

0 Distance-driven species turnover in Bornean rainforests: 53 homogeneity and heterogeneity in primary and post-logging forests 55

5 **R. L. Kitching, L. Ashton, A. Nakamura, T. Whitaker and Chey Vun Khen** 60

10 *R. L. Kitching (r.kitching@griffith.edu.au), L. Ashton and A. Nakamura, Environmental Futures Centre and Griffith School of Environment, Griffith Univ., Nathan, QLD 4111, Australia. – T. Whitaker, Crowtrees, Low Bentham, Lancaster, LA2 7EE, UK. – C. V. Khen, Forest Research Centre, Sabah Forestry Dept, Sepilok, Sandakan, Sabah 90715, Malaysia.*

15 Selective logging is practiced extensively within tropical rainforests of south-east Asia, and its impact on local biodiversity is well documented. Little is known, however, about the impact of selective logging on patterns of spatial heterogeneity of species. We set out to test the hypothesis that selective logging will lead to a homogenization of the associated faunal assemblages, using moths (Lepidoptera) as our subject taxa. 65

20 Large-scale transects were established within primary and post-logging lowland mixed dipterocarp rainforests around the Danum Valley Conservation Area and surroundings, Sabah, Malaysia (4°50'N–5°00'N and 117°35'E–117°45'E). Five study sites were located within each habitat with geometrically increasing inter-site distances. Macro-moths plus Pyraloidea were sampled by light trapping in 2007 and 2008. Vegetation state was also measured at each site. 70

25 A clear distance–decay relationship (decreasing assemblage similarity with increasing geographic distances) was observed in primary forest but was absent in the post-logging forest. Large, comparable numbers of macro-moth species were found in both primary and post-logging forests. There were no significant differences in moth assemblage composition between primary and post-logging forests. 75

30 There are important structural differences between primary and post-logging forests reflected in the moth assemblages. A two-stage hypothesis combining both neutral and niche concepts is probably the most parsimonious explanation of these results. First, the composition of the moth assemblage is almost certainly determined locally by the variety of plant–hosts available to larvae, with the plants representing important niche dimensions for the moth species. Second the turnover (or lack of same) in the underlying plant assemblage probably reflects clumping and, in turn, dispersal capacity of the commoner plants in each forest type. Although the impact of selective logging may be subtle, this study suggests that selective logging results in the spatial homogenization of macro-moth assemblages. 80

35 The physical disruption caused by logging operations on tropical rainforests has produced evidence that the biodiversity and ecology of such post-logging forests may be seriously impacted (Sist et al. 2003a, b, Meijaard et al. 2006, Paoli et al. 2008, Corlett 2009). In terms of increases or decreases in species richness, a range of studies of taxon- or habitat-specific assemblages have given mixed results (Holloway et al. 1992, Hill 1999, Willott 1999, Davis 2000, Willott et al. 2000, Schulze et al. 2004, Deblauwe and Dekoninck 2007, Dumbrell et al. 2008, Sodhi et al. 2010). Given the vast biological diversity associated with tropical rainforests such studies still concern a small proportion of taxa, locations and time periods. Further studies will shed light on the generality or otherwise of these earlier results. 85

40 In addition, anticipated post-logging impacts may be considerably more subtle than simple changes in species richness. As the physical structure of the forest is altered, so corresponding changes may be induced in community parameters such as food-web structure, guild partitioning, habitat diversity and, most pertinent to the present paper, patterns of spatial heterogeneity (Willott 1999, Hill and Hamer 2004, Beck et al. 2006). All of these changes can occur without changing species richness and yet may have dramatic impacts upon ecosystem functioning and service provision. In other words it is the composition and patterning of the richness which may change rather than the absolute richness itself. 90

45 One hypothesis derived from these concerns, is that the disturbance regime associated with the logging process may impose a spatial homogeneity on species assemblages, in place of a distance-mediated dynamic turnover in species composition which might be expected to occur within an intact 'primary' rainforest (Nekola and White 1999, Chave and Leigh 2002, Morlon et al. 2008). Should this prove to be the case then questions arise as to what sorts of ecological processes may produce these patterns. The current neutrality/ niche differentiation debates (Chesson 2000, Hubbell 2001, Leibold and McPeck 2006) are pertinent here, as are related issues of spatial scale as it relates to pattern in emergent properties of ecological communities. If neutrality is the 100

0 dominant process determining place to place turnover in
community composition, then once spatially explicit pro-
cesses are taken into account, a distance decay curve may
be expected with steepness associated with the clumping
regime of the underlying plants (Chave and Leigh 2002,
5 Morlon et al. 2008). Of course, such a relationship may
also arise if there is spatial habitat heterogeneity and the sort
of compartment-based specialisation of communities noted
for arthropods by, among others, Walter et al. (1998) for
mite assemblages, and C. Wardhaugh et al. (pers. comm.) for
10 beetles in rainforests. Further, if place to place turnover is
examined on too small a scale vis-à-vis the inherent or feasi-
ble vagility of the organisms being studied, then again no
distance-decay relationship may be detected.

15 We have used the relatively well-known moth fauna of
Sabah in northern Borneo to compare the patterns of species
turnover across primary and post-logging lowland forest. We
have used a mass sampling programme based on geometri-
cally increasing inter-site distances from 100 to 80 000 m
in each forest type to test the hypothesis outlined above.

20 We began with the a priori expectation that species turn-
over would be related to inter-site distance in undisturbed
forest whereas place to place change in post-logging forest
would show no such relationship.

25 Study site and methods

Study area

30 The Danum Valley Field Centre is located on the Segama
River in north-eastern Borneo in the Malaysian state of
Sabah. The Field Centre is adjacent to the 43 800 ha Danum
Valley Conservation Area (4°50'N–5°00'N and 117°35'E–
117°45'E) – a fully conserved region of undisturbed primary
35 lowland dipterocarp forest. Both the Field Centre and the
Conservation Area are embedded with the 1 million ha
Yayasan Sabah logging concession. This surrounding area
has experienced various intensities of logging from the 1960s
until very recently. Most of the post-logging areas have been
40 allowed to regenerate naturally although some restoration
by interplanting using dipterocarp saplings has occurred in
a few areas.

In general the primary forest has a high density of dip-
terocarp trees frequently forming a closed canopy with rela-
tively open understory. In contrast post-logging areas have
45 relatively open canopies and a dearth of dipterocarp species
(these being the primary targets of the logging industry).
The few large trees left standing are those less favoured by
the industry such as *Koompasia excelsor* (although following
some logging regimes a small number of dipterocarp 'seed
50 trees' also remain). The understory is frequently dense
with mass thickets of gingers, climbing bamboos *Dinochloa*
spp. and smothering vines as well as tree genera such as
Macaranga, *Octomeles* and *Neolamarkia* characteristic of
55 disturbed areas (Willott 1999). Detailed descriptions of the
flora and vegetation of the primary rainforests close to our
study areas are provided by Newbery et al. (1992). Studies
of the vegetation of the forests after logging are few but
Woods (1989), Brearley et al. (2004) and Bischoff et al.
60 (2005) provide useful introductions and some survey data.

Sampling design

We selected ten study sites, five in undisturbed primary
forest and five in post-logging forest, at each of which we
located three Pennsylvania-style light traps hung at about
65 head height (Frost 1957, Kitching et al. 2005). Figure 1 shows
the approximate location of each group of traps. All sites
were at < 300 m a.s.l. (primary forest sites 152–279 m a.s.l.;
logged-over sites 124–215 m a.s.l.). Traps were arranged
about a focal point such that no trap was visible from
70 any other. At each site three traps were run for several nights,
until a moth sample of at least 1000 individuals of macro-
moths with a wingspan greater than circa 8 mm, had been
accumulated. We have not used each trap as an independent
75 sample, first, because of their proximity to each other (gener-
ally < 20 m) and, second, because accumulating a suffi-
ciently large, statistically powerful, sample in each trap
(rather than sets of three traps) would have extended the
sampling period beyond the time resources available. We
used this approach as a way of circumventing the inherent
80 variability in nightly catches associated with light trapping.

85 Sampling was carried out during two field trips in the
same period (December–March) in 2007 and 2008. Simple
logistics prevented all 10 sites being sampled in the same
year, and this is an acknowledged weakness in the study.
Accordingly we sampled four primary forest and two post-
logging forest sites in 2007, and two primary and four
post-logging forest sites in 2008. We resampled one primary
and one secondary site in each year so that the year-to-year
90 variation in diversity could be assessed (see below).

Within each forest type, sampling foci were located
at geometrically increasing inter-site distances. From a base
location and set of samples (point 0), further samples
were collected at ca 100, 1000, 10 000 and 80 000 m dis-
95 tance (the most distant sites were located in the adjacent
Imbak Canyon Conservation Area). This design gave us
the ability to calculate assemblage similarities for inter-site
distances within each forest 'treatment'. All sites occurred
within a more or less continuous forest matrix.

All conventionally designated macro-moths (that is:
100 members of the clade 'Macrolepidoptera' together with
Hepialoidea, Zygaenoidea and Cossioidea) plus Pyraloidea
and Thyridoidea (Grimaldi and Engel 2005) were removed
from the samples and counted. This group of moths com-
prises a large portion of Lepidoptera in Borneo, representing
105 more than 6800 recognised species (Holloway 1986–2011,
Whitaker unpubl.). All moths were identified to morpho-
species and a substantial fraction have subsequently been
named using the 18 volumes of Holloway (1986–2011),
Robinson et al. (1994) and treatments in preparation for
110 [AQ2] the Pyraloidea and Thyridoidea (Whitaker et al. unpubl.).

Lepidoptera are almost universally herbivorous in their
larval stages (Scoble 1992) and hence information on plant
assemblages is useful in trying to explain moth diversity
115 patterns. Accordingly plants were surveyed within a circle of
20 m diameter, centred on each of the three light traps
per site. The number of trees and their size classes ('large'
> 50 cm dbh, 'medium' 25–50 cm dbh, 'small' < 25 cm
dbh) were recorded, and abundance levels of other vegeta-
tion including seedlings and herbs were estimated using
120 the semi-quantitative DAFOR scale where 5 = dominant,

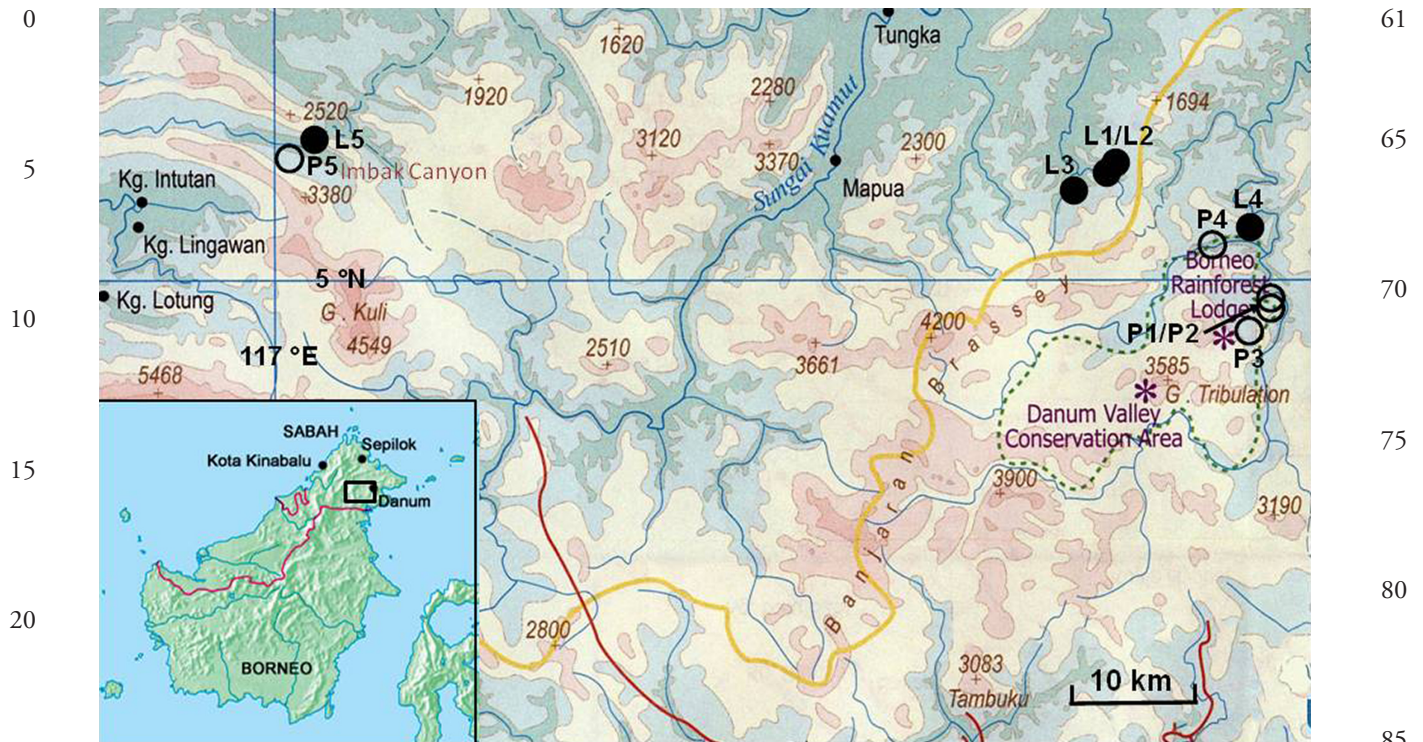


Figure 1. Map of the study sites and their locations on the island of Borneo. Sites in primary forest are indicated as open symbols and numbered with the prefix 'P', sites in logged-over forest are indicated by closed symbols numbered with the prefix 'L'. Spot heights are in feet above sea level. Topographic categories range from 0 to 150 m a.s.l. (mid-green) and then in 300 m steps through to > 1500 m (pale green to increasing shades of brown). The base map is reproduced with permission from the Sarawak/Sabah/Brunei 1:650000 sheet of the International Travel Maps produced by ITMB Publishing (<www.itmb.com>), Vancouver, Canada who retain its copyright.

4 = abundant, 3 = frequent, 2 = occasional, and 1 = rare (Butterfield et al. 1991). All plants were identified to families and, where possible, to genus and/or species.

Data analysis

We first compared moth species richness between primary and secondary forests. Although sampling intensity was standardized at approximately 1000 individuals, exact numbers varied from 1036 to 1269. Species richness was therefore adjusted to a sample size of $N = 1000$ individuals, using individual-based species rarefaction curves generated for each site, based on the expected richness function (Mao Tau) using EstimateS ver. 8.2.0 (Colwell 2009). Total species richness was estimated using the abundance-base coverage estimator (ACE) of Chazdon et al. (1998), based on a standard sample of $n = 1000$ individuals per site.

As year-to-year variation was evident (Results), statistical analyses treated sampling year as a random factor and habitat type as a fixed factor. For both univariate (species richness) and multivariate analyses (assemblage composition), we used a permutational multivariate analysis of variance (PERMANOVA) implemented in PRIMER 6 (ver. 6.1.13, Clarke and Gorley 2006) and PERMANOVA+ (ver. 1.0.3, Anderson et al. 2008) add-on software. The PERMANOVA routine tests for the effects of factors on one (such as species richness) or more (for example, assemblage composition) response variables, based on pseudo- F statistics of the

distance measures. Although PERMANOVA was developed primarily for multivariate analysis, univariate analysis is possible using Euclidean distances which yield Fisher's traditional univariate F statistic (Anderson et al. 2008). Type III sums of squares were used to calculate F statistics. Due to the limited number of possible permutations, Monte Carlo tests were conducted to obtain P values using 4999 permutations of residuals under a reduced model.

Before assemblage-level analyses, moth species were subdivided into 'common' and 'rare' species. Common species were selected following Novotny et al. (2007) who calculated the probability of observing a species (P) given N individuals from n sites, under an assumption of the extreme case where there is no beta-diversity within a given habitat, using the following equation: $P = 1 - (1 - 1/n)^N$. Threshold minimum abundance of common species ($N = 14$) was calculated with $P = 95\%$ chance of detection from $n = 5$ sites within each habitat type. Abundances of 'common' moth species were then transformed to presence/absence binary data, and a Sørensen similarity index was used to measure assemblage similarities among pairs of sites. Only common species were incorporated into the calculation of these similarity measures, as inadequate sampling of rare species results in overestimation of beta-diversity (Novotny et al. 2007). In addition we used the relative abundance of both common and rare species to calculate Chao's abundance-based Sørensen similarity index (Chao-Sørensen index, Chao et al. 2005) in order to cross-validate the results obtained using the Sørensen index of common moth species

0 (executed by EstimateS, ver. 8.2.0, Colwell 2009). Unlike other similarity indices that measure assemblage similarities using observed samples, the Chao–Sørensen index estimates the extent of shared species taking into account unseen shared species, based on the number of observed rare, shared
 5 species between two sites. The Chao–Sørensen index is effective when samples are undersampled and contain a substantial fraction of rare species (Chao et al. 2005).

Variations in moth assemblage composition were also investigated visually using non-metric multi-dimensional scaling (NMDS) ordination using PRIMER 6 software. Based on the triangular matrix of between-site similarity values, an NMDS ordination was generated using 25 random restarts with the first Kruskal fit scheme.

Pairwise comparisons among the five locations within each forest type are not wholly independent of each other (because the data from each location is involved in calculating similarities with several other sites). Accordingly we investigated distance–decay relationships between moth assemblage similarities and inter-site distances using Mantel tests calculated in R ver. 2 (R Development Core Team) and the vegan community ecology package ver. 2 (Oksanen et al. 2008). Mantel tests investigate whether two different matrices show similar patterns of inter-site variation using a correlation between two dissimilarity matrices (a Pearson correlation coefficient was used here), and test the significance of the statistic using Monte Carlo techniques. We tested the relationships between moth assemblage compositions and geographic distances between sites (in metres, log-transformed and measured as Euclidean distances). We carried out these analyses using Sørensen indices based on the presence or absence of species and the Chao–Sørensen metric which takes into account relative abundance of species. We repeated this analysis for the plant assemblages using Sørensen indices alone. Finally we examined the correlation between the moth assemblage and the tree assemblage.

Results

40 Primary forests were characterised by greater proportion of large trees and larger number of large and medium size tree species (Table 1). The proportion of dipterocarp trees was also greater within primary than secondary forest across all size classes. These differences, however, were not significant due to large between-site variations (Supplementary material Appendix 1).

In total, we sampled 13562 moths (6992 in primary forest and 6570 in post-logging forest), representing 1996 species (1393 in primary forest and 1468 in post-logging forest). Of these individuals, 7089 (1298 species) were caught in year 1 and 6473 (1465 species) in year 2. The similarity of abundances reflects the fact that we sampled each site until at least the requisite 1000 individuals were encountered (Table 2).

55 Two outcomes are of particular note based on the mean values of standardised species richness and ACE (both estimated at N = 1000 individuals) (Table 2). First, these values in primary and post-logging forest were comparable with no significant effect of habitat type (Table 3). Second, both standardized species richness and ACE in primary

Table 1. Mean and standard error (in parentheses) of: proportion of large trees to all other size classes (viz. large, medium and small trees); species richness of trees with different size classes, and seedlings and other vegetation; and proportion of Dipterocarp trees across three size classes between primary and post-logging forests.

	Primary forest	Post-logging forest
Proportion of large trees	0.420 (0.097)	0.267 (0.090)
Species richness		
Large trees	4.2 (0.9)	2.8 (0.9)
Medium trees	8.4 (1.9)	7.8 (1.0)
Small trees	1.8 (0.7)	3.2 (1.0)
Seedlings and other vegetation	10.2 (1.0)	8.8 (1.1)
All	19.0 (1.6)	18.2 (2.8)
Proportion of Dipterocarp trees		
Large trees	0.776 (0.091)	0.562 (0.167)
Medium trees	0.352 (0.088)	0.192 (0.041)
Small trees	0.400 (0.187)	0.107 (0.066)

forest were higher in year 2 than in year 1 although there was no significant effect of year, nor interaction between habitat and year (Table 3).

In both forest types across both years of sampling there were very large numbers of ‘rare’ species. In primary forest, 94% (1308 species) of all species encountered fell into this category, in secondary forest, 95% (1394 species). This is not an unexpected outcome given the size of the Bornean moth fauna.

Figure 1 represents the results of our ordination analysis based on Sørensen similarity measures of common moth species. Although within-year points for primary and post-logging forest cluster separately from each other, the introduction of two samples from the additional year in each case obfuscates these differences especially in the primary forest samples. A PERMANOVA test suggests that the year to year differences are significant whereas the forest type differences and any interaction, are not (Table 3). Similar results were found when we used Chao–Sørensen similarity measures of both common and rare species.

The situation, however, is much clearer and more interesting when we examine the relationship between species

Table 2. Mean and standard error (in parentheses) of moth abundance, species richness, estimated species richness (ACE) and the number of common and rare species per site. Values are also subdivided for the data collected in year 1 and 2.

	Primary forest	Post-logging forest
Number of individuals	1165 (40.9)	1095 (22.8)
Year 1	1211 (44.3)	1081 (24.1)
Year 2	1075 (33.0)	1124 (55.5)
Species richness at 1000 individuals	468 (17.5)	501 (8.3)
Year 1	453 (23.1)	500 (11.6)
Year 2	497 (7.6)	503 (15.0)
ACE at 1000 individuals	1236 (80.5)	1213 (39.2)
Year 1	1146 (90.3)	1182 (44.9)
Year 2	1415 (3.5)	1273 (73.8)
Number of common species	94 (2.2)	93 (0.8)
Year 1	96 (3.0)	93 (1.3)
Year 2	91 (1.5)	94 (0.5)
Number of rare species	362 (17.1)	397 (15.3)
Year 1	343 (18.5)	404 (19.4)
Year 2	402 (7.5)	383 (30.5)

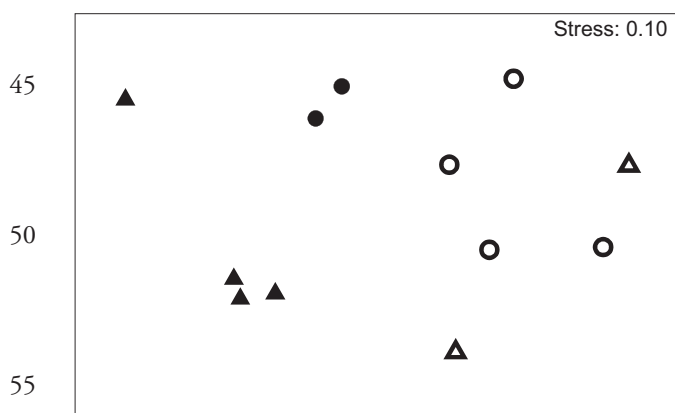
0 Table 3. Summary results of PERMANOVA, showing pseudo-*F* and *p* values (*p* values obtained from Monte-Carlo permutations) of habitat, year and their interaction effects on species richness (univariate) and assemblage (multivariate) data. Degrees of freedom for habitat, year, interaction and error were 1, 1, 1 and 8 respectively.

	Habitat		Year		Interaction	
	Pseudo- <i>F</i>	<i>p</i>	Pseudo- <i>F</i>	<i>p</i>	Pseudo- <i>F</i>	<i>p</i>
5 Univariate data						
Standardised species richness	1.26	0.453	1.09	0.324	1.40	0.282
ACE	0.09	0.813	1.27	0.300	5.19	0.053
Multivariate assemblage data						
Sørensen similarity measures on 'common' species only	3.34	0.083	4.98	0.005	0.69	0.640
10 Chao-Sørensen abundance-based estimated similarity measures	9.22	0.039	6.18	0.004	0.33	0.776

15 turnover and inter-site distance within primary and post-logging forest types (Fig. 2). We note, first, that the similarity values of moth assemblages in both forest types were remarkably high, ranging between 71 and 91% for Sørensen (that is: based on 'common' species only) and 65 and 95% for Chao-Sørensen similarity values (that is: based on all species). There was a negative relationship between assemblage similarity and the log of inter-site distance for primary forest. However, no such relationship existed for post-logging forests. Mantel tests confirmed the observed patterns, showing significant relationships between geographic distance and moth assemblages of primary, but not post-logging forest (Table 4). Plant assemblages, similarly, were significantly correlated with geographic distances within primary ($r = 0.85$, $p = 0.040$), but not post-logging forest ($r = -0.18$, $p = 0.749$). Moth assemblage composition was also correlated to those of plant assemblages. The relationships, however, were only significant for moth assemblage composition based on Chao-Sørensen index values (Table 4).

35 Discussion

In trying to erect hypotheses to underpin our observations on both richness and turnover, we first suggest that, almost without exception, local richness and assemblage structure for Lepidoptera will reflect locally available larval host plants. Although there are celebrated exceptions,



55 Figure 2. NMDS ordination based on Sørensen similarity measures of 'common' moth species, collected from primary (triangle) and post-logging forest (circle) in year 1 (closed symbols) and year 2 (open symbols).

(Williams 1930) most adult Lepidoptera are not very vagile (Wilson and Thomas 2002) and probably spend their lives within a few tens or, at most, hundreds of meters of their birth sites. A large proportion is also specialized by forest stratum with mixing between ground and canopy being the exception rather than the rule (Schulze et al. 2001, Schulze and Fiedler 2003, Brehm 2007, Ashton and Kitching unpubl.). In addition, most species are narrowly oligophagous often being restricted to a single genus or genus-group within a particular plant family (Basset 1992, Novotny et al. 2002, 2003, Dyer et al. 2007). If we accept these three generalisations as axiomatic, then explanations of spatial pattern are best sought in ideas about the spatial

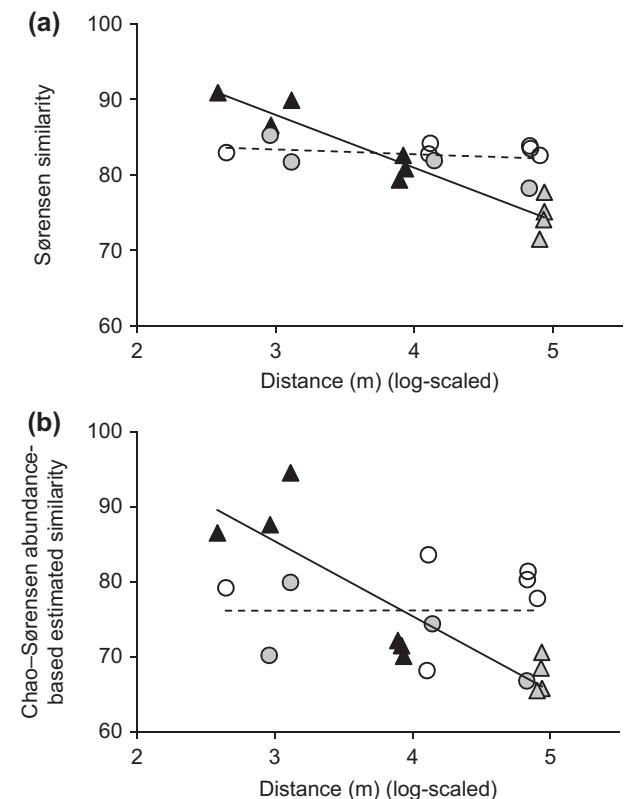


Figure 3. Relationships between geographical distance and (a) Sørensen and (b) Chao-Sørensen similarity values using moth assemblages collected from primary (triangles) and post-logging secondary (circles) forest. Shaded points represent similarity values based on comparisons of moth assemblages across the two years of the study. Trend lines were drawn for primary (solid line) and secondary (dotted line) forests.

0 Table 4. Summary results of Mantel tests showing *r* and *p* values of
 5 the matrix correlation between moth assemblages and distance
 10 matrix, and between moth and vegetation assemblages.

	Distance		Vegetation	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
5 Primary forest				
Sørensen	0.96	0.041	0.80	0.087
Chao–Sørensen	0.82	0.043	0.67	0.042
Secondary forest				
Sørensen	0.06	0.631	0.07	0.668
Chao–Sørensen	0.18	0.452	−0.50	0.872

15 patterning of the plant species which make up the local veg-
 20 etation. Here a rich and informative literature is available
 25 (Hubbell 2001, Condit et al. 2002, Losos et al. 2004).

30 Our comparisons of the species' totals in primary and
 35 post-logging secondary forests confirm earlier observations
 40 on Lepidoptera that each forest type presents similar levels
 45 of richness (Willott 1999, Hamer et al. 2003). Likewise
 50 we detected no significant overall differences in assemblage
 55 composition between these two habitat types, despite strong
 60 evidence of year-to-year variations. The similar levels of
 species richness encountered in primary and post-logging
 forest may be explained when we take into account the
 range of food-plant driven opportunities provided for estab-
 lishment of specific moth populations. The species compo-
 sition in the understorey of primary forest is likely driven
 by the availability of ombrophilous shrubs, seedlings of
 canopy trees, woody and non-woody vines, plus vascular
 and non-vascular epiphytes, plus a few species will originate
 in the leaf litter and fallen timber. Herbaceous plants are
 relatively rare under closed canopies. In contrast, in post-
 logging forests, the canopy is almost always substantially
 disturbed and simplified with concomitant loss of woody
 vines and epiphytes (Johns 1988). This may be compen-
 sated for, however, by vastly increased availability of non-
 woody vines, herbs, and ferns. Grasses, gingers, scrambling
 palms and other vigorous monocotyledons are a much more
 apparent part of the flora in these post-logging forests. It
 seems likely that this compensates for the inevitable loss
 of the canopy components of the fauna to produce the
 closely similar richness measures across the two forest types.

Turning to spatially driven turnover patterns, we found
 contrasting differences between the two habitat types: the
 presence of distance-mediated spatial heterogeneity was
 evident within primary forest but not within the post-
 logging forests. Effects of year-to-year variation may have
 confounded our results as the majority of primary and post-
 logging forests were sampled in different years. Neverthe-
 less, where there were sufficient points available from within
 year samples the contrasts in distance–decay relationship
 across the two forest treatments was comparable with those
 seen when all data were considered together. This reinforced
 our notion that such a relationship exists in primary but
 not post-logging secondary forests in Bornean rainforests.

Our finding bear direct comparison with those of
 Novotny et al. (2007) who found low beta diversity in New
 Guinean tropical rainforests. It is interesting to note that
 both Novotny et al. and we found relatively high species
 overlaps among sites (i.e. low beta diversity). Our study,

61 however, detected stronger inter-site differences with dis-
 65 tance than did Novotny et al. (2007). This apparent differ-
 70 ence between the two studies probably reflects two factors.
 First the Novotny study standardised each site for the
 plant diversity sampled whereas we did not. Indeed that
 study was based on explicit sampling of trees rather than use
 of traps. Second, the spatial scales employed in the two stud-
 ies differed substantially: our study examined inter-site
 distances of 0.4 to 80 km, whereas Novotny et al. (2007)
 examined the range, 100 to 600 km. Beck and Khen (2007)
 found distance–decay relationships in geometrid moth
 assemblages in Bornean rainforests, but the relationships
 they observed were more evident at smaller spatial scales
 with inter-site distances of < 20 km and were only detect-
 able after controlling for other parameters such as elevation
 and human-mediated disturbances.

The distance–decay relationship that we have identified
 in primary forest for both moths and plants has been
 widely supported and debated in the literature (for key refer-
 ences see Introduction). Much recent attention has been
 focussed on neutral explanations of vegetation in which
 local diversity is viewed as being drawn from a species pool
 with little if any determinism concerning local success
 of particular species (Hubbell 2001, Condit et al. 2002).
 Recent authors have incorporated explicit spatial dynamics
 into the fundamental theory of Hubbell (Chave and Leigh
 2002, Morlon et al. 2008) showing how the 'traditional'
 distance–decay curve emerges with only minimal additional
 parameters related to local, perhaps transient, 'clumping'
 of species. The most likely driver of such clumping is dispersal
 limitation. In their model, based on a Poisson cluster
 process acting upon presence or absence of species, Morlon
 et al. (2008) show in addition that this pattern is largely
 generated by the commoner species in any location with
 rare species playing only a minor role. This insensitivity to
 rare species even when abundance-based similarity measures
 are used is also confirmed by Nekola and White (1999).
 Morlon et al. (2008) also show that the shape of the rela-
 tionship is insensitive to overall species richness. It is feasible
 that place to place turnover in plant composition – and, in
 consequence, of moth assemblages – reflects topographic
 and pedological heterogeneity with distance producing
 new opportunities ('niches') for different species. This is not
 the most parsimonious explanation and, in any case, would
 not account for the absence of a distance decay relationship
 in the post-logging forest, where at least most of the topo-
 graphy and gross soil characteristics will persist, albeit in
 locally rearranged form.

We suggest, therefore, that the clear turnover we
 observe in moth assemblages in primary forest is adequately
 explained by neutral explanations of vegetation change.
 These changes then provide different available niche dimen-
 sions (through the availability of food plants) for moths
 thereby producing the patterns of moth turnover we observe.
 This combination of neutral and niche drivers of pattern
 may well have wider applicability for accounting for beta
 diversity in animal assemblages.

The same logic can be applied in seeking an explanation
 for the flat (or absent) distance–decay relationship in post-
 logging forest. Here our argument demands a more or less
 uniform set of available food plants. Under the spatially

- 0 explicit neutral model the most parsimonious way of posit- 61
ing this is by hypothesising that the post-logging forests
are dominated by plant species which have exceptionally
well developed dispersal mechanisms. This is not to say that
the same aggregative mechanisms would not apply in these
5 forests, just that they would operate over a much larger
spatial scale. The dominance of regenerating rainforests by
plants having a high vagility has been observed by several
authors (Willson and Crome 1989, Gorchov et al. 1993,
Dalling et al. 2002).
- 10 These results have considerable implications for conser-
vation. They suggest that the effectiveness of ecosystem man-
agement for conservation cannot be monitored simply by
assessing species richness. Species turnover is a vital marker
if vibrant healthy forests are to be maintained. Conceivably
15 this requires more landscape management to maintain
patches of intact canopies scattered through post-logging
forests. Depending on the target taxa this may require par-
ticular attention to the spatial scale of these patches.
- 20 *Acknowledgements* – This work was carried out at the Danum Valley
Field Studies Centre in Sabah and we gratefully acknowledge
Yayasan Sabah, the Danum Valley Management Committee
(particularly Waidi Sinun), the State Secretary, Sabah Chief
Minister's Dept, and the Economic Planning Unit of the Prime
25 Ministers Dept for permission to conduct this work. We also thank
Glen Reynolds for day to day advice and support during the field
work. Jamaludin Jamil, Alex Karolus, Anthony Karolus, Nasir
Majid and Nazran Yaakub provided able research assistance during
the field work. The study was project number RS263 of the Danum
Valley Rainforest Research and Training Programme and the
30 research was supported by the Royal Society (SEARRP) and by a
National Geographic Society, Washington (grant number 8024-06).
We gratefully acknowledge Stuart Pimm, Jane Hill and Chris
Hamer for their advice during the preparation of the research
proposal. Tom Fayle assisted us with statistical advice. These per-
35 sons together with Nigel Stork and Hamish McCallum kindly
commented upon an earlier version of the manuscript. Permission
to use the map base in Fig. 1 was provided free of charge by ITMB
Publishing, Canada and we are grateful to Ian Joyce of ITMB for
that permission.
- 40
- ## References
- Anderson, M. J. et al. 2008. PERMANOVA+ for PRIMER: guide
to software and statistical methods. – PRIMER-E, Plymouth.
- 45 Basset, Y. 1992. Host specificity of arboreal and free-living insect
herbivores in rain forests. – *Biol. J. Linn. Soc.* 47: 115–133.
- Beck, J. and Khen, C. V. 2007. Beta-diversity of geometrid
moths from northern Borneo: effects of habitat, time and
space. – *J. Anim. Ecol.* 76: 230–237.
- Beck, J. et al. 2006. Geometrid moths (Lepidoptera, Geometridae)
50 in Borneo: how homogenous are assemblages from a 'uniform'
lowland primary forest? – *J. Zool. Soc. Wallacea* 2: 44–53.
- Bischoff, W. et al. 2005. Secondary succession and dipterocarp
recruitment in Bornean rain forest after logging. – *For. Ecol.
Manage.* 218: 174–192.
- 55 Brearley, F. Q. et al. 2004. Structure and floristics of an old
secondary rain forest in central Kalimantan, Indonesia, and a
comparison with adjacent primary forest. – *For. Ecol. Manage.*
195: 385–397.
- Brehm, G. 2007. Contrasting patterns of vertical distribution in
60 two moth families in a Coasta Rican lowland rain forest.
– *Basic Appl. Ecol.* 8: 44–54.
- Butterfield, J. E. L. et al. 1991. The response of terrestrial inverte-
brates to climate change. – A report commissioned by Natural
Environment Research Council, Swindon.
- Chao, A. et al. 2005. A new statistical approach for assessing sim-
ilarity of species composition with incidence and abundance
65 data. – *Ecol. Lett.* 8: 148–159.
- Chave, J. and Leigh, E. G. 2002. A spatially explicit neutral model
of beta-diversity in tropical forests. – *Theor. Popul. Biol.*
62: 153–168.
- Chazdon, R. L. et al. 1998. Statistical methods for estimating
species richness of woody regeneration in primary and second-
ary rain forests of NE Costa Rica. – In: Dallmeier, F. and
Comiskey, J. A. (eds), *Forest biodiversity research, monitoring
and modeling: conceptual background and Old World case
studies*. Parthenon Publishing, pp. 285–309.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity.
– *Annu. Rev. Ecol. Syst.* 31: 343–366. 75
- Clarke, K. R. and Gorley, R. N. 2006. PRIMER v6: user manual/
tutorial. – Primer-E, Plymouth.
- Colwell, R. K. 2009. EstimateS: statistical estimation of species
richness and shared species from samples. – Version 8.2,
< <http://purl.oclc.org/estimates> >. 80
- Condit, R. et al. 2002. Beta-diversity in tropical forest trees.
– *Science* 295: 666–669.
- Corlett, R. T. 2009. *The ecology of tropical east Asia*. – Oxford
Univ. Press.
- Dalling, J. W. et al. 2002. Role of dispersal in the recruitment
limitation of neotropical pioneer species. – *J. Ecol.* 90:
85 714–727.
- Davis, A. J. 2000. Does reduced-impact logging help preserve
biodiversity in tropical rainforests? A case study from Borneo
using dung beetles (Coleoptera: Scarabaeoidea) as indicators.
– *Environ. Entomol.* 29: 467–475.
- 90 Deblauwe, I. and Dekoninck, W. 2007. Diversity and distribution
of ground-dwelling ants in a lowland rainforest in southeast
Cameroon. – *Insect Soc.* 54: 334–342.
- Dumbrell, A. J. et al. 2008. Changes in species diversity follow-
ing habitat disturbance are dependent on spatial scale:
theoretical and empirical evidence. – *J. Appl. Ecol.* 45:
95 1531–1539.
- Dyer, L. A. et al. 2007. Host specificity of Lepidoptera in tropical
and temperate forests. – *Nature* 448: 696–699.
- Frost, S. W. 1957. The Pennsylvania insect light trap. – *J. Econ.
Entomol.* 50: 287–292.
- 100 Gorchov, D. L. et al. 1993. The role of seed dispersal in the natu-
ral regeneration of rain forest after strip cutting in the Peruvian
Amazon. – *Vegetatio* 107/108: 339–349.
- Grimaldi, D. and Engel, M. S. 2005. *Evolution of the insects*.
– Cambridge Univ. Press.
- Hamer, K. C. et al. 2003. Ecology of butterflies in natural and
selectively logged forests of northern Borneo: the importance
105 of habitat heterogeneity. – *J. Appl. Ecol.* 40: 150–162.
- Hill, J. K. 1999. Butterfly spatial distribution and habitat require-
ments in a tropical forest: impacts of selective logging.
– *J. Appl. Ecol.* 36: 564–572.
- Hill, J. K. and Hamer, K. C. 2004. Determining impacts of habi-
tat modification on diversity of tropical forest fauna: the
110 importance of spatial scale. – *J. Appl. Ecol.* 41: 744–754.
- Holloway, J. D. 1986–2011. *Moths of Borneo*, Vol. 1–18.
– Southdene Sdn. Bhd.
- Holloway, J. D. et al. 1992. The response of some rain forest
insect groups to logging and conversion to plantation. – *Phil.
115 Trans. R. Soc. B* 335: 425–436.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity
and biogeography*. – Princeton Univ. Press.
- Johns, A. D. 1988. Effects of "selective" timber extraction on rain
forest structure and composition and some consequences for
120 frugivores and folivores. – *Biotropica* 20: 31–37.

0	Kitching, R. L. et al. 2005. The comparative assessment of Arthropod and tree biodiversity in Old-World rainforests, 2nd ed. – Rainforest CRC and Earthwatch Inst.	61
	Leibold, M. A. and McPeck, M. A. 2006. Coexistence of the niche and neutral perspectives in community ecology. – <i>Ecology</i> 87: 1399–1410.	
5	Losos, E. C. et al. 2004. The structure of tropical forests. – In: Losos, E. C. and Leigh, E. G. (eds), <i>Tropical forest diversity and dynamism: findings from a large-scale plot network</i> . Univ. of Chicago Press, pp. 69–78.	
	Meijaard, E. et al. 2006. Wildlife conservation in Bornean timber concessions. – <i>Ecol. Soc.</i> 11: 47.	
10	Morlon, H. et al. 2008. A general framework for the distance–decay of similarity in ecological communities. – <i>Ecol. Lett.</i> 11: 904–917.	
	Nekola, J. C. and White, P. S. 1999. The distance decay of similarity in biogeography and ecology. – <i>J. Biogeogr.</i> 26: 867–878.	
15	Newbery, D. M. et al. 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. – <i>Phil. Trans. R. Soc. B</i> 335: 341–356.	
	Novotny, V. et al. 2002. Low host specificity of herbivorous insects in tropical forest. – <i>Nature</i> 416: 841–844.	
20	Novotny, V. et al. 2003. Herbivore assemblages and their food resources. – In: Basset, Y. et al. (eds), <i>Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy</i> . Cambridge Univ. Press, pp. 40–53.	
	Novotny, V. et al. 2007. Low beta diversity of herbivorous insects in tropical forests. – <i>Nature</i> 448: 692–695.	
25	Oksanen, J. et al. 2008. <i>Vegan: community ecology package</i> . – R package ver. 1.11–4.	
	Paoli, G. D. et al. 2008. Soil nutrients affect spatial patterns of above-ground biomass and emergent tree density in south-western Borneo. – <i>Oecologia</i> 155: 287–299.	
30	Schulze, C. H. and Fiedler, K. 2003. Vertical and temporal diversity of a species-rich moth taxon in Borneo. – In: Basset, Y. et al. (eds), <i>Arthropods of tropical forests. Spatio-temporal</i>	
	<i>dynamics and resource use in the canopy</i> . Cambridge Univ. Press, pp. 69–85.	61
	Schulze, C. H. et al. 2001. Understorey versus canopy: patterns of vertical stratification among Lepidoptera in a Bornean rain forest. – <i>Plant Ecol.</i> 153: 133–152.	
	Schulze, C. H. et al. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. – <i>Ecol. Appl.</i> 14: 1321–1333.	65
	Scoble, M. J. 1992. <i>The Lepidoptera: form, function, and diversity</i> . – Oxford Univ. Press.	
	Sist, P. et al. 2003a. Sustainable cutting cycle and yields in a lowland mixed dipterocarp forest of Borneo. – <i>Ann. For. Sci.</i> 60: 803–814.	70
	Sist, P. et al. 2003b. Reduced impact logging in Indonesian Borneo: some results confirming the need for new silvicultural prescriptions. – <i>For. Ecol. Manage.</i> 179: 415–427.	
	Sodhi, N. S. et al. 2010. Conserving southeast Asian forest biodiversity in human-modified landscapes. – <i>Biol. Conserv.</i> 143: 2375–2384.	75
	Walter, D. E. et al. 1998. Mites in the mist: how unique is a rain-forest canopy-knockdown fauna? – <i>Aust. J. Ecol.</i> 23: 501–508.	
	Williams, C. B. 1930. <i>Migration of butterflies</i> . – Oliver and Boyd.	80
	Willott, S. J. 1999. The effects of selective logging on the distribution of moths in a Bornean rainforest. – <i>Phil. Trans. R. Soc. B</i> 354: 1783–1790.	
	Willott, S. J. et al. 2000. Effects of selective logging on the butterflies of a Bornean rainforest. – <i>Conserv. Biol.</i> 14: 1055–1065.	85
	Willson, M. F. and Crome, F. H. J. 1989. Patterns of seed rain at the edge of a tropical Queensland rain forests. – <i>J. Trop. Biol.</i> 5: 301–308.	
	Wilson, R. J. and Thomas, C. D. 2002. Dispersal and the spatial dynamics of butterfly populations. – In: Bullock, J. M. et al. (eds), <i>Dispersal ecology</i> . Blackwell, pp. 257–278.	90
	Woods, P. 1989. Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. – <i>Biotropica</i> 21: 290–298.	
		95
35	Supplementary material (available online as Appendix ECOG-0023 at < www.oikosoffice.lu.se/appendix >). Appendix 1.	
40		100
45		105
50		110
55		115
60		121