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The impact of disturbance on carrion- and fruit- feeding butterflies, in tropical peat-swamp forest, Indonesian Borneo

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Biodiversity and Conservation MRes Summer Project

Module: 5191M



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Abstract

1. South-east Asia is suffering high rates of deforestation and degradation, as a result of logging, agricultural conversion and fire. Tropical lowland peat-swamp forests are particularly badly affected, yet little is known about the biodiversity that resides within them; understanding the impacts of disturbance is crucial for effective conservation. Although Lepidoptera are well studied, there is a paucity of data for carrion-feeding butterflies, as most studies use fruit-feeding Nymphalidae; however, different functional guilds may have very different responses to disturbance, as has been shown for other taxa. This study used baited traps to study the responses of both carrion- and fruit-feeding butterflies to disturbance, in tropical peat-swamp forest in Central Kalimantan, Borneo.
2. The two functional guilds responded differently to disturbance. Logging increased the species richness and abundance of carrion-feeding butterflies. Evenness and distinctness of species assemblages was reduced however, indicating less complexity in heavily disturbed forest, although this was not due to a higher proportion of generalists with fewer restricted range species of higher conservation value. There was a slight decrease in the abundance of fruit-feeding butterflies in heavily disturbed forest, although species richness remained the same. Canopy and understorey species assemblages were distinct within both feeding guilds.
3. Forest structure was affected by disturbance, with an increase in species richness and tree density, but a decrease in size, canopy cover, and habitat heterogeneity with greater disturbance. The increased light levels may stimulate an increase in ground-dwelling plants providing extra nectar resources; as carrion-feeding butterflies feed primarily on floral nectar, rotting fruit or tree sap, with carrion providing supplementary micronutrients, this could account for the positive response of carrion-feeding butterflies to disturbance. The response of the fruit-feeding butterflies suggests that fruit may not increase in abundance. Carrion-feeding butterflies had lower rates of recapture, suggesting higher levels of mobility, and greater ability of colonising disturbed areas.
4. Care must be taken when evaluating the responses of butterflies to disturbance, especially when considering the use of butterflies as indicators of habitat degradation. Other factors such as scale and seasonal variation should be investigated further. Previous studies have shown that changes in species composition and abundance of butterflies post-disturbance often do not correlate well with other taxa; this study has demonstrated that within Lepidoptera there is a difference in response between feeding guilds. However, disturbed forest still has a high biodiversity value and so effort should be made to conserve it.

Introduction

Tropical forests are some of the most biodiverse habitats in the world (Whitmore, 1998), but are suffering incredibly high rates of habitat loss from deforestation and degradation (Gardner, 2010), the main factors driving the current global biodiversity crisis (Sala et al, 2000). The problem is especially severe in South-east Asia, where forest loss is occurring at an alarming rate (Sodhi et al, 2004).

The lowlands of South-east Asia contain 60% of the world's tropical peatlands, the international importance of which has become more significant in the last decade, as their value as the largest terrestrial carbon store has been established (Posa et al, 2011). The biodiversity value of tropical peat-swamp forests is less widely appreciated however. Peatlands have been thought in the past to be poor areas for biodiversity, owing to the challenging conditions created by the acidic, waterlogged, low-nutrient peat soils (Reiley, 1996). This, combined with their inaccessibility, has meant that tropical peat-swamp forests have been poorly studied and are not well understood (Posa et al, 2011) despite representing some of the most biodiverse tropical ecosystems on earth (Koh et al, 2009).

Although relatively few animal species are reliant solely on the peat-swamp forests of South-east Asia – 80 species of freshwater fish are restricted this habitat, but no species of terrestrial vertebrates (Page et al, 1997) - they provide important refuges for endangered or threatened species also associated with other kinds of forest, such as primates (Morrogh-Bernard et al, 2003; Cheyne et al, 2008; Ehlers Smith et al, 2013). They also harbour a rich floristic diversity, with 11% of plant species restricted to tropical peat-swamp, and distinctive species communities (Posa et al, 2011).

It has been estimated that the pre-disturbance extent of peatlands in South-east Asia was between 20 and 30 million hectares, of which only 36% is thought to remain. Additionally, further areas of forest could be degraded, for which there are no data (Miettinen et al, 2010). The peat swamp forests of Kalimantan, Borneo, account for nearly half of this remaining area, but have themselves suffered very high rates of deforestation, with only 47% left (Posa et al, 2011). Although a quarter of this area is protected, in many places protection is on paper only, with logging and other activities still allowed to continue (Curran et al, 2004). This increases the susceptibility of the peat swamp forest to fires, which can smoulder beneath the peat for months without being extinguished and are highly detrimental to biodiversity (Harrison et al, 2009). Although peatlands are not a highly-productive ecosystem for agriculture, as they must be cleared, drained, fertilised and limed before crop production, huge areas are cleared for oil-palm (Miettinen et al, 2010), as well as large tracts made available for logging, or conversion to industry (Posa et al, 2011).

There are not much data available on the impact of logging on peat-swamp forests. Evidence suggests that forest structure is changed; for example, the commercially important tree species ramin (*Gonystylus bacanus*) does not regenerate well after disturbance from logging, and is now listed as vulnerable on the IUCN Red List (Posa et al, 2011). Different taxonomic groups appear to respond differently, with birds (Page, 1987) and orang-utans (Morrogh-Bernard et al, 2003) documented to decline post-logging, but small mammals to increase (Doody et al, 1997). The effects of logging on tropical invertebrates have been less well studied however (Willott et al, 2000; Hill et al, 1995); this is particularly true in peat-swamp forests (Posa et al, 2011; Houlihan et al, 2013). Tropical forests are recognised to harbour exceptionally high invertebrate biodiversity (Hamer et al, 2006), the greatest current threat to which is habitat degradation (Basset et al, 2012).

Lepidoptera are among the best-studied tropical invertebrate fauna, and are often used as indicators of habitat disturbance (Basset et al, 2013); with short generation times, high habitat sensitivity and well-resolved identification systems (Bonebrake, 2010). Butterflies across their life stages play an important part in tropical ecology by impacting upon ecological processes such as pollination (Basset et al, 2013). Within the Lepidoptera however, most research in the tropics has focussed on nectar- and fruit-feeding butterflies, with relatively few data for carrion-feeding butterflies (Hamer et al, 2006). It is likely however that different functional guilds will behave differently to disturbance, as has been shown among birds (Gray et al, 2007), and tropical invertebrates (Edwards et al, 2012). Additionally, information on the diversity and distribution of species' populations is essential for establishing effective management schemes for conservation (Gardner, 2010).

This study was conducted in the Sabangau peat-swamp forest (5,300km²), located within the largest contiguous tract of lowland forest remaining in Borneo (Ehlers-Smith et al, 2013), in mixed-swamp forest where previous studies have suggested high animal abundance is found (Page et al, 1997). It is an important stronghold for biodiversity, with the largest extant populations of the Bornean orangutan (*Pongo pygmaeus*; Morrogh-Bernard et al, 2003) and the southern Bornean gibbon (*Hylobates albibarbus*; Cheyne et al, 2008) as well as large populations of many other endangered taxa, such as marbled cats, sun-bears, clouded leopards and 6 red-data book bird species (Page et al, 1997; Cheyne et al, 2008). It has been suggested that the relatively depauperate short forest on the habitat edges is that which accounts for previous assumptions of low species richness and diversity in peat-swamp forest (Page, 1997).

This study aimed to assess the impact of disturbance on the species richness, abundance and community composition of carrion-feeding butterflies of tropical peat-swamp forest, Borneo, at both the ground and the canopy strata, and compare responses to those of fruit-feeding butterflies. Changes were related to differences in vegetation structure and composition.

Methods

Study site

The fieldwork was carried out in the Natural Laboratory for the Study of Peat-swamp Forest (NLPSF), S2°19'00.3" E113°54'29.3", in Sabangau, Central Kalimantan; which is located 20km southwest of the provincial capital Palangka Raya. The NLSPF covers a 500km² area of peat-swamp forest, bordering the Sabangau National Park to the south and west and was established for research in 1997.

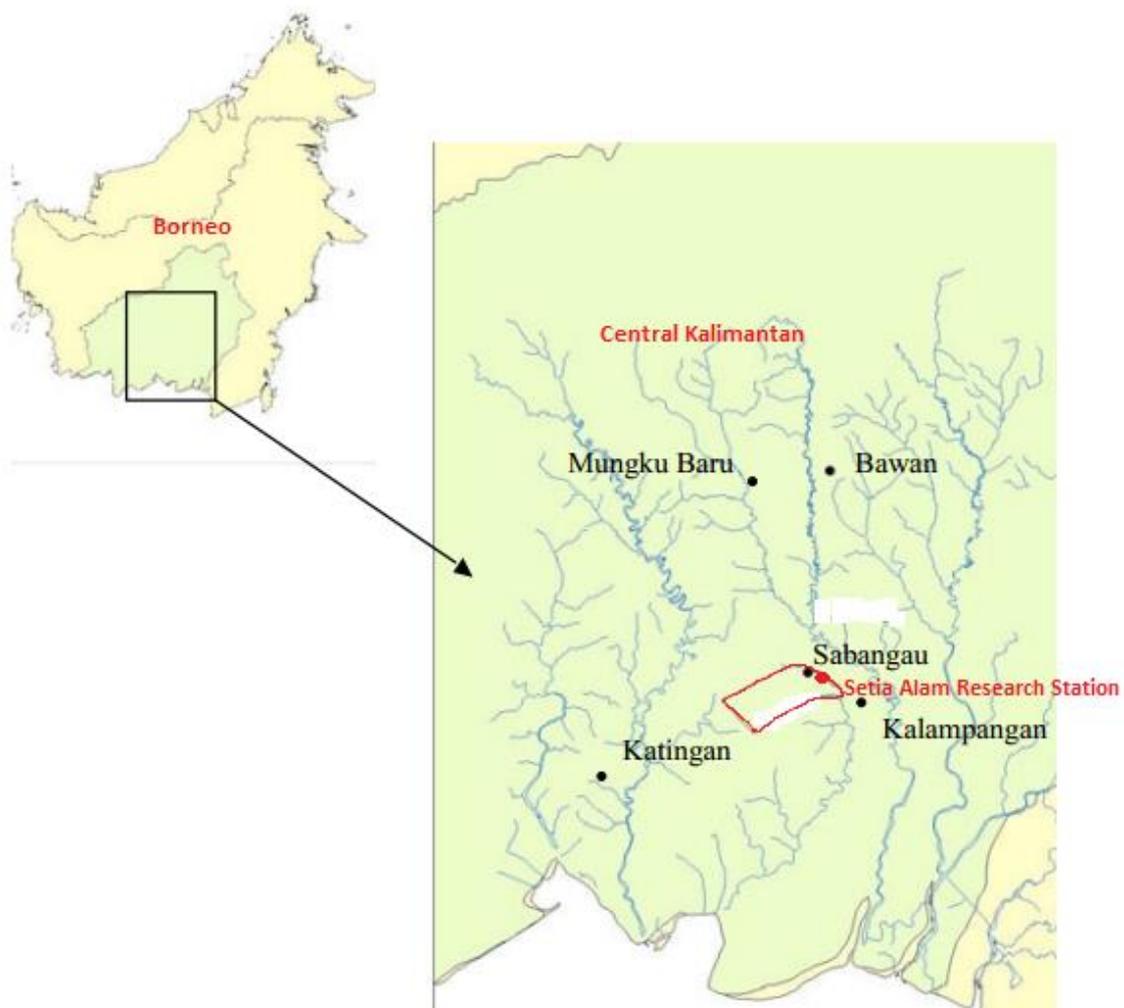


Figure 1. Showing the location of the Sabangau Forest in Central Kalimantan, Borneo, and the Setia Alam Research Station, where the reseach was carried out. Map from the OuTrop website (OuTrop, 2012).

The forest was subject to extensive logging activity in the past; first legally, as part of the Setia Alam Jaya logging concession, which operated for 25 years until 1997 (Gibson, 2005) and then by widespread uncontrolled illegal logging (Houlihan et al, 2013). It was originally selectively harvested for commercially valuable timber species, such as Ramin (*Gonystylus bacanus*) and

Meranti (*Shorea sp.*), extracted using a narrow-gauge railway, as well as small-scale harvesting of other forest products such as bark, rattan and latex (Morrogh-Bernard et al, 2003). Canals were constructed to extract timber, which drained the forest, resulting in greater susceptibility to fire; between 1997 and 2009, an estimated 15% of the forest area was burnt (Houlihan et al, 2013). In 2004 logging ceased, and a Community Patrol Team now fights fires during the dry season and prevents further disturbance from illegal activities (Houlihan et al, 2013; Harrison et al, 2009).

The study was undertaken in lightly disturbed and heavily disturbed forest, lightly disturbed forest representing the best realistic baseline forest condition; there is very little pristine peat-swamp forest left in Borneo (Miettinen et al, 2010). Six 250m transects were used in the study: three from each forest type.

The three transects used to survey heavily disturbed forest were located between the two old timber extraction railways where the most logging occurred, positioned parallel at 200m intervals from each other. The three transects used to survey lightly disturbed forest were located at least 550 metres from the main railway (the logging mostly occurred within a 30m zone to either side of the railway), and at least 800m from the heavily disturbed transects; also positioned at least 200 metres apart. A much lower intensity of activity occurred here, with selective removal of the most commercially valuable species, as opposed to more extensive, non-selective logging in the heavily disturbed forest.



Figure 2. A view over the peat-swamp forest of Sabangau, from a weather observation tower located 800 metres south of the camp.

Climate

Temperatures remain fairly consistent year round, with temperatures varying diurnally rather than seasonally. The wet season typically spans from November to May (Ehlers-Smith, 2013), and so incorporated the majority of the research period. During the study period, the mean daily rainfall was 6mm, and the mean temperature was 27.8°C (Wunderground, 2014).

Butterfly surveys

Carrion-feeding butterflies were sampled with traps baited with prawn paste, situated along the six transects described above. Ten traps were placed along each transect, in pairs of ground and canopy level, as it has been found that sampling in the canopy is crucial in order to obtain accurate species inventories (DeVries et al, 2012; Dumbrell & Hill, 2005; Koh, 2007). Pairs of traps were positioned 50m apart along each transect to ensure independence of data (see Hamer et al, 2003). The canopy traps were erected with catapults, and were hung 15-20 metres from the ground, while ground traps were hung at 1-2 metres. Traps used were in the style of DeVries, 1987. The replicates of traps aimed to ensure that localised variations in microhabitat and environment did not bias results (DeVries et al, 2012).



Figure 3. An example of a hung butterfly trap.

Traps were baited and checked for cycles of five days, with extra bait added each day to ensure a range of decay. This was the same methodology as for the existing fruit-feeding butterfly surveys, to better enable comparison of data. A 5-day pilot study was undertaken before data was collected, to ensure the method was successful for carrion-feeders. Each transect was sampled 4 times over

the study period, to attempt to mitigate for temporal variation in butterfly abundance and diversity. The use of baited traps is one of the most reliable and unbiased methods of surveying butterflies in the tropics (Bonebrake et al, 2010); although fewer guilds are attracted to the traps and are dependent on the bait offered, it is easier to identify butterflies in traps than when walking transects in a habitat with very high Lepidopteran diversity (Hamer et al, 2006), often with low visibility, low population sizes and cryptic species (Basset et al, 2013).

Traps were checked daily between the hours of 11:00 and 14:00, with the start point changed each day to account for any influences of time on butterfly activity (Basset et al, 2013). Butterflies were identified in the field using identification guides (Otsuka, 1991; Tsukada, 1982; D’Abrera, 1985), measured using callipers (body and forewing length), marked using a permanent marker pen with a unique number on the ventral side of the right forewing, and released. Sex was recorded where males and females exhibited sexual dimorphism, without necessitating dissection. *Tanaecia* species have not been identified to species level, as they are a poorly resolved clade, requiring dissection. Photos were taken of all species surveyed, in order to build up an identification library and help with future monitoring surveys. Specimens were taken of species difficult to identify in the field in order that more thorough identification could be carried out, and are stored at the NLPSF Research Station.



Figure 4. Examples of butterflies with unique markings on the right ventral wing surface: the letter denotes the species, and the number the individual of that species.

Trapping took place on a total of 60 days, over two study periods (12th October – 9th December and the 4th of January to the 19th of February), resulting in a total of 1200 trap days.

Fruit-feeding butterflies were sampled between the 22nd and the 28th of each month (October-February), using the same methodology (Houlihan et al, 2013), giving 500 additional trap days of data. These traps were baited instead with a mixture of bananas, sugar, and a local alcohol. Fruit-feeding butterflies were only sampled along two of the transects used for carrion-feeding

butterflies, as part of a longer-term study. As data from the feeding guilds will not be directly compared however, just the responses within the guild to disturbance, this should not present any issues during analysis. The standardization of the data collection techniques makes comparison of the two data sets more reliable (Magurran & McGill, 2011), even though sampling effort is unequal.

Forest structure surveys

A 10m x 10m plot was surveyed around each of the sixty carrion-feeding butterfly trap locations, and the GPS co-ordinates of the centre of the plot marked so that further monitoring can be undertaken in the future. Long-term study plots allow the monitoring of butterflies in relation to changes in vegetation and climate (Basset et al, 2013). In each plot, the following data was collected: numbers and species of trees present; circumference at breast height (CBH); basal circumference (BC); tree height; numbers and species of liana present; and percentage canopy cover at 10m above ground, 20m and 30m. Trees were classed as within the plot if the roots lay within plot boundaries. Only trees over 15cm in circumference were measured, with trees smaller than that considered saplings. Trees were measured over bark, at 1.3m from the ground, with a tape measure. For trees whose roots base extended at least 90cm above ground, the measurement was taken 30cm above the buttress. For trees with aerial roots, the measurement was taken 1.3m from the limit between the stem and the roots. Tree height was estimated by an experienced member of the OuTrop research team and put into 5m categories: 0-5m, 5-10m, 10-15m, 15-20m, 20-25m, 25-30m. Canopy cover was estimated using a densiometer; in this case, an empty CD case with dots marked on in rows. Canopy cover was calculated using the number of dots that had sky visible above when looked through from below, and was taken from the centre of each plot. The cover was calculated at three different heights above ground to get a more complete picture of forest structure and canopy stratification; for example, an area with a dense understorey at 10m and sparse canopy cover at 20m is very different to one in which the reverse is true. Stem density per m² could be calculated by dividing the number of trees in the quadrat by ten. Tree species were identified by local field staff from the OuTrop research team.

Data analysis

To determine whether differences in species richness and abundance between heavily and less disturbed forest were significant, generalized linear models (GLZs) were run in SPSS v. 21. A Poisson log-linear model was used, as the data is count data. GLZs were run for both fruit- and carrion- feeding butterflies, at the trap and transect level to attempt to control for the impact of sampling scale. Data was not normally distributed and variance was checked. Diversity indices were not calculated, as they are generally accepted to be of no more use than presenting the separate components of species richness and abundance (Gardner, 2010; Magurran, 2004).

To estimate the likely species pools, six commonly used species richness estimators (ACE, CHAO2, Jack1, Jack2, Bootstrap and MMM) were calculated using EstimateS v. 9, and analysed in SPSS v. 21. An independent t-test was used to test whether the differences between guilds and disturbance levels were significant. The mean predicted values were compared to observed values to make a judgement on the efficacy of the sampling regime.

In order to determine whether changes in species richness could be attributed to an influx of more widespread species to more disturbed areas, all the butterfly species trapped were ranked according to geographic distributions, using data from Tsukada, 1982, indicating taxonomic distinctiveness (see Hill et al, 1995). Species were ranked first according to the distribution of the sub-species found on Borneo, then on the distribution of the entire species. The lowest ranked species (35) was the most widespread, mid-ranked butterflies were found within the Sundaland area of Borneo, Java, Sumatra, Palawan and West Malaysia (see Hamer et al, 2003), and the highest ranked (1) was a species endemic to Borneo. The median rank of communities in heavily disturbed and less disturbed forest were then compared for fruit- and carrion- feeding butterflies, and a Mann-Whitney U-test was used to test the statistical difference in ranks between the communities.

Studies have shown that analysis of beta diversity and community similarity measure response to environmental change more sensitively than assessing species richness and abundance (Gardner, 2010). The estimated number of shared species, and the Bray-Curtis similarity index was calculated to examine the difference in community composition between carrion and fruit, and heavily and less disturbed forest, using EstimateS v. 9. The Bray-Curtis similarity index is one of the most commonly used abundance-based similarity measures (Magurran & McGill, 2011) and is a reliable measure of the distinctiveness of species assemblages (Magurran, 2004; Gardner, 2010).

ANOSIMs (non-parametric ANalysis Of SIMilarity) were also run, using PAST v. 2.17 software, using the Bray-Curtis measure of similarity, and the Bonferroni correction, to determine whether

differences in species composition between the communities were significant. The R_{ANOSIM} statistic produced is an absolute measure of the similarity of two communities; a value of 1 indicates that samples are more like others from within a group than between groups, while a value of 0 indicates no difference among groups (Cleary et al, 2005). Vertical stratification was investigated using the same mechanisms.

Diversity partitioning was used to further analyse the compositional differentiation between heavily and less disturbed forest for both feeding guilds. This involves partitioning gamma, or regional diversity, into alpha and beta components, representing within group diversity and between group diversity respectively (Jost et al, 2010). The contribution of different communities to regional diversity, and whether these are distinct, can then be determined, which gives an idea of species turnover (beta diversity), and the heterogeneity of the region. Multiplicative partitioning was used (following Chao et al, 2012; Woodcock et al, 2011), calculated using PARTITION software (Veech & Crist, 2009) to produce the alpha, beta and gamma diversity at three levels of q . When $q = 0$, all species are given equal weighting and abundances are not taken into account; when $q = 1.001$, species are weighted according to frequency; and when $q = 2$, abundant species are given a heavier weighting than rare species and therefore influence beta diversity proportionally more (Chao et al, 2012).

The contribution of singleton species (those which are represented by just one individual) to overall species richness, was investigated. Bar charts were produced to graphically present the differences in species richness between forest types when singletons were and were not excluded from the data, to remove the disproportionate impact of species that are not effectively sampled.

Substrate choice was investigated by calculating the proportions of butterfly species found on carrion or fruit, randomizing and standardizing trapping hours to account for differences in sampling effort. A carrion preference index (CPI) was calculated using the percentage of captures of each species on each substrate. A CPI of 1 indicates that the species was found only on carrion; 2, that the species was trapped on carrion in over 65% of captures; 3, that the species was trapped on both fruit and carrion, with between 35 and 65% of captures on carrion; 4, that the species fed mostly on fruit, with under 35% of captures on carrion; and 5, that the species was trapped exclusively on fruit. A mean CPI for each family was produced. A Generalized Linear Model was also run in SPSS v. 21, to determine if family had a significant effect on bait choice.

Sex ratios were calculated for carrion and fruit, using SPSS v. 21 and recapture rates calculated.

To examine the relationship between vegetation structure and butterfly species richness and abundance, *R*-mode multivariate analysis was carried out. The original forest structure variables were analysed, using a Principal Components Analysis (PCA) run in SPSS v. 21, in order to extract fewer, new, synthetic variables, which still accounted for most of the variance (Magurran & McGill, 2011). Variables inputted were: mean tree height, mean circumference at breast height (CBH), mean basal circumference (BC), number of tree species, stem density per m², number of lianas, number of liana species, and percentage canopy cover at 10m, 20m and 30m above ground. Suitability of factors for inclusion in the analysis is indicated by the Kaiser-Meyer-Olkin (KMO) measure; number of lianas and liana species, and number of tree species, were removed from the analysis due to a low KMO score. The final KMO was 0.76, which is above the minimum requirement of 0.6, and the Bartlett's test of sphericity was significant ($\chi^2 = 462.8$, $df = 21$, $p < 0.001$); these measure sampling adequacy and indicated that factorability was assumed and therefore factor analysis was appropriate (Leech et al, 2005).

Linear regressions were run in SPSS v. 21 to determine how much variation in butterfly abundance and species richness was attributable to the principal components produced by the PCA.

To investigate the differences in forest structure between heavily and less disturbed forest, independent t-tests were run to determine whether the original variables were statistically different between the two, as well as the two most influential principal components produced by the PCA. There were no outliers in the data, assessed visually with box-plots. Component scores were normally distributed, assessed using the Shapiro-Wilk's test ($p > 0.05$). Where variance was not homogenous, the *t* – value with equal variance not assumed was reported.

An ANOSIM was run to determine whether there was a significant difference in species composition of trees and lianas between both disturbance levels. Non-metric multi-dimensional scaling (NMDS) ordination, based on the Bray-Curtis similarity matrix, was used to produce a visual representation of the level of similarity between species composition, based on abundance. The Shepard's plot produced a straight line, indicating a good representation, and the Kruskal's stress value was 0.3. Both were produced using PAST software. NMDS has been found to be a robust technique in ecological studies, without strict model assumptions (Cleary et al, 2005; Magurran, 2004).

RESULTS

Carrion-feeding butterflies

A total of 589 butterfly captures was made over the 60 days of trapping, of which all but 7 were identified to species level. A total of 382 captures were made in heavily disturbed forest (65%), and 207 in less disturbed forest (35%). 363 of these were marked in total, and just 17 (5%) were recaptured. A total of 30 different species were recorded on carrion (see table 3).

Species richness and abundance

Species richness was higher in more disturbed forest, with 29 species trapped, than less disturbed forest, with 21 species (see table 2). There was a significant difference in the number of species sampled per trap ($\chi^2 = 22.6$, $df = 1$, $p < 0.001$; see table 1) and the abundance of butterflies per trap ($\chi^2 = 48.7$, $df = 1$, $p < 0.001$; see table 1). Disturbance had the same effect on species richness and abundance at transect level ($\chi^2 = 22.3$, $df = 1$, $p < 0.001$; $\chi^2 = 38.7$, $df = 1$, $p < 0.001$; see table 1).

CARRION:	Heavily disturbed	Lightly disturbed	x	p
Species richness per trap	0.5 ± 0.03	0.3 ± 0.02	22.6	<0.001
Butterfly abundance per trap	1.6 ± 0.08	1.3 ± 0.04	48.7	<0.001
Species richness per transect	5.0 ± 0.4	3.3 ± 0.3	22.3	<0.001
Butterfly abundance per transect	6.2 ± 0.7	3.7 ± 0.4	38.7	<0.001

Table 1. The species richness and abundance of carrion-feeding butterflies sampled in heavily and lightly disturbed forest, at the trap and transect level, ± SE. x is the Wald Chi-Square value produced by the Generalized Linear Model run in SPSS to determine whether the difference in species richness and abundance between the two forest disturbance types was significant. The p value shows the significance; green shading indicates a significant difference.

	Heavily Disturbed	Less Disturbed	<i>t</i>	<i>p</i>
Total species sampled	29	21		
Total individuals sampled	382	207		
ACE	41.9	26.2		
CHAO2	45.1	27.0		
Jack1	41.0	27.0		
Jack2	48.0	30.0		
Bootstrap	34.7	23.7		
MMM	48.0	22.3		
Mean of the above species richness estimators	43.1 ± 2.1	26.0 ± 1.1	7.3	<0.001

Table 2. The scores for six commonly used species richness estimators for heavily and less disturbed forest, calculated using EstimateS 9.0. Means of the species richness estimators are ± 1 SE. Results of an independent *t*-test testing differences in mean predicted species richness are shown.

Predicted overall species richness was much higher in heavily disturbed forest, with a mean of 43 species, than less disturbed forest with a mean of 26 species (see table 2). An independent *t*-test indicated that the difference in mean predicted species richness was significant ($t = 7.3$, $df = 10$, $p < 0.001$; see table 2).

Table 1 shows that 67.3% of predicted species richness was successfully sampled in heavily disturbed forest, and 80.8% in less disturbed forest; indicating that both habitats were sampled reasonably well.

	Carrion		Fruit		Total	Rank		Carrion		Fruit		Total	Rank
	HD	LD	HD	LD				HD	LD				
Hesperiidae:							Cyrestinae						
Coeliadinae							<i>Chersonesia peraka</i>	1	1	0	0	2	13
<i>Burara etelka</i>	89	42	0	0	131	20	Heliconiinae						
<i>Burara gomata</i>	9	6	0	0	15	24	<i>Vindula dejone</i>	1	0	0	0	1	15
<i>Burara harisa</i>	2	7	0	0	9	22	Limentidinae						
<i>Hasora badra</i>	2	0	0	0	2	19	<i>Athyma asura</i>	5	8	0	0	13	31
Lycaenidae:							<i>Dophla evelina</i>	0	0	42	34	76	28
Lycaeninae							<i>Moduza procris</i>	1	1	0	0	2	27
<i>Acytolepis puspa</i>	0	1	0	0	1	34	<i>Pandita sinope</i>	1	0	0	0	1	9
<i>Acytolepis ripte</i>	4	1	0	0	5	1	<i>Tanaecia munda</i>	0	0	0	3	3	2
<i>Arhopala sp.</i>	4	3	0	0	7	-	<i>Tanaecia sp.</i>	1	0	7	12	20	-
<i>Caleta elna</i>	14	7	0	0	21	33	Morphinae						
<i>Catapaecilma evansi</i>	1	0	0	0	1	8	<i>Zeuxidia aurelius</i>	0	0	2	2	4	3
<i>Nacaduba solta</i>	88	30	0	0	118	5	<i>Zeuxidia doubledayi</i>	0	0	1	0	1	6
Theclinae							Nymphalinae						
<i>Amblypodia narada</i>	21	6	0	0	27	14	<i>Lexius canescens</i>	1	0	1	2	4	11
<i>Eooxylides tharis</i>	2	0	0	0	2	17	<i>Lexius bangkana</i>	0	2	3	2	7	7
<i>Hypolycaena amabilis</i>	1	0	0	0	1	16	<i>Lexius pardalis</i>	7	15	2	11	35	26
<i>Hypolycaena amasa</i>	5	1	0	0	6	32	<i>Lexius sp.</i>	0	0	0	2	2	-
Nymphalidae:							Satyrinae						
Charaxinae							<i>Melanitis leda</i>	0	0	16	17	33	35
<i>Agatasa calydonia</i>	26	10	32	39	107	12	Papilionidae:						
<i>Charaxes bernadus</i>	75	57	60	52	244	29	Papilioninae						
<i>Charaxes borneensis</i>	0	0	13	7	20	10	<i>Graphium evemon</i>	1	0	0	0	1	21
<i>Charaxes solon</i>	1	2	2	4	9	30	<i>Papilio iswara</i>	2	0	0	0	2	4
<i>Polyura schreiber</i>	5	2	0	0	7	25	Pieridae:						
<i>Prothoe franck</i>	1	1	30	34	66	23	Coliadinae						
							<i>Eurema nicevillei</i>	5	4	0	0	9	18

Table 3. Butterfly species recorded on carrion and fruit in heavily (HD) and lightly (LD) disturbed forest during the study period, along with abundances and rank according to geographical distribution. The highest ranked species (1) is endemic to Borneo, while the lowest ranked (35) has the most widespread distribution.

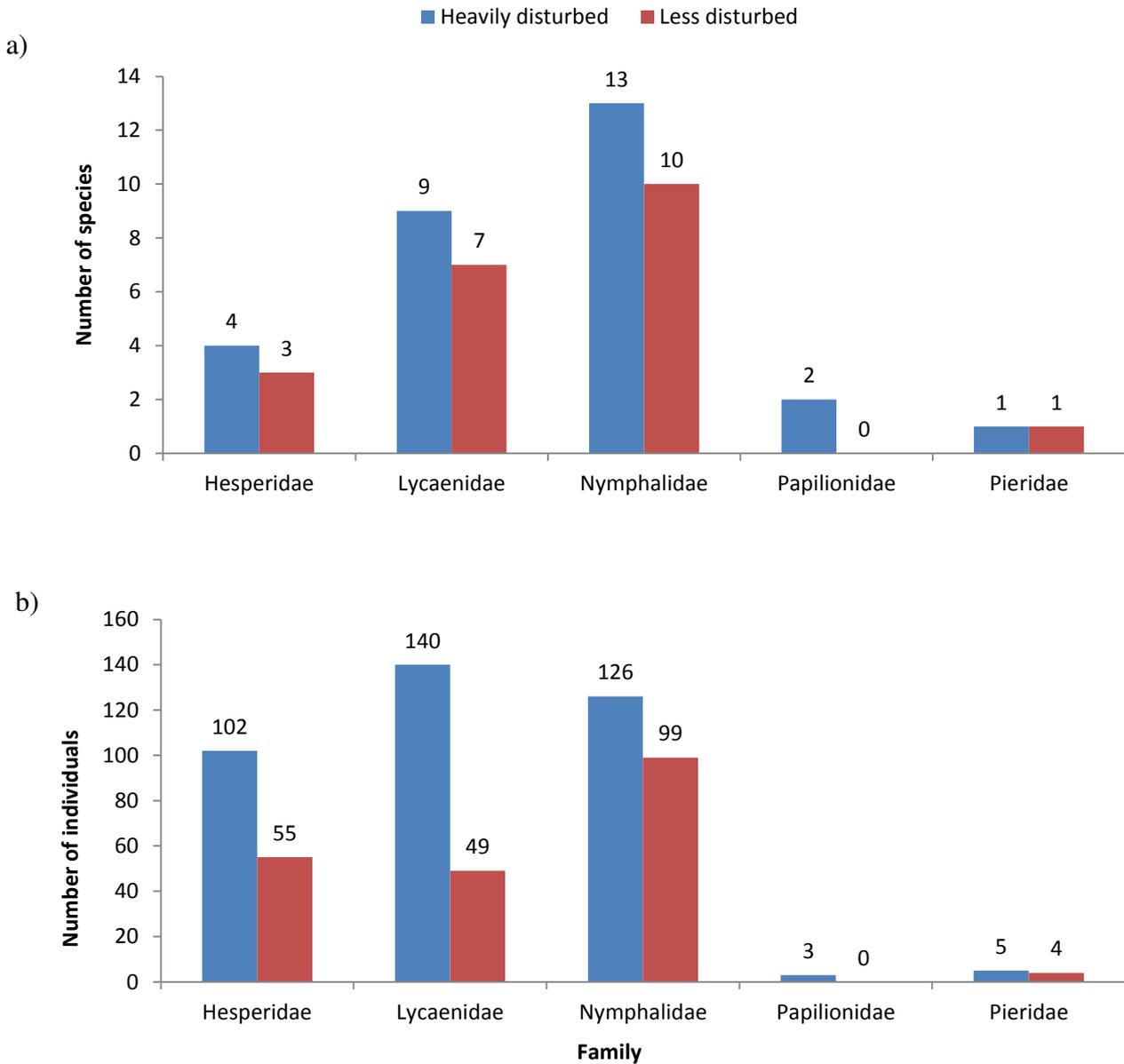


Figure 5. Total number of a) species and b) individuals of each family of carrion-feeding butterflies trapped in heavily and less disturbed forest.

All five families show an increase in abundance post-logging, with the effect most marked in the Hesperidae and the Lycaenidae (see figure 5b). Papilionidae are found only in heavily disturbed forest, but only three individuals were trapped. Four families showed an increase in species richness post-logging; Pieridae remained the same (see figure 5a).

Fruit-feeding butterflies

A total of 433 butterflies were captured during the 5 month study period, of 13 species; 211 in heavily disturbed forest (49%) and 222 in less disturbed forest (51%) (see table 5). Of these, 410 were marked, and 69 (17%) were recaptured.

Species richness and abundance

There was no significant difference in the abundance of fruit-feeding butterflies per trap between heavily and less disturbed forest ($\chi^2 = 0.28$, $df = 1$, $p = 0.60$; see table 4) or the number of species found per trap ($\chi^2 = 0.56$, $df = 1$, $p = 0.45$; see table 4). Disturbance had the same effect on butterfly abundance at transect scale ($\chi^2 = 0.29$, $df = 1$, $p = 0.59$; see table 4) but it did have a significant effect on species richness ($\chi^2 = 44.3$, $df = 1$, $p = <0.001$; see table 4). Overall observed diversity was the same, with 12 species found in each forest type.

FRUIT:	Heavily disturbed	Lightly disturbed	χ	p
Species richness per trap	0.67 ± 0.07	0.73 ± 0.06	0.56	0.45
Butterfly abundance per trap	0.84 ± 0.10	0.89 ± 0.09	0.28	0.60
Species richness per transect	9.48 ± 1.68	4.40 ± 0.51	44.27	<0.001
Butterfly abundance per transect	8.28 ± 2.03	8.72 ± 1.95	0.29	0.59

Table 4. The species richness and abundance of carrion-feeding butterflies sampled in heavily and lightly disturbed forest, at the trap and transect level, ± SE. χ is the Wald Chi-Square value produced by the Generalized Linear Model run in SPSS to determine whether the difference in species richness and abundance between the two forest disturbance types was significant. The p value shows the significance; green shading indicates a significant result.

When the mean total predicted species richness was estimated using six of the most common predictors (ACE, Chao2, Jack1, Jack2, Bootstrap and MM), it was predicted that heavily disturbed would contain 15 species and less disturbed forest 16 (see table 5). The sampling for fruit-feeding butterflies was more effective at sampling all species therefore, with 87.8% of the total predicted species surveyed in heavily disturbed forest, and 88.1% of those in less disturbed forest. Only one species was only trapped once.

	Heavily Disturbed	Less Disturbed	<i>t</i>	<i>p</i>
Total species sampled	12	12		
Total individuals sampled	222	211		
ACE	14.8	15.5		
CHAO2	14.5	15.3		
Jack1	16.0	17.0		
Jack2	16.0	16.0		
Bootstrap	14.5	16.2		
MMM	12.9	15.7		
Mean of the above species richness estimators	14.8 ± 0.5	15.9 ± 0.3	-2.2	0.055

Table 5. The scores for six commonly used species richness estimators for heavily and less disturbed forest, calculated using EstimateS 9.0. Means are ± 1 SE.

An independent t-test indicated that the difference in predicted species richness was not significant ($t = -2.2$, $df = 10$, $p = 0.055$; see table 5), although close to the threshold.

The response of the carrion-feeding Nymphalidae was quite different from the fruit-feeding Nymphalidae, the only family to be caught in fruit traps. Carrion-feeding Nymphalidae showed a marked increase in both species richness and abundance post-logging (see figure 5), but fruit-feeding butterflies showed no or very little change (see figure 6).

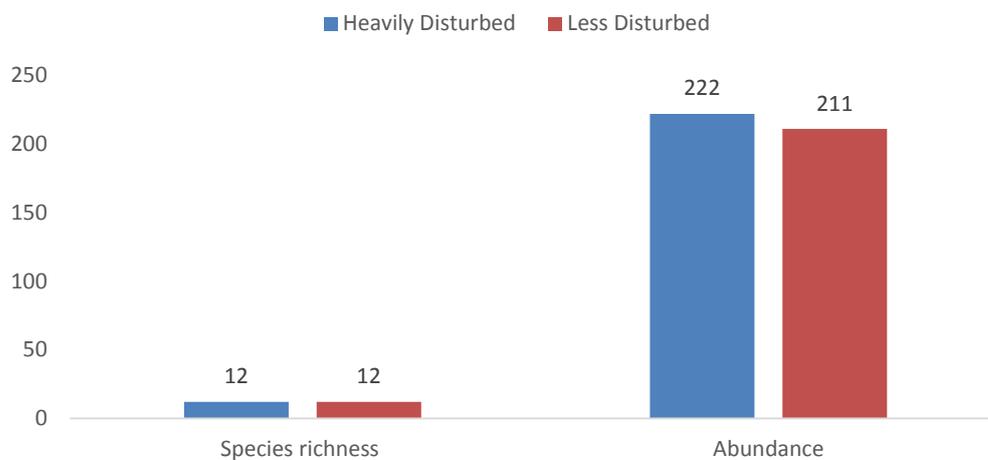


Figure 6. Number of species and individuals of fruit-feeding Nymphalidae sampled in heavily and less disturbed forest.

However, when only the species found on both substrates are considered, the difference in the response of both guilds is consistent, although less pronounced on fruit, with an increase in species richness and abundance post-logging (see figure 7).

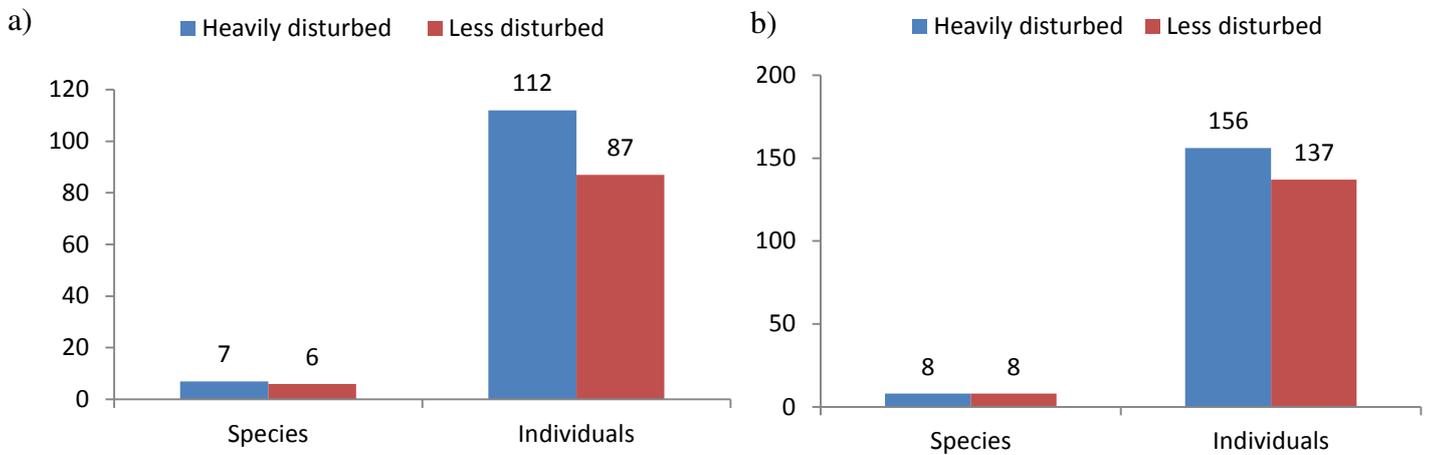


Figure 7. The impact on species richness and abundance of Nymphalidae post-disturbance sampled both on a) carrion and b) fruit, in heavily and less disturbed forest.

	Carrion		Fruit	
	Heavily disturbed	Less disturbed	Heavily disturbed	Less disturbed
Number of occurrences	382	207	211	222
Observed number of species	29	21	12	12
Estimated species pool	43.1 ± 2.1	26.0 ± 1.1	14.8 ± 0.5	15.9 ± 0.3
Mean number of species per transect	5 ± 0.4	3.3 ± 0.3	9.5 ± 1.7	4.4 ± 0.5
Mean number of species per trap	0.5 ± 0.03	0.3 ± 0.02	0.7 ± 0.1	0.7 ± 0.1

Table 6. A summary of the species richness and abundance of butterflies sampled on carrion and fruit. Means are ± SE.

Taxonomic distinctiveness:

The butterfly species were ranked according to geographic distribution. The highest ranked species (1), *Acytolepis ripte*, is endemic to Borneo, while the lowest ranked species (35), *Melanitis leda*, has a range which spans Australasian, African and Oriental regions (see table 3 for ranks).

For fruit-feeding butterflies, there was no significant difference in taxonomic distinctiveness between heavily and less disturbed forest (See figure 8 and table 7. Heavily disturbed: median = 28, $n = 204$, IQR = 15-30; less disturbed: median = 28, $n = 205$, IQR = 15-30; Mann-Whitney U -test: $Z = -4.7$, $p = 0.64$). For carrion-feeding butterflies however, heavily disturbed forest was taxonomically more distinctive than less disturbed forest (see figure 8 and table 7. Heavily disturbed: median = 20, $n = 372$, IQR = 12-29; less disturbed: median = 22, $n = 204$, IQR = 18-29; Mann-Whitney U -test: $Z = -4.0$, $p < 0.001$).

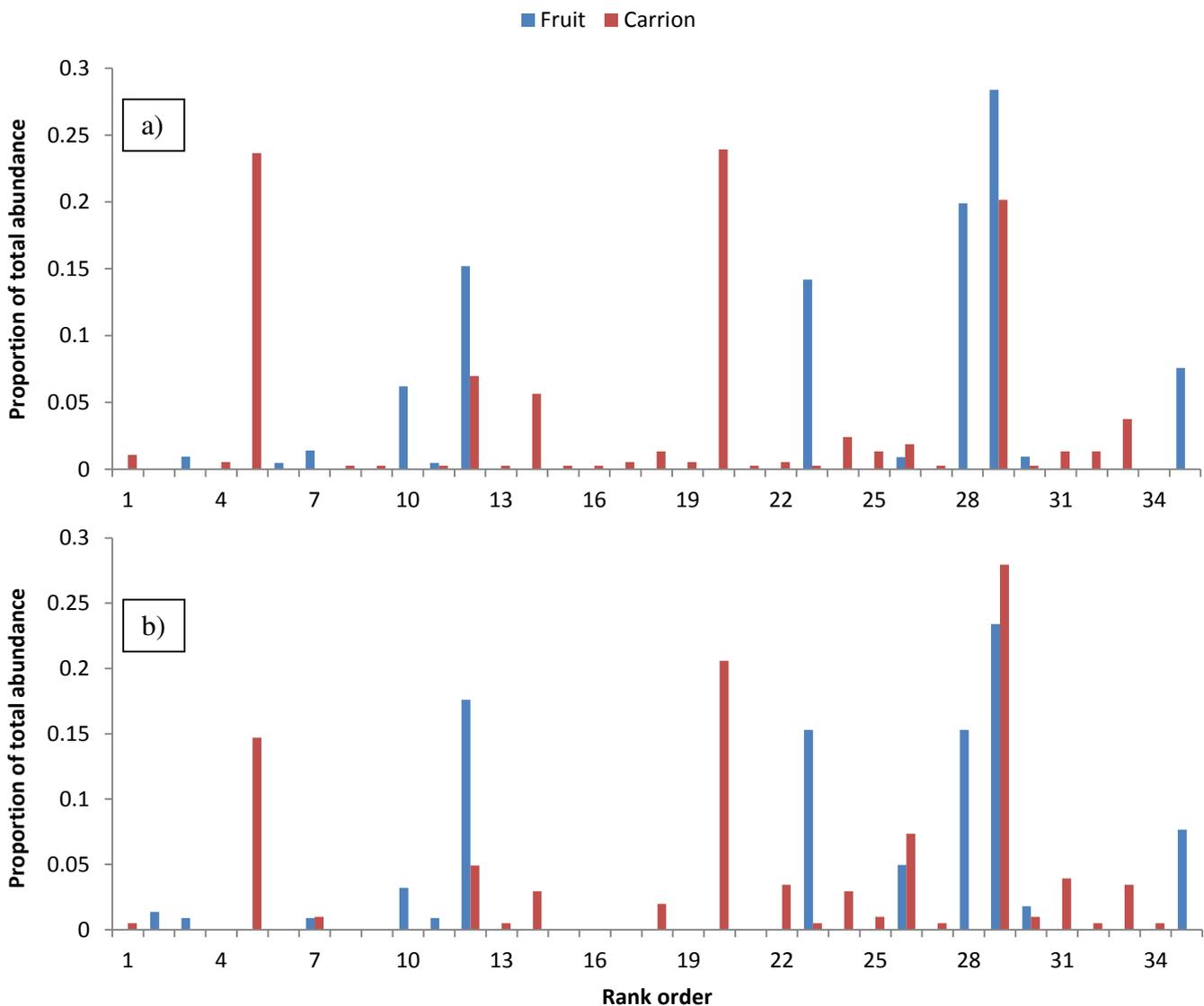


Figure 8. Proportional abundance distributions of butterfly species ranked by taxonomic distinctiveness for a) heavily disturbed forest, and b) less disturbed forest, for fruit- and carrion- feeding butterflies.

		Median rank	<i>n</i>	IQR	Z	<i>p</i>
Carrion	Heavily Disturbed	20	372	12-29	-4.0	< 0.001
	Less Disturbed	22	204	18-29		
Fruit	Heavily Disturbed	28	204	15-30	-4.7	0.64
	Less Disturbed	28	205	15-30		

Table 7. The taxonomic distinctiveness of butterfly communities in heavily and less disturbed forest for fruit- and carrion-feeding butterflies, as shown by the median rank and IQR (inter-quartile range). *n* is the number of ranked individuals. The results of the Mann-Whitney U-test used to determine whether the difference in rank distributions between the two disturbance types for each feeding guild was significant is also shown; *Z* is the Mann-Whitney U-test statistic, and *p* indicates level of significance. Significant *p*-values are shaded green.

Shared species:

When all fruit- and carrion- feeding butterfly data was analysed, the butterfly community composition was more similar between highly and less disturbed forest (See table 8; $C = 0.75$), than between the two feeding guilds ($C = 0.34$), with more shared species.

	Total number of species	Observed number of shared species	Chao estimate of total number of shared species	Bray-Curtis index, <i>C</i>
Carrion and fruit-feeding	39	8	10.7	0.34
Highly and less disturbed forest	39	27	31.1	0.75

Table 8. The observed and predicted number of shared species, between substrates and between forest types, and the Bray-Curtis index of similarity. A lower value of *C* indicates a lower level of similarity in community composition. The values were calculated using EstimateS.

However, ANOSIMs showed that both between forest types and substrates there is still a significant difference in community composition (See table 9. Forest types: $R_{ANOSIM} = 0.008$, $p = 0.0001$; substrates: $R_{ANOSIM} = 0.068$, $p = 0.0001$).

	R_{ANOSIM}	p
Between forest types	0.008	0.0001
Between substrates	0.068	0.0001

Table 9. The results of the ANOSIMs testing differences in community composition between forest types and between substrates. Significant p - values are shaded green.

When the data was separated in to the separate feeding guilds, ANOSIMs indicated a significant difference between community compositions between heavily and less disturbed forest for carrion (see table 10: $R_{ANOSIM} = 0.12$, $p = 0.0001$), but not fruit ($R_{ANOSIM} = 0.25$, $p = 0.25$).

	R_{ANOSIM}	p
Carrion	0.12	0.0001
Fruit	0.25	0.25

Table 10. The results of the ANOSIMs testing differences in community composition between traps in heavily disturbed forest and less disturbed forest. Significant p - values are shaded green.

For carrion-feeding butterflies, with increased disturbance, the species composition of butterfly communities at traps increased in similarity, with a higher number of shared species between traps in heavily disturbed forest than in less disturbed forest (see table 11). For fruit-feeding butterflies, this effect was reversed (see table 11).

	Mean shared species		Mean Bray-Curtis index, C	
	Heavily Disturbed	Less Disturbed	Heavily Disturbed	Less Disturbed
Carrion	2.62 \pm 0.1	1.65 \pm 0.1	0.36 \pm 0.0	0.31 \pm 0.0
Fruit	4.49 \pm 0.2	5.64 \pm 0.1	0.52 \pm 0.0	0.61 \pm 0.0

Table 11. The mean observed shared species, and Bray-Curtis index score, for heavily and less disturbed forest for carrion- and fruit-feeding butterfly assemblages between traps. Calculated using Estimate S v. 9.

Vertical stratification:

ANOSIMs also indicated a significant difference between community compositions at different trap heights for both fruit and carrion (see table 12. Fruit: $R_{\text{ANOSIM}} = 0.21$, $p = 0.006$; carrion: $R_{\text{ANOSIM}} = 0.13$, $p = 0.0002$).

	R_{ANOSIM}	p
Carrion	0.13	0.0002
Fruit	0.21	0.006

Table 12. The results of the ANOSIMs testing differences in community composition between traps at the ground level and the canopy level for both feeding guilds. Significant p - values are shaded green.

Both carrion- and fruit-feeding butterflies have more distinct community compositions at the canopy level, with lower similarity scores and fewer shared species (see table 13).

	Mean shared species		Mean Bray-Curtis index, C	
	Ground	Canopy	Ground	Canopy
Carrion	2.84 \pm 0.5	1.31 \pm 0.5	0.37 \pm 0.01	0.21 \pm 0.01
Fruit	5.6 \pm 0.2	4.87 \pm 0.2	0.59 \pm 0.02	0.59 \pm 0.01

Table 13. The mean observed shared species, and Bray-Curtis index score, for low and high carrion- and fruit-feeding butterfly assemblages between traps. Calculated using Estimate S v. 9.

A total of 28 species were sampled overall in high traps, and 36 in low traps. Three species were sampled only in the canopy, but they were sampled only once (*Vindula dejone*, *Pandita sinope* and *Catapaecilma evansi*), all in heavily disturbed forest. The majority of captures were at ground level; 597 in comparison to the 425 captures at canopy level.

Diversity partitioning:

For carrion-feeding butterflies, both species turnover (beta diversity) and species richness (alpha diversity) are higher in heavily disturbed forest than less disturbed forest (see table 14).

Carrion	Heavily Disturbed			Less Disturbed		
	q = 0	q = 1.001	q = 2	q = 0	q = 1.001	q = 2
Alpha	1.3	1.2	1.1	1.2	1.1	1.1
Beta	23.3	9.6	6.5	17.8	8.6	6.2
Gamma	30.0	11.4	7.4	21.0	9.7	6.7

Fruit	Heavily Disturbed			Less Disturbed		
	q = 0	q = 1.001	q = 2	q = 0	q = 1.001	q = 2
Alpha	2.3	2.0	1.8	1.5	1.3	1.2
Beta	5.6	6.3	6.9	7.8	5.0	4.6
Gamma	13.0	12.9	12.8	12.0	6.8	5.6

Table 14. Showing the alpha, beta and gamma diversity for fruit- and carrion- feeding butterflies in heavily and less disturbed forest at three values of q. The data was weighted equally and randomized 100 times. Calculated using PARTITION software (Veech & Crist, 2009).

For fruit-feeding butterflies, alpha diversity is higher in heavily disturbed forest, as is beta diversity when species abundances are not taken into account (when q is > 0) (see figure 9). However, when q > 0 beta diversity is higher in less disturbed forest, suggesting that species assemblages are more even in the less disturbed forest, with more rare species. The values for gamma diversity support this.

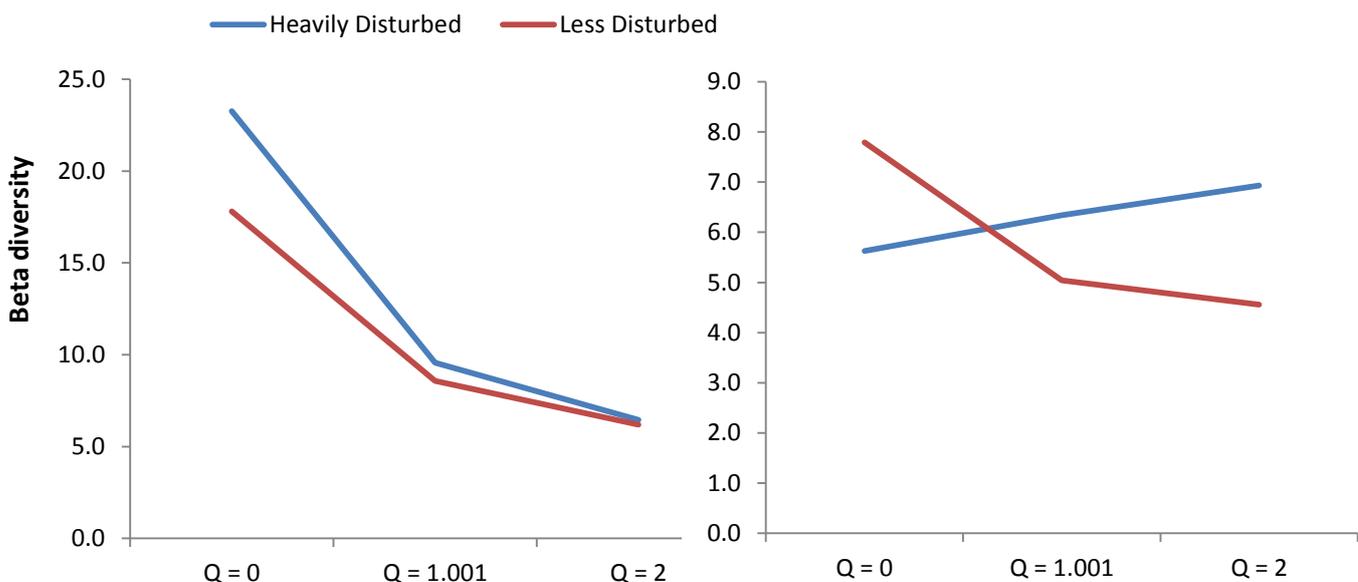


Figure 9. The multiplicative beta diversity of a) carrion- feeding and b) fruit-feeding butterflies in heavily and less disturbed forest, when q = 0, 1 and 2.

Singletons and site-specific species:

Singletons accounted for 27% of species of carrion-feeding butterflies; but only 7% of fruit-feeding butterflies, despite fewer trapping hours.

Two species were unique to less disturbed forest (0.05), with nine recorded only in heavily disturbed forest (0.24). However, when singletons were removed from the data, the proportion of species found only in heavily disturbed forest fell substantially, to 0.06, while the proportion found only in less disturbed forest fell slightly to 0.03 (see figure 10).

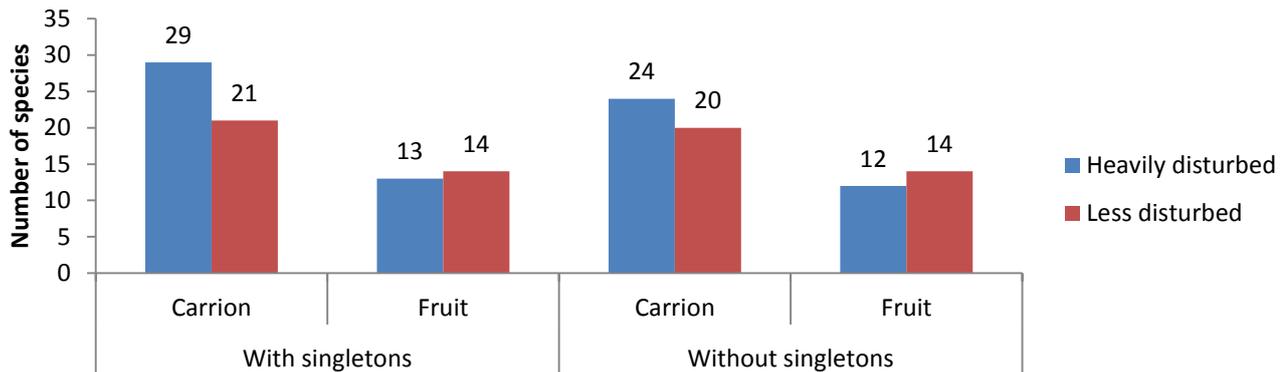
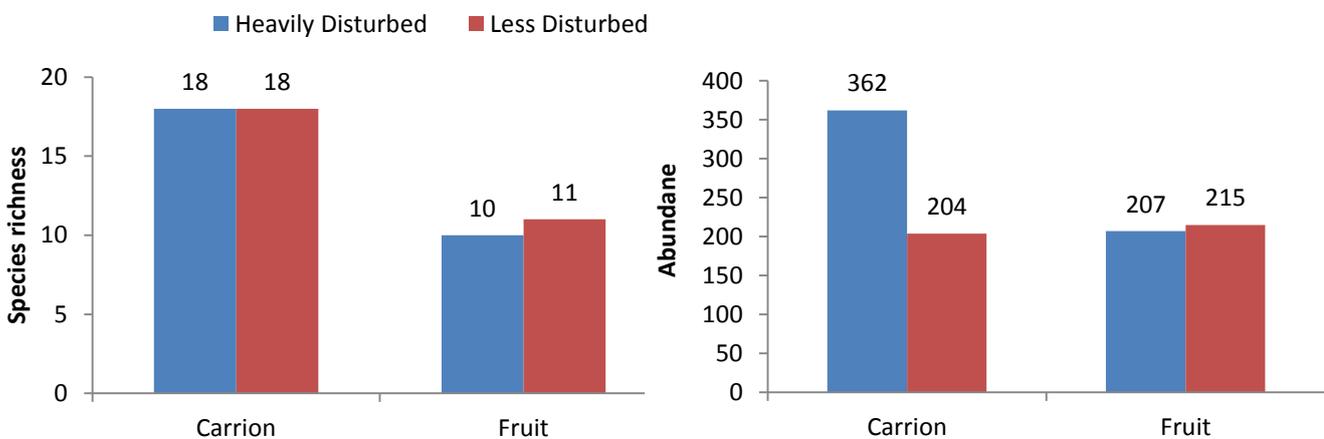


Figure 10. The number of species found within heavily and less disturbed forest when singletons are included or not .

A previous study of butterflies in Borneo only included butterflies in the analysis that numbered over 5 individuals, to reduce sampling error (Hamer et al, 2003). When butterflies of $n < 5$ were removed, there was no or negligible difference in species richness between heavily disturbed and less disturbed forest for carrion- or fruit-feeding butterflies (see figure 11), or in abundance on fruit; although abundance on carrion was still 1.8x higher in heavily disturbed forest (see figure 12). This was in large part due to the high numbers of *Burara etelka* and *Nacaduba solta*.



Figures 11 & 12. The species richness and abundance of carrion- and fruit- feeding butterflies when only species with >5 individuals are included in the analysis.

Substrate choice

Only 8 species (21% of the total) were recorded on both fruit and carrion; the other 30 showed clear preferences for one bait or the other. Among the 12 species with more than ten individuals recorded, the mean percentage of individuals on the bait with the greater abundance was 92.3% (SD \pm 14.5). Only three of these commonest species were more generalist: *Charaxes bernadus*, *Agatasa calydonia* and *Lexius pardalis*.

Species	Total number of individuals	% carrion	% fruit
<i>Charaxes bernadus</i>	166	32	67
<i>Burara etelka</i>	60	100	0
<i>Nacaduba sp.</i>	54	100	0
<i>Agatasa calydonia</i>	85	16	84
<i>Amblypodia narada</i>	11	100	0
<i>Lexius pardalis</i>	22	41	59
<i>Caleta elna</i>	11	100	0
<i>Prothoe franck</i>	65	2	98
<i>Tanaecia sp.</i>	19	0	100
<i>Dophla evelina</i>	76	0	100
<i>Melanitis leda</i>	33	0	100
<i>Charaxes borneensis</i>	20	0	100

Table 15. The percentages of total butterfly abundance found on carrion and fruit for the 12 species for which ten or more individuals were trapped. Nine showed clear preferences for one substrate or the other (green shading), with only 3 species more generalist (blue shading). Carrion data was randomized and standardized to equal trapping effort to fruit.

Family	Mean Carrion Preference Index
Hesperiidae	1 \pm 0
Lycaenidae	1 \pm 0
Nymphalidae	3.4 \pm 1.7
Papilionidae	1 \pm 0
Pieridae	1 \pm 0

Table 16. The mean carrion preference index of each of the five families trapped during the study period, on a scale of 1-5, and calculated using the percentage of captures of each species on each substrate. Values are presented \pm SD.

Family had a significant effect on bait choice ($\chi^2 = 23.3$, $df = 12$, $p = 0.025$), with 4 out of the 5 families feeding exclusively on carrion. Within the family Nymphalidae there was substantial variation, with 7 species feeding exclusively on carrion, 6 exclusively on fruit, 7 mostly on fruit, and one on both (see table 16).

Sex ratios

There was a strong male bias among species sampled on carrion, but not on fruit. 449 of the 515 carrion-feeding butterflies that were attributed a sex were male (87%), and 188 of the 328 fruit-feeding butterflies (57%). Even amongst the species that were trapped on both fruit and carrion, there was still a male bias on carrion (mean proportion on fruit = 0.61, $SD = 0.13$; mean proportion on carrion = 0.97, $SD = 0.05$).

Recapture rates

Recapture rates were much lower on carrion (5%) than on fruit (17%). Six of the carrion recaptures were originally trapped on fruit, not carrion, and so the true recapture rate on the carrion was lower, at 2%.

There was an average of 4.5 ± 1.2 days between original capture and recapture for carrion-feeding butterflies (see appendix 2). The mean distance travelled between captures was 285m (± 67), but variation was high. Only one carrion-feeding butterfly exhibited trap fidelity and was trapped twice in the same location. The furthest travelled was 500m, by a *Burara etelka* and a *Charaxes bernadus* individual.

Forest structure:

A total of 1189 trees and lianas were recorded in the sixty 10m² study plots: 1094 trees and 95 lianas. The highly disturbed forest plots had a total of 659 trees and lianas, of 102 species; the less disturbed forest had a total of 530 trees and lianas, of 89 species.

A factor analysis was run to reduce the number of variables to just those which account for most of the variation in vegetation structure between heavily and less disturbed forest. Principal components analysis (PCA) extracted four components of variation (FAC1, FAC2, FAC3 and FAC4), which accounted for 48, 15, 14 and 13% of the variability in the vegetation data respectively; 90% of the total cumulatively (see table 17).

Variable	Component			
	FAC1	FAC2	FAC3	FAC4
Mean CBH	.98	.01	-.09	-.01
Mean BC	.98	.01	-.09	-.04
Mean tree height	.96	.05	-.12	-.03
Stem density per m ²	.12	.89	-.13	-.07
Percentage cover at 10m	.19	.26	.91	.23
Percentage cover at 20m	.47	-.31	-.01	.69
Percentage cover at 30m	.43	-.35	.34	-.63

Table 17. The contributions of different variables to the four principal components of variation in forest structure produced by the PCA. The variables making the main contribution to each component are in bold.

FAC1 increases with increased circumference at base and breast height, increased tree height and increased percentage cover at the higher levels. It therefore reflects larger, taller trees, with bigger crowns. FAC2 increases with stem density, and decreases with increased canopy cover at 20m and 30m, so reflects dense forest, with a more open canopy at higher levels. FAC3 increases with percentage cover at 10m, so reflects increased cover at the understory level. FAC4 increases with increased percentage cover at 20m, so reflects mid-level canopy cover. So, FAC1 reflects tree architecture, FAC2 reflects the density of the forest, and FAC3 and FAC4 reflect canopy cover at understory and mid- level.

There was a significant difference in FAC1 between disturbance levels (*t*-test using unequal variance estimate: $t = -6.9$, $df = 35$, $p = <0.000$), with the mean FAC1 score for less disturbed forest 1.3 greater than for heavily disturbed forest (LD: -0.66 ± 0.6 ; HD: 0.66 ± 0.2). There was also a significant difference in FAC2 scores (*t*-test using unequal variance estimate: $t = 3.2$, $df = 51.2$, $p = 0.002$) with heavily disturbed forest having a mean score 0.78 (95% CI, 0.3 – 1.3) higher than less disturbed forest.

However, both FAC1 and FAC2 showed greater variability in less disturbed forest (FAC1: range = 4.5; FAC2: range = 4.0) than heavily disturbed forest (FAC1: range = 1.2; FAC2: range = 3.0), indicating a greater range of habitat heterogeneity in less disturbed forest.

Variable	Heavily disturbed		Less disturbed		<i>p</i>
	Mean	SD	Mean	SD	
Trees					
Mean height*	11.4	4.6	14.0	5.8	<0.000 ^b
Mean BC*	44.3	25.5	50.1	26.3	<0.000 ^b
Mean CBH*	36.0	21.8	41.2	23.6	<0.000 ^b
Stem density per m ² *	2.0	0.4	1.6	0.6	0.006 ^b
Number of tree species	15.2	3.1	13.0	4.8	0.033 ^b
Lianas					
Number of lianas	1.9	1.3	1.3	1.3	0.065 ^a
Number of liana species	1.3	0.8	0.9	0.7	0.018 ^a
Percentage cover					
10m*	43.7	23.0	47.9	27.9	0.524 ^a
20m*	27.7	26.1	50.3	26.7	0.002 ^a
30m*	4.7	10.8	7.7	15.3	0.384 ^a
Principal components					
FAC1	-0.7	0.3	0.7	1.0	<0.000 ^b
FAC2	0.4	0.7	-0.4	1.1	0.002 ^b

Table 18. The values for individual forest structure variables for heavily and less disturbed forest, with two principal components of variation. Variables marked with a * are those which were input into the final PCA to generate FAC1-4. The *p* value indicates the results of an independent *t*-test to determine whether the differences in means for heavily and less disturbed forest were significant. Green shading indicates a significant difference.

^a Levene's test indicated homogeneity of variances (>0.05), so equal variance assumed.

^b Levene's test indicated variance unequal, so the *t* statistic using unequal variances assumed was reported.

Habitat associations:

Mean butterfly abundance was not statistically significantly predicted by FAC1-4 in heavily disturbed ($F = 0.38$, $df = 4$, residual $df = 25$, $p = 0.82$) or less disturbed ($F = 0.54$, $df = 4$, residual $df = 25$, $p = 0.71$) forest. The forest types were analysed separately so that the difference in vegetation between habitat types did not artificially create an effect of vegetation on butterfly abundance. Mean number of species trapped was also not statistically significantly predicted by FAC1-4 in heavily disturbed ($F = 1.22$, $df = 4$, residual $df = 25$, $p = 0.33$) or less disturbed forest ($F = 0.88$, $df = 4$, residual $df = 25$, $p = 0.49$).

Species composition:

There was a significant difference in the species composition of trees and lianas between heavily and less disturbed forest ($R_{ANOSIM} = 0.36$, $p < 0.001$) with distinct communities of species (see figure 13).

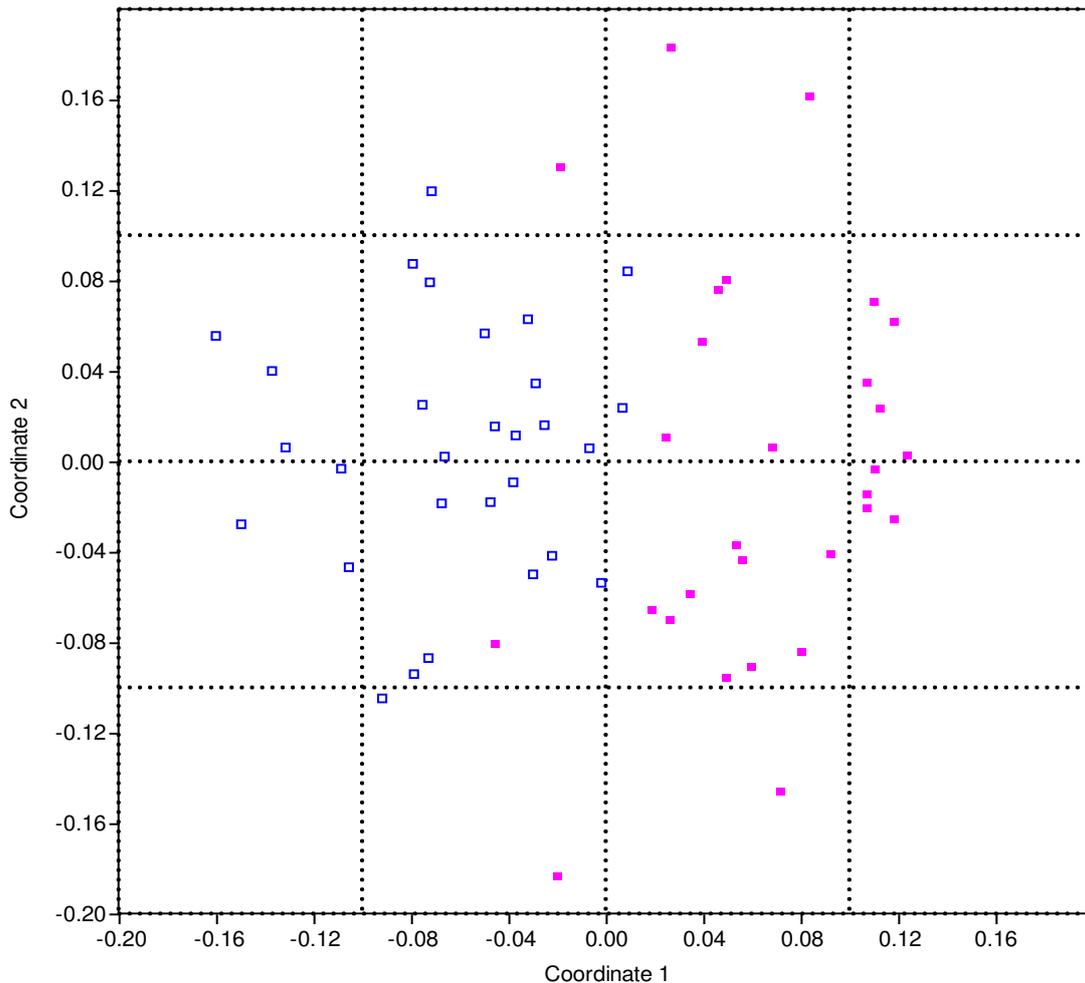


Figure 13. Non-metric multi-dimensional scaling of the community composition of tree and liana species in plots in heavily disturbed forest (blue squares) and less disturbed forest (filled pink squares), created using PAST software.

Discussion

The impact of logging on invertebrates is a critical concern, especially in South-east Asia, where many of the forests most threatened by logging are found (Cleary, 2005). In this study, logging was shown to influence the species richness, abundance and community composition of carrion- and fruit- feeding butterflies in tropical peat-swamp forest, Borneo, but that these guilds react differently to the disturbance.

As found elsewhere (Hamer et al, 2006; Holloway et al, 2013), species richness was significantly higher on carrion than on fruit, and this was still true at higher taxonomic levels; species richness recorded on the carrion traps was over double that of the fruit traps. This suggests that carrion is a very important food source for tropical butterflies, which has often been neglected in studies in the past (Hamer et al, 2006; Molleman, 2010). Abundance was greater on fruit when the difference in sampling effort was accounted for; although it is possible that overall populations were similar owing to the male bias observed on carrion, consistent with other studies (Hamer et al, 2006; Molleman, 2010). There were distinct communities feeding on carrion and fruit, with few butterfly species utilizing both as a food source.

Responses of animals to logging are varied, with both positive and negative impacts recorded (Berry et al, 2010; Fimbel et al, 2001; Morrogh-Bernard et al, 2003; Page, 1997). In this study, logging increased the species richness and abundance of carrion-feeding butterflies; while having little impact on fruit-feeding butterflies.

It is possible that an increase in small mammal abundance post-logging, as has been found in a previous study (Doody et al, 1997), would encourage an increase in numbers of other animal groups which feed upon them. This could contribute to a greater availability of food resources; both carrion, and faeces and secretions of vertebrates, which have all been observed to host 'puddling' behaviour by Lepidoptera (Molleman, 2010), thereby enabling an increase in the abundance and species richness of carrion-feeding butterflies.

Molleman (2005) acknowledges two distinct feeding guilds: nectar-feeders and fruit-feeders, with few butterflies regularly feeding on both. As carrion-feeding is thought to supplement diets with specific micro-nutrients, such as sodium or nitrogen (Molleman, 2010), rather than fulfilling all energy requirements, it is possible that other dietary resources are more available in disturbed forest. Higher light levels in the understorey of disturbed forest could allow an increase in herbaceous plants and nectar resources (Ghazoul & Hill, 2001; Berry et al, 2010), allowing an increase in nectar-feeding, which is a behaviour general to all five butterfly families sampled in this study (Beck & Fiedler, 2009), thereby increasing butterfly abundance. For example, members of

the Pieridae and Papilionidae, both of which were sampled in the carrion traps of this study, are known feed on nectar (Holloway et al, 2013).

Nymphalidae subsist almost entirely on fruit (DeVries et al, 1997); the ambivalent response to disturbance may suggest that there was not a sustained long-term increase in fruit resources in heavily disturbed forest, as has been found in other studies (e.g. Costa & Magnusson, 2003). A review of the response of different avian feeding guilds showed that frugivores declined significantly post-logging (Gray et al, 2007), possibly due to a decrease in fruit resources, although a study of bats found the opposite (Clarke et al, 2005). Several of the species sampled on fruit were also sampled on carrion, and the response of this subset to logging was still consistent with carrion-feeding butterflies overall. Nymphalinae and Charaxinae occur more often in gaps and exploit a wider variety of trees, shrubs and lianas (Hamer et al, 2003), and therefore may be expected to benefit from logging, which produces artificial gaps and increases short-term plant diversity (Berry et al, 2010). All of the Nymphalidae species found on both fruit and carrion were in the Nymphalinae and Charaxinae families, which may explain why this subset responded positively to disturbance; 31% of fruit-feeding Nymphalidae were in other families, which are likely to respond differently. A previous study found species richness of fruit-feeding butterflies at the same site to be positively correlated with percentage canopy cover (Houlihan et al, 2013), which was reduced in heavily disturbed forest, especially at higher levels.

The species composition of trees and lianas was significantly different between heavily and less disturbed forest; so it is likely that there is a difference in fruit and nectar production between the two areas. It is also possible that differences in larval host-plants present in each forest type could account for differences in species richness of adult butterflies, as well as seasonal variations in larval mortality (Hamer et al, 2005) and presence of courtship areas (DeVries et al, 2012).

Liana diversity and abundance was higher in logged forest. Butterflies that specialize on lianas have been found to increase in abundance post-logging, due in part to the increase in liana density (Cleary et al, 2005). As the species richness of carrion-feeding butterflies is much higher than that of fruit-feeders, it may be that there are more liana-specialists in that guild, which could help to explain the increase in abundance of carrion-feeders post-logging.

Logging can increase the species richness of generalists and herb feeders, by opening up with logging roads areas of forest previously impenetrable to species restricted to more open habitats (Cleary et al, 2005). The heavily disturbed transects were located closer to the forest edge, and so this may also have increased opportunities for migration of butterflies from areas outside of the forest. This may have increased the diversity of carrion-feeders in heavily disturbed forest by increasing numbers of non-forest-dependent species. The lack of increase in fruit-feeding

butterflies in heavily disturbed forest may indicate that this guild consists of forest-dependent specialists, with frugivory less common than puddling, and no opportunistic generalists able to spread to heavily disturbed forest from other areas. This is very possible, as fruit is more restricted to forests than carrion. Previous studies have found that some species of carrion-feeding butterfly have higher mobility than those that feed on fruit, in order to reach ephemeral food resources that can be widely scattered (Hamer et al, 2006; Hall & Wilmott, 2000). In this study, carrion-feeders had lower recapture rates than fruit-feeders, which supports this, meaning they could be more able to colonise disturbed areas. However, this could also be due to the dependence of fruit-feeding butterflies on fruit, whereas carrion-feeders only need to supplement their diet by puddling occasionally, and therefore probably visit carrion sources less (Hamer et al, 2006).

It is also likely that the contiguous nature of the forest areas of the study site would facilitate at least some migration of butterflies from less disturbed to heavily disturbed areas, keeping the species diversity of the latter higher than it would be in an isolated fragment. If carrion-feeders have higher mobility, this may be another reason that increased species richness increased with disturbance in this guild.

Previous studies have found more species of generalist butterflies in heavily disturbed forest, with butterflies with a restricted distribution and high conservation value more abundant in less disturbed forest (Hill et al, 1995; Ghazoul & Hill, 2001). This study found that while there was no difference between the two forest types for fruit-feeders, for carrion-feeders there were actually more highly ranked butterflies in heavily disturbed forest. A previous study of Nymphalidae in Borneo found that within the Satyrinae and Morphinae, species with narrower geographical ranges were more adversely affected by logging, while in the Nymphalinae and Charaxinae the opposite was true (Hamer et al, 2003). Over a third of all the butterflies trapped on carrion were in the Nymphalinae or Charaxinae, which could partly explain the tendency to narrow geographical distribution in heavily disturbed forest. It is likely that sub-families within the other families trapped on carrion show different relationships between disturbance and taxonomic distinctiveness.

Disturbance caused a significant change in species composition in both fruit- and carrion- feeding butterflies, but again this differed between the guilds. There were more distinct species assemblages of carrion-feeding butterflies in less disturbed forest, and significantly different community composition. This indicates that for carrion-feeding butterflies, a more complex butterfly community was present in unlogged forest; however, although species richness and abundance were greater in heavily disturbed forest, this was not due to an influx of widespread generalist species of lower conservation value, as discussed above. The lesser distinctness in community composition for fruit-feeding butterflies in less disturbed forest may be misleading, as fruit-feeding

is not as widespread as puddling, and all the species sampled were from the same family from a smaller species pool. Species evenness was higher in less disturbed forest.

A study of temporal variation in fruit-feeding butterflies in northern Borneo found that diversity was higher in logged forest during the wetter monsoon season and higher in primary forest during the drier season (Hamer et al, 2005). My study took place in the transitional and then the wet season, so it may be that the preference of fruit-feeding butterflies for less disturbed forest during the rest of the year is more pronounced. It is also possible that the higher values for diversity in heavily disturbed forest that were found for carrion-feeding butterflies are an artefact of the season, and misleading. However, different guilds may not respond in the same way to temporal variation. Fruit resources also exhibit seasonality (Levey, 1988; Kimura et al, 2001) which may impact on populations of fruit-feeding butterflies which time breeding peaks accordingly. The fruiting phenologies of the most common tree and liana species found in the study suggest that during the dry season in Sabangau there are more fruit resources available in less disturbed forest, whereas during the wet season it is more even (see appendix 1), which may mean that the preference of fruit-feeding butterflies for less disturbed forest is more pronounced in the dry season. Seasonal migratory and diapause strategies, along with population fluctuations, could also impact the diversity and abundance of butterflies sampled in the wet and dry seasons (Bonebrake et al, 2010).

Ideally, fruit and carrion data would have been collected together, subject to exactly the same environmental conditions. The fruit-feeding butterfly sampling was carried out as part of a longer-term study, and so the methodology could not be changed. It is possible therefore that differences in air temperature, rainfall, and other climatic variables could have accounted for some of the differences observed in the response to disturbance from carrion- and fruit-feeding butterflies (Basset et al, 2013); however, the length of the study should have mitigated for any potential effects.

Many Lycaenidae have mutual associations with ant species (Bonebrake et al, 2010). A personal observation during the study was the much greater presence of ants at traps in heavily disturbed forest; leaf-litter ants have been shown to increase in species richness, at least initially, after disturbance (Lawton et al, 1998; Berry et al, 2010). It is possible that the increased presence of Lycaenidae, all trapped only on carrion, in heavily disturbed forest was due in some small part to the increase in ants and subsequent opportunities for mutualistic relationships.

Previous studies of tropical butterflies in South-east Asia have shown both decreases and increases in butterfly diversity after anthropogenic disturbance (Cleary, 2004; Bonebrake et al, 2010; Hill et al, 1995; Willott et al, 2000). This demonstrates the idiosyncratic nature of responses to logging, highly dependent on various corroborating factors: the scale at which sampling takes

place, proximity to areas of different habitats or to neighbouring forest, sampling techniques, focus guilds, and different disturbance intensities (Hamer & Hill, 2000; Cleary, 2004; Hamer et al, 2003; Dumbrell & Hill, 2005). The use of Lepidoptera as habitat indicators is therefore dubious, exacerbated by a documented lack of correlation with diversity of other taxonomic groups (Hayes et al, 2009; Lawton et al, 1998; Bonebrake et al, 2010; Gardner, 2010).

One study showed that the impact of disturbance on butterflies can be predicted with high confidence knowing only the spatial scale of sampling, and that the smaller the scale of the study, the more likely a positive response to disturbance (Hamer & Hill, 2000; Hill & Hamer, 2004), with species richness and evenness exaggerated (Hamer et al, 2003). Although data was analysed at the trap and transect level, it is possible that at higher spatial scales the positive response of carrion-feeding butterflies in this study could be reversed. Fruit-feeding butterflies were studied on fewer transects than carrion-feeding, and therefore at a smaller scale; however, the likely species pool was sampled more effectively, with 62% of the total found during a year-long study conducted in the same area in 2012 trapped (Marchant et al, in press), so the difference in response between the two guilds should still be robust. Species richness was significantly higher in heavily disturbed forest for fruit-feeders at the transect level however. Less disturbed forest exhibited a greater range of vegetation densities and tree architecture than heavily disturbed forest, and increased structural complexity often positively correlates with biodiversity, with a greater variety of resources and micro-climates available for species to exploit (Gardner, 2010). Both dense shade and open gaps are more common in unlogged forest (Hamer et al, 2003). The scale of the study may not have been big enough to take the difference in habitat heterogeneity into account, and an enlarged study area may have produced a higher diversity of carrion-feeding butterflies in less-disturbed forest, to correspond with fruit-feeding butterflies which were more effectively sampled; as well as a greater species richness of trees. Species turnover was higher in heavily disturbed forest, meaning greater heterogeneity in species composition, which may also be reversed.

Both carrion-feeding and fruit-feeding butterflies seemed to show stratification of community composition according to trap height, as found in previous studies (DeVries et al, 2012; Houlihan et al, 2013; Dumbrell & Hill, 2005), with more distinct communities at the canopy level than at the ground level. It is possible however that this is a result of the use of baited traps, and is not maintained at all times (Hill et al, 1995). Three species were found only in the canopy, but as they were each only sampled once, it is unlikely that they are canopy-dependent species, just that they are uncommonly trapped. Disturbance resulted in a reduced and lower canopy, as found in previous studies (Willott et al, 2000), so this may be consistent with previous findings that undisturbed forest hosts a more complex assemblage of butterfly species (Hill et al, 1995). The canopy of mixed peat-swamp forest is lower than that of dipterocarp forest, which in addition to the

presence of fruits lodged high in trees, may mean butterflies do not have to descend to the floor to feed on rotting fruits (Houlihan et al, 2013).

There were many more carrion-feeding than fruit-feeding butterfly species trapped only once. This could suggest that many of the species that were found only in one forest type or another were not sampled effectively, although some may represent individuals of inherently rare species (Woodcock et al, 2011; Gardner, 2010). When only species with more than 5 individuals trapped were accounted for, species richness was the same in both forest types; suggesting that perhaps if sampling was more effective, the positive response of carrion-feeding butterflies to disturbance would reduce.

This study found then that the impact of logging on Lepidoptera differs between guilds, and that care should be taken therefore when evaluating or predicting the effects of disturbance using only one functional guild. Species richness and abundance of butterfly species may be maintained, or increased, post-disturbance, but species assemblages may become less complex and distinct; and other influencing factors such as seasonality and spatial scale also need investigating further. As found in other studies however, disturbed forest is clearly still of high conservation and biodiversity value (Berry et al, 2010; Woodcock et al, 2011; Edwards et al, 2011).

Further monitoring should be undertaken of the butterfly communities at the research site, to distinguish between real, long-term impacts of disturbance on abundance and species richness, and short-term, stochastic effects (Basset et al, 2012). It is also possible that with time, as the habitat recovers, species with restricted ranges may re-colonise, and the species assemblages would no longer be distinct (Liebsch et al, 2008).

Acknowledgements:

Fieldwork was undertaken in collaboration with OuTrop (the Orangutan Tropical Peatland Project), who work in partnership with CIMTROP (the Centre for International Cooperation for Sustainable Management of Tropical Peatland), based at the University of Palangka Raya in Central Kalimantan, Indonesia.

All relevant research permits and visas were obtained for the fieldwork, from the Indonesian Institute of Research and Technology (RISTEK) and other local authorities.

I would also like to thank my supervisors, Professor Keith Hamer, University of Leeds, and Dr Mark Harrison, the managing director of OuTrop, for their help and advice; as well as the assistants and volunteers who helped me in the field, especially Abdul Azis, Ari Purwanto and Fransiskus Agus Harsanto.

I would also like to thank the Whitley Wildlife Conservation Trust, without whose financial support the project would not have been possible.

Adding to existing knowledge of butterflies found in Sabangau

A guide to the carrion-feeding butterflies that were trapped during this study was produced for the research station, and is included in this report (on attached CD), along with raw data.

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Species	Heavily Disturbed		Less Disturbed		Fruiting frequency	Month											
	Rank	%	Rank	%		J	F	M	A	M	J	J	A	S	O	N	D
<i>Blumeodendron elateriospernum/tokbrai</i>	-	-	7	4	F		f				f	f	f				
<i>Calophyllum hosei</i>	10	2.3	2	6.4	R		f	f									
<i>Camposperma coriaceum</i>	-	-	5	4.9	F	f				f		f					f
<i>Cratoxylum arborescens / glaucum</i>	7	3	-	-	R										F*		
<i>Dactylocladus stenostachys</i>	3	4.1	9	3	I												
<i>Diospyros areolata</i>	-	-	10	3	-												
<i>Elaeocarpus mastersii</i>	8	2.9	-	-	I												
<i>Garcinia sp. 5/10/bancara</i>	5	3.5	-	-	R	F*										f	F*
<i>Horsfieldia crassifolia</i>	-	-	8	3.6	I												
<i>Lithocarpus sp. 4</i>	2	4.9	-	-	R		f										
<i>Neoscortechinia kingii</i>	-	-	3	5.5	I												
<i>Nephellium lappaceum</i>	6	3.5	-	-	I												
<i>Palaquium leiocarpum</i>	-	-	1	6.8	F	f	f				f	F*	F*	F*	F*	F*	f
<i>Shorea teysmanniana</i>	1	7.4	4	5.3	I												
<i>Tetramerista glabra</i>	9	2.8	-	-	F	f				f	f	F*	f	f	f	F*	f
<i>Uncaria sp. 1</i>	4	3.8	6	4.2	-												

Appendix 1. The fruiting phenology of the top ten most common species of tree and liana in heavily and less disturbed forest. % is the percentage of individuals accounted for by that species. Fruiting frequency denotes whether the species fruits frequently (F), regularly (R) or unknown (-). If time of fruiting is known, boxes were shaded in according to month, with green shading if the species was one of the ten most common in less disturbed forest, or red if the species was one of the ten most common in heavily disturbed forest. Orange denotes that it was common in both. Grey diagonal shading indicates the study period of this research project.

f = high likelihood of $\geq 1\%$ of stems bearing fruit, F* = high likelihood of $\geq 10\%$ of stems bearing fruit.

Information obtained from a report entitled 'The Fruiting Phenology of Peat-swamp Forest Tree Species at Sabangau and Tuanan, Central Kalimantan, Indonesia' (Harrison et al, 2010).

Code	Species	Originally trapped				Recaptured				Number of days between captures	Distance between captures, m	M/F	Colour	Wing condition	Trap fidelity?
		Date	Transect	Trap	Time	Date	Transect	Trap	Time						
D18	<i>Burara etelka</i>	09/11/2013	0.8	6	11:26	18/11/2013	0.4	4	11:12	9	450	M	1 (2)	1 (2)	No
H6	<i>Amblypodia narada</i>	18/11/2013	0.4	6	11:24	19/11/2013	0.4	5	12:45	1	50	M	1 (2)	1 (1)	No
B78	<i>Charaxes bernadus</i>	20/11/2013	0.4	3	11:25	21/11/2013	0.4	3	12:56	1	0	M	1 (1)	1 (2)	Yes
D17	<i>Burara etelka</i>	09/11/2013	0.8	3	11:13	21/11/2013	0.4	7	13:07	12	500	M	2 (2)	2 (1)	No
B113	<i>Charaxes bernadus</i>	03/02/2014	0.4	1	12:22	07/02/2014	0.4	9	12:58	4	450	M	1	1	No
B94	<i>Charaxes bernadus</i>	09/12/2013	0.8	1	12:30	13/02/2014	1B east	8	11:29	4	500	M	1	1	No
P4	<i>Polyura schreiber</i>	02/12/2013	1B east	9	11:04	07/12/2013	0.8	5	12:40	5	320	M	1 (2)	1 (2)	No
A23	<i>Agatasa calydonia</i>	10/01/2014	0.4	1	11:29	18/01/2014	0.8	1	11:29	8	400	M	1	1	No
B101	<i>Charaxes bernadus</i>	10/12/2013	2	15	12:39	11/02/2014	1.6 (2)	11	12:54	1	410	M	1	2	No
B91	<i>Charaxes bernadus</i>	09/12/2013	2	15	11:16	10/12/2013	2	16	12:36	1	10	M	1 (2)	1	No
A22	<i>Agatasa calydonia</i>	07/12/2013	2	13	11:26	11/12/2013	2	15	11:27	4	50	M	1	1	No

Appendix 2. The recaptured individuals on carrion; which were originally trapped on carrion.