Butterfly species and traits associated with selectively logged forest in Borneo

Daniel F.R. Cleary\textsuperscript{a,b,*}, Martin J. Genner\textsuperscript{a,c}, Lian P. Koh\textsuperscript{d}, Timothy J.B. Boyle\textsuperscript{e}, Titiek Setyawati\textsuperscript{f}, Rienk de Jong\textsuperscript{b}, Steph B.J. Menken\textsuperscript{a}

\textsuperscript{a}Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands
\textsuperscript{b}National Museum of Natural History, ‘Naturalis’, P.O. Box 9517, 2300 RA Leiden, The Netherlands
\textsuperscript{c}School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK
\textsuperscript{d}Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA
\textsuperscript{e}United Nations Development Program, GEF Unit, 304 E. 45th, 10th Floor, New York, NY 10017, USA
\textsuperscript{f}Institute of Land and Food Resources, University of Melbourne, Victoria 3010, Australia

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Abstract

Logging can significantly change the structure of rainforest communities. To better understand how logging drives this change, butterflies and environmental variables were assessed within both unlogged and logged forest in Indonesian Borneo. In the whole dataset, we found local environmental variables and geographic distance combined captured 53.1\% of the variation in butterfly community composition; 29.6\% was associated with measured local environmental variables, 13.6\% with geographic distance between sites, and 9.9\% with covariation between geographic distance and environmental variables. The primary axis of variation in butterfly community composition represented a disturbance gradient from unlogged to logged forest. Subsequent axes represented gradients influenced by variables such as canopy cover and total tree density. There were significant associations between environmental variables and geographic range and larval host plant use of species. Specifically, butterflies using trees as larval host plants and those with distributions limited to Borneo were more likely to be present in unlogged forest. By contrast, species that tended to be more abundant in logged forest were those with widespread distributions and those using lianas and grasses as larval host plants. The results of this study highlight the importance of environmental variables and disturbance, e.g., selective logging, in structuring rainforest community diversity. Moreover, they confirm how species traits, such as larval food use and geographic distributions can determine patterns of species abundance following environmental change.

\textsuperscript{*}Corresponding author at: National Museum of Natural History, ‘Naturalis’, P.O. Box 9517, 2300 RA Leiden, The Netherlands.
Tel.: +31 20 5256623; fax: +31 20 5255402.
E-mail addresses: cleary@science.uva.nl, cleary@naturalis.nnm.nl (D.F.R. Cleary).

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Zusammenfassung

Der Holzeinschlag kann die Struktur von Lebensgemeinschaften in Regenwäldern signifikant verändern. Um besser zu verstehen, wie der Holzeinschlag diese Veränderungen vorantreibt, wurden die Schmetterlinge und die

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**Introduction**

The influence of commercial logging on biodiversity is one of the most important issues facing forest ecologists (Summerville & Crist, 2002), and the effective management of logged forests will probably be one of the major determinants of global rainforest biodiversity in the coming decades (Costa & Magnusson, 2002). Many studies have been undertaken of the effects of selective logging on forest biodiversity, and in general rainforest communities tend to lose few species as a result of this activity. However, there is often a marked impact on community composition (Cleary, 2004; Cleary, Boyle, Setyawati, Angraeti, & Menken, 2007; Hamer et al., 2003; Lewis, 2001; Summerville & Crist, 2002; Willo, Lim, Compton, & Sutton, 2000). Species abundance changes are likely to be linked to both the physical effects that logging has on the environment, and the ecological and life history traits of species in the community. The primary change that selective logging brings is an increase in frequency and the size of gaps in the canopy leading to rapid germination of pioneer tree species and lianas. This is likely to favour some groups of species, but at the cost of those that thrive in pristine habitat.

In this study, spatial variation in butterfly composition was assessed within a rainforest in Central Kalimantan province, Indonesian Borneo. The study site is located within the Sundaland biodiversity hotspot (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000), and, like many rainforests of the region, logging continues to supply international demand for timber (Sohi, Koh, Brook, & Ng, 2004). In Southeast Asia, butterflies have been identified as important indicators for assessing biodiversity and monitoring ecosystem responses to environmental perturbations (Cleary, 2004). In particular, butterflies of the region show substantial responses to logging (Ghazoul, 2002), but little is known of the life history characters and species traits that are likely to influence species responses to the environmental changes brought about by logging. However, two species traits have been shown to influence species responses to disturbance, namely, larval feeding guild and geographic range (Charette et al., 2006; Koh, Soh, & Brook, 2004). Larval feeding habits are important in determining species responses to disturbance because many species are host-specific, and adults locate these plants for courtship and egg laying. As such, with a change in the local host plant availability we may expect concomitant changes in butterfly community composition. Geographic range has been linked to vulnerability to disturbance, with more narrowly distributed species being subject to higher extinction risk (Charette et al., 2006). A likely reason is that narrowly distributed species also tend to occupy narrow ecological niches and are less adaptable to temporal environmental changes (Koh et al., 2004).

Here, we investigated the responses of a diverse butterfly community to commercial selective logging. Firstly, we investigated differences between butterfly communities of pristine unlogged forests and selectively logged forests. Secondly, we tested to which extent butterfly communities are dependent upon a series of local environmental variables. Third, we investigated if the distance between sampling sites influences community composition, possibly due to dispersal limitation. Finally, we tested if spatial patterns of butterfly species abundance are linked to two species traits, namely, larval host plant use and geographic range.
Materials and methods

Sampling sites and species

Sampling was conducted within the 300,000 ha Kayu Mas logging concession in Central Kalimantan. The concession contained a mosaic of forest types, including unlogged forest or forest that had been logged once. Logging in the area has been selective, with a cutting cycle of 35 years, extracting mainly dipterocarp tree species. In total, 37 sites were sampled representing three habitat types; unlogged ‘primary’ forest (hereafter labelled ‘P’: 14 sites), forest logged in 1993/94 (‘L93’: 13 sites), and forest logged in 1989/90 (‘L89’: 10 sites). Survey sites were 3 ha (300 x 100 m²) and were designated "a-priori" on a digitalised elevation map using three physiographical classes: lower, middle and upper slope habitats. For a more detailed description of sites see Cleary, Genner, et al. (2005). Butterflies were sampled from July to October 1998 using methods described in Cleary (2003). Briefly, butterflies were sampled when encountered within ca. 15 m on either side of a 300 m transect in each site. Transects were traversed on foot at a steady pace until 200 butterflies were sampled. The number of days spent sampling a site was on average 5.2 days for L89, 6.4 days for L93 and 7.75 days for P. Individuals were caught with nets and identified in the field. Most of these individuals were marked and released to avoid multiple observations of the same individual. Sampling took place between 9:00 and 16:00 h, except during rain. Capture date and location were noted for each individual. Voucher specimens of selected species were preserved and deposited at the Zoological Museum of the University of Amsterdam. Individuals were identified to species following Maruyama and Otsuka (1991), Otsuka (1988), and Seki, Takanami, and Maruyama (1991). In a few cases, it was not possible to identify beyond a species-pair or species-group because morphological diagnostic characteristics could not be determined in the field. In total, data comprised 7400 individuals belonging to 332 butterfly species (mean 58 ± 12 S.D. species per sampling site). All the species sampled and their abundance per sample site is presented in Appendix A.

Habitat structure variables

Habitat structure variables were recorded in six 200 m² (10 x 20 m) subplots in each site using a systematic sampling design that constituted 4.0% of the total site area. The following variables were recorded within each 200 m² subplot: the volume of (1) fresh dead wood, (2) dead wood with sound wood, but flaking bark, (3) dead wood with sound wood, but no bark, (4) dead wood with rotting wood, but firm, (5) dead wood with wood rotten and soft, (6) fallen dead wood, (7) standing dead wood, (8) total volume of dead wood; the abundance of (9) non-woody lianas, (10) small-woody lianas (stem diameter < 5 cm), (11) large-woody lianas (stem diameter > 5 cm), (12) epiphytes, (13) bryophytes; the ground cover of (14) seedlings, (15) herbs, (16) ferns, (17) grasses, (18) small woody debris (dead wood less than 10 cm diameter), (19) mesophyll leaf litter, (20) notophyll leaf litter, (21) microphyll leaf litter, (22) mean litter depth (23) dbh (diameter at breast height) (24) tree height, (25) bifurcation index, (26) crown depth, (27) crown radius; the density of (28) short (< 5 m) saplings (< 5 cm dbh), (29) tall (> 5 m) saplings (< 5 cm dbh), (30) short (< 10 m) poles (5–10 cm dbh), (31) tall (> 10 m) poles (5–10 cm dbh), (32) trees (> 10 cm dbh), (33) mean canopy cover and (34) standard deviation in canopy cover. The importance of geographic distance between sampling sites in explaining variation in butterfly community composition was assessed by supplementing the spatial UTM coordinates (easting ‘x’ and northing ‘y’) with all the terms of a bi-cubic trend surface, (i.e., x, y, x², xy, y², x³, x²y, xy² and y³; see Borcard, Legendre, & Drapeau, 1992). See Cleary, Genner, et al. (2005) for a detailed description of habitat structure variables.

Butterfly species traits

Data on two species traits were compiled for each species from published data. These included (1) larval feeding guild and (2) geographic distribution. We distinguished seven larval feeding guilds: (1) herb feeders (feed on dicotyledonous or monocotyledonous herbs), (2) grass feeders, (3) liana feeders (feed on monocotyledonous and/or dicotyledonous vines), (4) palm feeders, (5) tree feeders (feed on woody dicotyledonous shrubs and/or trees), (6) carnivores (feed on insects such as aphids, coccids, membracids and psyllids) and (7) generalists (members of at least two of the previously mentioned guilds). Data on host plant use was obtained from Eliot, Corbet, Pendlebury, and D’Abera (1992), Igarashi and Fukada (1997, 2000), and Robinson, Ackery, Kitching, Beccaloni, and Hernández (2001). For the geographic distribution, each species was ranked on a scale of 1–4, as follows: (1) endemic to the island of Borneo; (2) endemic to the Sundaland Region (Malaysia, Southern Thailand, Sumatra, Java, Borneo, and satellite islands); (3) found in Sundaland and surrounding biogeographic regions; (4) Sundaland and extending into more distant biogeographic regions (e.g., Australia, Africa, Europe). Geographic distribution data were obtained from Igarashi and Fukada (1997, 2000), Otsuka (1988), Maruyama and Otsuka (1991), and Seki et al. (1991).
Data analysis

Community composition was assessed with unconstrained ordination, principal components analysis (PCA) and with constrained ordination, redundancy analysis (RDA), in CANOCO 6.1 (ter Braak & Smilauer, 1998). Input for these analyses consisted of log$_{10}(x+1)$ species abundance data transformed using the programme Transformation (http://www.fas.umontreal.ca/biol/casgrain/en/labo/transformations.html). Through this transformation, species abundance data were adjusted so that subsequent analyses preserved the chosen distance among sample sites. Here the Hellinger distance was used, as recommended by Legendre and Gallagher (2001).

The environmental dataset used in the RDA consisted of the following variables: elevation, slope position (lower: 1, middle: 2 and upper: 3), logging (P: 1, L89: 2 and L93: 3) and the log$_{10}(x+1)$ mean values of previously mentioned habitat structure variables. Within CANOCO, a forward selection procedure using a Monte Carlo permutation test (999 permutations) and the full model option (ter Braak & Smilauer, 1998) was used to test environmental and spatial variables for significance (ter Braak & Verdonschot, 1995). Only variables with $P < 0.1$ were included in the final model.

The significance of associations between species and environmental datasets was also assessed using Monte Carlo simulations (999 permutations) of constrained ordination scores against environmental variables. Variance partitioning (Borcard et al., 1992; Legendre, Borcard, & Peres-Neto, 2005; Økland, 2003), using partial RDA’s within CANOCO, was subsequently used to partition the spatial variation in composition into variation only explained by environmental (vegetation structure) variables, only by spatial variables, or by a combination of both (see Økland, 2003).

Species traits were directly linked to environmental variables with a three-table ordination method known as RLQ analysis (Dolédec, Chessel, ter Braak, & Champely, 1996; Ribera, Dolédec, Downie, & Foster, 2001) using the ADE4 software package (http://pbil.univ-lyon1.fr/ADE-4/) within R (http://www.r-project.org/). See Rachello-Dolmen and Cleary (2007) for a detailed description of the method.

Results

Principal component and redundancy analyses

Principal component axis 1 captured 11.8% of the variance in community composition while axis 2 captured 7.1% of the variance. There was a clear differentiation between sites (Fig. 1), strongly indicating that commercial selective logging had considerable influence on butterfly community composition. Along axis 1, sites from L89 appeared intermediate on average to sites from P and L93 suggesting that the greater the time since logging in L89 has allowed it to more closely resemble unlogged forest, at least in as far as butterfly composition is concerned. The cluster of L93 sites closest to P sites along axis 1 are all sites that were adjacent to unlogged forest in P, thereby indicating that the proximity to unlogged forest has a strong influence on the composition of butterflies in logged forest. Along axis 2, the sites in L89 seem distinct from sites in P and L93, which may be due to the greater distance between L89 and both other areas or a function of some global
environmental difference between L89 and both other areas.

In the RDA, the sum of all constrained (canonical) eigenvalues was 0.531 (Monte Carlo test of trace; \( P < 0.001 \)). The environmental variables and geographic distance between sites thereby captured 53.1% of the variation in the dataset of which 13.6% \( (P = 0.031) \) was due to geographic distance only, 9.9% due to covariance of geographic distance and local environmental variables, and 29.6% \( (P < 0.001) \) due to local environmental variables only. The eigenvalues of the first four axes of the ordination were 0.112, 0.064, 0.050 and 0.042 for the first, second, third and fourth axes respectively. The species-environment correlations of the first four axes were high (range: 0.929–0.978) indicating a strong association between the species matrix and the environmental matrix.

RDA ordinations linking butterfly species responses to significant environmental variables are shown in Fig. 2. Axis 1 represents a disturbance gradient characterised by variables including logging, non-woody liana abundance, tree density and elevation. Species such as *Eurema hecabe*, and the grass feeding *Ypthima baldus* and *Ypthima fasciata* were associated with selectively logged habitats, while the tree feeding *Euthalia iapis* and *Arhopala borneensis*, and the generalist *Drupadia theda* were associated with unlogged habitats. Axis 2 was primarily associated with canopy cover, axis 3 with tree and liana abundance and axis 4 with grass cover.

**RLQ analysis**

RLQ analysis revealed a highly significant (Permutation test; \( P < 0.001 \)) relationship between environmental variables and species traits. We only consider the first two RLQ axes, which together captured 80.37% of variance in the analysis. The RLQ analysis (Fig. 3A and B) showed that differences between logged forest with a high abundance of non-woody and small woody lianas, mesophyll leaf litter and small woody debris, and unlogged forest, with a high tall sapling, pole and tree density, microphyll leaf litter, and mean tree height accounted for most of the variation in species traits in as far as this could be related to the available set of environmental predictors (variance explained: 67.4%). Species with widespread distributions and those with larvae that feed on lianas were linked to environmental

Discussion

Local environmental variables, geographic distance between sampling sites and butterfly community structure

We were able to explain more than 50% of the variation in composition of a diverse tropical butterfly community. A highly significant proportion of this variation was associated with local environmental variables, thus the results confirm that local environmental conditions can significantly influence spatial structure of rainforest butterfly assemblages. This result is consistent with the hypothesis that niche differentiation among butterflies contributes to large-scale patterns of spatial abundance. Importantly, species composition differed considerably between forest that had been subject to commercial selective logging and unlogged forest. Moreover, logging was identified as the primary variable characterising the main axis in spatial variation in the butterfly community. It would seem that the principal drivers of community change in our sampled areas are logging activity and associated environmental changes. Several other studies have demonstrated logging to have significant impacts on insect community structure (e.g. Basset, Charles, Hammond, & Brown, 2001; Cleary, 2003; Cleary, Boyle, Setyawati, & Menken, 2005; Ghazoul, 2002). It is likely that these changes are linked directly to alterations in vegetation structure, as well as physical variables such as light availability and humidity.

The results of this study also revealed a significant effect of geographic distance between sampling sites on butterfly community composition. While some of this was linked to co-variance between environmental variables and geographic distance, a high proportion was associated with geographic distance alone. One factor driving this may be the relationship between dispersal ability and population demography, for example, spatial variation in population growth rates have been linked to dispersal rates (Baguette & Schtickzelle, 2006). Tropical butterflies can be strongly dispersal limited (Fauvelot, Cleary, & Menken, 2006), and there is also evidence that in general lepidoptera can differ in rates of dispersal depending on their morphology and patterns of resource use (Beck & Kitching, 2007).

Species traits and responses to commercial logging

Our results indicate that differences in the abundance of species within logged and unlogged habitats was significantly linked to their traits. Species from the larval tree feeding guild were more abundant in primary unlogged forest, while species belonging to grass and...
liana feeding guilds were more abundant in recently logged forest. Species that feed on herbs and palms were mainly found in areas of unlogged and recently logged forest with a relatively high mean canopy cover whereas insect feeders were mainly found in areas of older logged forest with a deep litter layer and abundant dead wood. Although butterfly larvae do not feed on dead wood, the presence of dead wood and its state of decay are indicators of local environmental conditions. For example, large volumes of rotten dead wood (state 5) were found in unlogged humid closed canopy forest.

Within logged forest there was also variation in species abundance patterns. Liana feeders and wide range species were associated with logged areas with high small woody liana abundance, whereas grass feeders were associated with areas dominated by non-woody lianas, recently fallen dead wood (DW2) and small woody debris. Although there is no direct association between, for example, dead wood and grass feeding butterflies, the presence of dead wood influences the environmental conditions within the sample site. As such dead wood may either influence environmental conditions critical to the presence of butterflies or be correlated with other variables that have a more direct effect on butterflies.

Although the specialist guilds were on average more abundant within logged forest, they tended to occupy somewhat different disturbance types. Interestingly, there was little association between the cover of grasses and grass feeders. There was also no significant difference in grass cover among the forest types (results not shown); severely disturbed logged areas were mainly dominated by lianas as opposed to grasses. The presence of grass-feeding butterflies in large open gaps dominated by non-woody lianas, recently fallen dead wood (DW2) and small woody debris. Although there is no direct association between, for example, dead wood and grass feeding butterflies, the presence of dead wood influences the environmental conditions within the sample site. As such dead wood may either influence environmental conditions critical to the presence of butterflies or be correlated with other variables that have a more direct effect on butterflies.

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likely that more fine-scale study of the traits of individual species will reveal close associations between species and environmental variables. It is particularly important to note the importance of environmental variables in structuring composition implying that there is considerable niche differentiation within the butterfly assemblage. This suggests that a key factor in the maintenance of high species richness within these environments is a naturally heterogeneous forest with high niche diversity.

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Appendix A. Supplementary Material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2008.03.004.

References


