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Assessing the Potential Influence of Vascular Epiphytes on Arthropod Diversity in Tropical Tree Crowns: Hypotheses, Approaches, and Preliminary Data

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Abstract. The canopies of tropical forests harbor a large proportion of global biodiversity. The largest fraction of this diversity is comprised of arthropods. For establishment and maintenance of such faunal diversity, vascular epiphytes may play an important role by substantially increasing the structural heterogeneity of the canopy habitat, providing resources for herbivores, and mitigating microclimatic extremes. Until now, the degree of this possible influence has not been studied at the community level within entire tree crowns. Here, we present an approach to investigate the relationships between the epiphyte flora of selected *Annona glabra* trees and their respective arthropod fauna. Currently, we are conducting a one-year survey of arthropods inhabiting tree crowns bearing distinct epiphyte assemblages in a tropical moist forest in Panama. We are collecting animals using long-term trapping techniques to address seasonal fluctuations. Four different types of traps are described and discussed. Composite flight interception traps yielded most arthropods, but tended to underestimate certain taxa, e.g., ants and springtails. Those were more successfully captured in branch traps. Preliminary results on the composition of the arboreal arthropod fauna are presented.

Key words: arthropods, diversity, epiphytes, structural herogeneity, canopy, trapping techniques

Introduction

Much of global biodiversity can be attributable to the diversity of canopy systems of tropical forests. Arthropods constitute a large fraction, though how large remains to be determined (Wilson 1990, Erwin 1982, 1983). The challenge of a comprehensive inventory has always fascinated biologists. Research is needed to help understand the processes that create and maintain high tropical diversity. Vascular epiphytes may be of great significance for the establishment and maintenance of arthropod diversity in tropical forest canopies (Benzing 1990, Nadkarni 1994). Aside from supplying resources for herbivorous species and mitigating climatic extremes, epiphytes could significantly affect occurrence and abundance of arboreal invertebrate species by increasing the structural heterogeneity of the canopy. For example, Freiberg (1997) showed that microclimatic gradients are largely dependent on organic matter accumulated on epiphyte-laden branches in a rainforest in Costa Rica, thereby counteracting the harsh and arid conditions of the upper canopy. In a large arthropod inventory, Stork (1987a) found that the abundance of certain taxa (Homoptera; Gryllidae; Chrysomelidae and Anthicidae, Coleoptera) was associated with a tree's epiphyte load (i.e., the presence or absence of ferns and vines). Furthermore, certain epiphyte species indirectly influence faunal communities by harboring ant species that promote the presence of Homoptera, keep the host tree clear of herbivores or potential bug predators, or prey upon other co-habitant arthropods (Buckley 1990, Davidson and Epstein 1989, Dejean et al. 1992, Dejean et al. 1995).

The role of epiphytes in determining arthropod diversity and abundance has not been thoroughly studied. Below, we present an approach to investigate the relationships between canopy epiphytes and their respective arthropod communities. Currently, a comprehensive one-year

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survey of arthropods is being carried out in a tropical moist forest in Panama. The questions we are addressing are as follows. Do vascular epiphytes as structural elements of the canopy affect arthropod assemblages in terms of relative abundance and species richness? Do different epiphyte species influence arthropod diversity in different ways? If so, what are the mechanisms of the influence? Does arthropod abundance fluctuate seasonally, and do epiphytes reduce these fluctuations by moderating climatic extremes?

Considering the complexity of most tree crowns, a feasible study system should be easily accessible and contain relatively few epiphyte species. This is the case for *Annona glabra* L. (Annonaceae), a small tree occurring abundantly on the lake shores of the Barro Colorado National Monument (BCNM) in Panama. Although *A. glabra* does not have the stature of an emergent rainforest tree, its crown microclimate is similar to the conditions in the upper strata of the forest due to its openness and exposure to sun and wind along the lake shore (Zotz et al. 1999). Many individual trees are dominated by only one epiphyte species (Zotz et al. 1999). Thus, tree crowns bearing distinct plant communities can be easily classified and the arthropod fauna compared among them. *Annona glabra* is inundated up to its lower stem portions during the rainy season and during most of the dry season. Access of terrestrial arthropods is therefore impeded, leaving primarily the arboreal species.

Arthropods are being sampled continuously with different trap types throughout one year. This enables us to assess seasonal fluctuations in species composition and relative abundance of the arboreal fauna. Below, we will describe the study system, the trapping techniques, and our approach toward describing arthropod diversity. The presented preliminary data on trap yields provide a first insight into the composition of the arthropod fauna.

Study System and Methods

Study Site

The investigations are being conducted in the BCNM (9°10′N, 79°51′W) in the Republic of Panama. Focal trees are located along mainland peninsulas of Lake Gatún. The vegetation of this biological reserve has been classified as 'tropical moist forest' (Holdridge et al. 1971). The area receives approximately 2600 mm of annual precipitation with a pronounced dry season from late December to April. Detailed descriptions of climate, vegetation, and ecology are reported by Croat (1978), Leigh et al. (1982), and Windsor (1990).

Study System

Our aim was to investigate the role of vascular epiphytes as structuring elements in forest canopies. Taking advantage of the natural differences in epiphyte colonization of *Annona glabra*, we defined four categories of host trees with distinct epiphyte assemblages. Each category except the control group is dominated by a particular species of epiphyte, thus providing a different set of structural features according to its architecture:

N—Trees free of epiphytes as a **control group.** In these trees, the composition of the arthropod fauna will not be influenced by epiphytes, but rather by the structure of the host tree itself and its trophic relations with herbivores.

V—Trees dominated by ***Vriesea sanguinolenta*** Cogn. & Marchal. This is a large bromeliad with broad leaves to one meter long. It can store more than two liters of rainwater in its tank and impound considerable amounts of leaf litter. Organic matter decomposes between the basal portions of the leaves, thus creating soil-like microsites.

T—Trees dominated by ***Tillandsia fasciculata*** Sw. var. *fasciculata.* This much smaller bromeliad with dense rosettes of numerous, lanceolate, somewhat stiff leaves of a maximum length of 40 cm, impounds only small amounts of water and less debris but provides a finer-grained spatial partitioning of the habitat than *Vriesea sanguinolenta.*

D—Trees dominated by the orchid ***Dimerandra emarginata*** (G. Meyer) Hoehne. This epiphyte has a rather simple structure, consisting of a cluster of erect, slender stems to 45 cm in height and bears linear leaves. *Dimerandra emarginata* does not impound leaf litter or water.

We selected seven trees of each category at different sites on peninsulas within BCNM, except for trees dominated by *Tillandsia,* of which we could find only four individuals. We chose sites where all four categories are present in close vicinity to account for spatial heterogeneity across different locations. The trees selected had no crown contact with neighboring trees and were cleared of vines where necessary.

Trapping Program

To sample arthropods continuously over an entire year, we designed a setup of traps that

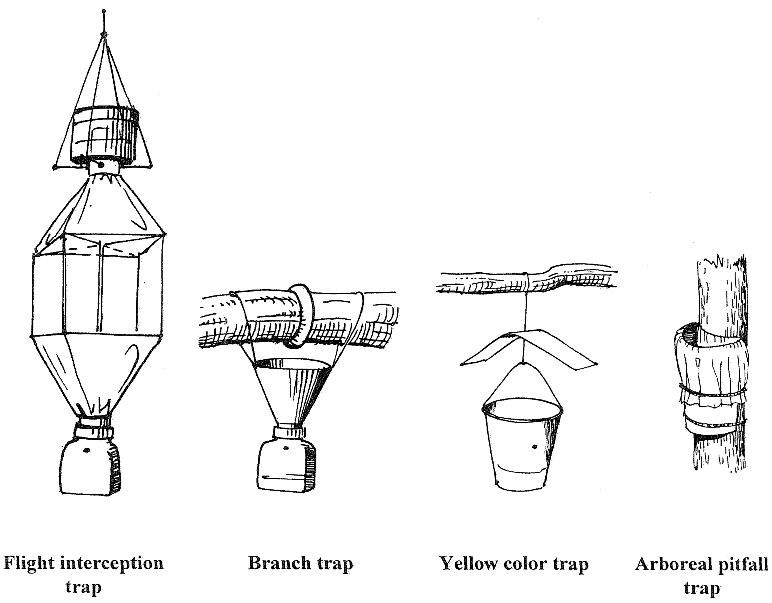

FIGURE 1. Illustration of the four trap types used. The center part of the flight interception traps consists of a cross-panel of clear plexiglass, the funnels above and beneath the windows are of darker plastic sheeting, each leading to a collecting jar. Trap size is only 30 × 80 cm, corresponding to our rather small tree crowns. The branch trap was described by Koponen et al. (1997). We use a yellow sand-bucket as yellow trap (diameter 15 cm), provided with an aluminum roof. For the arboreal pitfall trap, we cut a PVC tube half to support a plastic bag, which fits tightly against the stem (diameter ca. 8 cm).

would remain in selected tree crowns, with minimal maintenance. Four different trap types were used to sample the arboreal arthropod fauna (FIGURE 1). Flying insects and ballooning spiders are caught by composite flight-interception traps (two per tree) and yellow color traps (one per tree). Bark-dwellers are captured by branch eclectors (two per tree) and arboreal pitfall traps (one per tree). A 1% copper sulfate solution is used as a killing and preservation liquid. It kills arthropods quickly and prevents destruction of sampled animals by fungi. Traps are emptied every two weeks and arthropods transferred into 70% ethanol.

Assessing Arthropod Diversity

All arthropods are being quantified and identified to the ordinal level with the help of trained assistants. For a detailed inventory, we focus on three groups: Araneae, Formicidae (Hymenoptera), and Coleoptera. For the following evaluation, only two trapping periods are considered, and only spiders and ants of one trapping period were assigned to morphospecies.

We chose these taxa for methodological as well as ecological reasons. First, reliable identification keys are available at least for families and genera. Second, many morphological characteristics facilitate assignment to morphospecies. Third, each of the three groups either covers important ecological guilds in the canopy or is especially appropriate for our purposes:

1. Spiders (Araneae). Spiders are responsive to structural characteristics of the habitat they live in (Greenstone 1984, Gunnarson 1990, Gunnarson 1992, Hatley and MacMahon 1980, Robinson 1981). Furthermore, they are considered to be important arboreal invertebrate predators (Pfeiffer 1996) and might therefore strongly affect the composition of the entire arthropod faunas of tree crowns.
2. Ants (Formicidae, Hymenoptera). Ants are one of the most abundant insect taxa in tropical tree crowns (e.g., Adis et al. 1997, Brühl et al. 1998, Floren and Linsenmair 1997, Stork 1991). Similar to spiders, they are of major importance in determining the structure of arboreal arthropod communities by exerting a constant, high predation pressure (Floren and Linsenmair 1997, Stork 1987b). Finally, ants are often directly associated with epiphytes (Davidson and Epstein 1989, Dejean et al. 1992, Fisher and Zimmerman 1988).
3. Beetles (Coleoptera). Beetles are one of the most species-rich insect taxa in forest cano-

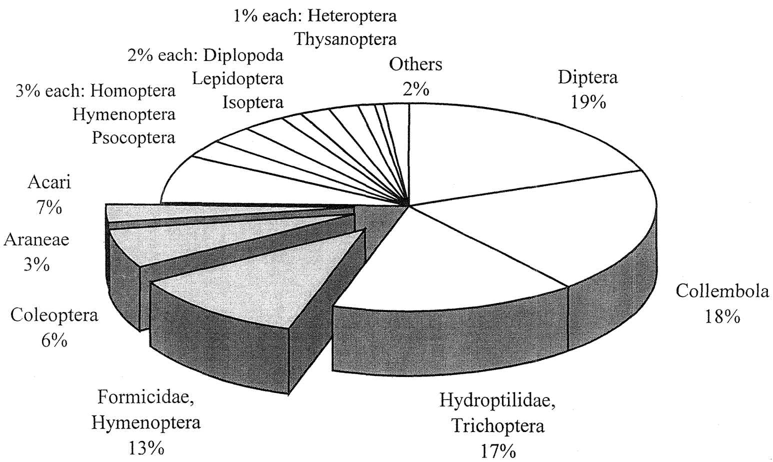

FIGURE 2. Composition of the fauna. Data are from two capture periods during early rainy season 1998. All traps combined yielded 36,875 individuals. "Hymenoptera" refers to Hymenoptera other than ants. "Others" include orders that contributed less than 1% to the total fauna (Odonata, Orthoptera, Blattodea, Embioptera, Neuroptera, Chilopoda, Scorpiones, Pseucoscorpiones, Isopoda, Trichoptera other than Hydroptilidae, Ephemeroptera, Dermaptera, Strepsiptera).

pies and cover all-important feeding guilds. Their taxonomic and ecological diversity makes beetles an especially good focal group.

Specimens of these three taxa are identified to family (beetles, some spiders) or genus level (ants, most spiders) and are sorted to morphospecies based on external morphology. Vouchers are deposited at the Smithsonian Tropical Research Institute, Panama, at the University of Panama, and at the University of Würzburg, Germany.

INITIAL RESULTS

Faunal Composition

A total of 36,875 arthropods belonging to 25 different orders were caught in the first two capture periods during April and May 1998, at the onset of the rainy season (FIGURE 2). The most abundant taxa were springtails (Collembola), flies (Diptera), ants (Formicidae, Hymenoptera) and caddisflies (Trichoptera), each representing 13–19% of the total number of individuals. The latter group was represented by a few species of the genus *Oxyethira* (Hydroptilidae, Microcaddisflies), that probably breed in the Lake Gatún (O. Flint pers. comm.). Especially abundant were two species, *O. circaverna* Kelley and *O. maya* Denning. The three focal taxa, spiders, ants, and beetles together constituted approximately one fifth of the total arthropod collection.

Trap Yields

The distribution of taxa among trap types was clearly heterogeneous (TABLE 1). This is expected from the diverse ways arthropods move about and the many microsites they occupy in tree crowns. TABLE 1 also shows that branch traps not only captured arthropods foraging on branches, but also flying insects. Similarly, flight traps collected not only flying insects, but also many unwinged arthropods. The highest overall yield was attained by the flight interception traps. Each of them caught an average number of 77.1 individuals in a two-week trapping period.

The orders that were mainly caught by flight interception traps were beetles, psocids (Psocoptera), microcaddisflies (Hydroptilidae, Trichoptera) and, somewhat unexpected, spiders. Many of the captured spiders were clearly too large to balloon (i.e., drift by their silk strand). Ants were also well represented in flight traps due to the preponderance of winged reproductives. To date, only ants of the worker caste could be identified properly, due to the lack of reliable keys for reproductives. Thus, the ant fraction in the flight interception traps is of limited utility when investigating species richness. However, these specimens may provide valuable information on seasonal patterns of flight activity of reproductive ants and colonization dynamics. Workers were trapped abundantly in branch traps, together with very high numbers of springtails (Collembola) and mites (Acari). Dip-

TABLE 1. Trap yields. Data are average numbers of individuals per trap per two weeks computed after the first two trapping periods. Arthropods were collected with 50 flight interception traps, 50 branch traps, 25 yellow color traps, and 25 pitfall traps. Numbers in bold indicate the trap type which sampled the largest proportion of specimens within each taxon. The large amount of ants in arboreal pitfall traps is due to two incidents when hundreds of workers of the same species were caught (see text).

Taxon	Flight interception trap	Branch trap	Yellow color trap	Arboreal pitfall trap
Araneae	**3.2**	1.0	1.1	0.9
Coleoptera	**6.3**	3.8	2.3	1.5
Formicidae	4.7	12.7	2.0	**37.8**
Diptera	16.7	6.9	**23.5**	9.0
Hydroptilidae, Trichoptera	**18.4**	5.5	12.7	4.9
Homoptera	2.1	2.1	**2.7**	0.7
Psocoptera	**3.5**	1.6	0.6	0.9
Hymenoptera (excl. Ants)	1.2	1.6	**4.3**	1.1
Collembola	10.5	**18.6**	4.0	18.0
Acari	3.8	**8.2**	2.1	0.8
Others*	**6.7**	5.0	3.4	1.4
Total	**77.1**	67.1	58.9	76.9

* Heteroptera, Isoptera, Thysanoptera, Diplopoda, Chilopoda, Lepidoptera, Odonata, Orthoptera, Blattodea, Embioptera, Neuroptera, Isopoda, Trichoptera other than Hydroptilidae, Scorpiones, Pseucoscorpiones, Ephemeroptera, Strepsiptera.

tera, Hymenoptera other than ants, and Homoptera were mainly caught in yellow color traps. The high average number of ants collected in arboreal pitfall traps was due to two traps inadvertently positioned close to *Azteca* trails, one capturing 580 workers of a single morphospecies, and the other 132 workers of the same species. After realizing that the captured ants overlap extensively with the species caught with branch traps, and that for most other orders except springtails the pitfall traps have the lowest yields of any trap type, we omitted arboreal pitfall traps from the array. We now collect arthropods only with flight interception, yellow color, and branch traps.

Species Composition—A First Look

Thus far, ants and spiders of one capture period have been separated to morphospecies. Clearly, this small sample of the entire fauna does not enable us to draw any valid conclusions, but represents a first glimpse at our study system (TABLE 2).

Spiders (Araneae)

The first two weeks of trapping in mid April 1998 yielded 303 spiders in 18 families, of which 220 were adults. The adult spiders were assigned to 69 morphospecies, whereas the remaining 83 immature were identified only to family level (except for later instars, where the genus could also be determined). Numbers of individuals caught per species were quite balanced, with no species clearly dominating the spider fauna; even the most common spider, *Cheiracanthium 1* (Clubionidae), was recorded with 10 individuals only. Forty morphospecies (58% of all spider species) were singletons. On average, 5.7 morphospecies of adult spiders

TABLE 2. Morphospecies composition in spiders and ants. Specimens were collected during one capture period of two weeks with 150 traps in 25 trees. Workers and winged reproductive ants are not summed up to an "ant total," because at this point we are unable to estimate the overlap between these castes. Similarly, there is very likely a certain overlap between juvenile and adult spider morphotypes.

	Spiders (Araneae)		Ants (Formicidae, Hymenoptera)	
	Adults	Juveniles	Workers	Reproductives
Species per tree (mean ± SD)	5.7 ± 2.9	2.5 ± 1.6	7.3 ± 3.0	4.2 ± 2.0
Range	0–13	0–6	2–14	1–9
Total number of morphospecies	69	14	34	35
Total number of individuals	220	83	1485	215

were collected per individual tree. The variation among trees was considerable, ranging from zero to 13 morphospecies per host tree (TABLE 2).

The most numerous families were Salticidae (51 individuals of adult spiders), Ctenidae (29), Clubionidae (21), Araneidae (13), and Corinnidae (10). In terms of species richness, jumping spiders (Salticidae) outnumbered the other families by far: 24 morphospecies of adult spiders could be determined. The second most diverse family was Araneidae (nine morphospecies); Gnaphosidae followed with seven morphospecies, Corinnidae with six, and Clubionidae and Ctenidae with five each.

Ants (Formicidae, Hymenoptera)

During the same, two-week trapping period, 1700 ants were collected (TABLE 2). Most of them (1485 individuals: 87%) were of the worker caste and could be identified to genus. Winged specimens (215 individuals) were morphotyped as well, but could not always be linked to the respective workers. In agreement with previous studies, alpha diversity in Formicidae is rather low compared to other arthropod taxa (e.g., Coleoptera) and does not correspond to their great abundance in most tropical sites (Floren and Linsenmair 1997, Stork 1991). Thirty-four morphospecies of workers belonging to 18 different genera were identified. The most diverse and numerous subfamily was Myrmicinae, accounting for 18 morphospecies and 601 individuals, followed by Dolichoderinae with 7 morphospecies and 534 individuals. The most abundant morphospecies belonged to the latter subfamily as well: one single *Azteca* morphospecies was collected with 319 individuals. Seven morphospecies were singletons (21% of all morphospecies), and another seven were represented by more than 50 individuals. In the genus *Pheidole* we counted a maximum of six morphospecies. Four morphospecies each belonged to the genera *Azteca* and *Camponotus,* while ten genera were represented by a single morphospecies. No morphospecies was clearly numerically dominant in the trees studied. Per single host tree, we trapped a mean of, respectively, 7.3 (worker caste) and 4.2 (reproductives) ant morphospecies (TABLE 2).

DISCUSSION

Faunal Composition

Comparison of the faunal assemblages in our samples is somewhat problematic because we are not aware of any study where arthropod communities have been collected by similar trapping techniques in the tropics. Most comprehensive arthropod surveys have been done by insecticide fogging (Adis et al. 1997, Floren and Linsenmair 1997, Stork 1991, Wagner 1997), which samples a slightly different part of the spectrum of canopy-dwelling arthropods (Basset et al. 1997).

However, the overall composition of the arthropod fauna in our samples matched the general trends found in previous surveys. One apparent difference, however, was the proportion of the Formicidae. These were rather rare in our samples (i.e., 13%, FIGURE 2), compared to 18.2% (Stork 1991), 36–49% (Wagner 1997); 45% (Adis et al. 1997), or 58% reported by Floren and Linsenmair (1997). On the other hand, Collembola and Trichoptera were present in much higher numbers. Collembola were found in large numbers in the branch traps (TABLE 1), whereas insecticide knockdown techniques tend to underestimate springtails. Perhaps more striking is the high abundance of microcaddisflies (Trichoptera, Hydroptilidae), that contributed fully 17% to the arthropod community in our study system. The proportion of Trichoptera in most canopy fogging studies was low enough to only mention them under "other arthropods" (Floren and Linsenmair 1997, Stork 1991, Wagner 1997), or not at all (Adis et al. 1997). Abundant Trichoptera are probably a peculiarity of the locations of the focal trees: our trap sites were along the shore of Lake Gatún, whereas the mentioned fogging surveys were carried out within rainforests. As the majority of caddisfly larvae are aquatic, and most adults are weak fliers, they are restricted to areas with nearby aquatic habitats. The abundant species *Oxyethira circaverna* and *O. maya* also dominated the caddisfly fractions in light trap samples on Barro Colorado Island (O. Flint pers. comm.). Lake Gatún apparently represents a very suitable habitat for these two species.

Trapping Techniques

Sampling arthropods with appropriate traps allows long-term, comparatively non-destructive assessment of representative portions of the arboreal community. To collect a comprehensive assemblage of arthropods with different activity patterns in time and space within a study area, a variety of sampling methods as well as both spatial and seasonal replicates are necessary (Basset et al. 1997). Long-term investigations conducted in BCNM revealed a very pronounced seasonality for several insect groups (Barrios 1997, Erwin and Scott 1980, Smythe 1882, Wolda 1982) and for spiders (Nentwig 1983). Considering this, continuous trapping is likely to more closely approximate actual species diversity than taking discrete spot samples (e.g., insecticide knockdown techniques). In a comparative study, Basset et al. (1997) collected about twice as many species of leaf-feeding beetles by sampling for several months with flight interception traps than they did in one fogging event.

However, the results of a study where arthropods are obtained by trapping will always be dependent on the setup. TABLE 1 displays the selectivity of different trap types. Using one kind of trap exclusively would bias the results toward certain taxa. For example, estimates of faunal composition obtained by sampling with flight interception traps only would have considerably underestimated the contribution of Formicidae to the total arthropod assemblage in our trees in terms of both abundance and species richness. A combination of various trap types is likely to reduce the capture bias and allows sampling of a broader spectrum of the canopy fauna.

Choosing a Feasible Identification and Model System

Monitoring arthropod diversity in a tropical rainforest is an extremely time- and money-consuming endeavor and is hindered by the existence of many millions of yet undiscovered and undescribed species (Erwin 1983, 1995, Wilson 1990). However, it may not be imperative to determine species to reveal diversity patterns. Oliver and Beattie (1996) showed that the outcome of a comparative invertebrate survey was affected very little, regardless of whether animals were identified to species level by specialists or sorted to morphospecies without the use of any keys (Didham et al. 1998, Erwin 1995).

Given the complexity of tropical forest canopies, another crucial factor for designing a comprehensive arthropod survey is the selection of an appropriate model system. We chose a single, rather small host tree species with dense, distinct epiphyte assemblages. These form suitable units for a comparison between tree crowns with different traits related to their epiphyte load, for example structural heterogeneity, resources available for herbivores, or microclimatic conditions.

OUTLOOK

Though fieldwork is still in progress, we believe the chosen methodology will yield sufficient numbers of arthropods to help find answers to the questions posed. The one-year survey should provide a basis for the investigation into diversity patterns among trees and epiphytes. In addition, measurements of microclimatic parameters and other host tree traits, studies on subsystems (e.g., the bromeliad-inhabiting fauna), and experimental manipulation of the trees and their epiphyte loads might lead us to a greater understanding of the communities we are studying. We hope this will eventually help us to answer the question about how the presence of epiphytes contributes to the establishment and maintenance of high arthropod diversity in tropical forest canopies.

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