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Species richness of phytophagous beetles in the tropical tree *Brosimum utile* (Moraceae): the effects of sampling strategy and the problem of tourists

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Abstract. 1. Phytophagous beetles on six mature living trees and two dead trees of *Brosimum utile* (Moraceae) were surveyed during 1 year in a tropical wet forest in Panama. The dead trees were surveyed both as suspended in the canopy and after falling down to the understorey.

2. Canopy access was provided by a construction crane and sampling was performed by beating and hand-collecting. The same amount of time was spent on each tree in order to standardise sampling effort. A list of all species associated with the tree is presented.

3. A total of 3009 individuals representing 364 species were collected. Tourists were excluded from the analyses by recording host associations directly and by probability assessments of host associations based on abundance categories. A total of 2603 individuals and 244 species were associated with the tree. The proportion of tourists in the trees increased with sample size.

4. A single mature living tree had on average 58.5 ± 6.5 species. The local species richness of *B. utile* was estimated as 2.5 times higher than in a single mature tree; however, a substantial increase in species richness was attained when dead wood habitats were included. Saproxylic species made up 82% of the total material.

5. The investigated habitat types of *B. utile* constituted distinct, complementary species assemblages. Similarity between saproxylic species of dead suspended wood and dead understorey wood of the same tree was 0.2 (Morisita–Horn index), confirming a prominent vertical stratification among this guild.

Key words. *Brosimum utile*, habitat types, host specificity, Panama, phytophagous beetles, sample size, species richness, tourists, tropical forests, vertical stratification.

Introduction

The number of arthropod species associated with tropical trees is one of the key determinants of species diversity in the tropics (Erwin, 1982; May, 1990; Basset *et al.*, 1996; Ødegaard, 2000a), and constitutes a most important ecological variable in studies of biotic relationships and processes that are important for the maintenance of biodiversity in tropical forests (May, 1990; Stork *et al.*, 1997; Basset *et al.*, 2003c; Novotny *et al.*, 2003).

The number of species associated with one plant species varies considerably, and it is influenced by several factors such as geographic range, local abundance and recent geological history (Southwood, 1960, 1961; Lawton & Schröder, 1977; Fowler & Lawton, 1982; Strong *et al.*, 1984), biochemical composition (Bernays & Chapman, 1994), habitat diversity (MacArthur, 1958; Anderson, 1978), and structural complexity of the host plant (Lawton, 1983).

In all studies of arthropod species richness in tropical trees, the recorded number of species tends to be lower than the actual number at a given time since all studies are restricted at temporal and spatial scales (Pimm, 1991). All species accumulation curves increase with sample size due to the fact that the sampling universe always expands in time and space because of, for example, mass effects

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(e.g. Shmida & Wilson, 1985; Rosenzweig, 1995; Novotny & Basset, 2000). At a local scale, species richness increases as more tree individuals or more tree habitats are studied, and at a regional scale, as larger parts of the geographical range of the trees are studied (e.g. Novotny & Missa, 2000).

Local species richness of arthropods in trees may be underestimated due to the high diversity of resources (microhabitats) that exist through the succession phases of big trees (Lawton & Schröder, 1977; Lawton, 1983; Novotny *et al.*, 2003). The proportion of different microhabitats investigated, and the extent to which these microhabitats have been sampled, are difficult parameters that may increase uncertainty in such estimates. Although many studies are restricted to living trees, there are many microhabitats, especially in the canopy (Lowman *et al.*, 1993), that may be ignored. For instance, Ødegaard (2000b) found 65 species of unknown beetles specialising on tendrils of lianas in the canopy of a Panamanian forest.

Furthermore, dead trees have an extraordinary rich fauna of arthropods (e.g. Dajoz, 2000). In Dumoga-Bone National Park, North Sulawesi, xylophagous and fungivorous species constituted 39.4% of the nearly 6000 species of recorded Coleoptera (Hammond, 1990). The proportion of dead suspended wood is very high in the tropics compared with temperate forest (Martinus & Bandeira, 1998), and subcanopy gaps are common (Connell *et al.*, 1997). Habitats for saproxylic species therefore are expected to appear discontinuously along vertical gradients in the forest, which, in turn, are important for the maintenance of distinct arthropod assemblages (Rodgers & Kitching, 1998). Vertical differences in resource availability, forest physiognomy, and abiotic conditions are important factors for stratification of species diversity in tropical forests (Basset *et al.*, 2003a). Species richness in dead wood, however, is expected to be highest on the ground (Hammond, 1990). Studies on host specificity of saproxylic beetles in the tropics (e.g. Beaver, 1979; Basset, 1992; Berkov & Tavakilian, 1997; Tavakilian *et al.*, 1997; Ødegaard, 2000b) indicate that generalists dominate. A high number of species that utilise a wide host range implicates that dead wood is an important resource for tropical arthropods.

Several studies have reported on the species richness of particular plant species but often without particular focus on the effects of the number of plants sampled (e.g. Basset & Arthington, 1992; Mawdsley & Stork, 1997; Barone, 1998; Ødegaard, 2000b; Basset, 2001; Novotny *et al.*, 2002; Barrios, 2003). Basset and Novotny (1999) showed how species richness of insect herbivores increased with 6800 tree-inspections of 15 *Ficus* tree species in Papua New Guinea, confirming the obvious correlation between sample size and species richness (Magurran, 1988; Novotny & Basset, 2000), both within and between tree species. Studies based on very few (one or two) target-plant individuals are particularly vulnerable to bias in species richness since insect herbivores are notoriously aggregated on their host plants (Novotny & Leps, 1997; Basset, 2000; Novotny & Basset, 2000).

Additional factors that rarely are accounted for include assessments of the degree of host association for each species and the proportion of tourists (*sensu* Moran & Southwood, 1982) in the samples. Host associations vary from strict monophagous species to broad polyphagous species (e.g. Janzen, 1973; Strong *et al.*, 1984). Some associations are strong, for example if all stages are dependent on the plant; or they can be weak, for example if the adult insect use the plant only for nectar consumption. Host specificity as a parameter is difficult to use in assessments of species richness (Mawdsley & Stork, 1997; Ødegaard, 2000a) due to its instability in space and time (Gould, 1979; Bernays & Chapman, 1994; Radtkey & Singer, 1995; Janzen, 2003). In order to assess host associations, it is important to control the major proportion of species in samples termed tourists, that accidentally, or due to mass effects (Shmida & Wilson, 1985), happen to rest on the plant (Overgaard Nielsen, 1975; Hammond *et al.*, 1997). The proportion of tourists in samples, and the ability to control them, depends on sampling strategy and general knowledge of the local species richness. Due to these factors, very few studies of species assemblages associated with specific trees are comparable.

The aim of this study was to survey the species composition and species richness of phytophagous beetles inhabiting one specific tree species in a tropical, wet, lowland forest in Panama in order to assess the effects of sample size, tourists, and three habitat types – mature living trees in the canopy, dead suspended wood, and dead wood on the ground – within and between trees.

Materials and methods

The study site was at the Canopy Crane in the San Lorenzo Protected Area, Colon Province in Panama (9°17′N, 79°58′W, ≈130 m a.s.l.). The annual precipitation at the site is 3152 mm and the average annual temperature 25.8 °C (Basset *et al.*, 2003b). Canopy access was provided by a 55-m tall construction crane with a horizontal arm of 54 m. The crane perimeter covers 0.88 ha of tropical, wet, evergreen lowland forest that includes more than 240 species of trees and lianas. About 70 species of woody plants can easily be studied from the crane gondola. The crane stands in a 6-ha plot, where all trees down to 1 cm in diameter breast height have been identified, measured, and mapped. The forest has escaped anthropogenic disturbance for more than 150 years (Basset *et al.*, 2003b).

The target tree for this study was *Brosimum utile* (Kunth) Pittier (Moraceae). *Brosimum* are tall canopy trees with 13 species known from north-western South America (Gentry, 1993). *Brosimum utile* ranges from northern Bolivia through north-western South America to Costa Rica, where it grows in moist tropical lowland forests. It may be up to 40 m tall with a crown diameter that may exceed 25 m. The tree is evergreen and replaces the old leaves simultaneously with leaf-flush over a 1-month period once a year (F. Ødegaard, pers. obs.). Leaves are glabrous, of a broadly elliptic shape with milky latex. The fruits resemble figs, but with a large seed instead of a hollow centre (Gentry, 1993). Within the crane perimeter there are 28 trees of *B. utile* with diameter breast height >1 cm of which 20 are big trees easily accessible from the crane.

Six mature living trees within the crane perimeter were studied during 1 year. Two additional trees within the crane perimeter were broken as a result of heavy winds during this period. Parts of these dead trees were suspended, resting on other trees in the canopy for some weeks before they fell to the ground. This accidental situation made it possible to study the succession of saproxylic beetles both in the canopy and on the ground.

Sampling procedure

Sampling procedure intended to survey a similar leaf and branch area of each tree, to maximise the number of microhabitats of each tree, and to minimise the influence of neighbouring trees. Thus, the six sampling trees were chosen conditionally based on the longest possible distance from conspecific trees and the most extensive, wide tree crowns. Trees with symptoms of weakening, like dead twigs, were preferred before healthy trees. Sampling was carried out from the crane gondola using a 1 m^2 beating sheet. Each sample was standardised by beating different parts of the tree for 30 min by moving from different positions within the tree both along vertical and horizontal gradients. The stays in each position within the tree included beating of two or three branches before the material was collected by an aspirator. Movements between positions were repeated six to eight times within the 30-min period. Accordingly, appropriate statistical replication was based on equal beating time as a rough substitute measurement for leaf area. Each tree was sampled regularly once a month during 1 year. The sampling procedure for the dead trees was similar but more frequent for a shorter time period in order to catch the faunal changes along with the decomposition of the trees (Table 1).

Target taxa

All species of Buprestidae, Chrysomeloidea, and Curculionoidea, which make up nearly all herbivorous and a major part of saproxylic beetles in this forest, were the targeted taxa of this study. All the beetle material was identified to species level (Appendix) and sorted to ecological guilds: leaf-chewers, leaf-miners, fruit-feeders, and saproxylic species (wood-borers and fungus-feeders).

Identifications were performed by the author or experts of the different taxonomic groups. A larger part of the material was deposited in the author's collection. Some material has been deposited in the collections of the taxonomists (see acknowledgements) and in the synoptic insect collection at Smithsonian Tropical Research Institute (STRI).

Host associations

At times of fruiting or leaf-flush, feeding observations on fruits or leafs were recorded. Feeding observations were also recorded for some wood-borers concealed in their holes surrounded by fresh borrowing dust. A host record was defined as at least one feeding observation (h1, Table 4). Other host observations were determined by probability assessments based on abundance categories according to Flowers and Janzen (1997) and Ødegaard (2000b), and assigned to the following host-occurrence categories: h2: 10 or more individuals recorded; h3: five to nine individuals recorded; h4: two to four individuals recorded; h5: one individual recorded and additional evidence for host association; tourists: species assessed as tourists based on the comparison with the beetle fauna of 60 other plant species within the crane perimeter (F. Ødegaard, unpubl. data) and additional evidence from literature, collections, etc. Species with proven host associations of the 60 other plants were treated as tourists on *Brosimum* when abundance was 20% less than of that of their host tree. It was not possible to set consistent abundance limits for treatment of tourists because many species appeared to be randomly distributed in the canopy as aerial drift material. Several species, often belonging to genera that are rather host specific in general (e.g. *Anthonomus* and *Apion*), were extremely abundant on *Brosimum*, but were treated as tourists due to their random distribution among the 60 other plants. All singletons among the leaf chewers, leaf miners, and fruit feeders were defined as tourists, whereas singletons among saproxylic species (excluding Conoderinae because their occurrences are poorly understood) found on dead wood were recorded as host records at the weakest level of confidence. The reason for the different treatment of singletons was the anticipation of relatively strong attraction of species to recently dead wood compared to that of mature living trees. The expected subsequent accumulation of species on

Table 1. Sampling periods, number of samples, and specific incidents of the sampled trees. M, Mature living tree; D, dead tree; C, canopy; U, understorey.

Tree	Sampling period (samples)	Incident
MC 1–6	6 March 2001 to 14 May 2002 ($n = 9$)	
DC 1	14 October 2001 to 28 December 2002 ($n = 12$)	Principal branch broke 7 October 2001
DC 2	24 January 2002 to 4 February 2002 ($n = 3$)	Stem broke 18 January 2002
DU 1	17 November 2001 to 14 May 2002 ($n = 18$)	Most branches fell to the ground 13 November 2002
DU 2	11 February 2002 to 14 May 2002 ($n = 3$)	Crown fell to the ground 10 February 2002

dead wood decreases the probability of accidentally occurring saproxylic species in such habitats.

Statistical methods

Beetle data were managed using a Microsoft Access Database. The total number of species in the samples was estimated by the Chao 1 estimator (Chao, 1984; Colwell & Coddington, 1994) and the ACE estimator (Abundance-base Coverage Estimator) (Chazdon *et al.*, 1998). The rarefied number of species present in samples was computed by Coleman's rarefaction (Coleman, 1981; Colwell & Coddington, 1994). Similarities in different insect communities were calculated with the Morisita–Horn index (Magurran, 1988). Accumulation curves based on the observed number of species (S_{obs}), Chao 1 estimators, ACE estimators, and Morisita–Horn statistics were calculated with 50 randomisations and computed by the program EstimateS (Colwell, 1997).

Detrended correspondence analysis with default choices was computed with the program CANOCO (ter Braak & Smilauer, 2002) to evaluate major trends and patterns in spatial distribution of the species in relation to their occurrences on host trees. Samples were pooled among study plants, emphasising individual plants and habitat types of the trees as the source of variation. Species occurring in only one pooled sample were removed to increase confidence of the data. The most abundant species are labelled according to the Appendix.

Results

Total species richness

A total of 3009 individuals representing 364 species was found in the pooled samples. Thirty-three per cent of the species and 13.5% of the individuals sampled were assessed to be tourists. After removing the tourists, the total number of species associated with *B. utile* was 244, and the estimated number was 285.3 ± 14.8 (Chao 1 ± SD) and 287.9 (ACE). Species richness of the mature living trees was levelling off after six trees; however, when the two dead canopy trees and the two dead trees in the understorey were added to the curve successively, they yield an extensive, almost linear jump to the accumulative number of species (Fig. 1).

Fig. 1. Species accumulation curve of phytophagous beetles associated with *Brosimum utile* (tourists excluded). The first six trees (●) represent mature living trees; tree numbers 7 and 8 (▲) represent dead trees in the canopy; tree numbers 9 and 10 (■) represent dead trees fallen to the ground.

Mature living trees

A total of 1782 individuals of 227 species were collected from the six living mature trees (Table 2). On average 84.3 ± 9.2 species (297.0 ± 73.1 individuals) were found on

Table 2. Number of species, individuals, and singletons in different samples and habitat types of *Brosimum utile*. Codes for trees as in Table 1.

	Species		Individuals		Singletons	
Tree	Total	Excl. tourists	Total	Excl. tourists	Total	Excl. tourists
MC 1	95	59	406	329	52	25
MC 2	76	49	308	232	34	15
MC 3	87	61	245	179	53	33
MC 4	81	60	215	161	44	29
MC 5	94	68	355	290	44	26
MC 6	73	54	253	209	43	30
MC total	227	123	1782	1400	97	29
DC 1	100	82	404	385	46	29
DC 2	40	38	254	252	15	13
DC total	115	95	658	637	43	24
DU 1	102	100	510	508	47	45
DU 2	37	36	59	58	25	24
DU total	113	110	569	566	51	48
D total	196	173	1227	1203	81	59
Total	364	244	3009	2603	139	58

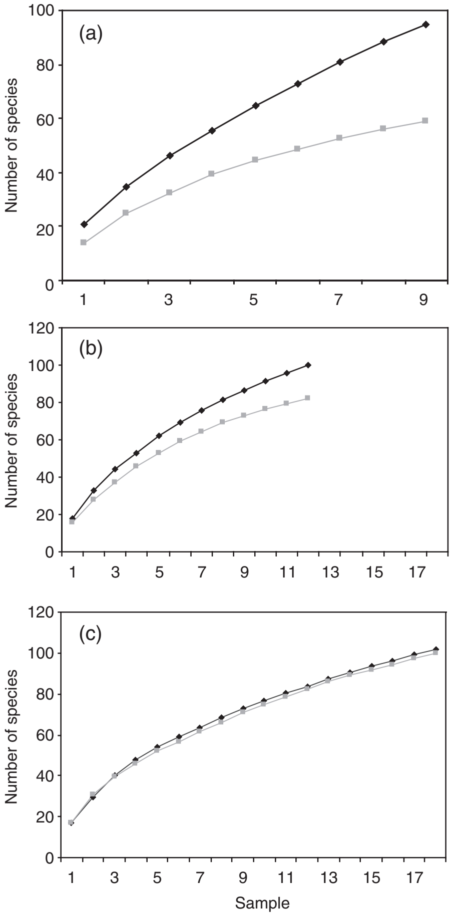

Fig. 2. Accumulation of beetle species as a function of samples for individual trees of *Brosimum utile*. (a) Mature living tree, (b) suspended dead wood, (c) dead tree in understorey. The upper curve in each graph represents total species richness; the lower curve represents species richness of host-associated species (tourists excluded).

each tree. This means that a six-fold increase in sampling effort, in terms of number of trees, gives 2.7 times more species.

A total of 1400 beetles representing 123 species was assessed as being host associated with *B. utile* (58.5 ± 6.5 species and 233.3 ± 65.0 individuals on average on each tree) (Table 2). A six-fold increase in sampling effort (six trees) gave a 2.1 times increase in species richness when tourists were removed. The proportion of tourists found on one tree represented on average 21.5% of the individuals and 30.6% of the species. The species accumulation curves for total species richness and host-associated species for each tree (Fig. 2a) indicate that the proportion of tourist species in the cumulative data set increases with sample size. The proportion of tourists on the six trees constituted 45.8% of the species.

The total number of species associated with mature living trees was estimated to 364.0 ± 40.0 (Chao 1 ± SD) and 365.5 (ACE). After removing the tourists, the number of host-associated species was estimated to 152.1 ± 15.6 (Chao 1 ± SD) and 146.5 (Table 3). The expected increase in species richness from one tree to the estimated total number of trees was 2.6 ± 0.3 (Chao 1 ± SD) and 2.5 (ACE) for the host-associated species. The estimated total proportion of tourists was 58.2% (Chao 1 ± SD) and 59.9% (ACE).

Dead trees

A total of 1227 individuals representing 196 species was found on dead branches in the canopy and dead wood in the understorey. Of these, 658 beetles of 115 species, and 569 beetles of 113 species were found in canopy and understorey respectively. Only 24 individuals of 23 species were assessed as tourists in the dead-wood samples (Table 2). The

Table 3. Estimators of species richness for different samples and habitat types of *Brosimum utile*.

	Chao 1 ± SD		ACE		Coleman ± SD	
Tree	Total	Excl. tourists	Total	Excl. tourists	Total	Excl. tourists
MC 1	197.2 ± 46.3	89.1 ± 19.0	183.6	87.9	89.1 ± 2.3	56.1 ± 1.6
MC 2	104.1 ± 13.7	55.6 ± 5.1	121.5	61.6	72.0 ± 1.9	47.1 ± 1.3
MC 3	202.0 ± 53.3	119.9 ± 34.7	190.4	111.2	81.0 ± 2.3	57.2 ± 1.8
MC 4	130.9 ± 21.9	85.4 ± 13.7	156.3	101.4	75.8 ± 2.1	56.6 ± 1.8
MC 5	149.7 ± 24.9	88.4 ± 11.6	160.4	98.0	88.9 ± 2.1	64.9 ± 1.7
MC 6	173.6 ± 55.0	108.6 ± 34.7	176.5	124.9	68.1 ± 2.1	50.6 ± 1.8
MC total	364.0 ± 40.0	152.1 ± 15.6	365.5	146.5	209.8 ± 3.8	117.5 ± 2.2
DC 1	149.2 ± 19.8	102.5 ± 10.2	155.5	107.1	96.0 ± 1.9	79.4 ± 1.5
DC 2	51.7 ± 9.6	46.8 ± 7.7	60.1	53.9	33.9 ± 2.1	32.6 ± 2.0
DC total	145.1 ± 12.7	104.5 ± 5.6	160.3	112.5	84.3 ± 4.2	74.1 ± 3.6
DU 1	190.4 ± 39.0	181.0 ± 36.2	179.8	172.0	99.4 ± 1.6	97.5 ± 1.6
DU 2	74.7 ± 25.5	70.7 ± 23.8	87.6	82.8	27.7 ± 2.5	27.1 ± 2.5
DU total	192.8 ± 34.3	180.6 ± 31.0	189.9	178.9	82.1 ± 4.1	80.6 ± 4.0
D total	288.4 ± 27.9	221.9 ± 17.5	300.9	234.0	173.3 ± 4.2	155.8 ± 3.7
Total	529.2 ± 38.0	285.3 ± 14.8	531.3	287.9	349.5 ± 3.6	237.8 ± 2.4

Table 4. The level of confidence in host observations of *Brosimum utile*; h1: feeding observations; h2: 10 or more individuals recorded; h3: five to nine individuals recorded; h4: two to four individuals recorded; h5: one individual recorded and additional evidence for host occurrence.

	MC 1	MC 2	MC 3	MC 4	MC 5	MC 6	DC 1	DC 2	DU 1	DU 2	**Total**
h1	1						3		2		6
h2	6	4	3	2	8	7	9	6	17		55
h3	10	6	7	6	11	4	7	5	9	2	37
h4	17	24	18	23	23	13	35	14	27	10	88
h5	25	15	33	29	26	30	28	13	45	24	58
Total	59	49	61	60	68	54	82	38	100	36	244

number of species associated with dead wood (excluding tourists) was estimated to be 104.5 ± 5.6 (Chao 1 ± SD) and 112.5 (ACE) in the canopy, and 180.6 ± 31.0 (Chao 1 ± SD) and 178.9 (ACE) in the understorey. The total number of species associated with dead wood was estimated to be 221.9 ± 17.5 (Chao 1 ± SD) and 234 (ACE) (Table 3). These estimators probably underestimate species richness of dead trees due to low sample size. The species accumulation curve of samples from dead trees for host-associated species and tourists showed no sign of levelling off in the understorey (Fig. 2c). The comparable curve for suspended wood (Fig. 2b) appeared to be approaching an asymptote. There was a discrepancy between host-associated species and total number of species in the canopy samples, while the understorey samples almost were free of tourists.

Host associations

Among the 244 host observations, there were only six species observed feeding, and 55 species (22.5%) were recorded with 10 or more individuals. For nearly 60% of the species the host observations belonged to the two weakest levels of confidence (Table 4).

Similarity and ordinations

The similarities of insect communities within habitat types were 0.68, 0.47, and 0.71 ± 0.09 for dead suspended wood, dead wood in understorey, and mature living trees in canopy respectively. On the other hand, the similarities across habitat groups were much lower, and, hence, very complementary (Table 5). Also, the similarity between saproxylic species in mature living trees and dead suspended wood was noticeably different (0.32). Similarity between dead suspended wood and dead wood in understorey (0.2) confirmed a prominent vertical stratification of insect communities in similar substrates as reported for leaf feeding insects in the same area (Basset, 2001). The fauna within dead trees in canopy and understorey was much more similar than between understorey and canopy of the same tree.

The detrended correspondence analysis confirmed the similarity within habitat types which represents the main variation of the material along the first axis. Most saproxylic species were clustered around the dead trees. Variation among mature living trees was explained along the second axis (Fig. 3). Species assemblages from different guilds were clustered along this axis. The total inertia of the detrended correspondence analysis was 2.210, and the cumulative percentage variance of species data was 34.5 for the first axis, 44.1 for the second axis, and 46.9 for the third axis, indicating that most of the variation in the system was explained by the first two axes.

Functional groups

The major proportion (71%) of the species associated with *B. utile* were saproxylic. Only one species was found in association with the fruits (Table 6).

The mature trees had 38 species feeding on living plant parts. Nine species of leaf-chewers were also found among dead branches in the canopy. These species were hiding among dead leaves, but proved to be associated with *B. utile* from data on living trees. A major part (65%) of the species on mature living trees was associated with dead wood or fungi. Altogether, the saproxylic species constituted 82% of the species.

Table 5. Similarities between different insect communities found on different habitats of *Brosimum utile*. MC = Branches of mature living trees in canopy; DC = dead trees in canopy; DU = dead trees in understorey; D = DC + DU; MC X = saproxylic species in mature living trees of the canopy; MC average = the average similarity between 15 combinations of samples from mature living trees in the canopy.

Sample 1	Sample 2	Morisita–Horn (incl. tourists)	Morisita–Horn (excl. tourists)
MC	DC	0.22	0.24
MC	DU	0.08	0.09
MC	D	0.22	0.23
DC	DU	0.20	0.20
DC	MC X	0.32	0.32
DU	MC X	0.11	0.11
D	MC X	0.29	0.28
DC 1	DC 2	0.68	0.69
DU 1	DU 2	0.47	0.47
MC average		0.71 ± 0.09	0.70 ± 0.10

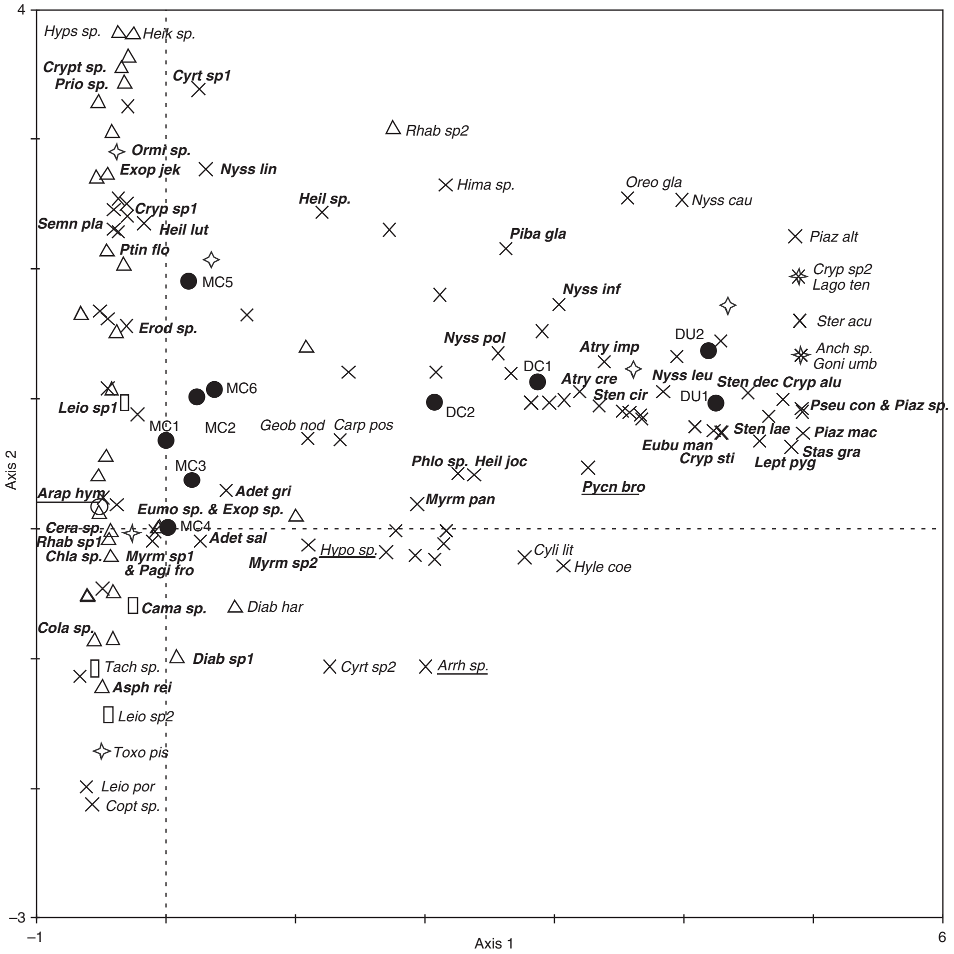

Fig. 3. Detrended correspondence analysis of 137 species of phytophagous beetles (× = wood-borers; △ = leaf-chewers; ▯ = leaf-miners; ✧ = fungus-feeders; ○ = fruit-feeders) across the 10 study trees (●). Codes for the trees are defined in Table 1. The plot represents axes 1 and 2 in the detrended correspondence analysis. Beetle species with 10 or more individuals and species with less than 10 individuals, but assumed to be ecologically important, are labelled bold and normal respectively, according to the appendix. Species with feeding records are underlined.

Discussion

Local species richness

The results indicate that *B. utile* harbour a very rich fauna of phytophagous beetles. A total of 244 host-associated species were recorded from the tree; however, species accumulation curves from dead wood indicate even a more extensive fauna. The estimators indicate a total species richness of 288 species for the study trees; however, sample size of dead trees unfortunately was too small for confident estimation of species richness. These estimators are dependent on sample size and in this case the estimated species richness has not reached the asymptote. Local species richness associated with the investigated habitat types of *B. utile* in this area in the forest therefore certainly includes more species. This number could be conservatively assessed to exceed 350 species.

The proportion of host-associated species vs. tourists in samples depends highly on sampling method (Basset *et al.*, 1997). The percentage of proven feeders among leaf beetles collected with hand-collecting/beating, flight interception traps, and pyrethrum knockdown in Papua New Guinea was 47.5, 19.5, and 30.0% respectively (Basset *et al.*, 1997). Stork (1987) assessed the proportion of arthropod tourists to 18.6% in a fogging study of 10 Bornean trees. In the present study the proportion of host-associated species was 67%, implying a relatively small proportion of tourists; however, as shown in Fig. 2, the proportion of tourists depends on sample size. Accordingly, based on the estimated species richness, 54% of the species in the present study are associated with the host tree. A limitation of the study was that nearly 60% of the data on host associations represented uncertain host observations belonging to the two lowest levels of confidence.

A crucial question in assessments of local species richness of arthropods in trees is the effect of sample size (number of trees), a factor that varies considerably in such studies (Basset *et al.*, 2003d). The present study showed that 58.5 ± 6.5 species were associated with a single mature

Table 6. Number of species representing different functional guilds among host-associated species totally, and in different habitat types (MC = mature living trees in canopy; DU = dead trees in understorey; DC = dead trees in canopy) of *Brosimum utile*.

	Total		MC		DU		DC	
Guild	Sp.	Ind.	Sp.	Ind.	Sp.	Ind.	Sp.	Ind.
Leaf-chewers	40	456	38	442	–	–	9	14
Leaf-miners	4	46	4	47	–	–	1	1
Fruit-feeders	1	97	1	97	–	–	–	–
Wood-borers	174	1905	73	767	97	539	77	599
Fungus-feeders	25	98	7	49	13	26	8	23

living tree (Fig. 1), and the estimated number of species would be around 150 (Table 3). Erwin (1982) found 682 species of phytophagous beetles by fogging of 19 trees of *Luehea seemannii* in Panama. If 30% of these species were associated with *L. seemannii*, as indicated for fogging studies in general (Basset *et al.*, 1997), there would be 205 species of that tree in the canopy of that forest. Ødegaard (2000b) found 96 species on two trees of the same species in Parque Natural Metropolitano in Panama. Hence, data of Erwin (1982) and Ødegaard (2000b) on *L. seemannii* would be comparable when accounting for sample size and tourists. Based on an ACE estimator, the present study concludes that species richness in a single living mature tree multiplied by 2.5 would account for the total local species richness of the living trees of that species, assuming that the estimated species richness for mature living trees are close to the asymptote of the species accumulation curve (Fig. 1). Provided similar host specificity of beetles utilising different habitat types within the tree, this ratio would be similar for total species richness of the tree.

There was a striking difference between the saproxylic fauna of dead suspended wood and dead wood in the understorey (Morisita–Horn index: 0.2). This level compares with the interval range of similarity found between communities of Coleoptera harbouring taxonomically distant trees in Australia (Kitching *et al.*, 2003). It is also interesting that similarity within habitats of different trees was much higher than between habitats of the same tree in canopy and understorey, a fact that indicates that saproxylic species in tropical forests are highly stratified. Similarity would be even lower if pseudoreplication (samples from the same tree) was an important factor.

Unfortunately, dead wood was sampled only from two trees for a short period (up to 2 months in the canopy and up to 6 months in the understorey) because the branches fell to the ground due to winds and termite attacks; however, beetle abundance of suspended wood decreased along with the increasing attacks from termites. In the understorey, the fauna switched from xylophagous species to fungivorous species along with increasing attacks from termites. Obviously, dead and living trunks, roots, and thick branches would house an additional set of species that was not recorded in this study. Another, additional set of species would probably be recorded if other sampling methods were introduced. Basset *et al.* (1997) showed that each method collects a different set of target taxa.

A main habitat missing in this study was small living trees. Sampling effort on saplings of *B. utile* would probably give an additional complementary set of species since communities of leaf feeding arthropods are highly stratified in this tropical forest, even within the same tree species (Basset, 2001; Barrios, 2003).

A major proportion of the species on *B. utile* was saproxylic (82%), which is a high number compared with data on the target taxa from similar studies of tropical trees (e.g. Erwin, 1983; Davies *et al.*, 1997). It could be that saproxylic species are undersampled in most canopy studies due to the temporal occurrence of suspended wood habitats or *B. utile* has relatively few chewers due to the obscure flowers with sticky latex as indicated by, for example, Dussourd and Eisner (1987). On the other hand, latex outflow was not a predictive variable of species richness of 15 *Ficus* trees in Madang, Papua New Guinea (Basset & Novotny, 1999).

Implications for regional species richness

Extending the study area to include the total geographical range of *B. utile* would probably increase the local species richness by a factor of at least 2.5. This factor is based on data from Gilbert and Smiley (1978) and subsequent assessments (May 1990; Thomas, 1990, Ødegaard, 2000a). It is therefore a reasonable guess that at least 900 species of the present target taxa could be found on the studied microhabitats of the tree through its geographical range. Studies of other groups of arthropods and other microhabitats would increase the species number even more. Although this is a high number of species it is probably not more than an average common tropical tree in terms of species richness of phytophagous beetles. On average, 58.5 ± 6.5 host-associated species were recorded from each mature living tree in the present study. In comparison, Ødegaard (2000b), recorded host-associated phytophagous beetles with comparable methods from a tropical, dry forest in Panama and found on average 55.8 ± 6.8 species on each of 24 mature living tree species; however, most studies on species richness in the tropics are performed on common trees. As shown for Hawaiian trees, abundant trees can be 25 times more species rich in insects than rare trees (Southwood, 1960). It is therefore difficult to assess the regional species richness of arthropods for the average tropical tree without such knowledge from rare tree species (Kennedy & Southwood, 1984; Ødegaard, 2000a).

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Appendix: species list including identified taxa of phytophagous beetles associated with *Brosimum utile*

Abbreviations in parentheses refer to species labels in Fig. 3.

Buprestidae

Leiopleura sp. (two sp.) (***Leio sp1***, *Leio sp2*).

Cerambycidae

Cerambycinae

Tomopterus vespoides White

Laminae

Adetus ?*salvadorensis* Franz (***Adet sal***), *Adetus bacillarius* Bates, *Adetus costicollis* Bates, *Adetus mucorens* Bates, *Adetus* ?*griseicauda* Bates (***Adet gri***), *Amphicnaea quinquevittata* Bates, *Amphicnaeia crustulata* Bates, *Amphionycha crassipes* Bates, *Anisopodus costaricensis* Lara & Shenefelt, *Anisopodus dispar* Bates, *Anisopodus scriptipennis* Bates, *Ataxia fulvifrons* Bates, *Atrypanius conspersus* (Germar), *Atrypanius cretiger* (White) (***Atry cre***), *Atrypanius implexus* (Erichson) (***Atry imp***), *Atrypanius irrorellus* Bates, *Callia albicornis* Bates, *Carphontes posticalis* Bates (***Carp pos***), *Chalastinus championi* Bates, *Cylicasta liturata* Fabr. (*Cyli lit*), *Cyrtinus* sp. (two spp.) (***Cyrt sp1***, *Cyrt sp2*), *Esthlogena porosa* Bates, *Estoloides longicornis* Breuning, *Estoloides* sp. (two spp.), *Hesychotypa heraldica* (Bates), *Hylettus coenobia* (Erichson) (*Hyle coe*), *Hyperplatys pusilla* Bates, *Leptostylus decipiens* Bates, *Leptostylus pilula* Bates, *Leptostylus pygidalis* Bates (***Lept pyg***), *Leptostylus vitriditinctus* Bates, *Lepturges festivus* Bates, *Lepturges navicularis* Bates, *Myoxinus pictus* (Erichson), *Nyssodrysina haldemani* (LeConte), *Nyssodrysina infima* (Bates) (***Nyss inf***), *Nyssodrysina leucopyga* (Bates) (***Nyss leu***), *Nyssodrysina lineatocollis* (Bates) (***Nyss lin***), *Nyssodrysina polyspila* (White) (***Nyss pol***), *Nyssodrysternum caudatum* (Bates) (*Nyss cau*), *Oreodera canotogata* Bates, *Oreodera glauca* (L.) (*Oreo gla*), *Ozineus cribripennis* Bates, *Pibanga* ?*glabricua* (Bates) (***Piba gla***), *Pycnomorphus centrolineatus* Bates, *Stenolis circumscripta* (Bates) (***Sten cir***), *Stenolis decemguttata* (Bates) (***Sten dec***), *Stenolis laetifica* (Bates) (***Sten lae***), *Taeniotes scalaris* (Fabr.), *Trestonia pulcherrima* D. & D., *Urgleptes amplicollis* (Bates), *Urgleptes laxicollis* Gilmour, *Urgleptes mixtus* (Bates), *Urgleptes* sp. nr. *laticollis* (Bates), *Urgleptes* sp. (two spp.), unidentified genus (one sp.).

Chrysomelidae

Clytrinae

Coleothropa sp., *Cryptocephalus* sp. (seven spp.) (***Crypt sp.***), *Griburius* sp. (two spp.), *Lexiphanes* sp., *Megalostomis amazona* Jac., *Megalostomis flavipennis* Jac., *Megalostomis* sp., ?*Chlamisus* sp. (***Chla sp.***).

Eumolpinae

Antitypona sp., *Colaspoides* sp. (***Cola sp.***), *Prionodera* sp. (***Prio sp.***), *Rhabdopterus* sp. (four spp.) (***Rhab sp1***, *Rhab sp2*), unidentified genus (one sp.) (***Eumo sp.***).

Galerucinae

Asphaera reichi Harold (***Asph rei***), *Calomicrus* sp., *Diabrotica godmani* Jac., *Diabrotica ?haroldi* Baly (*Diab har*), *Diabrotica* sp. (three spp.) (***Diab sp1***, *Diab sp2*), *Heikertingeria* sp. (*Heik sp.*), *Omophoita* sp.

Anthribidae

Brachycorynus sp., ?*Domoptolis championi* Jordan, *Eusphyrus* sp. (three spp.), *Goniocloeus umbrinus* Jordan (*Goni umb*), *Goniocloeus* sp. (seven spp.), *Gymnognathus* ?*thecla* Champ., *Lagopezus tenuicornis* Fabr. (*Lago ten*), *Ormiscus* sp. (six spp.) (***Ormi sp.***), *Phaenithon* sp., *Ptychoderes tricostifrons* Fåhr., *Toxonotus pistor* (Jordan), (*Toxo pis*), unidentified genus (one sp.).

Attelabidae

Eugnamptus sp. nr. *notatus* Voss.

Brentidae

Arrhenodes sp. (*Arrh sp.*)

Curculionidae

Curculioninae

Camarotus sp. (***Cama sp.***), *Ceratopus* sp. (***Cera sp.***), *Erodiscus* sp. (two spp.), *Myrmex panamensis* Champ. (***Myrm pan***), *Myrmex* sp. (three spp.) (***Myrm sp1***, ***Myrm sp2***), *Ptinopsis floccosa* Champ. (***Ptin flo***), *Tachygonus* sp. (*Tach sp.*).

Conoderinae

Copturus sp. (four spp.) (*Copt sp.*), *Eulechriops* sp. (two spp.), *Lechriops* ?*porcata* Champ. (*Leio por*), *Lechriops* sp. (three spp.), *Piazurus alternans* Kirsch (*Piaz alt*), *Piazurus caprimulgus* (Oliv.), *Piazurus maculipes* Gyll. (***Piaz mac***), *Piazurus* sp. (two spp.) (***Piaz sp.***), *Pseudopinarus condyliatus* (Boh.) (***Piaz con***), *Pseudopinarus* sp.

Cossoninae

Acamptus plurisetosus (Champ.), *Himatium* sp. (*Hima sp.*).

Cryptorhynchinae

Anchonus sp. (*Anch sp.*), *Cophes* ?*quadricostatus* Champ., *Cophes asperata* Champ., *Cophes* sp., *Cryptorhynchus* ?*paleatus* Champ., *Cryptorhynchus alboscutellatus* Champ. (*Cryp alu*), *Cryptorhynchus alutaceus* Champ., *Cryptorhynchus bifenestratus* Champ., *Cryptorhynchus bioculatus* Champ., *Cryptorhynchus carinifer* Champ., *Cryptorhynchus conspicillatus* Champ., *Cryptorhynchus diseiger* Champ., *Cryptorhynchus ignobilis* Champ., *Cryptorhynchus mesomelas* Champ., *Cryptorhynchus* sp. nr. *ignobilis* Champ., *Cryptorhynchus stigmatophorus* Champ. (***Cryp sti***), *Cryptorhynchus* sp. (nine spp.) (***Cryp sp1***, *Cryp sp2*), *Eubulus* ?*monachus* Schönh., *Eubulus lineatipleura* Champ., *Eubulus miser* Champ., *Eubulus munitus*

Kirsch (***Eubu mun***), *Eubulus nimbatus* Champ., *Eubulus stipator* Boh., *Eubulus* sp. (six spp.), *Macromerus succinctus* Champ., *Metriophilus horridulus* Champ., *Metriophilus minimus* Champ., *Metriophilus* sp. (two sp.), *Microxypterus* ?*binotatus* Champ., *Pisaeus* sp., *Semnorhynchus fulvopictus* Champ., *Semnorhynchus planirostris* Champ. (***Semn pla***), *Staseas granulata* Champ. (***Stas gra***), *Staseas* sp. (two spp.), *Sternocoelus acutidens* (Champ.) (*Ster acu*), *Sternocoelus tardipes* Boh., *Tyrannion unipustulatum* Champ., *Tyrannion* sp., unidentified genus (two spp.).

Entiminae

Exophthalmus jekelianus White (***Exop jek***), *Exophthalmus* sp. (***Exop sp.***), *Compsus auricephalus* Say, *Hypsonotus* sp. (*Hyps sp.*), *Exophthalmina* sp., *Macrostylus* sp.

Molytinae

Geobyrsa nodifera Pasc. (***Geob nod***), *Heilipus* sp. (three spp.) (***Heil sp.***), *Heilus bioculatus* (Boh.), *Heilipodus lutosus* (Pasc.) (***Heil lut***), *Heilipodus jocosus* (Boh.) (***Heil joc***), *Hilipinus* sp., *Heilipodus* ?*spinipennis* (Champ.), *Microhyus* sp. (five spp.).

Scolytinae

Araptus hymenaeae (Egg.) (***Arap hym***), *Araptus* sp., *Coccotrypes cyperi* (Beeson), *Hypothenemus opacus* (Eich.), *Hypothenemus* sp. (*Hypo sp.*), *Pagiocerus frontalis* (Fabr.) (***Pagi fro***), *Phloeotribus maurus* Wood., *Phloeotribus setulosus* Eich., *Phloeotribus subovatus* Bld., *Phloeotribus* sp. (***Ploe sp.***), *Pycnarthrum brosimi* Wood (***Pycn bro***), *Scolytodes* sp., *Theoborus* sp., *Xyleborus caraibicus* Egg., *Xyleborus affinis* Eich., *Xyloborinus protinus* (Wood), *Xylosandrus morigerus* (Bld.).

Platypodinae

Euplatypus segnis (Chap.), *Megaplatypus discicollis* (Chap.).