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Arthropods in epiphytes: a diversity component that is not effectively sampled by canopy fogging

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Abstract. Insecticide fogging is often used to document arthropod species richness in forest canopies, but this technique may not effectively sample invertebrates that are concealed within a variety of microhabitats. We quantified the effects of fogging on invertebrates in canopy epiphyte mats of a Costa Rican cloud forest by extracting arthropods from 18 paired pre- and post-fogging samples. Mean abundance and morphospecies richness of living arthropods were respectively reduced by 33 and 30% in epiphyte material after fogging, but most organisms survived the treatment. Relative abundances of major taxa were unaffected by fogging. Herbivores were less abundant after fogging than other trophic groups, and the median body length of non-mite arthropods present in epiphytes was significantly smaller after fogging. Examination of seven post-fogging samples showed that many arthropods killed by insecticide remained trapped within the epiphyte material. These results provide the first quantitative assessment of a specific component of arboreal arthropod biodiversity that is missed by the fogging technique.

Introduction

Fogging tree crowns with pyrethrin insecticide (e.g., Erwin and Scott 1980; Erwin 1983) is a popular method for collecting arthropods from forest canopies around the world (Stork et al. 1997). This technique is relatively efficient, generating a large survey of arboreal macroarthropods with minimal time expenditure (Erwin 1995; Stork et al. 1997). However, tree crowns, especially in tropical forests, include a variety of microarthropods (e.g., Acarina, Collembola) and microhabitats (e.g., bark crevices, tree holes, epiphytes, humus pockets) that may not be effectively sampled by fogging (Adis et al. 1984; Stork and Hammond 1997; Walter and Behan-Pelletier 1999). To our knowledge, no studies have quantified the fraction of arthropod diversity missed by fogging or the effects of fogging on the arthropods in specific arboreal microhabitats.

Epiphytes are a major microhabitat component of neotropical forest canopies, accounting for >33% of the plant species, >5% of the total vegetative biomass, and >50% of the nutrient capital in some locations (Gentry and Dodson 1987; Coxson and Nadkarni 1995; Rodgers and Kitching 1998; Nadkarni et al. 2000). In the

montane forests of Costa Rica, for example, bryophytes (mostly liverworts and mosses) and small ferns form a dense covering of low-stature vegetation on the woody portions of trees (e.g., Clark et al. 1998; Gradstein 2000). In old or 'primary' forests of this region, centuries of vegetative growth and concomitant accumulation of dead organic matter have resulted in development of thick carpet-like epiphyte mats on the upper surfaces of branches (Nadkarni 1981; Vance and Nadkarni 1990; Clark and Nadkarni 2000). Epiphytes are also typically diverse and abundant on relatively young trees in secondary forests (Nadkarni and Wheelwright 2000), but mats are generally much thinner in this setting.

Regardless of age and mat thickness, the vegetative portions of non-vascular epiphytes tend to contain a large variety of very small arthropods, especially mites (Acarina, mostly Oribatida) and Collembola (Walter and Behan-Pelletier 1999; Winchester et al. 1999; Yanoviak and Nadkarni 2001). Prior studies on this system showed that primary forest epiphyte mats support more arthropod morphospecies than secondary forest mats (Yanoviak and Nadkarni 2001). These invertebrates often occur in fogging samples (Walter and Behan-Pelletier 1999), but most are concealed within the epiphyte mat vegetation and are likely to be missed by insecticide fog. Similarly, the diverse arthropod assemblages within the litter and humic material associated with epiphytes (e.g., Nadkarni and Longino 1990; Rodgers and Kitching 1998) are probably missed by fogging.

No published studies have specifically examined the microdistribution of arthropods in non-vascular epiphytes. However, Usher and Booth (1984) showed that arthropod distributions vary predictably within turf mosses, which are superficially similar to mat-forming epiphytes. It is probable that some taxa and trophic groups (e.g., herbivorous beetles) are more abundant in the upper vegetative layers of epiphyte mats, whereas others (e.g., saprophytic mites) are more common in the underlying dead organic material. Thus, effects of fogging could differ among major taxa or trophic groups.

Body size distribution within an assemblage may also influence the composition of arthropod samples obtained by fogging. The small size of most arthropods living inside epiphyte mats makes them unlikely to appear in fogging knock-down samples, because the majority of dead individuals probably remain trapped within the mats. Moreover, some arthropods (especially microarthropods) that fall from the epiphytes may drift out of the collection zone (Floren and Linsenmair 2000). Several studies have quantified body size patterns in ecological surveys of canopy arthropods (e.g., Basset 1997), but none has examined the differential efficacy of fogging based on arthropod body size.

We designed this study to quantify the effects of insecticide fogging on arthropod assemblages living in epiphyte mats in a Costa Rican montane forest. We tested the null hypothesis that fogging would have no effect on characteristics of arthropod assemblages in epiphyte mats. Based on the alternative hypothesis of a measurable fogging effect, we predicted that: (1) fogging would significantly reduce arthropod species richness and abundance in epiphyte mats; (2) effects of fogging would differ between primary and secondary forest types; (3) major arthropod taxa or trophic groups would not be equally affected by fogging; (4) larger arthropods would be

more susceptible to fogging; and (5) most arthropods in epiphyte mats would die *in situ* instead of falling into fogging knock-down funnels. We tested these predictions by extracting, counting, and measuring arthropods from epiphyte mat samples collected before and after fogging selected tree crowns in primary and secondary forests.

Methods

This study was conducted in the Monteverde Cloud Forest Preserve (MCFP), Cordillera de Tilarán, Costa Rica (10°20′ N, 84°45′ W). The research forest at the MCFP falls within the lower montane wet forest life zone (Haber 2000). It is located on the Pacific slope of the Continental Divide at ca. 1500 m elevation and receives an average of 2500 mm of seasonal rainfall per year. The region also receives substantial (>1000 mm) precipitation in the form of cloud moisture wind-driven mist (see Nadkarni and Wheelwright (2000) for additional site details).

We fogged five trees with insecticide in primary forest and five trees in secondary forest at the MCFP between 15 and 20 May 2001 as part of a larger project (J. Gering, N. Nadkarni, and S. Yanoviak, unpublished data). To our knowledge, this study is the first attempt at fogging trees in a neotropical cloud forest. The crown of each tree was fogged for 3 min with a 1% pyrethrin formulation (Pyrethrins Fogging Concentrate 1-2-3, Summit Chemical Co., Baltimore, Maryland). Insecticide was dispersed using a portable fogger (Curtis Dyna-Fog, Ltd.; model 2610E, Series 3) set on a formulation flow rate of ca. 29 l/h and 25 μm particle size (dial position '5'; cf. Erwin 1983).

The fogger was equipped with a radio-controlled trigger and a guide rope attached to the exhaust nozzle, and was suspended from a pulley over a high branch following techniques described in more detail elsewhere (Erwin 1983; Stork and Hammond 1997; Gering and Crist 2000). Dispersal of insecticide throughout each tree crown was accomplished by rotating the fogger through a circular arc. Ten 1.0 m^2 circular collection funnels, each fitted with a plastic jar containing 70% ethanol, were placed in the understory beneath each tree before fogging (see Stork and Hammond (1997) for photos of the same equipment as used in this study). All fogging was conducted between 7.00 and 10.00 A.M, followed by a 2 h arthropod drop time.

Three small patches of mat-forming epiphytes (each patch ca. 5 × 5 cm and 100–200 ml volume) were collected from the crown of each of three focal trees in each forest type <20 h before fogging (n = 18; 3 epiphyte samples × 3 trees × 2 forest types). These pre-fogging samples were representative of the diversity of mat-forming epiphyte morphologies present in each tree. Samples were taken from branches and branch sections that were most likely to receive a substantial application of insecticide based on the location of fogger guide ropes. To standardize samples as much as possible, collections from both forests were restricted to smaller branches (<20 cm diameter) with epiphyte mats <3 cm in total thickness. An additional three epiphyte patches were collected from the crown of each tree 2–3 h

after fogging (n = 18 epiphyte samples). Each post-fogging sample was taken from the same region of the same epiphyte mat as the pre-fogging sample, so that pre- and post-fogging samples could be treated as pairs for analysis.

Secondary forest epiphyte samples were collected from three *Conostegia oerstediana* O. Berg ex Triana (Melastomataceae). This species comprises 95% of the stems in secondary forests in the region (N. Nadkarni, unpublished data). Primary forest samples were collected from two *Ocotea tonduzii* Standl. (Lauraceae) and one *Pouteria fossicola* Cronquist (Sapotaceae); both species are common in the MCFP (Nadkarni et al. 1995; Haber et al. 1996). Tree crowns were accessed using the single-line climbing technique (Perry 1978).

Arthropods were extracted from epiphytes in the laboratory using a series of Tullgren funnels (60 W incandescent bulb, 17 cm funnel diameter, 12–18 h). Extracted specimens were examined under a stereoscope (10–40× magnification), sorted to morphospecies within higher taxa (Oliver and Beattie 1996), counted, and stored in 70% ethanol for future study. Voucher specimens are currently being examined by taxonomists. A reference collection was deposited at the MCFP laboratory. Following arthropod extraction, epiphyte samples were dried at 60 °C for 24 h and weighed to the nearest 0.001 g on a Fisher® 7301A balance.

After they were processed in funnels and dried, seven post-fogging epiphyte samples were examined under the stereoscope to quantify the fraction of arthropods that had died *in situ*. Arthropods found in these samples were added to the original data gathered from Tullgren funnel extraction. The augmented post-fogging data were compared to their companion pre-fogging data to determine if differences before and after fogging could be accounted for by arthropods trapped dead in the epiphyte material. Due to time constraints, we did not similarly search the pre-fogging samples for dead arthropods. However, we previously examined collections of epiphyte material following Tullgren extraction for other studies of this system (Yanoviak and Nadkarni 2001). In all cases, the abundance of arthropods that died within the sample (i.e., during the extraction process) was $\ll$1% of total arthropod abundance.

Body size differences were assessed by measuring all arthropods in nine randomly selected pre-fogging samples and their post-fogging pairs under a stereoscope fitted with a reticle. We used total body length (measured to the nearest 0.05 mm on the longest body axis, excluding appendages) as an estimate of overall body size for each individual. The median body size in each sample was used for analyses. We also counted the number of non-mite herbivores, predators, and omnivores (including scavengers and saprophages) in these samples to determine effects of fogging on different trophic levels. Trophic assignments were based on information in general texts such as Borror et al. (1989).

Except where noted in Results, arthropod assemblage variables and median body size were compared between pre- and post-fogging samples using paired t-tests. We similarly analyzed differences in sample mass, because the abundance and diversity of arthropods in bryophytes and associated dead organic matter are often correlated to the quantity of material collected (e.g., Booth and Usher 1984). All data were tested for normality using Kolmogorov–Smirnov tests applied to ungrouped data

(Sokal and Rohlf 1995; SAS Institute 1999). Proportions were arcsine square root-transformed, and abundance and body size values were log-transformed before analysis to correct variance heterogeneity and improve normality (Sokal and Rohlf 1995). Means given in the Results are from untransformed data.

Results

In all, 1334 arthropods were extracted from the epiphyte samples. Mites (Acarina), springtails (Collembola), beetles (Coleoptera), and ants (Hymenoptera: Formicidae) together comprised 95% of the entire collection (Figure 1). The remaining 5% ('Others' in Figure 1) included thrips (Thysanoptera), scale insects (Homoptera), moth larvae (Lepidoptera), barklice (Psocoptera), parasitoid wasps (Hymenoptera: Chalcidoidea), and spiders (Araneae). These results are consistent with other studies of this system (Yanoviak and Nadkarni 2001).

The different forest types and trees (nested within forest type for analyses) did not influence morphospecies richness in pre-fogging or post-fogging samples (nested ANOVAs; forest type: $F_{1,12} < 1.33$, $P > 0.27$; trees: $F_{4,12} < 1.43$, $P > 0.28$ in both tests). Similar results, although marginal, were obtained for arthropod abundance ($F_{1,12} < 3.63$, $P > 0.08$; trees: $F_{4,12} < 3.13$, $P > 0.056$). Thus, we excluded 'tree' and 'forest type' variables from subsequent analyses and focused on overall pre- and post-fogging differences.

The average dry mass of epiphyte samples collected before (1.99 g $\pm$ 0.15 SE) and after fogging (1.88 $\pm$ 0.15 g) did not differ ($t = 0.46$, df = 17, $P = 0.65$), but arthropod abundance and morphospecies richness were significantly lower in epiphytic bryophytes after fogging ($t > 3.07$, df = 17, $P < 0.007$ in both tests; Figure 2). Despite these differences in absolute numbers of individuals and morphospecies, the mean relative abundance of each of the four major taxonomic

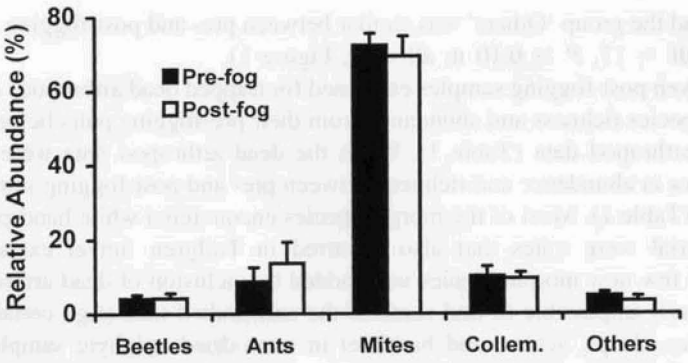

Figure 1. Mean relative abundance (%) of major taxonomic groups of arthropods found in epiphyte samples before and after fogging. Bars represent + 1 SE. $n = 18$ for each mean. 'Collem' = Collembola. Means do not differ within groups ($P > 0.10$ in all cases).

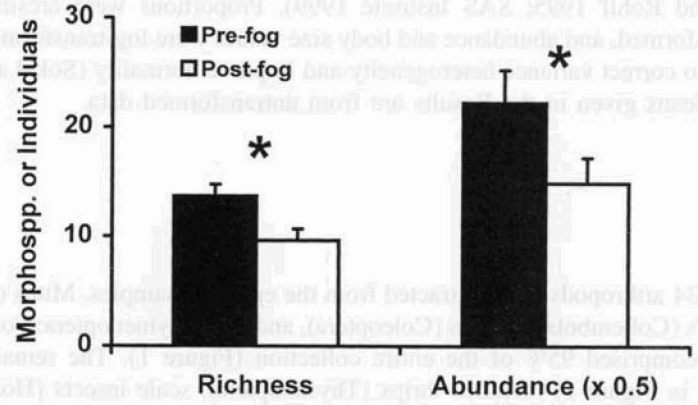

Figure 2. Mean morphospecies richness and abundance in epiphyte samples collected before (pre-fog) and after fogging (post-fog). Bars represent + 1 SE. $n = 18$ for each mean. $^*P < 0.05$ abundance results were divided by two for scaling.

Table 1. Mean (±SE) arthropod abundance and morphospecies richness in seven pairs of pre- and post-fogging epiphyte samples.

Variable	Pre-fog	Post-fog	t_{obs}
Extract abundance	39.9 ± 4.32	26.6 ± 5.60	3.06*
Extract richness	14.1 ± 1.96	10.3 ± 2.10	3.15*
Manual abundance	n/a	17.0 ± 3.74	n/a
Manual richness	n/a	5.4 ± 0.48	n/a
Final abundance	39.9 ± 4.32	43.4 ± 8.14	0.04
Final richness	14.1 ± 1.96	11.4 ± 2.10	2.28

Extract = data obtained by Tullgren funnel extraction of live arthropods. Manual = data obtained by examination of dry post-fogging epiphyte samples after funnel extraction. Final = result obtained by adding manual data to extraction data for post-fogging samples. Morphospecies overlap between extraction and manual data sets was corrected before analysis. $^*P < 0.025$ (Bonferroni-adjusted $\alpha = 0.025$).

groups and the group 'Others' was similar between pre- and post-fogging samples ($t < 1.73$, df = 17, $P > 0.10$ in all tests; Figure 1).

The seven post-fogging samples examined for trapped dead arthropods differed in morphospecies richness and abundance from their pre-fogging pairs before addition of dead arthropod data (Table 1). When the dead arthropod data were included, differences in abundance and richness between pre- and post-fogging samples were nullified (Table 1). Most of the morphospecies encountered while hand-picking the dry material were mites that also occurred in Tullgren funnel extractions, so relatively few new morphospecies were added by inclusion of dead arthropod data. It was nearly impossible to find some of the soft-bodied taxa (e.g., certain collembola, mites, thrips, scales, and barklice) in oven-dried epiphyte samples, so the number of trapped morphospecies was undoubtedly larger than the number found. Although we did not similarly examine pre-fogging samples after they were processed, adding a conservative 5% to raw abundance and richness data before

comparison with the augmented post-fogging data did not change the statistical outcome.

The nine pairs of samples used to generate body size data collectively contained 732 arthropods, or 55% of the total collection. Frequency distributions of body length were strongly right-skewed (Figure 3A) for both pre- and post-fogging data sets, due to the great abundance of small individuals (primarily mites) in all samples. Removal of mites improved normality in the distribution (Figure 3B). The average median body length of arthropods in pre-fogging samples (0.34 mm $\pm$ 0.014 SE) did not differ from their companion post-fogging samples (0.35 $\pm$ 0.015 mm) when all morphospecies were included ($t = 0.13$, df = 8, $P = 0.90$). However, a second test with mites removed from the data set showed that the average median body length of arthropods was significantly smaller after fogging (0.87 $\pm$ 0.101 mm) than before fogging (1.38 $\pm$ 0.136 mm; $t = 3.48$, df = 8, $P = 0.008$; Bonferroni $\alpha = 0.025$). The average number of non-mite herbivores per sample was marginally greater before (3.9 $\pm$ 0.89) than after (1.7 $\pm$ 0.55) fogging ($t = 2.40$, df = 8, $P = 0.043$), but mean abundances of non-mite predators and omnivores did not differ ($t < 0.84$, df = 8, $P > 0.42$; Figure 4).

Only preliminary sorting of the arthropods collected by fogging has been

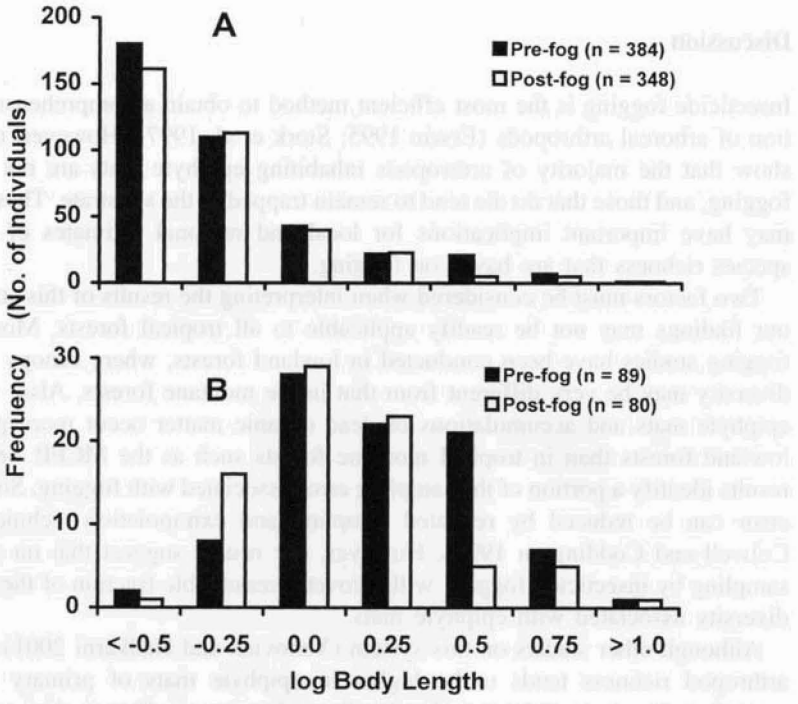

Figure 3. Frequency distributions of log-transformed arthropod body lengths in epiphyte samples collected before (pre-fog) and after fogging (post-fog). (A) All arthropods found in nine paired samples; (B) the same data as in (A) with mites removed.

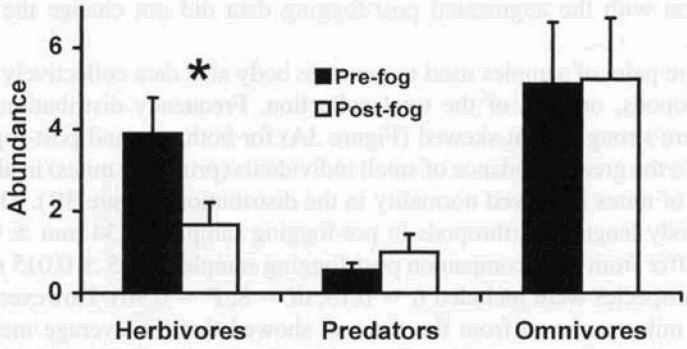

Figure 4. Mean abundance of major trophic groups of arthropods found in epiphyte samples before and after fogging. Bars represent + 1 SE. $n = 9$ for each mean. $^*P < 0.05$.

completed, so we were unable to quantify the occurrence of epiphyte-dwelling arthropods in the knock-down samples. However, mites, the most abundant group in epiphyte extractions, averaged only 7.6 individuals per m^2 (range = 0–46, SD = 8.64) in the 30 knock-down samples sorted to date.

Discussion

Insecticide fogging is the most efficient method to obtain a comprehensive collection of arboreal arthropods (Erwin 1995; Stork et al. 1997). However, our results show that the majority of arthropods inhabiting epiphyte mats are not killed by fogging, and those that do die tend to remain trapped in the substrate. These findings may have important implications for local and regional estimates of arthropod species richness that are based on fogging.

Two factors must be considered when interpreting the results of this study. First, our findings may not be readily applicable to all tropical forests. Most tropical fogging studies have been conducted in lowland forests, where canopy arthropod diversity may be very different from that in the montane forests. Also, very large epiphyte mats and accumulations of dead organic matter occur more patchily in lowland forests than in tropical montane forests such as the MCFP. Second, our results identify a portion of the sampling error associated with fogging. Some of this error can be reduced by repeated sampling and extrapolation techniques (e.g., Colwell and Coddington 1994). However, our results suggest that no amount of sampling by insecticide fogging will recover a reasonable fraction of the arthropod diversity associated with epiphyte mats.

Although other studies on this system (Yanoviak and Nadkarni 2001) show that arthropod richness tends to be higher in epiphyte mats of primary forest vs. secondary forest, we did not find a significant forest type effect in this study. There are differences in gross epiphyte structure (e.g., mat thickness) between primary and secondary forests, but we avoided those differences by standardizing the physical characteristics of the samples as much as possible. Thus, fogging effects appear to

be similar in structurally similar epiphyte mats regardless of forest type. Had we examined a range of epiphyte mat types, we would have predicted decreasing fogging effects with increasing epiphyte mat thickness.

We did not find a differential effect of fogging on relative abundances of major taxonomic groups as predicted. This lack of difference likely resulted from at least two factors. First, it may be an artefact of focusing on relatively broad taxonomic levels (i.e., non-uniform treatment effects among taxa may have occurred at lower taxonomic levels than we examined). Second, arthropods may have homogenized their otherwise stratified abundances and distributions (e.g., by hiding deeper in the mats or escaping by flight) in response to disturbance not directly related to the insecticide, such as vibration created by the fogger. Studies focusing on lower taxonomic levels, and perhaps conducted under laboratory conditions, are needed to better resolve differential effects of fogging among epiphyte-dwelling taxa.

The reduced number of non-mite herbivores in samples after fogging may be the result of stratified distributions of trophic groups. Epiphyte mats can be divided into well-defined vegetative and humic layers, and arthropod assemblages are not randomly distributed between these layers (Yanoviak and Nadkarni 2001). In a structurally and trophically similar terrestrial moss system, Usher and Booth (1984, 1986) found distinct 'green' layer and 'dead' layer arthropod assemblages, and showed that predators were the only randomly distributed trophic group. Although our results for effects of fogging on trophic levels are correlative, they suggest that herbivorous taxa were more likely to be present in the exposed vegetative mat layer, and were therefore more likely to be killed by the insecticide fog.

Differences in the average median body length of non-mite arthropods before and after fogging indicate that smaller arthropods are less susceptible to capture by this collection technique. This may be due to their relatively smaller spiracles, preventing or reducing uptake of the killing agent microdroplets. Also, the inability of larger arthropods to move freely within the epiphyte mat substrates probably forces them to remain at or near the vegetative surface, where they are more likely to encounter airborne insecticide.

In sum, here we provide the first quantitative assessment of the arthropod fauna missed by fogging-based surveys. Our results provide only a general perspective; focused microhabitat experiments and species-level resolution within epiphyte samples and within fogging knock-down samples are needed to determine the fraction of arthropod species richness that is missed. Also, assumptions of host–epiphyte specificity must be outlined and tested before a realistic approximation of the contribution of epiphyte mats to global arthropod diversity can be obtained. Finally, additional work specifically addressing the natural history and taxonomy of superdiverse or understudied groups (e.g., Acarina, Collembola, Thysanoptera) in epiphytes is essential to understanding the ecology of this system.

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