Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest

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Despite concern about the effects of tropical forest disturbance and clearance on biodiversity[1,2], data on impacts, particularly on invertebrates, remain scarce[3–8]. Here we report a taxonomically diverse inventory on the impacts of tropical forest modification at one locality. We examined a gradient from near-primary, through old-growth secondary and plantation forests to complete clearance, for eight animal groups (birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites and soil nematodes) in the Mbalmayo Forest Reserve, south-central Cameroon. Although species richness generally declined with increasing disturbance, no one group serves as a good indicator taxon[9–12] for changes in the species richness of other groups. Species replacement from site to site (turnover) along the gradient also differs between taxonomic groups. The proportion of 'morphospecies' that cannot be assigned to named species and the number of 'scientist-hours' required to process samples both increase dramatically for smaller-bodied taxa. Data from these eight groups indicate the huge scale of the biological effort required to provide inventories of tropical diversity, and to measure the impacts of tropical forest modification and clearance.

We chose birds and butterflies as groups to study because they frequently serve as 'flagship taxa' in biodiversity inventories[6,9,13]. The other six groups were chosen because they are all widespread and abundant invertebrates. The study area[14–16] is semi-deciduous humid forest representative of much of southern Cameroon, and is used for subsistence farming, experimental agriculture, and forestry trials[16], providing a mosaic of habitats. Study sites (Table 1) formed a gradient of increasing intensity and frequency of disturbance. For some taxa the inventories are almost complete; for others, because of lower sampling effort, they are far from complete (Table 2). The proportion of 'morphospecies'[11] (judged by expert systematists) that cannot currently be assigned to known (named) species is inversely related to log (body length) ($F_{1,5} = 11.07$, $P = 0.02$, ants included only once; values $>x$ in Table 2 regressed as x), emphasizing the huge disparity that exists between groups in the state of taxonomic knowledge.

Generally, as in previous studies[1,2,5–7,17,18], species richness

declined with increasing habitat modification (Fig. 1), although richness in some groups was surprisingly insensitive to extreme habitat modification, and not all taxa had maximum species richness in near-primary (NP) or old-growth secondary (OS) sites. No single group is a good indicator of changes in species richness for all, or even most, other groups (Table 3). Although sample sizes for the correlations in Table 3 are small, the number of positive, statistically significant correlations (5 in 45) is very low (to emphasize the point, we have not corrected for multiple comparisons). On average, only about 10–11% of the variation (mean $r = 0.33$) in species richness of one group is predicted by the change in richness of another group. Most r-values are positive, and 19 of the 45 exceed 0.5, but 10 correlations are actually negative (one significantly so)[11,12]. Data for birds and butterflies are uncorrelated. Changes in richness of only one group (canopy ants) are significantly positively correlated with changes in richness of three others; most groups are significantly positively correlated with only one or two others. Beetles caught in interception traps are not correlated with any other group. Malaise-trap beetles tend to be negatively correlated with other groups, significantly so with nematodes. One of the five significant positive correlations in Table 3 is between the same taxon (ants), sampled in the canopy and in the litter, but canopy beetles and understorey flying beetles are not correlated. Overall, the distribution of correlation coefficients in Table 3 appears idiosyncratic.

We conclude that attempts to assess the impacts of tropical forest modification and clearance using changes in the species richness of one or a limited number of indicator taxa[9–12] (including popular groups such as birds or butterflies) to predict changes in richness of other taxa may be highly misleading. Several other studies also cast serious doubt on the utility of indicator species to predict changes in species richness[11,12,19,20], presumably for the common-sense reason that different kinds of organisms (birds and nematodes, to take an extreme example) have very different ecological requirements, and hence are extremely unlikely to show similar responses to even major changes in habitat.

Even if richness changes little with disturbance, trophic structure may alter, and species characteristic of primary and old-growth secondary forest may be replaced by species associated with disturbed habitats[2,6,7,17,18,21]. With some exceptions[14,15], too little is known about the ecology of most of the taxa to comment in detail, although birds characteristic of primary forest disappear, and species from disturbed habitats are added along the gradient (Fig. 1a). A modified version of Whittaker's β (β-2; see Methods) quantifies species' replacement[22] (Table 2); higher values imply greater changes in species composition with disturbance. Rates of turnover appear to be very different in different groups.

The richness and composition of the regional species pool[23] may account for some of these patterns. For example, 66–80% of the bird species on the most severely disturbed plots (complete clearance (CC) and manually cleared farm fallow (FF)) do not occur in the forest, but have entered the area from natural grasslands and savannas well to the north. Because the Mbalmayo region currently lacks savanna butterflies and termites (which might otherwise colonize the severely disturbed plots), there is less species replacement, and more impact of severe disturbance on species richness, than might be observed at sites with forest and savanna species in close proximity.

Table 1 Study sites in the Mbalmayo Forest Reserve

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Near primary (NP)	Residual plots of near-primary forest, apparently lightly and selectively logged >70 years ago. Sample plots 2–3 ha in extent, surrounded by old-growth secondary forest.
Old-growth secondary (OS)	The dominant vegetation over large parts of south-central Cameroon; large tracts of second-growth forest, unlogged for >40 years. Sample sites (~2 ha) were representative of many parts of the Forest Reserve. Local tree species richness in one 22-ha sample plot was 149 spp.; data are not available for other parts of the forest.
Partial manual clearance, plus plantation (PManC)	1-ha plots. Felling and/or poisoning of up to 70% of old second-growth canopy trees, and understorey clearance in rows with machete. *Terminalia ivorensis* planted in 1987–88, at 5–8 m intervals, and 10–15 m tall at time of sampling. *T. ivorensis* is native to Cameroon, but does not grow wild in Mbalmayo. Resulting forest has closed canopy of native trees and *T. ivorensis*, with a dense understorey.
Partial mechanical clearance, plus plantation (PMechC)	1-ha plots. Bulldozer used to clear ~50% of understorey and larger old second-growth trees, resulting in some soil compaction. *T. ivorensis* planted in 1987–88, as above. More disturbed, and with less understorey than PManC.
Complete clearance, with young plantation (CC)	1-ha plots. All large trees felled with a chainsaw, smaller trees, remaining vegetation, and dead wood cleared manually and mechanically by bulldozer. Considerable soil compaction. Row-planted with *T. ivorensis* (1–2 m tall at time of sampling); considerable bare ground and no closed canopy. For some taxa (such as termites and nematodes) this is a more extreme disturbance than the farm fallow (which lacks small trees) because the topsoil is removed.
Manually cleared farm fallow (FF)	A ~3 ha plot, cleared manually of trees and other vegetation in 1990; some wood from felled trees spread and allowed to decompose. Weeded to prevent tree regeneration; ground cover of dense *Chromalaena*. Similar fallow fields created by local farmers occur throughout the forest.
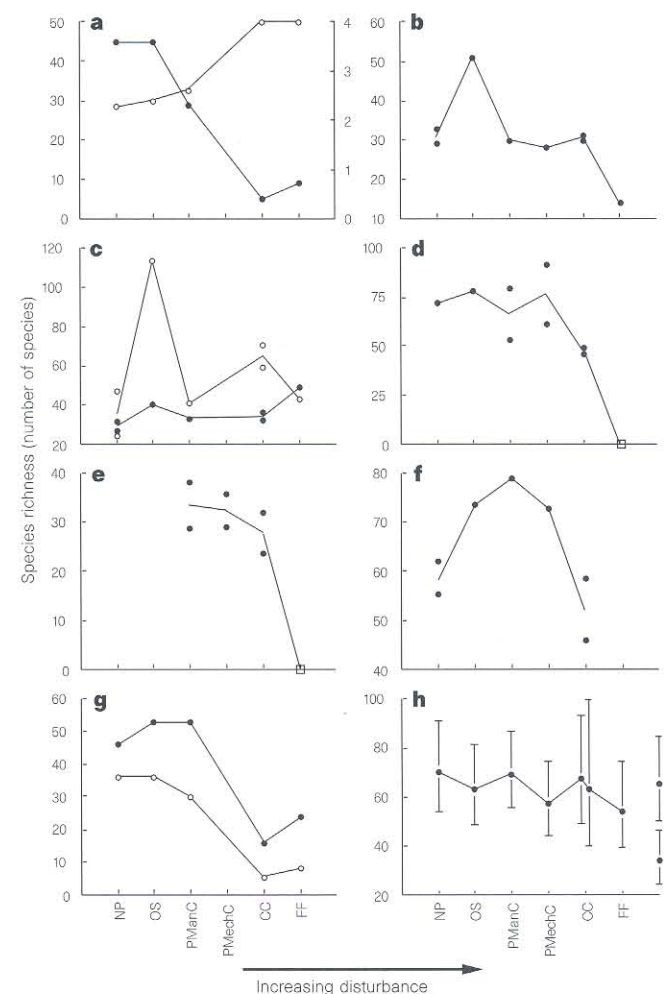
Figure 1 Species richness of animal groups along a gradient of increasing habitat modification (see Table 1). **a**, Birds (with mean habitat scores (open circles) on right ordinate); **b**, butterflies; **c**, flying beetles (malaise traps, filled circles; flight-interception traps, open circles); **d**, canopy beetles; **e**, canopy ants (open squares in **d** and **e** assume richness falls to zero in the absence of canopy); **f**, leaf-litter ants; **g**, termites (open circles, additional surveys not included in analyses); **h**, soil nematodes (with 95% confidence, and data from two even more heavily disturbed sites[14] not included in analyses).

Table 2 Important features of the taxa and inventory

Group surveyed	Total species recorded on study plots during survey*	Index of species turnover (β-2)	Geometric mean body length (range) (cm)	Scientist-hours to sample, sort and identify	Morphospecies that cannot be assigned to known species (%)
Birds (Aves)	78 (H)	18.3	26.5 (9–78)	50	0
Butterflies (Lepidoptera)	132 (I)	22.7	4.7 (2.0–11.1)	150	1
Flying beetles (Coleoptera)	358 (malaise) (L)	45.0	0.37 (0.06–2.26)	600 (both methods combined)	50–70
	467 (interception)	22.1			
Canopy beetles (Coleoptera)	342 (L)	39.4	0.45 (0.05–4.0)	1,000	>80
Canopy ants (Hymenoptera: Formicidae)	96 (I)	30.4	0.32 (0.1–1.0)	160	40
Leaf-litter ants (Hymenoptera: Formicidae)	111 (I)	6.8	0.32 (0.1–1.0)	160	40
Termites (Isoptera)	114 (H)	28.8	0.38 (0.2–0.75)	2,000	30
Soil nematodes (Nematoda)	374 (I)	21.0	0.089 (0.02–0.4)	6,000	>90

* H (high, >90%), I (intermediate, 50–90%) and L (low, <50%) are estimates of the degree of completeness in the species inventory for each group.

Table 3 Correlations between groups in change in species richness across plots on the disturbance gradient

	Butterflies	Flying beetles (malaise)	Flying beetles (interception)	Canopy beetles	Canopy ants	Leaf-litter ants	Termites	Nematodes
Birds	5, 0.67 *P* = 0.21	5, *–0.40* *P* = *0.50*	5, 0.28 *P* = 0.65	4, 0.98 **P = 0.02** (5, 0.78 *P* = 0.12)	2, – (3, 0.50 *P* = 0.66)	4, 0.47 *P* = 0.53	5, 0.90 **P = 0.04**	5, 0.51 *P* = 0.38
Butterflies		5, *–0.31* *P* = *0.61*	5, 0.82 *P* = 0.09	5, 0.40 *P* = 0.50 (6, 0.75 *P* = 0.09)	3, *–0.49* *P* = *0.67* (4, 0.97 **P = 0.03**)	5, 0.25 *P* = 0.69	5, 0.58 *P* = 0.30	6, 0.41 *P* = 0.42
Flying beetles (malaise traps)			5, 0.24 *P* = 0.71	4, 0.25 *P* = 0.75 (5, *–0.75* *P* = *0.15*)	2, – (3, *–0.99* *P* = *0.08*)	4, 0.43 *P* = 0.57	5, *–0.32* *P* = *0.61*	5, *–0.98* **P = 0.006**
Flying beetles (interception traps)				4, 0.28 *P* = 0.72 (5, 0.37 *P* = 0.54)	2, – (3, 0.30 *P* = 0.81)	4, 0.21 *P* = 0.80	5, 0.21 *P* = 0.74	5, *–0.17* *P* = *0.79*
Canopy beetles					3, 0.86 *P* = 0.33 (4, 0.97 **P = 0.03**)	5, 0.67 *P* = 0.22	4, 0.92 *P* = 0.08 (5, 0.73 *P* = 0.17)	5, *–0.28* *P* = *0.66* (6, 0.57 *P* = 0.24)
Canopy ants						3, 0.99 **P = 0.01**	2, – (3, 0.46 *P* = 0.70)	3, 0.04 *P* = 0.98 (4, 0.70 *P* = 0.30)
Leaf-litter ants							4, 0.84 *P* = 0.16	5, *–0.21* *P* = *0.73*
Termites								5, 0.50 *P* = 0.38

Where two estimates of species richness for a group exist at a particular point on the disturbance gradient (for example, butterflies in NP; Fig. 1b), values have been averaged. Data are then presented as sample size (number of plots available for pairwise comparison, from 2 to 6), Pearson's *r*, and associated probability, *P*. Values in parentheses are calculated using an assumed species richness of zero for canopy-inhabiting taxa in the absence of a canopy. Ten negative *r*-values and associated probabilities are in italics; *P*-values <0.05 are in bold. To simplify presentation, *r*-values are rounded to two significant figures, and hence similar values in the table (but not in the original calculations) may be associated with different *P*-values. Dashes indicate sample sizes too small for correlations to be calculated.

The number of scientist-hours required to process these samples (Table 2) is inversely related to each group's geometric mean body length $(\log_{10}(h) = -0.72 \log_{10}(cm) + 2.64; F_{1,5} = 11.64, P = 0.02$, including ants only once). In total, approximately 5 scientist-years (over 10,000 scientist-hours; Table 2) were required to sample, sort and catalogue the approximately 2,000 species. The total number of species present in all taxa must be at least 10 times, and may approach 100 times, this number, because many of the inventories are incomplete (Table 2) and numerous taxa (many very species rich, and many very small bodied) were not included in the surveys. We conclude that a detailed inventory, even from one area, of the impacts of tropical forest modification and disturbance on biodiversity will require a huge scientific effort, far exceeding anything attempted so far anywhere in the world. These data are also informative about the scale of effort required to produce an all-taxa biological inventory (ATBI)[11,24] for a 'representative hectare' of forest[25]. Such an inventory is unlikely to be possible without 1–2 orders of magnitude more effort than that devoted to the present

surveys. There were 12 systematists working on our material; two orders of magnitude more effort might absorb 10–20% of the estimated entire global workforce of 7,000 systematists[26] if an ATBI were to be completed in a reasonable time.

We do not argue against the critical importance of undisturbed forest for many species. Maximum diversity in tropical forests will be conserved by maintaining a mosaic of habitats, including large tracts of primary and old-growth secondary forest[27,28]. Our data do, however, suggest that some managed forests (plantations of native tree species, established by partial forest clearance[17,27]) may help to maintain diversity for both invertebrate and vertebrate[28] taxa. Most importantly, assessing the effects of habitat modification and disturbance on tropical biodiversity by using changes in species richness of familiar and well-studied groups (such as birds or butterflies) as indicators of changes in the diversity of other taxa gives a highly misleading picture of overall faunal changes. Monitoring changes in biodiversity resulting from forest modification and destruction requires a wide range of taxa to be studied,

embracing species with very different ecologies and life histories. The resources required to do this far exceed those currently available to taxonomists and ecologists worldwide. □

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Methods

Study area. Mbalmayo Forest Reserve (11° 25' to 11° 31' E, 3° 23' to 3° 31' N) is ~50 km south of Yaoundé in Cameroon, and at 650 m altitude. We did not establish experimental treatments ourselves (Table 1). We used existing areas of forest, silviculture demonstration plots created by the Institute of Terrestrial Ecology (UK) and later the Forest Management and Regeneration Project (a bilateral Government of Cameroon ONADEF, and UK Overseas Development Administration project), and experiments established by the International Institute of Tropical Agriculture field station[16]. Sites selected were representative of different parts of the forest habitat mosaic; replicate samples (Fig. 1) were taken from different sites. Human impacts have extirpated some species (including several large mammals) completely from the reserve; however, most other well-known groups (birds, butterflies and termites) remain rich in characteristic forest species.

Sampling. Sampling, concentrated in 1992–94, minimized edge effects by locating surveys and traps away from habitat boundaries. Within a group, sampling effort was identical on all plots (standardized by time, number of samples, or number of individuals sampled). Although some of the plots are relatively small (and hence data may not be representative of similar treatments applied over much larger areas), and although sampling of some groups is much less complete than others, our primary focus is on patterns of change along the gradient, not on absolute changes in species richness; the data are adequate for these purposes. Authors primarily responsible for data for each group are indicated in the following by initials.

Birds. (R.D.H., J.H.L.) Plots were censused visually and aurally, in morning or late-afternoon sessions lasting 1–2 h (10 h per plot, 7 h in July 1993 and 3 h in March 1994). Only birds using the plots (not flying over or through) were counted. Species 'characteristic habitat scores'[29] were assigned as follows: 1, 'true forest', primary forest, old-growth secondary forest; 2, 'forest'; 3, forest and other habitats, such as bush, second growth, clearings; 4, bush, scrub, farmland, gardens.

Butterflies. (T.B.L., D.S.S., N.E.S., A.D.W.) Plots were sampled in March 1994 (ref. 16) by netting by D.S.S., netting by four hired local collectors, rotated round plots to avoid collector bias, and by fruit-baited traps.

Flying beetles. (P.E., P.M.H., N.A.M.) Two methods, malaise and flight-interception traps[30], caught beetles from just above ground level to a maximum height of ~1 m (two traps in NP and CC plots, one in each OS, PmanC and FF plot; see Table 2 for definitions). Each trap was set for two periods of 4 days (July 1993). The two methods catch very different components of the flying-beetle fauna.

Canopy beetles and canopy ants. (B.B., N.S.E., A.D.W.) Sampling[16] was confined to planted *Terminalia ivorensis* in plantations (15 trees per plot) and to indigenous *T. superba* in NP and OS plots, by fogging with permethrin, an insecticide with rapid knock-down (ants, on four occasions between 1991 and November 1993; beetles in November 1993 only). There was no surviving tree canopy on the FF plot; canopy-insect species richness was assigned values of zero on this plot for some analyses.

Leaf-litter ants. (B.B., N.S.E., A.D.W.) Ten litter samples, each 1 m², taken in 50-m transects across each plot in November 1993. Leaf litter and the top few millimetres of soil were sieved in a coarse 1-cm sieve, and the residue extracted in 'Winkler bags'[16].

Termites. (D.E.B., P.E., J.H.L.) All species (up to 1 m above ground) were collected from transects (100 m × 2 m) run across each plot in November 1992 and July 1994 (ref. 16). Additional less comprehensive samples[15] (August 1992 and July 1993) are shown (Fig. 1) for comparative purposes only.

Nematodes. (G.F.B., M.H., J.H.L.) Core samples[14] taken from 18 sites in July 1993 comprise 200 nematodes identified to species in one core from each site, with similar sites grouped to obtain replicate measures (three each of NP, OS, PMechC and CC; four of PManC; and two of FF).

Body size. We used geometric mean body length (for butterflies, wingspan), hereafter referred to as 'length', of the largest and smallest species in each group (adult birds, beetles and nematodes, worker ants and termites) as an estimate of each group's characteristic body size.

Sampling effort. 'Scientist-hours' (Table 2) include fieldwork, extraction, sorting to morphospecies, identification where possible, and data compilation. They exclude training, travel, and domestic and logistic activities. Estimates (made for each taxon without consulting colleagues working on other groups) are minima, because sorting and identification involved world experts with direct access to NHM collections. Conversion from scientist-hours to scientist-years assumes 250 working days of 8 h per year.

Statistics. Data are total species recorded per plot, without errors; replicated plots, where available (Fig. 1), give similar results. For nematodes, 95% confidence intervals were calculated using replicate plots[14]. Where the total number of individuals sampled is known we also used a jack-knife technique (the program EstiMates; R. K. Colwell, University of Connecticut, unpublished) to calculate mean richness and 95% confidence intervals for data rarefied to uniform numbers of individuals sampled on all plots, and re-ran the analyses. Our general conclusions are unaffected. Pearson correlations (Table 3) were calculated with SPSS 6.1. β-2 (species' turnover along the gradient[22]) $= \{[(S/\alpha_{max}) - 1]/(N - 1)\} \times 100$, where S is the total number of species recorded, α_{max} is the maximum within-taxon richness per sample and N is the number of samples per taxon. β-2 is insensitive to trends in species richness, and allows comparison between transects of unequal size[22]. It ranges from 0 (no turnover) to 100 (every sample has a unique set of species). Because values reflect real turnover and pseudo-turnover (caused by incomplete inventories), and cannot be compared statistically, they must be interpreted cautiously; different ways[22] of calculating β, and of including or excluding duplicate samples, do not alter the general conclusions.

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