

Faunal turnover of arthropod assemblages along a wide gradient of disturbance in Gabon

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We examined the results of a study in Gamba, Gabon, focusing on the impacts of disturbance on arthropods, including more than 400 000 individuals, from which 21 focal taxa were separated into 1534 morphospecies by parataxonomists. Replication included the understorey of three sites in each of four different stages of forest succession and land use (= 'habitats') after logging (old and young forests, savanna and gardens), surveyed over a whole year with three sampling methods. Generally, there was a good correspondence between the number of species sorted by taxonomists and the number of morphospecies sorted by parataxonomists. Despite higher taxonomic groups being present in most habitats, a large proportion of insect species was site- or habitat-specific. Anthropogenic modification of habitats did not result in a monotonic decline of abundance and diversity, as many herbivore pests and their associated predators and parasitoids invaded gardens, where plant productivity was kept artificially high year-round through watering and crop rotation. Because gardens were colonized mostly by invasive crop pests with little relation with the forest fauna, these results emphasize the concept of maintenance of 'quality biodiversity' and the value of considering other variables than species richness alone in conservation studies. Further, several lines of evidence indicated that savanna habitats at Gamba supported a species-poor arthropod fauna distinct from that in nearby habitats. It is therefore questionable whether in Africa insect assemblages of savanna represent a smaller subset of their neighboring forest fauna.

Key words: biodiversity; parataxonomy; rainforest; savanna; species replacement, insect conservation.

INTRODUCTION

The distribution of plant and animal species is a major theme in ecology. Sadly, evaluating loss of species following anthropogenic disturbance is rapidly becoming another significant theme in ecology and one of the main research topics in conservation biology. The demise of tropical rain-

forests and the pace at which biodiversity is inventoried within these forests, especially arthropods, means that many organisms may go extinct before they are known to science (Wilson 2000). Whereas the magnitude of this process may be debatable, what is certain is that we know little of the majority of species' interactions within tropical rainforests and therefore how vulnerable they

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may be to anthropogenic disturbance, how quickly they will be lost and what can be attempted to slow down these extinctions (Lawton & May 1995).

Reliable data on the vulnerability of species to extinction and their extinction threats also require sound biological monitoring of tropical ecosystems, which is not limited to a few flagship or umbrella species (Lawton *et al.* 1998). Thus, a crucial problem is the consideration of multi-taxa assemblages, including functional guilds, to properly assess arthropod responses to disturbance (Didham *et al.* 1998; Lawton *et al.* 1998; Kotze & Samways 1999). Perhaps 80–90 % of tropical taxa have never been the focus of tropical conservation studies, and the consequences of this taxonomic selectivity urgently need to be assessed (Lewis & Basset 2007). Studies of tropical arthropods and disturbance rarely provided enough replication for a wide range of taxa, because of the huge scale of biological effort involved (Lawton *et al.* 1998). The task of monitoring a sufficient number of taxa at various locations with adequate time may appear daunting. In practice, training and working with parataxonomists (i.e. local assistants trained by professional biologists: Janzen 1992) can help to alleviate these problems and ensure that statistical replicates are representative of the system studied (Basset *et al.* 2004a).

In Africa, basic ecological information on described species of tropical arthropods is typically fragmentary and often relates to a few locality types. Largely as a result of Africa's colonial history, the insect fauna is probably better known than other tropical regions, but the information is stored in European museums and libraries and therefore often more difficult to locate (Miller & Rogo 2001). Gaps in our knowledge are evident, even for well-studied taxa (Miller & Rogo 2001). Further, studies focused on the impact of anthropogenic disturbance on arthropods (overview in Miller & Rogo 2001) are relatively few and often examine a handful of taxa, usually ants, dung beetles, butterflies, termites or mosquitoes (e.g. Nummelin & Hanski 1989; Eggleton *et al.* 1995; Watt *et al.* 1997; Wagner 2000; Zilihona & Nummelin 2001; Schulz & Wagner 2002; Stork *et al.* 2003; Minakawa *et al.* 2005; Bobo *et al.* 2006; Lachat *et al.* 2006). To the best of our knowledge, with perhaps the exception of Lawton *et al.* (1998), there has been no study (a) dedicated to studying a wide anthropogenic gradient of disturbance (as opposed to studying non-disturbed *vs* disturbed forests), and (b) selecting a wide range of focal taxa that represent

diverse taxonomic and functional guilds.

Further, although many studies adequately summarize their findings (i.e. by detailing different variables accounting for community characteristics and/or providing multivariate analyses displaying most of the variance of the study system), they often fail to discuss whether species may be replaced along disturbance gradients. Species replacement represents an important variable in conservation studies, which can only be discussed adequately with identified species (Summerville 2004). Species replacement may be evaluated statistically by testing whether species may be considered as site- or habitat-specific. This point is important if, for example, one wants to discuss the origin of arthropod assemblages associated with savanna in Africa (Fisher & Robertson 2002). There is currently a debate whether rainforest loss in Africa (and subsequent invasion of savanna) has been historically triggered by changes in climate or prehistoric human impacts (Brncic *et al.* 2007).

Here we examine the results of a study based on the work of trained parataxonomists in Gabon (Basset *et al.* 2004b). Replication included three sites in each of four different stages of forest succession and land use (= 'habitats') after logging, surveyed over a whole year using three sampling methods. We evaluated the impacts of disturbance on a range of arthropod assemblages representing different feeding guilds. Our specific questions in this contribution are explicitly focused on taxonomy, as opposed to analyzing community characteristics (Basset *et al.* 2004b; 2008), and include whether

- pre-sorting of the material by parataxonomists is reasonable compared to sorting by taxonomists;
- which higher arthropod taxa are most affected by habitat changes, in terms of abundance; and
- which morphospecies/species may be considered as site or habitat-specific in our study system.

MATERIAL AND METHODS

Study area and sites

The study area was in the Shell Gabon oil concession of Gamba (Table 1), 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

Table 1. 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	<i>Neochevalierodendron stephanii</i> (A. Chevalier) Léonard dominant, <i>Diospyros zenkeri</i> (Gurke) F. White and <i>D. verwoeseni</i> De Wild common
B	Old forest	02°42'54"S 10°00'00"E	84	Secondary forest, tallest trees = 45 m, sandy soil	<i>Neochevalierodendron stephanii</i> dominant, <i>Diospyros zenkeri</i> , <i>D. verwoeseni</i> and <i>Palisota ambigua</i> 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	<i>Diospyros verwoeseni</i> and <i>D. conocarpa</i> Gurke ex K. Schum common, <i>P. ambigua</i> and <i>Trichoscypha acuminata</i> 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	<i>Palisota ambigua</i> , <i>Aframomum</i> sp. and <i>Rauvolfia</i> sp. common; one pioneer <i>Musanga cecropioides</i> 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	<i>Xylopia hypolampra</i> Mildb. and <i>Xylopia</i> spp. dominant
F	Young forest	02°47'32"S 10°03'45"E	166	Secondary forest, plot at the edge of a thin tongue of forest connected to a large forested area; tallest trees = 30 m, important re-growth in the understorey, sandy soil	<i>Pachyodanthium staudtii</i> Engl. and Diels, <i>Diospyros verwoeseni</i> , <i>Palisota ambigua</i> , <i>Leptactina mannii</i> Hook.f., <i>Ouratea sulcata</i> (Van Tiegh.) Keay, <i>Sacoglottis gabonensis</i> (Baillon) Urb. and <i>Bertiera subsessilis</i> 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 %	<i>Borreria verticillata</i> (L.) GFW Mey and two unidentified Poaceae dominant, <i>Cyperus tenax</i> Boeck and <i>Dracaena</i> sp. present
H	Savanna	02°44'11"S 10°00'22"E	3.0	Surrounded by forest, sandy soil, bare soil = 25 %	<i>Borreria verticillata</i> , <i>Dracaena</i> sp. and one unidentified Poaceae dominant, <i>Cyperus halpan</i> J. Kern and <i>Heterotis decumbens</i> (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 %	<i>Merrremia tridentata</i> Hallier f., <i>Cyperus tenax</i> 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

following the selective logging of Okoumé (*Aucoumea klainiana* Pierre). 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 Gamba oil field has been active since 1967 and Gamba has grown from a small village in 1960 to a town of 8000 inhabitants. The earliest cultivated crop gardens of notable size were established near the town in 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) 'old forests', the understorey of the interior of old secondary rainforests; (b) 'young forests', the understorey of the edge of young secondary rainforests; (c) 'savanna', an area of rainforest cleared to install oil rigs and subsequently invaded by savanna; and (d) 'gardens', cultivated crop 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 1 (see also 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 epigeic arthropods of the understorey and litter: one ground Malaise trap, four ground yellow pan traps and five pitfall traps buried in the ground. At each site, a Malaise trap occupied the center of the set of traps, with four pitfall traps established to the North, South, East and West, 10 m distant from the Malaise trap. Four yellow-pan traps were set up at equal distances between the pitfall traps, again 10 m distant from the Malaise trap. The fifth pitfall trap was established 30 m north of the Malaise trap. Other details about the traps and mode of action are given by Basset *et al.* (2004b). The 120 traps were operated for three days during each of the 38 survey periods from July 2001 to July 2002. A team of eight parataxonomists was trained and supervised by a professional entomologist throughout the project; see Basset *et al.* (2004a) for detailed discussion of this strategy and Krell (2004) for critical considerations.

The material collected was first sorted into families or higher taxa by the parataxonomists.

The material belonging to 21 focal taxa (Table 2) was separated 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, *sensu* Cranston 1990) 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 rationale for selecting the focal taxa were (a) being well represented in the samples (so that much information was retained); (b) reasonably well-known taxonomically; (c) taxonomists having expressed interests in working on the material; and (d) representation of a variety of functional guilds and orders (Table 2). Specimens were 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

As far as possible, we considered data sets of highest possible taxonomic resolution, including a mixture of morphospecies and species (see results concerning the relationships between these two variables; hereafter referred to as 'species' for sake of simplicity). To gauge how sorting of insect material by parataxonomists affected our interpretation of the results and, particularly, the ranking of sites along the disturbance gradient, we performed a two step analysis. First, we chose a straightforward approach by quantifying faunal turnover among sites (beta-diversity) using detrended correspondence analysis (DCA), with options set as scaling with Hill's scaling, detrending the data by segments, and using untransformed data (ter Braak & 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. For this analysis, we considered the larger dataset, including the abundance of the most common species and morphospecies at the different sites (≥ 12 individuals; i.e. at least on average one individual collected at each site; 227 morphospecies). Results of this analysis are detailed and discussed in Basset *et al.* (2008). Second, we compared the scores of sites on Axis 1 of this DCA with similar scores originating from two similar analyses: (a) a DCA

Table 2. Focal taxa considered in this study. Guild assignment follows the system of Moran & Southwood (1982). Ind = no. individuals collected; Indm = no. individuals morphotyped by parataxonomists (some damaged or lost material could not be morphotyped; some material collected by flight-interception traps was not considered in this study); Mor = total no. of morphospecies sorted by parataxonomists from Indm.

Focal taxa	Order	Guild	Ind	Indm	Mor
Mantodea	Mantodea	Predators	98	50	19
Acrididoidea ¹	Orthoptera	Leaf-chewers	1129	360	40
Fulgoroidea ²	Hemiptera	Sap-suckers	4022	2345	233
Membracidae	Hemiptera	Sap-suckers	37	35	14
Buprestidae	Coleoptera	Wood-eaters	115	91	14
Scarabaeidae	Coleoptera	Leaf-chewers, scavengers	2240	1980	81
Coccinellidae	Coleoptera	Predators	1409	1200	32
Histeridae	Coleoptera	Predators	682	589	20
Cleridae	Coleoptera	Predators	45	18	12
Tenebrionidae	Coleoptera	Scavengers	839	605	54
Cerambycidae	Coleoptera	Wood-eaters	278	79	34
Chrysomelidae	Coleoptera	Leaf-chewers	2285	1,761	157
Neuroptera ³	Neuroptera	Predators	235	133	21
Asilidae	Diptera	Predators	409	333	47
Dolichopodidae ⁴	Diptera	Predators	7339	2113	38
Tephritidae	Diptera	Leaf-chewers ⁵	535	426	34
Syrphidae	Diptera	Predators, scavengers	459	369	32
Pipunculidae	Diptera	Parasitoids	123	97	16
Ichneumonidae	Hymenoptera	Parasitoids	2302	1880	420
Chalcidoidea ⁶	Hymenoptera	Parasitoids	4577	1302	175
Apoidea ⁷	Hymenoptera	Leaf-chewers ⁸	1239	1049	93

¹Including Acrididae (Acr), Pyrgomorphidae (Pyr), and many juveniles, not morphotyped.

²Including Achilidae (Ach), Cixiidae (Cix), Delphacidae (Del), Derbidae (Der), Dictyopharidae (Dic), Eurybrachidae (Eub), Flatidae (Fla), Fulgoridae (Ful), Issidae (Iss), Meenoplidae (Mee), Ricianiidae (Ric), Tettigometridae (Tem) and Tropiduchidae (Tro).

³Including Berothidae (Ber), Coniopterygidae (Con), Chrysopidae (Chy), Dilaridae (Dil), Hemerobiidae (Hem), Mantispidae (Mat), Myrmeleontidae (Mym) and Osmiidae (Osm).

⁴Only morphotyped from July–December 2001, then kept unassigned in alcohol.

⁵Subguild: fruit-feeders.

⁶Only >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).

⁷Including Apidae (Api), Halictidae (Hal) and Megachilidae (Meg).

⁸Subguild: pollinators.

comparing the most common species sorted by taxonomists and (b) a DCA comparing the most common morphotaxa as sorted by parataxonomists.

Overall abundance and observed species richness were extracted from raw data for each focal taxon at each site, since sampling effort was similar at each site (although not in terms of individuals collected, species rarefaction detailed in Basset *et al.* 2008). We pooled data of 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 arthropod abundance for higher taxa varied significantly across habitat types with one-way ANOVA and Tukey's

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. This procedure calculates the expected proportion of false positives among all significant hypotheses with $P < 0.05$ (García 2004).

To evaluate which species may be indicative of particular sites and habitats, we used the indicator value index (Dufrêne & Legendre 1997). The indicator values range from zero (no indication) to 100 (perfect indication). Perfect indication means that the presence of a taxon points to a particular site or habitat without error, at least with the data set in hand. We restricted the data set to the most

Table 3. Target taxa identified by taxonomists. Ide = no. individuals identified by taxonomist; Spp = no. of species sorted by taxonomist from Ide; Sm = no. of morphospecies sorted by parataxonomists from Ide (% error to no. of species sorted); Spl = no. spp. split by parataxonomists; Lum = no. spp. lumped by parataxonomists; Indw = no. individuals wrongly assigned by parataxonomists from Ide (% error to total identified); % G = % of generic identifications; % S = % of species-level identifications; Nov = no. of new species recognized in the material identified.

Target taxa	Taxonomist	Ide	Spp	Sm (%)	Spl	Lum	Indw (%)	%G	%S	Nov
Cerambycidae	S. Lingafelter	133	51	53 (4)	4	2	10 (8)	75	29	0
Chrysomelidae	T. Wagner	899	157	169 (8)	15	3	105 (12)	25	3	3
Galerucini	T. Wagner	259	37	49 (32)	15	3	95 (37)	81	11	3
Buprestidae	G. Curletti	95	16	16 (0)	2	2	11 (12)	100	50	0
Pipunculidae	M. De Meyer	95	22	16 (27)	9	15	32 (34)	100	32	3
Neuroptera	M.W. Mansell	106	25	25 (0)	1	1	7 (7)	64	36	0
Apoidea	C.D. Eardley	564	51	93 (82)	28	14	249 (44)	100	24	0

abundant morphospecies (≥ 12 individuals; $n = 227$) and tested whether morphospecies were indicative of particular sites ('site-specific' species), or of particular habitats ('habitat-specific' species), particularly for old and young forests (133 morphospecies). The significance of the highest indicator value for a given species across groups was tested for each species by Monte Carlo randomization with 1000 permutations, performed with PC-ORD (McCune & Medford 1999).

RESULTS

In total, 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 represented 16 855 individuals and 1534 morphospecies (Table 2). Further, 347 species were recognized from the seven focal taxa which to date have been examined by taxonomists (Table 3). On average, the parataxonomist team sorted 11 300 specimens for each survey. This represents a sorting rate of approximately 100 specimens sorted to family and order level per hour and per person. Most of the material examined by taxonomists could be assigned between 75–100 % to genera, and between 29–50 % to known species (Table 3). Generally, there was a significant and good correspondence between the number of species sorted by taxonomists and the number of morphospecies sorted by parataxonomists ($r = 0.96$, $P < 0.01$, $n = 7$). However, parataxonomists often erred on sorting known species, resulting in between 8 and 44 % of individuals being wrongly assigned. Most of the errors involved splitting species into different morphotypes (Table 3). Bees proved particularly difficult

to sort correctly by parataxonomists. There was a highly significant correlation between the scores of sites on Axis 1 of the DCAs performed with taxonomist data and with parataxonomist data ($r = 0.998$, $P < 0.001$). There were also highly significant correlations between the scores of sites on Axis 1 of the DCA based on the larger matrix (i.e. including all species and morphospecies) and similar scores from DCAs based on taxonomist and parataxonomist data ($r = 0.986$ and $r = 0.989$, respectively, $P < 0.001$).

Community characteristics accounting for the intensity of faunal changes between habitats (abundance; observed, rarefied and estimated species richness; proportion of rare species; diversity partitioning; evenness of assemblages; species turnover; nestedness; proportion of site-specific species and ratios of functional guilds) are detailed elsewhere for each focal taxon (Basset *et al.* 2004b, 2008). In sum, these analyses indicated that overall arthropod responses emphasized differences between forests and open habitats, with cleared forest subsequently invaded by savanna being the least populated and less diverse habitat. As far as species richness was concerned, we could not consider our disturbance gradient as a series of impoverished habitats derived from older forests. When considered at this local scale, anthropogenic modification of habitats did not result in a monotonic decline of diversity, as many herbivore pests and their associated predators and parasitoids invaded gardens, where plant productivity was kept artificially high year-round through watering and crop rotation. Responses to disturbance of most focal taxa were uncorrelated.

Of 55 families representing the focal taxa, 48, 47,

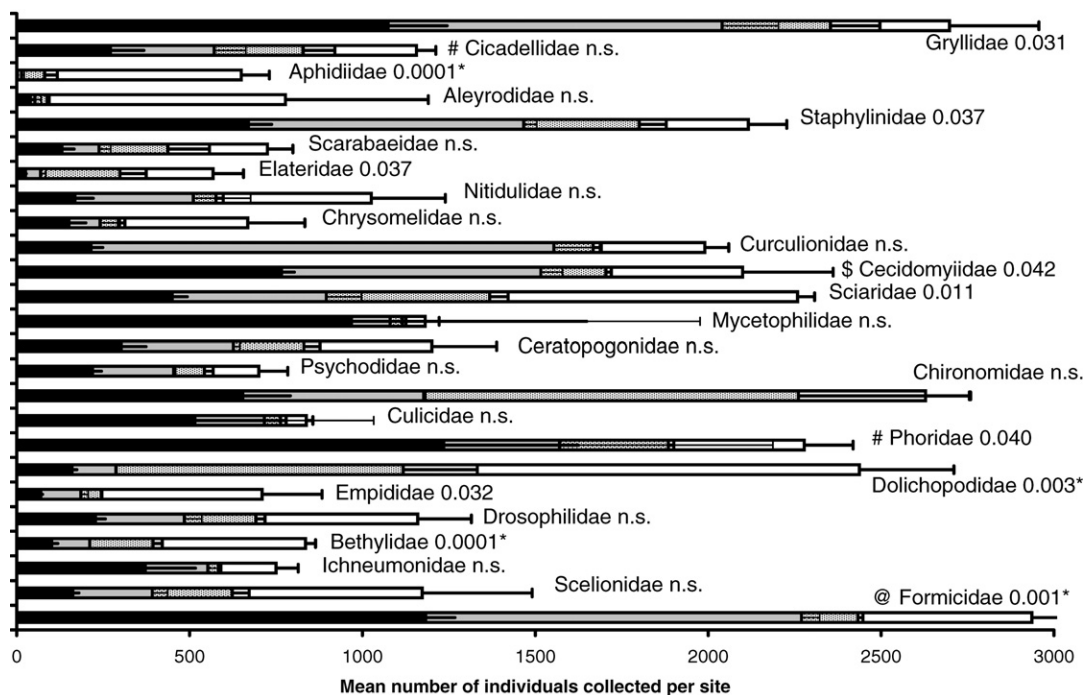


Fig. 1. Mean number of individuals (± 1 S.E.) collected per site for the 25 most common insect families, detailed per habitat (black = old forest, grey = young forest, stippled = savanna, white = garden). Figures indicate the P -value of an ANOVA with habitat as factor: n.s. = not significant; * = multiple test significant with the false detection rate method $P = 0.003$. For sake of clarity: # = all means per habitat scaled by a factor 1/3; \$ = all means per habitat scaled by a factor 1/5; @ = all means per habitat scaled by a factor 1/15.

42 and 48 families occurred in old forests, young forests, savanna and gardens, respectively. A few families of Fulgoroidea were missing in savanna, a few of Chalcidoidea in forests and savanna and a few of Neuroptera in all habitats. Family occurrence was not significantly different across habitats, as tested with a Kruskal-Wallis test ($W = 3.348$, $P = 0.341$). The abundance of 14 of 21 focal taxa was significantly different among habitats (Basset *et al.* 2008). Few taxa were significantly more abundant in forests than in open habitats (Cerambycidae, Cleridae and Ichneumonidae). Many taxa were more abundant in non-forested habitats and particularly in gardens (Fulgoroidea, Buprestidae, Coccinellidae, Tenebrionidae, Neuroptera, Dolichopodidae, Syrphidae, Pipunculidae, Chalcidoidea and Apoidea). Only Acridoidea were more abundant in savanna than in other habitats. As a further illustration of this trend, Fig. 1 details the abundance per habitat of the 25 most abundant insect families in our collections. Among them clear differences emphasized

the better representation of Formicidae, Phoridae, Cecidomyiidae, Staphylinidae and Gryllidae in forests, against the clear preferences of Aphidiidae, Sciaridae, Dolichopodidae and Bethylidae for gardens. Since, overall, arthropod abundance was correlated with observed species richness ($r = 0.530$, $P < 0.014$, $n = 228$; data presented in Basset *et al.* 2008), we can expect to some extent distribution patterns of species richness to follow those reported for abundance.

Most of the species tested could be considered habitat- or site-specific (92 % and 82 % of species tested, respectively). Four focal taxa included species indicative of all habitats, Fulgoroidea, Scarabaeidae, Dolichopodidae and Asilidae, (Fig. 2). A high proportion of Apoidea species was indicative of garden habitats (Appendix 1 online). When we restricted our comparison between old and young forests, 29 % of species could be considered as being significantly habitat-specific, including 21 species for old forests and 17 for young forests. The former category included 10 species of

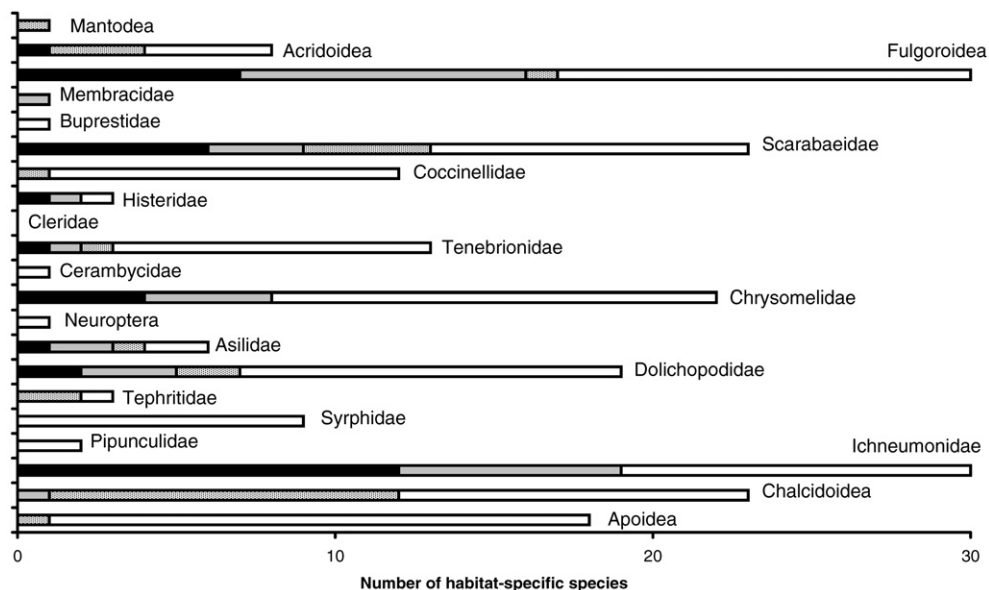


Fig. 2. Number of habitat-specific species for each focal taxon, detailed per habitat (black = old forest, grey = young forest, stippled = savanna, white = garden).

Ichneumonidae, three of Chrysomelidae, two each of Achilidae and Cixiidae, and one each of Fulgoridae, Scarabaeidae, Asilidae and Dolichopodidae. Significant indicator species for young forests included four species of Ichneumonidae, three each of Derbidae and Scarabaeidae, two of Chrysomelidae, and one each of Cixiidae, Histeridae, Tenebrionidae, Asilidae and Chalcididae. The most widespread species, as estimated by site occupancy, included 22 species present in all four habitats and at least in eight sites: ten species of Dolichopodidae, four of Scarabaeidae, and one each of Cixiidae, Histeridae, Chrysomelidae [*Galerudolphia tenuicornis* (Jacoby)], Asilidae, Ichneumonidae, Chalcididae and Apidae (*Apis mellifera* L.).

We now briefly discuss species replacement among habitats for species of focal taxa identified at least to genus (Appendix 1 online). Beside a species of *Coptops* common in gardens, Cerambycidae were only abundant in forests and included various species of *Monochamus*, *Pseudoxylamia*, *Litopus*, etc. Apart from two species of *Glenea* and *Pseudoxylamia*, common in both old and young forests, most species were collected in low numbers in one of the two forest habitats. Our chrysomelid samples from old and young forests included many species from a yet undescribed genus near *Barombiella*, typical from lowland rainforests of the

Guineo-Congolian forest block. Other species well-represented in our forest habitats included *Bonesia* sp. and *Galerudolphia tenuicornis*, a species which has been mainly recorded from forests through the Congo Basin to Zambia (Bolz & Wagner 2005). Many chrysomelid species recorded from gardens included crop pests, such as *Lema* spp. often feeding on Convolvulaceae and Dioscoreaceae; *Diacantha*, *Lamprocopa*, and *Leptaulaca* feeding on Cucurbitaceae and Solanaceae; and some rather polyphagous species in the genera *Luperus* and *Exosoma* (Jolivet & Hawkwood 1995).

Among Buprestidae, *Agilus* spp. mostly recruited from forest habitats but *Chrysobothris dorsata* could be considered as indicator of gardens. Forest habitats often included neuropteran genera such as *Podallea*, *Ankylopteryx*, *Oyochrysa* and *Spilosmylus*, whereas open habitats were more likely to include *Chrysoperla*, *Italochrysa*, *Myrmeleon* and *Nemoleon*. The pipunculid genera, *Eudorylas* and *Tomosvaryella*, were almost exclusively collected from savanna and gardens. *Eudorylas* spp. are confirmed parasitoids of Cicadellidae (Skevington & Marshall, 1997). Bees collected in the understorey mostly originated from savanna and gardens, with genera such as *Allodape*, *Apis*, *Braunapis*, *Lipotriches*, *Halictus*, *Lasiglossum* and *Patellapis* particularly common in gardens.

DISCUSSION

Limitations of the study

Our project is unusual for a study on the effects of anthropogenic disturbance on tropical arthropods because (a) it considers a wide gradient of disturbance beyond the usual disturbed/undisturbed forest dichotomy; (b) high spatial and seasonal replication; (c) use of different sampling methods; (d) it examines high numbers of individuals, morphospecies or species; and (e) considers a wide range of arthropod taxa, accounting for a variety of orders and functional guilds. That said, three caveats related to methodological constraints are evident in our study. First, although sampling methods used in this study were non-destructive and easily deployed and maintained during a year at all studied habitats, they were inadequate for many arthropod taxa (e.g. Lepidoptera are better collected with light traps, Agrilinae better collected with yellow sticky traps, etc.). Entomologists have devised protocols to survey specific taxa with the aims of maximizing species inventory. However, most of these rather qualitative protocols are difficult to implement in the context of biological monitoring for assessing the effects of ecosystem changes on arthropods. Thus, one must recall that protocols developed for biological monitoring, such as those used in this study, are not adequate to estimate local or regional species richness.

Second, forest canopies were not sampled, but most likely support a significant proportion of species not overlapping with those foraging in the understorey (Basset *et al.* 2001). For example, in central forests of Gabon at La Makandé, about 300 km from our sites, insect herbivores are 2.5 times more speciose in the upper canopy than in the understorey (Basset *et al.* 2001). Further, most species of *Agrilus* collected both at La Makandé and Gamba recruit from the understorey of old and young forests, not from the canopy (Curletti 2000, 2003). *Agrilus* species richness at La Makandé was estimated to be about four times higher in the canopy than in the understorey (Basset *et al.* 2001). Thus, overall estimates of species richness, including canopy habitats, are most likely higher in forests than in savanna or gardens. Third, even if the percentage of site-specific species may appear high (relative to the number of species tested), we consider these results as underestimates, as passive traps are more likely to collect common, rather unspecialized and

mobile species (Gaston & Lawton 1988). In practice, the fidelity of many insect species for particular habitats and study sites is probably higher than our data suggest.

Working with parataxonomists

Most of the field work, processing and pre-sorting of the material was achieved by a team of dedicated parataxonomists (Basset *et al.* 2000, 2004a). As far as we know, this is the first time a parataxonomist approach has been used on this scale in Africa for arthropods. The sorting accuracy of parataxonomists was reasonable, generally resulting in good correspondence between their morphospecies assignment and species sorting by taxonomists. There were notable exceptions (bees) that could have been improved by taxonomist feedback. This critical factor for a sound sorting of insect material by parataxonomists, not taken into account in Krell's (2004) critical review of parataxonomist studies, was difficult to implement in our study. Most errors in species assignment resulted from 'splitting' (see Krell 2004 for similar results), which was encouraged in our context of low taxonomist feedback. Since subsamples sent to taxonomists included a high proportion of 'doubtful' specimens, the parataxonomists probably assigned in reality a higher proportion of specimens correctly than proportions reported in Table 3. Although parataxonomists often sorted species with errors of less than 20 % of total species, it must be noted that overall levels of synonymy within the taxonomic community are also close to 20 % (May & Nee 1995). What might be the consequences of sorting errors for the interpretation of our data? Admittedly, our morphospecies assignment may preclude a sound discussion of local species richness for particular assemblages. However, since we checked that the ranking of sites along our obvious gradient of disturbance was not affected by either parataxonomists' or taxonomists' assignments, we conclude that this factor is unlikely to greatly modify the interpretation of our results. In summary, we agree with Krell (2004) that the work of parataxonomists in general has been a great benefit for biodiversity studies, but that it only represents the first step in sorting and identifying biological samples.

Overall differences among habitats studied

In Africa and elsewhere in the tropics, large arthropod surveys along anthropogenic gradients

of disturbance typically examined distribution patterns for less than 10 000 individuals representing fewer than 500 species, often belonging to one of a few taxa (Nummelin & Hanski 1989; Zilihona & Nummelin 2001; Stork *et al.* 2003; Bobo *et al.* 2006; Lachat *et al.* 2006). Studies performed with pyrethrum knockdown (Watt *et al.* 1997; Wagner 2000; Schulz & Wagner 2002) or targeting social insects or the minute soil fauna (Critchley *et al.* 1979; Eggleton *et al.* 1995; Noti *et al.* 1996) usually collected larger sample sizes but remained restricted to a few taxa. The pioneering multi-taxa study of Lawton *et al.* (1998) with a relatively large sample size remains unrivaled to date and, therefore, the generality of its conclusions are difficult to assess.

Overall differences, considering all focal taxa, among our habitats were clear. Plant productivity in gardens was kept artificially high year-round through watering and crop rotation. This resulted in higher insect abundance and observed species richness (Basset *et al.* 2008). Most arthropod variables emphasized large differences between forests and non-forests habitats. Despite higher taxonomic groups being present in most habitats and study sites, a large proportion of insect species was site- or habitat-specific. For example, in gardens, herbivores were not recruited from the pool of generalist herbivores in forests, but included many insect pests feeding on specific crops. However, despite the presence of several habitat-specific species, old and young forests were difficult to distinguish from one another. In sum, these results are consistent with other African studies that indicated few differences between old-growth and degraded forests when focusing on the observed richness of a variety of taxa (Lawton *et al.* 1998; Nummelin & Hanski 1989; Stork *et al.* 2003; Lachat *et al.* 2006). Our data also agree with a range of studies, detailed below, examining particular taxa and indicating either a decrease or increase of abundance in open habitats. Most of these patterns can be easily explained by the different life-histories and resource bases of relevant taxa.

Responses of particular focal taxa to disturbance

Three focal taxa showed obvious preferences for forests. As wood-eaters, Cerambycidae are tied with wood resources and their decline in savanna or in gardens is therefore understandable (Lachat

et al. 2006). Cleridae are often predators of other wood-eating species, such as Scolytinae, and are also expected to decline in open habitats. Desiccation seems to be a critical factor limiting the activity of parasitoids such as Ichneumonidae (Shapiro & Pickering 2000), which are rarely collected in hot, dry and sunny habitats (Gauld 1987).

The high abundance and diversity of African Acridoidea and Coccinellidae in open and disturbed habitats, and the fewer but distinct and specialized species belonging to these taxa in forests, is well documented (Couturier *et al.* 1984; Chazeau & Couturier 1985; Magagula & Samways 2001). Tenebrionidae are often generalist scavengers feeding on decaying matter of plant origin and tended to prefer gardens. Dolichopodidae are known to be particularly abundant in African savanna and gardens, where they may be preying on a variety of homopteran herbivores (Couturier & Duviard 1976). The latter may explain, along with good flying abilities, why some species of dolichopodid occurred at nearly all study sites. The high occurrence of Syrphidae and Pipunculidae in gardens is likewise probably related to the abundance of their homopterous prey (Aphidiidae, Aleyrodidae, Cicadellidae) in this habitat. There are at least two explanations to account for the high abundance and species richness of Apoidea in non-forested habitats. First, in forests bees tend to forage at the top of flowering trees, which were not sampled in this study. Second, many bees, especially social bees (*Apis*, *Allodape*, *Liotrigona*, *Meliponula*), are dependent on flower density and generalists and therefore are often more dominant in disturbed, weedy areas with a high diversity of flowering plants (Liow *et al.* 2001; Tylianakis *et al.* 2006).

Other focal taxa showed no obvious preferences for particular habitats. Fulgoroidea represent a diverse assemblage of several families of which Cixiidae, Derbidae and Fulgoridae preferred forests, and Delphacidae and Meenoplidae gardens. Dung beetles were more abundant in savanna than in other habitats, but of similar species richness in all habitats studied. In particular, few differences existed between old and young forests, as recorded by Nummelin & Hanski (1989) in Uganda. Dung beetle occurrence is mainly related to the presence of dung resources provided by mammals (Nummelin & Hanski 1989) and in our garden sites probably resulted from soil fertilization by compost and manure.

CONCLUSIONS

Noti *et al.* (1996) emphasized the faunal continuum of soil arthropods from forest to savanna sites in Congo. However, this situation may be different for epigeic and airborne arthropods. Several lines of evidence in this study indicated that savanna habitats at Gamba support a species-poor arthropod fauna distinct from that in nearby habitats. As noted for ants in Madagascar, it is therefore questionable whether insect assemblages of African savanna represent a smaller subset of their neighboring forest fauna (Fisher & Robertson 2002). Whether the faunal assemblages in coastal savannas of Gabon, which today are isolated from the rich and diverse savannas south and north of the Congolian forest block (Duviard & Pollet 1973), are different from assemblages in savannas elsewhere in Africa would equally represent an issue worthy of investigation.

Since 1998, garden sites at Gamba have been colonized mostly by invasive crop pests with little relation to the forest fauna. Garden assemblages at Gamba emphasize the concepts of maintenance of 'quality biodiversity' (Magagula & Samways 2001). While these assemblages have high local alpha diversity (Basset *et al.* 2008) and may be considered quite habitat-specific at the local or

meso-scale, they consist mostly of pests, vagrant and generalist species of lower conservation value which are unlikely to contribute to high spatial beta-diversity and overall species richness at the regional scale. Hence, conservation studies assessing the effects of ecosystem change should imperatively report additional variables to species richness, such as abundance or spatial and temporal partitioning of species turnover (Tylianakis *et al.* 2006), for a sound interpretation of results.

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Appendix 1. Total abundance of identified species (at least to genus) in the different habitats studied. Species are listed alphabetically by families, detailing the site for which the maximum indicator value was recorded (Site); the maximum indicator value (IV); and the *P*-value of Monte Carlo permutations testing the statistical significance of the maximum indicator value. Olf = Old forests; Yof = young forests; Sav = savanna; Gar = gardens.

Taxon/Code	Species	Olf	Yof	Sav	Gar	Site	IV (%)	<i>P</i>
Buprestidae								
COBUPR05	<i>Agrilus (Agrilus) kraatzii</i> Kerremans, 1899	1	1	–	–	–	–	–
COBUPR14	<i>Agrilus (Melagrilus) escaleraei</i> Obenberger, 1921	–	1	–	–	–	–	–
COBUPR04	<i>Agrilus (Pinarius) subgriseus</i> Kerremans, 1898	–	1	–	–	–	–	–
COBUPR06	<i>Agrilus (Robertius) africanus</i> Kerremans, 1899	2	–	–	–	–	–	–
COBUPR15	<i>Agrilus (Robertius) gibbosus</i> Kerremans, 1899	1	–	–	–	–	–	–
COBUPR10	<i>Agrilus (Robertius) pertener</i> Obenberger, 1935	–	1	–	–	–	–	–
COBUPR19	<i>Agrilus (Robertius) sp. 1</i>	1	–	–	–	–	–	–
COBUPR11	<i>Agrilus (Robertius) zebratus</i> Curletti, 1999	–	–	–	1	–	–	–
COBUPR02	<i>Aphanisticus cf. bourgoini</i> Obenberger, 1928	–	1	–	1	–	–	–
COBUPR08	<i>Aphanisticus sp. 1</i>	–	–	1	9	–	–	–
COBUPR01	<i>Chrysobothris dorsata</i> Fabricius, 1787	–	–	26	37	L	11	0.001
COBUPR18	<i>Habroloma cf. cara</i> Kerremans, 1913	1	–	–	–	–	–	–
COBUPR13	<i>Parataenia chrysochlora</i> Palisot, 1805	–	1	–	–	–	–	–
COBUPR12	<i>Sambus sp. 1</i>	–	–	2	2	–	–	–
COBUPR03	<i>Trachys sp. 1</i>	1	1	–	1	–	–	–
COBUPR17	<i>Zitella sp. 1</i>	–	–	–	1	–	–	–
Cerambycidae								
COCERA47	<i>Arrhytmus fenestratus</i> (Belon)	4	–	–	–	–	–	–
COCERA32	<i>Calybistum sp. 1</i>	–	1	–	–	–	–	–
COCERA05	<i>Chromalizus sp. 1</i>	1	–	–	–	–	–	–
COCERA07	<i>Coptops sp. 1</i>	–	1	–	14	K	8.6	0.004
COCERA26	<i>Cordoxylamia cordifera</i> (Chevrolat)	1	–	–	–	–	–	–
COCERA10	<i>Cordylomera apicalis</i> Thomson	1	1	–	1	–	–	–
COCERA12	<i>Domitia sp. 1</i>	2	1	–	–	–	–	–
COCERA13	<i>Freya floccifera</i> Quedenfeldt	–	1	–	–	–	–	–
COCERA02	<i>Glenea mephisto</i> Thomson	3	3	–	–	–	–	–
COCERA20	<i>Hippopsicon sp. ? lactollum</i> Thompson	–	1	–	–	–	–	–

Taxon/Code	Species	Olf	Yof	Sav	Gar	Site	IV (%)	P
COCERA30	<i>Litopus</i> sp. 1	5	–	–	–	–	–	–
COCERA29	<i>Litopus</i> sp. 2	1	–	–	–	–	–	–
COCERA25	<i>Metallyra</i> sp. 1	1	–	–	–	–	–	–
COCERA49	<i>Metallyra</i> sp. 2	–	1	–	–	–	–	–
COCERA38	<i>Monochamus griseoplagiatus</i> Thomson	–	1	–	–	–	–	–
COCERA18	<i>Monochamus</i> sp. 1	–	1	–	–	–	–	–
COCERA28	<i>Monochamus</i> sp. 2	–	1	–	–	–	–	–
COCERA27	<i>Nothophysis stuhlmanni</i> (Kolbe)	2	–	1	–	–	–	–
COCERA48	<i>Pachydissus</i> sp. 1	–	1	–	–	–	–	–
COCERA37	<i>Pachydissus</i> sp. 2	1	–	–	–	–	–	–
COCERA31	<i>Pellamnia gripha</i> Jordan	1	–	–	–	–	–	–
COCERA23	<i>Phytoecia (Blepisanus) incensa</i> (Pascoe)	–	1	–	–	–	–	–
COCERA09	<i>Promecidus linearis</i> (Linnaeus)	6	–	–	–	–	–	–
COCERA01	<i>Pseudoxylamia trianguligera</i> (Aurivillius)	6	4	–	–	–	–	–
COCERA24	<i>Velleda bassamensis</i> (Breuning)	–	1	–	–	–	–	–
Chrysomelidae								
COCHRY101	<i>Barombiella violacea</i> (Jacoby, 1894)	1	1	–	–	–	–	–
COCHRY64	cf. <i>Beiratia</i> sp. 1	–	–	1	–	–	–	–
COCHRY30	<i>Bonesia</i> sp. 1	–	29	–	1	E	29.6	0.001
COCHRY106	<i>Diacantha</i> sp. 1	–	2	–	–	–	–	–
COCHRY38	<i>Exosoma</i> sp. 1	–	2	–	–	–	–	–
COCHRY91	<i>Exosoma</i> sp. 2	–	–	–	5	–	–	–
COCHRY167	<i>Exosoma</i> sp. 3	–	1	–	–	–	–	–
COCHRY130	<i>Exosoma</i> sp. 4	–	–	–	1	–	–	–
COCHRY59	<i>Exosoma</i> sp. 5	3	–	–	–	–	–	–
COCHRY90	<i>Galerudolphia</i> sp. 1	–	–	1	–	–	–	–
COCHRY89	<i>Galerudolphia tenuicornis</i> (Jacoby, 1899)	8	64	2	5	D	13.3	0.002
COCHRY114	<i>Hespera</i> sp. 1	–	1	–	–	–	–	–
COCHRY112	<i>Lamprocopa</i> sp. 1	–	–	–	2	–	–	–
COCHRY28	<i>Lema</i> sp. 1	–	–	1	–	–	–	–
COCHRY126	<i>Lema</i> sp. 2	–	–	–	1	–	–	–
COCHRY128	<i>Lema</i> sp. 3	–	–	–	2	–	–	–

Taxon/Code	Species	Olf	Yof	Sav	Gar	Site	IV (%)	P
COCHRY118	<i>Lema</i> sp. 4	–	–	–	1	–	–	–
COCHRY107	<i>Lema</i> sp. 5	–	1	–	–	–	–	–
COCHRY108	<i>Lema</i> sp. 6	1	–	–	–	–	–	–
COCHRY25	<i>Lema</i> sp. 7	–	–	–	10	–	–	–
COCHRY93	<i>Lema</i> sp. 8	–	3	–	1	–	–	–
COCHRY60	<i>Lema</i> sp. 9	–	1	1	4	–	–	–
COCHRY58	<i>Lema</i> sp. 10	–	–	–	5	–	–	–
COCHRY36	cf. <i>Luperus</i> sp. 1	–	–	2	14	K	7.4	0.001
COCHRY76	<i>Leptaulaca</i> sp. 1	–	3	–	5	–	–	–
COCHRY70	<i>Medythia</i> sp. 1	–	–	–	3	–	–	–
COCHRY133	<i>Monolepta alwineae</i> Wagner, 2002	2	–	–	1	–	–	–
COCHRY02	<i>Neobarombiella prasina</i> (Weise, 1906)	–	3	–	1	–	–	–
COCHRY29	<i>Neobarombiella</i> sp. 1	2	7	–	1	–	–	–
COCHRY54	<i>Neobarombiella</i> sp. 2	–	5	–	–	–	–	–
COCHRY37	<i>Neobarombiella</i> sp. 3	–	–	3	1	–	–	–
COCHRY46	<i>Neobarombiella</i> sp. 5	–	18	–	–	D	14	0.001
COCHRY132	<i>Neobarombiella</i> sp. 6	1	–	–	–	–	–	–
COCHRY35	<i>Neobarombiella</i> sp. 7	19	–	–	–	A	6.1	0.011
COCHRY170	<i>Neobarombiella</i> sp. 8	1	–	1	2	–	–	–
COCHRY66	<i>Ootheca</i> sp. 1	–	4	–	–	–	–	–
COCHRY110	<i>Platyxantha</i> sp. 1	1	1	1	–	–	–	–
COCHRY32	<i>Platyxantha</i> sp. 3	1	–	–	–	–	–	–
COCHRY69	<i>Smaragrina scitula</i> Lacordaire, 1848	–	–	–	28	K	31.6	0.001
COCHRY116	<i>Sphaeroderma</i> sp. 1	1	–	1	25	–	–	–
COCHRY67	<i>Strobiderus</i> sp. 1	–	–	–	1	–	–	–
Berothidae								
NEBERO01	<i>Podallea</i> sp.	3	4	–	–	–	–	–
Chrysopidae								
NECHRY05	<i>Ankylopteryx</i> sp. 1	4	1	–	–	–	–	–
NECHRY06	<i>Chrysoperla pudica</i> (Navás, 1914)	1	–	2	1	–	–	–
NECHRY02	<i>Chrysoperla</i> sp. 1	–	–	–	4	–	–	–
NECHRY01	<i>Italochrysa</i> sp. 1	–	–	6	1	–	–	–

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NECHRY03	<i>Oyochrysa ancora</i> Brooks	3	1	–	1	–	–	–
NECHRY04	<i>Spilomyilus ? tristis</i> Tjeder, 1957	4	–	–	–	–	–	–
Dilaridae								
NEDILA01	<i>Nallachus</i> sp. 1	2	–	–	–	–	–	–
Myrmeleontidae								
NEMYRM05	<i>Creoleon nubifer</i> (Kolbe, 1898)	–	–	1	1	–	–	–
NEMYRM04	<i>Gymnoleon</i> sp. 1	–	–	1	1	–	–	–
NEMYRM07	<i>Macroleon lynceus</i> (Fabricius, 1787)	–	2	–	–	–	–	–
NEMYRM01	<i>Myrmeleon obscurus</i> Rambur, 1842	2	–	10	56	L	24.4	0.001
NEMYRM06	<i>Nemoleon iolanthe</i> (Banks, 1911)	–	–	–	1	–	–	–
NEMYRM02	<i>Nemoleon notatus</i> (Rambur, 1842)	–	–	1	–	–	–	–
NEMYRM13	<i>Nemoleon risi</i> (Esbe–Petersen, 1916)	–	–	2	1	–	–	–
NEMYRM03	<i>Nemoleon</i> sp. 1	1	–	4	3	–	–	–
Pipunculidae								
DIP1P117	<i>Cephalops vinnulus</i> Hardy	–	–	1	–	–	–	–
DIP1P107	<i>Eudorylas excisus</i> Hardy	–	–	–	4	–	–	–
DIP1P106	<i>Eudorylas mutilatus</i> (Loew)	–	–	1	–	–	–	–
DIP1P103	<i>Eudorylas</i> sp. 1	–	1	–	–	–	–	–
DIP1P109	<i>Eudorylas</i> sp. 2	–	–	–	1	–	–	–
DIP1P118	<i>Eudorylas</i> sp. 3	–	–	–	1	–	–	–
DIP1P110	<i>Eudorylas</i> sp. 4	–	–	5	2	–	–	–
DIP1P120	<i>Eudorylas</i> sp. 5	–	–	2	1	–	–	–
DIP1P121	<i>Eudorylas</i> sp. 6 (new)	–	–	–	1	–	–	–
DIP1P119	<i>Eudorylas</i> sp. 7 (new)	–	–	–	3	–	–	–
DIP1P123	<i>Eudorylas</i> sp. 8 (new)	–	1	–	1	–	–	–
DIP1P124	<i>Eudorylas</i> sp. 9	–	–	–	1	–	–	–
DIP1P102	<i>Eudorylas</i> sp. 10	–	–	–	2	–	–	–
DIP1P112	<i>Eudorylas</i> sp. 11	–	–	2	–	–	–	–
DIP1P122	<i>Eudorylas</i> sp. 12	–	–	–	1	–	–	–
DIP1P113	<i>Microcephalops fulvicaudus</i> De Meyer	–	–	–	6	–	–	–
DIP1P114	<i>Tomosvaryella ancylostyla</i> Hardy	–	–	4	18	K	6	0.011
DIP1P116	<i>Tomosvaryella</i> cf. <i>africana</i>	–	–	5	11	J	4.1	0.069

Taxon/Code	Species	Olf	Yof	Sav	Gar	Site	IV (%)	P
DIPII01	<i>Tomosvaryella cf. transvaalensis</i>	–	–	6	3	–	–	–
DIPII15	<i>Tomosvaryella mbuyensis</i> Hardy	–	–	1	2	–	–	–
DIPII11	<i>Tomosvaryella</i> sp. 1	–	–	–	3	–	–	–
DIPII08	<i>Tomosvaryella subvirescens</i> Loew	–	–	5	2	–	–	–
Apidae								
HYAPOI29	<i>Afranthidium (Immanthidium)</i> sp. 1	–	–	–	2	–	–	–
HYAPOI83	<i>Allodape interrupta</i> Vachal	–	–	5	6	–	–	–
HYAPOI13	<i>Allodape mea</i> Strand	1	–	3	7	–	–	–
HYAPOI72	<i>Amegilla kaimosica</i> (Cockerell)	–	–	1	–	–	–	–
HYAPOI10	<i>Apis mellifera</i> Linnaeus	4	5	18	33	L	15	0.001
HYAPOI36	<i>Braunsapis calidula</i> (Cockerell)	–	–	–	1	–	–	–
HYAPOI47	<i>Braunsapis facialis</i> (Gerstaecker)	–	–	–	21	L	31	0.001
HYAPOI64	<i>Braunsapis luapalana</i> (Cockerell)	–	2	45	29	I	12.4	0.001
HYAPOI02	<i>Braunsapis</i> sp. 1	–	–	3	95	L	26	0.001
HYAPOI16	<i>Ceratina (Ceratrina)</i> sp. 1	–	–	3	5	–	–	–
HYAPOI23	<i>Ceratina (Ceratrina)</i> sp. 2	–	–	1	–	–	–	–
HYAPOI43	<i>Ceratina (Ceratrina)</i> sp. 3	–	–	3	4	–	–	–
HYAPOI68	<i>Ceratina (Ceratrina)</i> sp. 4	–	–	3	7	–	–	–
HYAPOI14	<i>Ceratina (Pithitis) viridis</i> (Guerin)	–	–	1	3	–	–	–
HYAPOI19	<i>Liotrigona bottegoi</i> (Magretti)	1	–	2	2	–	–	–
HYAPOI18	<i>Meliponula lendliana</i> (Friese)	2	–	2	1	–	–	–
HYAPOI33	<i>Xylocopa imitator</i> Smith	1	–	–	–	–	–	–
Halictidae								
HYAPOI37	<i>Ceylalictus ?muiri</i> (Cockerell)	–	–	–	13	L	8.1	0.005
HYAPOI25	<i>Ceylalictus</i> sp. 1	–	–	2	27	L	10.8	0.001
HYAPOI49	<i>Lipotriches (Lipotriches)</i> sp. 1	–	1	1	54	K	16.4	0.001
HYAPOI50	<i>Lipotriches (Lipotriches)</i> sp. 2	–	–	2	70	L	20	0.001
HYAPOI48	<i>Lipotriches (Lipotriches)</i> sp. 3	–	–	1	33	K	39.6	0.001
HYAPOI78	<i>Lipotriches (Lipotriches)</i> sp. 4	–	–	–	5	–	–	–
HYAPOI74	<i>Lipotriches (Lipotriches)</i> sp. 5	–	–	1	3	–	–	–
HYAPOI27	<i>Lipotriches (Lipotriches)</i> sp. 6	–	–	–	1	–	–	–
HYAPOI65	<i>Lipotriches (Lipotriches)</i> sp. 7	–	–	–	1	–	–	–

Taxon/Code	Species	Olf	Yof	Sav	Gar	Site	IV (%)	P
HYAPOI22	<i>Lipotriches (Lipotriches)</i> sp. 8	2	–	–	1	–	–	–
HYAPOI71	<i>Lipotriches (Lipotriches)</i> sp. 9	–	–	1	–	–	–	–
HYAPOI28	<i>Halictus (Seladonia)</i> sp. 1	–	–	6	57	K	24.2	0.001
HYAPOI35	<i>Halictus (Seladonia)</i> sp. 2	–	1	1	14	K	11.8	0.001
HYAPOI12	<i>Lasioglossum (Ctenonomia)</i> sp. 1	–	–	33	53	K	13.3	0.001
HYAPOI73	<i>Lasioglossum (Ctenonomia)</i> sp. 2	–	–	–	25	L	37.9	0.001
HYAPOI58	<i>Lasioglossum (Ctenonomia)</i> sp. 3	1	–	–	20	K	25.6	0.001
HYAPOI30	<i>Nomia (Acunomia)</i> sp. 1	–	–	–	21	K	25.6	0.001
HYAPOI62	<i>Nomia (Acunomia)</i> sp. 2	–	–	–	2	–	–	–
HYAPOI76	<i>Nomia (Acunomia)</i> sp. 3	–	–	–	5	–	–	–
HYAPOI61	<i>Patellapis (Chaetalictus)</i> sp. 1	–	–	–	3	–	–	–
HYAPOI51	<i>Patellapis (Chaetalictus)</i> sp. 2	–	8	1	133	K	61.9	0.001
HYAPOI56	<i>Pseudapis (Pachynomia)</i> sp. 1	–	–	–	2	–	–	–
HYAPOI93	<i>Pseudapis (Pachynomia)</i> sp. 2	–	–	3	12	K	9.8	0.002
HYAPOI11	<i>Pseudapis (Pachynomia)</i> sp. 3	–	–	26	68	L	37.6	0.001
HYAPOI54	<i>Sphecodes</i> sp. 1	–	–	–	1	–	–	–
HYAPOI55	<i>Thrinchostoma (Thrinchostoma)</i> sp. 1	–	1	1	1	–	–	–
Megachilidae								
HYAPOI40	<i>Megachile (Chalicodoma)</i> sp. 1	1	–	–	–	–	–	–
HYAPOI79	<i>Megachile (Chalicodoma)</i> sp. 2	1	–	–	–	–	–	–
HYAPOI07	<i>Megachile (Creightonella)</i> sp. 1	–	–	1	–	–	–	–
HYAPOI45	<i>Megachile (Creightonella) discolor</i> Smith	–	–	5	–	–	–	–
HYAPOI20	<i>Megachile (Eutricharacea)</i> sp. 1	–	–	–	2	–	–	–
HYAPOI17	<i>Megachile (Eutricharacea)</i> sp. 2	–	–	–	1	–	–	–
HYAPOI42	<i>Megachile (Megella)</i> sp. 1	–	–	6	3	–	–	–
HYAPOI46	<i>Megachile (Megella)</i> sp. 2	–	1	–	–	–	–	–