

Diversity of Carabidae (Insecta, Coleoptera) in Epiphytic Bromeliaceae in Central Veracruz, Mexico

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ABSTRACT This paper documents the existence of carabid assemblages associated with bromeliads on the Cofre de Perote, Veracruz, Mexico. Based on bromeliads sampled over three altitudinal ranges, the assemblages included at least 26 species with an arboreal lifestyle and another 11 species that are not strictly arboreal. Seven species are new to science, urging us to pay attention to the arboreal fauna in forest conservation studies. Composition of carabid assemblages associated with bromeliads changes with altitude. In lowlands, it is comprised almost entirely of species of Lebiini, with the Platynini dominating assemblages found in bromeliads >1,000 m above sea level. Our data suggest that carabids use bromeliads to reduce stresses associated with drought periods, the exact timing of which depends on altitude. The unexpected low diversity of the carabid fauna associated with bromeliads at middle altitude is explained in terms of anthropogenic conversion of the original forest to pastureland. Given the importance of arboreal elements, further fragmentation of subtropical and tropical mountain forest significantly threatens overall carabid diversity.

Este trabajo presenta la existencia de ensambles de carábidos asociados con bromelias en el Cofre de Perote, Veracruz, México. Con base en un muestreo de bromelias efectuado en tres rangos altitudinales los ensambles incluyeron al menos 26 especies con afinidad arbórea y otras once sin esa afinidad. Siete especies de carábidos son nuevas especies con lo cual se llama la atención sobre la importancia de considerar la fauna arbórea en los estudios de conservación de bosques. La composición de los ensambles de carábidos asociados a bromelias cambia con la altitud. En tierras bajas se compone casi completamente por especies de la tribu Lebiini en tanto que especies de la tribu Platynini dominan en los ensambles que se encuentran en bromelias por arriba de los 1,000 metros de altitud. Nuestros datos sugieren que los carábidos usan las bromelias para reducir el estrés asociado con períodos de sequía, cuya ocurrencia depende de la altitud. La inesperada baja diversidad de carábidos asociados a bromelias que se encontró en altitudes medias se explica en términos de la conversión de los bosques originales a tierras de pastoreo. Dada la importancia de los elementos arbóreos, la continua fragmentación del bosque montano tropical y subtropical amenaza significativamente la diversidad de carábidos.

KEY WORDS altitude, bromeliads, carabids, diversity, Mexico

The role of epiphytic plants for establishment and maintenance of the extraordinary arthropod diversity in forest canopies has been well documented (Richardson 1999, Stuntz et al. 1999, Greeney 2001, Stuntz et al. 2002). For example, Beutelspacher (1999) recognized 47 insect families belonging to 14 orders in just one bromeliad species. In particular, beetles are well represented in such forest canopy communities (Floren and Linsenmair 1998). More

than 40 beetle families including ground beetles (Carabidae) have been recorded, even in tree crowns of old-growth temperate deciduous forest (Gering and Crist 2000). For tropical rain forests, the high number of carabid beetle species sampled from the canopy suggests that the diversity of this family is far higher than previously thought (Lucky et al. 2002). Beutelspacher (1972) reported four carabid species with “certain frequency” in epiphytes, and Murillo et al. (1983) concluded this family was one of the seven most abundant among the bromeliad-associated insect fauna. In an explanatory summary about the carabids of Mexico, Ball and Shpeley (2000) highlighted the importance of the arboreal lifestyle with respect to the diversity of the carabid fauna in tropical areas. They showed that 24% of the 172 genera of carabids extant in

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Mexico include arboreal species, and many such species have been collected from epiphytes, especially bromeliads.

Bromeliads and their associated fauna are well-defined biological systems (Picado 1913, Delamare-Deboutville 1948, Beutelspacher 1972, Benzing 1986, Willimas and Feltsmate 1992, Beutelspacher 1999, Richardson 1999). These epiphytic plants have rosetted, overlapping wide leaves that allow water and debris accumulation, which favors establishment of a variety of organisms. Leaves form a cup or small tank that becomes occupied by water and organic matter (sprigs, leaves, fruits, seeds, spores, pollen grains, flowers, etc.). Water from rain or mist condensation is deposited in the tank during the rainy season and slowly evaporates during the dry season. This water is partially absorbed by the plant itself, and it is also used by multiple organisms, which in return supply nutrients derived from their activities to the plant.

It is reasonable to suppose that tight relationships, perhaps even mutualisms, could develop between bromeliads and some animals that depend on them for particular aspects of their life cycles. For example, the metabolic wastes and remains of dead ants result in a large contribution of nutrients for the plants and for the bromeliad inhabitants as well (Rickson 1979, Davidson et al. 1989, Rico-Gray et al. 1989, Benzing 1990, Olmsted et al. 1995, Treseder et al. 1995, Benzing 2000). The benefits offered by epiphytes to their associated fauna are hypothesized to include cover and refuge against predators and/or extreme climatic conditions, a supply of water, resting sites, or aggregation sites useful for mating (Benzing 1970, 1984, 1990).

In this paper, we describe and analyze the carabid assemblage associated with epiphytic bromeliads in central Veracruz, Mexico. We show that there is a regular carabid assemblage associated with bromeliads that includes some species commonly living at ground level. Our data suggest that the association between carabids and bromeliads has a distinct seasonal component, underscoring the potential role of these epiphytes in relieving water stress during dry seasons. Moreover, this latter effect interacts with altitude so that patterns must be understood in the context of altitudinal zones. We conclude with a general discussion about the contribution of the bromeliads to the diversity of the carabid fauna of the study area.

Materials and Methods

Study Area. This study was conducted on the southeastern slope of the Cofre de Perote (CP), a mountain located in central Veracruz, Mexico, between 19°40', 19°20' N and 97°00', 97°15' W and reaching an elevation of 4,282 m. We studied carabids found associated with bromeliads over three altitudinal ranges: (A) low, from 280 to 450 m; (B) middle, from 1,300 to 1,550 m; and (C) high, from 2,200 to 2,600 m. Above 2,600 m, bromeliads were scattered and mainly inaccessible because of their height on trees. Within each range, we sought to sample in several locations ~1 ha in area

in which trees harbored many epiphytic bromeliads on trunks and branches. The spatial distribution of bromeliads in Veracruz is highly aggregated, but there is no evidence of further spatial segregation of bromeliad species within these aggregations (Hietz and Hietz-Seifert 1994, 1995). Therefore, in this study of carabid beetles, we considered all bromeliads, regardless of species, as equivalent potential habitats.

According to Hietz and Hietz-Seifert (1994), one can find 12 bromeliad species (*Tillandsia*) at the low altitude sites of range A, whereas the species number increases to 28 (3 *Catopsis* and 25 *Tillandsia*) at the middle altitude sites on range B. The number of expected bromeliad species decrease to ~10 (1 *Catopsis* and 9 *Tillandsia*) over range C. Those authors reported no bromeliads at >3,000 m of elevation.

Sampling Protocol. Bromeliads were sampled for carabids by at least two people once about every 45 d during a full year interval (July 2000 to June 2001) in each one of the altitudinal ranges. Because some epiphytic bromeliads are threatened through illegal trade of ornamental plants, we sought to minimize destruction of the plants as follows: (1) we sampled only from one of several possible sites in each altitude during each sampling period, (2) if five consecutive bromeliads were sampled from at least two trees at least 10 m apart with failure to find any carabids, sampling was terminated at that site for that sampling period, (3) a maximum of 25 bromeliads was sampled at a site during a particular sampling period, and (4) only bromeliads no more than 5 m above the ground were sampled (this was also partly a constraint of the cutting pole used). Samples came from isolated trees or groups of trees at least 10 m apart as they were encountered haphazardly in walking through the sites. Neither tree nor bromeliad species were identified nor specifically targeted in this study.

Bromeliads were cut and pulled down using extensible branch-cutters and a curved blade and immediately disassembled leaf by leaf and shaken over a plastic sheet placed on the ground. Individual carabids routed by these procedures were captured and preserved in tubes with vapor of ethyl acetate. To increase efficiency of collection, specimens belonging to other taxa were ignored. Although we conducted no tests of sampling efficacy, we felt that we collected virtually all the beetles in the bromeliads. Identification of subsequently pinned specimens was made to the specific level using dichotomous keys (G.E.B. and E.M.O., unpublished data) and by comparison with previously identified material held at the University of Alberta Strickland Museum (UASM). The material from this study is housed in the carabid collection of the Instituto de Ecología A.C. (Xalapa, Veracruz, Mexico) or the UASM (Edmonton, Alberta, Canada).

Results

Carabids in Bromeliads. We captured 153 individuals belonging to 37 species in bromeliads on the Cofre de Perote (Table 1). The Lebiini and Platynini were the two best represented tribes with 15 and 16 species,

Table 1. Species of carabids and no. individuals collected in bromeliads according to (A) low altitude sites, from 280 to 450 m; (B) middle, from 1,300 to 1,550 m; and (C) high, from 2,200 to 2,600 m

Species	No. individuals	Sites	Peak collection	Lifestyle
Clivinini				
<i>Schizogenius longipennis</i> Putzeys 1866	1	A	Jul	Hygrophilous
Odacanthini				
<i>Colliuris pilatei</i> Chaudoir 1848	1	A	Mar	Mesophile geophilous
Harpalini				
<i>Selenophorus</i> UASM-16	14	A	Feb	Mesophile hygrophilous
<i>Selenophorus</i> UASM-4	6	A	Jul	Mesophile hygrophilous
<i>Pelmatellus nitescens</i> Bates 1882	3	B	Jul	Mesophile geophilous
Bembidiini				
<i>Paratachys monostictus</i> Bates 1872	1	A	Feb	Mesophile geophilous
Lebiini				
<i>Cymindis latiuscula</i> Chaudoir 1875	2	A	Feb	Mesophile arboreal
<i>Lebia xanthogaster</i> Bates 1883	1	A	Mar	Mesophile arboreal
<i>Lebia callizona</i> Bates 1878	1	A	Feb	Mesophile arboreal
<i>Lebia analis</i> Dejean 1825	2	A	Feb	Mesophile
<i>Lebia</i> UASM-109	4	A	Feb	Mesophile
<i>Lebia quadriplagiata</i> Chaudoir 1871	2	A	Feb	Mesophile arboreal
<i>Lebia</i> UASM-10	1	A	Oct	Mesophile arboreal
<i>Lebia urania</i> Bates 1883	1	A	Feb	Mesophile arboreal
<i>Lebia translucens</i> Bates 1883	3	A	Feb	Mesophile arboreal
<i>Calleida truncata</i> Chevrolat 1835	2	A	Feb-Mar	Mesophile arboreal
<i>Calleida planulata</i> LeConte 1848	1	A	Mar	Mesophile arboreal
<i>Calleida cyanippa</i> Bates 1883	2	A	Feb-Mar	Mesophile arboreal
<i>Calleida sumptuosa</i> Bates 1883	2	B, C	Nov	Mesophile arboreal
<i>Eucheila planipennis</i> Bates 1891	1	A	Jul	Mesophile arboreal
<i>Phloeoxena batesi</i> Ball 1975	5	C	Jul	Mesophile
Platynini				
<i>Onypterygia iris</i> Chaudoir 1863	1	B	Jul	Mesophile arboreal
<i>Platynus aphaedrus</i> Chaudoir 1859	1	B	Jul	Mesophile arboreal
<i>Platynus fratellus</i> Chaudoir 1878	24	B	Mar & Jul	Mesophile arboreal
<i>Platynus convexulus</i> Casey 1920	1	B	Jun	Mesophile arboreal
<i>Platynus</i> Cofre sp. 4 n.sp.	2	B	Jul	Mesophile
<i>Platynus variabilis</i> Chaudoir 1837	10	B, C	Jul	Mesophile
<i>Platynus caeruleus</i> Chaudoir 1859	3	B, C	Nov	Mesophile
<i>Platynus columbinus</i> Chaudoir 1878	12	B, C	Nov	Mesophile
<i>Platynus</i> UASM-218	3	B, C	Nov	Unknown
<i>Platynus cupripennis</i> Lap. de Cast. 1835	4	B, C	Feb & Nov	Mesophile geophilous
<i>Platynus obscurellus</i> Bates 1878	2	B, C	Feb & Nov	Mesophile arboreal
<i>Platynus acutulus</i> Bates 1891	2	C	Feb	Mesophile geophilous
<i>Platynus gracilis</i> Chaudoir 1859	22	C	Jul & Nov	Mesophile arboreal
<i>Platynus</i> UASM-155	2	C	Feb	Mesophile geophilous
<i>Platynus delicatulus</i> Chaudoir 1878	6	C	Feb	Unknown
<i>Platynus sexfoveolatus</i> Chaudoir 1878	2	C	Jul	Mesophile arboreal
37	153			

Peak collection refers to months. For lifestyle, see text.

respectively, and together comprised 83% of the overall catch (19.6% Lebiini and 63.4% Platynini). The Harpalini with three species represented 15%, and the remaining 2% consisted of one species and a single individual each of Clivinini, Odacanthini, and Bembidiini.

Five species represented by 10 or more individuals comprised 53.6% of the total catch, included four platynines (*Platynus variabilis*, *P. columbinus*, *P. gracilis*, and *P. fratellus*) and one undescribed harpaline species (*Selenophorus* [*Gynandropus*] UASM-16). Twenty of the collected species were represented by two to six individuals each and accounted for 38.6% of the total catch, with nine species each of lebiines (15.7%) and platynines (17%). Twelve species comprised of the remaining 7.8% of the total catch were represented by a single specimen each and included six species of lebiines (3.9%) and three of platynines (2%).

Altitude and Diversity. Overall, 18 carabid species were found in bromeliads at low altitude, and

13 species were collected at both middle and high altitude ranges. Based on our estimate of relative abundance, the probability of finding a beetle in a bromeliad was highest in the highest elevation range (Fig. 1).

Rarefaction (Magurran 1988) suggests that our sample is fairly complete at the two highest elevations but that we should expect more species to be found with additional sampling effort at lower altitude. Clearly, the diversity of bromeliad-inhabiting carabids is greatest in the lowest elevation range. In a sample of 46 individuals (the lowest number collected over all three altitudes), the expected number of species is 17.8 ± 0.194 (SE) for low altitude, 12.3 ± 0.626 for middle altitude, and 12.3 ± 0.619 for high altitude ranges (Fig. 2).

The relative abundance of carabid species adjusted to standardize sampling effort at each altitudinal range is shown in Fig. 3. Of the 18 species found at low

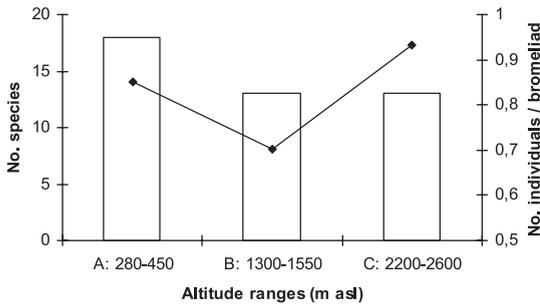


Fig. 1. Number of species and individuals of carabids collected in bromeliads at three altitudinal ranges.

altitude, 2 harpaline *Selenophorus* were the most abundant species. The 13 lebiines and the other 3 species sampled at this range were represented at low abundances (Fig. 3A). *Platynus fratellus* was the most abundant species at middle altitude and was four times more abundant than two other species of *Platynus* (*P. variabilis* and *P. columbinus*) encountered there. The other eight *Platynus* species, *Pelmatellus nitescens*, and *Calleida sumptuosa* were found in lower abundances (Fig. 3B). Finally, at high altitude, *Platynus gracilis* was most commonly collected, and its relative abundance was four times higher than that of the two next most abundant *Platynus* species (*P. delicatulus* and *P. columbinus*) and of *Phloeoxena batesi*. The other eight species of *Platynus* and *Calleida sumptuosa* encountered in bromeliads at this range were less common (Fig. 3C).

The carabid assemblages found associated with bromeliads differed strikingly with altitude. None of the species collected at low altitude (30.1% of the collected individuals) were recorded at the two higher altitudes (Figs. 3A and 4). Six species were exclusively found at middle (20.9%) and high (25.5%) altitudes (Figs. 3B and C and 4). Seven species (23.5% of the specimens collected) were found at both of the two higher altitude ranges and included six platynines (*P.*

columbinus, *P. variabilis*, *P. caeruleus*, *P. UASM-218*, *P. cupripennis*, and *P. obscurellus*) and the lebiine *C. sumptuosa* (Fig. 4).

The altitudinal separation of the carabid assemblages has a major taxonomic basis. Most of the Lebiini occurred in range A, and all the Platynini occurred at the two highest altitudinal ranges (Fig. 4). Just 2 of the 15 lebiine species did not occur at the lowest altitudes. *C. sumptuosa* was found at the two upper altitude ranges and *P. batesi* at high altitude. This latter species was the most commonly encountered species among lebiines, followed by an undescribed species *Lebia* sp. 109 at low altitude (Figs. 3A and C and 4). Among platynines, *P. fratellus* and *P. gracilis* were the most common species occurring exclusively at middle and high altitudes, respectively (Figs. 3B and C and 4).

Seasonality. There seems to be a strong seasonal component to associations between carabids and bromeliads. Overall, the maximum number of species was encountered in February when 17 (46%) of the 37 species were collected. The next highest peak occurred in July with 13 species (35%). Eight species (22%) were recorded in November and March. Carabids were also more numerous in the bromeliads sampled in February, July, and November. No carabids were collected from bromeliads during August, December, January, April, and May (Fig. 5).

Seasonal effects on species richness and carabid abundance associated with bromeliads depended strongly on altitude but did not follow the same pattern. The February peak in diversity was accounted for mainly by the higher number of species at low altitude, whereas July peak was found mainly at middle altitude. Finally, the November peak reflected data mainly from the high altitude range (Fig. 6, top). Interestingly, peaks of species richness do not correspond strongly to peaks in abundance. Peaks in numbers of carabids occurred in July, November, and February, respectively, at low, middle, and high altitudes (Fig. 6, bottom).

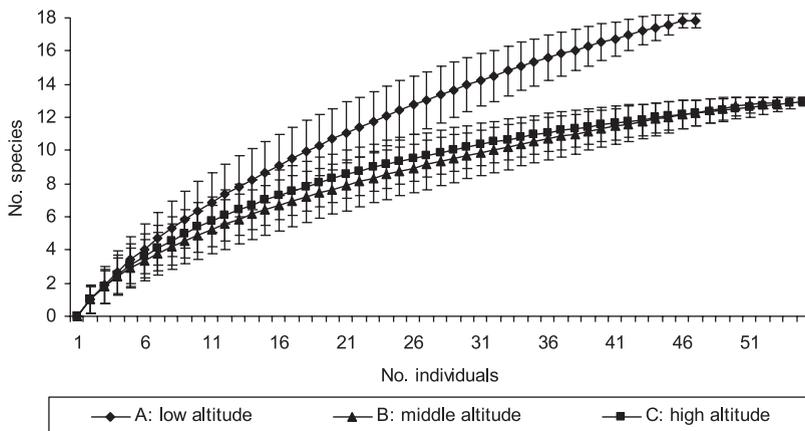


Fig. 2. Rarefaction curves of the carabids found in bromeliads at different altitudinal ranges. Vertical discontinuous lines indicate SE.

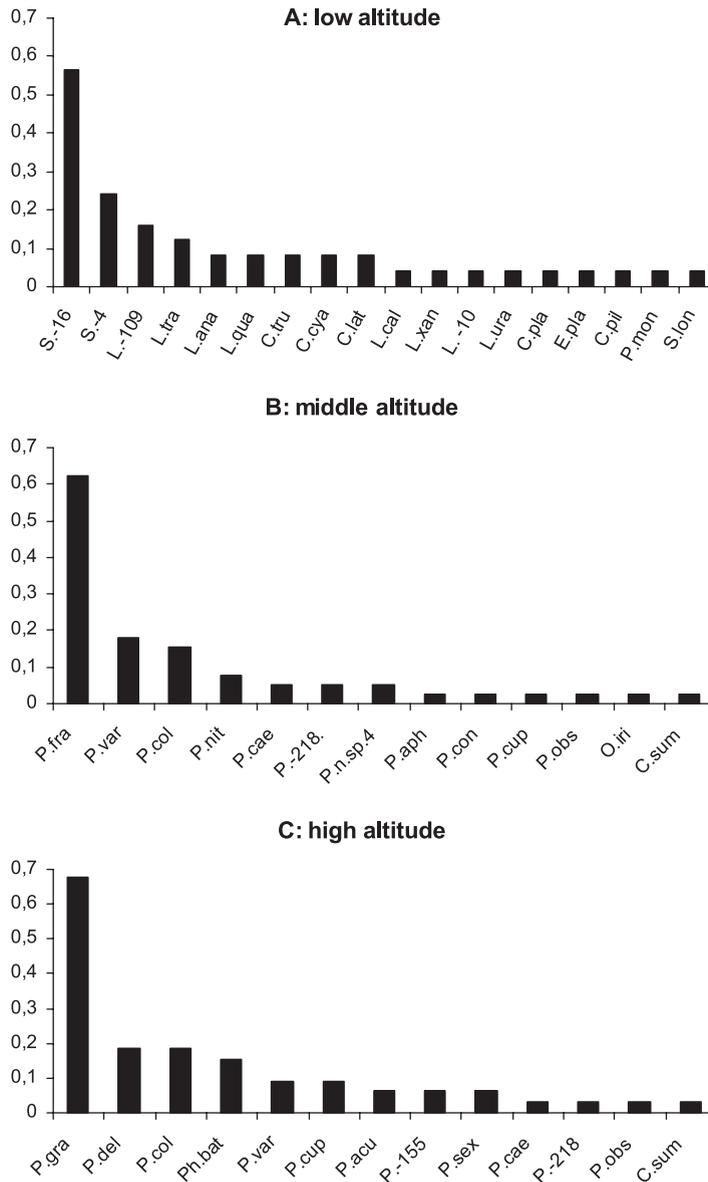


Fig. 3. Standardized abundance ($[\text{number of individuals of each species}/\text{total at each altitudinal range}] \times 100/[\text{n}]$ number of bromeliads sampled) of the carabid species (A: $n = 54$, B: $n = 74$, C: $n = 59$).

Given the conspicuous association between altitude and taxonomic composition of carabid assemblages, it is not surprising that most of the lebiines (12 of the 15 species), a tribe generally restricted to the lowlands, were collected in February–March (Table 1). Nevertheless, three species were found in July (*Lebia analis*, *P. batesi*, and *Eucheila planipennis*) and one species each was found in October (*Lebia* UASM-10) and November (*C. sumptuosa*). The platynines were more widely distributed among the collecting periods, with six species found in two or more periods. *P. delicatulus* was collected in February and October, *P. cupripennis* and *P. obscurellus* in February and November, *P. gra-*

cilis in July and November, *P. fratellus* in March, July, and September, and *P. variabilis* in March, June, July, and November.

Discussion

Carabid Assemblages Associated with Bromeliads. In this study, we found 37 species of carabids in bromeliads. The fact that 7 of these 37 species (19%) are new to science underscores how much we have yet to learn about tropical arboreal faunas. Twenty-six of the 37 species (70%) are clearly recognized as arboreal or mesophilic, i.e., based on previous work they are as-

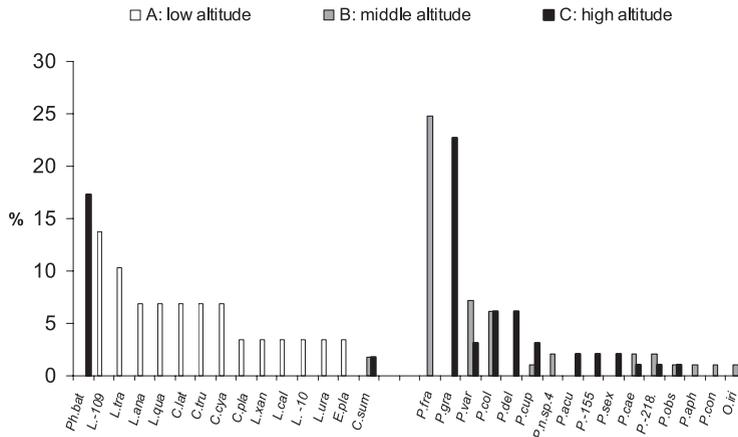


Fig. 4. Proportion of Lebiini (left, n = 30) and Platynini (right, n = 97) species found in bromeliads by altitudinal range.

sociated with life in shrubs and trees, with the moisture conditions provided by well-developed vegetation cover, or both. These species include all 15 lebiines and 11 platynine species (Table 1). Given that the three known specimens of *P. UASM-218* were collected only in bromeliads and that many individuals of *P. delicatulus* were also found in bromeliads, these two species probably also have arboreal affinities. However, additional knowledge of their respective patterns of habitat use is needed to support this inference.

We expected to find other species with known arboreal habits in bromeliads (G.E.B., unpublished data). For example, species such as the lebiines *Coprodora aurata*, *C. festiva*, *Cymindis basipunctata*, *Calleida decora*, and the platynine species *Onypterygia tricolor*, *O famini*, *O. fulgens*, and *O. angustata*, were not found in bromeliads in this study but were collected recently at light and by branch-beating in the

same area (E.M.O. and G.E.B., unpublished data). The limited sampling in this study is likely sufficient to explain the absence of the above species in this data set. Nevertheless, our data set shows that at least 37 carabid species are associated in some degree with bromeliads.

The exact function of bromeliads for carabids remains poorly understood. Previous authors (Murillo et al. 1983) have suggested that bromeliads provide refuge from dry conditions to a variety of insects of different families, including Carabidae. In addition, foraging in bromeliads may increase opportunities of finding prey among the diverse arthropod fauna harbored within. Epiphytic bromeliads increase the volume of arboreal soil and litter by creating water-filled interfoliar tanks in which litter accumulates and soil forms (Paoletti et al. 1991). In this substrate, mites and springtails are particularly abundant and diverse (Palacios-Vargas 1981, Nadkarni and Longino 1990,

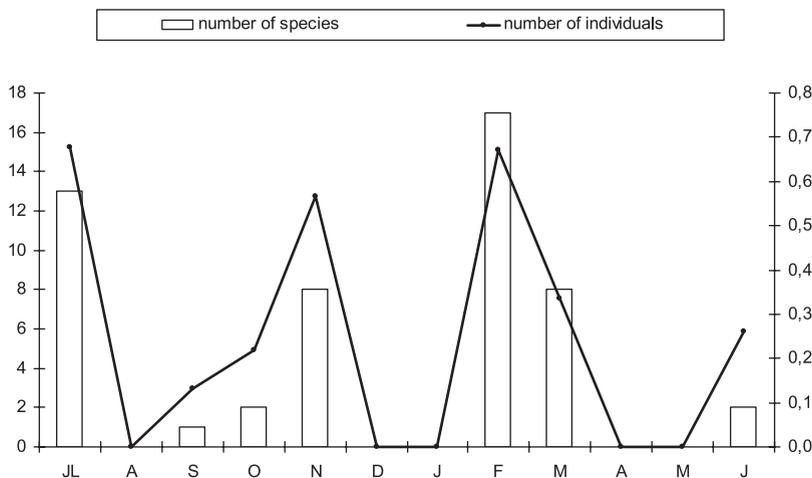


Fig. 5. Seasonal distribution of species richness and standardized relative abundance of carabids found in bromeliads in the Cofre de Perote.

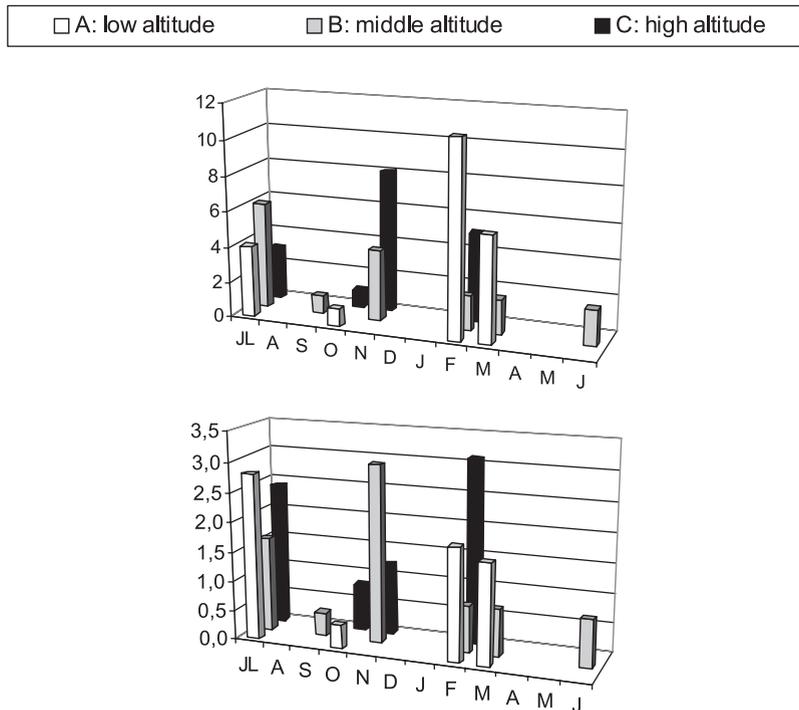


Fig. 6. Number of species (top) and standardized relative abundance (bottom) of carabids found in bromeliads by altitudinal range along a year.

Paoletti et al. 1991, Palacios-Vargas and Castaño-Meneses 2001, Castaño-Meneses 2002). These conditions could provide a rich source of food for some of the arboreal carabid species, especially during time where food is scarce elsewhere.

Some carabid species have developed apparent structural adaptations for living in bromeliads. For example, adults of the *P. bromeliarum* species group on Jamaica are extremely flat and are apparently adapted for life among the leaf rosettes of bromeliads (Darlington 1970). The flattened body of the most common arboreal species of *Platynus* (e.g., *P. fratellus* and *P. gracilis*) taken in bromeliads at middle and high altitudes in this study also suggests such adaptation.

Most of the species gathered in bromeliads exhibit an arboreal life style or at least have strong mesophile affinity. Most of the arboreal lebiines were found only in bromeliads, but some of them were caught also at light during their nocturnal flight periods. With exception of *P. batesi*, none of the lebiine species were caught in pitfall traps, and thus, there is little evidence that the adults ever occur on the ground (E.M.O., unpublished data).

Few specimens of species normally living on the ground were collected in bromeliads (Table 1). Based on collecting records from elsewhere, three Harpalini, the single specimens of Clivinini, Odacanthini, and Bembidiini, and three Platynini species found in bromeliads are not strictly arboreal. Rather, they seem to be mesophilic and geophilous, i.e., living in moist situations on open ground and/or hydrophiles associated

with fresh water stream banks (Table 1). With the exception of *Schizogenius longipennis* and *Colliuris pilatei*, all of these species have been collected with other methods such as light, by hand, and by pitfall trapping (E.M.O., unpublished data). They could be attracted occasionally to the moist and humic environment provided by bromeliads and might be best considered as "tourists" or "accidentals" in the bromeliads.

Carabid assemblages associated with bromeliads are comprised mostly of arboreal species but also includes some nonarboreal elements. For these latter species, bromeliads may occasionally act as passive traps for insects washed in from the canopy or that wander in from the forest floor (Richardson 1999, Armbruster et al. 2002). However, for truly arboreal carabids, bromeliads are not random microhabitats but valuable resources that provide shelter during unsuitable external environmental conditions and possibly food.

Altitude, Bromeliads, and Carabids. Carabids associated with bromeliads showed a clear altitudinal replacement pattern at Tribe level: Lebiini occurred mostly at low altitudes and Platynini were found exclusively in the two higher altitudinal ranges. This pattern has been described for the carabid fauna in Mexico and postulated to have resulted from climatic adaptation (Ball and Shpeley 2000). However, these authors also expected maximum diversity for both Platynini and Lebiini in mid-altitudinal tropical forests. In contrast, we found that the number of carabid species found in bromeliads decreased from lowland to higher altitudes and showed a sharp break in the

altitudinal ranges of species representing these two tribes.

The altitudinal pattern of carabid species richness in bromeliads that we observed on the southeastern slope of the Cofre has some plausible explanations. It may be a simple result of the claim that abundance of some bromeliads and other plant species decreases with an increase in altitude (García-Franco and Peters 1987, Cowling and Samways 1994), although earlier studies on the relationships between altitude and epiphytic abundance showed the contrary; abundance increases with an increase in altitude (Gilmartin 1964). More likely, we believe the pattern reflects the effect of extreme anthropogenic conversion of habitats that formerly dominated the middle altitude ranges on the CP.

It has been generally recognized that the greatest diversity of epiphytic bromeliads occurs in mid-altitudinal montane or mesophilous forests (Gentry and Dodson 1987, Hietz and Hietz-Seifert 1994). For example, in some locations between 1,200 and 2,000 m close to our study area, it is possible to find 39 vascular epiphytic species in a 625-m² plot (Hietz and Hietz-Seifert 1994, 1995). This situation still exists in tracts of mesophilous forest restricted to inaccessible slopes and private lands (Castillo-Campos 1991, Hietz and Hietz-Seifert 1994, 1995). In contrast, the sites that we sampled were only small remnants of forest existing as patches or even isolated trees surrounded by pastureland that currently occupy this altitudinal range. This situation has likely promoted a reduction of bromeliad abundance and diversity within sites. The loss of arboreal habitats may then in turn explain the reduction in arboreal carabid abundance that we observed (Fig. 1). In particular, we suggest that the extensive development of rangeland at middle altitudes on the Cofre has led to the pronounced separation of lebiine and platynine elements. This has resulted in loss of the high diversity situation that presumably existed when habitat configuration permitted the overlap of these two fauna elements.

Seasonality. Abundance and composition of arthropod assemblages associated with bromeliads vary spatially and temporally (Richardson 1999, Stuntz et al. 1999, Stuntz 2001, Armbruster et al. 2002, Castaño-Meneses 2002). The joint effect of variation in these two dimensions was significant for the richness of arboreal carabid species in tropical rain forest canopy where seasonality is not obvious (Lucky et al. 2002). In our study conducted in a subtropical region with evident seasonality, bromeliads were used by carabids mostly during drought periods at specific altitudes. The maximal species richness and abundance in the three altitudinal ranges is explained by aggregation of species and individuals in bromeliads during different periods of the year when environmental conditions are much drier elsewhere.

The results of our study and that of Murillo et al. (1983) suggest that carabid use of bromeliads varies with local climatic patterns. A general pattern of strong seasonality with a dry season between November and April (mid-fall, winter, early spring) and a wet season from May to October (spring, summer, mid-fall) prevails in central Veracruz. This summer rainfall regime is modified by a short dry period determined by midsummer

heat in the middle of the rainy season (the "dog days" that occur between late July and early September). The extent of this modification is conspicuously affected by altitude (Gómez 1991, Giddings and Mehltreter 2003), and we hypothesize that this complex interaction between altitude and seasonal rainfall can explain the pattern carabid on bromeliads that we observed (Fig. 6). At lower altitude, notable drought periods are present during the dog days of summer and also during the latter part of the dry season, and this pattern is reflected for both beetle carabid species richness and carabid abundance. At middle altitude, the local effect of late summer drought is also important. However, the carabid data also seem to reflect a more pronounced dryness in November, characteristic of the general climatic pattern for the region. In the lowland regions, the period of high humidity is prolonged by northerly winds that bring humidity inland from the Caribbean. Finally, at high altitude, the late dry season is associated with most severe drought because of lower temperatures and less annual precipitation (from which <5% occurs in winter), and this is consistent with the high abundance of carabids in bromeliads observed during February at the highest elevations.

In summary, epiphytic bromeliads are a valuable resource for arboreal carabids. They provide shelter and may increase food availability during dry conditions, the timing of which varies according to altitude. We suggest that severity and temporal distribution of these dry periods determine the abundance and species richness of carabids associated with bromeliads at different altitudinal ranges.

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References Cited

- Armbruster, P., R. A. Hutchinson, and P. Coatgrave. 2002. Factors influencing community structure in a South American tank bromeliad fauna. *Oikos* 96: 225–234.
- Ball, G. E., and D. Shpeley. 2000. Carabidae (Coleoptera), pp. 363–399. In J. Llorente-Bousquets, E. González-Soriano, and N. Papaverio (eds.), *Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México. Hacia una Síntesis de su conocimiento*, vol. II. Universidad Nacional Autónoma de México, Mexico City, Mexico.
- Benzing, D. H. 1970. An investigation of two bromeliad myrmecophytes: *Tillandsia butzii* Mez, *T. caput-medusae* E. Morren, and their ants. *Bull. Torrey Botanical Club* 97: 109–115.
- Benzing, D. H. 1984. Vascular epiphytes: a survey with special reference to their interactions with other organisms, pp. 11–24. In S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (eds.), *Tropical rain forest: ecology and management*. Blackwell Scient. Pub., Oxford, UK.
- Benzing, D. H. 1986. Foliar specializations for animal assisted nutrition in Bromeliaceae, pp. 235–256. In B. E.

- Juniper, and T.R.E. Southwood (eds.), *Insects and the plant surface*. Edward Arnold, London, UK.
- Benzing, D. H. 1990. *Vascular epiphytes. General biology and related biota*. Cambridge University Press, New York.
- Benzing, D. H. 2000. *Bromeliaceae: profile of an adaptive radiation*. Cambridge University Press, New York.
- Beutelspacher, C. R. 1972. Fauna de *Tillandsia caput-medusae* E. Morren, 1880 (Bromeliaceae). *An. Inst. Biol. Univ. Nal. Autón. México Ser. Zool.* 1: 25–30.
- Beutelspacher, C. R. 1999. Bromeliáceas como ecosistemas. Con especial referencia a *Achmea bracteata* (Swartz) Griseb. Edit. Plaza y Valdés, Mexico City, México.
- Castaño-Meneses, R. G. 2002. Estructura de la comunidad de artrópodos epífitos y su papel en el crecimiento de *Tillandsia violacea* (Bromeliaceae) en un bosque templado de Hidalgo, México. PhD dissertation, Facultad de Ciencias, UNAM, Mexico City, Mexico.
- Castillo-Campos, G. 1991. Vegetación y flora del Municipio de Xalapa, Veracruz. MAB-Unesco, Instituto de Ecología, A.C. y H. Ayuntamiento de Xalapa, Veracruz, Mexico.
- Cowling, R. M., and M. J. Samways. 1994. Predicting global patterns of endemic plant species richness. *Biodiv. Lett.* 2: 127–131.
- Darlington, P. J., Jr. 1970. Carabidae on tropical islands, especially the West Indies. *Biotropica* 2: 7–15.
- Davidson, D. W., R. R. Snelling, and J. T. Longino. 1989. Competition among ants for myrmecophytes and the significance of plant trichomes. *Biotropica* 21: 64–73.
- Delamare-Deboutville, C. 1948. Étude quantitative du peuplement animal des sols suspendu et des epiphytes en forêt tropicale. *Compt. Rend. de l'Acad. du Sci.* 226: 1544–1546.
- Floren, A., and K. E. Linsenmair. 1998. Non-equilibrium communities of Coleoptera in trees in a lowland rain forest of Borneo. *Biotropica* 4: 55–67.
- García-Franco, J. G., and C. M. Peters. 1987. Patrón espacial y abundancia de *Tillandsia* spp. a través de un gradiente altitudinal en los Altos de Chiapas, México. *Brenesia* 27: 35–45.
- Gentry, A. H., and C. H. Dodson. 1987. Diversity and biogeography of neotropical vascular epiphytes. *Ann. Mo. Bot. Gard.* 74: 205–233.
- Gering, J. C., and T. O. Crist. 2000. Patterns of beetle (Coleoptera) diversity in crowns of representative tree species in an old-growth temperate deciduous forest. *Selbyana* 21: 38–47.
- Giddings, L., and Y. K. Mehlreter. 2003. Base de datos del clima de México. Extraídos de ERIC (2000). Instituto de Ecología, Xalapa, Mexico.
- Gilmartin, A. J. 1964. Ecuador. Bromeliad country. *Broml. Soc. Bull.* 14: 4–7.
- Gómez, C. M. 1991. Atlas climático del Municipio de Xico (Estado de Veracruz). Instituto de Ecología, Xalapa, Mexico.
- Greeney, H. F. 2001. The insect of plant-held waters: a review and bibliography. *J. Trop. Ecol.* 17: 241–260.
- Hietz, P., and U. Hietz-Seifert. 1994. Epífitas de Veracruz. Guía ilustrada para las Regiones de Xalapa y SpaceqqLos Tuxtlas, Veracruz/Epiphytes of Veracruz. An illustrated guide for the regions of Xalapa and Los Tuxtlas, Veracruz. Instituto de Ecología, Xalapa, Veracruz, Mexico.
- Hietz, P., and U. Hietz-Seifert. 1995. Structure and ecology of epiphyte communities of a cloud forest in central Veracruz, Mexico. *Vegetat. Sci.* 6: 719–728.
- Magurran, A. 1988. *Ecological diversity and measurement*. Princeton University Press: Princeton, NJ.
- Murillo, R. M., J. G. Palacios, J. M. Labougr, E. M. Hentschel, J. E. Llorente, K. Luna, P. Rojas, and S. Zamudio. 1983. Variación estacional de la entomofauna asociada a *Tillandsia* spp. en una zona de transición biótica. *Southwest. Entomol.* 8: 292–302.
- Lucky, A., T. L. Erwin, and J. D. Witman. 2002. Temporal and spatial diversity and distribution of arboreal Carabidae (Coleoptera) in a western Amazonian Rain Forest. *Biotropica* 34: 376–386.
- Nadkarni, N. M., and J. T. Longino. 1990. Invertebrates in canopy and ground organic matter in a Neotropical Montane Forest, Costa Rica. *Biotropica* 22: 286–289.
- Olmsted, I. C., A. Dejean, and R. R. Snelling. 1995. Tree epiphyte-ant relationships of the low inundated forest in Sian Ka'an Biosphere Reserve, Quintana Roo, México. *Biotropica* 27: 57–70.
- Palacios-Vargas, J. G. 1981. Collembola asociados a *Tillandsia* en el Derrame lávico del Chichinautzin, Morelos, México. *Southwest. Entomol.* 6: 87–98.
- Palacios-Vargas, J. G., and G. Castaño-Meneses. 2001. Collembola associated with *Tillandsia violacea* (Bromeliaceae) in Mexican *Quercus-Abies* forests. *Pedobiologica* 46: 395–403.
- Paoletti, M. G., R.A.J. Taylor, B. R. Stinner, D. H. Stinner, and D. H. Benzing. 1991. Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. *J. Trop. Ecol.* 7: 373–383.
- Picado, C. 1913. Les Bromeliacées epiphytes, considérés comme milieu biologique. *Bul. Scient. Fr. Belg.* 46: 215–360.
- Richardson, B. A. 1999. The bromeliad microcosm and the assessment of faunal diversity in a neotropical forest. *Biotropica* 31: 321–336.
- Rickson, F. R. 1979. Absorption of animal tissue breakdown products into a plant stem. The feeding of a plant by ants. *Am. J. Bot.* 66: 87–90.
- Rico-Gray, V., J. T. Barber, L. B. Thien, E. G. Ellgaard, and J. J. Toney. 1989. An unusual animal-plant interaction: feeding of *Schomburgkia tibicinis* (Orchidaceae) by ants. *Am. J. Bot.* 76: 603–608.
- Stuntz, S. 2001. The influence of epiphytes on arthropods in the tropical forest canopy. PhD dissertation, Bayerischen Julius-Maximilians-Universität Würzburg, München, Germany.
- Stuntz, S., U. Simon, and G. Zotz. 1999. Assessing the potential influence of vascular epiphytes on arthropod diversity in tropical tree crowns: hypotheses, approaches and preliminary data. *Selbyana* 20: 276–283.
- Stuntz, S., Ch. Ziegler, U. Simon, and G. Zotz. 2002. Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. *J. Trop. Ecol.* 18: 161–176.
- Treseder, K. K., D. W. Davidson, and J. R. Ehleringer. 1995. Absorption of ant-provided carbon dioxide and nitrogen by a tropical epiphyte. *Nature* 275: 137–139.
- Williams, D. D., and B. W. Feltmate. 1992. *Aquatic insects*. CAB International, University Arizona Press. Wallingford (UK)/Tucson, AZ.

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