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The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests

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Abstract

Aim Insect assemblages associated with lianas in tropical forests are poorly studied compared with those associated with trees. The importance of lianas for the maintenance of local species richness of insect herbivores in tropical forests is therefore poorly understood. With this in mind, a comparative study of the relative importance of trees and lianas as hosts for phytophagous beetles was carried out.

Location The study area was located in the canopy of a dry tropical forest in Parque Natural Metropolitano, Panama province, Republic of Panama.

Methods A crane system was utilized to access the canopy. The number of species and host specialization of adult phytophagous beetles associated with twenty-six liana species of ten different families, and twenty-four tree species of twelve different families were compared.

Results A total of 2561 host associations of 697 species of beetles were determined (1339 for trees and 1222 for lianas). On average 55.8 ± 6.8 beetle species were found to be associated with each tree species while the comparable number for lianas was 47.0 ± 6.1.

The pooled numbers of phytophagous beetle species associated with trees and lianas, respectively, were not significantly different. However, there were significantly more species feeding on green plant parts on lianas than on trees, and there were significantly more wood eaters on trees than on lianas.

Phytophagous beetles associated with lianas were significantly more specialized than the tree associates due to a higher degree of specialization among the species feeding on green plant parts of lianas. Wood eaters and flower visitors showed no differences in host specialization on different growth forms.

Main conclusion The present study shows that lianas are at least as important as trees for the maintenance of local species diversity of phytophagous beetles at this site. The mechanisms that drive the patterns can only be hypothesized. Plant architecture, size, and length of growing season are probably involved. Further studies, should include measurements of plant traits to elucidate experimentally what mechanisms that drive the patterns. Additional insight would come from similar studies in other forest types, and also studies of other major taxonomic groups of arthropod herbivores.

Keywords
Biodiversity, canopy, host specificity, lianas, Panama, phytophagous beetles, species richness, trees, tropical forests.

INTRODUCTION

Trees and lianas are the most dominant major life forms of plants, in terms of species richness, biomass and production, in dry tropical forests (Gentry & Dodson, 1987; Gentry, 1991; Hegarty & Caballé, 1991; Prance, 1995). Although lianas have been called the single most important physiognomic feature differentiating tropical from temperate forests (Croat, 1978), ecologists have paid little attention to this life form (Putz, 1984). Similarly, studies of species richness and host specificity of tropical forest herbivorous arthropods

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are mostly focused on tree hosts (Erwin & Scott, 1980; Stork, 1987; Basset, 1992; Basset *et al.*, 1996; Kitching & Zalucki, 1996; Allison *et al.*, 1997; Davies *et al.*, 1997; Wagner, 1997). Consequently, little is known about the importance of lianas as hosts for phytophagous beetles, although they have been suggested to have an important role in the maintenance of high local species diversity (Wolda, 1979; Stork, 1987). Phytophagous beetles probably also exert the major evolutionary pressure on plants because herbivory by large herbivores is trivial when compared to that of insects (Janzen, 1981; Clark & Clark, 1991), and phytophagous beetles make up about one third of all phytophagous insects (Strong *et al.*, 1984).

Many insect groups are intimately linked to lianas. In the neotropics, linkages of this kind are exemplified by, *Heliconius* butterflies on Passifloraceae (Benson, 1978; Gilbert & Smiley, 1978), and Ithomiinae butterflies on Solanaceae (Neto, 1991). These butterflies demonstrate a high degree of host specialization, and they possess intricate Muellerian mimicry complexes. Jewel beetles (Buprestidae) of the genus *Hylaeogena* associated with Bignoniaceae lianas (Hespenheide, 1974) are another example of a very species-rich insect group specialized on a taxonomically narrow group of lianas. These patterns induced Gentry (1985) to propose that lianas may support coevolutionary radiations as they rely on specific kinds of biochemical defence rather than such generalized defences as tannins and sclerified tissues that typify tropical trees. Furthermore, they are characterized by a life history featuring rapid growth, hence they show a prevalence of soft young edible vegetative parts. Several empirical studies suggest that such coevolutionary patterns are rare in trees because the paucity of insects feeding on species-rich groups of trees (e.g. Dipterocarpaceae) (Holloway, 1989), and the lesser influence of phytochemistry of host trees among tree feeding insects (Craig *et al.*, 1988; Scriber, 1988). In contrast, other species groups of trees (e.g. *Ficus* spp.) support a rich insect fauna (Basset *et al.*, 1997). If species radiation of insects associated with lianas is a common phenomenon, lianas could be hosts for considerable numbers of insect species.

Lianas are found in at least 133 plant families, indicating that the scandent habit of plants has evolved repeatedly and independently (Gentry, 1991). The fact that lianas are so widespread throughout the plant kingdom could be an indication that the evolution of insect–liana associations is also widespread.

If lianas support high numbers of arthropod herbivores, they will be of great importance both in structuring ecosystems and maintenance of local diversity of arthropod species. Tree species more than 10 m tall make up 15.4% of all species of flowering plants in the region of the study site, compared to scandent plants which constitute 19.4% (Croat, 1978). Furthermore, as pointed out by Wolda (1979), the lianas may exert a greater influence on local species richness of insects than the trees due to differences in leaf production, although, no data are available to support this. Indirect evidence of the importance of lianas was found by Stork (1987), studying the faunal similarity of ten Bornean tree species. He noted that the similarity in amount of vines and epiphytes was more important for faunal similarity than taxonomic relatedness of the trees. There are thus several indications that diversity and host specificity of insects associated with lianas in tropical forests may be of considerable importance.

A comparative study of tropical trees and lianas with respect to their insect faunas needs access to all habitats of the plants, especially in the canopy. The canopy comprises a major volume of the tropical forests and include a wide range of habitats which are scattered or nonexistent in the understory, and the greater part of production and structural diversity of lianas occur in the canopy (Hegarty & Caballé, 1991). Spatial heterogeneity within trees is shown to be higher in the canopy than in other layers due to the dominance of young leaves (Basset, 1991). In total, canopy plants account for more than 90% of tropical forest leaves (Wright & Colley, 1994). With respect to arthropod diversity, the importance of canopy habitats of tropical forests is pointed out by Erwin (1983) and Stork *et al.* (1997).

On this background this study aims to test the relative importance of trees *v.* lianas as resources for phytophagous insects in the canopy of a tropical forest with respect to both pooled and unpooled species richness and host specificity of beetles associated with each growth form or species of plant. The implications of these parameters for the maintenance of local diversity of insect herbivores in tropical forests are discussed.

METHODS

Study site and canopy access

The study was carried out in the Parque Natural Metropolitano in the province of Panama in Panama. This park of natural forest comprises an area of 270 ha, adjacent to Panama City. A larger complex of national parks is connected to the north. The total area of protected natural forests is 370 km^2 (Wright & Colley, 1994). The forest is characterized as a dry tropical forest (Holdridge *et al.*, 1971). The average annual rainfall is 1740 mm, of which 85% falls between May and November. Annual mean temperature is 28 °C (Kaoru Kitajima, unpublished data).

The study was carried out from a canopy crane consisting of a gondola connected to a tower crane. Access to all levels of the forest canopy is facilitated from the gondola. The crane is 42 m tall and has a horizontal boom of 51 m. The canopy of the forest under the crane ranges from 20 to 38 m in height. Thus, the crane facilitates the study of approximately 8000 m^2 and 200,000 m^3 of forest (Wright & Colley, 1994).

Insect groups collected and identification of species

Coleoptera of the families Buprestidae, Cerambycidae, Chrysomelidae (incl. Bruchinae), Brentidae (incl. Apioninae), and Curculionidae (incl. Scolytinae and Platypodinae), families were collected (Table 1). These beetle families comprise the major part of the ecologically defined phytophagous beetles. Phytophagous beetles, in this sense, include herbivorous (feeding on green plant parts flowers or fruits), xylophagous (feeding on wood), xylomycetophagous (feeding on tree associated fungi), and phloeophagous (feeding on bark) species.

Table 1 Number of species and individuals of phytophagous beetles in different major taxonomic groups.

Taxonomic group	No. of species	No. of individuals
Buprestidae	47	1512
Cerambycidae	55	511
Chrysomelidae	196	15744
Bruchinae	15	412
Cryptocephalinae	38	2061
Chlamisinae	26	458
Lamprosomatinae	6	547
Eumolpinae	23	7162
Galerucinae	13	247
Alticinae	45	4369
Hispinae	10	48
Cassidinae	15	406
Other *Chrysomelidae*	5	34
Anthribidae	7	173
Brentidae	17	408
Attelabidae	3	195
Curculionidae	372	15193
Otiorrhynchinae	7	208
Anthonominae	15	819
Baridinae	129	3024
Cryptorrynchinae	80	2676
Erirrhininae	14	4669
Otidocephalinae	24	530
Hylobiinae	19	305
Zygopinae	49	2583
Scolytinae	18	89
Other *Curculionidae*	17	290

All specimens were sorted to species level even for difficult groups. Genitalic dissections were performed systematically to reveal complex species groups and to understand intraspecific variation. Species names of described species were obtained as far as possible by comparing museum collections, and by sending specimens to expert taxonomists. The taxonomy of phytophagous beetles in the area is poorly known. Between 10% and 85% of the known species, dependent on taxon, are described (Hespenheide, 1994). In addition, there is an unknown proportion of species that remains to be discovered.

The plant species

The flora at the site is characterized by a dominance of trees and lianas in the canopy; epiphytes are rather few and scattered. Forty species of trees and thirty-five species of climbers (lianas, vines, and hemiepiphytes) are within reach of the crane. In addition, the forest contains an unknown number of species of treelets (small trees), shrubs, herbs and epiphytes.

Plant species across a broad taxonomic range were chosen for the investigation of beetle associations. A sampling regime was established on twenty-four tree species of twelve families and twenty-six liana species of ten families (Table 2). I tried to sample two individuals of each species. However, eleven tree species and twelve liana species were represented only by single individuals under the crane. Since the proportion of single individuals for trees and lianas was virtually the same, there was no bias in sampling effort between life forms (Table 3).

Sampling

Plants exceeding a certain biomass were chosen to be able to rotate the location of the sampling station between branches of the plant individual. Rotating was important to ensure that a variety of natural microhabitats for beetles was covered, and to minimize damage to the plants. The foliage biomass of a sampling station was measured immediately above a 1-m^2 beating sheet, and expressed in foliage units (Futuyma & Gould, 1979). One sampling station was established on each plant individual and each sampling station consisted of five to ten foliage units. However, it was not possible to select sampling stations of exactly the same size (biomass) due to considerable variation in leaf production and leaf loss throughout an annual cycle (Wright & van Schaik, 1994). The sampling stations were visited approximately once a week, alternating visits by day and by night throughout one year («frequent sampling»). A head lamp with red light was used at night. First, at each visit on a station, 5 min was spent on behavioural observations to record feeding, oviposition, and resting behaviours. Finally, a beating sheet was used to collect cryptic beetles.

In periods of leaf production and plant reproduction a qualitative sampling regime was carried out. It was based on the methods above, but independent of biomass of the sampled plant individuals, and independent of frequency of visits («additional sampling»). Each plant individual was subject to additional sampling when in the appropriate phase, e.g. leaf flush or flowering. Sampling once a week could lead to considerable underestimation of beetle species associated with a plant, especially when leaf flushing or flowering is of short duration, due to a positive correlation between the abundance of insects and the amount of young leaves or flowers (Basset, 1991).

These two sampling methods were selected to optimize insect species richness and recording host observations.

Definitions of host observations

A major problem in studies of host specificity of adult arthropods is how to treat those species occurring accidentally on a plant (i.e. 'tourists' or transient species) (Basset *et al.*, 1996). In the present study, species known to be transients on a particular plant species were ignored as host associates of that plant species. Some species show weak plant associations when avoiding predators (Stork, 1988), or using plants exclusively for mating purpose (Corbet, 1961). Species using a plant purely for such purposes are defined as transients of that plant species. Generally, most transients were eliminated through the procedure of host definition described below.

Generally, host specificity cannot be estimated if the number of specimens of an insect species is much lower than the number of host species (Colwell & Futuyma, 1971) because

Table 2 The twenty-four tree species (thirty-seven individuals) and twenty-six liana species (forty individuals) investigated. Lianas are marked with *. The number of plant individuals sampled of each plant species is indicated in front of each species name.

ARECACEAE
1 *Acrocomia aculeata* (Jacq.) Lodd. ex Mart.

MORACEAE
1 *Castilla elastica* Cerv.
2 *Cecropia longipes* Pitt.
2 *Cecropia peltata* L.
2 *Ficus insipida* Willd.
1 *Ficus maxima* Mill.
1 *Chlorophora tinctoria* (L.) Gaud.

LAURACEAE
1 *Nectandra membranacea* ssp. *cuspidata* (Nees & Mart.) Rohwer
1 *Nectandra globosa* (Aubl.) Mez
1 *Phoebe cinnamomifolia* (H.B.K.) Nees

CONNARACEAE
1 **Cnestridium rufescens* Planch.

FABACEAE
2 *Albizia adinocephala* (Donn. Sm.) Britt. & Rose
1 *Andira inermis* (Wright) H.B.K.
2 **Calopogonium caeruleum* (Benth.) Hemsl.
1 **Canavalia bicarinata* Standley
2 **Dioclea guianensis* Benth.
2 *Enterolobium cyclocarpum* (Jacq.) Griseb.

MALPIGHIACEAE
1 **Banisteropsis muricata* (Cav.) Cuart.
2 **Stigmaphyllon hypargyreum* Tr. & Planch.

ANACARDIACEAE
2 *Anacardium exelsum* (Bert. & Balb.) Skeels
2 *Astronium graveolens* Jacq.
2 *Spondias mombin* L.
1 *Spondias radlkoferi* Donn.

SAPINDACEAE
1 *Matayba scrobiculata* (H.B.K.) Radlk.
2 **Serjania mexicana* (L.) Wild.
1 **Serjania rhombea* Radlk.

RHAMNACEAE
2 **Gouania lupuloides* (L.) Urban

VITIACEAE
2 **Vitis tiliifolia* H. & B. ex Roem. & Schult.

TILIACEAE
2 *Luehea seemannii* Tr. & Planch.

BOMBACACEAE
1 *Pseudobombax septenatum* (Jacq.) Dugand

COMBRETACEAE
2 **Combretum fruticosum* (Loefl.) Stuntz.

ARALIACEAE
1 *Didymopanax morototoni* (Alub.) Dec. & Planch.

SAPOTACEAE
2 *Chrysophyllum cainito* L.

CONVOLVULACEAE
2 **Bonamia trichantha* Hall.
1 **Jacquemontia hirtifolia* (Mart. & Gal.) O'Donell

BORAGINACEAE
2 *Cordia alliodora* (R. & P.) Oken

BIGNONIACEAE
1 **Anemopaegma orbiculatum* (Jacq.) DC.
2 **Amphilophium paniculatum* (L.) H.B.K.
2 **Arrabidaea candicans* (L. Rich.) DC.
1 **Arrabidaea corallina* (Jacq.) Sandw.
2 **Arrabidaea patellifera* (Schlecht.) Sandw.
1 **Callichlamys latifolia* (L. Rich.) K. Schum.
1 **Cydista aequinoctalis* (L.) Miers
1 **Paragonia pyramidata* (L. Rich.) Bur.
1 **Phryganocydia corymbosa* (Vent.) Bur.
2 **Pithecoctenium crucigerum* (L.) A. Gentry
1 **Stizophyllum riparium* (H.B.K.) Sandw.
2 **Tynnanthus croatianus* A. Gentry

RUBIACEAE
2 *Antirrhoea tricantha* (Griseb.) Hemsl.

ASTERACEAE
2 **Mikania leiostachya* Benth.

Table 3 Comparison of sampling effort and taxonomic relatedness of the trees and lianas includes in this study.

	Trees	Lianas
No. of species where two ind. were sampled	13	14
No. of species where one ind. was sampled	11	12
No. of plant families	12	10
No. of plant genera	20	23
No. of congeneric pairs	4	2

rare species always look more specialized than they in fact are. Accordingly, only those beetle species encountered more than fifty times should be considered in this study. However, rare species are also important to consider since they always constitute a major proportion of the species in studies of tropical arthropods because they may be different from the common ones in their patterns of host specificity due to their rare occurrences (Price *et al.*, 1995). Host observations of species recorded fewer than fifty times were also considered if they fulfilled one of the following criteria.

1 If two or more feeding observations were recorded. Single feeding observations are also included when there are host observations of the same beetle species on other plant species (Table 4).

2 If there are five or more observations of a beetle species on a plant species, even if behavioural observations are lacking. The reliability of the host observations of this kind is ranked in two levels (≥ ten individuals, and five to nine individuals) (Table 4) according to Flowers & Janzen (1997). This procedure is just a guideline, and every possible host association of this kind is evaluated carefully in accordance with the circumstances around each record (see Ward, 1988). A few observations of one beetle species on tree species *A* would not be considered as a host association if there are certain circumstances that weigh heavily against such a treatment. For instance, if this beetle species is a very abundant associate of the neighbouring tree species *B*. Additional sampling on neighbouring trees/lianas, other than the fifty species investigated in the study, was carried out to help identify transient species.

3 If there are two to four observations of a beetle species on a plant species, establishment of host associations had to

Table 4 The nature of the host observations on trees and lianas for those beetle species recorded fifty times or more, and those species recorded less than fifty times. Host observations are given a score according to the confidence level of the observed associations (Flowers & Janzen, 1997).

	No. host observation ≥ 50 ind.		No. host observation ≤ 50 ind.			
	Trees	Lianas	Trees	Lianas	Total	Score
Feeding/oviposition	49	69	63	149	330	5–6
≥ 10 individuals	176	116	101	80	473	3–4
5–9 individuals	100	85	118	95	398	2–3
2–4 individuals	265	233	467	395	1360	1–2
Total	590	503	749	719	2561	

be supported from taxonomic arguments, references, or feeding damage that could reasonably be attributed to the respective beetle species (Table 4). Taxonomic arguments relate to the fact that taxonomically related plant species within a plant family tend to have a similar fauna compared to another plant family, and some plant species have a highly distinct, specialized fauna (Strong *et al.*, 1984). For example, if six species of *Octhispa* (Chrysomelidae, Hispinae) all are oligophagous on Bignoniaceae, there is a certain probability that a seventh *Octhispa* species also is a Bignoniaceae associate, independent of which plant it is recorded from. The same argument can be inversely addressed for polyphagous species. There are host references both in the applied literature and in reference collections for some of the species. Such information was never used on its own, but carefully as affirmative or additional information.

The present study is mainly based on observations of adult individuals. For many species, larval host preferences are different from that of the adults (Jolivet & Hawkeswood, 1995). However, that does not affect the value of the analyses because the distribution of adult insects among host plants is a phenomenon of its own interest, analogous to a similar investigation of host specificity in larvae (Mawdsley & Stork, 1997). In any case, life cycle stage differences in host specificity does not prevent a satisfactory comparison of lianas and trees as a resource for adult herbivorous beetles.

As pointed out by Basset (1992), it is also important to separate free-living (e.g. green feeders) and concealed species (e.g. wood eaters) since they are expected to show differences in host specificity. In the present study, green feeders include all species feeding on green vegetative plant parts and wood eaters include the following feeding habits: phloeophagy, xylophagy and xylomycetophagy, as defined by Atkinson & Equihua (1986). Flower visitors, defined as all species found in association with buds, flowers, or fruits, were also kept separate in this study. Beetles in flowers presumably take nectar, feed on flower parts, or feed on pollen as adults (Samuelson, 1994). They can also serve as pollinators (Endress, 1994) hence they are expected to behave differently than other guilds regarding host specificity.

Estimation of host specificity

Host specificity for insects is defined as the taxonomic range of plant species utilized and the plant-parts or plant-individuals being preferred (Janzen, 1973). Host specificity is an evolutionarily labile property (Gould, 1979; Wasserman & Futuyma, 1981; Radtkey & Singer, 1995), and often a species as a whole has a greater host range than a single individual of the same species (Fox & Morrow, 1981; Mawdsley & Stork, 1997). Testing of host specificity can never be accurate unless all possible plant species in the total range of the insect species are included (i.e. one can never prove monophagy). Consequently, host specificity has to be a relative measure dependent on both temporal and spatial scale (i.e. sampling period and taxonomic composition of host plant species). This study focuses on the total number of host plants utilized by the beetle species at the local scale defined by the accessible area below the crane boom.

Host specificity of tropical forest herbivore arthropods is still poorly known, but some large-scale surveys, mostly focused on tree hosts, have been performed (e.g. Janzen, 1980, 1988; Basset, 1992; Basset *et al.*, 1996). These studies showed percentages of monophagous species to vary considerably from 3% to 75%. Unfortunately, due to methodological differences, these percentages of monophagy are not comparable. Nonetheless, as indicated by Stork (1987), host specificity is a sliding scale, which means that every measurement of host specificity must give every species an inverse weight in accordance with the number of hosts on which the insects are found (Mawdsley & Stork, 1997). May (1990) described a method for calculation of host specificity (termed effective specialization) based on this principle. For a plant species k, in a community of T plant species, the proportion of beetles that are effectively specialized on k, f_k, is given by:

$$f_k = \sum_{i=1}^{T} (1/i) p_k(i) \tag{1}$$

were $p_k(i)$ is the proportion of beetles associated with plant species k, that are also associated with i other plants. An insect species that is shared between two plant species ($i = 2$) is then half as specialized as an insect species restricted to one plant species. Hence, the fewer hosts of an insect species, the more that insect species contributes to the value of effective specialization (f_k). Accordingly, the monophagous species are given the heaviest weight. The effective number of beetle species specialized on each plant species (k) is given as S_f:

$$S_f = S_k f_k \tag{2}$$

Table 5 Number of phytophagous beetle species, number of phytophagous beetle species of functional groups, and number of species exclusively associated with a given group of plant. Percentage refers to the total number of the given category.

		Lianas				
	Trees (n = 24)	Total (n = 26)	Bignoniaceae (n = 12)	Other species (n = 14)	Total (n = 50)	Species common to trees and lianas
Species associated with trees and lianas	424 (61%)	441 (63%)	276 (40%)	306 (44%)	697	169 (24%)
Species exclusively associated with trees or lianas	256 (48%)	272 (52%)	135 (26%)	137 (26%)	528	—
Flower visitors	118 (84%)	106 (75%)	58 (41%)	105 (74%)	141	83 (59%)
Flower visitors exclusively associated with group of plant	35 (60%)	23 (40%)	1 (2%)	22 (38%)	58	—
Green feeders	131 (41%)	223 (70%)	138 (43%)	125 (39%)	320	34 (11%)
Green feeders exclusively associated with group of plant	97 (34%)	189 (66%)	98 (34%)	91 (32%)	286	—
Wood eaters	175 (74%)	112 (47%)	80 (34%)	79 (33%)	236	52 (22%)
Wood eaters exclusively associated with group of plant	124 (67%)	60 (33%)	33 (18%)	27 (15%)	184	—

where S_k is the number of beetle species found to be associated with plant species k.

The average effective specialization across T plant species, which is a weighted average, is denoted F_T:

$$F_T = S_T/(\bar{S}_T \times T) \tag{3}$$

where S_T is the total number of beetle species associated with T plant species ($S_T = \Sigma S_f$), and $\bar{S}_T$ is the average number of insect species associated with each plant species. Then,

$\bar{S}_T \times T$ is the number of host observations.

Using reasonably accurate data from known biology of beetles associated with British *Quercus* trees, May (1990) found that effectively 10% of their herbivores were specialized on the genus. This method is also used indirectly on data from canopy fogging studies of ten rain forest trees in Borneo, suggesting an effective specialization of less than 10% (Mawdsley & Stork, 1997).

One weakness of the concept of effective specialization is its treatment of taxonomic related host plants as independent. A beetle feeding on just two closely related species within a plant genus will acquire the same degree of host association as a species feeding on two distantly related plant species, which could lead to considerable bias in estimation of effective specialization. Due to this problem, it was important to select trees and lianas with similar distribution on taxonomic categories. There were twelve families, twenty genera and four congeneric species pairs of trees and ten families, twenty-three genera and two congeneric pairs of lianas (Table 3). One possible skewness in this distribution could appear in the Bignoniaceae since twelve of the twenty-six liana species belong to this plant family. Therefore, calculations of host specificity parameters (S_k, S_f and F_T) for lianas are compared to analogous calculations excluding the Bignoniaceae to balance for effects of taxonomic relatedness of plants.

Another weakness relates to the fact that two hosts are considered independent of beetle density per biomass of host plants. This is critical because rare occurrences of insects on certain host plants inflate the estimates of both an insect's host range and a plant's variety of insect associates above the levels apparent in the field (Futuyma & Gould, 1979). When comparing trees and lianas in this context, it was considered more important to record as many host associations as possible through the procedure of additional sampling, than to obtain an accurate measure of degree of specialization such as diet breadth (*sensu* Futuyma & Gould, 1979).

RESULTS

A total of 35,479 individuals belonging to 1167 species of phytophagous beetles were collected. Of these, 1743 individuals, belonging to 470 species, were omitted because their host associations were not found. A total of 1339 host observations were recorded from trees and 1222 from lianas. Thus, this study treats 2561 host observations based on 33,736 individuals belonging to 697 species. Most species and individuals belong to the families Chrysomelidae and Curculionidae (Table 1).

Species richness

The twenty-four tree species were hosts to a total of 424 beetle species, of which 256 were exclusively tree associates. The twenty-six liana species were hosts to 441 beetle species, of which 272 were exclusively liana associates. Accordingly, 24.2% (697 – (256 + 272) = 169) of the species were found to be associated with both trees and lianas. Division of species into functional groups shows that trees have more wood-eating species than lianas (175 compared to 112) while lianas have more species of the green-feeding guild (223 compared to 131). The high percentage (59%) of flower visitors common to both trees and lianas indicates a low degree of specialization among species of this functional group. In contrast, only 11% of the green feeders were shared between trees and lianas (Table 5).

In total, there were not significantly more species associated with trees than lianas, even when Bignoniaceae were excluded (*t*-test: $z = -1.106$, n.s.). However, there were large differences in their reciprocal distribution across functional groups. The

Table 6 Mean number of phytophagous beetle species associated with each species of trees and lianas, S_k (SE). *T*-test 1 compares trees and all lianas, *t*-test 2 compares Bignoniaceae and other lianas, *t*-test 3 compares trees and other lianas.

	Trees (n = 24)	Lianas (n = 26)	*t*-test 1	Bignoniaceae (n = 12)	Other lianas[a] (n = 14)	*t*-test 2	*t*-test 3
Total	55.8 (6.78)	47.0 (6.05)	$0.970^{\text{n.s.}}$	49.5 (8.7)	44.9 (8.7)	$0.376^{\text{n.s.}}$	$0.987^{\text{n.s.}}$
Flower visitors	17.8 (3.34)	13.6 (2.84)	$0.957^{\text{n.s.}}$	9.7 (3.5)	16.9 (4.3)	$-1.270^{\text{n.s.}}$	$0.158^{\text{n.s.}}$
Green Feeders	17.0 (1.90)	19.2 (2.27)	$-0.734^{\text{n.s.}}$	24.0 (3.8)	15.1 (2.3)	2.075*	$0.535^{\text{n.s.}}$
Wood Eaters	21.0 (3.29)	14.2 (1.98)	$1.805^{\text{n.s.}}$	15.8 (2.8)	12.7 (2.8)	$0.740^{\text{n.s.}}$	$0.099^{\text{n.s.}}$

[a] All lianas investigated in this study excluding the species of Bignoniaceae.
* $P < 0.05$.

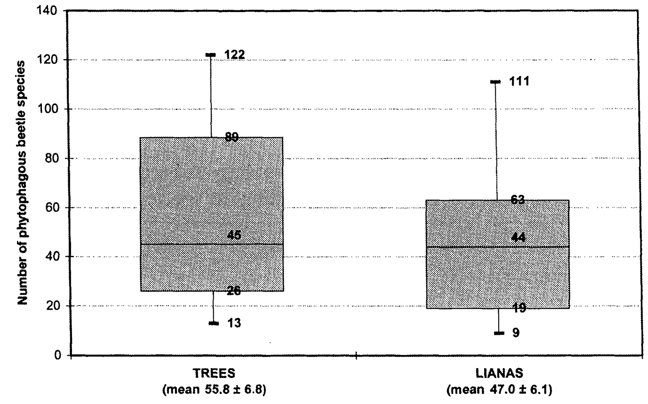

Figure 1 A Box & Wisker plot of the number of phytophagous beetle species associated with each species of trees and lianas (S_k).

green feeders were significantly more speciose on lianas than on trees (*t*-test: $z = -4.230$, $P < 0.001$), and the wood eaters were significantly more speciose on trees than lianas (*t*-test: $z = 6.416$, $P < 0.001$). These relations remained the same when Bignoniaceae were excluded (green feeders: *t*-test: $z = -4.793$, $P < 0.001$; wood eaters: *t*-test: $z = 6.302$, $P < 0.001$). The flower visitors were only slightly different in species numbers on trees compared to lianas (*t*-test: $z = 1.680$, n.s.). Their weak dominance on trees was inverted when Bignoniaceae were excluded since only few flower visitors were associated with that plant family (*t*-test, $z = -2.062$, $P < 0.05$).

Calculated across the tree species and across the liana species, there was no significant difference in the average number of phytophagous beetle species per tree *v.* per liana species, neither in total nor considering each functional group (flower visitors, green feeders, and wood eaters). However, there was a tendency for trees to support a greater number of wood eaters than lianas (*t*-test: $z = 1.805$, $P = 0.077$). Within the lianas, there were significantly more green-feeding species associated with Bignoniaceae than with other lianas. However, excluding the Bignoniaceae, did not affect the nonsignificant difference between the number of green feeders of trees *v.* lianas (Table 6).

The number of species associated with each plant species varied greatly both in trees and lianas. A Box & Wisker plot shows that the 75th percentile was considerably higher in trees than lianas while the medians were similar (Fig. 1).

All plants supported green feeders and wood eaters, and all plant species that flowered also supported flower visitors (*Astronium graveolens* Jacq. and *Cydista aquinoctalis* (L.) Miers were sterile during this study). Some species were especially attractive to flower visitors: four trees (*Nectandra membranacea* ssp. *cuspidata* (Nees & Mart.) Rohwer, *Luehea seemannii* Tr. & Planch., *Cordia alliodora* (R & P.) Oken and *Albizzia adinocephala* (Donn. Sm.) Britt. & Rose) and four lianas (*Amphilophium paniculatum* (L.) H.B.K., *Mikania leiostachya* Benth. and *Cnestridium rufescens* Planch.) supported more than thirty regular flower visitors each. *Ficus maxima* Mill. and *F. insipida* Willd. supported far more species of wood eaters than any other plant species (fifty-nine and sixty species, respectively). Four Bignoniaceae lianas (*Amphilophium paniculatum, Arrabidaea candicans* (L. Rich.) DC., *A. patellifera* (Schlecht.) Sandw. and *Tynnanthus croatianus* A. Gentry) had more than thirty species of green feeders associated with each. Among the trees, only *Anacardium exelsum* (Bert. & Balb.) Skeels and *Spondias mombin* L. held more than thirty species of green feeders (Appendices 1 and 2).

Considering the plant families with both tree and liana species in this study (Fabaceae and Sapotaceae), only a few beetle species were associated with both life forms of plants, although Sapotaceae and Fabaceae had twenty-two and thirty-six beetle species, respectively, specific to each plant family. Only broad generalist beetle species, having on average twenty-four different hosts, had confamilial tree and liana species as hosts (two cases in Sapotaceae and seven cases in Fabaceae).

Host specificity

The distribution of number of hosts for each beetle species (i.e. the number of beetle species associated with 1, 2, ... *n* plant species; Fig. 2) suggests a prevalence of specialized species (of 322 species, 46.2%, had only one host). On the other hand, as many as 159 species (22.8%) had more than five hosts.

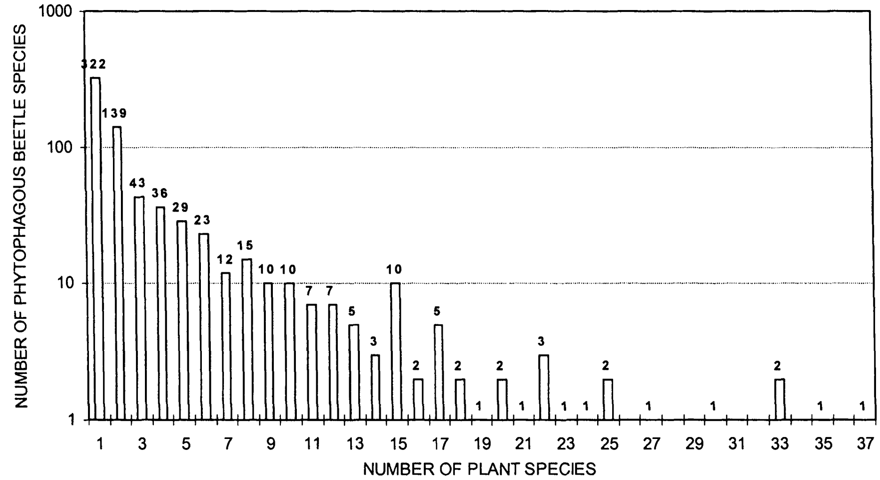

Figure 2 Distribution of diet richness of 697 phytophagous beetle species. The number beetle species utilizing 1, 2, 3,....50 host plants.

Table 7 Mean effective number of phytophagous beetle species specialized to trees and lianas, S_f (SE). *T*-test 1 compares trees and all lianas, *t*-test 2 compares trees and lianas excluding the species of Bignoniaceae.

	Trees (n = 24)	Lianas (n = 26)	*t* -test 1	Lianas[(a)] (n = 14)	*t*-test 2
Total	14.4 (2.21)	13.5 (1.83)	$0.312^{\text{n.s.}}$	12.9 (2.52)	$0.400^{\text{n.s.}}$
Flower visitors	3.2 (0.84)	2.5 (0.63)	$0.689^{\text{n.s.}}$	3.6 (0.96)	$-0.322^{\text{n.s.}}$
Green Feeders	4.8 (0.73)	7.8 (1.03)	-2.287^{*}	6.6 (1.17)	$-1.340^{\text{n.s.}}$
Wood Eaters	6.4 (1.36)	3.2 (0.57)	2.191^{*}	2.8 (0.81)	$1.894^{\text{n.s.}}$

[(a)] All lianas investigated in this study, excluding the species of Bignoniaceae.
* $P < 0.05$.

There was no difference in the total effective number of species specialized (S_f) on tree species compared to liana species. However, significantly more species of the green-feeding guild were effectively specialized on liana species than on tree species (*t*-test: $z = -2.287$, $P < 0.05$), and significantly more wood eaters were effectively specialized on tree species than on liana species (*t*-test: $z = 2.191$, $P < 0.05$). When lianas of Bignoniaceae were excluded, no significant differences of this kind were detected (Table 7). These patterns are probably due to the fact that (a) green feeders of Bignoniaceae are somewhat more specialized than those of other lianas (Fig. 4), and (b) number of specialized wood eaters of Bignoniaceae are less variable than that for other liana species (Table 7).

A Box and Wisker plot on the effective number of specialized species (S_f) (Fig. 3) shows a large variation in effective number of specialized species, a pattern similar to that for total number of species (S_k) (Fig. 1). A relation suggesting that the amount of specialized species increases proportionally with the total number of species utilizing the plant.

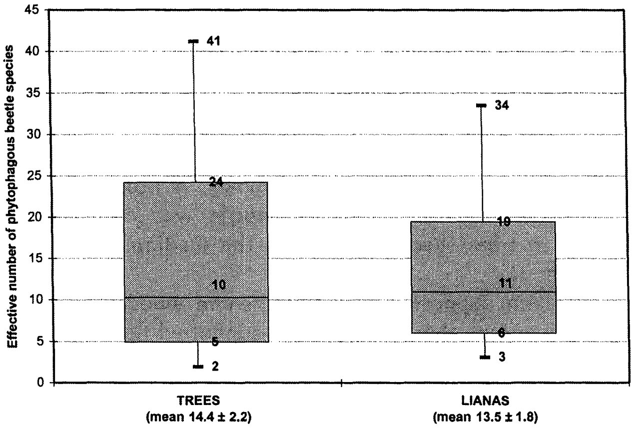

Figure 3 A Box & Wisker plot of the effective number of phytophagous beetle species specialized on each species of trees and lianas (S_f).

The calculated values of F_T indicate that lianas have a fauna of phytophagous beetles slightly more specialized than trees. However, the green feeders on lianas are much more specialized than those on trees, while the wood eaters on trees are somewhat more specialized than those on lianas. None of these patterns were affected when species of Bignoniaceae were excluded. Flower visitors on trees and lianas showed very similar degrees of host specialization; however, this value was lower here than in other guilds (Fig. 4).

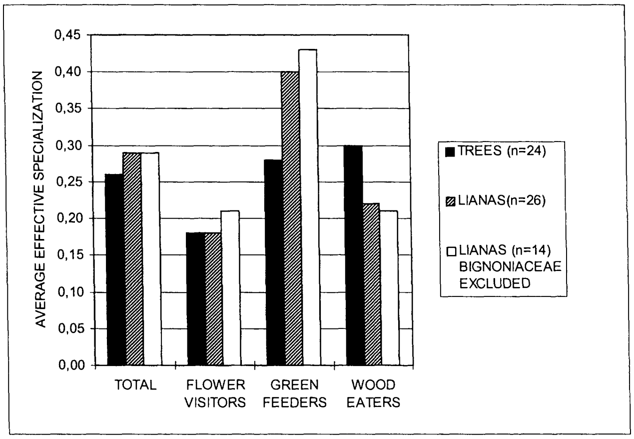

Figure 4 Average effective specialization (F_T) of phytophagous beetle species associated with trees and lianas. Flower visitors, green feeders, and wood eaters are treated separately. The values of F_T are also shown when the lianas of Bignoniaceae are excluded from the data set.

DISCUSSION

Species richness

In general, the number of insect species associated with a plant species depends on the geographical range, local abundance of the plant species (Southwood, 1960; Fowler & Lawton, 1982), and intrinsic characteristics of the plant such as size, structural complexity (e.g. Lawton, 1983) and biochemical properties (e.g. Bernays & Chapman, 1994). Finally, evolutionary radiations of insects are dependent on the degree of taxonomic and chemical isolation of host plants (Connor *et al.*, 1980; Strong *et al.*, 1984; Niemelä & Mattson, 1996). For this reason, abundant close relatives (confamilial or congeneric plants) generally acquire more insect species than otherwise taxonomically or chemically isolated plants (Strong *et al.*, 1984; Tahvanainen & Niemelä, 1987).

When comparing life forms of plants, the major determinants of the differences in number of insect species associated with particular life forms refers to structural complexity and size. Increased structural complexity implies more microhabitats available for occupation, while an increase in size implies larger population size which reduces extinction risk (Lawton & Schröder, 1977; Strong & Levin, 1979; Moran, 1980; Lawton, 1983).

In this study, lianas and trees had virtually the same number of associated beetle species, despite the relatively smaller size of lianas (i.e. lower biomass and leaf area). These results could be related to the fact that lianas possess relatively high structural complexity (Caballé, 1993). Structures specific for lianas are related to their climbing mechanisms, particularly the tendrils. They appear to be a very important microhabitat for many beetle species feeding within the plant families Bignoniaceae, Rhamnaceae, Sapindaceae and Vitiaceae. In this study some eighty beetle species were specific tendril feeders within these plant families. Obviously, an extreme radiation of species has taken place within the weevil tribe Baridini of which forty-nine closely related species are found to be exclusively associated with tendrils, buds, or leaflets of the Bignoniaceae. Analogous examples of species radiations are also found in the *Aulacochlamys* (Chrysomelidae, Chlamisinae), a complex species group including sixteen species feeding on tendrils of *Serjania* (Sapindaceae) and Bignoniaceae; and in the *Hylaeogena* (Buprestidae) which include ten species of leaf miners on Bignoniaceae. Species radiations in these beetle taxa were seemingly the reason why the Bignoniaceae had significantly more beetle species associated than other lianas These findings empirically support Gentry's suggestion (Gentry, 1985) that lianas are preadapted for the development of intricate biotic interactions, causing species radiations. (These preadaptations are specific kinds of biochemical defences correlated with a life history featuring rapid growth and thus a prevalence of soft, young edible vegetative parts.) Whether such a pattern arises as a result of intrinsic properties specific to lianas, or because the high degree of taxonomic relationship within liana species compared to tree species, is not known. However, these possibilities are not mutually exclusive. A comparison with confamilial tree could elucidate if these radiations are dependent of plant growth forms rather than being characteristic for some taxonomic groups of plants. It is unknown whether, or not, radiations of beetles are common in tree species belonging to the Bignoniaceae. However, several species of the Dorynotini (Cassidinae) (Windsor *et al.*, 1992; Buzzi, 1994) and *Oedionychus* (Alticinae) (Rockwood, 1974; Ribeiro *et al.*, 1994) are associated with Bignoniaceae tree species.

It is proposed that the length of the growing season of a plant species also influence the number of herbivorous insect species exploiting it due to altered exposure time (Lawton, 1978; Niemelä & Haukioja, 1982; Niemelä *et al.*, 1982). The amount of young leaves is positively correlated with leaf damage from herbivory (Coley, 1983) and abundance of herbivorous insect species because young leaves are soft and easy digestible and high in content of nitrogen (Basset, 1991). Lianas and trees are somewhat different in this respect. In general, lianas produce new leaves for long periods throughout the year, and they have a higher total production rate of new leaves than trees (Hegarty & Caballé, 1991). In this study, lianas on average produced new leaves for a longer period (200 ± 74 days per year) than trees (157 ± 97 days per year) (t-test: $z = 2.114$, $P = 0.038$). With this in mind, it is suggested that length of growing season could be a concurrent factor for explaining the relatively higher than expected species richness of beetles associated with lianas compared to trees.

Wood-eating beetles were more numerous in trees than lianas. The actual difference may be even larger than that detected in this study because the whole range of woody microhabitats of trees (i.e. thick branches and limbs) in the canopy could not be sampled properly. Generally, wood eaters are underestimated in species numbers because of their concealed habit.

The flower visitors, associated both with trees and lianas, was the feeding guild that showed the highest variance in species richness. The number of flower visitors of a plant species is probably highly dependent on the pollination strategy of the plant. The involvement of beetles in such processes is highly variable (Endress, 1994), a fact that correlates well with the present results.

There are great differences in numbers of beetles associated with each plant species, considering both trees and lianas separately (Fig. 1). These patterns suggesting that the factors determining whether a plant is considered as an available resource for an insect species, is more dependent on chemical, biotic and structural characteristics of each plant taxon (independent of life form), than on the life form to which the plant belongs. Nevertheless, extreme radiation seems to be a feature typical to some groups of feeders of lianas. Furthermore, within plant families consisting of both trees and lianas, no beetle species was associated with both life forms of plants. These results suggest that life form is more important than taxonomic relationship within plant families regarding species composition and faunal overlap of herbivores. Although, such relations could in turn be caused by different chemical, biotic and structural characteristics of these trees and lianas as well.

Host specificity

The distribution of number of hosts for each beetle species (Fig. 2) suggests a prevalence of specialized species. Additional sampling would increase the number of host associations of polyphagous species, however, at the same time, new monophagous associations will be detected. The rate of increase of these two processes depends on the data set and can be elucidated by fitting models of species accumulation curves of subsamples (e.g. Colwell & Coddington, 1994).

It should be noted that a large proportion (53%) of the host associations was of the weakest level of confidence (Table 4). Accordingly, these observations should be supported by more evidence to be treated as adequate host records. However, the distribution of reliability scores of host observations for trees and lianas, respectively, were virtually similar (Table 4), hence the comparison itself should be insensitive to such variation.

Young leaves have more specific kinds of biochemical defence, which could promote specialization (Janzen, 1984). Cates (1980, 1981) has shown that monophagous and oligophagous species are more strongly dependent on young leaves than polyphagous species. Increased abundance of insects on young foliage may also provide specialization due to increased competition between or within species (Burdon & Chilvers, 1974). Competition for limited high quality resources may occur even at low population densities (Price, 1992). Besides the favourable properties of young leaves, the diversity of microhabitats among young, green tissue of lianas (e.g. the tendrils) is suggested as another factor providing a greater specialization of the species associated with lianas than those associated with trees.

It is interesting that five tree species of the Moraceae (the genera *Ficus*, *Castilla*, and *Cecropia*) have the greatest degree of specialization amongst the beetles associated regarding both green feeders and wood eaters (f_k values, Appendices 1 and 2). This plant family is characterized by sticky latex, containing defensive compounds (Thomen, 1939; Janzen, 1979). The general properties of *Ficus* spp. for insect herbivores and, in particular, the predominance of wood-eating taxa and specialized feeders are pointed out in Basset *et al.* (1997). Specialization in these insects could be related to the needs for adaptations to the host (Farrell *et al.*, 1992; Bernays & Chapman, 1994). In addition, similar arguments could be made to explain the existence of a specialized liana fauna, due to the fact that leaf production in the two species of *Ficus* is prominent throughout the year. The special architecture of the studied *Ficus* species, consisting of leafs in typical layers and great amounts of dead twigs below, provides a sustainable resource for the wood-dependent fauna. The specialization of the *Cecropia*-associated beetles is presumably necessary for coexistence with the ants that defend these plants (e.g. Longino, 1991).

Flower visitors were generally less specialized than other guilds. There were no significant differences among trees and lianas within this guild (Fig. 4). Slobodkin *et al.* (1967) argue that herbivores associated with fruits and flowers would be expected to compete for scarce resources, which, in turn, should lead to specialization, a hypothesis not supported by these data. On the other hand, eating pollen and nectar, rich in nutrients and low in toxic substances, means a general dietary supplement for many species, promoting a generalized flower fauna of a particular plant species (Samuelson, 1989; Jolivet & Hawkeswood, 1995). Accordingly, the degree of host specialization for flower visiting insects is probably dependent on whether the flowers are the primary host, essential for the insects' development, or a secondary resource utilized for obtaining supplementary energy. For most beetle species in this study, the latter situation seems to be the case because many flower visitors are known to have other primary hosts. However, there are three plant species having a relatively host-specific flower fauna including *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. ($f_k = 0.36$), the only palm at the crane site. This figure is consistent with the fact that palms are known to have a species-rich fauna of specialized flower associated weevils (C. O'Brien, pers. comm.). Secondly, the high specialization of the flower fauna of *Stigmaphyllon hypargyreum* Tr. & Planch. ($f_k = 0.52$) could be explained through the dominance of specialized species of weevils of the tribe Anthonomini. According to Burke & Clark (Burke, 1976; Clark & Burke, 1985; Clark, 1988), many species within this tribe are associated with Malphigiaceae. In general, the species with larval development in seeds and buds are more specialized than those species visiting flowers as adults for nutrient purposes (Burke, 1976; Janzen, 1980; Samuelson, 1994). However, it was hard to separate these two groups in the present study since no rearing was done. Thirdly, the flower visitors in *Calopogonium caeruleum* (Benth.) Hemsl. also show a relatively high degree of specialization ($f_k = 0.48$). Legume seeds are known to be attacked by a variety of bruchid beetles (Rehr *et al.*, 1973), patterns fitting well with the specialized flower fauna of this plant.

It is interesting that the relatively specialized green-feeding fauna of the Bignoniaceae, seems to have a conspicuously general flower-visiting fauna (f_k mean = 0.09). According to Gentry (1976), these liana species are pollinated by different groups of bees. Since phytophagous beetles are not directly involved in the pollination process, it is not surprising that they are lower in numbers and in the degree of specialization.

This study has shown a higher degree of effective specialization of beetles associated with lianas than trees in this tropical dry forest. This result is offset by the slightly lower number of beetle species associated with each liana species, causing the pooled numbers of species associated with lianas and trees to be nonsignificantly different (Table 7). Accordingly, at this local scale, lianas are at least as important as trees for maintenance of local species diversity of phytophagous beetles. The mechanisms that drive the patterns can only be hypothesized. Plant architecture, size, and length of growing season are probably involved. Further studies of this topic should include measurements plant traits and manipulations to elucidate experimentally what mechanisms being involved. Additional insight would come from similar investigations of other forest types to see if the patterns remain when the species pool and the densities of major growth forms are different. Other major groups of herbivores, such as Lepidoptera and Orthoptera, should also be included in the analysis since they may be different regarding host specificity (Basset *et al.*, 1996).

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BIOSKETCH

Frode Ødegaard received his PhD at the Norwegian University for Science and Technology in 1999. Currently, he works as a research scientist at the Department of Conservation Biology, Norwegian Institute for Nature Research in Trondheim, Norway. The present work is a part of his doctoral thesis, which deals with host specificity as a parameter in estimates of species richness. In addition to tropical entomology, he also works on faunistics and ecology of Nordic Coleoptera and Heteroptera.

Appendix 1 Total numbers of phytophagous beetle species associated with each tree species (S_k) and the effective specialization (f_k) of the beetle fauna on tree species k, and the effective number of species specialized on each tree species (S_f). These values are also given for functional groups (F = flower visitors; G = green feeders, and W = wood eaters). The species are ranked in order of those tree species having the most specialized fauna associated.

Tree species	S_k	f_k	S_f	SF	F f_k	F S_f	SG	G f_k	G S_f	SW	W f_k	W S_f
Ficus insipida	102	0.40	41.2	18	0.14	2.5	24	0.44	10.5	60	0.47	28.2
Cecropia longipes	44	0.35	15.2	9	0.17	1.6	12	0.28	3.4	23	0.45	10.3
Cecropia peltata	51	0.33	16.9	13	0.27	3.6	14	0.32	4.4	24	0.37	8.9
Castilla elastica	22	0.32	7.1	4	0.04	0.2	5	0.42	2.1	13	0.37	4.8
Ficus maxima	78	0.31	23.9	7	0.12	0.8	12	0.29	3.5	59	0.33	19.5
Andira inermis	14	0.28	4.0	5	0.19	1.0	7	0.39	2.7	2	0.13	0.3
Enterolobium cyclocarpum	71	0.28	19.6	22	0.17	3.7	27	0.38	10.2	22	0.26	5.7
Luehea seemannii	96	0.27	26.4	37	0.21	7.9	30	0.35	10.6	29	0.27	7.9
Cordia alliodora	93	0.27	25.3	42	0.19	7.9	24	0.35	8.3	27	0.34	9.1
Pseudobombax septenatum	38	0.27	10.3	10	0.29	2.9	14	0.12	1.7	14	0.41	5.7
Spondias mombin	102	0.26	26.8	25	0.12	3.1	39	0.32	12.3	38	0.30	11.4
Nectandra membranacea ssp. *cuspidata*	122	0.26	31.5	76	0.26	19.9	27	0.22	6.0	19	0.30	5.7
Anacardium exelsum	99	0.25	24.6	25	0.15	3.6	31	0.30	9.4	43	0.27	11.6
Chlorophora tinctoria	46	0.22	10.3	8	0.08	0.7	12	0.16	1.9	26	0.30	7.7
Phoebe cinnamomifolia	44	0.22	9.8	17	0.16	2.7	12	0.32	3.8	15	0.22	3.3
Nectandra globosa	26	0.21	5.4	10	0.11	1.1	12	0.34	4.0	4	0.06	0.3
Acrocomia aculeata	16	0.21	3.3	8	0.36	2.9	5	0.03	0.1	3	0.10	0.3
Albizia adinocephala	84	0.20	17.2	34	0.16	5.3	23	0.31	7.1	27	0.17	4.7
Antirrhoea tricantha	36	0.18	6.6	13	0.11	1.5	16	0.27	4.3	7	0.11	0.7
Chrysophyllum cainito	47	0.16	7.5	14	0.11	1.5	20	0.19	3.8	13	0.17	2.2
Didymopanax morototoni	13	0.15	1.9	1	0.04	0.0	7	0.20	1.4	5	0.10	0.5
Astronium graveolens	38	0.12	4.5	12	0.11	1.4	19	0.12	2.2	7	0.12	0.9
Spondias radlkoferi	19	0.11	2.1	7	0.05	0.4	5	0.16	0.8	7	0.14	1.0
Matayba scrobiculata	38	0.11	4.1	10	0.10	1.0	12	0.10	1.2	16	0.12	1.9

Appendix 2 Total numbers of phytophagous beetle species associated with each liana species (S_k) and the effective specialization (f_k) of the beetle fauna on liana species k, and the effective number of species specialized on each liana species (S_f). These values are also given for functional groups (F = flower visitors; G = green feeders, and W = wood eaters). The species are ranked in order of those liana species having the most specialized fauna associated.

Liana species	S_k	f_k	S_f	SF	F f_k	F S_f	SG	G f_k	G S_f	SW	W f_k	W S_f
Stigmaphyllon hypargyreum	48	0.50	23.9	16	0.52	8.3	24	0.61	14.5	8	0.13	1.1
Calopogonium caeruleum	16	0.48	7.6	5	0.48	2.4	9	0.51	4.6	2	0.29	0.6
Paragonia pyramidata	27	0.45	12.0	2	0.10	0.2	21	0.55	11.5	4	0.08	0.3
Cydista aequinoctalis	14	0.43	6.0	0	0.00	0.0	7	0.60	4.2	7	0.26	1.8
Canavalia bicarinata	9	0.41	3.7	2	0.04	0.1	5	0.69	3.4	2	0.11	0.2
Jacquemontia hirtifolia	15	0.39	5.9	3	0.10	0.3	7	0.59	4.1	5	0.30	1.5
Dioclea guianensis	19	0.36	6.9	2	0.04	0.1	8	0.59	4.7	9	0.23	2.1
Arrabidaea candicans	98	0.34	33.5	13	0.10	1.2	48	0.48	23.3	37	0.24	9.0
Tynnanthus croatianus	49	0.32	15.7	3	0.11	0.3	35	0.34	11.9	11	0.31	3.4
Serjania mexicana	77	0.31	23.9	26	0.19	4.9	30	0.46	13.9	21	0.24	5.0
Banisteropsis muricata	19	0.29	5.5	4	0.18	0.7	10	0.43	4.3	5	0.10	0.5
Amphilophium paniculatum	111	0.29	31.8	46	0.18	8.1	36	0.42	15.0	29	0.30	8.7
Gouania lupuloides	111	0.29	31.7	47	0.17	7.8	30	0.44	13.3	34	0.31	10.6
Phryganocydia corymbosa	28	0.27	7.7	6	0.07	0.4	12	0.39	4.7	10	0.25	2.5
Stizophyllum riparium	45	0.26	11.7	8	0.09	0.7	21	0.27	5.7	16	0.33	5.3
Mikania leiostachya	94	0.26	24.4	45	0.23	10.2	17	0.41	7.0	32	0.23	7.3
Arrabidaea patellifera	75	0.26	19.5	10	0.08	0.8	41	0.34	13.8	24	0.21	4.9
Combretum fruticosum	63	0.26	16.2	23	0.13	3.0	21	0.44	9.2	19	0.21	4.1
Serjania rhombea	52	0.25	13.2	21	0.27	5.7	18	0.29	5.2	13	0.17	2.3
Anemopaegma orbiculatum	23	0.24	5.4	5	0.10	0.5	11	0.36	4.0	7	0.13	0.9
Arrabidaea corallina	47	0.23	10.9	10	0.10	1.0	25	0.31	7.9	12	0.17	2.0
Pithecoctenium crucigerum	34	0.21	7.3	4	0.08	0.3	14	0.25	3.5	16	0.22	3.5
Cnestridium rufescens	57	0.19	11.0	33	0.21	6.8	14	0.21	3.0	10	0.13	1.3
Callichlamys latifolia	43	0.18	7.8	10	0.11	1.1	17	0.27	4.6	16	0.14	2.2
Vitis tiliifolia	18	0.17	3.1	3	0.06	0.2	12	0.22	2.7	3	0.08	0.2
Bonamia trichantha	30	0.16	4.7	7	0.07	0.5	7	0.31	2.2	16	0.13	2.0