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Consistency of effects of tropical forest disturbance on species composition and richness relative to use of indicator taxa

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Abstract

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A citation-classic study published almost twenty years ago found that the species richness of eight taxa each responded differently to anthropogenic disturbance in Cameroon forests. Recent developments in conservation biology suggest that net number of species is an insensitive measure of change and that understanding which species are affected by disturbance is more important. In addition, it is recognized that all disturbance types are not equal in their effect on species and that grouping species according to function rather than taxonomy is more informative of responses of biodiversity to change. In a reanalysis of most of the original Cameroon dataset (canopy/ground ants, termites, canopy beetles, nematodes and butterflies) using more a inclusive measure of forest disturbance, which recognised four component drivers of change, we found disturbance effects are always stronger on species composition than on species richness and are mostly concordant between taxa. Further, the magnitude of compositional change relative to reference site was correlated across several taxa. In contrast to findings in the original study, species richness for most groups did not decline with disturbance level, providing additional support to the view that trends in species richness at local scales do not reflect the resilience of ecosystems to disturbance. Although disturbance generally caused changes in composition, the strength of this relationship depended on the disturbance driver and the functional group of organisms considered. This re-analysis suggests consideration of the impact of different forms of disturbance on species composition rather than net numbers of species, and the functional similarity of different taxa are important for conservation management when assessing the impacts of disturbance on biodiversity.

Introduction

Human transformation of the world's ecosystems, their biodiversity and other ecosystem goods and services has led to suggestions that we are now in a new geological era: the Anthropocene (McGill et al. 2015; Millenium Ecosystem Assessment 2005). Measuring the impact of anthropogenic disturbance on biodiversity is difficult, however, because of the large numbers of poorly known and taxonomically intractable species, especially in groups such as invertebrates and fungi. Surveying a few well-known and relatively easily identifiable species or taxonomic groups such as birds, butterflies and dung beetles, and using these as indicators or surrogates for the impact of disturbance on the rest of the biota therefore has great appeal and has become a classic concept in conservation biology (Lindenmayer & Burgman 2005; Lindenmayer et al. 2000). However, it has been difficult to determine whether such well-known taxa actually do act as surrogates, which are the best metrics to use, and what the usefulness of these surrogates is for conservation management decisions (Kerr et al. 2000; Lewandowski et al. 2010; Lindenmayer et al. 2000; Lovell et al. 2007; McGeoch 1998; Schulze et al. 2004). Further, the term 'indicator' has been used in many different ways in the literature with Caro (Caro 2010) identifying at least five different meanings for this term.

One of the most highly-cited studies of the indicator species concept, now a recognized citation classic, compared eight groups of invertebrates and vertebrates, in tropical forests in Cameroon (Lawton et al. 1998). Although the species richness of most groups appeared to show some change over a gradient in forest disturbance, no single group was a good indicator of changes in the others, a result subsequently observed in a number of other studies in different ecosystems (Barlow et al. 2007; Schulze et al. 2004).

We have been motivated to re-examine the Lawton *et al.* study by several recent developments within conservation biology. First, it has been argued repeatedly that the goal of conserving global biodiversity requires an understanding of which species are affected by forest disturbance, rather than the net number of species within disturbed versus undisturbed forest (Bengtsson et al. 2000;

Gardner et al. 2009; Lindenmayer & Franklin 2002). Disturbance may select for widespread or generalist species, so that local diversity may be maintained following disturbance while the rare, endemic or specialised species, which are the most important to regional and global biodiversity, decline. At local scales, therefore, conservation biology is more concerned by shifts in species composition and loss of particular species from the ever-decreasing areas of old growth forest, than by changes in the total number of species (Dunn 2004; Gibson et al. 2011).

The second development has been a growing recognition that species richness is either an insensitive or contingent metric of ecological change (Supp & Ernest 2014). Recent meta-analyses of temporal trends in local richness trends have provided conflicting results, either no net change over time (Dornelas et al. 2013; Vellend et al. 2013) or declines in diversity following disturbance (Murphy & Romanuk 2014). Understanding how individual species within communities are affected by anthropogenic change may be the key to determining local community responses and their impact on ecosystem services (Wardle et al. 2011).

A third development in conservation biology has been a growing realization that all disturbance types are not equal in their effect on biodiversity (Sodhi et al. 2009). The effects of logging depend critically on the scale and methods used (Hill & Hamer 2004) and how much ecosystem integrity is compromised (Lindenmayer et al. 2000; Stork et al. 1997). For example, logging with heavy machinery affects both canopy cover and soil compaction. Replanting trees may mitigate for the loss of cover, but not necessarily the effects of soil compaction. Lawton *et al.* (1998), as others, made no attempt to distinguish the different components of disturbance in their analysis.

A fourth issue is whether grouping species according to function rather than traditional taxonomy is more informative when considering the responses of biodiversity to anthropogenic change (Didham *et al.* 1996).

In the Lawton *et al.* study, butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites, soil nematodes and birds were sampled and sorted to species or morphospecies for multiple experimentally disturbed 1ha tropical rainforest plots. The treatments were originally ranked on a disturbance gradient, from near-primary forest through secondary forest to plantation forest and to completely cleared plots. Here, we re-examine data for six of these groups in the light of these new developments in conservation biology, particularly an assessment of the impact of different measure of disturbance on species composition. We also consider the spatial locations of the plots relative to each other and account for this explicitly in our analyses. We hypothesise that:

- 1) species composition is more sensitive to forest disturbance than species richness because changes in composition reflect the responses of individual species to disturbance.
- 2) disturbance can have congruent effects on the composition of different faunal groups, even when it has divergent effects on their species richness, and that functionally similar groups using similar resources or microhabitats will show similar effects of disturbance on composition (eg soil dwellers, such as nematodes and termites, or canopy dwellers such as canopy beetles and ants).
- 3) subsuming multiple trophic and functional levels within a single, large, taxonomically-defined group is too coarse a resolution to detect congruent patterns of faunal change with disturbance, and that herbivores (for beetles and nematodes) and decomposers (for termites) are more affected by tree loss than other guilds that are less directly associated with particular plants.

Lawton *et al.* (1998) ordered the different forest treatments in a broad, single gradient of disturbance or habitat modification. By not explicitly defining the gradient they may have omitted

important mechanistic links. Here we examine whether groups differ in sensitivities to four components of disturbance: years since disturbance, tree cover, soil compaction, and degree of tree removal and we hypothesise that:

4) herbivorous groups will be most affected by loss of plant diversity and tree cover and soil dwellers will be most sensitive to soil conditions.

The practical problem we tackle in our study is similar to that faced by many conservation studies and, recognising the many ways in which the term indicators has been used (Caro 2010), it is extremely time-consuming to sample all groups of organisms, and hence are we justified in basing our conservation decisions on just one or a couple groups of organisms? We would be justified if the response of any groups of organisms to forestry disturbance was actually fairly similar to the collective response. So, to be precise, we are asking if the response of taxonomic group X1 is indicative of the general response of taxonomic groups X1, X2...Xn where n is the total number of taxonomic groups in the forest. Here we approximated n to 6, as a complete biodiversity inventory of a hectare of tropical forest has eluded even the world's best biologists.

Methods

Study area, forest treatments, and sampling of taxa

Samples were taken within the Mbalmayo Forest Reserve (3°23' to 3°31' N, 11°25' to 11°31' E) in Southern Cameroon, at that time a mosaic of lightly to highly disturbed evergreen and deciduous rainforest (Fig. 1). Many plots have been experimentally disturbed in different ways and measured for various biotic and abiotic parameters. Plots were selected to represent a number of different stages of disturbance from old growth through to farm fallow (Lawton *et al.* 1998).

Sampling methods

Sampling was conducted between 1992 and 1994 using standard sampling methods as described below and elsewhere: nematodes (Bloemers et al. 1997); termites (Eggleton et al. 1995); butterflies (Stork et al. 2003); ants and beetles (Watt et al. 2002; Watt et al. 1997a).

Butterflies (NES, ADW, DSS) were sampled by hand-netting by NES, ADW and DSS and by four local collectors, rotated around plots to avoid collector bias, and by fruit-baited traps. *Nematodes* (MH) - were sampled by examination of soil cores. *Termites* (PE) - all species were collected from ground based transects (100m x 2 m: up to 1m above ground) run across each plot. *Canopy beetles* and *canopy ants* (NES, ADW) - sampling was confined to planted *Terminalia ivorensis* in plantations (15 trees per plot) and to indigenous *T. superba* in Near Primary and Old Secondary plots, by fogging with permethrin, an insecticide with rapid knock-down (ants, on four occasions; beetles once). *Leaf-litter ants* (NES, ADW) - ten litter samples, each 1m², were collected in 50-m transects across each plot. Leaf litter and the top few millimetres of soil were sieved in a coarse 1cm sieve, and the residue extracted in Winkler bags. Ants were sorted to species by Barry Bolton.

Species of beetles (b), termites (t) and nematodes (n) were allocated to the following feeding guilds: herbivores/plant feeders (b,n) algal feeders (n), wood-fungus-feeders (b,t), fungivores (b,t,n), scavengers/omnivores (b,n), humus feeders (t), microbivores (n), soil ingestors (n, t), predators (b,n), parasitoids (n)..

Data selection and categorization of disturbance

Datasets were those used by Lawton et al. (1998) omitting flying beetles and birds because these data were unavailable. Data were selected so that all plots used for a taxonomic or ecological group had similar sampling effort (number of sampling periods and samples per plot). The number of plots/species for each group were as follows: butterflies 8/132, termites 5/73, canopy beetles 8/342,

litter ants 7/111, canopy ants 8/63, nematodes 25/428 (termites sampled in two seasons).

Supplementary Table 1 shows most target taxa were sampled at the same 5-8 sites.

The intensity of initial disturbance was categorized in four ways:

- i. *Tree biomass removed*: categorized as none, partial or complete. Where biomass was partially removed, the exact proportion remaining was difficult to quantify, but was in the range 30–50% canopy cover (Lawson *et al.* 1990).
- ii. *Soil compaction*: categorized as none (uncleared forest), low (forest partially cleared by hand), medium (forest completely cleared by hand), high (forest partially cleared mechanically) and very high (forest completely cleared mechanically). Manual clearance involved felling larger trees by chainsaw and smaller trees by machete, and cutting vegetation to knee height, resulting in minimal soil compaction. Mechanical clearance involved use of bulldozers to remove trees and the undergrowth resulting in substantial soil compaction.
- iii. *Time since disturbance*: determined as years between the sampling date (typically 1993) and the last known felling of trees. This was known in plots receiving experimental forestry treatments, but was estimated for uncleared old growth and regenerating forest. For these plots, time since disturbance was estimated based on the size of trees and local knowledge, ranging from 30 years (Eboufek old secondary) to 70 years (Bilik near primary (Bloemers *et al.* 1997; Eggleton *et al.* 1996)). The Ebogo near primary plot was evaluated as near primary but younger than the Bilik near primary plot (Stork *et al.* 2003).. Time since disturbance data was log transformed to capture the difference in rate of change as re-vegetation and tree growth are typically fastest soon after tree felling then slow down with time.

iv. *Tree cover/diversity at time of sampling*: estimated on a six-point ranked (ordinal) scale. In order of increasing tree cover the rankings were: (A) farm fallow with no trees; (B) completely cleared plots replanted with spaced trees 1–2 years prior to sampling; (C) completely cleared plots replanted with spaced trees 4–6 years prior to sampling or partially cleared plots replanted 1 year prior to sampling; (D) partially cleared plots replanted 5–6 years prior to sampling; (E) partially cleared plots replanted 11–21 years prior to sampling; (F) uncleared. Tree density and basal area data were available for eight of the plots confirming that the measured values matched the assumed rank order of (A), (D) and (F).

Statistical analysis

i) To test whether species composition in some taxa was more related to disturbance than for others, for each taxon we examined the Pearson correlation between dissimilarity in species composition for all pairs of plots with the dissimilarity in disturbance of the same pairs of plots (as described below). As such correlations are based on non-independent data-points (each plot contributes to multiple plot pairs), we tested the significance of each correlation coefficient with a Mantel test (10,000 permutations of plots with mantel function, vegan package, R vers. 3.1.2). Distance between plots varied from 100m to 9 km, so we removed potential effects of spatial autocorrelation by employing partial Mantel tests, which partialled out effects of space on species composition from effects of disturbance on species composition (Leduc et al. 1992). An alternative approach would have been to ordinate the raw data matrices, however such raw data methods do not permit us to compare the strength of taxa responses to a single multivariate disturbance gradient and so were not pursued here (but see separate publications for nematodes (Bloemers et al. 1997); termites (Eggleton et al. 1996; Eggleton et al. 1995); butterflies (Stork et al. 2003; Watt et al. 1997b); ants and beetles (Watt et al. 2002; Watt et al. 1997a)).

A species composition dissimilarity matrix was generated for each taxon by calculating the Morisita-Horn dissimilarity metric for each pair of plots (veg dist function, package vegan, R). We selected the Morisita-Horn metric as it is one of the most robust metrics to differences between plots in species richness and sample size (Magurran 1988; Morisita 1959; Wolda 1981). This metric can be sensitive to highly abundant species so we log-transformed our abundance data as recommended (Wolda 1981) prior to calculating the dissimilarity values. We also explored the robustness of our results to changes the similarity index (to Bray Curtis) and the correlation metric (to Spearman); in each case results were qualitatively similar to the Pearson correlations based on Morista-Horn similarity values that we report here.

The disturbance dissimilarity matrix was based on the four different measures of disturbance and recovery: log age since disturbance, tree cover at time of sampling, tree removal rank, and soil compaction rank. The log age of plots ranged from 0 to 5.24, so we scaled the ranks of the remaining three disturbance measures to encompass the same 5.24 range between plots. This scaling meant that each disturbance measure was equally weighted in the overall disturbance dissimilarity matrix. Given the standardized range between our four dissimilarity measures, we could use one of the simplest measures of dissimilarity, Euclidean distance, to generate our disturbance dissimilarity matrix (more complex dissimilarity indices are needed, for example, when species differ in mean abundance). As with the species dissimilarity matrix, the distance dissimilarity matrix compared pairs of plots - in this case combining information from the four disturbance metrics.

To create a spatial distance matrix we located all plots either either on Google Earth for plots more than 1km apart (Fig. 1) or in published figures of the arrangements of the plots where they were less than 1 km apart (Stork et al. 2003). We used those locations to calculate the distances between all possible plot combinations.

ii) Species richness was recalculated from the values in Lawton *et al.* (1998) using only the plots in the current analysis. We first used Mantel tests to test whether plot differences in species richness (dissimilarity estimated as Euclidean distance) correlated with dissimilarity in disturbance, using the same methods as given in (i). We also tested whether those plots that were of intermediate disturbance might exhibit higher species richness than less or more disturbed plots, according to the intermediate disturbance hypothesis (Connell 1978), by plotting species richness separately for each taxon against a univariate disturbance index. The univariate disturbance index was simply the average of the four components of disturbance (see (i)), scaled to vary from 0 to 1.

iii) We also used Mantel tests to determine whether feeding guilds of canopy beetles, nematodes and termites responded differently to disturbance gradients. The feeding guilds and their presumed equivalences are listed in Table 1.

iv) We tested which measure of disturbance correlated best with compositional change for each dataset by re-running the partial Mantel tests, but with a disturbance dissimilarity matrix based on just one of the disturbance measures (i.e. four sets of tests in total). We again partialled out spatial effects as detailed above.

With only eight study plots for most of the taxa considered some of the disturbance levels within disturbance types are not replicated, making the results potentially dependent on the specific characteristics of individual study plots. However, our intention here is to demonstrate how different ways of assessing disturbance may produce different results.

Results

Most taxonomic groups showed strong species composition responses to forest disturbance. Specifically, plots that were most different in disturbance were also most different in species

composition. This applied to butterflies, canopy beetles and litter ants, with marginally non-significant results for nematodes and termites, both before (Fig. 2) and after (Table 1) we partialled out spatial autocorrelation (Supp. Material Table 2 for full correlations). Canopy ants showed no correlation between disturbance and composition dissimilarities (Table 1, Fig. 2).

In contrast, species richness was generally uncorrelated with disturbance. Of the six target taxa, only termites showed a significant correlation between plot dissimilarities in species richness and disturbance (full correlations: Suppl. Mat Table 2; partial correlations Table 1). For the other five taxa, the lack of correlation was not an artefact of an underlying nonlinear relationship between disturbance and species richness. To demonstrate this, we first summarized the four components of disturbance in a univariate disturbance index (see Methods). No taxa had a quadratic relationship between species richness and this disturbance index, and again only termites exhibited a linear relationship (Fig. 3). Spatial autocorrelation, which was significant for the species composition of butterflies, canopy beetles and nematodes, did not affect patterns in species richness (Table 1).

When the four different drivers of disturbance were analyzed separately, taxonomic groups diverged in their compositional response (Table 2). Composition of butterflies, litter ants and nematodes was particularly correlated with amount of tree cover on plots at the time of sampling, composition of canopy beetles was most strongly correlated with time since disturbance, and composition of termites was most strongly correlated with degree of initial soil disturbance.

There were also moderately divergent responses to disturbance between functional feeding groups; differences between plots in disturbance were most strongly correlated with compositional

differences of herbivores (within beetles and nematodes) and humus feeders within termites (Table 3).

Discussion

In our analysis we found that, for at least three of our six taxonomic groups, disturbance of a tropical forest affects species composition more strongly than species richness, as we had hypothesised. This was particularly true for those groups where more disturbance-tolerant species replaced less disturbance-tolerant species, with total species richness remaining the same. Only termites showed effects of disturbance on species richness but not on composition. In this group, disturbance resulted in progressive loss of species in order of disturbance sensitivity, resulting in stronger negative effects on species richness. Our largely insignificant results for species richness contrast with those of Lawton et al. (1998), who suggested that the species richness of most groups responded, albeit in idiosyncratic ways, to disturbance. There are at least two reasons for this apparent discrepancy. First, the datasets are not completely identical. The bird data were not available for our analysis, and this group showed the clearest decline in species richness with disturbance. Lawton et al. (1998) also assumed that two sites with no canopy would have no canopy ants or canopy beetles, and this assumption alone resulted in the appearance of declines in species richness for these groups, whereas our analyses did not consider sites where data were not collected. Second, we statistically tested responses of taxa to disturbance and accounted for spatial autocorrelation, whereas Lawton et al. visually assessed patterns. We found that although butterflies and nematodes tended to decline in species richness over the disturbance gradient (in both Lawton et al. 1998 and Figure 3 of this paper), such declines were not actually significant. Hence our results for species richness are actually similar to those of Lawton et al. but arguably our interpretation is more robust. Our observations in part support the conclusion of several meta-

analyses that overall temporal trends in plot-scale species richness for both marine and terrestrial communities are not significantly different from zero (Dornelas et al. 2014; Supp & Ernest 2014; Vellend et al. 2013)(but see Elahi et al. (2015)), even following some disturbance (McGill et al. 2015). This trend of temporal constancy in local species richness is highlighted as one of the 15 forms of biodiversity trends that ecologists and conservation biologists should recognize and assess in the Anthropocene (McGill et al. 2015). Further, our results support the growing consensus that at local scales, species composition is a more sensitive and consistent indicator of ecological change than other measures of biodiversity, such as species richness (Dornelas et al. 2013; Supp & Ernest 2014; Vellend et al. 2013).

Our main conclusion is that the overall responses of taxonomic groups to disturbance were generally similar. However, this does not mean that there were no ecological differences evident in finer-scale analyses. As predicted, these differences generally reflected both the main habitats preferred by the taxonomic groups and, within taxa, the food resources for different functional feeding groups. For example, when disturbance was separated into four component drivers, different taxa were most sensitive to different components. Termites, many of which live in the soil, were particularly affected by the degree of initial soil compaction, and, within termites, humus feeders were more affected by disturbance than were wood and fungus feeders (Eggleton et al. 2002). Butterflies, which consume leaves and floral resources at different life stages, and litter ants, which use tree litter as habitat, were particularly affected by changes in the amount of tree cover. These results support those of others (Barlow et al. 2007).

The use of higher taxonomic levels to look at environmental gradients, biogeographic patterns or to predict species richness (Balmford et al. 2000; Beccaloni & Gaston 1995) appears to have some merit at least for levels up to the family. However, treating all trophically diverse beetles, nematodes or termites together as a single group, as we did previously (Lawton et al. 1998), is like lumping together all vertebrates and expecting there to be a single response to disturbance gradients. Beetles, for example, which appeared in the geological record around 285mya (Hunt et al. 2007).are generally conservative in their feeding guild up to tribe and often to family level (Hammond 1994) .

Although there has been some debate about the usefulness of functional groups in observing environmental change (Lindenmayer et al. 2000) others suggest that they are more likely to identify responses to disturbance than taxonomic grouping (Didham et al. 1996). Our separation of beetles, termites and nematodes into different feeding guilds demonstrated that the greatest response to disturbance in species composition was from the groups feeding on plant material (living or dead), confirming the usefulness of the functional guild approach (Didham et al. 1996) and the sensitivity of herbivorous invertebrates to disturbance. Canopy ants, unlike litter ants, showed little compositional shift in response to disturbance. It has previously been found that canopy ants in tropical forest exhibit a spatial 'ant mosaic', whereby species composition is determined by antagonistic interactions of dominant species on other species (Blüthgen et al. 2004). Such behaviourally enforced spatial patterns may override the influences of local habitat on species composition.

In summary, our study indicates that species composition is a more sensitive measure of the effect of disturbance on biodiversity than species richness. Species composition in at least some taxa

responds similarly to overall disturbance and particular types of disturbance. For conservation management, biodiversity indices such as species richness have the appeal of being comparable among groups in directionality. However, as we discussed above, there is now very strong evidence that trends in species richness at small scales does not reflect the resilience of ecosystems to disturbance. On the other hand, here (Fig. 2) we demonstrate that a number of taxa all exhibit compositional differences that correlate with disturbance differences. This provides some hope that monitoring of select groups can be used to set conservation policy for the ecosystem as a whole. Compositional data also provide the opportunity to examine the ecological function of rare and threatened status of the species affected to help guide conservation decisions. In a further analysis not presented here we found that for most groups (except termites) the change in species composition with increasing disturbance is due to the loss of disturbance-sensitive species and addition of disturbance-tolerant species.

We suggest that a critical element in monitoring the disturbance effects on biodiversity is to separate out the impacts of various forms of disturbance because, as we have demonstrated, some taxa respond only to particular kinds of disturbance or not at all. To the best of our knowledge this is the first time this has been demonstrated.

Our results suggest that of the taxa we sampled, the most sensitive to multiple drivers of disturbance and which respond in similar ways in changes in species composition are butterflies, canopy beetles and litter ants, and herbivores. In contrast, canopy ants, termites and nematodes appear to respond differently. A more complete understanding of the response of biodiversity to disturbance would, therefore, require that a wider range of taxa known, or suspected, to show

different responses are also sampled. Where taxa are known to show similar compositional shifts, the length of time to sample and sort them becomes important since indicator taxa should be easier to measure than the groups they are indicating. In our study the time to sample and sort was 1,000-6,000 hrs for nematodes, termites and canopy beetles, whereas litter ants, canopy ants and butterflies each took 150-160 hours (Lawton et al. 1998)). Taking these issues into account, of the taxa we have reanalysed, butterflies and litter ants would appear to be useful indicator taxa. However, a fuller assessment of biodiversity would require that other taxa are also sampled.

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Table 1. Partial correlations (Pearson's r) of plot differences in disturbance with either differences in species composition or species richness, after controlling for the spatial distance between plots (see Supplementary Table 2). The significance of all partial correlations were evaluated with Mantel tests.

¹Note canopy ants included a hyper-abundant species (*Technomyrmex 2*), but removal of this species did not substantially change the results.

Taxa	Disturbance & species composition		Disturbance & species richness	
	r	p	r	p
Butterflies	0.577	0.001	0.094	0.221
Termites	0.450	0.060	0.793	0.034
Canopy beetles	0.680	0.001	0.098	0.272
Litter ants	0.517	0.005	0.075	0.265
Nematodes	0.107	0.065	-0.008	0.506
Canopy ants ¹	-0.160	0.774	-0.137	0.759

Table 2. Partial correlations (Pearson's r) of plot differences in particular disturbance components with plot differences in species composition. The significance of all partial correlations were evaluated with partial Mantel tests which partialled out the effects of spatial distance between plots.

Taxa	Age (log)		Tree cover		Soil disturbance		Tree removal	
	r	p	r	p	r	p	r	p
Butterflies	0.406	0.033	0.591	0.001	0.572	0.001	0.540	0.001
Termites	0.251	0.193	0.347	0.176	0.673	0.015	0.296	0.115
Canopy beetles	0.774	0.001	0.699	0.001	0.496	0.004	0.543	0.007
Litter ants	0.417	0.098	0.537	0.005	0.423	0.005	0.488	0.006
Nematodes	0.123	0.084	0.131	0.042	0.050	0.232	0.069	0.167
Canopy ants	-0.146	0.703	-0.232	0.867	-0.085	0.644	-0.240	0.881

Table 3. Partial correlations (Pearson's r) of plot differences in disturbance with differences in the species composition of particular feeding guilds of canopy beetles, termites and nematodes. The significance of all partial correlations were evaluated with partial Mantel tests which partialled out the effects of spatial distance between plots. In a few cases, as noted, one or more sites were omitted from analyses because similarity between pairs of sites with zero values cannot be computed in a Mantel test.

Feeding Guilds	Disturbance & species composition	
	r	p
Beetle herbivores (n=131 species)	0.506	0.005
Beetle fungivores, xylophages (n=87)	0.248	0.135
Beetle predators, scavengers (n=51)	0.306	0.061
Termites: fungus (n=7)	-0.606	0.983
Termites: wood (n=11, 1 site omitted)	0.222	0.375
Termites: humus (n=27)	0.434	0.008
Termites: soil (n=27, 1 site omitted)	0.636	0.167
Nematodes: herbivores (n = 146)	0.186	0.005
Nematodes: fungivores (n = 22, 5 sites omitted)	-0.002	0.478
Nematodes: microbivores (n = 122)	-0.037	0.692
Nematodes: predators (n=77)	0.044	0.246
Nematodes: omnivores (n = 55)	-0.055	0.798

Fig. 1. Map of the study area in Cameroon showing the positions of the sampling plots. The inset maps show the arrangement of treatment plots at Bilik, Ebogo and Eboufek.

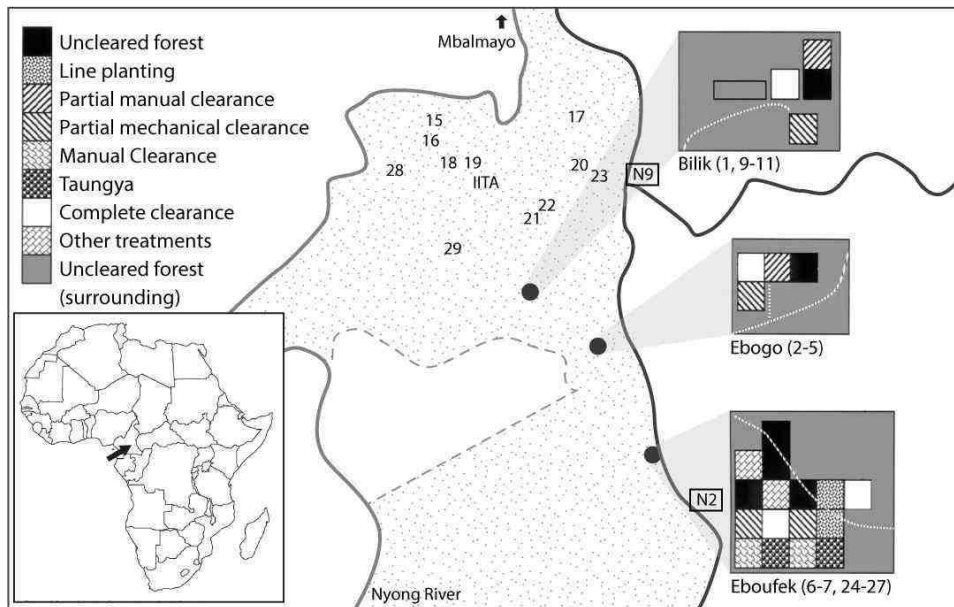


Fig. 2. Community dissimilarity in species composition between plots was often correlated to plot dissimilarity in forest disturbance. After correcting for spatial autocorrelation, correlations were significant for butterflies, beetles and litter ants (solid lines), marginally significant for termites, nematodes (dotted lines) and non-significant for canopy ants. Note darker points are where several points overlap.

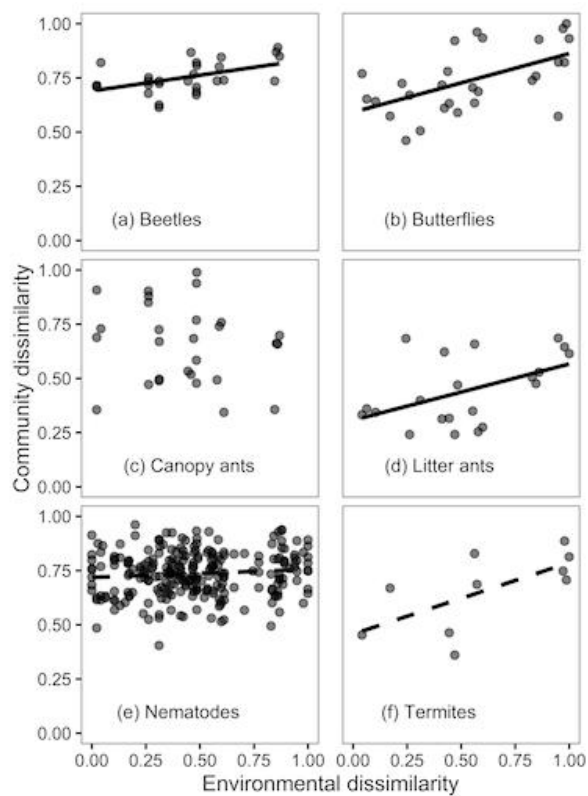


Fig. 3. Species richness within plots was often unrelated to the disturbance history of the plot; disturbance here is measured by a composite index that increased with tree biomass removal and degree of soil compaction and decreased with tree cover and age of forest . Of the six target taxa, only termites exhibited a significant linear relationship with disturbance (solid line).

