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# Choice of metrics for studying arthropod responses to habitat disturbance: one example from Gabon

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**Abstract.** 1. The choice of metrics comparing pristine and disturbed habitats may not be straightforward. We examined the results of a study in Gabon including 21 arthropod focal taxa representing 16 855 individuals separated into 1534 morphospecies. Replication included the understorey of 12 sites representing four stages of land use after logging (old and young forests, savanna and gardens), surveyed for 1 year using three sampling methods.

2. For all focal taxa, we calculated a suite of 13 metrics accounting for the intensity of faunal changes between habitats, namely: abundance; observed, rarefied and estimated species richness; proportion of rare species; additive diversity partitioning; evenness of assemblages; higher taxonomic composition; species turnover; ordination scores of multivariate analyses; nestedness; proportion of site-specific species and ratios of functional guilds.

3. Most metrics showed large differences between forests and non-forest habitats, but were not equally discriminating for particular taxa. Despite higher taxonomic groups being present in most habitats, many insect species were site or habitat specific. There was little evidence that the disturbance gradient represented a series of impoverished habitats derived from older forests. Rather, entire suites of species were being replaced as habitats were modified.

4. Metrics based on species identity had a high sensitivity to disturbance, whereas measurements describing community structure were less discriminating in this regard. We recommend using metrics based on abundance, estimated species richness, species turnover estimated by multivariate analyses and guild structure, to avoid misleading interpretations that may result from comparisons of species richness alone.

**Key words.** Additive diversity partitioning, biodiversity, nestedness, parataxonomist, species loss.

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**Table 1.** Metrics/concepts examined in this contribution to assess the impact of disturbance on tropical arthropod assemblages. As far as possible, examples include empirical references relevant to tropical arthropod assemblages.

| Metric/concept (algorithm) | Advantage(s) | Example(s) |
|---|---|---|
| A. Metrics describing community structure (with no reference to species identity) | | |
| A1. Overall abundance | Straightforward; time-saving; easy to report to the public | Shahabuddin *et al*., 2005 |
| A2. Observed species richness | Straightforward; easy to report to the public | Shahabuddin *et al*., 2005 |
| A3. Rarefied species richness (Coleman's rarefaction) | Accounts for unequal sample size | Klein *et al*., 2002 |
| A4. Estimated (projected) species richness (Chao1 estimates) | Projections for larger sampling effort | Shahabuddin *et al*., 2005<br>Tylianakis *et al.*, 2005 |
| A5. Percentage of 'rare' species (percentage of singletons) | Focus on (putative) threatened species | Novotny & Basset, 2000<br>Hilt & Fiedler, 2005 |
| A6. Additive diversity partitioning (Shannon index, see text) | Examines the relative contribution of diversity at different spatial and temporal scales | Summerville *et al*., 2003<br>Tylianakis *et al*., 2005 |
| A7. Evenness of assemblages (Bulla's index) | Accounts for subtle assemblage modifications before eventual species loss | Basset *et al*., 2001 |
| B. Metrics based on taxonomic identity (with species either named or not) | | |
| B1. Higher taxonomic composition (absence/presence of insect families) | Information based on low resolution of sorting | Basset *et al.*, 2004b |
| B2. Species turnover and replacement (ANOSIM) | Makes best use of species identification data | Basset *et al*., 2004b |
| B3. Multivariate analyses (detrended correspondence analysis with Hill's scaling) | Focus on changes in abundance of multiple species; may be coupled with direct ordination techniques to identify explanatory factors | Basset *et al.*, 2001<br>Avendaño-Mendoza *et al.*, 2005 |
| B4. Nestedness of assemblages (nestedness temperature) | Test the occurrence of nested subset of species | Avendaño-Mendoza *et al.*, 2005 |
| B5. Percentage of habitat-specific species (indicator value index) | Focus on threatened species threatened by habitat destruction | Lewis & Basset, 2007 |
| B6. Guild composition (percentage data, predator–prey ratio) | Focus on functional aspects and their losses | Didham *et al*., 1996<br>Klein *et al*., 2002 |

## Introduction

The demise of tropical rainforests and the pace at which biodiversity, especially arthropods, is inventoried within these forests mean that many organisms may go extinct before they are known to science (Lawton & May, 1995). The general public and decision makers may be unimpressed by putative mass-scale extinction, unless species losses are demonstrated by biologists. Practical conservation decisions are more likely to consider arguments based on species identity and precise autoecological information, such as endemism, habitat and resources requirements, geographical distribution, etc. Unfortunately, this is likely to be impractical for the majority of poorly known tropical rainforest arthropods (Lewis & Basset, 2007). This imposes pressure on conservationists to provide figures easily understood by the public. Such simple statistics to monitor faunal changes often include estimates of species richness and species loss.

However, the choice of metrics in such assessments is not straightforward. Species richness or species diversity may seem sensible metrics to measure, but in practice these measures often increase with disturbance, concurrent with a *decrease* in conservation *value*. For example, in many butterfly assemblages, forest disturbance allows a suite of mobile, widespread and generalist taxa to colonise and co-exist with much of the existing fauna (Lewis *et al.*, 1998), enhancing overall diversity. These newcomers are typically species of low conservation concern, and it does not make sense to give them equal weighting to restricted range habitat specialists in conservation assessments (Lewis & Basset, 2007). Alternative metrics may include a range of measurements or it may be possible to weight the conservation value of a species to reflect its geographical range or rarity.

Here, we explore alternative metrics and contrast inferences based solely on species richness and abundance data against those based on other metrics, for a large data set of wide taxonomic scope. We restricted our attention to metrics or concepts where disturbance effects have been previously shown for tropical arthropod assemblages. These 13 metrics (Table 1) may be classified into two main categories: (i) metrics describing community structure, with no explicit reference to species identity across samples (metrics A1–A7); and (ii) metrics based on (higher) taxonomic identity, with species either named or not (B1–B6). This compilation is not exhaustive but represents recent analytical trends in the study of tropical arthropod diversity in relation to disturbance (review in Lewis & Basset, 2007).

Observed abundance and species richness represent standard variables (metrics A1–A2). The use of rarefied and estimated species richness (A3–A4) is also customary in conservation biology. Ideally, considering changes altering the population dynamics of endemic species would represent a sound strategy (Lewis *et al.*, 1998). However, assigning the majority of tropical species to categories of endemicity is a near-impossible task because of lack of biological information and low sampling effort for most species. Alternatives may include considering 'rare' species (A5) or measuring the ratio of 'wider countryside' to forest specialist (Lewis & Basset, 2007), or, more generally, focusing on habitat-specific species (B5). Instead of focusing on species diversity within assemblages, we considered the wider concept of 'additive diversity partitioning' (A6; Crist *et al*., 2003),

which allowed us to examine the relative contribution of species diversity at different spatial and temporal scales. This metric may further help to evaluate the scale-dependence of impacts of anthropogenic disturbance (Tylianakis *et al.*, 2005). Although we considered species' abundance distribution with evenness (A7), discussing fit to particular distribution models was beyond the scope of this work.

Metrics B1–B3 are often routinely used in conservation biology. Rainforest fragmentation may promote co-existence of nested subsets of species within fragments (B4; Patterson & Atmar, 2000). Loss or simplification of functional traits has sometimes been studied with particular reference to predator–prey ratios (B6; Klein *et al*., 2002). This emphasises the wider challenge of considering multi-taxic assemblages, including functional guilds, to properly evaluate arthropod response to disturbance, as opposed to monitoring a few 'indicator species' (Didham *et al*., 1996; Lawton *et al*., 1998). Perhaps 80% to 90% of tropical taxa have never been the focus of tropical conservation studies, and it is an open question what might be the consequences of this taxonomic selectivity (Lewis & Basset, 2007). Few studies involve sufficient replication for a wide range of taxa, because of the huge scale of biological effort involved (Lawton *et al.*, 1998). In practice, training parataxonomists (i.e. local assistants trained by professional biologists; Janzen, 1992) can help to alleviate these problems (Basset *et al*., 2004a).

Here, we examine the results of a study based on the work of trained parataxonomists in Gabon. Replication included 12 sites representing four stages of forest succession and land use (='habitats') after logging, surveyed during a whole year with three complementary sampling methods. We evaluate the impacts of disturbance on a range of arthropod assemblages representing different feeding guilds and contrast our conclusions when based either only on abundance and species richness, or on a range of alternative metrics as detailed above. We restrict our results and discussion to comparison among metrics. Concepts such as parataxonomist performance, faunal changes along the disturbance gradient, spatial congruence of taxa and seasonality for this data set will be discussed elsewhere. Our specific questions are:

1 What is the percentage loss of species along the disturbance gradient, when reported with comparable metrics?
2 Do metrics vary significantly among habitats?
3 Are species gradually replaced along the disturbance gradient or do whole assemblages disappear and appear?
4 Finally, can we recommend the use of a particular metric or group of metrics which may be useful with regard to the conservation of species-rich but poorly-known rainforest arthropods?

## Material and 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 southeast 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 amounts to 2093 mm per year, with the major dry season from June to August (Alonso *et al*., 2006). The earliest cultivated crop gardens of notable size were established near the Gamba town as recently as 1998.

We considered four distinct habitats of increasing anthropogenic disturbance (i.e. increasing forest clearing and introduction of exotic vegetation) and selected three sites (replicates) within each habitat. The four habitat types were: (i) the understorey of the interior of old secondary rainforests, *old forests*; (ii) the understorey of the edge of young secondary rainforests, *young forests*; (iii) an area of rainforest cleared to install oil rigs and subsequently invaded by savanna, *savanna*; and (iv) cultivated crop gardens, *gardens*. At the time of the study, there were no substantial plantations in the area and these four habitat types were predominant in the Gamba oil field. Salient characteristics of the study sites (coded A to L) are indicated in Table 2 and Fig. S1, Supplementary material (see further details in Basset *et al*., 2004b).

### *Arthropod collecting and processing*

Each site was equipped with an identical set of traps recommended for biological monitoring of the flying and epigaeic arthropods of the understorey and litter: one ground Malaise trap, four ground yellow pan traps and five pitfall traps buried in the ground. Details about the traps, their placement and mode of action are given by 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. A team of eight parataxonomists were trained and supervised by a professional entomologist throughout the project (see Basset *et al*., 2004a for a detailed discussion of this strategy).

The material collected was first sorted into families or higher taxa by the parataxonomists. The material belonging to 21 focal taxa (Table 3) was mounted and sorted to morphospecies (i.e. unnamed species diagnosed using standard taxonomic techniques) by the parataxonomists. Formal taxonomic study of this material is ongoing but sub-samples of the material belonging to seven taxa have been examined by taxonomists (Table 3). The 21 focal taxa were selected as (i) being well represented in the samples; (ii) being workable taxonomically; and (iii) representing of a variety of functional guilds and orders (Table 3). Focal taxa were assigned to the following feeding guilds (Moran & Southwood, 1982): chewers, sap-suckers, scavengers, wood-eaters, parasitoids and insect predators. The first four categories were considered as *prey*, the others as *predator* in calculating predator–prey ratios. Specimens were stored at the Smithsonian Biodiversity Conservation Center in Gamba, and vouchers have been deposited at the National Museum of Natural History (Washington) and with taxonomists that helped in species identification.

### *Statistical methods*

We calculated metrics of Table 1 for each of the 21 focal taxa, and also for all focal taxa together. The later approach, combining

**Table 2.** Main characteristics of study sites within the Shell-Gabon Gamba oil field. For gardens, the main crops cultivated during the study period are listed.

| Code | Habitat | Coordinates | Fragment size (ha) | Physiognomy | Vegetation characteristics |
|---|---|---|---|---|---|
| A | Old forest | 02°42′20″S 09°59′49″E | 700 | Secondary forest, tallest trees = 45 m, sandy soil | *Neochevalierodendron stephanii* (A. Chevalier) Léonard dominant, *Diospyros zenkeri* (Gurke) F. White and *D. vermoeseni* De Wild common |
| B | Old forest | 02°42′54″S 10°00′00″E | 84 | Secondary forest, tallest trees = 45 m, sandy soil | *Neochevalierodendron stephanii* dominant, *Diospyros zenkeri*, *D. vermoeseni* and *Palisota ambigua* CB. Clarke 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 | *Diospyros vermoeseni* and *D. conocarpa* Gurke ex K. Schum common, *P. ambigua and Trichoscypha acuminata Engler* 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 | *Palisota ambigua*, *Aframomum* sp. and *Rauvolfia* sp. common; one pioneer *Musanga cecropioides* R. Br. ex Tedlie present |
| E | Young forest | 02°46′08″S 10°02′25″E | 19 | Secondary forest, very open canopy, tallest trees = 30 m, swampy soil | *Xylopia hypolampra* Mildb. and *Xylopia* 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 re-growth in the understorey, sandy soil | *Pachypodanthium staudtii* Engl. and Diels, *Diospyros vermoeseni*, *Palisota ambigua*, *Leptactina mannii* Hook.f., *Ouratea sulcata* (Van Tiegh.) Keay, *Sacoglottis gabonensis* (Baillon) Urb. and *Bertiera subsessilis* Hiern 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% | *Borreria verticillata* (L.) GFW Mey and two unidentified Poaceae dominant, *Cyperus tenax* Boeck and *Dracaena* sp. present |
| H | Savanna | 02°44′11″S 10°00′22″E | 3.0 | Surrounded by forest, sandy soil, bare soil = 25% | *Borreria verticillata*, *Dracaena* sp. and one unidentified Poaceae dominant, *Cyperus halpan* J. Kern and *Heterotis decumbens* (Pal.Beauv.) H. Jacques-Félix present |
| I | Savanna | 02°48′23″S 10°03′21″E | 2.5 | Surrounded by forest, sandy soil, bare soil = 25% | *Merremia tridentata* Hallier f., *Cyperus tenax* and one unidentified Poaceae dominant |
| J | Garden | 02°44′47″S 10°01′10″E | 2 | Sandy soil fertilised with compost | Amaranth, aubergine, cabbage, carrot, lettuce, pepper, spinach, sweet pepper, tomato and water melon |
| K | Garden | 02°43′36″S 10°02′06″E | 0.5 | Clayish sand fertilised with compost | Aubergine, banana, maize, manioc, pepper, pineapple, spinach, sugar cane and taro |
| L | Garden | 02°44′09″S 10°01′06″E | 0.8 | Sandy soil fertilised with compost | Amaranth, aubergine, cabbage, cucumber, gombo, pepper, sorrel, spinach and tomato |

all data available, (i) represents the closest analysis to estimating responses of whole arthropod assemblages to disturbance in the study system (although it still relates to a small proportion of the material collected, see Results); and (ii) provides a convenient way to summarise and visualise most of results. For metrics B2–B5, when considering all focal taxa, we restricted the data set to the most abundant morphospecies (≥ 12 individuals; $n = 227$), but calculated metrics for individual focal taxa without restriction of abundance. For most analyses, we pooled data from the three sampling methods at a site (data from ten traps) for the 38 surveys and considered this to be a sample ($n = 12$). Next, we tested whether sample measurements varied significantly across habitat types with one-way ANOVA (degrees of freedom = 3 and 8 for factor and error terms, respectively) and Tukey tests, after log(x + 1) transforming data to satisfy assumptions of normality (Kolmogorov–Smirnov–Lilliefors tests, $P > 0.05$). We used the false discovery rate method to correct for multiple tests ($N = 21$). This procedure calculates the expected proportion of false-positives among all significant hypotheses with $P < 0.05$ (García, 2004).

Several options may exist for the computation of metrics considered here. Whenever possible, we used methods routinely used in the ecological literature, for ease of comparison with previous studies. We considered three cases for species rarefaction: (a) taxa abundantly distributed in all habitats and sites, for which we considered a minimum sample size of 30 individuals and calculated a rarefied number of species for both sites and habitats (six taxa); (b) taxa less evenly distributed across habitats, for which it was only meaningful to compute rarefied species for a taxa-specific minimum number of $n$ individuals across habitats (10 taxa); and (c) taxa too unevenly distributed across habitats so that a minimum sample size was too small to compute an informative rarefaction (minimum sample size < 5 individuals; 5 taxa). For ease of comparison of results for categories (b) and (c), we

**Table 3.** Focal taxa considered in this study. Ind, no. individuals collected; indm, no. individuals morphotyped by parataxonomists (§); mor, total no. of morphospecies sorted by parataxonomists from indm; spp., no. of species sorted by taxonomists from a sub-sample of indm (full data presented and discussed elsewhere); authority, taxonomist in charge of the material, abbreviated for co-authors of this article; code, abbreviations used in figures.

| Focal taxa | Order† | Guild‡ | Ind | Indm | Mor | Spp. | Authority | Code |
|---|---|---|---|---|---|---|---|---|
| Mantodea | Ma | Pr | 98 | 50 | 19 | – | – | Man |
| Acrididoidea¶ | Or | Lc | 1129 | 360 | 40 | – | – | Acr |
| Fulgoroidea†† | He | Ss | 4022 | 2345 | 233 | – | – | Ful |
| Membracidae | He | Ss | 37 | 35 | 14 | – | – | Mem |
| Buprestidae | Co | Wo | 115 | 91 | 14 | 13 | GC | Bup |
| Scarabaeidae | Co | Lc, Sc | 2240 | 1980 | 81 | – | – | Sca |
| Coccinellidae | Co | Pr | 1409 | 1200 | 32 | – | – | Coc |
| Histeridae | Co | Pr | 682 | 589 | 20 | – | – | His |
| Cleridae | Co | Pr | 45 | 18 | 12 | – | – | Cle |
| Tenebrionidae | Co | Sc | 839 | 605 | 54 | – | – | Ten |
| Cerambycidae | Co | Wo | 278 | 79 | 34 | 30 | S. Lingafelter | Cer |
| Chrysomelidae | Co | Lc | 2285 | 1761 | 157 | 146 | TW | Chr |
| Neuroptera‡‡ | Ne | Pr | 235 | 133 | 21 | 21 | MWM | Neu |
| Asilidae | Di | Pr | 409 | 333 | 47 | – | – | Asi |
| Dolichopodidae§§ | Di | Pr | 7339 | 2113 | 38 | – | – | Dol |
| Tephritidae | Di | Lc¶¶ | 535 | 426 | 34 | – | – | Tep |
| Syrphidae | Di | Pr, Sc | 459 | 369 | 32 | 25 | C. Thompson | Syr |
| Pipunculidae | Di | Pa | 123 | 97 | 16 | 22 | MDM; M. Foldvari | Pip |
| Ichneumonidae | Hy | Pa | 2302 | 1880 | 420 | – | – | Ich |
| Chalcidoidea††† | Hy | Pa | 4577 | 1302 | 175 | – | – | Cha |
| Apoidea‡‡‡ | Hy | Lc§§§ | 1239 | 1049 | 93 | 51 | CE | Apo |

†Orders: 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, sap-suckers; Wo, wood-eaters (system of Moran & Southwood 1982).
§Some damaged or lost material could not be morphotyped; some material collected by flight-interception traps was not considered in this study.
¶Including Acrididae (Acr), Pyrgomorphidae (Pyr), and many juveniles, not morphotyped.
††Including Achilidae (Ach), Cixiidae (Cix), Delphacidae (Del), Derbidae (Der), Dictyopharidae (Dic), Eurybrachidae (Eub), Flatidae (Fla), Fulgoridae (Ful), Issidae (Iss), Meenoplidae (Mee), Ricaniidae (Ric), Tettigometridae (Tem) and Tropiduchidae (Tro).
‡‡Including Berothidae (Ber), Coniopterygidae (Con), Chrysopidae (Chy), Dilaridae (Dil), Hemerobiidae (Hem), Mantispidae (Mat), Myrmeleontidae (Mym) and Osmylidae (Osm).
§§Only morphotyped from July–December 2001, then kept unassigned in alcohol.
¶¶Subguild: fruit-feeders.
†††Only > 2 mm and including Agaonidae (Aga), Chalcididae (Cha), Elasmidae (Ela), Encyrtidae (Enc), Eucharitidae (Euc), Eulophidae (Eul), Eupelmidae (Eup), Eurytomidae (Eur), Leucospidae (Leu), Perilampidae (Per), Pteromalidae (Pte), Tetracampidae (Tet) and Torymidae (Tor).
‡‡‡Including Apidae (Api), Halictidae (Hal) and Megachilidae (Meg).
§§§Subguild: pollinators.

graphically reported the percentage of rarefied species number in each habitat. We calculated individual-based rarefaction curves (Coleman curves) and Chao1 richness estimates (performing well when many species are rare) with 50 randomizations using ESTIMATES software (Colwell, 2005). We defined rare species as those represented by only a single specimen in the sample (singletons). We considered both local singletons (species collected as a single individual at particular study sites) and unique singletons (species found as a single individual in the combined data set).

We evaluated the additive version of species diversity with the Shannon index, since it is widely used, less sensitive to common species (as the Simpson index is) and because it is distinct from species richness (Crist *et al*., 2003). Following Tylianakis *et al*. (2005), our sampling scheme allowed to partition total ($\gamma$) diversity within habitats as:

$$\gamma = \alpha + \beta T + \beta S$$

where $\alpha$-diversity is the average diversity within samples (the mean Shannon index per site and per survey in our case) and $\beta$-diversity is the average diversity among samples, estimated as $\beta = \gamma - \alpha$. $\beta$-diversity is further partitioned into temporal ($\beta T$) and spatial ($\beta S$) turnover. Specifically, $\beta T$ was calculated as the Shannon index for a site over all 38 surveys minus the mean Shannon index per survey for this site ($\alpha$). $\beta S$ was calculated as the Shannon index within a habitat over all 38 surveys minus the mean Shannon index per site of that habitat type (over all 38 surveys). $\alpha$ and $\beta T$ were replicated within sites and were analyzed as a proportion of $\gamma$ in one-way ANOVAS with habitat type as factor. We calculated the evenness of insect assemblages at each site with the index of evenness E, proposed by Bulla (1994) for abundance data. Evenness equalled 1 for totally even assemblages and was assigned to 0 whenever assemblages were empty at a particular site.

Higher taxonomic composition was simply defined as presence or absence of insect families including focal taxa. Species

 

turnover among habitats was estimated with a non-parametric analysis of similarity (ANOSIM) on untransformed data to test for differences in the rank similarities of sites grouped by habitats (Clarke, 1993). ANOSIM s were calculated with Bray–Curtis distances for each focal taxa and their significance was tested with 10 000 random permutations using the program PAST (Hammer *et al*., 2001). We chose a straightforward approach by quantifying beta-diversity using detrended correspondence analysis (DCA) with Hill's scaling, using untransformed data (ter Braak and Smilauer, 1998). The differences between the scores of any two sites on the first axis of the DCA represent a measure of species turnover between these two sites. We tested for differences among habitats by performing ANOVAS on the scores of Axis 1 of the DCA calculated for each focal taxon by the program CANOCO (ter Braak and Smilauer, 1998). We calculated the nestedness temperature to compare the degree of nestedness of our target assemblages within our sampling universe (Patterson & Atmar, 2000). We used BINMATNEST software (Rodrígues-Gironés & Santamaría, 2006) to compare the degree of nestedness in insect assemblages, based on presence–absence data. We ran BINMATNEST with recommended default parameters to generate 1000 random assemblages.

To evaluate which species may be indicative of particular sites and habitats, we used the indicator value index (Dufrêne & Legendre, 1997). Using morphospecies occurrence in the 38 surveys at each site, we first tested whether morphospecies were indicative of particular site ('site-specific' species) and then tested whether the mean percentage of site-specific species was different among habitats by ANOVA. Similarly, we also tested whether morphospecies were indicative of particular habitat ('habitat-specific' species). The significance of the maximum indicator value was tested for each taxon by a randomization procedure implemented in PC-ORD (Monte Carlo permutation tests; 1000 permutations; McCune & Medford, 1999).

To analyze guild composition, we compared the percentage individuals per site and survey for each guild among habitats, for the combination of all focal taxa. Similarly, we considered the slope of predator–prey ratios across each habitat to perform a nested analysis of covariance (ANCOVA) with prey as dependent variable, predator as covariable and habitat as effect. In summary, to compare the different metrics calculated, we considered (i) the number of focal taxa with significant differences among habitats; (ii) ANOVAS testing in differences in mean metric per site between habitats across the 21 focal taxa; (iii) Spearman correlation coefficients among metrics, which could be calculated for 228 combinations of focal taxa x sites; (iv) effect sizes averaged across habitats and taxa, standardised relative to average values for old forests (i.e. effect size scaled to 1.0 for old forests); and (v) other factors related to computation, protocols and biological interpretation.

## Results

Overall, 400 404 arthropods were collected by all collecting methods during the 38 sampling events, representing 31 orders and at least 218 families. The 21 focal taxa used in this study represented 16 855 individuals and 1534 morphospecies (Table 3). Furthermore, 347 species were recognised from the seven focal taxa which to date have been examined by taxonomists (Table 3). Figure 1 summarises comparisons among habitats for most metrics when all focal taxa were considered together. Arthropod abundance was significantly different among habitats with mean abundance per site in gardens being significantly higher than in other habitats (Fig. 1a; $F_{3,8} = 11.81$, $P = 0.003$). The abundance of 14 focal taxa (67% of taxa tested) was significantly different among habitats (Fig. 2a). Overall observed arthropod species richness was also significantly higher in gardens than in savanna, with intermediate values for forests (Fig. 1b, $F_{3,8} = 5.33$, $P = 0.026$). This trend persisted for estimated species richness ($F_{3,8} = 5.41$, $P = 0.025$), but not for rarefied species richness (expressed as average per site and survey, Fig. 1b, $F_{3,8} = 1.52$, $P = 0.28$). However, rarefaction curves computed when pooling all focal taxa by habitats (i.e. average of three sites per survey, Fig. 3) indicated that species accumulation rates were steeper in forests than in non-forest habitats and highest in young forests. Eleven out of 21 focal taxa (52%) showed significant differences in observed species richness among habitats (Fig. 2b) but differences were less marked than for abundance.

Large differences in abundance among habitats made it difficult to apply rarefaction techniques (Table S1, Supplementary material). None of the six taxa tested showed significant differences in rarefied species richness among habitats. Comparing the percentage of rarefied species richness for taxa amenable to analyses ($n = 15$), we noted that the proportion of rarefied species was significantly higher in gardens than in savanna ($t$-test, $t = 2.63$, $P < 0.02$). There was a tendency for the proportion of rarefied species to be higher in forests vs. non-forest habitats, and in young vs. old forests, but differences were not significant ($t$-tests, $P > 0.05$). Estimated species richness varied significantly among habitats for seven taxa (Table S1). Overall, singletons represented a high proportion (41.9%) of all species sorted. For all focal taxa, percentage local singletons was significantly higher in forests than in savanna or gardens (Fig. 1c, $F_{3,8} = 16.93$, $P = 0.001$). Target assemblages included many local singletons, sometimes > 70% of species (Table S2, Supplementary material). However, there was no obvious correlation between the total number of individuals sorted and the percentage of local singletons ($r = 0.304$, $P = 0.180$, $n = 21$). After correcting for multiple tests, no taxa showed significant differences when comparing between habitats the mean percentage of local singletons per site (Table S2).

For all focal taxa considered together, within-sample diversity was significantly higher in gardens than in other habitats (Fig. 1d, $F_{3,8} = 9.45$, $P = 0.005$). However, within-sample diversity was not significantly different across habitats for any of the focal taxa individually (Table S3, Supplementary material). For all focal taxa, there was a trend for temporal turnover to be smaller in gardens, but this was not significant ($F_{3,8} = 2.25$, $P = 0.16$). This trend was significant when comparing the mean proportions across the 21 focal taxa, emphasizing the lower temporal turnover in gardens as compared to young forests ($F_{3,80} = 2.724$, $P = 0.049$). Across the 21 focal taxa, the mean proportion of diversity accounted for by spatial turnover was significantly different among habitats, emphasizing low and high spatial turnover in gardens and young forests, respectively ($F_{3,80} = 3.838$,

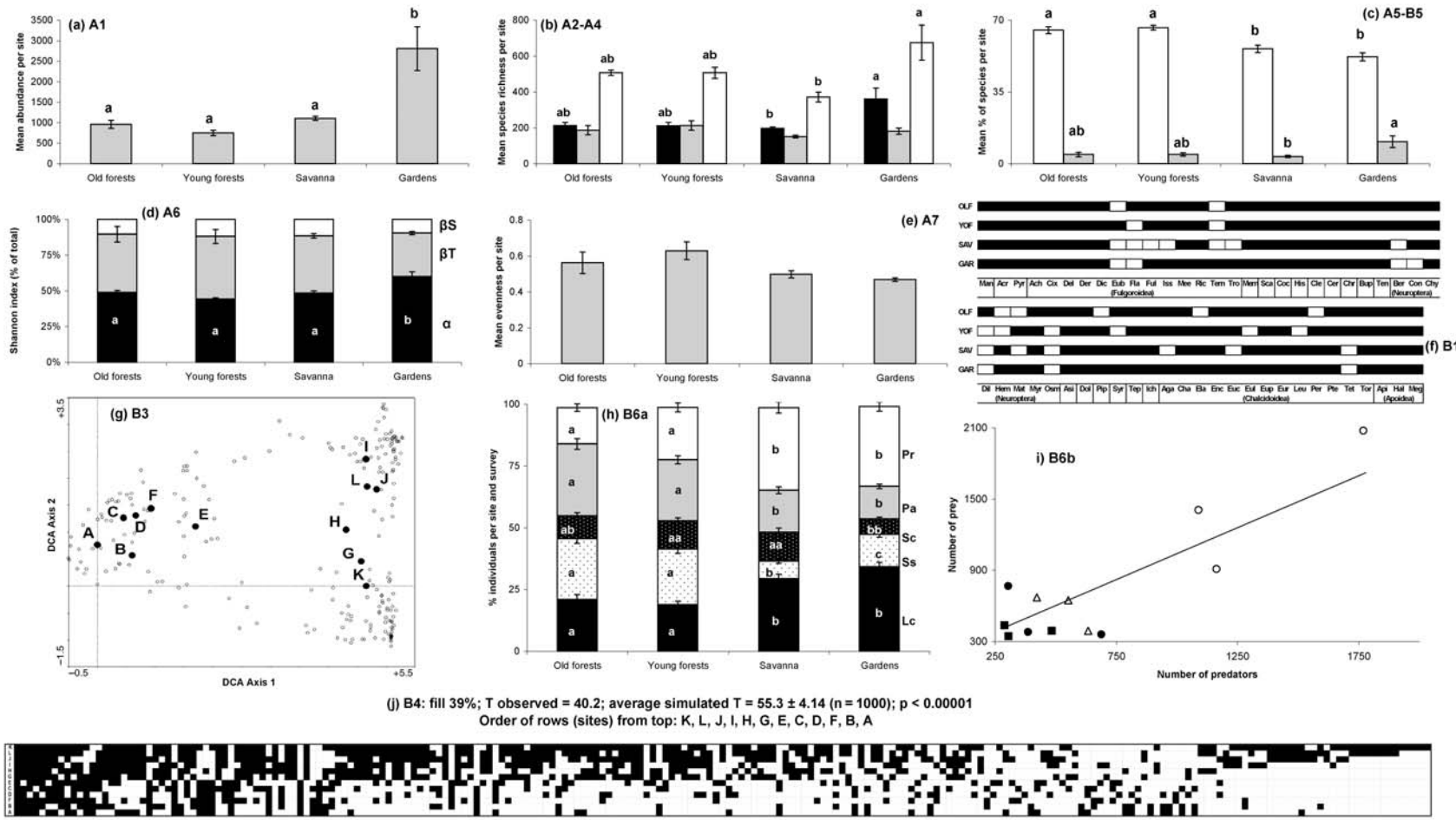


**Fig. 1.** Mean values (± s.e.) per site of most metrics compared across habitats, for all focal taxa combined: (a) abundance (metric A1); (b) observed species richness (black bars), rarefied species richness to a minimum sample size of 650 individuals (grey bars) and estimated species richness (white bars; metrics A2–4); (c) percentage of local singletons (white bars) and site-specific species (grey bars; metrics A5 and B5); (d) proportion of species diversity (metric A6) accounted by within-sample diversity (black bars), temporal turnover (grey bars) and spatial turnover (white bars); (e) evenness (metric A7); (f) higher taxonomic composition (metric B1): presence (closed bars) or absence (open bars) across habitats (OLF, old forests; YOF, young forests; SAV, savanna; GAR, gardens) of 55 families representing focal taxa, coded as in Table 3; (g) multivariate analysis (metric B3): 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; mean Axis 1 scores in Table S4; (h) detail of guild composition (metric B6): percentage individuals of leaf chewers (Lc, black bars), sap-suckers (Ss, light stippled bars), scavengers (Sc, dark stippled bars), parasitoids (Pa, grey bars) and predators (Pr, white bars; wood-eaters represent < 2% of individuals and are not figured here); (i) guild composition (also metric B6): scatter plots of predator vs. prey in old forests (closed circles), young forests (closed squares), savanna (open triangles) and gardens (open circles), with significant regression line over the pooled data; and (j) nestedness: maximally packed matrix of absence (empty cells) – presence (filled cells) of 227 morphospecies (columns) × 12 sites (rows), with details of *T* and result of simultation test (metric B4). Within each metric category, different letters denotes different means (Tukey tests, $P < 0.05$). For metric B2, see Table S4.

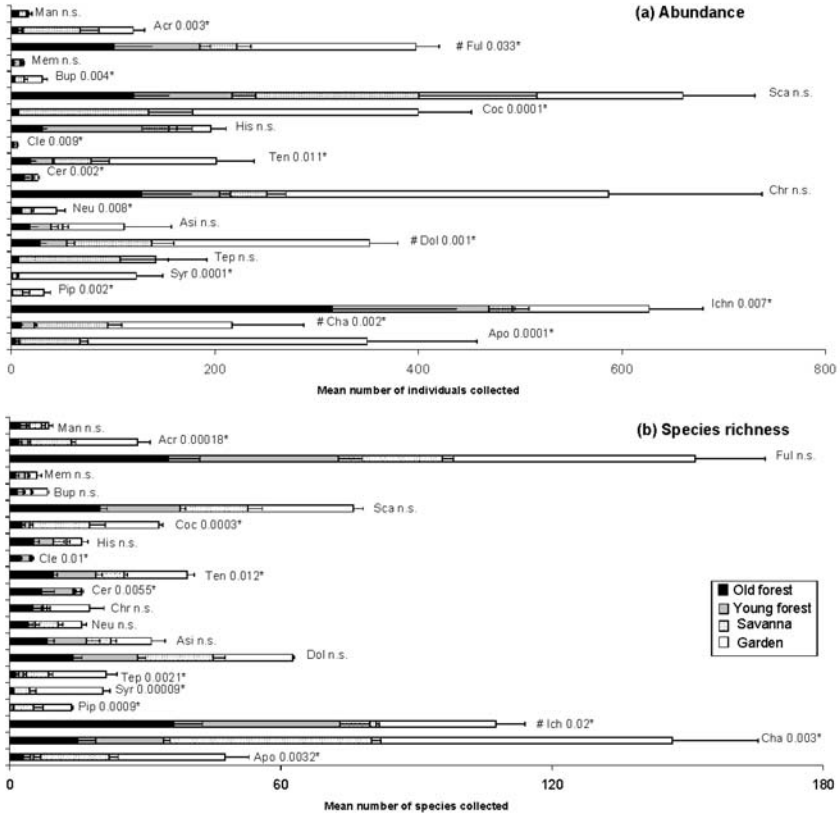


**Fig. 2.** Mean metric (+ 1s.e.) per site detailed per habitat (black, old forest; grey, young forest; stippled, savanna; white, garden): (a) abundance; (b) observed species richness. Figures indicate the *P*-value of an ANOVA with habitat as factor: n.s., not significant; *multiple test significant with the false detection rate method: (a) $P \leq 0.033$, (b) $P \leq 0.0198$, respectively. For sake of clarity: #, all figures × 1/2. Taxa coded as in Table 3.

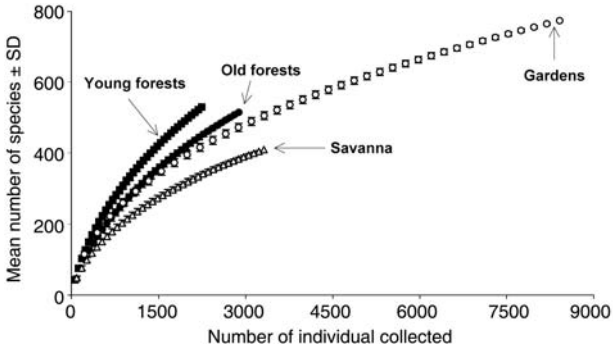


**Fig. 3.** Rarefaction curves ($n = 50$ randomizations) calculated by pooling all focal taxa collected in different habitats: old forests (closed circles), young forests (closed squares), savanna (open triangles) and gardens (open circles).

$P = 0.013$). For all focal taxa, evenness was not significantly different among habitats (Fig. 1e, $F_{3,8} = 3.55$, $P = 0.068$). The evenness of insect assemblages was often < 0.5 (Table S2).

Higher taxonomic composition varied little across habitats (Kruskal–Wallis test, $W = 3.348$, $P = 0.341$; Fig. 1f). Out of 55 families representing all focal taxa, 48, 47, 42 and 48 families occurred in old forests, young forests, savanna and gardens, respectively. Species turnover among habitats as measured by ANOSIM was significant for all focal taxa together and for 18 different taxa (Table S4, Supplementary material). High values of dissimilarity (high *R*-values) were noted for most of the species-rich groups. However, old and young forests could not be considered as statistically different ($R = 0.444$, $P = 0.10$). Considering all focal taxa, the mean scores of sites on Axis 1 of the DCA were significantly different among habitats (Fig. 1g, Table S4, $F_{3,8} = 142.7$, $P < 0.0001$). The DCA emphasised large faunal differences between forests and non-forest habitats (Tukey tests, $P < 0.05$), and less so between either old and young forests or savanna and gardens (Tukey tests, $P > 0.05$; Fig. 1g). Out of the 21 focal taxa, 14 showed significant differences when comparing their DCA scores among habitats (Table S4). Most of the differences observed related to comparisons of forest and non-forest habitats (Tukey tests, $P < 0.05$).

The absence–presence matrix including all focal taxa was significantly nested (Fig. 1j). The most *hospitable* sites, according to the terminology of Patterson and Atmar (2000), were gardens (topmost sites in the packed matrix, Fig. 1j). Leaving out garden sites resulted also in a significantly nested matrix for all focal taxa, with savanna being the most *hospitable* sites (observed $T = 45.6$, average simulated $T = 56.3 \pm 5.88$, $P < 0.00001$). Fourteen insect assemblages could be considered as being significantly nested, often with gardens being the most *hospitable* sites (Table S4). Most of the species tested could be considered habitat or site specific (92% and 82% of species tested, respectively). For all focal taxa, percentage of site-specific species was higher in gardens than in other habitats (Fig. 1c, $F_{3,8} = 4.40$, $P = 0.042$). Old and young forests supported significantly higher

 

percentages of sap-suckers and parasitoids than savanna and gardens did (Fig. 1h; $F_{3,8} = 30.1$, $P < 0.0001$ and $F_{3,8} = 20.3$, $P < 0.0001$, respectively). On the other hand, gardens and savanna supported higher percentages of leaf chewers and predators than forests (Fig. 1h; $F_{3,8} = 15.9$, $P < 0.0001$ and $F_{3,8} = 22.9$, $P < 0.0001$, respectively). Overall, there was a significant relationship between the number of predators and prey (Fig. 1i; $F_{1,10} = 33.4$, $P < 0.00001$, $R^2 = 0.75$). However, the simple ANCOVA performed with data pooled over surveys did not suggest that these slopes were significantly different among habitats (Table S5, Supplementary material). A more comprehensive analysis of particular guild ratios (Fig. 1h), their seasonal trends and interaction with habitats is beyond the scope of the present article.

Table 4 summarises comparisons among most metrics calculated in this study. Metrics B2, A1, B3, B4 and A2 were good discriminants of habitats for many focal taxa. Worst in this regard were metrics A3, A5, A6 (α) and A7. Few metrics, beside B5, A3 and A6 (βS), showed consistent differences between habitats and across focal taxa. The metrics most closely correlated with each other were A1, A2 and A4, whereas B3 was not correlated with any other metric (Table S4; Table S6, Supplementary material).

## Discussion

Most metrics emphasised large differences between forests and non-forest habitats. With regard to species loss along the disturbance gradient, we need to consider two different situations. First, loss of species occurred when forests were cleared to yield savanna habitats, from a modest 7.5% of observed species, to much larger loss of 29% and 27% when rarefied and estimated species richness were considered, respectively (Fig. 1b). This included losses of 10% of rare species (singletons, Fig. 1c). These losses are likely to be more severe when accounting for the loss of canopy habitats and associated species, not studied here. Second, there was a gain of species richness when open habitats such as savanna were fertilised, transformed into gardens and watered all year round, from 45% in observed species richness against 17% and 45% in rarefied and estimated species richness, respectively. Thus, as far as species richness is concerned, we cannot consider our disturbance gradient as a series of impoverished habitats derived from older forests. This is consistent with the observation that most metrics based on taxonomic identity indicated that, with the exception of comparisons between old and young forests, entire suites of species were being replaced as habitats were modified.

A more accurate interpretation of our results is that species foraging in forests, savanna or gardens recruit from different species pools and that metrics describing community structure without reference to taxonomic identity are evidently misleading on this account. In our study system, it may be more legitimate to ask what might be the proportion of species affected by disturbance, rather than estimating the percentage of species lost. We can estimate the former by considering the percentage of habitat-specific species, since these species are mostly confined to a particular habitat and may decline elsewhere. This is a rather high figure, 92%, to compare with, for example, a loss of 7.5% of observed species.

**Table 4.** Comparisons of metrics discussed in this contribution and amenable to analysis (B1 and B6 cannot be compared with other metrics): number of focal taxa with significant difference among habitats; *P*-value of ANOVA testing for differences in mean metric per site between habitats across the 21 focal taxa; number of significant correlations with other metrics (Corr., see Table S6 for full results); effect size for young forests (Yof), savanna (Sav) and gardens (Gar), compared to an effect size of 1.0 in old forests (see text); ease of computation and remarks. All multiple tests are corrected with the false detection rate method.

| Metric | No. taxa | ANOVA p | Corr. | Effect size Yof/Sav/Gar | Computation | Remark |
|---|---|---|---|---|---|---|
| A1. Abundance | 14 | 0.034 | 6 | 0.8/1.1/2.9 | Straightforward | Sensitivity to protocol and trap location |
| A2. Species richness | 11 | 0.455 | 5 | 1.0/0.9/1.7 | Straightforward | Highly correlated with abundance, metric A1 |
| A3. Rarefied species richness | 0 | 0.005* | – | 1.1/0.8/1.0 | Complex | Comparing vastly different samples sizes may be difficult |
| A4. Estimated species richness | 7 | 0.412 | 5 | 1.0/0.7/1.3 | Intermediate | Depends on sample size, aggregation and provides lower bound only |
| A5. Percentage of local singletons | 0 | 0.138 | 2 | 1.1/1.0/0.9 | Straightforward | Highly correlated with evenness, metric A7 |
| A6. Additive diversity partitioning: | | | | | | |
| α | 0 | 0.143 | 4 | 1.0/1.0/1.4 | Intermediate | Specific protocol needed with extensive replication |
| βT | 3 | 0.049 | 3 | 1.2/0.9/0.8 | Intermediate | Specific protocol needed with extensive replication |
| βS | – | 0.013* | – | 1.1/1.0/1.1 | Intermediate | Specific protocol needed with extensive replication |
| A7. Evenness | 2 | 0.146 | 3 | 1.1/0.9/0.8 | Intermediate | Highly correlated with singletons, metric A5 |
| B2. Species turnover | 18 | – | – | – | Complex | Canonical partitioning more suitable (Legendre *et al*., 2005)? |
| B3. Multivariate analyses | 14 | 0.431 | 0 | 3.1/12.7/13.3 | Complex | 'Empty' sites impossible to score for specific assemblages |
| B4. Nestedness | 14 | – | – | – | Intermediate | Biological interpretation not straightforward |
| B5. Percentage of site-specific species | 3 | 0.00001* | 2 | 1.2/1.0/4.3 | Complex | Results depend on definition of sampling universe |

 

All metrics considered in this study have specific merits, as they quantify rather different types of invertebrate responses to disturbance. Most algorithms proposed for the calculation of estimated species richness are sensitive to sample size and aggregation and provide, at best, a lower bound for species estimates (Mao & Colwell, 2005). Rarefied species richness is an attractive concept but may be of limited use for multi-taxic comparisons when taxon abundance differs greatly among sampling units (i.e. the choice of a minimum sample size is problematic). To estimate well the different components of species diversity, a specific sampling protocol with extensive spatial and temporal replication is needed (Gering & Crist, 2002). Evenness and proportion of local singletons were highly correlated and the former appeared more discriminating than the later. The metric based on ANOSIM (B2) was the most discriminant of all metrics tested. ANOSIM represents a form of Mantel test, which is considered by Legendre *et al*. (2005) as being less appropriate for analyzing beta diversity than canonical partitioning (but see counter-arguments in Tuomisto & Ruokolainen, 2006). A related multivariate technique also of high discriminating power proved to be the scores of DCA, metric B3. One drawback of this method is the impossibility to compute site scores (and to compare them) when sites are 'empty', a problem similar to the one mentioned for rarefied species richness. Considering guild structure (B6) along disturbance gradients is certainly insightful (Tylianakis *et al*., 2005), but our data suggest that comparing percentage data (Fig. 1h) may be more discriminant than simple predator–prey ratios (Fig. 1i). In practice, this approach is limited to diverse assemblages including different feeding guilds. The estimation of the proportion of site-specific species depends on the sampling universe (number and classification of sites) and can lead to misleading interpretation. For example, a generalist, cosmopolitan pest species may appear to be highly habitat specific. Although this metric did not appear to be very discriminant among habitats, it has advantages since, as previously noted, it can provide coarse estimates of the overall proportion of species affected by disturbance.

Higher taxonomic composition (B1) proved to be of limited value in assessing changes along our disturbance gradient (Basset *et al*., 2004b). Although many assemblages appeared to be significantly nested (B4), we reject nestednesss as describing adequately the structure of observed assemblages along our disturbance gradient for several reasons. First, it can only be conceptually explained from the requirements of vagile, generalist and pest species in 'hospitable' gardens moving into less hospitable (and less diverse) savanna and forests. This is likely to be an artefact as forests support probably more species, with an unknown proportion thriving in the canopy. Second, an important condition for the development of nestedness is not met in our study system, as our sites were not open to colonization by a common species pool (Patterson & Atmar, 2000). Garden sites have been mostly colonised since 1998 by invasive crop pests with little relation with the forest fauna. Last, nestedness may be merely related to passive sampling (Fischer & Lindenmayer, 2002).

Metrics describing community structure which proved to be informative (A1, A2, A4) indicated that 33–67% of focal taxa were affected by the disturbance gradient studied (Table 4). On the other hand, metrics based on taxonomic identity and deemed to be informative (B2, B3) showed that a higher proportion of focal taxa (67–86%) were sensitive to disturbance. Many focal taxa which showed non-significant A1, A2 or A4 metrics (Fig. 2), had significant B2 and B3 metrics (Table S4). In other terms, metrics based on species identity reflect a high sensitivity of arthropod assemblages to disturbance, whereas measurements based solely on describing community structure are less discriminating in this regard (Su *et al*., 2004).

Based on Tables 1, 4 and S6, our best choice of metrics would include A1, A2, A4, B2, B3 and, if applicable, B6 (Fig. 1h). A more restricted and recommended set of metrics would include A1, A4 (less correlated with A1 than A2 is), B3 (analyses and interpretation more straightforward than B2 and the strength of interactions between taxa may be estimated by the same token) and B6. An estimation of the percentage of species affected by the disturbance (related to metric B5), not just lost, may also be informative. As this study made clear, it is imperative to move from metrics solely describing community structure to include also more discriminating metrics based on species identity. Interpretation based on species richness estimates alone may be misleading and may not reflect the full extent of species turnover occurring when habitats are modified or lost. In the context of this study, this would have included reporting a 7.5% species loss whereas in fact, 92% of species may have been affected by disturbance.

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## Supplementary Material

The following supplementary material is available for this article:

**Fig. S1.** Aerial photograph indicating 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.

**Table S1** Mean values per site, compared by habitats, for (a) estimated species richness and (b) rarefied species richness for a minimum sample size of $n$ individuals across habitats ($S_r$, total number of rarefied species across all habitats; n.a., not available, sample size too small within habitats, see text). P, $P$-values of ANOVAS comparing means [*multiple test significant with the false detection rate method: (a) $P \leq 0.014$, (b) $P \leq 0.008$]. Olf, old forests; Yof, young forests; Sav, savanna; Gar, gardens.

**Table S2** Mean values per site, compared by habitats, for (a) rarity: mean percentage of local singletons (to total number of species), Uni, percentage of singletons in the combined data set for this taxa; (b) mean evennesss of assemblages per site, Eve, evenness in the combined data set for this taxa; and (c) mean percentage of site-specific species, Hab, percentage of habitat-specific species in the combined data set for this taxa. P, *P*-values of ANOVAs comparing means [*multiple test significant with the false detection rate method: (a) $P \leq 0.002$, (b) $P \leq 0.003$), (c) $P \leq 0.04$]. Olf, old forests; Yof, young forests; Sav, savanna; Gar, gardens.

**Table S3** Additive diversity partitioning compared by habitats: (a) mean percentage of alpha to gamma diversity; (b) mean percentage of temporal turnover to gamma diversity; and (c) percentage spatial turnover to gamma diversity. P, *P*-values of ANOVAs comparing means [*multiple test significant with the false detection rate method: (a) $P \leq 0.002$, (b) $P \leq 0.007$]. Olf, old forests; Yof, young forests; Sav, savanna; Gar, gardens.

**Table S4** Metrics B2, B3 and B4. (a) Results of ANOSIM (metric B2) comparing species turnover among habitats: *R* statistics and *P*-values; (b) mean DCA scores of sites on Axis 1 (metric B3), compared by habitats and *P*-value of ANOVA; (c) nestedness (metric B4): observed T (*T* obs), average simulated T±SD (*T* simul), *P*-value testing the null model, most 'hospitable' habitat (three topmost sites in the packed matrix, Hosp), Spearman rank correlation coefficient with fragment size ($R_s$ frg) and scores of sites on the Axis 1 of the DCA ($R_s$ DCA). *multiple test significant with the false detection rate method: (a) $P \leq 0.039$, (b) $P \leq 0.016$, (c) $P \leq 0.022$). Olf, old forests; Yof, young forests; Sav, savanna; Gar, gardens.

**Table S5** Results of ANCOVA with prey as dependent variable, predator as covariable and habitat as effect. Data points are the 38 surveys pooled for each of the 12 study sites ($n = 12$).

**Table S6** Lower Pearson correlation coefficient between metrics computed for combinations of focal taxa and study sites ($n = 228$). Coefficients in gray cells are significant after correction for multiple tests with the false detection rate methods ($P < 0.014$).

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