Monitoring arthropods in a tropical landscape: relative effects of sampling methods and habitat types on trap catches

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Abstract To discuss the challenge of monitoring multi-species responses of tropical arthropods to disturbance, we considered a large dataset (4×10^5 individuals; 1,682 morphospecies representing 22 focal taxa) based on the work of parataxonomists to examine the effects of anthropogenic disturbance on arthropods at Gamba, Gabon. Replication included three sites in each of four different stages of forest succession and land use after logging, surveyed during a whole year with four sampling methods: pitfall, Malaise, flight-interception and yellow pan traps. We compared the suitability of each sampling method for biological monitoring and evaluated statistically their reliability for 118 arthropod families. Our results suggest that a range of sampling methods yields more diverse material than any single method operated with high replication. Multivariate analyses indicated that morphospecies composition in trap catches was more strongly influenced by habitat type than by sampling methods. This implies that for multi-species monitoring, differences in trap efficiency between habitats may be neglected, as far as habitat types remain well contrasted. We conclude that for the purpose of monitoring large arthropod assemblages in the long-term, a protocol based on operating a set of different and non-disruptive traps appears superior in design than summing a series of taxa-specific protocols.

Introduction

The Millennium Ecosystem Assessment (*2005*) report makes clear that: (1) loss in biodiversity due to human activities has been more rapid in the past 50 years than at any time in human history; (2) the most important drivers of biodiversity loss are habitat change (including loss and fragmentation of forests) and climate change; (3) in the tropics, habitat change contributes much more to biodiversity loss than climate change and this situation will continue for a significant period (Sala et al. *2000*); and (4) rates of biodiversity loss are projected to accelerate. In particular, tropical forests are likely to turn into extinction hotspots (May et al. *1995*) and these extinctions will primarily involve arthropods (Dunn *2005*).

Because of their short generation time, invertebrates respond quickly to modifications of their environment (Kremen et al. *1993*; Basset et al. *2001*) and may be more discriminating in this regard than vertebrates (Moritz et al. *2001*). Arthropod populations are thought to be sensitive to short-term impacts of land management, as well as to longer-term general ecosystem changes (Kremen et al. *1993*; Underwood and Fisher *2006*). Relatively high number of arthropods can be easily collected with a variety of techniques without harming their populations. For these various reasons, they represent choice organisms for biological monitoring (Kremen et al. *1993*).

The usual goal of a species inventory is to document as completely as possible the taxonomy and ecology of taxa within a certain area (see Longino and Colwell *1997* for a good example related to ants). In contrast, biological monitoring seeks to repeat sampling over time to identify population patterns (Stork et al. *1995*; Niemelä *2000*; Yoccoz et al. *2001*; Underwood and Fisher *2006*; Conrad et al. *2007*). Monitoring goals may include detecting the presence of invasive species; detecting population trends of threatened, endangered or keystone species; evaluating land management decisions; or assessing ecosystem change (Underwood and Fisher *2006*). Our research framework relates to the latter and seeks to assess the effects of anthropogenic disturbance, such as land conversion and clearance, on tropical arthropods. This subject is not well understood and warrants further investigations since perhaps 80–90% of tropical taxa have never been the focus of tropical conservation studies (review in Lewis and Basset *2007*).

It is increasingly clear that a multi-species approach, including functional guilds, appears to be better than using indicator species to monitor the responses of tropical invertebrates to disturbance (Kremen et al. *1994*; Didham et al. *1996*; Lawton et al. *1998*; Kotze and Samways *1999*; Basset et al. *2001*). The task of monitoring a sufficient number of taxa at various locations with adequate time may appear daunting. In practice, working with parataxonomists (i.e., local assistants trained by professional biologists) with adequate taxonomic feedback can help to alleviate these problems and ensure that statistical replicates are representative of the system studied (Basset et al. *2004b*).

Entomologists have devised quantitative protocols to survey or monitor specific taxa in the tropics, such as for example ants (Longino and Colwell *1997*; Agosti et al. *2000*; Underwood and Fisher *2006*), termites (Jones and Eggelton *2000*), or butterflies (Sparrow et al. *1994*; DeVries and Walla *2001*). While some recommendations are available to survey whole arthropod assemblages in the tropics (e.g., Noyes *1989*;

Gadagkar et al. *1990*; Stork and Brendell *1993*; Basset et al. *1997*; Adis et al. *1998*; Kitching et al. *2001*), few guidelines exist for designing monitoring protocols targeting multi-assemblages in the tropics (Finnamore *1997*; see Rohr et al. *2007* for one temperate example). There are multiple reasons for this, owing notably to complex issues of sampling methodology, spatio-temporal replication to characterize well assemblages and taxonomic impediment (Niemelä *2000*; Rohr et al. *2007*). This contribution focuses on sampling methodology and emphasizes the three following questions: (a) which trap/method may be suitable for monitoring? (b) Which higher taxa are best collected by particular trapping method, when several trapping methods are used? (c) Does trap efficiency vary between different habitat types?

With regard to the first question, entomologists have devised an impressive range of techniques and traps (e.g., Southwood and Henderson *2000*). The challenge is less about collecting insects, but rather how to use available methods with maximum efficiency, and how best to interpret the resulting data. Sampling methods can be broadly classified in three categories. The first category allows estimating population density by surveying a defined area/volume of habitat (e.g., visual counts, soil coring). The second category includes traps that passively collect arthropods as they move in the habitat (e.g., pitfall, Malaise and flight interception traps). In this case, differing levels of activity among species complicate the interpretation of these trap catches. However, large numbers of individuals can often be collected with relatively little effort. The last category uses the attraction of arthropods for a particular scent, food or visual cue to lure and trap them (e.g., light, pheromone and colored pan traps). These techniques can be very effective for focal taxa but their results are the most difficult to interpret as catches are affected by population density, individual activity and stimulus attraction, all three of which tend to differ among species (Southwood and Henderson *2000*).

When the emphasis is on comparing species densities, sampling methods belonging to the first category are often the best choice. However, since they are often destructive and labor intensive, they may be unsuitable for biological monitoring. For baseline surveys and biological monitoring, trapping techniques may be preferable, especially when comparing different habitats or the same habitat over time. Trapping methods used in biological monitoring must fulfill several criteria. Ideally, they should: be simple, inexpensive, non-destructive and non-disturbing to the study system; have a negligible impact on arthropod populations; be easy to deploy, service and maintain in the field; behave more or less consistently across sites (including both control and impact sites) with respect to the profile of arthropods collected; be relatively insensitive to abiotic factors (or the potential effects of abiotic factors on trap catches should be measurable); quickly provide representative baseline data and repeatable results with low stochastic variance; produce seasonal and annual replicates of the same sampling units; provide a variety of material and/or be efficient for specific focal taxa; provide quality material and taxonomically tractable taxa; and avoid redundancy of information (Kitching et al. *2001*). These quantitative criteria preclude using specific but mainly qualitative protocols developed by taxonomists for their favorite taxa.

While many papers consider the relative merits of modifying a particular sampling method, relatively few compared meaningfully different methods of sampling terrestrial arthropods for biological monitoring (reviews in Muirhead-Thomson *1991*; Basset et al. *1997*; Southwood and Henderson *2000*; Kitching et al. *2001*). Comparisons have often been impeded by low spatial and taxonomic replication. Choice of methods relied more on scientific traditions than on rigorous statistic analyses. Nevertheless, four of the most used sampling methods for arthropods are furthermore recommended for biological monitoring: pitfall, Malaise, flight-interception and yellow pan traps (Finnamore *1997*; Niemelä *2000*; Southwood and Henderson *2000*; Kitching et al. *2001*; Rohr et al. *2007*). The first three are passive traps whereas yellow pan traps collect arthropods that are attracted to a small area of water in a yellow container. In this contribution, we consider these four methods, which may be complemented by automatic light traps, if one is more concerned about nocturnal insects (Wolda et al. *1998*; Kitching et al. *2001*).

Several authors have emphasized the value of using a range of sampling methods for inventorying tropical arthropods (Noyes *1989*; Gadagkar et al. *1990*; Stork *1994*; Basset et al. *1997*; Longino and Colwell *1997*; Kitching et al. *2001*). If one of the goals of biological monitoring is assessing the long-term effects of ecosystem changes on multiple arthropod assemblages with a range of sampling methods, then the relative affinities of particular taxa for particular methods need to be quantified for a sound interpretation of monitoring data. As for question (b), above, the entomological literature is surprisingly scarce on applying rigorous statistics to estimating arthropod affinity for particular trapping methods. A major exception is Kitching et al. (*2001*), who identified subset of both trapping methods and target taxa across a latitudinal transect spanning from Australia to Borneo. However, these authors discussed mainly biodiversity inventorying and detailed information only at the ordinal level. An optimal design for a monitoring programme would require some information on the relative affinity of taxa for particular trapping method at least at the familial level (see Rohr et al. *2007* for a temperate example).

With regard to question (c) above, a dissimilar trap efficiency in different habitats may result from the effect of habitat structure on the trappability of different taxa (Melbourne *1999*), from faunistic differences between habitats, or from both factors. This issue has rarely been well quantified (see discussions for pitfall, Malaise and light traps in Bowden *1982*; Longino and Colwell *1997*; Melbourne *1999*; King and Porter *2005*) and deserves particular attention when designing a monitoring programme assessing long-term ecosystem changes, for example.

Here we consider a study based on the work of trained parataxonomists in Gabon, which examines the effects of a wide anthropogenic gradient of disturbance on a range of focal arthropod taxa that represent diverse taxonomic and functional guilds. Replication included three sites in each of four different stages of forest succession and land use after logging, surveyed during a whole year with four sampling methods recommended for biological monitoring (pitfall, Malaise, flight-interception and yellow pan traps). The major results of this study are reported elsewhere (Basset et al. *2004a*, *2008*). Although this specific study was not designed as a monitoring exercise, we believe that its scope in

terms of diversity of habitats surveyed, sampling methods used, sample size, replication, and taxonomic coverage allow us to discuss some issues which may be important for designing monitoring programmes assessing the effects of ecosystem changes on multiple assemblages of arthropods in the tropics. In this context, our key questions are:

- Do the four sampling methods used in this study appear suitable for biological monitoring? Additionally, what are their relative efficiency (in terms of abundance and species richness) and complementarity to collect rapidly baseline information?

- Which taxa are most likely to be collected in a baseline study using these four sampling methods?

- What are the relative effects of sampling methods per se and habitat types on the composition of trap catches?

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 south-east 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. Primary rainforests are absent from the Gamba oil field, following the selective logging of Okoumé (*Aucoumea klaineana* Pierre). The mean annual temperature in the area is 26°C and annual rainfall amounts to 2,093 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 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: (a) the understorey of the interior of old secondary rainforests, ‘old forests’; (b) the understorey of the edge of young secondary rainforests, ‘young forests’; (c) an area of rainforest cleared to install oil rigs and subsequently invaded by savanna, ‘savanna’; and (d) 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–L) are indicated in Table 1 (see also Basset et al. *2004a*).

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

Code	Habitat	Coordinates	Fragment size (ha)	Physiognomy	Vegetation characteristics

Code	Habitat	Coordinates	Fragment size (ha)	Physiognomy	Vegetation characteristics
A[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[a]	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[a]	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[a]	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	2.7	Surrounded by	*Borreria verticillata* (L.)

Code	Habitat	Coordinates	Fragment size (ha)	Physiognomy	Vegetation characteristics
		09°59′55″E		forest; isolated bushes and trees, sandy soil, bare soil = 50%	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 fertilized 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 fertilized 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 fertilized with compost	Amaranth, aubergine, cabbage, cucumber, gombo, pepper, sorrel, spinach and tomato

For gardens, the main crops cultivated during the study period are listed
[a]Sites equipped with a flight-interception trap

Arthropod collecting and processing

Each site was equipped with an identical set of traps recommended for the biological monitoring of the flying and epigaeic arthropods of the understorey and litter (Finnamore *1997*; Niemelä *2000*; Southwood and Henderson *2000*; Kitching et al. *2001*; Rohr et al. *2007*). At each site, one ground Malaise trap (hereafter MT), four ground yellow pan traps (YPT) and five pitfall traps buried in the ground (PT) were used. In addition, four flight-intercept traps were also set up at forest sites (FIT; Table 1).

The collecting surface of one MT was 2.7 m^2 (model similar to Townes *1972*; Santé Traps, 739 Cooper Drive, Lexington, Kentucky, USA 40502). Collecting fluid was 70% ethanol. YPT were 27 cm in diameter by 8 cm deep and filled with a mixture of water

(ca. 80%), 70% ethanol (ca. 20%) and a few drops of liquid detergent to break the surface tension of the water. They were placed in the soil so that the rim was level with ground surface, thus also intercepting crawling arthropods (Finnamore *1997*). PTs were small 0.5-l plastic cups (6 cm in diameter) filled with the same water, ethanol and detergent mixture. At each site, a MT occupied the center of the set of traps, with four PTs established to the north, south, east and west, 10 m distant from the MT. Four YPTs were set up at equal distances between the PT, again 10 m distant from the MT. The fifth PT was placed 30 m north of the MT. In addition, 4 FITs were hung 3 m off the ground above the fifth PT, in four of the six forest sites. The collecting surface of one FIT was about 4 m^2 (Santé Traps; model similar to Springate and Basset *1996*). All of these traps have specific advantages and limitations, as discussed for example in Adis (*1979*) and Basset et al. (*1997*).

The 120 traps operated for 3 days each week and were intended to be surveyed weekly (=one survey) from July 2001 to July 2002. However, the amount of material collected required us to spread surveys and eventually only 38 surveys were obtained during the above period (12 in the dry season and 26 in the wet season). The longest gap between two surveys was one month (December 2001). A team of eight parataxonomists was trained and supervised by a professional entomologist throughout the project (see Basset et al. *2004b* for a detailed discussion of this strategy). The material collected was first sorted into families or higher taxa by the parataxonomists (see exceptions below). The material belonging to 22 focal taxa (Table 2) was isolated and pinned, and each individual was identified by a unique specimen number. The focal taxa were 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 2). The rationale for selecting the 22 focal taxa were (a) being well represented in the samples (so that much information was retained); (b) being workable taxonomically; (c) taxonomists having expressed interests in working on the material; and (d) representation of a variety of functional guilds and orders (Table 2).

Table 2 Focal taxa sorted by parataxonomists

Focal taxa	Order[a]	Guild[b]	Ind	Indm[c]	Mor	Spp.	Authority
Mantodea	Ma	Pr	98	56	22	–	–
Acrididoidea[d]	Or	Lc	1,129	360	40	–	–
Fulgoroidea[e]	He	Ss	4,022	2,842	242	–	–
Membracidae	He	Ss	37	36	15	–	–
Buprestidae	Co	Wo	115	95	16	16	GC
Scarabaeidae	Co	Lc, Sc	2,240	2,031	88	–	–
Coccinellidae	Co	Pr	1,409	1,203	34	–	–
Histeridae	Co	Pr	682	624	25	–	–
Cleridae	Co	Pr	45	38	19	–	–
Tenebrionidae	Co	Sc	839	644	60	–	–
Cerambycidae	Co	Wo	278	149	53	51	S. Lingafelter

Focal taxa	Order[a]	Guild[b]	Ind	Indm[c]	Mor	Spp.	Authority
Chrysomelidae	Co	Lc	2,285	1,961	169	157	TW
Neuroptera[f]	Ne	Pr	235	152	25	25	MWM
Asilidae	Di	Pr	409	351	50	–	–
Dolichopodidae[g]	Di	Pr	7,339	2,121	38	–	–
Tephritidae	Di	Lc[h]	535	429	35	–	–
Syrphidae	Di	Pr, Sc	459	375	34	25	C. Thompson
Pipunculidae	Di	Pa	123	97	16	22	MDM; M. Foldvari
Ichneumonidae	Hy	Pa	2,302	1,916	429	–	–
Chalcidoidea[i]	Hy	Pa	4,577	1,315	179	–	–
Formicidae	Hy	An	134,912	na	na	–	–
Apoidea[j]	Hy	Lc[k]	1,239	1,060	93	51	CE

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
[a]Orders: Co = Coleoptera, Di = Diptera, He = Hemiptera, Hy = Hymenoptera, Ma = Mantodea, Ne = Neuroptera, Or = Orthoptera
[b]Guilds: An = ants, Lc = leaf-chewers, Pa = parasitoids, Pr = predators, Sc = Scavengers , Ss = sap-suckers, Wo = wood-eaters (system of Moran and Southwood *1982*)
[c]Some damaged or lost material could not be morphotyped
[d]Including Acrididae, Pyrgomorphidae and many juveniles, not morphotyped
[e]Including 14 families
[f]Including eight families
[g]Only morphotyped from July to December 2001, then kept unassigned in alcohol
[h]Subguild: fruit-feeders
[i]Only >2 mm and including 13 families
[j]Including Apidae, Halictidae and Megachilidae
[k]Subguild: pollinators

There were a few exceptions to the sorting and mounting pattern. Non-insect material was mostly sorted to order. Lepidoptera were not sorted to families, since being wet material they were useless. In the Diptera, the Nematocera, Brachycera and Aschiza were treated at the family level; numerous Schizophora were often identified as Calyptera or Acalyptera because of taxonomic difficulties. A number of other taxa were identified to superfamily level for the same reasons: Coccoidea, Aphidoidea, some Cucujoidea, Chalcidoidea, Cynipoidea and Proctotrupoidea. Chalcidoidea smaller than 2 mm were counted, but not morphotyped. Two focal taxa that were very abundant in samples, Dolichopodidae and Formicidae, were partly processed and morphotyped. Specimens are stored at the Smithsonian Biodiversity Conservation Center in Gamba, and vouchers have been deposited at the National Museum of Natural History (Washington D.C.) and with taxonomists who helped with species identification.

Statistical methods

Our analyses often considered three datasets of increasing taxonomic resolution and accuracy: (a) higher taxa (mostly families); (b) morphospecies sorted by parataxonomists from focal taxa; and (c) species sorted by taxonomists from focal taxa. Datasets at the ordinal resolution lack discriminating power, as indicated by earlier analyses of part of the material collected (Basset et al. *2004a*). We also often contrasted data related to forest vs. non-forest habitats. For most analyses, we pooled the data of a particular sampling method for a survey and considered this to be a sample (n = 38). One needs to recall that a sample is equivalent to three days of collecting of 60 PTs, 48 PYTs, 4 FITs and 12 MTs.

First, we compared the abundance and diversity of the material collected by the four sampling methods with a series of standard statistics and curves routinely used in ecology (Magurran *1988*; Colwell *2005*): Kruskal–Wallis tests, coefficient of variation, Coleman rarefaction, non-parametric Chao1 estimate of species richness, evenness (=Shannon diversity index/ln[no. morphospecies/species observed]) of species rank abundance curves, and randomized species accumulation curves. We also compared the three main sampling methods (PT, YPT and MT) with regard to the shared number of morphospecies/species between methods and computed two relevant statistics: Morisita–Horn index of faunal similarity and complementarity. The Morisita–Horn index is a special case of the NESS index where sample size parameter is set to 1 and is most sensitive to common species (Grassle and Smith *1976*). Complementarity between methods was estimated with the Marczewski–Steinhaus distance (proportion of all species collected by two methods that were captured by only one method; varies from 0, when both methods share all species, to 1, when methods have no species in common; Colwell and Coddington *1994*). Most of these statistics were calculated with EstimateS version 7.5, with 50 randomizations whenever applicable (Colwell *2005*).

Second, to evaluate which higher taxa were best collected by each sampling method, we used the indicator value index, which ranges from 0 (no indication) to 100 (perfect indication; Dufrêne and Legendre *1997*). Perfect indication means that presence of a taxon points to a particular sampling method without error, at least with the dataset in hand. For this analysis, we considered the sum of individuals collected within higher taxa for a particular combination of site and sampling method ($12 \times 3 + 4 = 40$ samples). We restricted the dataset to the most abundant higher taxa (≥40 individuals; i.e., at least on average one individual collected in each sample; 151 higher taxa were considered). The significance of the maximum indicator value was tested for each taxon by a randomization procedure implemented in PC-ORD (Monte Carlo permutation tests; 1,000 permutations; McCune and Medford *1999*).

Last, we performed multivariate analyses to estimate the relative contribution of sampling methods, habitat type and seasonality on the composition of arthropod catches, for the higher taxa, morphospecies and species datasets. For each dataset, we pooled data from a combination of sites, sampling methods and seasons ($12 \times 3 \times 2 + 4 \times 2 = 80$ samples). Seasons were defined as being ‘dry’ (June–August) or ‘wet’ (other sampling months). We restricted datasets to the most abundant higher taxa (≥40 individuals, n = 151, 80 samples), morphospecies (≥40 individuals, n = 86, 80 samples) and species (≥20

individuals, $n = 43$, 67 samples). First, we performed unconstrained ordinations (detrended correspondence analysis, DCA, ter Braak and Smilauer *1998*) for each dataset to examine the grouping of samples with regard to sampling methods and habitat types, especially forest vs. non-forest habitats. Second, we performed constrained ordinations (canonical correspondence analysis, CCA, ter Braak and Smilauer *1998*) for each dataset to evaluate the effects of independent (factor) variables. These included sampling methods (four dummy variables re-coded as advised in Leps and Smilauer *2003*), habitats (four dummy variables) and seasons (two dummy variables). Partitioning of variance followed Borcard et al. (*1992*).

Results

Overall, 430,448 arthropods were collected during the 38 sampling events (4,712 samples), representing 31 orders and at least 218 families. The 22 focal taxa represented 17,822 individuals and 1,682 morphospecies (Table 2). Further, 347 species were sorted from the seven focal taxa which to date have been examined by taxonomists. Most individuals were collected by PTs and MTs (Table 3). Catch rates expressed per trap-day were significantly different among methods (Kruskal–Wallis test, $W = 1390.9$, $P < 0.001$). MTs provided the highest catch rate, but when considering catch rates per unit surface area, PTs were most efficient, with the notable high efficiency of YPTs. Catches with YPTs also had the lowest coefficient of variation (Table 3). Distribution of arthropod abundance in the four habitat types was broadly similar for each of the four sampling methods, being usually high and similar at forest sites, lowest in the savanna, and intermediate to high in gardens (Table 3).

Table 3 Statistics related to the abundance and diversity of arthropod material collected by each sampling method

Variable	PT	YPT	FIT	MT
No. ind. collected	148,591	106,963	30,044	144,850
Mean ± SE ind. collected per survey	3,910 ± 434	2,814 ± 219	791 ± 96	3,812 ± 306
CV for survey samples (%)	68.4	47.9	75.0	49.4
Catch rate (mean ± SE ind. collected per trap-day)	21.7 ± 1.8	19.5 ± 0.9	65.9 ± 5.6	105.9 ± 6.2
Catch rate (mean ind. × day × m^{-2})	7676.3	341.4	16.5	39.2
Mean ± SE ind. collected per survey in old forests	1,359 ± 253.4	656.4 ± 106.6	427.6 ± 64.0	1202.8 ± 175.9
Mean ± SE ind. collected per survey in young forests	1326.7 ± 249.2	830.9 ± 103.4	363.1 ± 38.8	807.9 ± 103.4
Mean ± SE ind. collected per survey in savanna	370.3 ± 44.5	461.8 ± 30.7	–	562.7 ± 59.5
Mean ± SE ind. collected per survey in gardens	854.2 ± 132.8	865.8 ± 60.0	–	1238.4 ± 121.3

Variable	PT	YPT	FIT	MT
No. morphospecies collected	274	767	272	1,108
No. spp. collected[a]	46	159	100	254
No. of singletons collected (% of total)	139 (50.7)	379 (49.4)	169 (62.1)	504 (45.5)
No. of singletons collected (% of total) in forests	81 (58.3)	244 (55.1	169 (62.1)	306 (57.6)
No. of singletons collected (% of total) in non-forests	76 (48.7)	196 (48.5)	–	296 (42.2)
Evenness of morphospecies rank abundance curve	0.72	0.75	0.80	0.81
Evenness of spp. rank abundance curve[a]	0.74	0.77	0.87	0.80
Coleman morphospecies; sample size = 1,700 ind.	265.5 ± 0.4	375.1 ± 1.6	277.5 ± 0.3	508.2 ± 1.9
Coleman spp.: sample size = 150 ind.[a]	45.5 ± 0.2	56.7 ± 0.7	69.2 ± 0.6	68.4 ± 0.8
Chao1 ± SE: morphospecies	504.2 ± 7.8	1447.9 ± 13.8	677.1 ± 12.9	1842.9 ± 12.8
Chao1 ± SE: spp.[a]	103.0 ± 4.4	299.2 ± 6.0	288.4 ± 10.2	409.9 ± 6.2

CV = coefficient of variation; ind. = individuals; spp. = species
[a]Seven focal taxa: Table 2

Most morphospecies and species were collected by MTs and YPTs. Rarefaction indicated that this pattern remained true for morphospecies, but many species were also collected by FITs. Patterns were also broadly similar for morphospecies and species when estimating the total number of taxa present in the area or considering the evenness in rank abundance plots among sampling methods. The number of singletons collected by MTs and YPTs was appreciable. The PTs tended to have their collections dominated by a few morphospecies (Scarabaeidae and Histeridae; evenness of rank abundance plots, Table 3). PTs, YPTs and MTs collected higher proportion of singletons in forest than in non-forest habitats (Table 3). With larger sampling effort, MTs and YPTs may have collected many more species in the study area (Chao1, Table 3). Evenness was highest for FIT catches and lowest for PT catches (Table 3; morphospecies/species rank abundance plots not presented here). With the present protocol, one MT collected as many arthropods as four YPTs or five PTs; the catches of four YPTs and five PTs were 26 and 48% less diverse than one MT, respectively (Coleman rarefaction on morphospecies, Table 3).

Our sampling methods only collected a fraction of the local arthropod fauna, as suggested by morphospecies accumulation curves (Fig. 1a; patterns were broadly similar for species and are not presented here). Also, as indicated by the rarefaction, accumulation of morphospecies was steeper for MTs than for PTs, suggesting that PTs may have sampled a higher proportion of the epigaeic fauna when compared to the proportion of flying fauna sampled by MTs. For PTs, YPTs and MTs, morphospecies accumulation curves

were steeper in forest than in non-forest habitats, suggesting that a lower fraction of the fauna was sampled in the former than in the latter (Fig. 1b).

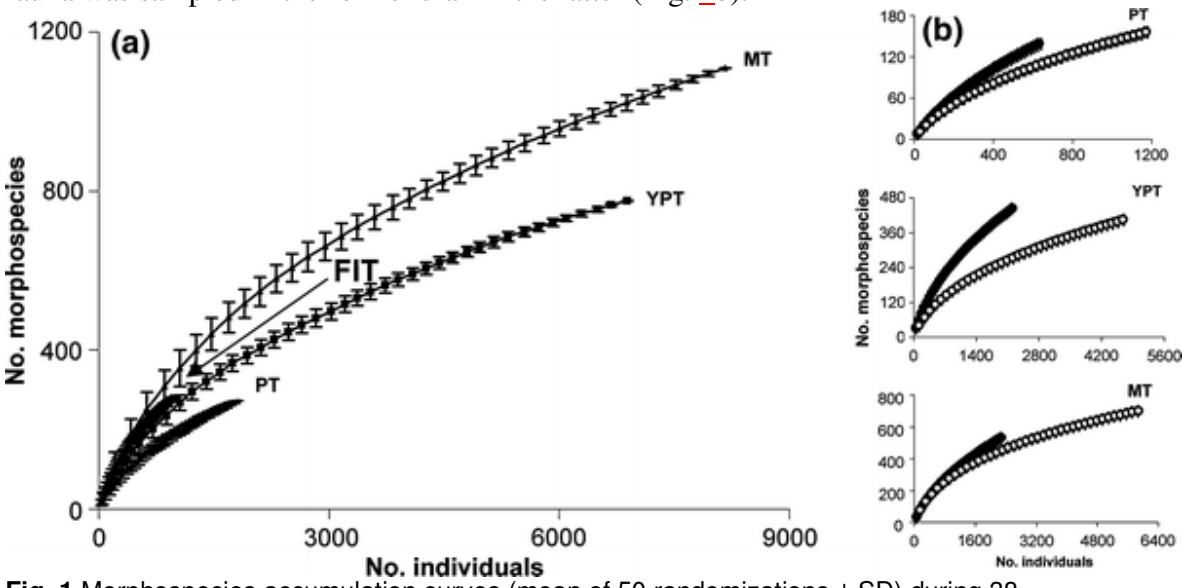

Fig. 1 Morphospecies accumulation curves (mean of 50 randomizations ± SD) during 38 arthropod surveys, for (**a**) different sampling methods, all habitats being pooled; and (**b**) particular sampling methods operating either in forest (closed circles) or non-forest habitats (open circles)

The distribution of unique and shared taxa was broadly similar for morphospecies and species. Both for morphospecies and species, MTs produced a high proportion of unique species (55–60%), whereas this was lower for PTs (19–26%; Fig. 2). Only 35 morphospecies (2.1% of total sorted) were collected by the four sampling methods. Faunal similarity was closest between the catches in MTs and FITs (Morisita–Horn indices of 0.40 for morphospecies) and furthest between the catches in MTs and PTs (Fig. 2). For both morphospecies and species, complementarity was highest between PTs and MTs (Fig. 2).

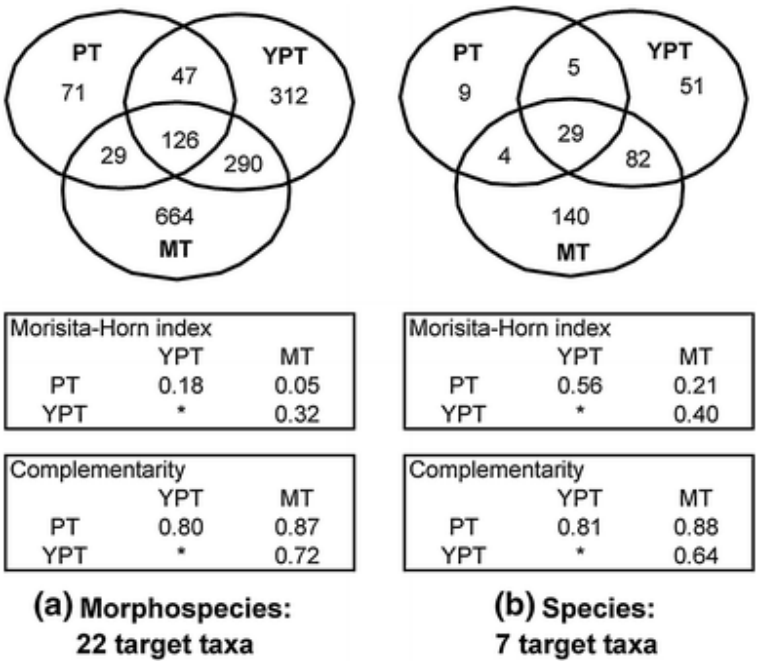

Fig. 2 Shared species statistics between the three main sampling methods (PT, YPT and MT), for (**a**) morphospecies and (**b**) species. Circles, above: no. of morphospecies/species uniques and shared between the three methods. Boxes, below: upper matrix of similarity (Morisita–Horn index) and complementarity between sampling methods

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Sampling methods each collected a different spectrum of fauna and often substantial variation in trap catches existed among habitat types (Fig. 3). Furthermore, the distribution of a few abundant taxa equally well collected by the three main sampling methods was not uniform across habitats (PT, YPT and MT; Formicidae, Collembola, Phoridae, Acalyptera, Calyptera, Cicadellidae and Scelionidae; *G*-tests on 3×4 matrices, all with $P < 0.001$), suggesting that different sampling methods collect different subsets of the fauna that are well-adapted to specific habitat types (and see multivariate analyses, below).

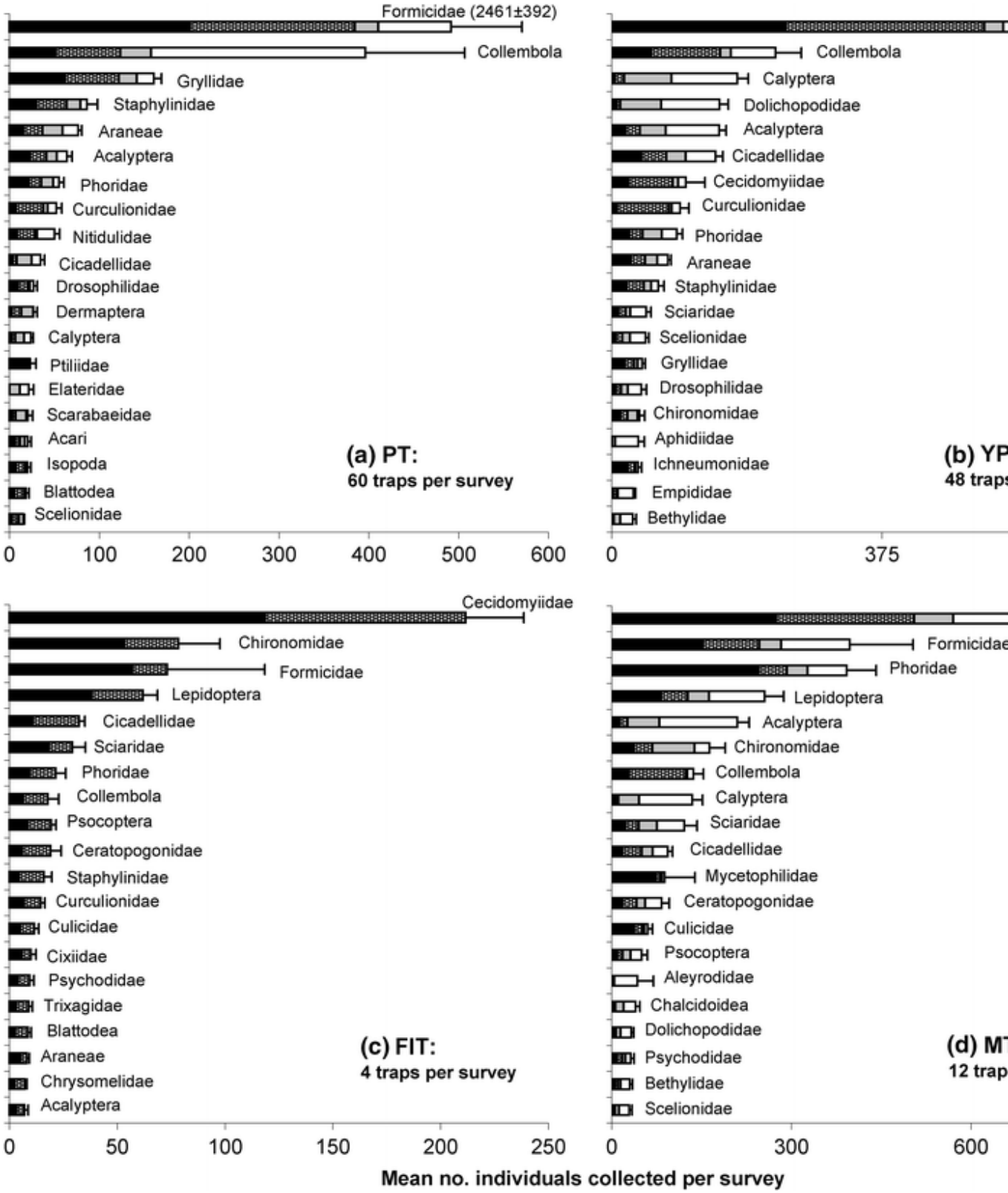

Fig. 3 The 20 most abundant higher taxa collected by each sampling method. Mean (±SE) number of individuals collected per survey, detailed for old forests (closed bars), young forests

(stippled bars), savanna (gray bars) and gardens (open bars). Standard errors relate to the mean of total individuals collected per survey for each taxon. For sake of clarity, Formicidae data for PT were all scaled by a factor 0.2 (actual value in brackets)

About half of the higher taxa tested (61 insect families) could be considered as indicators for particular sampling methods (Appendix A: indicator values with $P < 0.05$, 151 higher taxa tested representing 118 families). These results can be used by entomologists to compare the relative reliability of the four sampling methods used in this study for arthropod taxa. Most of this information has been previously reported in the literature (sometimes without statistical rigor), but other observations may not be widely known and are detailed below.

PTs are known to sample predominantly arthropods foraging on the ground, such as Gryllidae, Carabidae, Formicidae, Acari, Dermaptera and Diplopoda (all with indicator values with $P < 0.01$). YPTs sampled a mixture of taxa foraging on the ground or flying close to the ground, such as Dolichopodidae, Encyrtidae, Salticidae, Thysanoptera, Ceraphronidae, Sphecidae and Araneae (all with $P < 0.01$). The relative high catches of Stratiomyidae, Diopsidae and Anthicidae in YPTs are noteworthy. FITs were especially good to collect flying insects that tend to drop when hitting surfaces (many Coleoptera), such as Eucnemidae, Trixagidae, Coniopterygidae, Anthribidae, Cerambycidae, Cleridae, Scyrtidae, Termitidae, Aderidae and Psylloidea (all with $P < 0.01$). The high incidence of Coniopterygidae and alate Termitidae in the FITs are noteworthy. MTs often collected reasonably good fliers, such as Tabanidae, Buprestidae, Scoliidae, Evaniidae, Eurytomidae, Braconidae and Myrmeleontidae (all with $P < 0.01$). The good indicator scores for MTs of Buprestidae, Myrmeleontidae and Chrysidae are also noteworthy.

The first and second axes of the DCA explained 23.7 and 11.0% of variance in the composition of arthropod higher taxa (sum of eigenvalues of DCA = 2.165). They clearly separated samples on the basis of sampling methods (first axis) and habitat types, especially forests and non-forests (second axis; Fig. 4a). The second axis affected more strongly YPT and MT samples than PT samples (paired *t*-tests for differences in sample scores on axis 2 for PT, YPT and MT samples in forest and non-forest habitats: $t = -2.60$, $P < 0.05$; $t = -13.12$, $P < 0.001$; $t = -10.47$, $P < 0.001$, respectively). The CCA confirmed that the effect of sampling method influenced more strongly the composition of higher taxa than the effect of habitats. The first canonical axis explained 49.9% of the variance in the CCA (21.8% of the total variance). The dummy variable 'PT' was best correlated with the first axis ($r = -0.85$, $P < 0.001$; Fig. 4a). The second canonical axis explained 27.2% of the variance in the CCA (11.9% of the total variance). The dummy variables 'YPT', 'Garden', and 'Old forest' were best correlated with the second axis ($r = 0.61$, $r = 0.56$ and $r = 0.51$, respectively, $P < 0.001$; Fig. 4a).

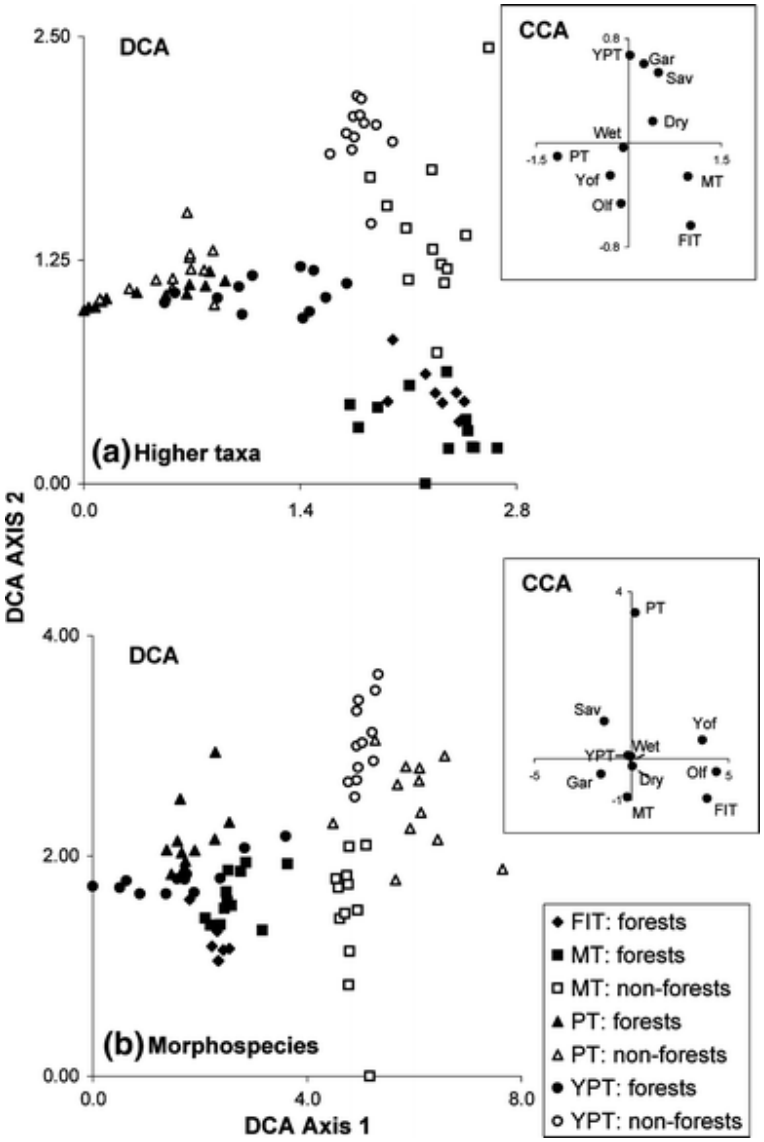

Fig. 4 Multivariate analyses of (**a**) 151 higher taxa and (**b**) 86 morphospecies, ordered by sites, methods and seasons. Plot of samples (closed symbols = forests, open symbols = non-forests) in the first and second axis of the DCA. Inset: plot of centroids of environmental variables in the first and second canonical axes of the CCA CCA (Olf = old forest, yof = young forest, sav = savanna, gar = garden, dry = dry season, wet = wet season)

Patterns were different when examining morphospecies composition. In this case, the first and second axes of the DCA explained a lower fraction of variance (9.6 and 6.1%, respectively; sum of eigenvalues = 9.305), emphasizing that many factors may influence morphospecies distribution. The first axis separated samples on the basis of habitat type, especially forests and non-forests, whereas the meaning of the second axis was more difficult to interpret (Fig. 4b). The first axis affected similarly PTs, YPTs and MTs (paired *t*-tests for differences in sample scores on axis 1 for PT, YPT and MT samples in closed and open habitats: $t = -17.00$; $t = -11.28$; $t = -14.12$; respectively; all with $P < 0.001$). The first canonical axis of the CCA explained 28.8% of the variance (9.3% of

the total variance) and was best correlated with the dummy variables ‘Old forest’ and ‘Garden’ ($r = 0.78$ and -0.64, respectively, $P < 0.001$). The second canonical axis explained 21.6% of the variance 6.9% of the total variance) and was best correlated with the dummy variables ‘PT’ and ‘MT’ ($r = 0.91$ and -0.57, respectively, $P < 0.001$). Multivariate analyses of the species dataset were broadly similar to the morphospecies dataset, particularly the first axes of the DCA and CCA being related to habitat type, and are not detailed here.

Discussion

Suitability of sampling methods for biological monitoring

The four sampling methods used in this study were non-destructive and easily deployed and maintained during a year at all studied habitats. However, there are at least four major impediments related to these traps and our study. First, sedentary arthropods were less likely to be collected by these rather passive traps. Thus, measurements of faunal similarity (for example calculated between habitat types) derived from these data are likely to be rather high. Our conclusion that many morphospecies/species are specialized to particular habitats (see below) may thus be further strengthened. Second, these methods were inadequate for many arthropod taxa (e.g., Lepidoptera are better collected with light traps, Kitching et al. *2001*). Third, non-forest habitats (savanna and gardens) were better surveyed than forests since traps operated in the understorey. The rich fauna of the forest canopy (Erwin *1983*) was probably only occasionally collected, as suggested by steep species accumulation curves and high occurrence of singletons in forests (Fig. 1b, Table 3). Last, taxonomic impediment prevented all focal taxa from being examined by taxonomists, although the studies of certain taxa are pending. This limited our analyses related to species richness. In most cases, our species and morphospecies datasets showed similar patterns, but species identifications are crucial for sound biological monitoring.

PTs are inexpensive, easy to deploy in the field and allow high spatial replication for habitat comparisons. However, particular care must be taken to keep the rim of the pitfall level with the ground surface, to ensure maximum efficiency. They need to be serviced often to prevent rain from flooding the trap contents and arthropods to start decomposing. A small roof over the trap may stop rain from diluting the preserving fluid, but this is at the expense of further trap bias (Adis *1979*). YPT share most qualities and shortcomings of PTs: being inexpensive; easy to use and possibility of high replication; sensitive to rainfall and frequent servicing needed. However, no roof can be placed over the trap to protect it from rainfall, as this would decrease catches of insects attracted to yellow, which tend to be phytophagous (Kirk *1984*). Unlike most authors, we emplaced YPTs with the rim level with the ground surface (Finnamore *1997*). This detail explains our high catches of both crawling and flying insects. Abundant material is collected in FITs and MTs (and better preserved than in the case of PTs and YPTs), which takes a lot of time to sort. However, by restricting operations to a short period with frequent servicing

(3 days at weekly intervals, such as in the present study), one may greatly decrease catches size and allow one to consider all taxa within (the smaller) samples. For long-term studies and monitoring, this approach may result in more representative samples (Gadagkar et al. *1990*). Both types of traps are expensive and, thus, spatial replication is more difficult to achieve than with the other two methods. The larger FITs and MTs are also more prone to disruption from humans and animals (with concomitant difficulty and costs to replace them) than the smaller PTs and YPTs, particularly in Africa in areas where large mammals are abundant.

Complementarity of sampling methods and reliability for collecting particular taxa

Sampling methods strongly influenced arthropod composition in trap catches, as they targeted different components of the fauna, either foraging on the ground (PTs, YPTs) or flying low in the vegetation (YPTs, FITs, MTs). Trap complementarity was highest for traps best designed to exploit these different behaviors, PTs and MTs. Each sampling method was biased towards specific higher taxa and morphospecies, resulting in different species rank abundance distributions. Most of the 35 morphospecies that were collected by all four collecting methods were more readily sampled by a particular method. As a result, faunal similarities calculated between the catches of different sampling methods were low. The implications are clear: a range of sampling methods (at the expense of lower replication) is likely to yield more diverse material for inventorying and monitoring arthropods than any single method operated with high replication (Noyes *1989*; Gadagkar et al. *1990*; Stork *1994*; Basset et al. *1997*; Longino and Colwell *1997*; Kitching et al. *2001*). Arguably, more systemic sampling methods exist than used in this study (e.g., pyrethrum knockdown, net sweeping, e.g., Noyes *1989*; Watt et al. *1997*), but they are unsuitable for long-term monitoring as they dramatically disturb study sites by fumigation and trampling.

Further, the extensive dataset of this study allowed statistical testing of the reliability of sampling methods used in this study for 118 arthropod families (in terms of relative abundance, Appendix A). This statistical approach is more accurate than relying on scientific tradition for choice of taxa and methods, which often prevails in the entomological literature (Kitching et al. *2001*).

Effects of habitat structure on trap efficiency

The effect of habitat structure on the trappability of different taxa is an important topic (Melbourne *1999*). However true faunistic differences between habitat types, such as those considered in the present study are likely to be far more significant, as suggested by the magnitude of faunal turnover observed (only 39 morphospecies common to all habitats, 2.4% of all morphospecies sorted; data presented and discussed elsewhere). As far as higher taxa are concerned, given that sampling methods had a larger impact on arthropod composition than habitat type (Fig. 4a), the most efficient method for a particular taxon is likely to remain the same across all habitat types. That said, we

observed that the higher taxa composition of MTs varied more between forests and non-forest habitats than that of PTs, YPTs being intermediate in this regard. MTs and YPTs may be more efficient in open habitats because of increased visibility and attractiveness (Noyes *1989*). Alternatively, MTs and YPTs are more likely to collect mobile taxa that may forage in different habitats. Interestingly, these patterns were different when considering the morphospecies/species composition of trap catches: the effects of habitat type were stronger than the effects of sampling method. This confirms that many morphospecies/species are specialized foragers in particular habitats and that datasets sorted at the level of species/morphospecies are much more discriminating with regard to arthropod composition in different habitats than those sorted at the level of higher taxa (Basset et al. *2004a*). This implies that monitoring should be preferably performed at the level of morphospecies/species and that for this type of data differences in trap efficiency or taxa trappability between habitat types may be neglected, as far as habitat types remain well contrasted and contain dissimilar fauna.

Conclusions and recommendations

The two concepts of inventorying and monitoring biodiversity are connected, since baseline data are needed for monitoring (Rohr et al. *2007*). For inventorying purposes, a combination of methods targeting different faunal components may be optimal, as they may collect a wider range of taxa than a single method (Noyes *1989*; Gadagkar et al. *1990*; Stork *1994*; Basset et al. *1997*; Longino and Colwell *1997*; Kitching et al. *2001*). Including a few MTs in the protocol may be valuable since they accumulate faster species in trap catches and provide high quality material for further taxonomic analyses. Note that a possible improvement of the protocol developed in the present study would be to establish more sites for each habitat type (i.e., nine sites per habitat instead of three) and to randomly move the 12 traps operating within this set of sites every month (or other relevant period). The amount of material collected would be similar but, most likely, more diverse. Further, it would improve statistical power, with analyses being less-site and more habitat-dependent. Adequate inventory of the canopy fauna, often different from that in the understorey within tall closed rainforests (Basset et al. *2003*), remains a challenge (Basset et al. *1997*). With regard specifically to long-term monitoring, one possibility may include operating compact FITs, modified YPTs or automatic light traps lifted on pulleys high in the canopy (Springate and Basset *1996*; Wolda et al. *1998*; De Dijn *2003*).

For general monitoring purposes, the situation is more complex, as species abundance in traps ideally needs to reflect actual species abundance. Given that each method tends to target a different component of the fauna and has its own biases, it would be preferable to statistically analyze species data separately for each sampling method, the results of one complementing the results of the other(s). In case only one sampling method can be deployed, YPTs represent an acceptable compromise, as they samples both crawling and flying arthropods and accumulate specimens and species reasonably fast. Further, since higher taxa composition in YPTs differed consistently between forest and non-forest habitats than in MTs or PTs, YPTs may be particularly useful for monitoring arthropod recovery in degraded and open habitats.

As noted in the introduction, several quantitative protocols exist to survey specific arthropod taxa in the tropics. For biological monitoring, it may be possible to implement in parallel taxa-specific protocols, but this approach is likely to be obtrusive (by trampling required to performed 5–10 protocols alone), or even destructive (e.g., ant and termite protocols, Agosti et al. *2000*; Jones and Eggelton *2000*), or time-consuming (as different training skills may be required for operators). The following alternative, based on the present study, may be considered: implement a common set of passive, non-obtrusive sampling methods (such as PTs, YPTs and MTs), extract focal taxa with the help of local parataxonomists (Basset et al. *2004b*), and refine species identifications with taxonomists' feedback. In addition to this multi-taxic monitoring programme, 1–3 taxa-specific protocols could be implemented in parallel, to validate the results of the wider monitoring programme. This strategy has at least four added advantages: (1) development of baseline datasets that are wider in taxonomic scope; (2) monitoring of a larger number of focal taxa belonging to different functional guilds; (3) long-term studies with non-disruptive methods may allow collection of rare species, which represent a substantial proportion of tropical arthropod assemblages (Novotny and Basset *2000*); and (4) wider training base for parataxonomists.

In conclusion, taxa-specific sampling protocols are certainly the best strategy when evaluating the effects of anthropogenic disturbance on particular arthropod taxa. However, for the purpose of monitoring large and diverse arthropod assemblages in the long-term, a protocol based on operating a set of different and non-disruptive traps appears superior in design and rewards than summing a series of taxa-specific protocols.

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Appendix A: Results of species indicator analysis with regard to sampling methods for the 151 most abundant higher taxa

Taxa	Method	Indicat. val. (%)	*P*-value
Acari	PT	54.8	0.001
Araneae	YPT	38.1	0.008
Salticidae	YPT	65.7	0.001

Taxa	Method	Indicat. val. (%)	*P*-value
Archaeognatha			
Meinertellidae	MT	14.3	0.755
Blattodea	FIT	37.7	0.219
Coleoptera			
Aderidae	FIT	62.8	0.008
Anthicidae	YPT	52.2	0.032
Anthribidae	FIT	69.8	0.001
Bostrichidae	MT	28.7	0.280
Bruchidae	MT	39.1	0.452
Buprestidae	MT	78.0	0.001
Carabidae	PT	68.7	0.001
Cerambycidae	FIT	63.0	0.001
Chrysomelidae	MT	32.9	0.746
Clambidae	YPT	40.5	0.224
Cleridae	FIT	78.9	0.002
Coccinellidae	YPT	41.7	0.296
Corylophidae	FIT	39.4	0.283
Cucujoidea	PT	26.2	0.431
Curculionidae	YPT	47.4	0.349
Elateridae	PT	34.4	0.644
Endomychidae	MT	74.7	0.013
Eucnemidae	FIT	83.9	0.001
Histeridae	YPT	43.2	0.109
Hydrophilidae	PT	61.6	0.055
Lagriidae	FIT	34.4	0.174
Leiodidae	YPT	35.4	0.635
Mordellidae	MT	44.4	0.076
Mycetophagidae	FIT	26.5	0.337
Nitidulidae	PT	54.5	0.011
Phalacridae	FIT	40.7	0.062
Pselaphidae	FIT	47.4	0.018
Ptiliidae	PT	51.9	0.091
Scarabaeidae	MT	37.8	0.480
Scydmaenidae	FIT	35.3	0.461

Taxa	Method	Indicat. val. (%)	*P*-value
Scyrtidae	FIT	75.3	0.004
Staphylinidae	PT	40.3	0.040
Tenebrionidae	MT	41.8	0.247
Trixagidae	FIT	81.7	0.001
Coleoptera: unknown	PT	39.9	0.103
Collembola	PT	48.6	0.019
Entomobryidae	MT	39.2	0.112
Dermaptera	PT	82.2	0.002
Diplopoda	PT	67.7	0.009
Diptera			
Acalyptera	MT	47.2	0.034
Anthomyiidae	MT	41.2	0.021
Asilidae	MT	61.5	0.013
Calliphoridae	YPT	47.4	0.047
Calyptera	YPT	51.0	0.031
Cecidomyiidae	MT	48.8	0.063
Ceratopogonidae	MT	55.0	0.013
Chironomidae	FIT	53.2	0.018
Culicidae	MT	59.8	0.087
Diopsidae	YPT	53.2	0.024
Dolichopodidae	YPT	77.2	0.001
Drosophilidae	YPT	43.8	0.035
Empididae	YPT	52.2	0.180
Limoniidae	MT	48.4	0.043
Micropezidae	YPT	61.3	0.055
Muscidae	YPT	25.6	0.194
Mycetophilidae	MT	78.5	0.059
Phoridae	MT	65.0	0.016
Pipunculidae	MT	47.1	0.031
Platystomatidae	YPT	38.4	0.088
Psychodidae	MT	38.8	0.145
Sarcophagidae	YPT	49.4	0.040
Scatopsidae	MT	70.6	0.064
Sciaridae	MT	45.8	0.014

Taxa	Method	Indicat. val. (%)	*P*-value
Stratiomyidae	YPT	48.6	0.023
Syrphidae	MT	63.3	0.046
Tabanidae	MT	81.9	0.001
Tephritidae	MT	61.1	0.191
Tipulidae	MT	54.9	0.021
Diptera: unknown	YPT	61.9	0.011
Embioptera	YPT	31.2	0.300
Hemiptera (Heteropterans)			
Anthocoridae	FIT	34.2	0.171
Ceratocombidae	FIT	42.5	0.029
Coreidae	YPT	29.4	0.313
Cydnidae	PT	40.8	0.225
Lygaeidae	YPT	36.2	0.453
Miridae	MT	36.7	0.232
Reduvidae	MT	30.7	0.589
Salpingidae	FIT	27.3	0.355
Heteroptera: juveniles	FIT	21.4	0.863
Heteroptera: unknown (Homopterans)	FIT	32.0	0.434
Achilidae	FIT	53.4	0.040
Aleyrodidae	MT	58.3	0.328
Aphidoidea	YPT	54.5	0.098
Aphrophoridae	YPT	78.9	0.010
Cercopidae	YPT	46.7	0.043
Cicadellidae	YPT	38.9	0.035
Cixiidae	FIT	51.5	0.035
Coccoidea	PT	40.6	0.081
Delphacidae	YPT	74.5	0.012
Derbidae	MT	57.2	0.043
Fulgoridae	MT	25.6	0.395
Meenoplidae	MT	57.8	0.079
Psylloidea	FIT	49.3	0.008
Fulgoroidea: juveniles	MT	39.0	0.419
Hymenoptera			
Apidae	MT	53.3	0.045

Taxa	Method	Indicat. val. (%)	*P*-value
Apoidea	MT	34.3	0.380
Aulacidae	MT	46.9	0.045
Bethylidae	MT	42.4	0.194
Braconidae	MT	64.7	0.006
Ceraphronidae	YPT	73.4	0.006
Chalcididae	MT	65.9	0.014
Chalcidoidea	MT	49.4	0.124
Chrysididae	MT	42.6	0.035
Crabronidae	MT	46.5	0.067
Cynipoidea	MT	61.4	0.014
Diapriidae	MT	42.1	0.237
Elasmidae	MT	31.1	0.113
Encyrtidae	YPT	73.3	0.001
Eucoilidae	YPT	16.4	0.570
Eupelmidae	MT	38.4	0.129
Eurytomidae	MT	66.9	0.002
Evaniidae	MT	72.3	0.002
Formicidae	PT	66.6	0.001
Halictidae	MT	54.4	0.086
Ichneumonidae	YPT	58.5	0.045
Mutilidae	YPT	42.7	0.171
Platygastridae	MT	30.2	0.577
Pompilidae	YPT	47.8	0.018
Proctotrupoidea	MT	30.9	0.236
Scelionidae	YPT	45.2	0.135
Scoliidae	MT	62.2	0.001
Sphecidae	YPT	54.2	0.007
Tiphiidae	YPT	42.8	0.096
Torymidae	MT	58.0	0.016
Vespidae	YPT	50.1	0.029
Hymenoptera: juveniles	MT	31.8	0.405
Isopoda	PT	57.5	0.029
Isoptera	FIT	39.0	0.139
Termitidae	FIT	55.6	0.005

Taxa	Method	Indicat. val. (%)	*P*-value
Lepidoptera	MT	54.5	0.017
Geometridae	YPT	31.1	0.384
Lepidoptera: juveniles	PT	39.7	0.192
Mantodea	MT	43.2	0.122
Neuroptera			
Coniopterygidae	FIT	78.3	0.001
Myrmeleontidae	MT	68.1	0.007
Opiliones	MT	18.7	0.865
Orthoptera			
Acrididae	YPT	37.3	0.274
Gryllidae	PT	73.0	0.001
Pyrgomorphidae	PT	25.3	0.490
Tetrigidae	PT	41.9	0.068
Tettigoniidae	MT	33.1	0.362
Tridactylidae	YPT	36.6	0.270
Pseudoscorpiones	PT	21.6	0.521
Psocoptera	FIT	47.5	0.043
Thysanoptera	YPT	65.7	0.002
Trichoptera	FIT	51.7	0.014

Taxa are listed alphabetically by order, detailing the sampling method for which the maximum indicator value was recorded; the maximum indicator value; and the *P*-value of Monte Carlo permutations testing the statistical significance of the maximum indicator value. Indicator values for taxa indicated in bold are significant with $P < 0.05$

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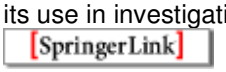

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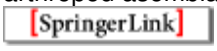

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