



Butterfly diversity and silvicultural practice in lowland rainforests of Cameroon

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Abstract. Butterfly diversity and abundance were sampled across eight 1-ha silvicultural treatment plots in southern Cameroon. The plots included a cleared and unplanted farm fallow, cleared and replanted forest plots, and uncleared forest plots. The replanted plots were line-planted with *Terminalia ivorensis*, but differed in the degree and method of clearance. A total of 205 species of butterflies were collected over two different seasons. Several sampling methods were used, including hand collecting and baited canopy traps. Sites with the greatest degree of disturbance and lowest level of tree cover had the lowest number of individuals and species of butterflies. The farm fallow had substantially fewer individuals and species of butterflies than the other plots. The replanted plots were intermediate between the farm fallow and uncleared forest in terms of abundance, richness and composition. With all three forms of multivariate analysis (Morisita similarity index clustering, detrended correspondence analysis and two-way indicator species analysis) largest differences were found between the farm fallow and uncleared forest plots. The butterfly fauna of the uncleared forest more closely approximated that of the manually cleared plot than that of the mechanically cleared plot. We found that although, in general, young replanted forest plots are a poor substitute for native forest, they do provide habitat for some forest species and that this may increase over time as the plots mature.

Introduction

Forests continue to show massive loss in many tropical countries around the world (FAO 1999). Deforestation is as high as or, in some countries, even higher than in previous decades (Myers 1980, 1989). The combination of such high rates of tropical deforestation with the high species richness of tropical forests means that tropical forests are likely to be extinction hotspots (Lovejoy 1980; May et al. 1995). However, empirical data demonstrating the link between tropical logging or total deforestation and extinction are largely lacking, particularly for diverse groups such as invertebrates (Brown and Brown 1992; Heywood et al. 1994; Mawdsley and Stork 1995; Brooks and Balmford 1996).

There are two options for reducing the area of tropical forests deforested each

year: reducing the level of timber extraction, or concentrating timber extraction in smaller areas by intensifying production (e.g., by replanting). So far, intensification of forestry in temperate forests and tropical forests has led to both increased levels of pests, particularly insect pests, and the loss of biodiversity. Many tropical silvicultural practices are being developed to improve the rate of regeneration of disturbed or harvested areas, such that harvesting of tropical forests can be both sustainable and economic (e.g. Leakey and Newton 1994). In one such programme of research in Cameroon a number of different silvicultural treatments have been tested to determine their usefulness for improved yields of the endemic hardwoods, *Triplochiton scleroxylon* and *Terminalia ivorensis*. Selective logging of natural forest for such species might normally be expected to produce 1–2 usable stems per hectare. Intensification through various silvicultural treatments might be expected to increase the yield 20- to 40-fold. These treatments have been studied to determine the likelihood of insect pest damage (Watt and Stork 1995) and to see how silvicultural practice affects the diversity, abundance and community structure of insects (Watt et al. 1997a, b, 2002). These treatments have also formed the focus for a detailed study of the impacts of forest change on a wide range of other organisms including termites, ants, beetles, soil nematodes, birds and butterflies (Eggleton et al. 1995, 1996; Lawton et al. 1998). Lawton et al. (1998) included summary data on butterfly abundance across forest treatments ranging from uncleared forest through replanted forest to fallow land. Here we examine in more detail how the diversity and abundance of butterflies differ in these forest treatments in the context of other studies of butterflies and other insects in disturbed forest habitats.

Butterflies are arguably the best known of all invertebrate taxa and with around 20,000 species worldwide, they often figure prominently in conservation or biodiversity assessments. The butterfly fauna of Cameroon numbers about 1500 species, or about 45% of the known Afrotropical butterfly fauna (Ackery et al. 1995). Cameroon is probably the richest country for butterflies in Africa and outranks all other countries in the world, except for the South American tropical rainforest countries such as Peru, Ecuador, and Brazil. The impact of logging and silviculture on butterflies is therefore of considerable conservation interest.

Butterflies are also a particularly useful group to examine the effects of forestry on biodiversity for practical reasons: the butterflies of West Africa are well known, can usually be readily identified and, being very visible insects, are relatively easy to catch in a replicable manner. Furthermore, previous studies of the effects of forest disturbance or silvicultural treatment on insect diversity and community structure have concentrated on groups that are predominantly ground-based decomposers or predators such as termites, nematodes, ants and dung beetles (Nummelin and Hanski 1989; Holloway et al. 1992; Belshaw and Bolton 1993; Eggleton et al. 1995, 1996). There also have been numerous studies on butterfly community structure and how this changes with both natural gradients and disturbance (e.g. DeVries 1987; Bowman et al. 1990; Kremen 1992; Pinheiro and Ortiz 1992; Spitzer et al. 1993, 1997; Hill et al. 1995; DeVries et al. 1997; Hamer et al. 1997; Hill 1999; Hamer and Hill 2000), but none have looked directly at the impact of silvicultural treatments on butterfly communities. In the present study we address this issue and have used a

variety of sampling techniques to determine the impact of silvicultural treatment on butterfly diversity and abundance.

Methods

Study sites

Field work was carried out on eight 1-ha treatment plots (Figure 1; see also Watt et al. 1997a) in the Mbalmayo Forest Reserve (11°2′–11°31′ East, 3°23′–3°31′ North, altitude about 650 m above sea level) some 50 km to the south of Yaounde, the capital of Cameroon. The Mbalmayo Forest Reserve covers about 9000 ha of primary and near-primary forest and, although under some form of government protection, includes areas of secondary forest, forest and farm experimental areas. Hunting, foraging and subsistence agriculture, often illegally, are undertaken by local villagers. The forest of this area is generally consistent with the moist pre-montane tropical forest classification of Holdridge et al. (1971) with annual rainfall averaging 1520 mm, most falling during two wet seasons (March–June and September–November). Average monthly temperatures range from 22.6 °C in August to 25.5 °C in January. Although logging has taken place several times within the reserve, there was no evidence of recent logging in this area. Plantation trials have been established in the reserve since 1970 and the study plots are situated in three areas which are about 10 km apart. Four 1-ha treatment plots were established at both Ebogo and Bilik and planted with *T. ivorensis* seedlings in 1987 and 1988, respectively (Lawson et al. 1990). A more extensive programme of 1-ha research plots was established at Eboufek in 1991 and planted with both *T. ivorensis* and *Tr. scleroxylon*. The plots follow a gradient of disturbance, arranged below from least to most disturbed:

The **Bilik uncleared forest** plot^(a) was left undisturbed apart from minor manual ground vegetation clearing for narrow access lines. The lack of logging roads and presence of larger trees (10% larger than on the Ebogo uncleared forest plot, below) suggest that this is the oldest forest amongst our plots and has been labeled as ‘near primary’ in other papers (Eggleton et al. 1995; Lawton et al. 1998). The **Ebogo uncleared forest** plot^(b) was also left undisturbed. Again, there is no indication of previous tree removals on this plot (G. Lawson, personal communication). The **Eboufek uncleared forest** plot^(c) was also left intact, but there was some indication of recent disturbance as one of the unmade access roads passed through one corner. Eggleton et al. (1995) termed this ‘old secondary forest’. In the **Ebogo partial manual clearance** plot^(d), ground vegetation and some trees were removed in 1987 by chainsaw and poisoning. The plot was then line planted with *T. ivorensis* at 5 m spacings. In the **Ebogo partial mechanical clearance** plot^(e) a bulldozer was used in 1987 to remove most undergrowth and some large trees, resulting in the loss of about 50% canopy cover. Planting was as in the previous plot. All trees in the **Ebogo complete clearance** plot^(f) were felled by chainsaw in 1987 and removed by

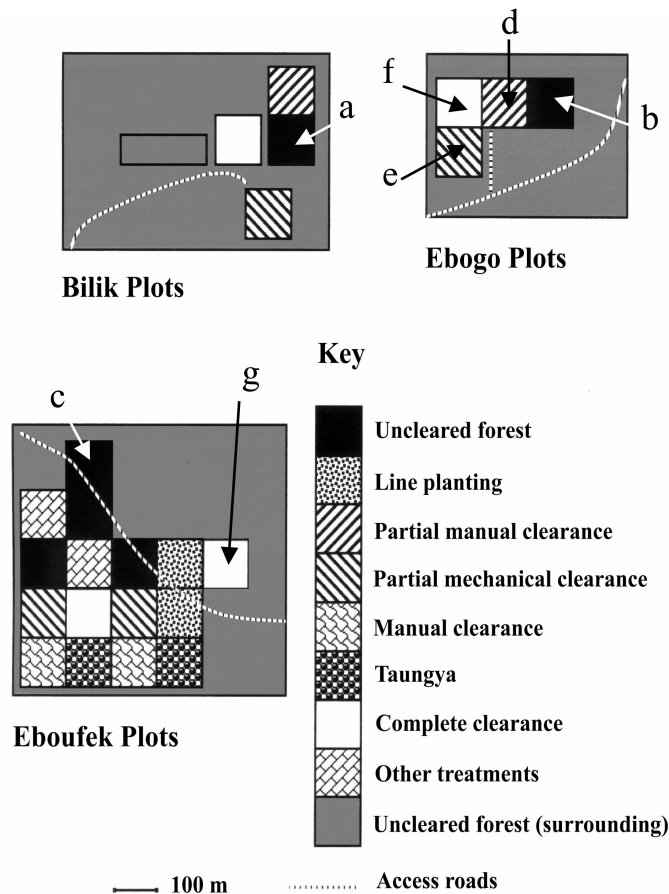


Figure 1. Map of the section of the Mbalmayo Forest Reserve area in southern Cameroon showing the location of the three main study sites and the different silvicultural treatment plots at each site (see Watt et al. (1997a) for a full explanation of all available silvicultural plots). Those plots used for this study are marked (a)–(g) (see Methods); the farm fallow plot (h) was at a farm site nearby.

bulldozers, along with tree stumps, other smaller trees and remaining vegetation. Planting was as in the previous two plots. The **Eboufek complete clearance** plot^(g) was also completely cleared with chainsaw and bulldozers and then replanted, but the clearing and planting were carried out later, in 1991. The **farm fallow** plot^(h) was previously secondary forest which had been manually cleared of trees by chainsaws and machetes (without the use of heavy machinery) in 1990 and then left fallow. The site was not replanted with trees, and was weeded to prevent tree regeneration (Eggleton et al. 1995). This plot was sited at the International Institute of Tropical Agriculture farm less than 20 km from the other sites.

These plots represent a gradient in disturbance allowing us to examine general effects of disturbance intensity on butterfly communities. The plots at Ebogo

compare three methods of clearance with an uncleared forest control plot. Although these treatments are not replicated over sites in the study, the other two uncleared forest plots at Eboufek and Bilik give an indication of the range of variation between sites. Although we have not surveyed these plots through time, temporal changes can be approximated by comparing the more recently cleared plot at Eboufek with the older complete clearance plot at Ebogo.

Butterfly sampling

Butterflies were sampled in November 1993, in the early part of the wet season, and in March 1994, at the very beginning of the dry season. In both years, sampling included collecting specimens for later identification by T.B.L. In March 1994 sampling also included estimates of abundance using visual counts. In all cases, butterflies were killed by thoracic compression (squeezing between head and thorax), and stored in appropriately labeled wax envelopes. We had three aims behind our collecting strategy: to collect both ground and canopy species, to compare abundance and richness between plots by carefully ensuring equal sampling effort amongst plots, and to catch enough butterflies to allow useful comparisons of composition and rarefied richness between plots. These multiple goals required using a combination of methods, described below. We emphasize that although several methods were used, all plots were sampled using the same suite of methods and with equal sampling effort for each method.

Local collectors (November 1993 and March 1994): Experienced local butterfly collectors were used to collect butterflies with hand nets. Collectors were rotated every 15 (November 1993) or 20 min (March 1994, including handling time) between plots to give a total each year of approximately 16 h sampling per plot. Differences between collectors in the number of butterflies collected on the same plot were only marginally significant in 1993 ($F_{3,15} = 3.30$, $P = 0.05$) and not in 1994 ($F_{3,9} = 1.23$, $P > 0.05$). Any effect of collector bias on our final results was minimized by circulating collectors evenly around the plots and pooling butterflies for each plot. All plots were sampled in 1994, and all plots except Bilik uncleared and the farm fallow were sampled in 1993. Note that in November 1993 it rained for short periods during the sampling at the two Eboufek plots, probably affecting abundances.

Timed catches (March 1994): In each plot, butterflies were caught by D.S. using a hand net during six 10-min periods (three in the morning, three in the afternoon). Unlike the collecting periods for the local collectors, these 10-min periods exclude handling time, giving a more accurate estimate of abundances. No sampling was done on the very edge of the plot. March represents the interface of the dry and wet seasons in Cameroon, so most plots were sampled in roughly equal proportions of sunny and cloudy weather (no sampling in rain). Collecting periods at Ebogo manual were cloudier than average and at Ebogo complete clearance were sunnier than average.

Baited traps (March 1994): The previous two methods only collect butterflies at ground level. Butterflies were also collected higher in the canopy with standard

butterfly traps (BMNH 1974), baited with a semi-fermented mixture of bananas and beer. One trap was hung in the center of each plot, at canopy height, which ranged from 2.5 m in complete clearance plots to 12 m in uncleared plots. Butterflies were trapped on two separate days (ca. 9 h/day) for each plot, and pooled over days.

Extra catch (March 1994): When the butterflies collected using the above three methods were summed, it was obvious that some plots were represented by fewer specimens than the rest. Since we did not want differences in abundance to affect our analyses of composition, extra butterflies were caught by D.S. with a hand net until all plots were represented by at least 50 specimens.

In all of the four methods described above, all butterflies captured were killed and retained for identification.

The above methods give a rough indication of abundance, but such estimates are compromised by differences between plots in weather conditions and time-of-day (even though we tried to minimize these effects). More accurate estimates of relative abundance are provided by abundance counts conducted in March 1994. The number of butterflies observed in each of several 5-min walks around each plot was recorded. No attempt was made to catch or identify the butterflies and therefore care was taken not to include repeat observations of the same butterflies during each walk. Walks were only done in sunny weather from 10:30 A.M. to 1:00 P.M. to minimize weather and time-of-day effects. Abundances were recorded for a total of 10–16 walks per plot.

Data analysis

Species richness

Variable numbers of butterflies were collected from each site. We rarefied the species richness estimates (Hurlbert 1971; Krebs 1989) to allow comparison for a standard sample size (either 29 or 47 individuals per site, depending on year and comparison). Rarefaction calculates the expected species richness when a given number of individuals are randomly selected (without replacement) from species-abundance data.

Composition

The similarity in the species composition of the butterfly fauna of different plots was assessed using the Morisita index (C_λ) (Morisita 1959; Krebs 1989). Average linkage cluster analysis (SAS 1999), using the resulting similarity index values, was then carried out to group sites according to their similarity. In addition, different plots were classified according to their butterfly species composition by detrended correspondence analysis (DECORANA) and two-way indicator species analysis (TWINSPAN) (Hill et al. 1975; Hill and Gaunch 1980; Hill 1994).

Butterfly identification

The butterflies were identified by Torben Larsen, who has been working on the origins, natural history, diversity and conservation of the butterflies of West Africa

Table 1. Summary of the number of individuals and species of butterflies caught by all methods in November 1993 and March 1994.

Site	Nov. 1993		March 1994											
	Local collectors		Local collectors		Timed collections		Weather timed collections		Baited traps		Extra catch		Sum of all methods	
	Indivs	Spp.	Indivs	Spp.	Indivs	Spp.	Indivs	Spp.	Indivs	Spp.	Indivs	Spp.	Indivs	Spp.
Farm fallow	-	-	18	19	9	5			14	2	8	4	49	14
Eboutek complete	44	23	27	17	8	8		s, c	18	10	13	9	66	31
Ebogo complete	56	45	26	19	25	16		p, s	7	5	2	2	60	30
Ebogo mechanical	39	31	24	16	22	16		s, p	7	5	4	4	57	28
Ebogo manual	43	36	20	14	8	6		s, s	4	4	21	20	53	30
Eboutek uncleared	31	17	23	20	24	21		p p	26	16	-	-	73	51
Ebogo uncleared	65	48	23	16	16	12		s, p	6	3	9	8	54	33
Bitik uncleared	-	-	28	17	19	10		p, s	7	6	4	4	58	29
Total	278	123	189	81	131	61			89	29	61	24	470	132

A full list of species is provided in Appendix 1. Weather data during both timed catch periods: s – sunny, p – partially cloudy, c – cloudy.

for over a decade (Dall'Asta et al. 1994; Larsen 1997). The authorities for species and subspecies taxa are found in Ackery et al. (1995).

Results

Faunal composition

A total of 748 butterflies of 205 species were collected; 278 individuals of 123 species in November 1993 and 470 individuals of 132 species in March 1994 (Table 1 and Appendix 1).

Abundance

The most accurate estimates of relative abundance are provided by the 5-minute walks. Abundances in the three uncleared forest plots were several times higher than those in the three completely cleared/farm fallow plots (Figure 2; Tukey's tests following plot effect in ANOVA, $F_{7,92} = 25.7$, $P < 0.05$). The two partially cleared plots had abundances intermediate between those of the uncleared forest and complete clearance plots (Figure 2).

The same general trends in abundance between plots are apparent in the timed catches, with fewer individuals caught in the more cleared plots (Table 1). The unexpectedly low capture rate for Ebogo manual and high capture rate for Ebogo complete clearance are due to weather differences (always semi-cloudy during Ebogo manual collections, always sunny during Ebogo complete clearance collections). By contrast, the numbers of butterflies caught by the local collectors, in either year, do not reflect these patterns in abundances (Table 1). Presumably, this is

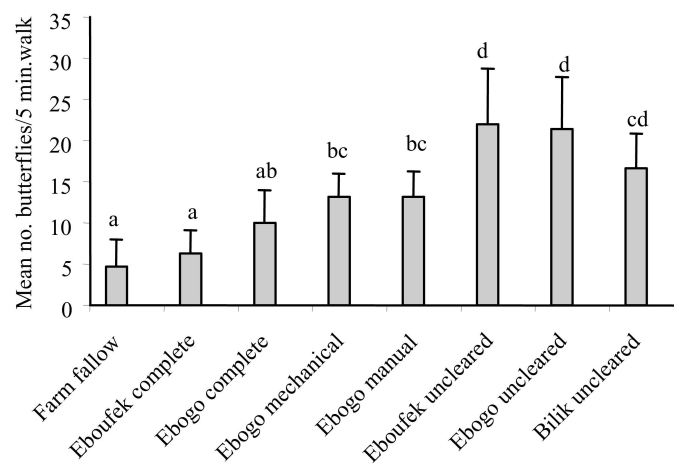


Figure 2. Mean number of butterflies encountered in 5-min walks averaged over 2 days (plus positive standard deviations) on different plots. Sites which do not significantly differ (Tukey's tests, $P > 0.05$) in abundance are identified by a common letter (a–c).

because handling time was not excluded from total sampling time (collectors were limited by how quickly they could process the butterflies, not by how quickly they could encounter them).

Species richness

For between-plot comparisons within each year, we rarefied richness using the maximum possible number of individuals (29 in 1993, 47 in 1994). The between-year comparisons are based on 29 individuals for both years. For this analysis, data are pooled across methods but not years. In both years, many of the plots did not differ significantly in terms of rarefied richness (Figure 3). In 1993, the only significant pairwise comparisons occurred between Eboufek and Ebogo plots. Eboufek plots had significantly lower rarefied richness than the Ebogo plots (two-tailed Tukey's tests, $P < 0.05$, rarefied $n = 29$), which may simply reflect the poor weather conditions during the collection of the Eboufek butterflies. In 1994, we also sampled the farm fallow and Bilik plots. Again, rarefied richness was generally uniform amongst plots with the following exceptions. Rarefied richness was markedly lower in the farm fallow plot than in the other plots and substantially higher in the Eboufek forest plot than in the other plots (two-tailed Tukey's tests, $P < 0.05$; rarefied $n = 47$). The rarefied richness of the Ebogo forest plot was significantly different from that of all plots but the Ebogo manually cleared plot, and intermediate in value between that of the Eboufek forest plot and the remaining plots (two-tailed Tukey's tests, $P < 0.05$, rarefied $n = 47$). All other pairwise comparisons amongst plots were nonsignificant (two-tailed Tukey's tests, $P > 0.05$; rarefied $n = 47$).

Finally, there are obvious seasonal effects in the data; the four Ebogo plots had consistently more species per 29 individuals in November 1993 than in March 1994

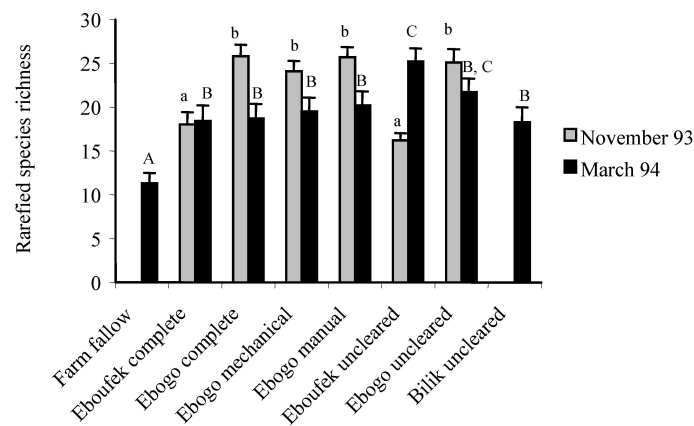


Figure 3. Rarefied species richness estimates (number of species/29 individuals) plus positive standard deviations for (a) (grey bars) the baseline collections in November 1993; (b) (black bars) all collections in March 1994. Sites which do not significantly differ (Tukey's tests, $P > 0.05$) are identified by a common letter (lowercase for 1993, uppercase for 1994; note: no comparison is made between years).

(Figure 3; two-tailed Tukey's tests, $P < 0.05$), although this pattern did not hold in the two Eboufek plots (Eboufek complete: $P > 0.05$; Eboufek forest: March $>$ November, $P < 0.05$).

In 1994 the Ebogo plots differed greatly in abundance but only slightly in rarefied richness. This suggests that when sampling is carried out in these plots over limited periods of time, plot differences in the recorded number of species should track abundance closely. Although we were not able to identify butterflies to species on our 5-min abundance walks, we can estimate from the above rarefaction curves that the mean number of species seen per walk would have been lowest in Ebogo complete clearance (8.3 ± 0.9 species), intermediate in Ebogo mechanical and manual clearance (10.8 ± 0.7 species; 10.9 ± 0.7 species), and highest in Ebogo uncleared (17.0 ± 1.1 species). These differences are predicted to disappear with infinitely long sampling periods if, and only if, the patterns in species accumulation rate suggested by our rarefaction curves (Figure 3) are accurate when extrapolated to much larger sample sizes.

Faunal similarity between plots

Three different methods were used to analyze similarity in species composition amongst the plots. These multiple analyses allow us to identify as spurious those results particular to only one type of analysis and concentrate instead on the common trends.

In all three analyses, the largest difference in butterflies assemblages occurred between the farm fallow plot and the uncleared forest plots, especially Bilik. The Average linkage analysis of the Morisita index separated the farm fallow plot first from the Bilik uncleared forest plot and then from the other forested plots (Figure 4A). The TWINSpan analysis separated the farm fallow and other heavily disturbed plots from the uncleared forest plots (Figure 4B). The DECORANA analysis (Figure 4C) also widely separates the farm fallow and Bilik plots. While all three analyses emphasize treatment differences, site differences are also evident in the DECORANA ordination plot: axis 1 (eigenvalue 0.72) ranks the plots from low to high disturbance, while axis 2 (eigenvalue 0.29) separates the four sites (Eboufek, farm fallow at IITA, Bilik, Ebogo).

Butterfly assemblages in the partially cleared and replanted plots were generally intermediate between the complete clearance/farm fallow plots and the uncleared forest plots. For example, in the Morisita similarity analysis, one partially cleared plot clustered with the complete-clearance plots while the other clustered with the uncleared forest plots. By contrast, the TWINSpan analysis clustered all the partially cleared plots with the complete clearance/farm fallow plots. The DECORANA analysis placed the Ebogo partially cleared plots closer to the older complete clearance plot at Ebogo than to the Ebogo uncleared forest plot, but at an intermediate position between the other uncleared forest plots and the younger complete clearance/farm fallow plots.

Finally, in all the analyses, the butterfly fauna of uncleared forest appears to be more closely approximated by the manually cleared plot than the mechanically cleared plot. This is most dramatically shown in the Morisita cluster diagram, but is

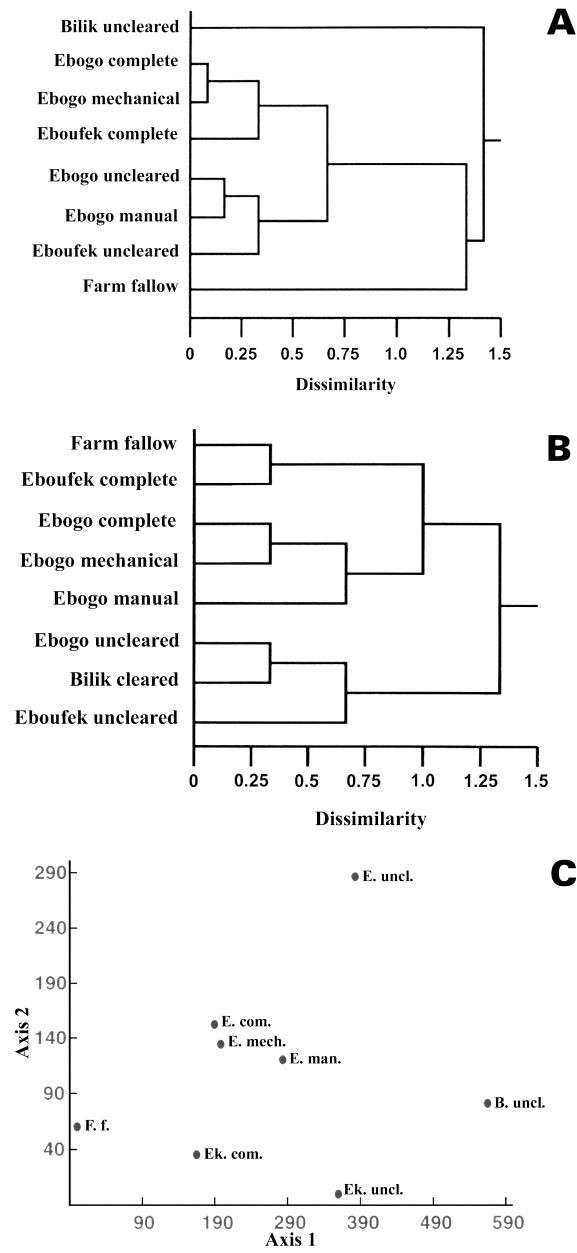


Figure 4. Faunal relationships of the eight sample plots based on summed butterfly species data using: (A) Morisita similarity index tree, (B) TWINSpan average linkage cluster tree, and (C) Detrended Correspondence Analysis ordination (using DECORANA; note that axes 1 and 2 are effectively scaled in terms of β -diversity).

also evident in the DECORANA analysis. The TWINSPAN analysis illustrates the same pattern in a different way, showing the butterfly fauna of the Ebogo complete-clearance plot to resemble more the mechanically cleared than the manually cleared plot.

Discussion

Are plantations useful surrogates for intact forest in terms of butterfly habitat?

The answer to this question is complex. Clearly, a replanted forest is superior butterfly habitat compared to a completely deforested area. Compared with the farm fallow plot, replanted plots had substantially higher abundance and diversity of butterflies, and contained more species characteristic of intact forest (Figures 2–4). However, replanted plots were by no means identical to the uncleared forest plots in terms of butterfly habitat. Replanted plots had consistently lower butterfly abundance than uncleared plots (Figure 2).

Of course, species richness is not a fail-safe indicator of a site's conservation value: a site with a few species but all with restricted ranges may be far more valuable than a site with many ubiquitous species. In other words, species identity is also critical. In all our analyses of community similarity, butterfly communities were substantially different between replanted and uncleared plots, and usually intermediate in composition between those of the farm fallow plot and uncleared forest plots (Figure 4).

Although the replanted plots were generally poor substitutes for the butterfly habitat provided by intact forest, they did provide habitat for some forest species. The degree to which these replanted plots substituted for intact forest depended on the method of clearance (although, since we sometimes sampled only one plot per clearance method, the following comments are more speculative than statistically accurate). The differences between replanted plots are subtle and are more apparent in the analysis of community similarity (Figure 4) than in the comparisons of abundance or diversity (Figures 2–4). Generally, butterfly communities of the intact forest were more closely approximated by communities of the partially cleared plots than by communities of the completely cleared plots (even the complete clearance plot of equal age). Amongst the partially cleared plots, the manually cleared plot had butterfly assemblages most characteristic of intact forest. The manually cleared plot had less soil compaction and more large trees left than the mechanically cleared plot, which in turn had more undisturbed vegetation than the complete-clearance plot. Obviously, the butterfly communities in each replanted plot will change over time as the vegetation matures (evidenced by the differences in abundance, richness and composition between the younger and older complete-clearance plots: Figures 2–4). It is possible that, as they age, the replanted plots will become indistinguishable from uncleared forest in terms of butterfly habitat.

Scale dependent diversity

Although we are not aware of any other studies directly examining the effects of

silvicultural treatment *per se* on tropical butterflies, there are a number of studies comparing tropical butterfly communities in logged and unlogged forests. These have been analyzed by Hamer and Hill (2000), who found that in some studies butterfly abundance and diversity are greater in unlogged forests and (e.g. Holloway et al. 1992; Hill et al. 1995) in other studies are less in unlogged forests (Raguso and Llorente-Bousquets 1990; Hamer et al. 1997), and sometimes the same in both logged and unlogged forests (Wolda 1987). Their analyses of these studies showed that the effects of forest disturbance on species diversity are heavily scale dependent. They found that both species richness and species evenness increased at a significantly greater rate with spatial scale in unlogged forest than in logged forest. The plots we sampled in the current study were relatively small (1 ha) and differences between plots therefore reflect small-scale habitat preferences rather than large-scale processes. It would probably be difficult to extrapolate from our study on the impacts of converting large areas of intact forest to plantation management on butterfly diversity. In addition, our treatments were unreplicated across sites and only the plots at Ebogo and Eboufek represented several treatments. Differences between the farm fallow plot and the other plots could represent either site or treatment effects. Similarly, differences between the uncleared forest at Bilik and completely or partially cleared plots could reflect either site or treatment effects. We attempted to partially remedy the lack of replication by surveying uncleared plots at several sites, which gives an indication of spatial variation in butterfly communities.

The effect of plantation forestry on animal species may depend critically on the tree species in cultivation, as shown for moth communities in Sabah by Chey (1994). Obviously the results from our study cannot be generalized beyond the plantation species, *T. ivorensis*. Similarly, our conclusions cannot be extended to other invertebrate or vertebrate taxa. Termites, ants, beetles, birds, and nematodes have also been studied on the same plots as used in the study (Eggleton et al. 1995; Bloemers et al. 1997; Watt et al. 1997a, b; Lawton et al. 1998), and often show fairly different patterns in species richness (Lawton et al. 1998). These taxa are very different from each other in both a taxonomic and ecological sense, however, and it is possible that groups more closely related to butterflies (e.g. moths) or occupying a similar niche (e.g. hummingbirds) may show similar responses to forestry management (Didham et al. 1996).

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Appendix 1

Summary of the number of individuals of each species of butterfly collected at each site in November 1993 and March 1994 including assessments, where available, of the species preference for particular kinds of habitats (as in Larsen 1997) as follows: WEF – centred on wet evergreen forest, MEF – centred on moist evergreen forest, ALF – found in all forests, DRF – centred on dry forest, DIS – common in disturbed areas, SPE – special habitat (swampy), GUI – centred on the Guinea savannah and forest fringes, '+' – species of forest clearings, '-' – species of undisturbed forest; species listed alphabetically by families and subfamilies: Papilionidae – Papilioninae (Pa); Pieridae – Coliadinae (Co), Pierinae (Pi); Lycaenidae – Lycaeninae (Ly), Lipteninae (Li), Miletinae (Mi), Theclinae (Th), Polyommatainae (Po), Riodininae (Ri); Nymphalidae – Danainae (Da), Satyrinae (Sa), Charaxinae (Ch), Nymphalinae (Ny), Acraeinae (Ac); Hesperiidae – Pyrginae (Py), Hesperinae (He) (authority for names as in Ackery et al. 1995).

Disturbance	Habitat	Subfamily	Species	Sum of abundance															
				March 1994				March 1994 total				November 1993				November 1993 total			
				Bitik uncleared	Ebogo complete	Ebogo uncleared	Ebogo manual	Ebogo mechanical	Ebouték complete	Ebouték uncleared	Farm fallow	Ebogo complete	Ebogo uncleared	Ebogo manual	Ebogo mechanical	Ebouték complete	Ebouték uncleared		
			Papilionidae																
		Pa	<i>Papilio bromius</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	
ALF		Pa	<i>P. cyorta</i>	1	0	0	1	0	0	1	0	3	0	1	1	0	0	2	
MEF		Pa	<i>P. menestheus</i>	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	
ALF		Pa	<i>P. zanobia</i>	1	0	1	0	1	0	0	0	3	0	0	0	0	0	3	
MEF		Pa	<i>Pieridae</i>																
		Co	<i>Eurema lapale</i>	0	3	1	0	3	1	0	0	8	1	2	0	1	0	4	
SPE		Co	<i>E. hecabe</i>	0	5	2	6	2	1	1	0	17	1	0	0	0	1	2	
DIS		Co	<i>E. senegalensis</i>	0	3	0	2	0	0	2	0	7	1	0	0	0	0	19	
MEF		Pi	<i>Appias phacela</i>	0	0	0	0	0	1	0	0	1	0	0	0	0	0	3	
MEF		Pi	<i>Appias sylvia (=perlicans)</i>	0	0	0	1	0	0	0	0	1	0	0	0	0	0	10	
WEF		Pi	<i>Lepossia hybrida</i>	4	0	0	0	0	0	1	0	5	0	0	0	0	0	1	
MEF		Pi	<i>L. marginata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	
MEF		Pi	<i>L. medusa</i>	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	
MEF		Pi	<i>L. napia</i>	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	
WEF		Pi	<i>Mylothris cf. hilara</i>	0	0	2	0	0	0	0	0	2	0	0	0	0	0	2	
MEF		Pi	<i>M. nr. rhodope</i>	0	0	0	0	0	0	0	0	0	1	2	2	5	0	10	

Appendix I. (continued)

		Sum of abundance																	
Disturbance	Habitat	Subfamily	Species	Site															
				March 1994			Nov. 1993			March 1994 total			Nov. 1993 total			Grand total			
				Blik uncleared	Ebogo complete	Ebogo uncleared	Ebogo manual	Ebogo mechanical	Ebouték complete	Ebouték uncleared	Farm fallow	Ebogo complete	Ebogo uncleared	Ebogo manual	Ebogo mechanical	Ebouték complete	Ebouték uncleared	Nov. 1993 total	
MBF	+	Ny	<i>Ananartia eldus</i>	0	0	0	0	0	1	0	0	2	0	0	0	2	0	4	5
ALF		Ny	<i>Ariadne albifascia</i>	0	0	0	1	2	0	0	0	3	0	0	0	0	0	0	3
ALF		Ny	<i>Ar. enotrea</i>	0	6	0	0	4	3	2	0	15	0	0	0	0	0	0	15
WEF		Ny	<i>Ar. pagenstecheri</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
ALF		Ny	<i>Atericia gatene</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
ALF		Ny	<i>Bebearia absolon</i>	0	0	0	1	0	0	2	0	3	1	2	1	0	0	4	7
WEF	-	Ny	<i>Be. ellensis</i>	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	2
WEF	-	Ny	<i>Be. flammia</i>	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
MBF	-	Ny	<i>Be. mandinga</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
WEF	-	Ny	<i>Be. nr ellensis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3
WEF	-	Ny	<i>Be. portia</i>	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	3
ALF		Ny	<i>Be. phanassina</i>	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	2
ALF		Ny	<i>Be. tenyris</i>	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	2
ALF		Ny	<i>Be. zomara</i>	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	3
DIS		Ny	<i>Byblia avatara</i>	0	1	0	0	0	1	0	1	3	1	0	0	0	0	0	4
MEF	-	Ny	<i>Catana angustata</i>	2	0	2	0	0	1	0	0	4	0	1	0	0	0	0	5
ALF		Ny	<i>Ca. crithca</i>	3	0	1	0	0	2	3	0	9	0	1	0	0	0	1	11
MEF	-	Ny	<i>Ca. oberthueri</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
WEF	-	Ny	<i>Cymatocera antitargis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
WEF	-	Ny	<i>Cy. beckeri</i>	1	0	0	0	0	0	2	0	3	0	1	0	0	0	0	4
ALF	+	Ny	<i>Cy. caenis</i>	0	0	0	2	1	1	1	0	5	0	0	1	0	0	0	6
MEF		Ny	<i>Cy. cteronis</i>	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1
MEF		Ny	<i>Cy. egesta</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
MEF		Ny	<i>Cy. fumana</i>	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1
WEF	-	Ny	<i>Cy. jodatta</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
		Ny	<i>Cymatocera sp. 1</i>	0	1	1	0	0	0	1	0	3	0	0	0	0	0	0	3

ALF		Ny	<i>Eriphaedra cerea</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
WEF		Ny	<i>Eu. cf simplex</i>	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
WEF	-	Ny	<i>Eu. dargeana</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
MEF		Ny	<i>Eu. elans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
		Ny	<i>Eu. lewintoni</i>	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
		Ny	<i>Eu. preussi</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
DRF		Ny	<i>Eu. rasilina</i>	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3
		Ny	<i>Eriphaedra sp. 1</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ny	<i>Eriphaedra sp. 2</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
MEF	-	Ny	<i>Eu. spatiosa</i>	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	3
MEF		Ny	<i>Eu. thernis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MEF	-	Ny	<i>Euriphene atossa</i>	1	0	0	0	0	1	1	0	3	1	0	0	0	0	0	8
ALF		Ny	<i>Eu. barombina</i>	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	2
MEF	-	Ny	<i>Eu. gambuae</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	4	5	6
		Ny	<i>Euryphora isuka</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
DRF		Ny	<i>Euryphora dryope</i>	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	2
MEF		Ny	<i>Hama thobene</i>	0	0	0	3	0	2	0	0	5	1	0	0	0	0	2	7
ALF	+	Ny	<i>Hypolimnas antileon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
WEF		Ny	<i>Hy. dinaracha</i>	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
ALF		Ny	<i>Hy. salmacis</i>	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
ALF		Ny	<i>Janania sophia</i>	0	0	0	0	0	0	0	5	5	0	0	0	0	0	0	5
ALF	+	Ny	<i>J. stygia</i>	0	2	0	0	7	0	0	0	9	3	1	0	0	0	4	13
ALF		Ny	<i>J. tera</i>	0	0	0	0	0	2	1	6	9	0	0	0	0	0	0	9
MEF	+	Ny	<i>Kallimoides ramia</i>	0	0	1	0	0	0	0	0	1	2	0	1	0	0	3	4
MEF		Ny	<i>Lachnoptera anticlia</i>	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
MEF		Ny	<i>La. anticlia (=tole)</i>	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
MEF		Ny	<i>Mesoxantha ethoxea</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
DIS		Ny	<i>Nepitidopsis ephione</i>	0	7	0	1	0	3	0	0	11	0	0	0	0	0	1	12
ALF		Ny	<i>Nepis agouale</i>	0	1	0	0	3	0	2	0	6	1	0	0	0	2	0	9

Appendix I. (continued)

		Sum of abundance																		
Disturbance	Habitat	Subfamily	Species	Site																
				March 1994					March 1994 total					Nov. 1993					Nov. 1993 total	
				Bilik uncleared	Ebogo complete	Ebogo uncleared	Ebogo manual	Ebogo mechanical	Ebogo complete	Eboufek complete	Eboufek uncleared	Fiam fallow	Ebogo complete	Ebogo uncleared	Ebogo manual	Ebogo mechanical	Eboufek complete	Eboufek uncleared		
ALF		Ny	<i>N. medicata</i>	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	3
ALF		Ny	<i>N. metella</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ALF		Ny	<i>N. nemetes</i>	0	0	0	2	0	0	0	0	0	2	0	0	1	0	0	0	1
ALF		Ny	<i>N. nicoteles</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ALF		Ny	<i>N. nysiades</i>	0	0	1	1	0	0	0	0	0	2	0	1	0	1	0	0	2
WEF	-	Ny	<i>N. puella</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
MEF		Ny	<i>N. strigata</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
ALF		Ny	<i>Phalantha erytis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
ALF		Ny	<i>Precis pelarga</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
MEF		Ny	<i>Pseudacraea semire</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MEF		Ny	<i>Ps. warburgi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
MEF		Ny	<i>Pseudoneptis bigandensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ALF	+	Ny	<i>Silamis parhassus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
ALF		Ny	<i>Sallya amula</i>	1	2	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1
DRF		Ny	<i>S. umbrina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
MEF	+	Ny	<i>Vanessula mica</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
WEF		Ac	<i>Acraea ?indemita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
MEF		Ac	<i>Ac. alciope</i>	0	0	1	2	0	0	0	0	0	1	0	0	3	1	0	0	7
WEF	-	Ac	<i>Ac. althoffi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ALF	+	Ac	<i>Ac. bonasia</i>	0	0	1	2	0	0	0	0	0	0	0	0	0	1	0	0	6
MEF		Ac	<i>Ac. cepheus</i>	0	2	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1

References

- Ackery P.R., Smith C.P. and Vane-Wright R. (eds) 1995. Carcasson's African Butterflies. An Annotated Catalogue of the Papilionoidea and Hesperoidea of the Afrotropical Region. CSIRO Publishing, Melbourne, Australia, 816 pp.
- Belshaw R. and Bolton B. 1993. The effect of forest disturbance on the leaf litter ant fauna in Ghana. *Biodiversity and Conservation* 2: 656–666.
- Bloemers G.F., Hodda M., Lamshead P.J.D., Lawton J.H. and Wanless F.R. 1997. The effects on diversity of tropical soil nematodes. *Oecologia* 111: 575–582.
- BMNH 1974. Insects. Instructions for Collectors no. 4a. 5th edn. Trustees of the British Museum (Natural History), London, 169 pp.
- Bowman D.M.J.S., Woinarski J.C.Z., Sands D.P.A., Wells A. and McShane V.J. 1990. Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: response of birds, butterflies and reptiles. *Journal of Biogeography* 17: 227–239.
- Brooks T. and Balmford A. 1996. Atlantic forest extinctions. *Nature* 380: 115.
- Brown K.S. and Brown G.G. 1992. Habitat alteration and species loss in Brazilian forests. In: Whitmore T.C. and Sayer J.A. (eds), *Tropical Deforestation and Species Extinction*. Chapman & Hall, London, pp. 119–142.
- Chey V.K. 1994. Comparison of biodiversity between plantation and natural forests in Sabah using moths as indicators, Ph.D. Thesis, University of Oxford, Oxford, UK, 284 pp.
- Dall'Asta U., Hecq J. and Larsen T.B. 1994. L'emploi de papillons de jour (Insectes: Rhopalocera & Grypocera) comme 'espèces monitrices' et 'espèces indicatrices' dans le projet de rehabilitation des forêts dans l'Est de la Côte d'Ivoire. Rapport Lepidoptera, nr. 1. Musée Royal de l'Afrique Centrale, Brussels, Belgium, pp. 1–47.
- DeVries P.J. 1987. *The Butterflies of Costa Rica and their Natural History*. Princeton University, Princeton, New Jersey.
- DeVries P.J., Murray D. and Lande R. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 62: 343–364.
- Didham R.K., Ghazoul J., Stork N.E. and Davies A.J. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* 11: 255–260.
- Eggleton P., Bignell D.E., Sands W.A., Mawdsley N.A., Lawton J.H., Wood T.G. et al. 1996. The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transactions of the Royal Society, series B* 351: 51–68.
- Eggleton P., Bignell D.E., Sands W.A., Waite B., Wood T.G. and Lawton J.H. 1995. The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Journal of Tropical Ecology* 11: 85–98.
- FAO 1999. *State of the World's Forests 1999*. Food and Agriculture Organization, Rome.
- Hamer K.C. and Hill J.K. 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology* 14: 1435–1440.
- Hamer K.C., Hill J.K., Lace L.A. and Langan A.M. 1997. Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography* 24: 67–75.
- Heywood V.H., Mace G.M., May R.M. and Stuart S.N. 1994. Uncertainties in extinction rates. *Nature* 368: 105.
- Hill M.O. 1994. DECORANA and TWINSpan for Ordination and Classification of Multivariate Species Data: A New Edition, together with Supporting Programs, in FORTRAN 77. Institute of Terrestrial Ecology, Huntingdon, UK.
- Hill J.K. 1999. Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *Journal of Applied Ecology* 36: 564–572.
- Hill M.O. and Gaunch H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47–58.
- Hill M.O., Bunce R.G.H. and Shaw M.W. 1975. Indicator species analysis, a diverse polythetic method of

- classification, and its application to a survey of native pinewoods in Scotland. *Journal of Ecology* 63: 597–613.
- Hill J.K., Hamer K.C., Lacey L.A. and Banham W.M.T. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology* 32: 754–760.
- Holdridge L.R., Grenke W.C., Hatheway W.H., Liang T. and Tosi J.A. 1971. *Forest Environments in Tropical Life Zones*. Pergamon Press, Oxford, UK.
- Holloway J.D., Kirk-Spriggs A.H. and Khen C.V. 1992. The response of some rain forest insect groups to logging and conversion to plantation. *Philosophical Transactions of the Royal Society, series B* 335: 425–436.
- Hurlbert S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52: 577–586.
- Krebs C.J. 1989. *Ecological Methodology*. HarperCollins, New York.
- Kremen C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2: 203–217.
- Larsen T.B. 1997. Korup butterflies – Biodiversity writ large. Report on a butterfly study mission to Korup National Park in Cameroon during January and February of 1997. WWF and Korup National Park, Cameroon, pp. 1–69.
- Lawson G.J., Mason P.A., Ngeh P.A., Musoko M., Eamus D. and Leakey R.R.B. 1990. Endomycorrhizal and nutrient cycling in indigenous hardwood plantations in Cameroon – effects of different systems of site preparation. UK Overseas Development Administration, London.
- Lawton J.H., Bignell D.E., Bolton B., Bloemers G.F., Eggleton P., Hammond P.M. et al. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391: 72–76.
- Leakey R.R.B. and Newton A.C. 1994. *Tropical Trees: The Potential for Domestication and the Rebuilding of Forest Resources*. HMSO, London, 284 pp.
- Lovejoy T.E. 1980. A projection of species extinctions. Council on Environmental Quality (CEQ): The Global 2000 Report to the President. Col CEQ, Washington, DC, pp. 328–331.
- Mawdsley N.A. and Stork N.E. 1995. Species extinction in insects: ecological and biogeographical considerations. In: Harrington R. and Stork N.E. (eds), *Insects in a Changing Environment*. Academic Press, London, pp. 321–369.
- May R.M., Lawton J.H. and Stork N.E. 1995. Assessing extinction rates. In: Lawton J.H. and May R.M. (eds), *Extinction Rates*. Oxford University Press, Oxford, UK, pp. 1–24.
- Morisita M. 1959. *Memoirs of the Faculty of Science of Kyushu University Series E (Biology)* 3: 65–80.
- Myers N.M. 1980. *Conversion of Tropical Moist Forests*. Report to the National Academy of Sciences. National Research Council, Washington, DC.
- Myers N.M. 1989. *Deforestation Rates in Tropical Forests and their Climatic Implications*. Friends of the Earth, London.
- Nummelin M. and Hanski I. 1989. Dung beetles of the Kibale forest, Uganda; comparisons between virgin and managed forest. *Journal of Tropical Ecology* 5: 349–352.
- Pinheiro C.E.G. and Ortiz J.V.C. 1992. Communities of fruit-feeding butterflies along a vegetation gradient in central Brazil. *Journal of Biogeography* 19: 505–511.
- Raguso R.A. and Llorente-Bousquets J. 1990. The butterflies (Lepidoptera) of the Tuxtla Mts., Vera Cruz, Mexico, revisited: species-richness and habitat disturbance. *Journal of Research on the Lepidoptera* 29: 105–133.
- SAS 1999. *SAS/STAT User's Guide*. Version 6. 4th edn. SAS Institute Inc., Cary, North Carolina.
- Spitzer K., Jaros J., Havelka J. and Leps J. 1997. Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation* 80: 9–15.
- Spitzer K., Novotny V., Tonner M. and Leps J. 1993. Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rain forest, Vietnam. *Journal of Biogeography* 20: 109–121.
- Watt A. and Stork N.E. 1995. *Ecology of Insects in Cameroon Plantation Forests*. Final Consultancy Report. UK Overseas Development Administration (ODA)/GOC Office.
- Watt A.D., Stork N.E. and Bolton B. 2002. The diversity and abundance of ants in relation to forest

- disturbance and plantation establishment in southern Cameroon. *Journal of Applied Ecology* 39: 18–30.
- Watt A.D., Stork N.E., Eggleton P., Srivastava D.S., Bolton B., Larsen T.B. et al. 1997a. Impact of forest loss and regeneration on insect abundance and diversity. In: Watt A.D., Hunter M. and Stork N.E. (eds), *Forests and Insects*. Chapman & Hall, London, pp. 273–286.
- Watt A.D., Stork N.E., McBeath C. and Lawson G.L. 1997b. Impact of forest management on insect abundance and damage in a lowland tropical forest in southern Cameroon. *Journal of Applied Ecology* 34: 985–998.
- Wolda H. 1987. Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society* 30: 313–323.