

Changes in Arthropod Assemblages along a Wide Gradient of Disturbance in Gabon

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Abstract: Searching for indicator taxa representative of diverse assemblages, such as arthropods, is an important objective of many conservation studies. We evaluated the impacts of a wide gradient of disturbance in Gabon on a range of arthropod assemblages representing different feeding guilds. We examined 4×10^5 arthropod individuals from which 21 focal taxa were separated into 1534 morphospecies. Replication included the understory of 3 sites in each of 4 different stages of forest succession and land use (i.e., habitats) after logging (old and young forests, savanna, and gardens). We used 3 complementary sampling methods to survey sites throughout the year. Overall differences in arthropod abundance and diversity were greatest between forest and open habitats, and cleared forest invaded by savanna had the lowest abundance and diversity. The magnitude of faunal differences was much smaller between old and young forests. When considered at this local scale, anthropogenic modification of habitats did not result in a monotonous decline of diversity because many herbivore pests and their associated predators and parasitoids were abundant and diverse in gardens, where plant productivity was kept artificially high year-round through watering and crop rotation. We used a variety of response variables to measure the strength of correlations across survey locations among focal taxa. These could be ranked as follows in terms of decreasing number of significant correlations: species turnover > abundance > observed species richness > estimated species richness > percentage of site-specific species. The number of significant correlations was generally low and apparently unrelated to taxonomy or guild structure. Our results emphasize the value of reporting species turnover in conservation studies, as opposed to simply measuring species richness, and that the search for indicator taxa is elusive in the tropics. One promising alternative might be to consider “predictor sets” of a small number of taxa representative of different functional groups, as identified in our study.

Keywords: indicator taxa, predictor sets, rainforest, species loss, species turnover

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Cambios en Ensamblajes de Artrópodos a lo largo de un Gradiente de Perturbación Amplio en Gabón

Resumen: La búsqueda de taxa indicadores representativos de ensamblajes diversos, como lo artrópodos, es un objetivo importante de muchos estudios de conservación. Evaluamos los impactos de un gradiente de perturbación amplio en Gabón sobre ensamblajes de artrópodos representando gremios alimentarios diferentes. Examinamos 4×10^5 individuos de artrópodos de los cuales 21 taxa focales fueron separados en 1534 morfoespecies. La replicación incluyó el sotobosque de tres sitios en cada una de cuatro etapas diferentes de la sucesión de bosques y de uso de suelo (i.e., hábitats) después de ser talados (bosques jóvenes y maduros, sabana y jardines). Utilizamos tres métodos de muestreo complementarios para estudiar los sitios a lo largo del año. Las diferencias generales en la abundancia y diversidad de artrópodos fueron mayores entre bosques y hábitats abiertos, y el bosque talado invadido por sabana tuvo la menor abundancia y diversidad. La magnitud de las diferencias fue mucho más pequeña entre los bosques maduros y viejos. Al considerarla en esta escala local, la modificación antropogénica de hábitats no resultó en una declinación monótona de la diversidad porque muchas plagas de herbívoros y sus depredadores y parasitoides asociados fueron abundantes y diversas en los jardines, donde la productividad de plantas fue mantenida artificialmente a lo largo del año mediante riego y rotación de cultivos. Utilizamos una variedad de variables de respuesta para medir la robustez de las correlaciones en los sitios de muestreo entre taxa focales. Estos pudieron ser clasificados, en términos del número decreciente de correlaciones significativas, como sigue: renovación de especies > abundancia > riqueza de especies observada > riqueza de especies estimada > porcentaje de especies específicas de sitios. El número de correlaciones significativas generalmente fue bajo y aparentemente sin relación con la taxonomía ni la estructura del gremio. Nuestros resultados enfatizan el valor de reportar la renovación de especies en los estudios de conservación, en lugar de simplemente medir la riqueza de especies, y que la búsqueda de taxa indicadores es elusiva en los trópicos. Una alternativa prometedora pudiera ser la consideración de "conjuntos pronosticadores" de números pequeños de taxa representativos de grupos funcionales diferentes, como los identificados en nuestro estudio.

Palabras Clave: bosque lluviosos, conjuntos pronosticadores, pérdida de especies, renovación de especies, taxa indicadores

Introduction

Understanding and maintaining the distribution of biodiversity across habitat mosaics, including varying levels of disturbance, is a central issue for conservation biology and the related field of agrobiodiversity. Arthropods represent a significant fraction of biodiversity and play major roles in ecosystem function, yet the theory and practice of assessing their response to fragmented habitats remain poorly developed (Kremen et al. 1993). Arthropods include a variety of functional guilds (Moran & Southwood 1982); hence, their responses to anthropogenic disturbance may vary greatly, even among congeneric species (Basset et al. 2001). Furthermore, the concepts of indicator and umbrella species appear untenable, especially in the tropics (Didham et al. 1996; Lawton et al. 1998). This has led to repeated pleas to consider multispecies and multiguild-assemblage responses to anthropogenic disturbance (Didham et al. 1996; Kotze & Samways 1999).

The impacts of disturbance on multitaxic assemblages have rarely been studied in tropical rainforests, due principally to a lack of workforce, relevant expertise, and funding (reviewed in Lewis & Basset 2007). Studies including several taxa and guilds are uncommon but growing in number (Didham et al. 1996; Lawton et al. 1998; Schulze et al. 2004; Pineda et al. 2005; Barlow et al. 2007). Still, there have been few studies dedicated to examining

arthropod responses over a wide anthropogenic gradient of disturbance (as opposed to examining undisturbed vs. disturbed forests) and selecting a wide range of arthropod taxa that represent diverse taxonomic and functional guilds.

In their seminal study, Lawton et al. (1998) surveyed 8 animal groups (1 vertebrate, 6 arthropod, and 1 invertebrate taxa) at 12 sites that ranged from near-primary forests and old-growth secondary forests to plantations and cleared farm fallows. Although sampling effort was not particularly large (56 trap days), it was deemed sufficient to characterize the arthropod fauna at these different sites. The results of this study appear especially relevant to species-rich assemblages (1620 arthropod species considered) and to conservation biology in general: species richness generally declined with increasing disturbance; no single group served as a good indicator taxon of the species richness of others; the matrix of correlation coefficients among taxa appeared idiosyncratic; and these data indicated the huge scale of the biological effort required to measure the effect of tropical-forest disturbance.

Similar studies in Sulawesi, Mexico, and in the Amazon surveyed 5, 3, and 15 groups, respectively (including 2, 1, and 8 arthropod taxa, respectively) at different sites ranging from old and young secondary forests to plantations and crop fields (Schulze et al. 2004; Pineda et al.

2005; Barlow et al. 2007). Although the general results of Schulze et al. (2004) were similar to those of Lawton et al. (1998), species richness was significantly correlated among taxonomic groups (and in particular between the 2 arthropod groups). Schulze et al. (2004) did not embrace the concept of indicator groups for predicting local patterns of species richness; rather, they stressed that animal and plant groups may be affected similarly by disturbance. Species richness was rather weakly correlated among taxonomic groups in other studies (Pineda et al. 2005; Barlow et al. 2007).

Most of the researchers cited earlier used observed species richness to calculate correlations among taxa. Barlow et al. (2007) noted that cross-taxon congruence in response patterns is stronger when evaluated with community similarity than with species richness data. In a previous analysis of the study system described later, species richness was not always the best variable to quantify the effect of anthropogenic disturbance on arthropods (Basset et al. 2008). Out of a range of variables tested, abundance, estimated species richness, percentage of habitat-specific species, and species turnover were also interesting in this regard and sometimes of higher discriminating power than observed species richness. Thus, the concept of indicator taxa (e.g., Pearson & Cassola 1992) should not be discarded before considering this full set of variables.

Furthermore, Lawton et al. (1998) commented on the high costs involved with biodiversity surveys in tropical systems, but did not consider including local parataxonomists in their protocols (Janzen et al. 1993; Basset et al. 2004a). We do not dispute the huge taxonomic effort involved in identifying tropical species, but at least the preparation and implementation of complex protocols, including adequate spatial and temporal statistical replicates, all aspects of specimen preparation and pre-sorting, and entering data into a database, can be handled by parataxonomists.

Motivated by Lawton et al. (1998), we based our study on the work of trained parataxonomists in Gabon. We examined 4×10^5 arthropod individuals, from which 21 focal taxa were separated into 1534 morphospecies (Basset et al. 2004b, 2008). Replication included 3 sites in each of 4 different stages of forest succession and land use (i.e., habitats). We evaluated the effects of this wide gradient of disturbance on a range of arthropod assemblages that represented different feeding guilds, and contrasted our conclusions with observed species richness and other variables. Our specific aims were to (1) evaluate the strength of correlation in richness among various arthropod taxa across study sites along a wide disturbance gradient, (2) examine whether conclusions are modified if alternative variables to observed species richness are used, and (3) examine whether correlation matrices among taxa appear idiosyncratic or may be struc-

tured by taxonomy or functional guilds. This information should be widely helpful to conservation biologists concerned with documenting the impacts of human modification of tropical forests on the arthropod assemblages they support because it will allow them to focus future sampling efforts on particularly informative sets of taxa and particular metrics of diversity.

Methods

Study Area and Sites

The study area was in the Shell Gabon oil concession of Gamba, within the Gamba complex of protected areas in southeastern Gabon (see Alonso et al. [2006] for background and botanical information). The Gamba oil field includes a mosaic of old-growth secondary rainforests, younger secondary rainforests, and savanna areas, resulting mainly from anthropogenic action. The mean annual temperature in the area is 26 °C and annual rainfall is 2093 mm per year, with the major dry season from June to August (Alonso et al. 2006). The Gamba oil field has been active since 1967 and since then Gamba has grown from a small village in 1960 to a town of 8000 inhabitants. The earliest cultivated crop gardens of notable size were established near the town as recently as 1998.

We considered 4 distinct habitats of increasing anthropogenic disturbance (i.e., increasing forest clearing and introduction of exotic vegetation) and selected 3 sites (replicates) within each habitat. The 4 habitat types were (1) understory of interior of old secondary rainforests (old forests), (2) understory of the edge of young secondary rainforests (young forests), (3) rainforest cleared to install oil rigs and subsequently invaded by savanna (savanna), and (4) cultivated crop gardens (gardens). At the time of the study, there were no substantial plantations in the area, and these 4 habitat types were predominant in the Gamba oil field. Salient characteristics of the study sites (coded A-L) are indicated in Table 1 (see also Fig. 1 and Basset et al. 2004b).

Arthropod Collecting and Processing

Each site was equipped with an identical set of traps recommended for biological monitoring of flying and epigeic arthropods of the understory and litter: 1 ground Malaise trap, 4 yellow pan traps on the ground, and 5 pitfall traps buried in the ground. Details about the traps, their emplacement, and mode of action are in Basset et al. (2004b). The 120 traps were operated for 3 days during each of the 38 survey periods from July 2001 to July 2002 (total 13,680 trap days). A team of 8 parataxonomists was trained and supervised by a professional entomologist throughout the project (see Basset et al. [2004a] for a detailed discussion of this strategy).

Table 1. Main characteristics of study sites within the Shell-Gabon Gamba oil field.

Code	Habitat	Coordinates	Fragment size (ha)	Physiognomy	Plant cover (level of cover)*
A	old forest	02°42'20''S 09°59'49''E	700	secondary forest, tallest trees 45 m, sandy soil	<i>Neochevalierodendron stephanii</i> (dominant); <i>Diospyros zenkeri</i> , <i>D. vermoeseni</i> (common)
B	old forest	02°42'54''S 10°00'00''E	84	secondary forest, tallest trees 45 m, sandy soil	<i>N. stephanii</i> (dominant); <i>Diospyros zenkeri</i> , <i>D. vermoeseni</i> , <i>Palisota ambigua</i> (common)
C	old forest	02°44'27''S 10°00'11''E	28	secondary forest, tallest trees 40 m, but many small trees 10–20 m tall, sandy soil	<i>D. vermoeseni</i> , <i>D. conocarpa</i> (common); <i>P. ambigua</i> , <i>Trichoscypha acuminata</i> (less common)
D	young forest	02°45'38''S 10°01'37''E	12	secondary forest, tallest trees 20 m, many small trees and bushes, sandy soil	<i>P. ambigua</i> , <i>Aframomum</i> sp., <i>Rauvolfia</i> sp. (common); <i>Musanga cecropioides</i> (present)
E	young forest	02°46'08''S 10°02'25''E	19	secondary forest, very open canopy, tallest trees 30 m, swampy soil	<i>Xylopia hypolampra</i> , <i>X.</i> spp. (dominant)
F	young forest	02°47'32''S 10°03'45''E	166	secondary forest, plot at the edge of a thin tongue of forest connected to a large forested area; tallest trees 30 m, important regrowth in the understory, sandy soil	<i>Pachypodanthium staudtii</i> , <i>D. vermoeseni</i> , <i>P. ambigua</i> , <i>Leptactina mannii</i> , <i>Ouratea sulcata</i> , <i>Sacoglottis gabonensis</i> , <i>Bertiera subsessilis</i> (present)
G	savanna	02°42'51''S 09°59'55''E	2.7	surrounded by forest; isolated bushes and trees, sandy soil, bare soil 50%	<i>Borreria verticillata</i> , 2 unidentified Poaceae (dominant); <i>Cyperus tenax</i> , <i>Dracaena</i> sp. (present)
H	savanna	02°44'11''S 10°00'22''E	3.0	surrounded by forest, sandy soil, bare soil 25%	<i>B. verticillata</i> , <i>Dracaena</i> sp., 1 unidentified Poaceae (dominant); <i>Cyperus halpan</i> , <i>Heterotis decumbens</i> (present)
I	savanna	02°48'23''S 10°03'21''E	2.5	surrounded by forest, sandy soil, bare soil 25%	<i>Merremia tridentata</i> , <i>C. tenax</i> , 1 unidentified Poaceae (dominant)
J	garden	02°44'47''S 10°01'10''E	2	sandy soil fertilized with compost	amaranth, aubergine, cabbage, carrot, lettuce, pepper, spinach, sweet pepper, tomato, water melon (present)
K	garden	02°43'36''S 10°02'06''E	0.5	clayish sand fertilized with compost	aubergine, banana, maize, manioc, pepper, pineapple, spinach, sugar cane, taro (present)
L	garden	02°44'09''S 10°01'06''E	0.8	sandy soil fertilized with compost	amaranth, aubergine, cabbage, cucumber, gombo, pepper, sorrel, spinach, tomato (present)

*For gardens, the main crops cultivated during the study period are listed.

The material collected was first sorted into families or higher taxa by the parataxonomists. The material belonging to 21 focal taxa (Table 2) was isolated, and each individual was identified by a unique specimen number. Focal taxa were sorted to morphospecies (i.e., unnamed species diagnosed with standard taxonomic techniques) by the parataxonomists. Formal taxonomic study of this material is ongoing but subsamples of the material belonging to 7 taxa have been examined by taxonomists (Table 2). We selected focal taxa so there would be good representation in the samples (so that much information was retained), because it would be workable taxonomically, because taxonomists expressed interests in the material, and so there would be representation of a variety of functional guilds and orders (Table 2). Specimens were stored at the Smithsonian Biodiversity Conservation Center in Gamba, and vouchers were deposited at the National Museum of Natural History (Washington, D.C.) and with taxonomists who helped with species identification.

Statistical Methods

We calculated correlations among taxa collected at study sites with the following variables: abundance, observed and estimated species richness, percentage of habitat-specific species, and species turnover. Overall abundance and observed species richness were extracted from raw data for each focal taxa at each site because sampling effort was similar at each site (although not in terms of individual collected). To calculate estimated species richness, we considered the results of consecutive surveys at each study site, pooling the results of all sampling methods ($n = 38 \times 12 = 456$ samples). For ease of comparison with previous studies, we used EstimateS software to calculate Chao1 richness estimates (adequate when many species are rare) with 50 randomizations (Colwell 2005).

To evaluate which species may be indicative of particular sites and habitats, we used the indicator value index (Dufrene & Legendre 1997). We restricted the data set to the most abundant morphospecies (≥ 12

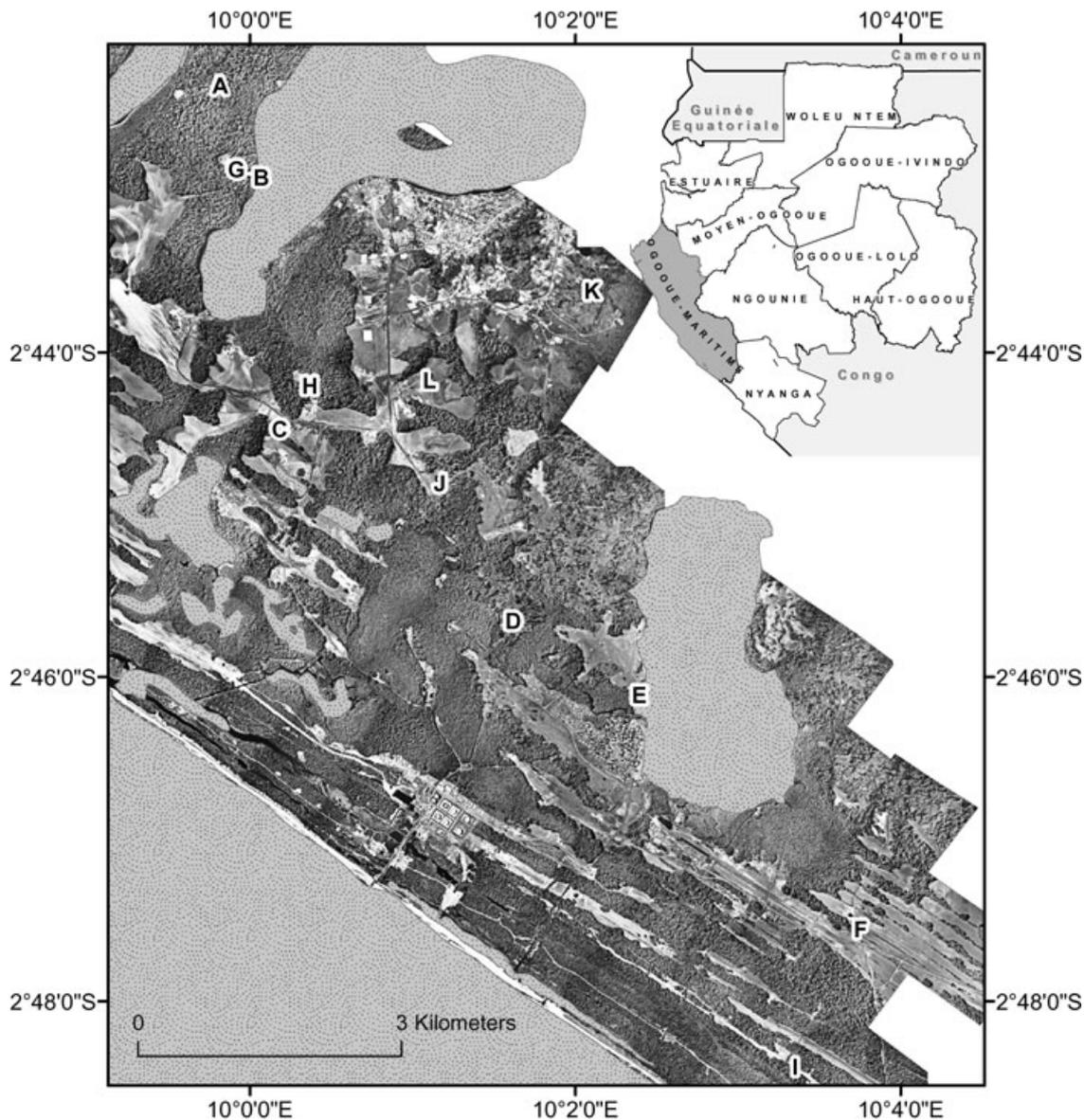


Figure 1. Aerial photograph of the location of study sites within the Gamba oil field. Sites coded as in Table 2. The town of Gamba is located between sites B and K. Water bodies indicated as stippled areas.

individuals; i.e., on average at least 1 individual collected per site; 227 morphospecies) and tested whether morphospecies were indicative of particular sites (site-specific species) or of particular habitats (habitat-specific species), particularly for old and young forests (133 morphospecies). The significance of the statistic was tested for each taxon by Monte Carlo randomization with 1000 permutations, performed with PC-ORD (McCune & Medford 1999).

To quantify overall species turnover, we used detrended correspondence analysis (DCA) with Hill's scaling on untransformed data. The differences between the scores of any 2 sites on the first axis of the DCA represent a measure of species turnover between these 2 sites (ter

Braak & Smilauer 1998). We again restricted our data set to the most abundant morphospecies ($n = 227$) and computed DCA with CANOCO (ter Braak & Smilauer 1998). To compare the species turnover of 2 taxa, we used a Procrustean randomization test (PROTEST) to compare the concordance between the raw data of 2 species-by-sites matrices (Peres-Neto & Jackson 2001; rationale detailed in Supporting Information). The significance of the m^2 statistic computed between all matrix pairs was assessed by Monte Carlo randomization with 1000 permutations in ade4 package of R Project software (Chessel et al. 2004).

Before calculating correlations among focal taxa, we checked for spatial autocorrelation and the independence of the data points (sites) with Mantel tests

Table 2. Focal taxa considered in this study of tropical arthropods and disturbance.

Focal taxa	Order ^a	Guild ^a	Individuals ^b	Indm ^c	Mor/Spp. ^d	Mantel ^e	P ^e	Code ^a
Mantodea	Ma	Pr	98	50	19	-0.204	0.881	Man
Acrididoidea ^f	Or	Lc	1129	360	40	-0.071	0.664	Acr
Fulgoroidea ^g	He	Ss	4022	2345	233	0.010	0.409	Ful
Membracidae	He	Ss	37	35	14	-0.071	0.669	Mem
Buprestidae	Co	Wo	115	91	16 ^b	-0.003	0.428	Bup
Scarabaeidae	Co	Lc, Sc	2240	1980	81	0.002	0.472	Sca
Coccinellidae	Co	Pr	1409	1200	32	0.075	0.275	Coc
Histeridae	Co	Pr	682	589	20	-0.081	0.769	His
Cleridae	Co	Pr	45	18	12	0.325	0.055	Cle
Tenebrionidae	Co	Sc	839	605	54	0.199	0.052	Ten
Cerambycidae	Co	Wo	278	79	51 ^b	0.121	0.213	Cer
Chrysomelidae	Co	Lc	2285	1761	157 ^b	-0.049	0.634	Chr
Neuroptera ⁱ	Ne	Pr	235	133	25 ^b	0.328	0.036	Neu
Asilidae	Di	Pr	409	333	47	0.108	0.235	Asi
Dolichopodidae ^j	Di	Pr	7339	2113	38	-0.080	0.731	Dol
Tephritidae	Di	Lc ^k	535	426	34	0.150	0.175	Tep
Syrphidae	Di	Pr, Sc	459	369	25 ^b	0.126	0.388	Syr
Pipunculidae	Di	Pa	123	97	22 ^b	0.272	0.113	Pip
Ichneumonidae	Hy	Pa	2302	1880	420	0.204	0.046	Ich
Chalcidoidea ^l	Hy	Pa	4577	1302	175	0.031	0.385	Cha
Apoidea ^m	Hy	Lc ⁿ	1239	1049	51 ^b	-0.119	0.692	Apo

^aOrders: Co, Coleoptera; Di, Diptera; He, Hemiptera; Hy, Hymenoptera; Ma, Mantodea; Ne, Neuroptera; Or, Orthoptera. Guilds: Lc, leaf chewers; Pa, parasitoids; Pr, predators; Sc, Scavengers; Ss, sapsuckers; Wo, wood eaters (Moran & Southwood 1982). Code, abbreviations used in tables.

^bNumber of individuals collected.

^cNumber of individuals morphotyped by parataxonomists (some damaged or lost material could not be morphotyped; some material collected by flight-interception traps was not considered).

^dTotal number of morphospecies sorted by parataxonomists from Indm.

^eMantel statistic (τ) testing for spatial autocorrelation and associated probability, p.

^fIncluding Acrididae, Pyrgomorphidae, and many juveniles, not morphotyped.

^gIncluding Achilidae, Cixiidae, Delphacidae, Derbidae, Dictyopharidae, Eurybrachidae, Flatidae, Fulgoridae, Issidae, Meenoplidae, Ricaniidae, Tettigometridae, and Tropiduchidae.

^hNumber of species sorted by taxonomists from a subsample of Indm.

ⁱIncluding Berothidae, Coniopterygidae, Chrysopidae, Dilaridae, Hemerobiidae, Mantispidae, Myrmeleontidae, and Osmylidae.

^jOnly morphotyped from July–December 2001, then kept unassigned in alcohol.

^kSubguild: fruit feeders.

^lOnly > 2 mm and including Agaonidae, Chalcididae, Elasmidae, Encyrtidae, Eucharitidae, Eulophidae, Eupelmidae, Eurytomidae, Leucospidae, Perilampidae, Pteromalidae, Tetracampidae, and Torymidae.

^mIncluding Apidae, Halictidae, and Megachilidae.

ⁿSubguild: pollinators.

appropriate for this purpose. We tested the independence between the distance matrix of study sites (cartesian coordinates; euclidean distance) and the dissimilarity matrix of each focal taxa (sites \times species; abundance data; distance equivalent of the Morisita-Horn index) with the vegan package of R Project software (Oksanen et al. 2006).

For ease of comparison with previous studies, we computed correlations for insect abundance and species richness variables between each focal taxa with Pearson coefficients. We are aware of the potential problem of double zeros in these calculations. This concerned a minority of comparisons for most insect variables but not for the percentage of site-specific species. To reduce the occurrence of double zeros, we calculated correlations only for focal taxa with site-specific species present at least at half of the study sites (9 taxa). For correlation

analyses, we used the false discovery rate method to correct for multiple tests (García 2004). For species turnover (PROTEST procedure), we did not adjust p values because Monte Carlo simulations provided strong control of type I error rates (Peres-Neto 1999).

Results

In total 400,404 arthropods were collected with all collecting methods during the 38 sampling events. Thirty-one orders and at least 218 families were represented (see Supporting Information). The 21 focal taxa represented 16,855 individuals and 1,534 morphospecies (Table 2). Furthermore, 347 species were recognized from the 7 focal taxa that to date have been examined by taxonomists (Table 2). Generally, there was good correspondence

between the number of species sorted by taxonomists and the number of morphospecies sorted by parataxonomists ($r = 0.96$, $p < 0.01$, $n = 7$), but these results will be discussed in detail elsewhere. Comparisons of mean insect variables among habitats are also presented elsewhere (Basset et al. 2008).

When the mean abundance of all arthropods collected among habitats was considered, abundance was significantly higher in forests and gardens than in savanna (Fig. 2a). Nevertheless, this pattern was different when we excluded ants from analyses (Fig. 2a): arthropod abundance was significantly higher in gardens than in savanna and intermediate in forests. Finally, when we considered only the abundance of our

focal taxa (Fig. 2a), abundance in gardens was significantly higher than in other habitats. The abundance of 14 focal taxa (67% of taxa tested) was significantly different among habitats. Many taxa were more abundant in unforested habitats (Supporting Information) and particularly in gardens. Nevertheless, a certain number of taxa not sorted to species were notably more abundant in forests than in gardens and particularly abundant in old forests (Supporting Information: Gryllidae, Endomychidae, Mycetophilidae, Phoridae, and Formicidae). In addition, Blattodea, Curculionidae, Staphylinidae, Cecidomyiidae, and Isoptera were either equally well represented in both old and young forests or better represented in the latter. Collectively, these

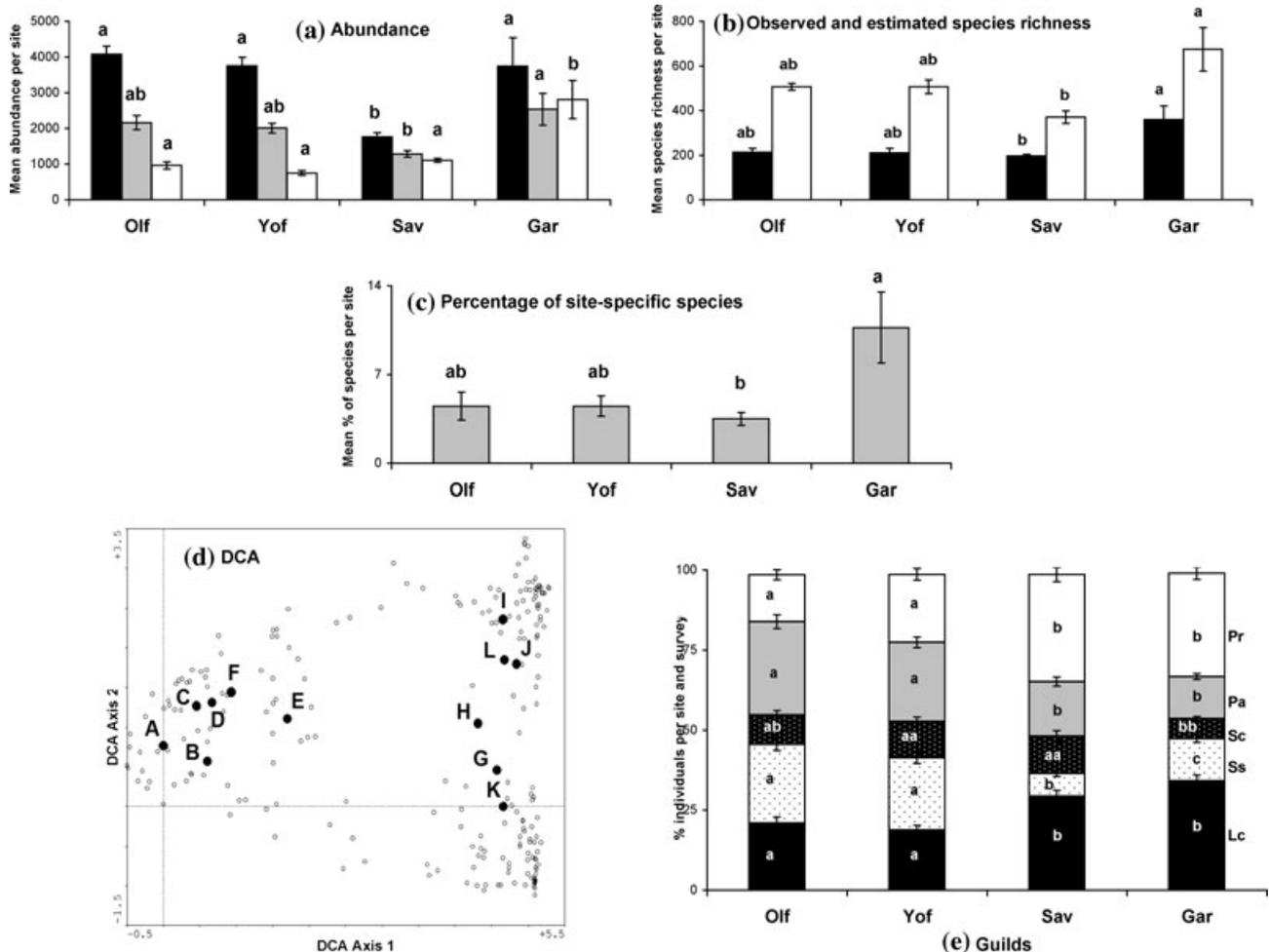


Figure 2. Mean (SE) per site of insect variables compared across habitats (Olf, old forests; Yof, young forests; Sav, savanna; Gar, gardens): (a) abundance of all arthropods (black bars), all arthropods without ants (gray bars), all focal taxa (white bars); (b) observed species richness (black bars) and estimated species richness (white bars); (c) percentage of site-specific species (gray bars); (d) species turnover: plot of 227 morphospecies (small, open circles) and sites (coded A-L, large closed circles) in the plane formed by axes 1 and 2 of the DCA; (e) detail of guild composition: percent individual leaf chewers (Lc, black bars), sapsuckers (Ss, light stippled bars), scavengers (Sc, dark stippled bars), parasitoids (Pa, gray bars), and predators (Pr, white bars) (wood eaters represent <2% of individuals and are not figured in here). In (a), (b), (c) and (e) for each variable, different letters denote different means (Tukey tests, $p < 0.05$). Figures 2b-e refer to all focal taxa.

observations explained most of the differences in abundance pattern between habitats (Fig. 2a).

When all focal taxa were considered, observed arthropod species richness was significantly higher in gardens than in savanna and intermediate in forests (Fig. 2b). This trend was similar for estimated species richness (Fig. 2b). Most of the species tested were significantly habitat or site-specific (92% and 82% of species tested, respectively). The percentage of site-specific species was significantly higher in gardens than in other habitats (Fig. 2c). When we restricted our comparison to old and young forests, 29% of species were significantly habitat specific, including 21 species for old forests and 17 for young forests. Considering all focal taxa, the mean scores of sites on axis 1 of the DCA were significantly different among habitats. The DCA revealed large faunal differences between forested and unforested habitats (Tukey tests, $p < 0.05$) and less of a difference between old and young forests and savanna and gardens (Tukey tests, $p > 0.05$; Fig. 2d). Of the 21 focal taxa, 14 differed significantly in their DCA scores among habitats. Most of these differences concerned again forested and unforested habitats (Tukey tests, $p < 0.05$). Old and young forests supported significantly higher percentages of sapsuckers and parasitoids than savanna and gardens (Fig. 2e). On the other hand, gardens and savanna supported higher percentages of leaf chewers and predators than forests. The percentage of scavengers was also significantly higher in savanna than in gardens (Fig. 2e).

Only 2 focal taxa were weakly spatially autocorrelated (Table 2). Therefore, we considered the data points for correlations as independent overall and did not adjust the degree of freedom in our calculations. Correlations of abundance among focal taxa were rather low (average [SE] $r = 0.176$ [0.029], $n = 210$). Of 210 possible combinations, only 50 correlations were significant with $p < 0.05$, including only 21 correlations significant after correction for multiple tests (Supporting Information). There was no obvious structure in the matrix of correlation, either when grouping correlations by functional guilds (Supporting Information) or by insect orders. In particular, there was no significant difference between the average values of correlation coefficients resulting from intraguild and interguild comparisons ($t = 1.298$, $p = 0.222$). Similarly, there was no significant difference between the average values of correlation coefficients resulting from intraorder and interorder comparisons ($t = -0.835$, $p = 0.405$). Although there was a trend for correlations between leaf chewers and parasitoids to be rather high, they were not significantly higher than other correlations (1-sample t test, $t = 1.637$, $p = 0.130$, $n = 12$). Similarly, correlations between Diptera and Hymenoptera appeared higher than other correlations, but not significantly so ($t = 1.623$, $p = 0.124$, $n = 15$). The 4 best indicator taxa were only each significantly correlated with 4 other taxa (Bupresti-

dae, Chrysomelidae, Syrphidae, and Apoidea, Supporting Information).

Correlations of observed species richness between focal taxa followed similar trends as for correlations of abundance (Table 3). They were also rather low (average [SE] $r = 0.193$ [0.029]; 48 correlations significant with $p < 0.05$, including only 18 correlations significant after correction for multiple tests). There was no significant difference between the average values of correlation coefficients resulting from either intraguild and interguild comparisons and intraorder and interorder comparisons ($t = -0.914$, $p = 0.362$ and $t = -0.356$, $p = 0.722$, respectively). Correlations either between leaf chewers and parasitoids or between Diptera and Hymenoptera were not significantly higher than other correlations ($t = 1.724$, $p = 0.113$ and $t = -0.939$, $p = 0.364$, respectively).

There was a sharp decrease in the number of significant correlations derived from estimated species richness (average [SE] $r = 0.054$ [0.024]; Supporting Information). Only a single correlation could be considered significant after correction for multiple tests. For taxa amenable to analysis, no correlation was significant after correction for multiple tests within the matrix on the basis of percentage of site-specific species (average $r = 0.202$ [0.052], $n = 36$; Supporting Information). Nevertheless, comparisons of species-by-sites matrices (species turnover) provided the highest share of significant comparisons (42 of 210 possible comparisons, 20%; Supporting Information). In particular, distribution patterns of Dolichopodidae were correlated with distribution patterns of 9 other taxa (at least 1 in each major guild), that of Pipunculidae and Syrphidae with 8 other taxa, and that of Apoidea with 7 taxa. Still, there was no obvious structure when considering significant statistics within the matrix (Supporting Information).

Discussion

We examined spatial congruence among arthropods, the most important component of terrestrial biodiversity. Our sample size was unusually large (in terms of trap days, number and variety of arthropod taxa considered, individuals collected, and number of species and morphospecies analyzed) and was obtained with adequate spatial and seasonal replicates. In addition, we used different methods to collect specimens. As far as we know, this represents one of the best tropical data sets of its kind, one that is adequate to evaluate arthropod responses to large-scale disturbance within an area of approximately 70 km² (Fig. 1). We further examined arthropod responses and possible correlations among these responses in our consideration of several variables (abundance, observed and estimated species richness, percentage of site-specific species, and species turnover), whereas other researchers focused

mainly on observed species richness (but see Barlow et al. 2007). The variety of assemblages we considered also allowed us to test whether taxa belonging to the same order or guild showed similar responses.

The problem that remains is the choice of focal taxa. The majority of conservation studies on arthropods examine only a small amount of local terrestrial biodiversity, usually 1 or 2 taxa that are not particularly speciose (Lewis & Basset 2007). Despite a massive collecting effort rarely equaled in the literature, we could only evaluate the influence of forest disturbance for 4% of the material collected. This raises serious questions about the choice of focal taxa and their representativeness. Had we considered taxa abundant in forests such as Formicidae and a few others (Supporting Information), our conclusions regarding relative arthropod abundance along the disturbance gradient would have been different. In fact, overall arthropod abundance was not lower in forests than in gardens (Fig. 2a).

We also strongly suspect that, overall, arthropod species richness is higher in forests than in gardens because (1) we targeted understory arthropods in forests, and most tropical forests harbor a significant and different canopy fauna, which may sometimes be as speciose as the understory fauna (Basset et al. 2003), (2) estimated species richness was lower in forests than in gardens but not significantly so, and it is notoriously difficult to survey all local rainforest species (Longino et al. 2002), (3) seasonal turnover was higher in forests than in gardens (Basset et al. 2008), and (4) regional species richness of garden assemblages is probably much lower than that of forest assemblages. We conclude that a massive project considering an even wider choice of focal taxa than ours would probably emphasize the sheer diversity of arthropod life histories and concomitant variety of responses to disturbance, decreasing further the proportion of significant correlations among arthropod taxa.

Overall arthropod responses to disturbance emphasized differences between forests and open habitats, with cleared forest subsequently invaded by savanna being the least populated and diverse habitat for arthropods. Few faunal differences were apparent between old and young forests, but this observation needs to be considered in the context of the wide disturbance gradient at Gamba. Despite this, 29% of species tested could be considered as habitat specific for either old or young forests, when comparing these 2 forest types. Hence, our data provide information on the biodiversity value of the wider, human-degraded landscape, indicating that many, but not all, taxa persist in these habitats. Thus, conservation strategies that promote secondary forests may maintain reasonably high species richness (Wright & Muller-Landau 2006), but a proportion of species across all taxa is likely to be lost with unknown long-term functional consequences (Brook et al. 2006).

Detailed analysis of a major herbivore group (Chrysomelidae) indicated that gardens were very distinct from other habitats and were invaded by a pest fauna mostly associated with crops (Basset et al. unpublished data). Sandy soils in gardens are fertilized by compost, which also increases water retention. Plant productivity is kept artificially high in gardens year-round through watering and crop rotation. Arthropods probably responded to these favorable conditions, notably leaf-chewing species and associated enemies. Hence, our results emphasize that anthropogenic modification of habitats, when considered at a local scale, does not necessarily result in a monotonous decline of diversity. This is in agreement with the results of many studies in which old-growth forests were compared with forest plantations in the tropics (Speight et al. 2003). Although garden assemblages had high local alpha diversity (Basset et al. 2008) and may be considered quite habitat specific at the meso- or local scale, they consisted mostly of pests and generalist species of lower conservation value, which are unlikely to show high spatial beta diversity and overall species richness at the regional scale.

Insect response variables could be ranked as follows in terms of decreasing number of significant correlations among focal taxa: species turnover > abundance > observed species richness > estimated species richness > percentage of site-specific species. As discussed elsewhere, conservation studies should as a matter of priority report species turnover along with observed species richness as a more accurate assessment of disturbance effects on faunal assemblages (Barlow et al. 2007; Tylianakis et al. 2007; Basset et al. 2008). Misleading conclusions are likely to be drawn if focusing solely on species richness (or a species diversity index) to assess human impacts, even when considering multiple taxa or guilds.

That said, our matrix of concordance accounting for species turnover included only 20% of significant concordances, a rather low figure if one is interested in identifying potential indicator taxa. Worse, there was no apparent structure in this matrix in terms of either taxonomy or functional guilds. In particular, concordance between taxa belonging to the same guilds was not noticeably higher than concordance between taxa belonging to different guilds. On the basis of species turnover, the best indicator taxon was Dolichopodidae. These flies are reasonably good fliers whose adults prey on a wide array of arthropods and respond quickly to habitat modification (Couturier & Duviard 1976). Nevertheless, their abundance and species richness was poorly correlated with that of other taxa. Furthermore, a reasonably good indicator for a particular disturbance gradient may not necessarily be good for narrower or wider gradients. For example, of the 38 arthropod species that were habitat specific for either old or young forests, only one was a dolichopodid. Because strong concordances between

taxa and related clear biological arguments to explain them are lacking, we believe correlation matrices mostly reflect idiosyncrasies related to the variety of arthropods examined (Lawton et al. 1998; Barlow et al. 2007).

The concept of indicator species represents one of the perennial issues in conservation-oriented literature. Similar to other arthropod-oriented studies (Didham et al. 1996; Lawton et al. 1998), our results emphasize the futility of using one taxon as an indicator for studies of anthropogenic disturbance, despite the ubiquity of single-taxon studies in the literature. Different taxa have different ecological requirements, and their responses to anthropogenic disturbance may therefore be different (Lawton et al. 1998), even at the congeneric level (Basset et al. 2001). This severely limits any generalization of studies derived from a selected group of taxa, both for biodiversity assessments and analyses of anthropogenic disturbance. One depressing option may be to admit that present resources will never be able to cope with the magnitude of effort needed to properly survey tropical habitats (Lawton et al. 1998) and, consequently, we will never be able to grasp the full extent and consequences of anthropogenic changes that are being induced on this planet.

A more stimulating alternative may be to standardize the choice of focal taxa, because only patterns for matching taxa can be meaningfully compared across disturbance gradients, and then use "predictor sets," which are composed of a small number of taxa representative of different functional groups (Kitching 1993; Didham et al. 1996; Basset et al. 2004b). Such predictor sets are properly selected only following statistical analysis of a larger, relatively complete, data set including all taxa and the catches from several complementary sampling methods. We suggest baseline surveys be run in different habitats, taxa selection be refined by analyzing species turnover between these habitats, and performing such surveys at a few tropical sites to determine how general patterns may be. For example, selection of Dolichopodidae, Pipunculidae, Apoidea, Fulgoroidea, and Buprestidae, which recruit from 5 major guilds and account together for 71% of significant concordances in species turnover, may represent a pertinent strategy to monitor the effects of anthropogenic disturbance on arthropods within the Gamba area. In the context of long-term management of tropical forests, similar information could be used by conservationists to assess to what extent arthropod communities of secondary forests approach those of undisturbed forests as time progresses.

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Supporting Information

Six tables are available as part of the on-line article (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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