

Generalist flowers and phytophagous beetles in two tropical canopy trees: resources for multitudes

Frode Ødegaard¹ & Dawn Frame²

¹ Norwegian Institute for Nature Research (NINA), Tungasletta 2, 7485 Trondheim, Norway.
frode.odegaard@nina.no (author for correspondence)

² Herbarium, Institut de Botanique, 163 rue A. Broussonnet, 34090 Montpellier, France

In the Republic of Panamá, phytophagous beetles were collected by hand and beating from superficially similar generalist blossoms of *Nectandra umbrosa* (Lauraceae) and *Tapirira guianensis* (Anacardiaceae), two phylogenetically distant Neotropical canopy trees. Beetles were sorted into three functional groups (guilds): general flower visitors, species developing in buds, and seed predators. Out of a total of 1,564 collected specimens belonging to 177 beetle species, 55 species or 31% were identifiable to specific epithet. These small- to medium-sized beetles belonged to four families: Cerambycidae, Chrysomelidae, Brentidae, and Curculionidae. A total of 723 beetles representing 121 species, and 841 beetles representing 121 species were recorded from *N. umbrosa* and *T. guianensis*, respectively. Of the beetles collected, 65 species were common to both trees, which equates to a similarity index value of 0.46 (Jaccard) or 0.34 (Sørensen). With respect to functional groups, there was no significant difference in the number of beetle species between the two tree species. Overall, beetle abundance patterns on flowers of the two trees are similar in terms of phytophagous beetle subfamily dominance. There are differences however, significantly more leaf beetles (Cryptocephalinae, Eumolpinae, Galerucinae) were collected per hour on *T. guianensis* than on *N. umbrosa*. Moreover, among beetles shared between the two tree species, Baridinae weevils showed a tendency to be more abundant on *N. umbrosa*. Nearly three-quarters of the flower feeders (72%) were shared between the two trees. The large overlap in beetle species between the two plant species suggests that the fauna is fairly general in terms of host use. We discuss the possible significance of our results to phytophagous beetle and host plant evolution. The combined effects of large species numbers, high abundance and broad diet breadth across generalist flowers of tropical canopy trees suggests that small- to medium-sized beetles play a crucial role in maintenance of species biodiversity and forest ecosystem function.

KEYWORDS: canopy, Coleoptera, florivory, Panama, tropical forests

INTRODUCTION

Overall, the greatest species diversity on Earth is found in tropical forests, and this is true for both phytophagous beetles and angiosperms. The most speciose organisms are arthropods, and recent estimates suggest that there are 7 to 10 million species (Ødegaard, 2000a, 2006; Novotny & al., 2002); such estimates are usually based on extrapolations from herbivory studies and the different values obtained relate to the hypothetical percentage of generalist feeders, the greater the proportion of generalists, the lower the estimated value of arthropods (Erwin, 1982; Ødegaard, 2000a). Phytophagous beetles are thought to be the most species-rich group and they are estimated to represent 700,000 to 1 million species, or about 20% of all arthropods (Ødegaard, 2000a). Vascular plants represent another species-rich higher order group with about 400,000 species, the great majority of which are angiosperms (May, 2000). So, we have an intriguing relationship between the most speciose organisms, phytophagous beetles, and vascular plants, their hosts.

There has been little field research directed at understanding the interplay between phytophagous beetles and generalist flowers, the most notable exception being Kirmse & al. (2003). For the purposes of our discussion, a generalist flower is one that has an open morphology and allows access to a diversity of animal visitors, such flowers typically have more visitors than principal pollinators (Frame, 2003). Studies of visitors to generalist flowers in the tropics are rare, probably because of the difficulties associated with identifying the numerous and varied insects from different orders, many of which may be undescribed or lack recent revisionary treatment or for which no taxonomist exists. With respect to beetles in general, Bernhardt (2000) writes “From the entomological perspective, the taxonomy of most Coleoptera is so poorly understood that it is often impossible to identify flower-visiting specimens beyond the level of subfamily...” Generalist flowers are often described by biologists as having many small insect visitors and left at that.

Strong & al. (1984), among others, have defined phytophagous insects as those insects that feed on living

tissue of higher plants; this narrow definition includes leaf-, flower-, and fruit-eaters, but excludes algae-, moss-, and lichen-feeders, granivorous species and wood-borers. A broader, possibly more realistic concept such as that of Ødegaard (2000b) includes all plants and dead plant tissue (such as wood). Strict adherence to the first definition is problematic; for instance, wood-borers (xylophages) feed mainly on dead plant tissue as larvae, however, many of these insects are regularly attracted to flowers as adults where they feed on living plant tissue. Florivory is a form of phytophagy wherein animals feed on flowers. With respect to beetle specialists, they may feed either as adults, larvae, or both. Florivorous insects may be important pollinators for their host plants (Endress, 1994). Frame (2003) has argued that flower eating is just a form of herbivory and that this is a fundamental phenomenon—pollination, as one possible outcome of florivory, therefore, is secondary. The issue of whether florivores are “principal” pollinators may, therefore, be irrelevant in some contexts.

It is believed that beetles are guided to flowers by certain cues, especially color (see Waser, 1983) and scent (Gottsberger, 1989). As pointed out by Forel (1910), color forms a cue for insects but has no attraction in and of itself, and color displays by blossoms (flowers or aggregations of flowers, e.g., inflorescences) may be important for beetles as a form of “advertisement” (Waser, 1983). Cues aid beetles to orient themselves within their environment, and those cues which lead beetles to food and/or mates, result in what we, as observers of the phenomenon, call “attraction”.

We studied phytophagous beetle visitors to superficially similar generalist flowers and inflorescences of two phylogenetically distant canopy trees, *Nectandra umbrosa* (Lauraceae) and *Tapirira guianensis* (Anacardiaceae), in order to document species composition of the phytophagous beetle fauna found there. This information was subsequently analyzed with respect to beetle diversity and functional groups and used as a basis of comparison between the two trees. This pilot study was carried out as part of a wider study of beetle diversity by the first author (Ødegaard, 2006) at the San Lorenzo Protected Area, Republic of Panama using the Smithsonian Tropical Research Institute (STRI) canopy crane located at this site. The beetle fauna of this region is relatively well known compared to the rest of the tropics, permitting us to dis-

tinguish and identify the collected specimens. Our study represents one of the few quantitative studies of beetle visitors to generalist flowers of the tropical canopy.

MATERIALS AND METHODS

Site. — The study was carried out in an evergreen, wet Panamanian lowland forest in San Lorenzo Protected Area (9°17' N, 79°58' W, ca. 130 m a.s.l.), Colon province, 4.4 km inland from the Atlantic coast. Average annual temperature and precipitation is 25.8°C and 3,140 mm, respectively. There is a pronounced dry season from mid-December to the end of April; at this time the forest receives about 10% of its yearly precipitation. The forest is dominated by 35 to 45 m tall trees; lianas and epiphytes occur regularly in the canopy. The San Lorenzo Protected Area includes 9,600 ha of relatively old-growth tropical forest that has escaped anthropogenic disturbance for about 200 years (Basset & al., 2003).

The canopy was reached using a 54 m tall crane having an arm length of 55 m. The projected area accessible for study is 0.88 ha. Within the crane perimeter there are ca. 40 tree species and ca. 35 species of climbers that can be reached from the gondola. There are two individuals of *Nectandra umbrosa*, a short canopy tree, and several individuals of *Tapirira guianensis*, a surmounting tree. There was a minimum distance of 10 m between study trees and 20 m between conspecific trees. At the site, *T. guianensis* flowers first, followed about a week or so later by *N. umbrosa*; there is no overlap in flowering between the two species.

Plants. — Here follows a detailed description of the study plants with an emphasis on the flowers, a brief summary of floral and inflorescence characters likely to be relevant to small beetle attraction are presented in Table 1.

Nectandra umbrosa (Lauraceae) (Fig. 1A–B)

Tree to 25 m growing from Honduras south to Colombia, often found below 50 m altitude in rainforests and beach thickets, or even secondary forest. Inflorescences lateral near apex of branches, emergent above leaf canopy. Seen from a distance, inflorescences appearing as an irregularly undulating white carpet, each inflorescence

Table 1. Comparison of selected floral and inflorescence characters potentially relevant to beetle visitors to *Nectandra umbrosa* and *Tapirira guianensis*.

	Attractivity of Inflorescences in days (height)	Flower diameter in mm (petals/tepals)	Petal or tepal number/color/ pubescent	Stamen length in mm/ shorter or equaling petals-tepals	Nectar/ scent
<i>Nectandra umbrosa</i>	21 (7)	5 (2.5)	6/white/yes	To 1.0/shorter	Yes (3 glands)/sweet
<i>Tapirira guianensis</i>	7 (3)	2.5 (1.2–1.5)	5/white/yes	To 1.5/equaling	Yes (interstaminal disk)/sweet musky

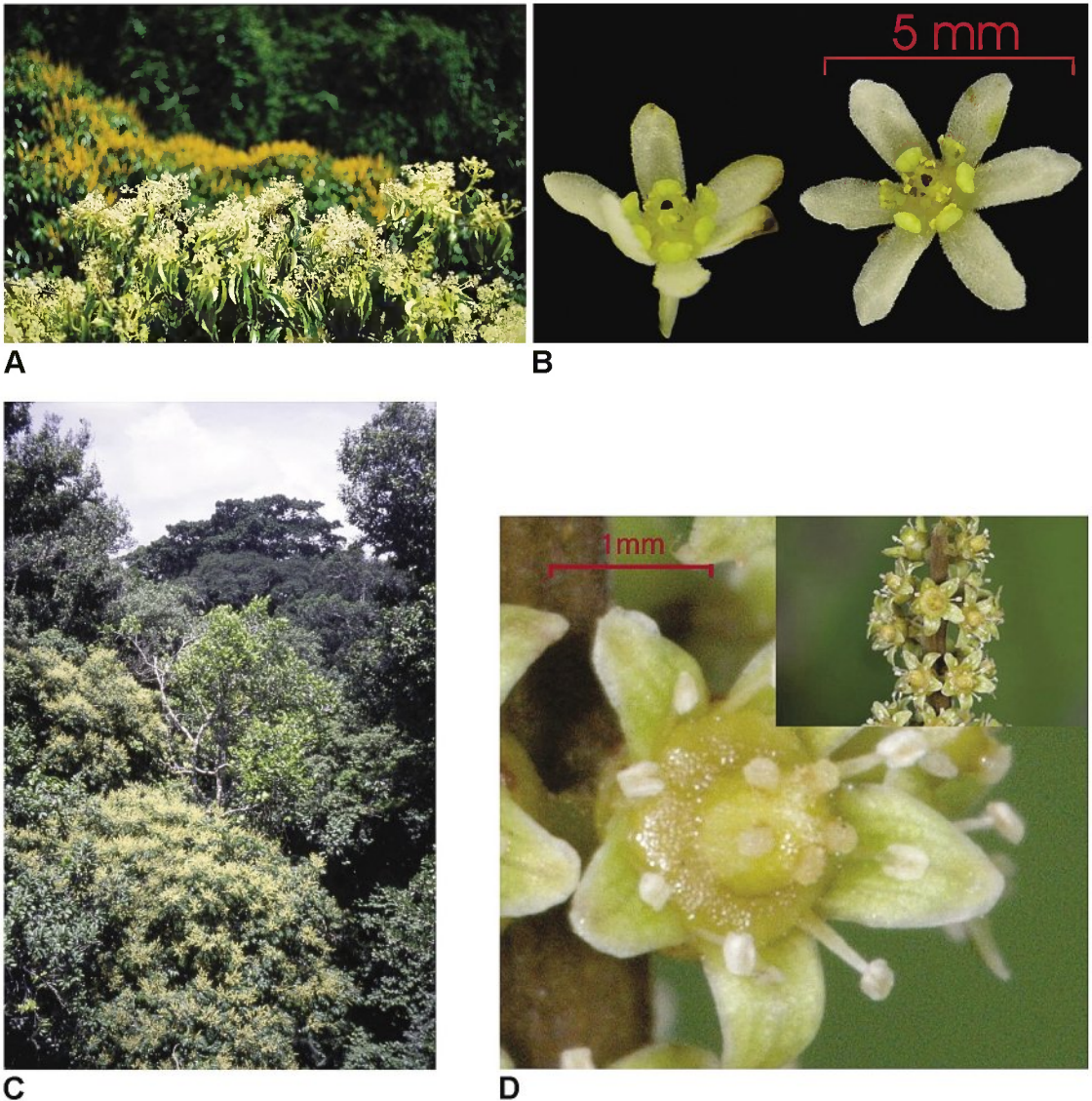


Fig 1. Flowers of *Nectandra umbrosa* and *Tapirira guianensis*. A, *N. umbrosa* as seen from the STRI canopy crane, San Lorenzo Protected Area, Panama (Photo: F. Ødegaard); B, close-up of flowers (Photo: S. Paton); C, *T. guianensis* as seen from canopy crane (Photo: F. Ødegaard); D, unisexual flower of *T. guianensis* from a dioecious tree, Recife, Brazil (Photo: L. Krause).

up to 13 cm long. The small flowers (5 mm) are usually disposed in clusters of 2 to 10 or more on short branches mostly arising from secondary inflorescences axes, overall shape of inflorescences hemispherical. Pedicels (to 0.6 mm) hirsute, bearing flowers with 6 white adaxially papillose, horizontally spreading, ligulate in outline tepals, arranged in two whorls of three, each about 2.5 mm long and 0.6–1.0 mm wide. Androecium composed of four whorls, the outer two have 3 stamens each as does the third whorl, which has extrorse locules; the inner (fourth) whorl alternates with the third and is staminodial, much reduced and appears as small cylindrical threads. All stamens and staminodia are inserted opposite the tepals. The stamens

of the third whorl bear two globose glands at their base, which secrete minute amounts of nectar. Stamens upright, appearing as a small crown, not quite one-third the length of the tepals. Anthers each having 4 half-thecae, opening by broadly elliptical flaps; when dehiscent appearing brilliant yellow because of the pollen. Gynoecium ca. 1 mm long, hirsute ovary globose to plumply ellipsoid terminated by a short style. Flowers sweet-smelling? Each flower lasts 1–2 days. In *Nectandra*, flowers are bisexual but dichogamous; there is a distinct female and male phase separated temporally by a short dormant period (Henk van der Werff, pers. comm.). Usually flowers are protogynous, i.e., are functionally female first.

Tapirira guianensis (Anacardiaceae) (Fig. 1C–D)

Tree to 35 m or more, growing from Honduras south to Bolivia in the west, through Paraguay to Santa Catarina, Brazil in the east; common in Amazonia and the Guianas. A widespread polymorphic species of the New World tropics, equally at home in lowland wet rainforest, lower montane forests and cerrado. Paniculate inflorescences lateral near apex of branches, emergent above leaf canopy. Seen from a distance, inflorescences appear as white, broadly tapering masses about 250 cm long. The minute (2 mm) flowers are disposed singly or in clusters of up to 7–8 flowers on short branches mostly arising from secondary inflorescence axes. The near orthotropic inflorescence axes become longer as they approach the branch apex. On expanded inflorescences, flowers are located on the distal three-quarters of the axes. The hirsute pedicels (to 0.7 mm) elongate as the floral buds mature. The connate, yellow, sparsely hirsute 5-lobed sepals are leathery and alternate with the 5 free petals. The strongly concave ovate liquid-filled petals are 1.2–1.5 mm long and 0.7–1.0 mm at their widest point. The ten equal free stamens are inserted opposite the sepals and petals below the spongy intrastaminal disk, those opposite the sepals maturing first. Mature stamens (to 1.5 mm), more or less equaling the petals. The small versatile anthers are sagittate, dehiscent to expose the pale yellow translucent pollen. The pale yellow moist spongy intrastaminal disk (1.0 mm in diameter) is more or less 10-lobed, the notches corresponding to the sites of filament insertion. Ringing the style and growing on it, are short hairs. The central style appears as a five-pointed star, the points opposite the petals; it is just emergent above the intrastaminal disk. Besides the hairs along the style, the tips of which reach to the edges of the moist stigma, there is a central core of hairs between the stigma lobes. Flowers give off a sweet musky scent and are open a single day. Inflorescences are in flower 3–7 days, with the height of flowering, that is, the greatest number of flowers open at the same time, lasting about 1–3 days. At our site the flowers appeared to be bisexual (pollen was present in anthers but we do not know if it is viable—it may function as “fodder” pollen), and all *T. guianensis* trees in the crane perimeter set fruit; however sexuality in this species appears to be unstable, and in other parts of its range, it may be dioecious (north of Recife, L. Krause, pers. comm.).

Beetle sampling and processing. — Phytophagous beetles of the Chrysomeloidea and Curculionoidea were collected from *Nectandra umbrosa* and *Tapirira guianensis* inflorescences by hand and beating over two consecutive flowering seasons (2001–2002). Each sampling lasted 30 minutes per tree and took place between 06:30 and 18:15. The first author (FØ) conducted night sampling on many trees within the crane perimeter, and found that in a gen-

eral manner, few additional beetle species were collected at this period. For this reason, there was no night sampling of the two study tree species. The greatest yield of beetles was found to occur from 07:30 to 10:00, and so most sampling was done at this time. Two trees of each species were chosen and visited about twice a week during the flowering period (here, the period when flowers attracted beetles), which lasted from mid-April to the start of May (about 3 weeks) for *T. guianensis* and from the beginning of May until early June (about 5 weeks) for *N. umbrosa*. In total, 5 and 8.5 hours were spent sampling inflorescences of *T. guianensis* and *N. umbrosa*, respectively.

Beetles were identified whenever possible to genus and species, unidentified species were denoted sp. 1, sp. 2, etc. Most beetles were dissected to expose genitalia; many species recognizable by this means were undescribed. Whenever it was unclear if the specimen represented a new species or genus, the taxon to which it resembled is given followed by a question mark (?). A list of all taxa can be found in the Appendix. Specimens are deposited in the collection of the first author at the Norwegian Institute for Nature Research (NINA, Trondheim). The species were assigned to three functional groups (guilds) on the basis of known biology for the genus: general flower visitors (F), species developing in buds (FB) and seed predators (FS).

Data analyses. — After a general characterization of the collected beetles, we analyzed the beetle data from the two trees with respect to functional group and diversity (richness and abundance). Species overlap was measured as presence/absence data using the Sørensen- and the Jaccard-index (Magurran, 2004). Statistical testing for comparisons between the trees was carried out using the software SPSS 12.0 (LEAD Technologies, Inc., Chicago).

RESULTS

Out of a total of 1,564 specimens belonging to 177 phytophagous beetle species collected, 55 species or 31% were identifiable to specific epithet. All beetles belong to families recognized as having many flower-visiting species: Cerambycidae, Chrysomelidae, Brentidae, and Curculionidae. Table 2 provides a brief description of life-history characters and adult size of beetles from the different subfamilies.

The total number of phytophagous beetles from all functional groups is presented in Table 3. Insect surveys from the tropics always include a high proportion of species represented by a single specimen, known as a “singleton” (Novotny & Basset, 2000). The percentage of singletons gives an indication of sampling completeness (Magurran, 2004). Our collection yielded 31% singletons which may be considered very good for invertebrate sam-

Table 2. General characteristics related to life history of the study beetles.

Family	Subfamily	Size of adults in mm (excluding antennae)	Larval hosts	Adult hosts
Brentidae	Brentinae	5–7	Woodborers/feed on wood fungi	Many spp. attracted to flowers
Cerambycidae	Cerambycinae	6–35; mostly 8–20	Woodborers	Many spp. attracted to flowers, pollen feeders
	Lepturinae	6–20; mostly 8–15	Develop in rotten wood	Attracted to flowers, pollen feeders
Chrysomelidae	Cryptocephalinae	1–8; mostly 2–5	Develop in soil/feed on detritus	Flowers/young shoots and leaves
	Eumolpinae	2–10; mostly 3–5	Develop in soil/feed on roots	Flowers/leaves
	Galerucinae	2.5–10; mostly 6–9	Some spp. with free living phytophagous larvae; others in soil/feed on roots?	Flowers/leaves
Curculionidae	Baridinae	1–8; mostly 2–5	Various tissue/woodborers	Flowers
	Curculioninae	1–5; mostly 2–3	Tribus Anthonomini develop in flower buds Tribus Derelomini associated with various tissues of monocots	In flowers, frequently on the same as their larval host plants

Table 3. Total number of phytophagous beetles from all functional groups.

	Species	Individuals	Shared	Shared singletons	Unique singletons
<i>Nectandra umbrosa</i>					
F	98	644	50	32	20
FB	6	7	4	5	2
FS	17	72	11	8	4
Total	121	723	65	45	26
<i>Tapirira guianensis</i>					
F	95	782	50	38	22
FB	9	16	4	6	3
FS	17	43	11	8	4
Total	121	841	65	52	29

Abbreviations: F, general flower visitors; FS, seed predators; FB, species developing in buds.

ples from tropical forests as many studies report more than 50% (e.g., Kirmse & al. 2003).

A total of 723 beetles representing 121 species, and 841 beetles representing 121 species were recorded from *N. umbrosa* and *T. guianensis*, respectively. Evidently, *T. guianensis* showed a stronger attraction rate for beetles than *N. umbrosa* (paired *t*-test: $z = -2.87, p = 0.021$). Of the collected beetle species, 65 were common to both trees, which equates to a similarity index value of 0.46 (Jaccard) or 0.34 (Sørensen). With respect to functional groups, there was no significant difference in the number of beetle species between the two plant species (F: paired *t*-test: $z = -1.80, p = 0.36$; FB: paired *t*-test: $z = -2.17, p = 0.15$; FS: paired *t*-test: $z = 0.03, p = 0.51$) (Fig. 2).

Beetle abundance patterns on flowers of the two trees are similar in terms of subfamily dominance (Fig. 3).

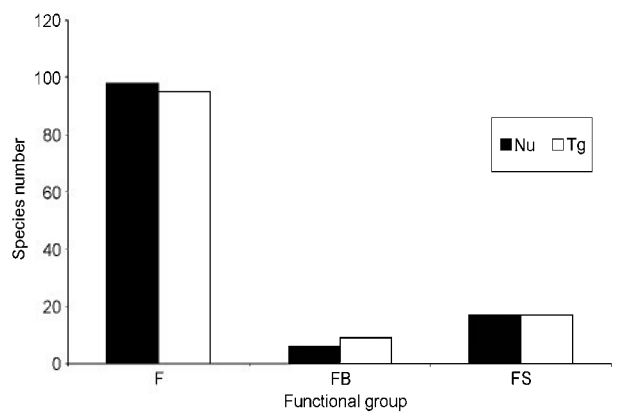


Fig 2. Beetle species by functional group (guild). F, general flower visitors; FB, species developing in buds; FS, seed predators; Nu, *Nectandra umbrosa*; Tg, *Tapirira guianensis*.

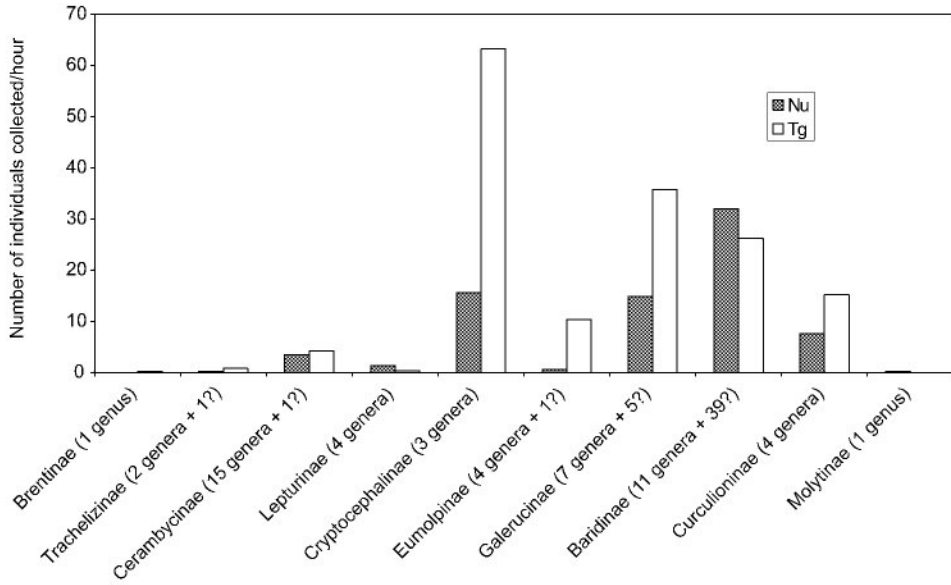


Fig 3. Abundance of general flower feeders (abundance per collecting hour) of *Nectandra umbrosa* (Nu) and *Tapirira guianensis* (Tg) as a function of beetle subfamilies.

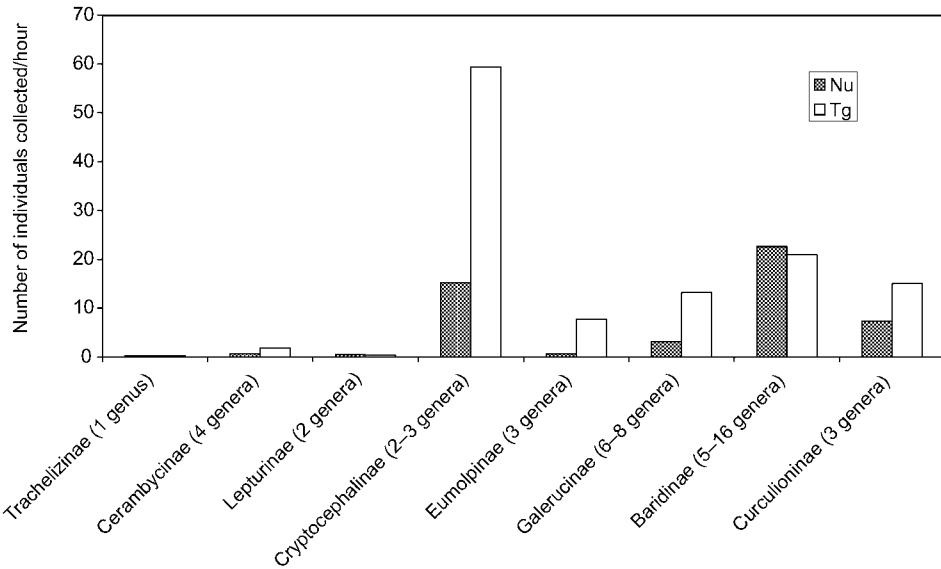


Fig 4. Abundance of general flower feeders (abundance per collecting hour) common to both *Nectandra umbrosa* (Nu) and *Tapirira guianensis* (Tg) as a function of beetle subfamilies.

However, with respect to detail there are some pronounced differences that merit mention. Significantly more leaf beetles (Cryptocephalinae, Eumolpinae, Galerucinae) were collected per hour on *T. guianensis* than on *N. umbrosa* (Paired *t*-test: $z = -2.95, p = 0.016$). On the other hand, among beetles shared between the tree species, Baridinae weevils showed a tendency to be more abundant on *N. umbrosa* (Fig. 4) (Paired *t*-test: $z = -2.38, p = 0.086$). Nearly three-quarters of the flower feeders (72%) were shared between the two tree species.

DISCUSSION

Taking into account the relatively small sampling effort (13.5 h), species richness and abundance of phytophagous beetles are extremely high in flowers of the study trees, and up to an order of magnitude higher than results obtained from studies of leaf chewers on individual trees using similar methods (e.g., Basset, 1990; Ødegaard, 2000b; Barrios, 2003). Clearly, generalist flowers support a very high species diversity of phytophagous beetles in

tropical forests. Although we were not specifically investigating beetle-pollination, it is evident that some pollen transfer between conspecific trees must occur given this number of beetles. In a study of insect visitors to two canopy trees in a Mata Atlantica forest fragment north of Recife, Brazil, Krause & Gottsberger (2005) found pollen on beetle visitors to female flowers of *Tapirira guianensis* (dioecious at this site), and they consider beetles to be a pollinator of this species; such data challenges the view that beetle-pollinated canopy trees are rare in lowland Neotropical wet forests (Bawa & al., 1985); the afore cited researchers nevertheless concede that pollination studies within this vegetation are biased towards large-flowered species. The issue of whether common flower visitors are pollinators is a tricky one (see Waser & al., 1996), it may very well be true that beetles are not always the most efficient of pollinators (especially in generalist systems) even if they are often the first to arrive, but given their richness and abundance in our study trees, they are likely to contribute to pollination, even if bees, which are universal tropical canopy flower visitors (to greater or lesser degrees), are very efficient pollen collectors and have the ability to move quickly between trees. In any case, the contribution to pollination of generalist flowers by various insect visitors is likely to vary considerably with respect to space and time (see, e.g., Herrera, 1988; Waser & al., 1996; and references therein). It is an inescapable fact that whether or not beetles pollinate, canopy flowers in generalist flower systems represent an important source of food and a meeting place for individuals. For the purposes of this paper, we will assume that most of the beetle “general flower visitors” were at the very least, rare to occasional pollinators of the study trees even if we did not check for pollen.

Our results indicate that phylogenetically distant plants bearing superficially similar flowers and inflorescences can attract the same groups (subfamilies) of beetles. This was not the conclusion arrived at by Kirmse & al. (2003) studying beetle visitors to the canopy trees *Matayba guianensis* (Sapindaceae) and *Tachigali guianensis* (Caesalpinaceae) in Venezuela; they write “The similarity of the beetle fauna among the tree species was low despite a comparable structure of flowers.” There are several possible reasons for the observed differences, the flowers may have been more different than they took them to be. *Tachigali guianensis* had fewer beetles overall and the fauna was dissimilar to that of *Matayba guianensis*, which at the level of beetle subfamily more resembled our study plants. The *Tachigali* is likely to be very attractive to bees, as are most members of its family, and this is certainly indicated by Kirmse & al.’s (2003) mention that its flowers produce a strong sweet scent. Unpublished data of the first author respecting the flower beetle fauna of *Tachigali guianensis* and a different sapindaceous

species, *Cupania scrobiculata*, at our study site also indicates that the latter species, more closely resembles that of *Nectandra umbrosa* and *Tapirira guianensis*, while *Tachigali guianensis* attracted a different beetle fauna and overall fewer beetles; a total of 92 beetle species were recorded from the flowers of *C. scrobiculata* whereas only 14 from *Tac. guianensis* given the same sampling effort (Ødegaard, unpub. data). It is therefore possible that *Tac. guianensis* is much less of a generalist beetle flower than a generalist, strongly bee-dominated one. It is also possible that seasonal and regional differences in insect fauna play a role and this may explain differences in the observed beetle fauna between *Tac. guianensis* and the other study trees.

An interesting difference between the study trees is that more generalist leaf beetles (Chrysomelidae) were collected from *Tapirira guianensis*, than *Nectandra umbrosa*. Conversely, the opposite is true with respect to Baridinae weevils. Regarding these differences, we have to keep in mind that the datasets of this pilot study were not large enough to test if infraspecific variation in beetle load within trees differed significantly from between tree species variation. Future studies should, therefore, include several trees of each species and blossom size should be quantified. However, results from a broader study of 50 plants in the same area indicate that attractiveness of canopy trees and lianas bearing small white generalist flowers clustered in large inflorescences may be different, both in terms of general and differential attraction rate across beetle groups and that, among other things, this may relate to beetle life history (Ødegaard, 2006). Other trees and lianas within the crane perimeter having small white flowers clustered in large inflorescences that seem to be especially attractive to the Baridinae include the sapindaceous canopy lianas *Serjania mexicana* and *Paulinia fibrigera*, and the canopy trees *Cupania scrobiculata* (Sapindaceae) and *Humiriastrum diguense* (Humiriaceae) (Ødegaard, data not shown).

In a review/theoretical article, Bernhardt (2000) traces beetle pollination modes and other phenomena along and across phyletic lines, and presents a classification system for beetle pollination recognizing four overlapping morphological modes: Bilabiate, Brush, Chamber Blossoms and Painted Bowl. He goes on to say beetle pollination modes are determined by suites of evolving characters but that there are distinguishable patterns, for example, biogeographical, e.g., Brush and Chamber Blossoms predominate in the wet tropics. Bernhardt explains that many flower-beetle patterns are the result of convergent evolution, a logical conclusion based on existing evidence. Indeed, one of the pivotal issues in coleopteran systematics and evolution is host lability. Blossoms of both of the trees we studied are Brush—they “usually consist of many, small, often unisexual flowers with reduced, or

absent perianth segments massed together but devoid of overarching-enveloping bracts at the time when anthers dehisce and stigmas are receptive” (Bernhardt, 2000).

Morphologically-speaking, the inflorescences of *Nectandra umbrosa* and *Tapirira guianensis* are functioning as flowers; it has been suggested that in beetle-pollinated plants, aggregations of small, few-staminate flowers act to produce a multi-staminate condition in the blossom (Bernhardt, 2000) as polyandry is characteristic of beetle-pollinated systems (Gottsberger, 1977; Bernhardt & Thien, 1987). We observed general flower feeders to feed on pollen and, although small amounts of floral nectar are available in both species, we suspect that the principal food was pollen. The largest phytophagous beetles collected were about 8–20 mm long (Cerambycidae) while members of other subfamilies were less than this (Table 2), and about the size or smaller than an individual flower. The cerambycids frequently formed clouds above the inflorescences and would settle on blossoms to feed on pollen and mate (F. Ødegaard & D. Frame, pers. obs.). Although long, these beetles are slender and easily moved between flowers on inflorescences. It is recognized that the physical size of such inflorescences, encourages conspecific beetle interactions (as meeting and copulating sites) and beetle-flower ones possibly leading to pollen deposition and transfer to receptive stigmas (Bernhardt, 2000). Inflorescences composed of small flowers, as in our study plants, provide a large surface area and diverse topography, which may be important for beetle circulation and spatial segregation (see Frame & Durou, 2001). It is significant that the stamens are included or equal the petals (Table 1), and so easily reachable by small beetles; well-exserted stamens in dense aggregated blossoms are better manipulated by other sorts of animals, e.g., bees and mammals.

Bawa & al (1985) conclude, and we concur (for reasons given below), that there are fewer sorts of pollination systems in the canopy. Tree canopies are exposed habitats, during the day they can be hot, dry and receive high solar insolation (Parker, 1995). Canopy flowers may represent small oases to beetles and other animals. It seems likely that there are a limited number of blossom forms in the canopy—partly related to the biophysical conditions found there—among the most common are large trumpet flowers (usually oriented perpendicular to mid-day sun) and clusters of many small flowers (variously oriented, but sometimes parallel to mid-day sun). We speculate that the latter, dissected form (as in our study plants) is likely to disperse heat efficiently and depending on flower pigmentation, may also reflect ultra-violet light. Large flowers are also thought to be good at dispersing heat (see Dieringer & al., 1999). There exist temperature optima for beetle species and some beetle-flowers are thermogenic, possibly constituting a “reward” (Seymour & al., 2003). We have no rea-

son to suspect this and found beetle activity to be greatest from 07:30 to 10:00, suggesting that temperature, whatever the source, was sufficient during this period. Interestingly, Bernhardt (2000) holds that Chamber Blossoms attract the greatest diversity of beetles although it is unclear what he means by diversity. This proposition may be true at the family level, however, our data would argue that in terms of beetle genera and species, Brush Blossoms attract the greatest diversity. Moreover, the number of beetle Brush blossoms has been greatly underestimated (see estimates in Bernhardt, 2000), presumably because of the paucity of studies focussing on beetle visitors to generalist flowers of lowland tropical wet forest canopy trees.

Both pollen feeding and nectar drinking are common among phytophagous beetles; pollen provides complementary proteins to a beetles’ diet and nectar is rich in sugar and a source of amino acids (Jolivet & Hawkeswood, 1995). Generalist phytophagous beetles, which are herbivores on numerous different plants, such as many Chrysomelidae, are often facultative florivores, feeding on pollen and nectar or other tissues (Samuelson, 1994; Held & Potter, 2004). Other generalist chrysomelids may be restricted to petals and other flower parts, yet without great specificity possibly because of a parallel lack of profound chemical specificity of corresponding tissues.

Oviposition in buds and flowers is common among many Anthonomini and Baridinae (Burke, 1976), respectively; the resulting larvae develop at the site. Such relationships imply specialized factors for host recognition. Hence, it is likely that there are subtle chemical differences among generalist flowers, yet to be discovered, which determine the composition of the beetle fauna attracted to them (see also Bernhardt, 2000). Our findings that there may be different attraction rates of phytophagous beetles even among generalist flowers (Fig. 3) would tend to support this idea.

With respect to beetle functional groups, the study plants were practically identical, suggesting that these plants offer the same kind of resources for beetles. It is a common phenomenon that functional groups (guilds) remain more or less constant, but species change over space and time (Strong & al., 1984; Ødegaard, 2006). This would seem to be true for both the flowers/inflorescences (as morphological guilds) as well as the beetles, that is, the flowers are functionally similar in terms of general attractivity to beetles but the plants are not closely related. In this instance, floral bauplan is convergent and may reflect the organization and evolution of beetle nervous systems’ as “blossom”-beetle interaction is a reciprocal relationship (see also Silberbauer-Gottsberger & al., 2001). Thus, theoretically, insect neurology should provide clues to the interpretation of floral characters.

The large overlap in beetle species between the two plant species suggests that the beetle fauna is fairly gen-

eral in term of host use. Kirmse & al. (2003) report a lower overlap (Sørensen-index: 0.25 compared with ours 0.34), but their proportion of singletons was higher, probably due to their predominate use of traps, which normally catch a higher proportion of tourists than hand collecting. Ødegaard (2000b, 2006) found that flower visitors were significantly more general than both leaf chewers and woodborers among phytophagous beetles.

The combined effects of large species numbers, high abundance and broad diet breadth across generalist flowers of tropical canopy trees suggests that small- to medium-sized beetles play a crucial role in maintenance of species biodiversity and, hence, forest ecosystem function.

ACKNOWLEDGEMENTS

We are grateful to the Canopy Crane Team at STRI (S.J. Wright, Y. Basset, M. Samaniego, J. Herrera, E. Andrade, and O. Saldana) for providing crane access in Panama. L. Krause kindly shared valuable information on *Tapirira guianensis* and allowed us to use his photos of flowers. Additionally, Ana Laccia and Tom Wendt provided helpful advice about the biology of *Tapirira guianensis*. The descriptions of *Nectandra umbrosa* and *Tapirira guianensis* benefited from the expertise of Henk van der Werff and John Mitchell, respectively. We thank S. Paton for providing the photo of *Nectandra umbrosa* flowers. Several taxonomists kindly identified beetles: W.E. Clark, R.W. Flowers, F.T. Hovore, J. M. Kingsolver, and H.P. Stockwell. The manuscript benefited from the suggestions and criticisms of three reviewers. The first author received financial support for this study from the Norwegian Research Council, Smithsonian Institution Fellowship Program and Norwegian Institute for Nature Research. The second author thanks the French government for support from the CAF program.

LITERATURE CITED

- Barrios, H.** 2003. Insect herbivores feeding on conspecific seedlings and trees. Pp. 282–290 in: Basset, Y., Kitching, R.L., Miller S. & Novotny, V. (eds.), *Arthropods of Tropical Forests. Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge Univ. Press, Cambridge.
- Basset, Y.** 1990. The arboreal fauna of the rainforest tree *Argyrodendron actinophyllum* as sampled with restricted canopy fogging: composition of the fauna. *The Entomologist* 109: 173–183.
- Basset, Y., Horlyck, V. & Wright, S.J.** 2003. *Studying Forest Canopies from Above: The International Canopy Crane Network*. STRI and UNEP, Panama.
- Bawa, K.S., Bullock, S.H., Perry, D.R., Coville, R.E. & Grayum, M.H.** 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *Amer. J. Bot.* 72: 346–356.
- Bernhardt, P.** 2000. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. *Pl. Syst. Evol.* 222: 293–320.
- Bernhardt, P. & Thien, L.** 1987. Self-isolation and insect pollination in the primitive angiosperms: new evaluations of older hypotheses. *Pl. Syst. Evol.* 156: 159–176.
- Burke, H.R.** 1976. *Bionomics of Anthonominae weevils*. *Annual Rev. Entomol.* 21: 283–303.
- Dieringer, G., Cabrera R.L., Lara, M., Loya, L. & Reyes-Castillo, P.** 1999. Beetle pollination and floral thermogenicity in *Magnolia tamaulipana* (Magnoliaceae). *Int. J. Pl. Sci.* 160: 64–71.
- Endress, P.K.** 1994. *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge Univ. Press, Cambridge.
- Erwin, T.L.** 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bull.* 36: 74–75.
- Forel, A.** 1910. *Das Sinnesleben der Insekten*. E. Reinhardt, München.
- Frame, D.** 2003. Generalist flowers, biodiversity and florivory: implications for angiosperm origins. *Taxon* 52: 681–685.
- Frame, D. & Durou, S.** 2001. Morphology and biology of *Napoleonaea vogelii* (Lecythidaceae) flowers in relation to the natural history of insect visitors. *Biotropica* 33: 458–471.
- Gottsberger, G.** 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Pl. Syst. Evol., Suppl.* 1: 211–226.
- Gottsberger, G.** 1989. Beetle pollination and flowering rhythm of *Annona* spp. (Annonaceae) in Brazil. *Pl. Syst. Evol.* 167: 165–187.
- Held, D.W. & Potter, D.A.** 2004. Floral affinity and benefits of dietary mixing with flowers for a polyphagous scarab, *Popillia japonica* Newman. *Oecologia* 140: 312–320.
- Herrera, C.M.** 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.* 35: 95–125.
- Jolivet, P. & Hawkeswood, T.J.** 1995. *Host-plants of the Chrysomelidae of the World*. Backhuys Publishers, Leiden.
- Kirmse, S., Adis, J. & Morawetz, W.** 2003. Flowering events and beetle diversity in Venezuela. Pp. 256–265 in: Basset, Y., Kitching, R.L., Miller, S. & Novotny, V. (eds.), *Arthropods of Tropical Forests. Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge Univ. Press, Cambridge.
- Krause, L. & Gottsberger, G.** 2005. Reproductive features of five insect-pollinated tree species in an Atlantic Rainforest remnant of northeast Brazil. Pp. 119 in: Del Claro, K. (ed.), *Frontiers in Tropical Biology and Conservation. The 2005 Association of Tropical Biology and Conservation Meeting*. Universidade Federal de Uberlândia, Uberlândia, Brazil.
- Magurran, A.E.** 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford.
- May, R.M.** 2000. The dimensions of life on Earth. Pp. 30–45 in: Raven, P. (ed.), *Nature and Human Society: The Quest for a Sustainable World*. National Academy Press, Washington D.C.
- Novotny, V. & Basset, Y.** 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89: 564–572.
- Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd, P.** 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature* 416: 841–844.

- Ødegaard, F. 2000a. How many species of arthropods? Erwin's estimate revised. *Biol. J. Linn. Soc.* 71: 583–597.
- Ødegaard, F. 2000b. The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests. *J. Biogeogr.* 27: 283–296.
- Ødegaard, F. 2006. Host specificity, alpha- and beta-diversity of phytophagous beetles in two tropical forests in Panama. *Biodivers. Conservation* 15: 83–105.
- Parker, G.G. 1995. Structure and microclimate of forest canopies. Pp. 73–98 in: Lowman, M.D. & Nadkarni, N.M. (eds.), *Forest Canopies*. Academic Press, San Diego.
- Samuelson, G.A. 1994. Pollen consumption and digestion by leaf beetles. Pp. 179–183 in: Jolivet, P.H., Cox, M.L. & Petitpierre, E. (eds.), *Novel Aspects of the Biology of Chrysomelidae*. Kluwer Academic Publishers, Dordrecht.
- Seymour, R.S., White, C.R. & Gibernau, M. 2003. Heat reward for insect pollinators. *Nature* 426: 243–244.
- Silberbauer-Gottsberger, I., Webber, A.C., Kückmeister, H. & Gottsberger, G. 2001. Convergence in beetle-pollinated Central Amazonian Annonaceae, Araceae, Arecaceae, and Cyclanthaceae. *Diss. Bot* 346: 165–183.
- Strong, D.R., Lawton, J.H. & Southwood, S.R. 1984. *Insects on Plants*. Harvard Univ. Press, Cambridge.
- Waser, N.M. 1983. The adaptive nature of floral traits: ideas and evidence. Pp. 241–285 in: Real, L.A. (ed.), *Pollination Biology*. Academic Press, New York.
- Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043–1060.

Appendix. Species list of phytophagous beetles recorded from flowers of *Nectandra umbrosa* (Nu) and *Tapirira guianensis* (Tg), and affiliation to guild (G).

	Nu	Tg	G		Nu	Tg	G
Cerambycidae				<i>Amblycerus whiteheadi</i> Kingsolver	5	2	FS
Cerambycinae				<i>Amblycerus</i> n.sp.	0	1	FS
<i>Acyphoderes</i> n.sp.	0	1	F	<i>Caryedes godmani</i> (Sharp)	1	0	FS
<i>Callichroma viridipes</i> Bates	1	0	F	<i>Ctenocolum martiale</i> Kingsolver & White	0	2	FS
<i>Coscinedes gracilis</i> Bates	1	1	F	Cryptocephalinae			
<i>Cosmisoma plumicornis</i> Dury	2	0	F	<i>Cryptocephalus</i> sp.	1	16	F
<i>Gnomidolon laetabile</i> Bates	1	0	F	<i>Cryptocephalus</i> sp.	0	2	F
<i>Kunaibidion panamensis</i> Giesbert	0	1	F	<i>Cryptocephalus</i> sp.	0	3	F
<i>Linsleychroma monnei</i> Giesbert	2	0	F	<i>Cryptocephalus</i> sp.	0	8	F
<i>Megacyllene panamensis</i> Bates	0	1	F	<i>Lexiphanes</i> sp.	16	37	F
<i>Ommata elegans</i> White	4	0	F	<i>Lexiphanes</i> sp.	4	25	F
<i>Ommata minuens</i> Giesbert	2	3	F	<i>Lexiphanes</i> sp.	101	200	F
<i>Ommata</i> n.sp.	0	1	F	<i>Lexiphanes</i> sp.	0	2	F
<i>Ommata</i> n.sp.	0	4	F	<i>Lexiphanes</i> sp.	2	11	F
<i>Pandrosus phthisicus</i> (Klug)	2	0	F	<i>Lexiphanes</i> sp.	2	0	F
<i>Pronuba incognita</i> Hovore & Giesbert	11	0	F	<i>Lexiphanes</i> sp.	1	4	F
<i>Rhinotragus longicollis</i> Bates	0	3	F	<i>Lexiphanes</i> sp.	0	1	F
<i>Rhopalophora vericolor</i> Chevrolat	0	1	F	<i>Lexiphanes</i> sp.	1	4	F
<i>Terpnissa listropterina</i> Bates	1	1	F	<i>Lexiphanes</i> sp.	0	2	F
<i>Tetranodus xanthocollis</i> Chemsak	2	4	F	<i>Lexiphanes</i> sp.	1	0	F
Unidentified genus sp.	1	0	F	Chlamisinae			
Lepturinae				? <i>Chlamisus</i> sp.	3	1	F
<i>Megachoriolaus spiniferus</i> (Linsley)	2	0	F	Eumolpinae			
<i>Pseudotypocerus virescens</i> Chemsak & Linsley	2	1	F	<i>Brachypnoea</i> sp.	2	12	F
<i>Strangalia beltii</i> (Bates)	1	0	F	<i>Brachypnoea</i> sp.	0	3	F
<i>Strangalia panamensis</i> Giesbert	1	0	F	<i>Parachalcoplacis</i> sp.	0	1	F
<i>Strangalidium chemsaki</i> Giesbert	3	0	F	<i>Spintherophyta</i> sp.	0	7	F
<i>Strangalidium kunaium</i> Giesbert	2	1	F	<i>Spintherophyta</i> sp.	1	11	F
Chrysomelidae				<i>Trichospinthera pilosa</i> (Lefevre)	2	16	F
Bruchinae				Unidentified genus sp.	0	2	F
<i>Acanthoscelides puellus</i> (Sharp)	1	3	FS	Galerucinae (incl. Alticinae)			
<i>Acanthoscelides</i> sp.	0	2	FS	<i>Calomicrus</i> sp.	1	0	F
<i>Acanthoscelides</i> sp.	0	1	FS	<i>Calomicrus</i> sp.	1	17	F
<i>Amblycerus anosignatus</i> (Chevrolat)	0	1	FS	<i>Diabrotica</i> sp.	36	77	F
<i>Amblycerus biolleyi</i> (Pic)	1	5	FS	<i>Diabrotica</i> sp.	1	3	F
<i>Amblycerus cerdanicola</i> Kingsolver	1	0	FS	<i>Diabrotica</i> sp.	1	0	F
<i>Amblycerus championi</i> Pic	2	13	FS	<i>Diabrotica</i> sp.	0	8	F
<i>Amblycerus tachigaliae</i> Kingsolver	3	3	FS	<i>Diabrotica</i> sp.	0	2	F
				<i>Diabrotica</i> sp.	3	0	F

Appendix. Continued.

	Nu	Tg	G		Nu	Tg	G
<i>Diabrotica</i> sp.	0	1	F	<i>Madarus</i> sp.	0	1	F
<i>Diabrotica</i> sp.	0	17	F	<i>Madarus</i> sp.	1	0	F
<i>Diabrotica</i> sp.	3	4	F	<i>Pachybaris</i> sp.	1	0	F
<i>Diabrotica</i> sp.	0	2	F	<i>Parisoschoenus expositus</i> (Champion)	6	10	F
<i>Epitrix</i> sp.	3	15	F	<i>Parisoschoenus</i> sp.	4	4	F
<i>Hypolampis</i> sp.	2	21	F	Unidentified genus sp.	7	0	F
<i>Hypolampis</i> sp.	0	6	F	Unidentified genus sp.	0	1	F
<i>Lupraea</i> sp.	5	1	F	Unidentified genus sp.	6	0	F
<i>Rhinotmetus</i> sp.	2	0	F	Unidentified genus sp.	0	2	F
<i>Trichaltica</i> sp.	7	1	F	Unidentified genus sp.	1	0	F
Unidentified genus sp.	46	0	F	Unidentified genus sp.	12	1	F
Unidentified genus sp.	8	0	F	Unidentified genus sp.	18	8	F
Unidentified genus sp.	3	1	F	Unidentified genus sp.	8	0	F
Unidentified genus sp.	2	0	F	Unidentified genus sp.	1	0	F
Unidentified genus sp.	2	3	F	Unidentified genus sp.	1	6	F
				Unidentified genus sp.	3	0	F
				Unidentified genus sp.	2	2	F
				Unidentified genus sp.	7	2	F
Brentidae				Unidentified genus sp.	11	1	F
Brentinae				Unidentified genus sp.	7	0	F
<i>Brentus caudatus</i> Herbst	0	1	F	Unidentified genus sp.	10	3	F
Trachelizinae				Unidentified genus sp.	31	3	F
<i>Hephebocherus mexicanus</i> Sharp	0	2	F	Unidentified genus sp.	5	0	F
<i>Paratrachelizus lineatus</i> Sharp	2	1	F	Unidentified genus sp.	13	2	F
Unidentified genus sp.	0	1	F	Unidentified genus sp.	13	1	F
				Unidentified genus sp.	3	0	F
Curculionidae				Unidentified genus sp.	0	3	F
Curculioninae				Unidentified genus sp.	0	1	F
<i>Andranthobius palmarum</i> (Champion)	0	1	F	Unidentified genus sp.	0	1	F
<i>Anthonomus alboscuteallatus</i> Champion	1	1	FB	Unidentified genus sp.	0	1	F
<i>Anthonomus aptus</i> Clark	0	2	FB	Unidentified genus sp.	3	0	F
<i>Anthonomus arrogans</i> Clark	1	0	FB	Unidentified genus sp.	2	0	F
<i>Anthonomus occularis</i> Champion	0	1	FB	Unidentified genus sp.	0	2	F
<i>Anthonomus</i> sp.	1	6	FB	Unidentified genus sp.	2	0	F
<i>Anthonomus</i> sp.	10	5	F	Unidentified genus sp.	2	0	F
<i>Anthonomus</i> sp.	23	67	F	Unidentified genus sp.	3	0	F
<i>Anthonomus</i> sp.	0	1	FB	Unidentified genus sp.	6	1	F
<i>Loncophorus fusiformis</i> (Champion)	2	1	FB	Unidentified genus sp.	14	0	F
<i>Loncophorus myrmecodes</i> Clark	0	1	FB	Unidentified genus sp.	1	0	F
<i>Loncophorus santarosae</i> Clark	0	2	FB	Unidentified genus sp.	2	0	F
<i>Melexerus</i> sp.	1	1	FB	Unidentified genus sp.	0	1	F
<i>Phyllotrox</i> sp.	1	1	F	Unidentified genus sp.	0	2	F
<i>Pseudanthonomus</i> n.sp.	1	0	FB	Unidentified genus sp.	0	1	F
<i>Tereris</i> ? <i>pilosa</i>	29	2	F	Unidentified genus sp.	1	0	F
<i>Tereris</i> sp.	1	0	F	Unidentified genus sp.	0	2	F
				Unidentified genus sp.	0	1	F
Baridinae				Cryptorhynchinae			
<i>Cnagius</i> sp.	1	0	F	<i>Thrasyomus uniformis</i> Champion	2	0	FS
<i>Coelonertus nigrirostris</i> Solari	0	1	F	Molytinae			
<i>Coelonertus</i> sp.	1	0	F	<i>Conotrachelus aristatus</i> Champion	0	1	FS
<i>Coleomerus</i> sp.	2	1	F	<i>Conotrachelus divrigatus</i> Champion	1	3	FS
<i>Cylindrocercus circumlineatus</i> Champion	2	0	F	<i>Conotrachelus</i> ? <i>paleatus</i> Champion	1	0	FS
<i>Eutoxus lacordairei</i> Champion	0	2	F	<i>Conotrachelus punctiventris</i> Champion	2	1	FS
<i>Geraeus</i> sp.	0	2	F	<i>Conotrachelus</i> sp.	42	1	FS
<i>Geraeus</i> sp.	1	0	F	<i>Conotrachelus</i> sp.	1	0	F
<i>Geraeus</i> sp.	4	0	F	<i>Conotrachelus</i> sp.	1	2	FS
<i>Geraeus serratispinis</i> Champion	0	1	F	<i>Conotrachelus</i> sp.	3	1	FS
<i>Limnobaris</i> sp.	51	29	F	<i>Conotrachelus</i> sp.	1	0	F
<i>Loboderes flavicornis</i> Gyllenhal	1	3	F	<i>Conotrachelus</i> sp.	2	1	FS
<i>Loboderes sulphureiventris</i> Champion	3	27	F	<i>Conotrachelus</i> sp.	3	0	FS
<i>Loboderes</i> sp.	0	1	F	<i>Cleogonus rubetra</i> (Fabricius)	1	0	FS
<i>Madarus bisignatus</i> Champion	0	1	F				
<i>Madarus</i> sp.	1	1	F				

F, general flower visitors; FB, species developing in buds; FS, seed predators.