Host specificity, alpha- and beta-diversity of phytophagous beetles in two tropical forests in Panama

FRODE ØDEGAARD
*Norwegian Institute for Nature Research (NINA), Tungasletta 2, NO-7485 Trondheim, Norway
(e-mail: frode.odegaard@nina.no; phone: +47-73-80-15-55; fax: +47-73-80-14-01)*

Abstract. Species diversity, host specificity and species turnover among phytophagous beetles were studied in the canopy of two tropical lowland forests in Panama with the use of canopy cranes. A sharp rainfall gradient occurs between the two sites located 80 km apart. The wetter forest is located in San Lorenzo Protected Area on the Caribbean side of the isthmus, and the drier forest is a part of the Parque Natural Metropolitano close to Panama City on the Pacific slope. Host specificity was measured as effective specialization and recorded by probability methods based on abundance categories and feeding records from a total of 102 species of trees and lianas equally distributed between the two sites. The total material collected included more than 65,000 beetles of 2462 species, of which 306 species were shared between the two sites. The wet forest was 37% more species rich than the dry forest due to more saproxylic species and flower visitors. Saproxylic species and flower visitors were also more host-specific in the wet forest. Leaf chewers showed similar levels of species richness and host specificity in both forests. The effective number of specialized species per plant species was higher in the wet forest. Higher levels of local alpha- and beta-diversity as well as host specificity based on present data from a tropical wet forest, suggests higher number of species at regional levels, a result that may have consequences for ecological estimates of global species richness.

Abbreviations: PNM – Parque Natural Metropolitano, Panama Province, Panama; SLA – San Lorenzo Protected Area, Colon Province, Panama

Introduction

Biodiversity is not only an issue of curiosity, but stands firm on the political agenda as a resource for humanity (Heywood 1995). Many species are under continuous threat as more natural ecosystems are changed, polluted, affected by climatic change, or exploited too heavily. To know the number of species, their ranges and ecology is therefore an important topic in conservation biology, for instance when estimating the rate of extinction and decline of species both locally and worldwide. More specifically, elucidation of the variation in host specificity and insect species richness along geographical gradients would be essential for refining our knowledge on the magnitude of local or even

global species richness (May 1994; Mawdsley and Stork 1997; Stork 1997; Ødegaard 2000a) as well as ecosystem structure and dynamics, and eventually for thorough based decisions in nature management.

Ecological estimates of regional species diversity are almost entirely based on studies reporting insect species diversity from single tropical sites (e.g., Erwin 1982; Basset et al. 1996; Ødegaard 2000a; Novotny et al. 2002a). However, such alpha diversity studies are of limited value in terms of predicting species richness on larger spatial scales due to incomplete sampling caused by temporal and spatial limitations. It is even hard to predict regional species diversity based on data from very extensively studied areas because the influence from mass effects increases with sample size (Shmida and Wilson 1985; Novotny and Basset 2000).

Species composition and host specificity of phytophagous beetles may vary considerably between sites (Basset 1992). This variation can be explained by differences in resource availability or other determinants for insect species diversity, such as hostplant abundance, distribution and species richness (e.g., Southwood 1960, 1961; Neuvonen and Niemelä 1983; Condit et al. 2000), plant architecture (Lawton and Schröder 1977), chemical composition of plant tissue (e.g., Connor et al. 1980; Bernays and Chapman 1994), and interactions among animals e.g., competition for resources and enemy-free space and several abiotic factors (Strong et al. 1984). For these reasons, comparisons of insect communities may have a higher probability of being of general validity if replicates are taken in different types of forests.

Beta diversity is the extent to which the diversity of two or more spatial units differs (Magurran 2003). Originally, beta diversity measures the extent of difference between two or more areas relative to the total species richness (e.g., Whittaker 1960), but more commonly it is used for comparing similarity between sites through different indices based on abundance or presence/absence data (Magurran 2003). Beta diversity has been widely used also for estimation of regional species richness through application of the classical species–area relationship (Gleason 1922; Connor and McCoy 1979; Mawdsley 1996; Ricotta et al. 2002). The main factors explaining beta diversity is range and habitat restrictions (Harrison et al. 1992). While there is an increasing understanding of patterns and mechanisms responsible for species turnover in tropical plants (Condit et al. 2002), there are relatively few studies on beta diversity of tropical insects (Hespenheide 1994; Novotny and Missa 2000).

Beta diversity among phytophagous insects is obviously linked to species turnover among host plants. Similarity in tropical tree communities declines with distance between sites (Condit et al. 2002). If all species were monophagous, the species turnover among phytophagous insects would be similar or higher than that of their host plants. Host specialization among insects complicates the patterns of beta diversity, however. The effective specialization among tropical insect communities is probably as low as 5–10% (Basset et al. 1996; Ødegaard et al. 2000; Novotny et al. 2002a), and it is unknown how the large proportion of generalists among tropical insects affects species turnover.

Generalists tend to have wider geographical ranges than specialized species (Gaston 1991), but these relations are hard to study because geographical range of insect species in tropical forests is very poorly known for most groups, and even less knowledge exists about similarity among insect communities between sites (Basset 2001).

The aim of this study was to examine how different terrestrial insect communities are structured with regard to species richness and host specificity in two different tropical lowland forests in Panama. The model group for this study was phytophagous beetles which constitute a dominant component of biodiversity on Earth (Hammond 1992). Host specificity and taxonomic composition of beetle communities in tropical forests are therefore important parameters structuring terrestrial ecosystems and basic for development of a better knowledge of species richness and beta diversity.

The geography of Panama particularly lends itself to understanding patterns in species turnover. The sharp rainfall gradient between the two sites causes an almost complete turnover of plant species. In addition, population variability of insect assemblages is in some cases more prominent between dry and wet tropical forests than it is between temperate and tropical forests (Wolda 1978; Pimm 1991). It would be of fundamental ecological interest to test if related parameters such as host specificity and beta diversity of insect communities also differ between these forest types. The results may in turn give further implications about the validity of current ecological estimates of global species richness.

Methods

Study sites

The study was carried out at two Panamanian lowland forest sites which represent different tropical forest types. The first site is the Parque Natural Metropolitano (PNM), which consists of 265 ha dry tropical forest in Panama province, close to Panama City and 2 km from the Pacific coast (8°59′ N, 79°33′ W, ca. 30 m a.s.1.). The average annual temperature is 28 °C, and annual precipitation is 1740 mm. The dry season is distinct from December to April, when rainfall is usually less than 100 mm per month. This is a secondary forest that has escaped major human disturbance for about 90 years. The vegetation at this site is characterized by dominance of deciduous trees (30–35 m height) and lianas in the canopy (Wright et al. 2003).

The other site is located in an evergreen, wet forest in San Lorenzo Protected Area (SLA) (9°17′ N, 79°58′ W, ca. 130 m a.s.1.), Colon province, 4.4 km away from the Atlantic coast of the isthmus. The average annual temperature is 25.8 °C, and average annual precipitation is 3140 mm. There is a pronounced dry season from mid December to end of April that receives nearly 10% of the yearly precipitation. This forest is dominated by trees at 35–45 m height with

lianas and epiphytes occurring regularly in the canopy. The San Lorenzo Protected Area includes 9600 ha of relatively old-growth tropical forest which has escaped anthropogenic disturbance for about 200 years (Wright et al. 2003).

Annual rainfall drops linearly from 3.1 to 1.7 m crossing the isthmus from north to south with little confounding elevational change. The study sites are located ca. 80 km apart in a contiguous protected forest along the Panama Canal with a total area of 370 km^2 (Wright and Colley 1994).

Canopy access

The canopy was accessed by two canopy cranes erected at the sites. The crane in PNM is 44 m tall with an arm length of 52 m that gives access to ca. 0.8 ha of projected area. About 40 species of trees and ca. 35 species of climbers reach the middle or upper levels of the canopy which could be accessed from the crane gondola. The SLA-crane is 54 m tall with an arm length of 55 m. Hence, the projected area accessible for study was 0.88 ha. About 70 species of trees and ca. 10 species of lianas were easily accessible for study from the crane gondola in SLA.

Focal taxa

The focal groups of this study were adult beetles of Buprestidae, Chrysomeloidea, and Curculionoidea, which make up nearly all herbivorous and a major part of saproxylic beetles in this forest. All the beetle material was identified to species level. Identifications were performed by the author or experts studying the different taxonomic groups. A species list from PNM is available in Ødegaard (2003). A large part of the material was deposited in the author's collection at the Norwegian Institute for Nature Research (NINA). Material of current taxonomic importance for the taxonomists has been deposited in their respective collections (see Acknowledgements), while a representative selection of the material were deposited in the synoptic insect collection at Smithsonian Tropical Research Institute (STRI) and the University of Panama.

For statistical treatment leaf chewers, saproxylic species, and flower visitors were distinguished as grouping variables. Leaf chewers were defined as all species feeding on green plant parts. Saproxylic species included species feeding on dead wood or wood associated fungi. Flower visitors included species attracted to flowers, presumably feeding on nectar or pollen. Fruit eaters and seed predators were included in this group as well. Taxonomically, the material was treated statistically at family level for small groups, and at subfamily level for Curculionidae, according to Alonzo-Zarazaga and Lyal (1999).

Target plants

The phytophagous beetle fauna of a total of 50 and 52 plant species were studied in PNM and SLA, respectively. Selection of plant species for study was limited by the crane perimeter, but as far as possible confamilial species at the two sites, and a representative proportion of trees and lianas at the sites were chosen. Additional criteria for the selection of target plant included size of plant biomass, and that the target plants as far as possible appeared without confounding epiphytes and lianas in order to minimize the influence from neighbouring plants. The number of plant taxa belonging to different life forms and taxonomic categories is indicated in Table 1.

Only two plant species were shared between the two sites; the lianas *Phryganocydia corymbosa* (Vent.) Bur., and *Cydista aequinoctalis* (L.) Miers of the family Bignoniaceae. The following genera among the study plants were common to the two sites: *Cecropia* (Cecropiaceae), *Cordia* (Boraginaceae), *Nectandra* (Lauraceae), and *Arrabidaea* (Bignoniaceae). A total of 14 plant families were shared between the two sites which include 82 and 58% of species in PNM and SLA, respectively (Table 2). Trees and lianas as prominent life forms of plants were considered separately as grouping variables for statistical treatment.

Sampling programme

The sampling procedure intended to survey a similar leaf and branch area of each plant species, and to maximize the number of microhabitats of each plant. Sampling was carried out from the crane gondola using a 1 m^2 beating sheet. Each sample was standardized by beating different parts of the tree or liana for 30 min by moving from different positions within the tree both along vertical and horizontal gradients. Each sampling 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

Table 1. Number of plant species distributed on life forms and taxonomic categories in PNM and SLA.

	PNM	SLA
No. of plant species	50	52
Trees	24	43
Lianas	26	9
No. of plant genera	43	48
No. of plant families	21	26
No. of congeneric pairs	6	5

Table 2. Plant families represented by the study plants shared between PNM and SLA, and the number of plant species studied in each family.

Families	PNM	SLA
Anacardiaceae	4	1
Araliaceae	1	1
Arecaceae	1	2
Bignoniaceae	12	6
Boraginaceae	1	1
Combretaceae	1	1
Cecropiaceae	2	1
Fabaceae	6	8
Lauraceae	3	1
Moraceae	4	2
Rubiaceae	1	1
Sapindaceae	3	3
Sapotaceae	1	1
Tiliaceae	1	1

(Ødegaard 2000b, 2004). Each tree crown was sampled regularly day and night once a month during 1 year. The range of height surveyed in the forest included canopy habitats from 10 to 40 m, but not the understorey. In addition, sampling was performed more frequently in periods of leaf flush or flowering in order to optimize insect species richness and the number of host observations. This sampling strategy was termed 'additional sampling' by Ødegaard (2000b). One individual plant of each species was sampled except for the big tree *Brosimum utile* in SLA. A total of six trees of this species were surveyed with similar methods in order to study the effect of sample size (i.e. number of tree individuals) (Ødegaard 2004).

The sampling effort was similar in PNM and SLA. The sampling period lasted from *primo* March 1995 to *medio* May 1996, and *primo* March 2001 to *medio* May 2002 for PNM and SLA, respectively. The beginning of the rainy season *(primo* May) was sampled two subsequent years at each site since this is a period of very high insect activity in Panama (Wolda 1980; Wolda et al. 1998).

Host observations

Feeding observations were recorded at times of flowering, fruiting or leaf-flush. A host record was defined as at least one feeding observation. Generally, host specificity is overestimated if the number of specimens of an insect species is lower than the number of host species (Colwell and Futuyma 1971). Accordingly, the feeding observations of species recorded 50 times or more (h0), were distinguished from those encountered less than 50 times (h1). Rare species always constitute a major proportion of species in samples, and they

may differ from common ones regarding patterns of host specificity (Price et al. 1995). Therefore, also host observations attended with lower level of confidence were included and determined by probability assessments based on abundance categories (Flowers and Janzen 1997; Ødegaard 2000b). These host occurrences were assigned to the following categories according to the number of individual records from the assumed host plant; h2: 10 or more records; h3: 5–9 records; h4: 2–4 record; h5: 1 record and additional evidence for host association based of collections or literature. Singletons recorded on a plant were treated as tourists unless additional evidence about host associations was available from collections or literature. Species of aerial drift (randomly distributed species) were treated as tourists although some of these were extremely common on the studied plants. These species are small in body size (often less than 2 mm), which seem to be rare among broad generalists. Frequently, they also belong to taxonomic groups which in general tend to be specialists (e.g., Anthonomini and Apioninae) *(personal observation)*. Species with proven host associations on trees other than the specific target trees were treated as aerial drift material when abundance was 20% less than of that of their host tree (Ødegaard 2004). Otherwise, aerial drift material was distinguished from polyphagous species through feeding records.

Statistical methods

Host specificity was measured as effective specialization (May 1990; Ødegaard et al. 2000). The principle behind effective specialization of a plant's insect fauna is to weight each insect species in accordance with its degree of specialization on other plants in the community. The monophagous species are given the heaviest weight, while broadly polyphagous species adds insignificant to the value. For a plant species k, in a community of T plant species, the proportion of beetles effectively specialized on k, f_k, is given by

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

where $p_k(i)$ is the proportion of beetles associated with plant species k and i other plants. Knowing f_k, the number of insect species effectively specialized on each plant species (k) is given as S_f:

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

where S_k is the number of beetle species associated with plant species k. This is the parameter that implies the plants' relative contribution to the maintenance of insect species richness in the community.

The rarefied number of species present in samples was computed by Coleman's rarefaction (Coleman 1981; Colwell and Coddington 1994). Beta diversity between different insect communities was calculated both as

presence/absence data (Jaccard and Sørensen index), and abundance data with Sørensen and Morisita-Horn statistics (Magurran 2003). Accumulation-curves and effective specialization-curves based on the observed number of species (S_{obs}) in each plant species, and similarity indices, were calculated with 50 randomizations by the programme Estimates (Colwell 1997). Comparisons of means were done by one sample t-tests using the program package SPSS 11.5.

Results

A total of 35,479 beetles of 1165 species were recorded from PNM (Ødegaard 2003), while 30,352 beetles including 1603 species were recorded from SLA. The higher number of species from SLA (37%) was due to higher number of flower visitors and saproxylic species (Figure 1). These differences between the ecological guilds were seen also among taxonomic groups representing the guilds. Among the saproxylic species the difference was mostly due to Cerambycidae, Anthribidae (incl. Brentidae), Cryptorynchinae (incl. Molytinae), Conoderinae, and Scolytinae (incl. Platypodinae and Cossoninae). All these groups were nearly twice as species rich in SLA than in PNM. In contrast, flower visitors such as Bruchinae and Baridinae were more species rich at PNM. Large groups of leaf chewers like Chrysomelidae and Buprestidae (mostly leaf miners) had a similar number of species at the two sites (Figure 2).

Similarity between sites

The total material included 2462 species of which 306 species were shared between the two sites. This proportion constitutes 12% of the species (Jaccard
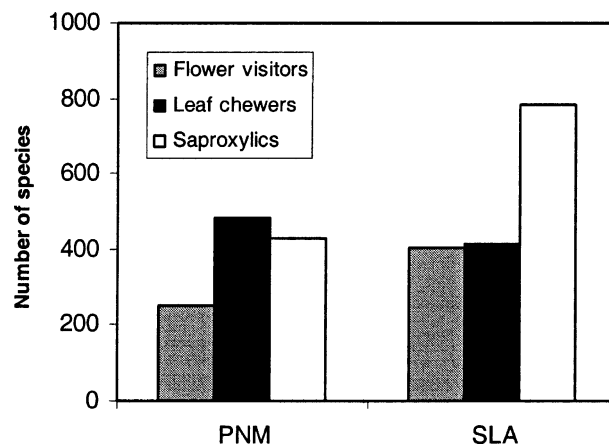

Figure 1. The total number of phytophagous beetle species belonging to different guilds at each of the two study sites.
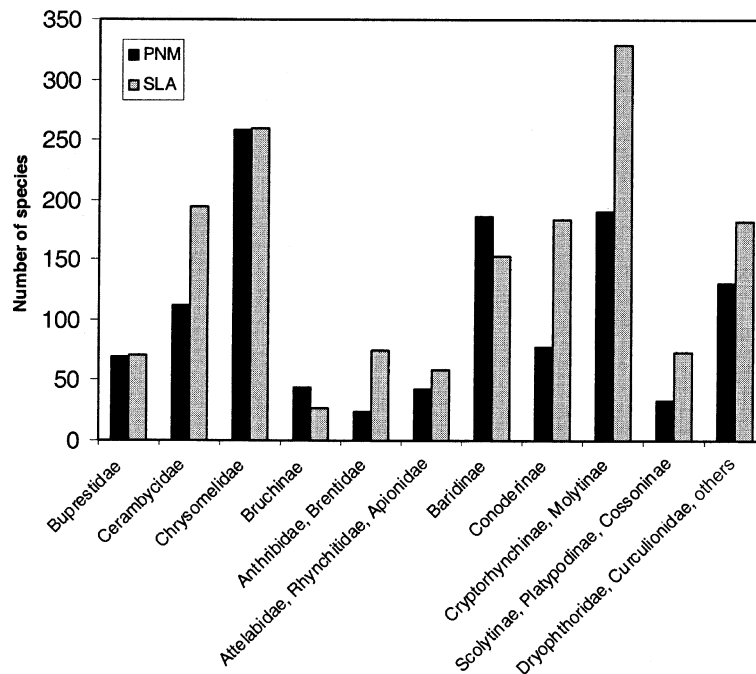
Figure 2. The number of beetle species belonging to different taxonomic groups at each of the two sites.

index). Abundance-based similarity indices for the total material were 0.08 (Sørensen Abundance index) and 0.07 (Morisita-Horn index) (Table 3). Presence/absence similarity indices on taxonomic subgroups indicated the lowest species turnover among Baridinae, Chrysomelidae, and Cerambycidae, and the highest among Anthribidae (incl. Brentidae) and Conoderinae. Abundance similarity indices indicated a relatively low turnover among Cerambycidae, Chrysomelidae, Scolytinae, while the Bruchinae and the remaining groups of Curculionidae showed a relatively high turnover (Morisita-Horn index, Table 3).

Among the three guilds of phytophagous beetles there were a higher proportion of leaf chewers in PNM than in SLA, and a higher proportion of saproxylic species in SLA than in PNM. The proportion of flower visitors was similar at the two sites. Among the species shared between the two sites, the relative proportion of flower visitors was higher than that at each of the sites. The relative proportion of leaf chewers and saproxylic species among the shared fauna was at an intermediate level relative to the sites (Figure 3a).

Regarding host relationships among the total beetle fauna, the relative proportion of tourists, generalists and specialists (up to family level of plants) were similar at the two sites. The fauna common to each site, was dominated by tourists and generalists that made up 47 and 36%, respectively. Specialists

Table 3. Number of species in taxonomic subgroups at each site, and the number of shared species between the sites along with similarity indices; $\pm$, = presence/absence; abd. = abundance.

Taxa	PNM	SLA	Shared	Jaccard $\pm$	Sørensen $\pm$	Sørensen abd.	Morisita-Horn
Buprestidae	69	70	10	0.08	0.14	0.02	0
Cerambycidae	112	194	38	0.14	0.25	0.15	0.14
Chrysomelidae[a]	258	260	71	0.16	0.27	0.09	0.15
Bruchinae	44	26	7	0.11	0.2	0.05	0.03
Anthribidae, Brentidae	24	73	5	0.05	0.1	0.04	0.01
Attelabidae, Rhynchitidae, Apionidae	42	58	12	0.14	0.24	0.03	0.01
Baridinae	186	153	47	0.16	0.28	0.1	0.08
Conoderinae	77	184	14	0.06	0.11	0.06	0.11
Cryptorhynchinae, Molytinae	190	329	54	0.12	0.21	0.09	0.05
Scolytinae, Platypodinae, Cossoninae	33	73	10	0.09	0.17	0.05	0.13
Dryophthoridae, Curculionidae, others[b]	130	182	38	0.14	0.24	0.08	0.03
Total species	1165	1602	306	0.12	0.21	0.08	0.07

[a]Includes Megalopodidae and Orsodacnidae, but excludes Bruchinae.
[b]Includes Curculioninae, Entiminae, Mesoptiliinae.

up to family level of plants constituted only 17% of the shared fauna (Figure 3b).

The number of beetles per plant species

Despite that more species were surveyed at SLA, the number of host-associated beetle species per plant species was not significantly different between the two sites, neither within life forms of plants, nor within insect guilds (Table 4). On average 49.1 ± 4.3 species were associated with plants in PNM, based on revised data from Ødegaard (2000b), while 59.4 ± 5.3 species were associated with plants in SLA. The number of species per plant varied from only a few to more than 150 species both within trees and lianas (Figure 4). Plotting the rates at which the host associated species accumulate when adding host plants to the samples clearly indicated that more species were recorded per plant in SLA, and that their accumulation rate was higher (Figure 5). Details on number of species associated with trees and lianas within flower visitors, leaf chewers, and wood eaters are given in Table 4.
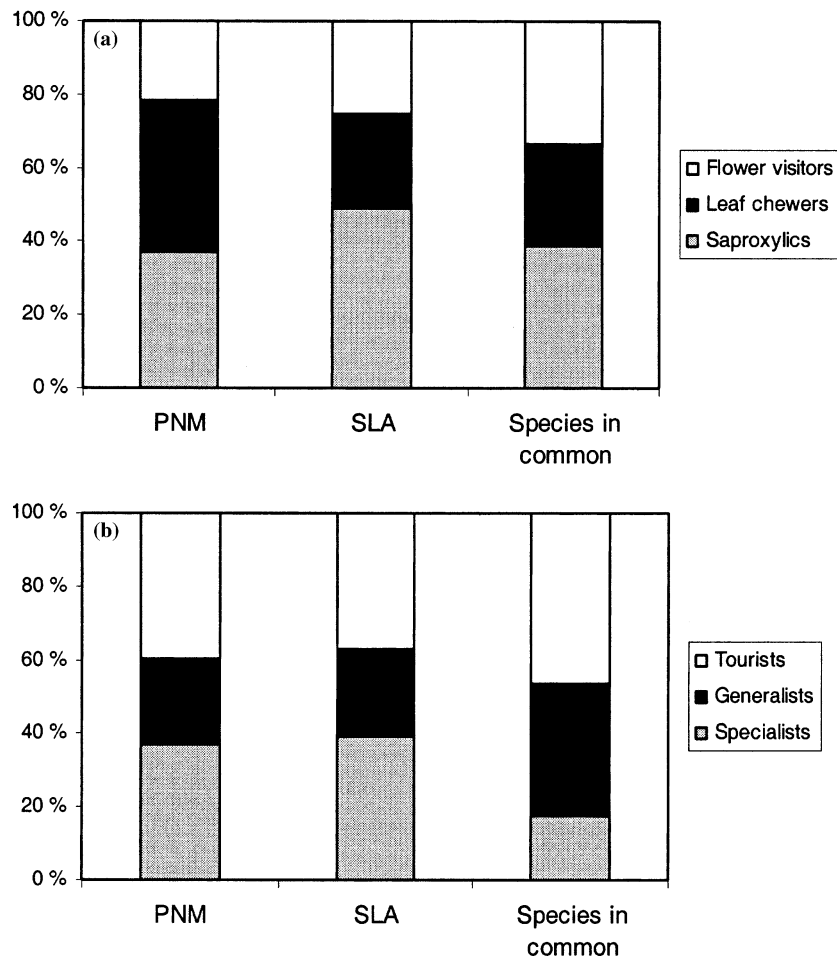
Figure 3. The relative proportion of species belonging to different guilds (a) and different categories of host associations (b) at each of the two sites and among the species shared between the sites. The specialists are defined as species associated within a plant family.

Host specificity

A total of 3088 and 2453 host observations were recorded in SLA and PNM, respectively. Only 2.6 and 3.8% of the host observations were of the highest level of confidence in SLA and PNM, respectively. More than half of the data reflected host observations of the two lowest levels of confidence (Table 5). Hence, individual host observations should be treated with caution, although for the purpose of comparisons between sites and groups, they are useful as long as being consistent across entities compared.

Table 4. The average number of beetle species per plant for flower visitors, leaf chewers and saproxylic species on trees and lianas at the two sites.

| Species	PNM	SLA	*t*-test	df	*p*
S total	49.1 ± 4.3	59.4 ± 5.3	1.499	100	0.137
S lianas	45.5 ± 5.8	45.1 ± 9.0	−0.31	33	0.975
S trees	53.0 ± 6.5	62.4 ± 6.1	0.99	65	0.326
S flower visitors total	13.6 ± 2.1	20.7 ± 3.6	1.689	100	0.094
S flowers lianas	12.2 ± 2.6	20.9 ± 10.2	1.175	33	0.248
S flowers trees	15.1 ± 3.4	20.6 ± 3.8	0.969	65	0.336
S chewers total	18.2 ± 1.5	15.8 ± 1.5	−1.164	100	0.247
S chewers lianas	19.2 ± 2.3	13.7 ± 3.1	−1.273	33	0.212
S chewers trees	17.0 ± 1.9	16.2 ± 1.6	−0.329	65	0.744
S saproxylic total	17.3 ± 1.9	23.0 ± 2.8	1.624	100	0.108
S saproxylic lianas	14.0 ± 1.9	10.4 ± 2.1	−1.016	33	0.317
S saproxylic trees	20.9 ± 3.3	25.6 ± 3.3	0.928	65	0.357
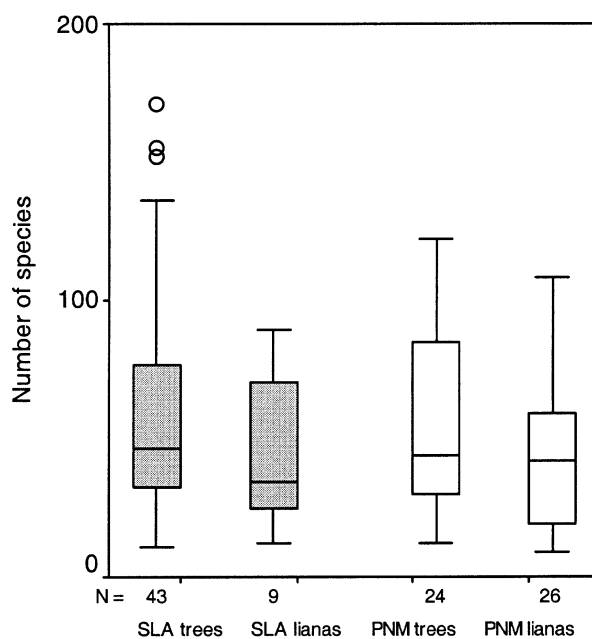
Figure 4. A Box and Wisker plot of the number of phytophagous beetle species per plant species of trees and lianas at each of the two sites.

Species associated with few host plants dominate among species at both sites. The proportion of monophagous insect species among the study plants was 47 and 54% in PNM and SLA, respectively. There was no obvious pattern regarding the proportion of beetles associated with two or more host plants across the sites, although there was a tendency that the proportion of generalists utilizing five or more plant species was higher in PNM (Figure 6).
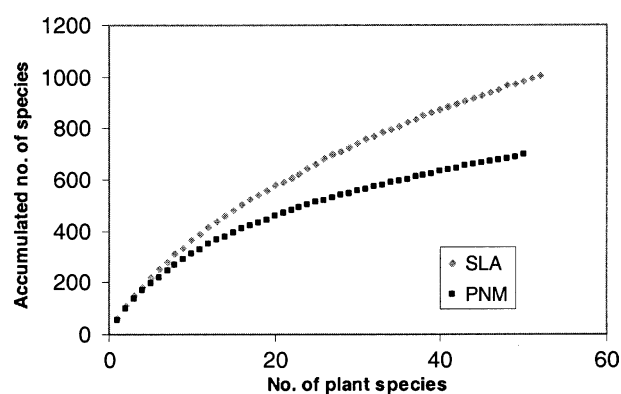
Figure 5. Rarefied accumulation curves of phytophagous beetle species with increased number of host plants at each of the two sites.

Table 5. Confidence level of host observations.

	SLA	PNM[a]
h0: feeding ($\geq$50 specimens)	65	118
h1: feeding (<50 specimens)	173	212
h2: >10 individuals	438	470
h3: 5–9 individuals	401	381
h4: 2–4 individuals	1057	1272[b]
h5: 1 individual	954	–
Total	3088	2423

Feeding observations of species recorded 50 times or more were distinguished from those recorded less than 50 times in the total material.
[a]Revised data from Ødegaard (2000b).
[b]Includes also h5.
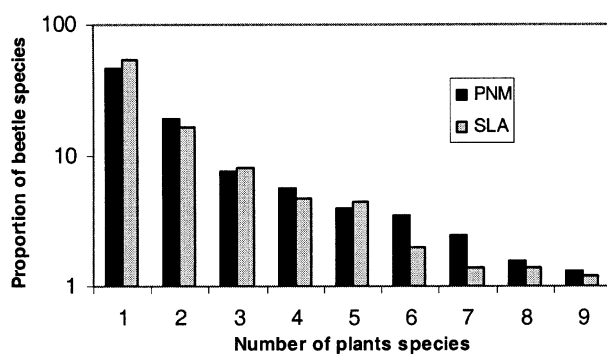
Figure 6. The relative proportion of phytophagous beetle species associated with one to nine plant species at each of the two sites.

The average effective specialization was significantly higher in SLA than in PNM ($t = 3.035$, df $= 100$, $p = 0.003$). The magnitude of effective specialization of the beetle assemblages depends on the number of host plants studied (Ødegaard et al. 2000). A calculation of average effective specialization of beetle assemblages on each of 1 to 50 plant species at each site reveals that the fauna in SLA was more specialized than in PNM independent on the number of plants studied (Figure 7). All guilds on both trees and lianas showed the tendency of being more specialized in SLA, and significant differences were found among saproxylic species ($t = 4.657$, df $= 100$, $p < 0.001$), and flower visitors ($t = 3.839$, df $= 100$, $p < 0.001$), but not among leaf chewers ($t = 0.69$, df $= 100$, $p = 0.492$). The higher degree of effective specialization among flower visitors in SLA was only significant in trees ($t = 3.2$, df $= 65$, $p = 0.002$) (Figure 8).

The number of beetle species effectively specialized on plants was higher in SLA than in PNM. ($t = 2.255$, df $= 100$, $p = 0.026$). This difference was due to flower visitors ($t = 2.536$, df $= 96$, $p = 0.013$) and saproxylic species ($t = 2.426$, df $= 100$, $p = 0.017$). The number of leaf chewers effectively specialized at the two sites was similar ($t = -0.798$, df $= 100$, $p = 0.427$) (Figure 9).

Discussion

Alpha diversity

Plant species diversity in tropical forests correlates strongly with annual precipitation (Gentry 1988; Wright 1992; Leigh 1999), and the number of
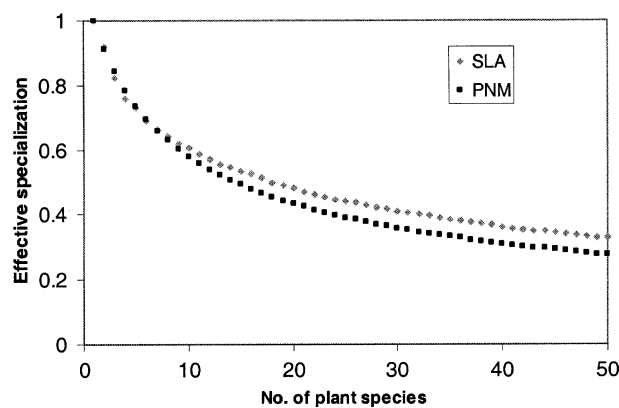

Figure 7. Effective specialization (F_T) as a function of the number of plant species at the two sites. The curves represent the average effective specialization of beetle assemblages on 1 to 50 plant species.
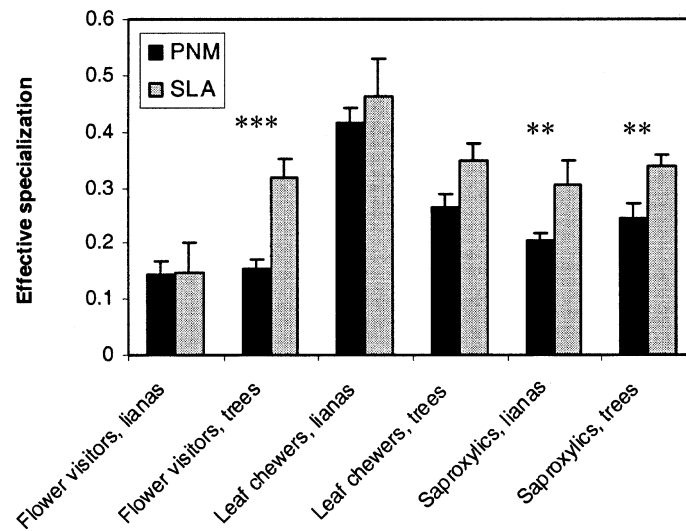
Figure 8. The average effective specialization per plant species (+SE) among different guilds on trees and lianas at each of the two sites. ** $p < 0.01$, ***$p < 0.005$.
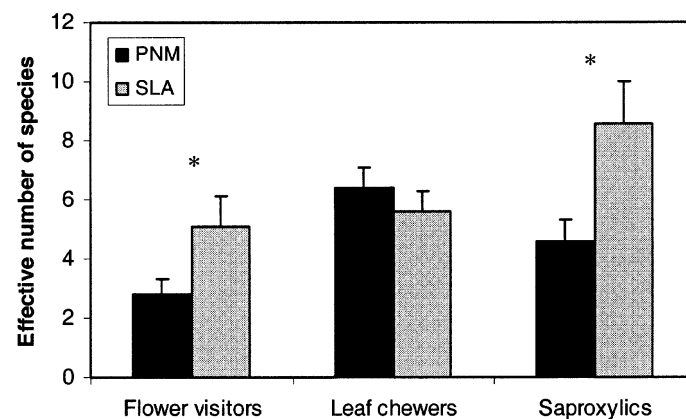

Figure 9. The average effective number of species per plant species (+SE) among different guilds at each of the two sites. *$p < 0.05$.

phytophagous insect species correlates strongly with the number of plant species in a community (e.g., Strong et al. 1984; Andow 1991). Thus, it is not surprising that the total number of phytophagous beetle species recorded from the wet forest was higher than from the dry forest. Similar patterns are also observed in butterflies (De Vries 1994).

A larger local species pool of insects also affects the average number of insects per plant species as the number of generalists among the insects will

increase proportionally with the degree of host specificity in the insect community. In the present study, more flower visitors and saproxylic species were recorded per plant species in SLA. Species richness of leaf chewers per plant was similar between sites, however. The contribution of a larger local species pool to species richness was probably counteracted by the higher effective specialization of the phytophagous fauna in SLA. A more specialized fauna has a more restricted range (Strong et al. 1984; Gaston 1991), and thus, a lower probability to be collected within the crane perimeter.

Apart from this, the higher species diversity in the wet forest may be due to differences in habitat characteristics. There were significantly more saproxylic species on trees than on lianas ($t = 3.040$, df $= 100$, $p = 0.003$). Thus, the low proportion of wood borers in the dry forest might be explained by the dominance of lianas in PNM. The number of species among fungus feeders (Anthribidae and most Scolytinae) was more than twice in the wet forest, a fact that probably relates to the greater diversity of fungus resources in wet forests, and thus, greater habitat diversity for saproxylic species in the wet forest.

Regarding flower visitors, many species, especially within the Baridinae and Cerambycidae, are specialized wood borers as larvae. The adults are general flower visitors that may be attracted to plants in blossom from long distance. Consequently, many pollinator–flower interactions maintain 'loose niches' that may change from year to year (Roubik 1992). The number of flower visiting species on a plant would therefore be a trait more related to the local species pool (alpha diversity) than to specific host plants. This explains the higher number of flower visitors in SLA.

Human impact factors including forest age, fragmentation, and edge effects related to management history may also be relevant to species richness of arthropods (e.g., Hanski and Gilpin 1991; Saunders et al. 1991; Didham et al. 1998; Floren and Linsenmair 2001; Colville et al. 2002; Basset et al. 2004). It has been shown that species richness increase with forest age (Grove 2002; Floren and Linsenmair 2003), and species diversity decrease with increasing degree of disturbance (Ghazoul 2002). These facts imply greater species richness in older, undisturbed forests, which is particularly relevant for saproxylic beetles (Grove 2002).

Beta diversity

The high species turnover among insects is not surprising regarding the almost complete change in plant composition. The figure compares well with Broadhead and Wolda (1985) who studied the diversity of Psocoptera in two tropical forests in Panama. They found even less overlap between sites (Jaccard index 0.03 opposed to 0.12 in this study), but their localities were more distant, and also separated by a significant difference in elevation. More relevant for comparison are studies of species turnover of Conoderinae and Buprestidae between La Selva, Costa Rica and Barro Colorado Island (BCI), Panama

(Hespenheide 1994). The faunas of these relatively distant sites were more similar than that of the same groups in the present study (for Conoderinae, Jaccard index: 0.23 opposed to 0.08 in the present study; for Buprestidae, Jaccard index: 0.14 opposed to 0.08 in the present study). In this case, the precipitation gradient is probably more important than geographical distance. This is supported by studies of the butterfly fauna of La Selva that is more similar to that of BCI (Jaccard index: 0.42), than that of the dry forests in Guanacaste, Costa Rica (Jaccard index: 0.27) (DeVries 1994; Hespenheide 1994).

The beetle studies from La Selva are mostly ground based in contrast to the present canopy study, which may indicate an additional stratum differences in species turnover when assuming higher beta diversity among specialists than generalists (Gaston 1991). Saproxylic species like Conoderinae and many Buprestidae, are likely to be more specialized in the canopy than on ground, as wood resources there are fresher and less dominated by fungi. In contrast, the understorey is dominated by wood resources of different decomposing stages that probably require a more generalized fauna of saproxylic insects (Price 1992; Bernays and Chapman 1994). These speculations, however, need further study.

Erwin (1983, 1991) suggested extremely high beta diversity among tropical insect communities. He recorded 1080 species of beetles in four neotropical forest types in the same area (at most 67 km apart). Only 1% of the species was shared between the sites. Among Lepidoptera species sampled in Beni, Bolivia (933 species and 1748 individuals), and in Paitza, Peru (1006 species and 1731 individuals; the two sites are 500 km apart), only 3.2% of the species were shared between sites (Erwin 1991). These arguments were used as indications of restricted distribution patterns and evidence for huge species richness. However, it is important to be aware of that calculations of beta-diversity of tropical forests tend to overestimate species turnover due to the dominance of rare species (Mawdsley 1996; Stork 1997) and small sample size (Chao et al. 2000). Simulations reveal that high species turnover will occur randomly given a small sample size and a large species pool (Chao et al. 2000). In the case of Erwin (1991), there were less than two specimens per species, an indication of a sample size representing a very small fraction of alpha diversity. On the other hand, comparisons of sites based on similar number of individuals but different species richness (as in the present study) may underestimate beta diversity because rare species shared between the sites may be unrecorded (Colwell and Coddington 1994).

It is obvious that species turnover increase across forest types where resources are completely different (Harrison et al. 1992). Likewise, abiotic factors like temperature are assumed to be more important than vegetation changes for species turnover in phytophagous insects as exemplified by geometrid moths in montane rainforests (Brehm et al. 2003). Additional insight would probably come from comparisons within similar forest types. However, it is difficult to find sites that are similar enough with regard to climate, habitat

type, and other environmental factors, while also being geographically distant enough to be relevant (Bartlett et al. 1999).

It would also be important to study beta diversity in different regions, especially with respect to variation in geology and climate. For these reasons, species turnover among phytophagous insect communities in Panama may be relatively high compared with other tropical forests as beta diversity of trees in Panamanian forests is higher than in western Amazonian forests due to steeper climatic gradients (Condit et al. 2002).

Host specificity

Although many hypotheses have been suggested for the evolution of host range (e.g., Basset 1992), very few studies, if any, have reported different levels of host specificity among comparable groups of herbivorous insects at different tropical sites. In many ways the patterns found in the present study fit well with current hypotheses. With basis in forests of different ages, the young forest should be dominated by pioneer plants investing more resources in growth than defence against herbivory (Coley 1983; Coley et al. 1985), a factor that promotes polyphagy (i.e. resource availability hypothesis). The dominance of deciduous species in PNM may have similar consequences (MacLean and Jensen 1985), although the outcome is not obvious since plant phenology is also seasonally predictable. Fluctuations in insect populations are likely to be higher in dry forests than in wet forests (Wolda 1978) which may be caused by unpredictable environments. Specialists may be more vulnerable than generalists if resources are unstable (e.g., Redfearn and Pimm 1988). In addition, dry forests are more isolated and vulnerable against human impact (Janzen 1988), a fact that probably affect specialists more than generalists due to smaller range (Ghazoul 2002). On the other hand, common species may be more heavily affected by fragmentation because rare species are better dispersers (Didham et al. 1998).

These hypotheses were mainly developed for leaf chewing insects, and it is unknown to what extent they apply for flower visitors and saproxylic species. The higher degree of specialization among flower visitor in SLA in the present study may be influenced by different phenology of the host plants. In seasonal forests (PNM), flowering events tend to synchronize in dry season, while they are more distributed over the year in wet forests (*personal observation*). Since flower visitors are mainly generalists and loosely associated with their flowers (Roubik 1992), synchronized flowering season may attract several seasonal insect populations simultaneously resulting in a lower effective specialization as the same insect species visits several flowers of different plant species. On the other hand, dispersed flowering events attract only those insect populations that happen to be in phase (adults) at the time of florescence. Thus, the high

level of effective specialization among flower visitors in SLA may be an artefact caused by the current availability of resources.

Hypotheses for the evolution of host range may apply for saproxylic species as well as leaf chewers since the wood borers are dominated by species attracted to recently dead wood that may have certain levels of plant defence (Bernays and Chapman 1994). An additional hypothesis for explaining the higher degree of specialization among saproxylic species in SLA relates to the increased frequency of fungal diseases in wet forests. If insects escape from fungal attack trough specialization, this phenomenon works similar as increased predation pressure which is a major selection pressure towards specialization (Jermy 1988; Novotny et al. 1999).

The measured level of host specificity may be influenced by sample size because generalists and specialists accumulate in samples at different rates (Novotny et al. 2002b), a fact that may bias smaller samples towards higher specialization, as in SLA. This is probably of minor importance since sample sizes are not very different, and that the observed differences in host specificity only apply for saproxylic species and flower visitors. Another problem relates to the fact that effective specialization does not account for phylogeny of host plants. This is probably not critical given the present sample size and the procedure of selection of target plants.

Implications for regional species richness

Global arthropod species richness was revised by Ødegaard (2000a) based on the present data set from PNM. He concluded that a working figure of 5 million species would be appropriate. Results from the present study suggest some consequences for ecological estimates of regional species richness. Higher alpha- and beta-diversities as well as more host specific faunas based on data from wet forests, all points in the same direction towards a higher number of species. More importantly, Ødegaard (2004) substantiated that the number of phytophagous insect species on a tropical tree might be an order of magnitude higher than that reported from extensive studies, because sample size, important microhabitats, and successional stages of trees linked to vertical stratification of insect assemblages are ignored or heavily underestimated in most studies (Basset et al. 2003). The conciliation in estimates of global arthropod species richness as indicated by Ødegaard (2000a) and Novotny et al. (2002a) might therefore be challenged by estimates based on data sets considering these confounding variables.

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