

Effects of Logging on Forest Structure and Drosophilid Diversity in Tropical Lowland Forests of Sabah, Malaysia

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Introduction

Tropical forests are the most diverse and ecologically complex of the world's ecosystems and their disappearance has been a major issue in conservation ecology since the 1980s (Bowles et al. 1998). The importance of both ecosystem services and the biological value of tropical forests has been emphasized by scientists and has caught the interest of citizens throughout the world. Sustaining biodiversity in tropical forests is a primary objective of conservation ecology. In addition, understanding the mechanisms of biodiversity degradation caused by logging disturbances in tropical forests is an important area of research in community ecology (Widodo et al. 2004).

In tropical forests that have regenerated after clearcut or that have been converted to plantations, insect diversity decreases from pre-disturbance levels (Eggleton et al. 1996). However, the effects of selective logging (i.e., a relatively moderate disturbance) on insect diversity remain unclear (Eggleton et al. 1996). In Sabah, Malaysia, a recently adopted logging method, i.e., reduced impact logging (RIL), has been launched to maintain sustainable forest use with minimal forest disturbance (Lagan et al. 2007). RIL was designed to limit forest disturbance and conserve large commercial trees as potential seed sources. Nevertheless, logging operations cause distinct changes in forest structure such as canopy destabilization and decreases in the density of trees or saplings (Hall et al. 2003).

The vertical distribution of the drosophilid community is closely related to the vertical foliage structure (Toda 1992; Tanabe et al. 2001). Specifically, drosophilid diversity tends to be higher in vertically complex than in simple forests (Tanabe et al. 2001). This difference in diversity can be explained in part by the "habitat heterogeneity hypothesis" whereby structurally complex habitats may provide more niches and more diverse ways of exploiting environmental resources and may thus increase species diversity (MacArthur and MacArthur 1961). Furthermore, drosophilid flies are useful indicators of biodiversity because their short lifespan (approximately 1 month) promotes rapid responses of their populations to environmental changes. In addition, their mobility allows quick relocation from unfavorable to favorable habitats (van der Linde and Sevenster 2002).

To test the habitat heterogeneity hypothesis, we investigated the effects of forest structural changes caused by various logging intensities on the species diversity of the drosophilid community. In addition, we discuss the relationship between biodiversity conservation and forest use by humans.

Material & Methods

Study plots

To assess the effects of various logging intensities on forest structure and the drosophilid community, we chose five study plots that experienced different disturbance regimes in the Deramakot Forest Reserve (DFR), Sabah, Malaysia. The disturbance regimes were characterized by two factors: the logging method [RIL or conventional (i.e., non-RIL) methods (CV)] and the time elapsed after logging. The five plots were differentiated according to the disturbance regimes (Table 1): “PRI” (primary forest with no logging), “80s” (harvested in the 1980s by CV), “RIL95” (harvested in 1995 by RIL), “RIL00” (harvested in 2000 by RIL), and “CV” (harvested continuously by CV).

Forest structure

In March 2005, the three-dimensional forest structure was measured using a portable lidar system. Details of the system were described by Parker et al. (2004). To measure vertical forest profiles, each plot was separated into lattices of each square 10-m on a side. Measurements were conducted at 2-m intervals along each separated line. For each 10-m section, vertical foliage densities were calculated at 1-m height intervals using the MacArthur–Horn method (MacArthur and Horn 1969) by combining data (i.e., height differences between the lidar system and the nearest foliage) from five measurement points.

Insect sampling

We used a bait (fermented banana) trap designed specifically for collecting drosophilid flies (Toda 1977). We selected 1–2 trees adjacent to each plot (within 5 m) for the placement of traps. Traps were set vertically from the understory to the canopy at each trapping site, with the lowest trap set at 0.5 m above the ground surface. The next trap was placed at 1.5 m aboveground, and remaining traps were set at 5-m intervals up into the canopy. The top traps varied in height depending on the canopy height of the forest (Table 1). Several (up to four) upper traps were suspended from the same rope using a pulley that was hung from a branch of the selected tree, and the lowest two traps were tied directly to the trunk of the same or a nearby tree (Table 1). We sampled four times in July–August and October–November 2003, and January–February and April–May 2004. During each sampling period, trapped insects were collected and trap baits were renewed three times at 10-day intervals. Samples from the most productive (determined from the sum of drosophilid flies across all plots) 10-day period during each season were selected for analyses. Flies were identified to species or morphospecies of Drosophilidae.

Data analyses

Forest structure

To estimate the vertical complexity of foliage, the foliage height diversity (FHD) was measured using the Shannon–Wiener index (Tanabe et al. 2001) for each 10-m section, and the mean FHD was calculated for each plot. Because of differences in plot shape (Table 1) and limited access caused by large fallen trees, the number of 10-m sections differed among plots (30 at PRI, RIL95, and RIL00; 24 at 80s; and 29 at CV). As an additional measure of foliage structure, the horizontal variance of the vertical foliage profile (HVF) was calculated as follows: the coefficient of variance for foliage densities at each 1-m height interval across all

10-m sections within each plot was calculated, and then the coefficients were averaged for all 1-m height intervals. Heights with no foliage across all 10-m sections were omitted from the calculations.

Differences in FHD or HVF were tested using one-way ANOVA. When a significant difference was detected among plots, multiple comparisons were performed using Tukey's honestly significant difference (HSD) test.

Diversity of the drosophilid community

The species richness and several diversity indices were calculated for each plot during each sampling period. Because the number of collected individuals and thus the number of species may have been biased by the number of traps, which varied among plots, species richness was estimated using sample rarefaction (Heck et al. 1975), based on the plot containing the lowest number of individuals in each season. Alpha, beta, and gamma diversity were calculated according to the concept of "additive partitioning of species diversity"; i.e., gamma (total) diversity can be partitioned into alpha and beta diversity (Levins 1968, Tanabe et al. 2001, Veech et al. 2002). Gamma diversity was calculated using the Shannon-Wiener formula, based on summed data for all traps in each plot. Alpha (intra-trap) diversity was estimated as the average Shannon-Wiener diversity calculated for each trap. Beta (inter-trap) diversity caused by species' compositional differences among traps was calculated as the difference between gamma and alpha diversity (gamma – alpha). As a measure of equitability, interspecific variation in the number of individuals was measured using Pielou's J' , based on gamma diversity and the observed number of species in each plot.

Generalized linear models in R (R Development Core Team 2004) were used to estimate the effects of forest structure. Separate analyses were conducted for species richness and each diversity index of the drosophilid community. Species richness was assumed to be Poisson distributed, whereas the diversity indices were assumed to be Gaussian distributed. The link functions were set as logarithmic. In addition, the four sampling periods were incorporated into the analyses as a categorical variable (the sampling period July–August was incorporated into the intercept). From all possible model combinations (including the null model with no variables) that incorporated the covariates (FHD and HVF) and one cofactor (season), the best model was selected using the Akaike information criterion (AIC; Akaike 1973). The deviance improvement was evaluated for the selected model. The percentage improvement compared to the deviance of the null model was used to estimate the relative explanatory power of the selected model.

Results

Forest structure

FHD was highest in the undisturbed plot of PRI and lowest in the most disturbed plot of CV. The moderately disturbed plots (80s, RIL00, and RIL95) were intermediate in FHD, between PRI and CV (Fig. 1). FHD differed significantly among plots (ANOVA, $P < 0.01$). PRI was significantly different from all the other plots (Tukey HSD, $P < 0.01$), but no other plots were significantly different from each other. Thus, all logging operations (even RIL) clearly affected forest structure by reducing FHD.

The mean HVF also differed significantly among plots (ANOVA, $P = 0.014$). This was primarily driven by the difference between PRI and RIL95 (Tukey HSD, $P = 0.039$; Fig. 1). HVF tended to be higher in the

moderately disturbed plots.

Changes in drosophilid diversity with respect to forest structure and season

In total, 20883 individuals representing 80 species of drosophilid fly were identified (PRI: 5149 individuals, 52 species; 80s: 4348, 45; RIL00: 4398, 49; RIL95: 4344, 44; CV: 2644, 45). All of the diversity measures, with the exception of equitability, fluctuated significantly among seasons (Fig. 2). In particular, the variation in species richness was largely explained by season (76.07% deviance improvement; Table 2). The number of species, gamma diversity, and alpha diversity were lowest in May and highest in January. Throughout the four seasons at DFR, the most rainy days occurred in December–January, whereas the least rain fell in April–May. Because most drosophilid species are vulnerable to desiccation, moisture conditions are a key factor for drosophilid survival. Of the two measures of forest structure, only FHD positively affected beta diversity (Table 2). Equitability was not affected by either season or forest structure.

Discussion

Effects of logging disturbances on forest structure

Logging disturbances decreased the vertical heterogeneity of foliage density. Logging in DFR targets mature Dipterocarpaceae trees (diameter at breast height > ca. 60 cm) and has removed several large foliage crowns from the canopy and/or emergent layers. These losses of canopy foliage reduce the complexity of the vertical foliage structure and promote the growth of subcanopy and/or pioneer trees (Okuda et al. 2003). As this gap regeneration proceeds, the vertical foliage structure slowly recovers. However, our results indicate that the effects of logging remain prevalent in the vertical foliage structure of forests harvested by both conventional logging as early as the 1980s and by RIL in 1995.

In contrast, the horizontal heterogeneity of foliage density tended to be higher in moderately disturbed forests. According to theories addressing light acquisition by subcanopy trees, the foliage distribution is predicted to be stratified in mature forests with a closed canopy (Terborgh 1985), thus forming a horizontally continuous structure of dense and sparse foliage layers. The selective removal of large trees from the canopy layer and the subsequent gap regeneration may disturb this horizontal constancy of the foliage structure. However, at the most strongly disturbed plot (CV), the horizontal foliage heterogeneity was relatively low. This may be attributed to the disappearance of virtually all trees in the top layer by heavy logging, as well as the concomitant growth of subcanopy and pioneer trees.

Relationship between drosophilid diversity and forest structure

Species richness was independent of forest structure and fluctuated significantly among the four seasons. The stability of equitability throughout the seasons suggests that seasonal changes in gamma and alpha diversity were caused by seasonal changes in species richness. In contrast, beta diversity (representing the degree of vertical habitat segregation in the drosophilid community) was positively affected by FHD. These results are consistent with the habitat heterogeneity hypothesis, which predicts that structurally complex habitats usually accommodate more species than homogeneous habitats by providing a greater variety of microhabitats. Paradoxically, in forests with less obviously stratified standing trees, weakened habitat

segregation may strengthen resource competition within the drosophilid community if component species use similar food resources (Shorrocks 1977; Tanabe et al. 2001). This strengthened competition may accelerate the extinction of species and may ultimately decrease local species richness.

In DFR, decreases in FHD caused by forest logging were related to decreases in beta diversity, but not to changes in species richness. Selective logging, especially RIL, in DFR has been operated to minimize the widespread effects of logging, thus reserving forest stands with diverse mosaics of foliage structure. Although species richness may decrease through strengthened competition in poorly stratified forest stands, adjacent stands with sufficient foliage stratification may function as regional sources of species to compensate for the local depletion of species richness. This seeding effect would be especially strong for highly mobile organisms such as flying insects and may thus serve as a reason why drosophilid species richness did not significantly vary among the study plots that differed in vertical foliage structure.

From a conservation ecology standpoint, we conclude that logging operations in DFR appear to be successful in terms of the conservation of drosophilid biodiversity. However, we caution against the generalization of our results to other organisms that may vary in mobility and in their responses to different sizes of habitat patchiness.

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Table 1 The disturbance regime, shape, canopy height, and trapping profile of each study plot.

Plot name	Abbreve	Disturbance regime	Plot size (m x m)	Canopy height (m)	Tree species at trap-sites	Trap heights (m)
Ecological trail	PRI	No impact of logging	20 x100	31.5-36.5	<i>Polyglaccae affine</i> <i>Shorea exelliptica</i>	0.5, 1.5, 6.5, 11.5, 16.5, 21.5, 26.5, 31.5, 36.5
C54	80s	Harvested in the 1980s by CV	40 x 50	26.5-31.5	<i>Lithocarpus sp.</i> <i>Shorea macroptera</i>	0.5, 1.5, 6.5, 11.5, 16.5, 21.5, 26.5, 31.5
C63 bawah	RIL00	Harvested in 1995 by RIL	20 x 100	26.5-31.5	<i>Shorea sp.</i>	0.5, 1.5, 6.5, 11.5, 16.5, 21.5, 26.5
Mannan	RIL95	Harvested in 2000 by RIL	20 x 100	26.5-31.5	<i>Dipterocarpus sp.</i> <i>Dorio sp.</i>	0.5, 1.5, 6.5, 11.5, 16.5, 21.5, 26.5
Tangkulap 1	CV	Continued intermittent harvest by CV	20 x 100	21.5-26.5	<i>Shorea parviforia</i>	0.5, 1.5, 6.5, 11.5, 16.5, 21.5

Abbrev; Abbreviation

Table 2 Parameter estimates and percentage deviance improvement of the selected models explaining the spatio-temporal variation in species richness and diversity indices of the drosophilid community.

	Intercept		FHD		HVF		January		May		October		(%) [#]
	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	
Species richness	2.986	0.100	NS*		NS		0.408	0.130	-0.238	0.151	0.159	0.139	76.07
Equitability	-0.560	0.039	NS		NS		NS		NS		NS		0.00
Gamma diversity	0.597	0.077	NS		NS		0.180	0.100	-0.203	0.122	0.073	0.105	44.60
Alpha diversity	0.408	0.084	NS		NS		0.181	0.110	-0.230	0.135	-0.027	0.121	41.93
Beta diversity	-2.721	0.769	0.646	0.309	NS		0.217	0.214	-0.054	0.242	0.455	0.197	46.37

Est: Estimate, *NS: not selected, #;Deviance improvement

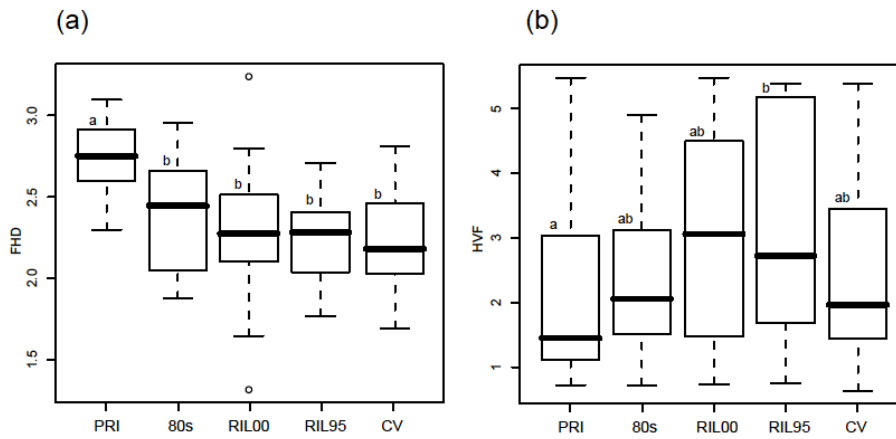


Fig. 1 Box-plots indicating the median (bold solid line), lower and upper hinges, extreme lower and upper whiskers, and outliers of (a) foliage height diversity (FHD) and (b) horizontal variance of foliage (HVf) within each plot. Different letters indicate statistically significant differences ($P < 0.05$) according to Tukey's HSD.

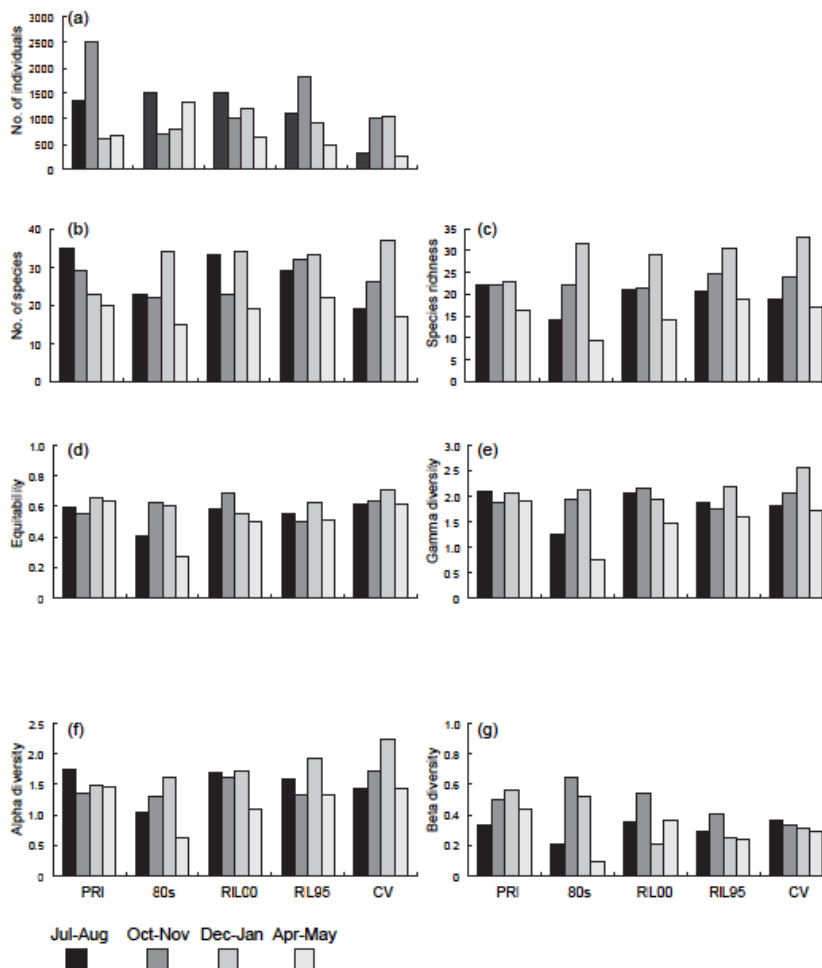


Fig. 2 Seasonal and among-plot variation in the (a) number of collected individuals, (b) number of collected species, (c) species richness estimated by rarefaction, (d) equitability, (e) gamma diversity, (f) alpha diversity, and (g) beta diversity.