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Arthropod Assemblages in Epiphyte Mats of Costa Rican Cloud Forests

Stephen P. Yanoviak[1,3], **Nalini M. Nadkarni**[1,4], and **Rodrigo Solano J.**[2]

[1]The Evergreen State College, Olympia, Washington 98505, U.S.A.

[2]Monteverde, Santa Elena de Puntarenas, Costa Rica

ABSTRACT

Tropical cloud forests are functionally important ecosystems, but are severely threatened due to deforestation and fragmentation. Epiphyte mats, accumulations of live vegetation and dead organic matter on tree trunks and branches, are a conspicuous component of cloud forests and harbor diverse assemblages of meso- and microarthropods. We compared the morphospecies richness, composition, and abundance of arthropods in epiphyte mats between primary and secondary forests of Monteverde, Costa Rica, and at two nearby replicate sites. Epiphyte mats were thinner and less structurally diverse in secondary forest. We collected *ca* 36,000 micro- and mesoarthropods from epiphyte mats in the 2-yr study. Whereas arthropod morphospecies richness did not differ among forest types, arthropod abundance was significantly higher in secondary forest due to larger numbers of ants, especially *Solenopsis* spp. Arthropod assemblages showed a high degree of taxonomic overlap both within and between primary and secondary forests (Jaccard abundance-based similarity = 0.93–0.96). Although characteristics of the arthropod fauna proved to be similar among sites and between forest types, there was a significant temporal effect: arthropod morphospecies richness in epiphyte mats generally was lower in the dry season (February–May), when many taxa probably became dormant or sought shelter against desiccation in deeper portions of mats.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: abundance; disturbance; tropical cloud forest.

LIKE CRITICAL OR "KEYSTONE" SPECIES IN FOOD WEBS (*e.g.*, Power *et al.* 1996), tropical cloud forests may be considered keystone ecosystems; their functional importance is large relative to their abundance. Among other ecosystem services, cloud forests regulate regional hydrology, influence local and global climate, and harbor diverse endemic biota (*e.g.*, Nadkarni & Wheelwright 2000, Budd *et al.* 2004). However, cloud forests compose only a small fraction of the tropical landscape. The need to understand the effects of anthropogenic disturbance on these systems is becoming urgent as the number and magnitude of threats they face increase (Pounds *et al.* 1999, Lawton *et al.* 2001, Thomas *et al.* 2004). At present, deforestation for agriculture is the most critical and immediate threat to most cloud forests (UNDP *et al.* 2000, Budd *et al.* 2004, Thomas *et al.* 2004).

The secondary forests that develop following deforestation in the tropics generally support different faunal assemblages from the original primary forest. In particular, species richness tends to decline with increasing disturbance on a landscape scale (*e.g.*, Whitmore & Sayer 1992). Whereas this trend is supported by field data for several vertebrate taxa (*e.g.*, Estrada *et al.* 1994, Canaday 1996) and soil microbes (Borneman & Triplett 1997), patterns for arthropods are less clear. Effects of deforestation on arthropods may be taxon- or functional group-specific (Lawton *et al.* 1998) and, whereas local diversity measures may be unchanged, arthropod composition often differs between regenerating forests and relatively undisturbed forests within the same geographic area (Floren & Linsenmair 1999, 2003; Wagner 2000). Identifying large-scale patterns in a diverse and widespread faunal component in forests (*e.g.*, arthropods) can be difficult if not impossible in a short-term field study. Here, we chose to focus on the arthropod fauna of a specific abundant microhabitat—epiphytes—which are very common in Neotropical cloud forests, but poorly studied in terms of their associated fauna.

Independently, arthropods and epiphytes are significant biodiversity components of tropical forest canopies (*e.g.*, Fittkau & Klinge 1973, Erwin 1982, Gentry & Dodson 1987, Nadkarni *et al.* 1995, Nadkarni & Wheelwright 2000, Basset *et al.* 2003). These two biological elements share a link in cloud forests via the presence of epiphyte *mats*—accumulations of living and dead plant material on the upper surfaces of branches (*e.g.*, Clark & Nadkarni 2000, Yanoviak *et al.* 2004)—that harbor a diverse but inconspicuous arthropod fauna. Although often casually called "moss mats," true mosses are a minor component of Neotropical cloud forest epiphyte mats; leafy liverworts and filmy ferns dominate the flora. However, the resident arthropod assemblages of epiphyte mats resemble the fauna of terrestrial mosses and the accompanying humus layer of the soil. Both systems are dominated by mites (Acarina), springtails (Collembola), ants (Hymenoptera: Formicidae), and minute beetles (Coleoptera) (Yanoviak *et al.* 2003b, 2004). Studies of the arthropods inhabiting these and related habitats have been few (Gerson 1982, Nadkarni & Longino 1990, Paoletti *et al.* 1991) but are growing in number and now include data from sites in the Asian and Australian tropics (Rodgers & Kitching 1998, Ellwood *et al.* 2002, Ellwood & Foster 2004).

The principal objective of this project was to determine how arthropod assemblages in epiphyte mats of Neotropical cloud forests differ as a result of historical anthropogenic disturbance, especially deforestation. Specifically, our goal was to compare morphospecies

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[3] Current address: Florida Medical Entomology Laboratory, 200 9th Street SE, Vero Beach, FL 32962, U.S.A.

[4] Corresponding author; e-mail: NadkarnN@evergreen.edu

richness, abundance, and higher taxonomic composition of canopy arthropod assemblages in epiphyte mats between primary and secondary forests in a Costa Rican montane forest setting. Secondary forests of the region are structurally less complex (in qualitative terms and in terms of precipitation storage capacity; Clark *et al.* 2000) and have epiphyte mats that are thinner and support lower floristic diversity (S. Y. & N. N., pers. obs.). Given the assumption that arthropod diversity is partly linked to structural and species diversity in the vegetative portion of epiphyte mats, we expected to find significantly lower arthropod abundance and morphospecies richness in mats of secondary versus primary forests.

METHODS

The majority of the field and lab work for this project was conducted in the research forest and facilities at the Monteverde Cloud Forest Preserve (MCFP), Cordillera de Tilarán, Costa Rica (10°20′ N, 84°45′ W). Fieldwork was also conducted at two additional cloud forest sites, both within 5 km of MCFP: (1) private land owned by Mario Solano adjacent to the Santa Elena Cloud Forest Reserve (hereafter, "Mario's"); and (2) a biological field station located between the populated areas of Monteverde and Santa Elena (hereafter, "Station"). The three sites are described in detail elsewhere (Yanoviak *et al.* 2003a). Nadkarni and Wheelwright (2000) provide a comprehensive biological and cultural overview of the region.

Individual samples consisted of a small patch of epiphyte mat removed by hand down to the bark layer and standardized by approximate area (max. 10 cm × 10 cm). We used modifications of the single rope technique (Perry 1978) to gain access to treecrowns for collection of canopy–level samples (*i.e.*, secondary forest = *ca* 15 m, primary forest = *ca* 25 m). Each mat fragment was placed in a plastic bag upon collection and transported to the lab for processing within 3 h.

Tullgren funnels were used to extract arthropods from the epiphyte material (60 W incandescent light, 17-cm-diameter funnel). The funnels were timer–controlled to run only during daylight hours to avoid contamination from nocturnal insects attracted to the lights. Total run time for each funnel was 18–30 h, depending on sample moisture content and ambient relative humidity. In all cases, the funnels were run until the sample material was completely dry. Collected arthropods were assigned to morphotypes within higher taxa (Oliver & Beattie 1996).

After arthropod extraction, the residual epiphyte material was dried at 50°C for ≥ 24 h and weighed to the nearest 0.001 g on an electronic balance (Fisher Scientific 7301A, Waltham, MA, U.S.A.). Mat samples from November 1999 were further examined to determine the percent cover of each of six distinct foliage morphologies: cushion, long turf, short turf, spreading (weft), frondose, or pendent, following Gradstein *et al.* (2001) and Malcolm and Malcolm (2000). We also included the percent cover of liverwort thalli, foliose lichens, and "fine erect" plant parts (*e.g.*, short emergent vegetative or reproductive structures not qualifying as pendent or frondose).

Most of the focal tree species (Table 1) are common in the region (Haber *et al.* 1996). We collected samples from the same trees within a forest type on successive collection dates. Such repeated sampling was unavoidable because of the limited number of safely climbable trees, especially in secondary forest patches. Epiphytes were collected from different sections of each treecrown on each sample date.

TABLE 1. *Focal tree species in primary and secondary forests at the three research sites.*

Site	Species	Family	Individuals	Samples
		Primary Forest		
MCFP	*Dussia macroprophyllata*	Fabaceae	1	20
	Ficus crassiuscula	Moraceae	2	20
	Ficus tuerckheimii	Moraceae	2	10
	Matayba oppositifolia	Sapindaceae	1	20
	Ocotea tonduzii	Lauraceae	7	160
	Pouteria exfoliate	Sapotaceae	1	20
	Pouteria fossicola	Sapotaceae	1	10
Mario's	*Alfaroa costaricensis*	Juglandaceae	1	5
	Ficus crassiuscula	Moraceae	1	10
	Guarea tonduzii	Meliaceae	1	5
	Meliosma vernicosa	Sabiaceae	1	10
	Sapium rigidifolium	Euphorbiaceae	3	20
Station	*Gordonia brandegeei*	Theaceae	1	10
	Pouteria reticulate	Sapotaceae	4	30
	Quercus corrugate	Fagaceae	1	10
		Secondary Forest		
MCFP	*Conostegia oerstediana*	Melastomataceae	7	220
	Hampea appendiculata	Malvaceae	2	40
Mario's	*Conostegia rufescens*	Melastomataceae	6	50
Station	*Conostegia oerstediana*	Melastomataceae	3	20
	Hampea appendiculata	Malvaceae	2	20
	Persea Americana	Lauraceae	2	10

Individuals = number of individuals of a species sampled within a site. Samples = number of epiphyte samples taken from each species within a site for the forest type comparison.

The first year of epiphyte collections focused on the MCFP site. Five epiphyte mat samples were collected from each of seven treecrowns in primary and secondary forest every other month from November 1999 to September 2000 ($N = 420$; 2 forest types × 7 trees in each × 5 samples per tree × 6 dates). Differences in arthropod abundance, morphospecies richness, and relative abundance of higher taxa between the two forest types were analyzed with separate repeated-measures ANOVAs. Diptera, Lepidoptera, Trichoptera, Blattaria, nonformicid Hymenoptera, Pseudoscorpiones, Opiliones, Diplopoda, Chilopoda, and Orthoptera each comprised < 1 percent of the total collection and were pooled into a single group ("Others") for analysis of relative abundance. Individual trees nested within forest types served as the subject for error estimation in the repeated-measures model (Littell *et al.* 1996).

Forests at the Station and Mario's were added in October 2000 to serve as replicate sites for comparison with MCFP. Five epiphyte samples were collected from the crowns of each of five trees in primary and secondary forest at each of the three sites in October 2000 and March 2001 ($N = 300$;

3 sites × 2 forest types × 5 trees per forest type × 5 samples per tree × 2 sample dates). These dates were selected to represent the wet and dry seasons, respectively. Differences in arthropod assemblage parameters were analyzed with a nested ANOVA using season, and forest type nested within season, as main effects. Random factors in the mixed model were site, and tree nested within forest type, season, and site.

We examined beta-diversity between primary and secondary forests at MCFP and replicate sites (pooled) with rarefaction techniques computed using EstimateS (Colwell 2005). We also used EstimateS to assess taxonomic similarity between the two assemblages with the abundance-based Jaccard index developed by Chao *et al.* (2005). To simplify the similarity analyses, we pooled arthropod abundance from all MCFP samples within a forest type on a given collection date, such that the primary–secondary forest comparisons for MCFP were based on six dates. Likewise, we pooled data from the individual samples of the year 2 replicate sites within sampling dates and sites, resulting in comparisons of six assemblages (3 sites × 2 dates). Similarity values were then compared between forest types with ANOVAs.

Arthropod abundance and epiphyte dry mass data were log-transformed to improve homogeneity of variance, and proportional data were arcsine-transformed before analysis (Sokal & Rohlf 1995). Normality was confirmed with normal probability plots and Kolmogorov-Smirnov tests applied to ungrouped data (Sokal & Rohlf 1995, SAS Institute 2002). Sequential Bonferroni adjustments (Rice 1989) were used as necessary to control for multiplicity. ANOVAs were conducted using mixed model procedures, and all repeated-measures tests used autoregressive covariance structure and the Kenward–Roger method for estimation of degrees of freedom (Littell *et al.* 1996; Saavedra & Douglass 2002; SAS Institute 2002).

RESULTS

Epiphyte mats differed in structure between the two forest types. Based on percent cover estimations for the November 1999 samples, mats in primary forests were more complex in terms of vegetative composition (mean ± SD: 3.3 ± 1.21 foliage classes per sample) than secondary forest (2.0 ± 0.77 classes; $F_{1,56} = 29.7$, $P < 0.001$). On average, mats in primary forest contained a larger percentage of long turf and frondose foliage than mats in secondary forest (Fig. 1; $F_{1,56} > 7.05$, $P < 0.01$).

Epiphyte mats were thinner in the secondary forests at all sites. At MCFP (year 1) the average dry mass of mats collected in secondary forest was about 40 percent lower (overall mean ± SD: 4.06 ± 1.514 g) than mat samples from primary forest (6.68 ± 2.829 g; Table 2). Likewise, sample mass was about 25 percent lower in secondary forest (3.34 ± 1.190 g) than in primary forest (4.35 ± 1.190 g) at the year 2 replicate sites (forest type nested within season: $F_{2,54} = 8.56$, $P < 0.001$). There was no relationship between the dry mass of a sample and the number of arthropod morphospecies present in year 1 (linear regression: $F_{1,418} = 0.80$, $P = 0.372$, $R^2 = 0.004$) or for the replicate forests in year 2

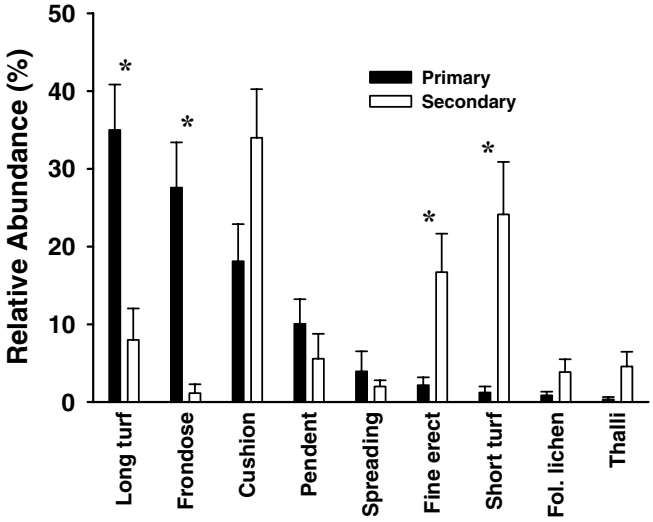

FIGURE 1. Mean (± SE) percent abundance of different foliage morphologies in epiphyte mat samples from primary and secondary forests at MCFP in November 1999. $N = 35$ for each mean. Asterisks indicate differences in means between forest types within a given morphology after sequential Bonferroni adjustment.

($F_{1,298} < 2.44$, $P > 0.119$, $R^2 < 0.009$). However, arthropod abundance weakly declined with increasing dry mass of the samples ($F_{1,418} = 32.02$, $P < 0.001$, $R^2 = 0.071$). These patterns were consistent when data were analyzed separately by sample date and forest type.

A total of 22,715 arthropods were collected in the first year of the project (MCFP only): 9553 from primary forest and 13,162 from secondary forest. Average arthropod abundance was greater in the secondary forest epiphytes (Fig. 2A). The average number of arthropod morphospecies showed a tendency to be higher in primary forest (Fig. 2B), but the pattern was not statistically significant following Bonferroni adjustment (Table 2). Rarefaction analysis provided similar results (Fig. 3). Both the abundance and morphospecies richness of arthropods varied over time (Fig. 2), but time × forest type interactions were not significant for either parameter (Table 2).

Mites (Acarina) composed approximately 65 percent of the arthropods collected (Fig. 4), and were similar in relative abundance between primary and secondary forest at MCFP (Table 2). However, several major taxonomic groups differed in mean relative abundance between forest types: Formicidae and Collembola were proportionally more abundant in samples from secondary forest; Coleoptera, Homoptera, Psocoptera, and "Others" represented larger percentages of collections from primary forest (Fig. 4; Table 2). Posthoc univariate tests indicated that these patterns were consistent over time except in May 2000, when relative abundances of all taxa were statistically similar in the two forests. Seasonal variation in relative abundance differed between forest types for Thysanoptera, Homoptera, Psocoptera, and Isopoda, as indicated by significant time × forest type interactions for these groups (Table 2). Overall,

TABLE 2. *Mixed model repeated-measures ANOVA output for effects of forest type on arthropod morphospecies richness, abundance, sample mass, and relative abundance of major taxa at MCFP (year 1).*

	Effect	df	*F*	*P*	Covariance Parameters	
Richness	Forest	1, 126	5.01	0.027	Tree (Forest × Time)	0.2307
	Time	5, 126	5.31	<0.001*	Residual	22.276
	Forest × Time	5, 126	0.77	0.573		
Abundance	Forest	1, 116	16.9	<0.001*	Tree (Forest × Time)	0.2299
	Time	5, 116	5.01	<0.001*	Residual	0.0691
	Forest × Time	5, 116	0.83	0.528		
Mass	Forest	1, 72	105.7	<0.001*	Tree (Forest × Time)	0.0215
	Time	5, 72	20.9	<0.001*	Residual	0.0473
	Forest × Time	5, 72	2.80	0.023		
Coleoptera	Forest	1, 122	12.1	<0.001*	Tree (Forest × Time)	0.2522
	Time	5, 122	14.1	<0.001*	Residual	0.0069
	Forest × Time	5, 122	2.76	0.021		
Formicidae	Forest	1, 105	21.8	<0.001*	Tree (Forest × Time)	0.4429
	Time	5, 105	3.04	0.013	Residual	0.0240
	Forest × Time	5, 105	1.99	0.087		
Acarina	Forest	1, 118	0.06	0.803	Tree (Forest × Time)	0.2991
	Time	5, 118	15.6	<0.001*	Residual	0.0154
	Forest × Time	5, 118	0.33	0.891		
Collembola	Forest	1, 115	7.07	0.009	Tree (Forest × Time)	0.2389
	Time	5, 115	3.34	0.008	Residual	0.0122
	Forest × Time	5, 115	0.96	0.447		
Araneae	Forest	1, 126	1.05	0.307	Tree (Forest × Time)	0.1685
	Time	5, 126	5.49	<0.001*	Residual	0.0030
	Forest × Time	5, 126	1.34	0.251		
Hemiptera	Forest	1, 140	1.57	0.212	Tree (Forest × Time)	0.1095
	Time	5, 140	6.39	<0.001*	Residual	0.0028
	Forest × Time	5, 140	0.71	0.615		
Thysanoptera	Forest	1, 131	0.72	0.398	Tree (Forest × Time)	0.1556
	Time	5, 131	6.02	<0.001*	Residual	0.0044
	Forest × Time	5, 131	4.73	<0.001*		
Homoptera	Forest	1, 111	20.2	<0.001*	Tree (Forest × Time)	0.1416
	Time	5, 171	8.08	<0.001*	Residual	0.0021
	Forest × Time	5, 171	6.31	<0.001*		
Psocoptera	Forest	1, 141	10.7	0.001*	Tree (Forest × Time)	0.0053
	Time	5, 141	2.86	0.017	Residual	0.0010
	Forest × Time	5, 141	3.01	0.001*		
Isopoda	Forest	1, 121	2.31	0.131	Tree (Forest × Time)	0.2029
	Time	5, 121	6.43	<0.001*	Residual	0.0029
	Forest × Time	5, 121	3.32	0.008*		
Other	Forest	1, 141	14.1	<0.001*	Tree (Forest × Time)	0.0098
	Time	5, 141	7.64	<0.001*	Residual	0.0035
	Forest × Time	5, 141	2.13	0.065		

*Significant based on sequential Bonferroni adjustment.

Jaccard similarity indices were consistently high within and among forest types at MCFP. Average (± SE) taxonomic similarity among sample dates within secondary forest (0.96 ± 0.009) and within primary forest (0.93 ± 0.012) did not differ from each other or from overall between-forest similarity (0.95 ± 0.007; $F_{2,63} = 2.03$, $P = 0.14$).

Abundance differences between the forest types were driven by larger numbers of ants in secondary forest versus primary forest.

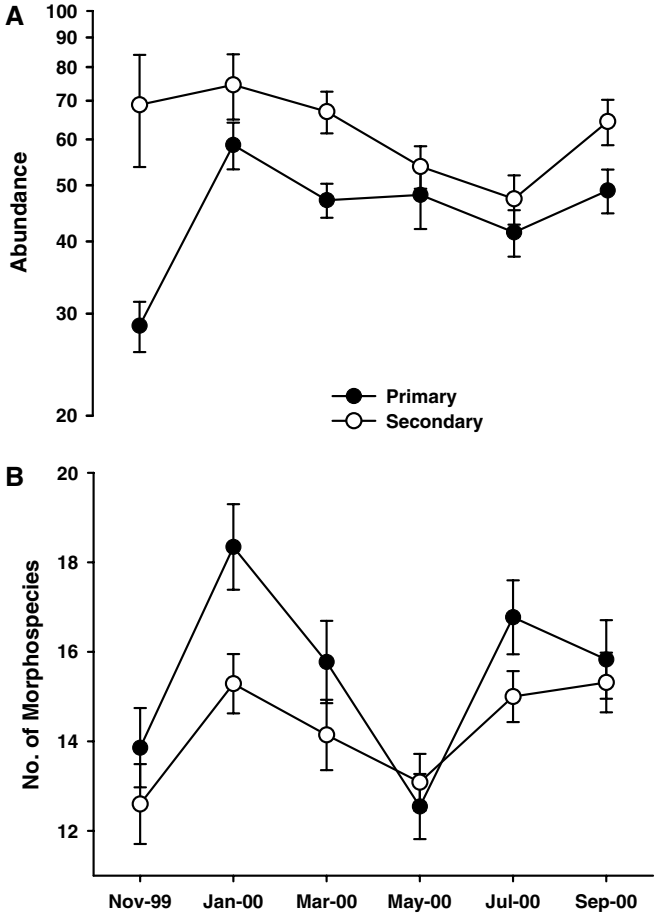

FIGURE 2. Mean (±SE) arthropod abundance (A) and morphospecies richness (B) in primary and secondary forests at MCFP. $N = 35$ for each mean (7 trees per forest type, 5 epiphyte samples per tree per sample date).

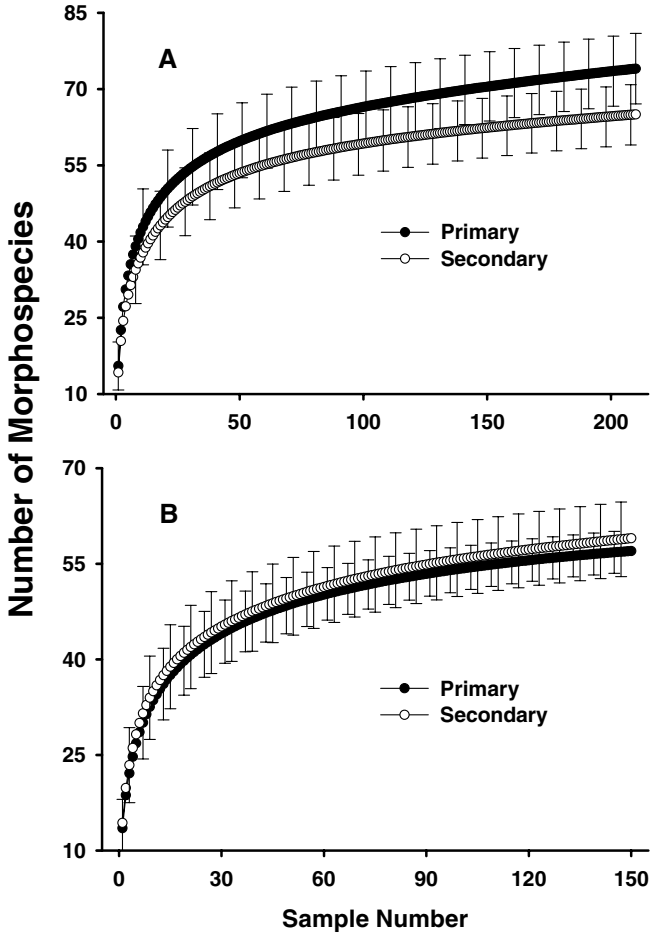

FIGURE 3. Mao Tau species accumulation curves (±95% ci) based on 50 randomized iterations for primary and secondary forests at MCFP (A) and the three replicate forests (B). Many 95% ci bars were omitted for clarity.

The frequency of epiphyte samples containing ≥ 10 ants was about seven times higher in secondary forest (11.4%) than in primary forest (1.7%; *G*-test with Williams' correction = 38.6, df = 1, $P < 0.001$). The most abundant ants, especially *Solenopsis* spp. (Longino 2000, Schonberg *et al.* 2004), were generally found in the dead organic matter at the interface between the tree bark and the epiphyte mats, and occurred in several different tree species. When ant data were excluded, the difference in overall arthropod abundance between forest types was nullified ($F_{1,112} = 2.03$, $P = 0.157$) and morphospecies richness became marginally greater in primary forest ($F_{1,124} = 7.31$, $P = 0.008$; $\alpha = 0.0071$). However, time effects and time × forest type interactions were unchanged by exclusion of ant data. Morphospecies richness declined with increasing ant abundance in samples (linear regression: $F_{1,418} = 12.69$, $P = 0.0004$), but this relationship explained only a small percentage of the variation in richness ($R^2 = 0.029$).

In the second year of the project, we collected 13,069 arthropods in epiphyte samples from the three replicate sites. Average arthropod abundance did not differ between wet and dry seasons, but (as with the year 1 results) more arthropods were collected from secondary forest than from primary forest (Fig. 5A; forest type nested within season: $F_{2,54} = 3.79$, $P = 0.029$). Secondary forest samples showed a tendency for higher morphospecies richness compared to primary forest samples (Fig. 5B), but the average difference was by a margin of one morphospecies or less and (again, consistent with year 1) was not statistically significant. Rarefaction analysis provided a similar result (Fig. 3).

There was a marginally significant seasonal effect on morphospecies richness at the year 2 replicate sites, with the average number of arthropod morphospecies *ca* 10 percent higher in the wet season samples (Fig. 5B; $F_{1,54} = 4.31$, $P = 0.043$). Relative abundances of major taxa did not differ between forest types during the wet season ($F_{3,24} < 2.87$, $P > 0.05$; Fig. 6A). In contrast, Coleoptera, Thysanoptera, and Homoptera were proportionally more abundant in secondary forest than in primary forest during the dry season ($F_{3,24} > 3.13$, $P < 0.045$; Fig. 6B). As with the MCFP (year 1) arthropod assemblages, there was a high degree of taxonomic overlap within primary (0.95 ± 0.014) and secondary (0.94 ± 0.009) forests, and between the two forest types (0.94 ± 0.006).

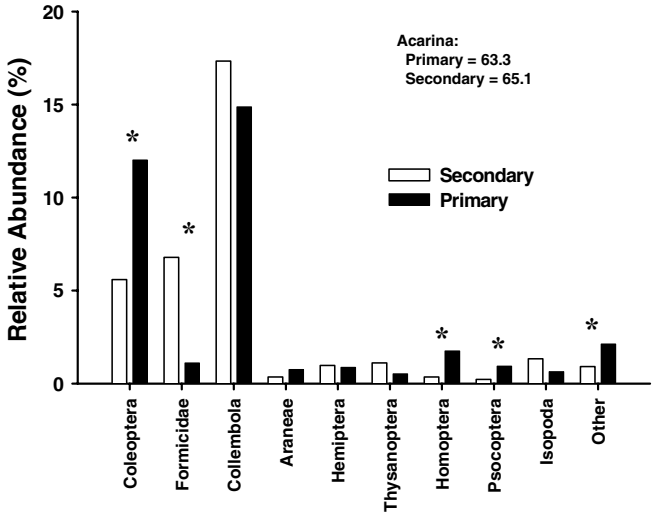

FIGURE 4. Relative abundance of major taxonomic groups collected in epiphyte mats in primary and secondary forests at MCFP between November 1999 and September 2000. Values were calculated from pooled data (samples from different dates combined by forest type). Asterisks indicate differences between forest types within a group based on repeated-measures ANOVAs (Table 2).

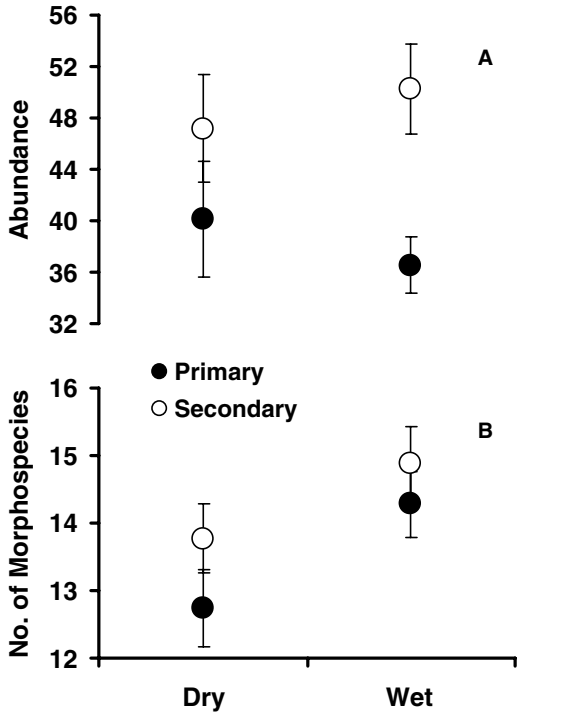

FIGURE 5. Mean (± SE) arthropod abundance and morphospecies richness in wet season (A) and dry season (B) samples from primary and secondary forests sampled in year 2. $N = 15$ for each mean.

These values did not differ from each other ($F_{2,63} = 0.25$, $P = 0.78$).

DISCUSSION

As we expected, and as observed in other projects conducted at the site (Yanoviak *et al.* 2003a,b, 2004), epiphyte mats tended to be significantly thinner and morphologically less diverse in the secondary forests. Despite these differences and the lower mass of samples from secondary forest, arthropods were generally more abundant there than in mats of primary forests. These results were consistent across years and replicate sites, suggesting that the age difference between the two forest types had minimal effects on basic arthropod assemblage parameters in epiphyte mats.

In part, the very high taxonomic similarity and lack of difference in arthropod morphospecies richness between forest types may be attributed to their spatial arrangement. All of the secondary forests used in this study were embedded in, or adjacent to primary forests. Under such circumstances, colonization of epiphyte mats in regenerating forests, even by uncommon and less vagile taxa, is probably facilitated by the proximity of the source pool of species in primary forest. However, this is very unlikely to occur where secondary trees are isolated from primary forests, which is currently the predominant situation in this and many other Neotropical regions.

The very high Jaccard similarity (*i.e.*, low beta-diversity) we observed within and among forest types reflects the dominance of a relatively specialized epiphyte mat fauna (*e.g.*, the ubiquity of certain mite, collembola, and beetle morphotypes). However, the high similarity values are also partly a consequence of pooling the data for analysis, and of substantial lumping with respect to assignment of individuals to morphospecies. Reference material examined by taxonomic specialists showed that we underestimated diversity such that our morphospecies designations (*e.g.*, within Acarina) more closely corresponded to genus- or family-level differences. Thus, our beta-diversity results should be viewed as preliminary until more focused studies on specific taxa are complete.

The greater abundance of ants in the secondary forest may be due to abiotic differences between the forest types (*i.e.*, greater insolation leading to warmer and drier conditions in secondary forest treecrowns). This pattern may also be the result of biotic differences between forest types, such as greater abundance of preferred trophobionts (*e.g.*, homopterans; Davidson *et al.* 2003) or absence of dominant competitor ant species in secondary forest. Determining the relevance of these possible explanations will require additional data collection and experimentation.

Time effects were not altered when we removed ants from the data set, suggesting that seasonal changes in ant abundance or activity were not driving temporal variation in arthropod assemblages in the mats. The slight negative relationship between ant abundance and arthropod morphospecies richness suggests that ants may reduce local diversity in epiphyte mats via top–down effects. This is plausible, given that many tropical arboreal ants are territorial and may compete with other insects for patchy resources in tropical forest canopies (Davidson 1997, Yanoviak & Kaspari 2000).

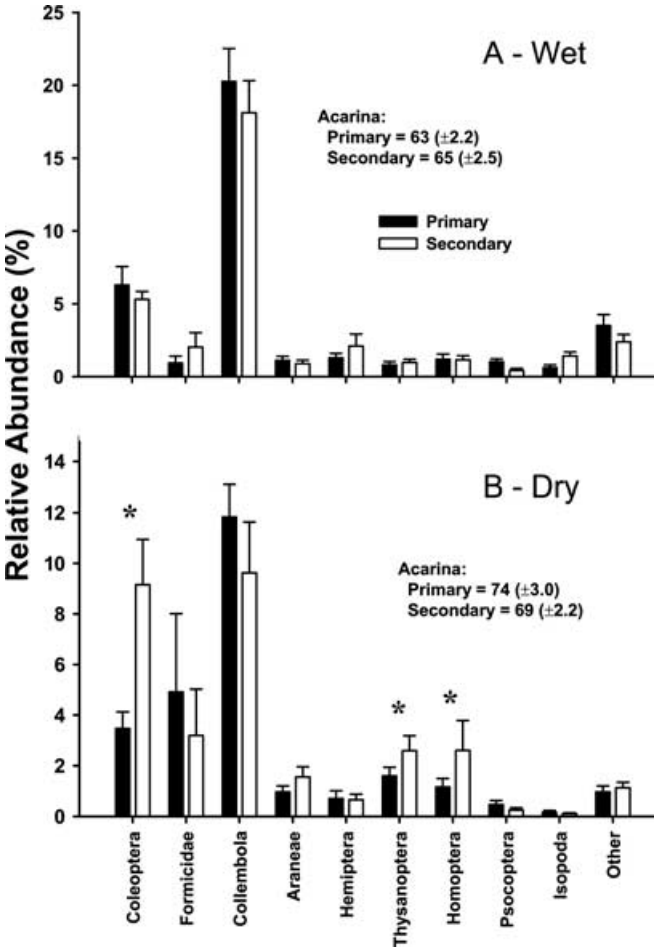

FIGURE 6. Mean (± SE) relative abundance of major taxonomic groups in primary and secondary forests at three replicate sites in wet season (A) and dry season (B). Asterisks indicate significant differences between forest types within taxa based on nested ANOVAs. Arthropod abundance in the five samples collected from each tree was pooled to generate relative abundance values on a per tree basis. Thus, each mean is based on $N = 15$ trees.

Results from MCFP and the two replicate sites suggest that seasonal effects are much more important than forest type effects in determining basic arthropod assemblage parameters within epiphyte mats. Drying disturbance can be extreme in this system (Bohlman *et al.* 1995), which may explain lower arthropod morphospecies richness during the dry season (February–May). We suggest two possible mechanisms for this seasonal effect. First, most of the arthropods extracted from the mats are very small and highly mobile, and may seek shelter deep in bark crevices or other inaccessible humid places during the dry season. These hidden arthropods would have been missed by our collection methods. Second, some taxa (*e.g.*, those living in highly exposed mat foliage) may become inactive during dry periods, and therefore would not be extracted with the Tullgren funnel technique. Seasonality was more strongly reflected by morphospecies richness than abundance in both years of the study, further suggesting that seasonal differences may be linked to the behavior of certain taxa, especially isopods and members of the group "Others," which tended to decline in relative abundance in the dry season.

The lack of a significant positive relationship between dry mass of samples and abundance of arthropods is atypical for this type of system (Booth & Usher 1984; Yanoviak *et al.* 2003b, 2004). We attribute this result to several factors. First, the inherently patchy nature of arthropod distributions in epiphyte mats may override the effects of sample volume at the scale of this study. Second, the slight but significant negative relationship between sample mass and arthropod abundance in primary forest was likely due to the presence of bark fragments, especially in samples collected from *Ocotea*, which added to the total mass of the sample without adding many individual arthropods. Moreover, primary forest mat samples included larger relative amounts of fine dead organic matter per sample, which generally contains fewer arthropods per gram dry weight than the vegetative portion of the mats (Yanoviak *et al.* 2004). Finally, above a certain optimal size, the effectiveness of Tullgren funnels declined with increasing volume, mass, and moisture content of a sample. This may have contributed to the low arthropod abundance observed in the November 1999 samples, which were exceptionally wet. We suspect that morphospecies richness was unaffected but abundance was reduced in those samples as a result of the slow drying time caused by excessive moisture.

Although epiphyte mats are a conspicuous component of tropical cloud forests and support diverse animal communities, no studies have examined the factors that regulate the structure of their resident arthropods. Our results provide the first quantitative assessment of large-scale patterns of arthropod species richness, abundance, and general composition in this system. Assessing variation in beta-diversity of arthropods in epiphyte mats and forest canopies in general is a daunting task due to the abundance of both species and life stages (*e.g.*, Paoletti *et al.* 1991, Floren & Linsenmair 2003). Nevertheless, more detailed taxon-based studies of the material collected in this project will build on current work with ants and beetles (Schonberg *et al.* 2004), enabling us to better understand the factors influencing variation in diversity between forests and seasons. On a smaller scale, investigations of linkages between arthropod diversity and epiphyte plant structure and composition would be a potentially interesting extension of this project. Finally, given that cloud forests are a functionally important yet rapidly disappearing ecosystem, greater efforts are needed to accurately predict the broader consequences of their loss.

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LITERATURE CITED

Basset, Y., V. Novotny, S. E. Miller, and R. L. Kitching (Eds.). 2003. Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, Cambridge, UK.

Bohlman, S., T. Matelson, and N. M. Nadkarni. 1995. Moisture and temperature patterns of canopy humus and forest floor soils of a montane cloud forest, Costa Rica. Biotropica 27: 13–19.

Booth, R. G., and M. B. Usher. 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: Effects of the physical and chemical environment. J. Anim. Ecol. 53: 879–893.

Borneman, J., and E. W. Triplett. 1997. Molecular microbial diversity in soils from eastern Amazonia: Evidence for unusual microorganisms and microbial population shifts associated with deforestation. Appl. Environ. Microbiol. 63: 2647–2653.

Budd, P., I. May, L. Miles, and J. Sayer. 2004. Cloud forest agenda. UNEP-WCMC. http://www.unep-wcmc.org/resources/publications/UNEP_WCMC_bio_series20.htm.

Canaday, C. 1996. Loss of insectivorous birds along a gradient of human impact in Amazonia. Biol. Conserv. 77: 63–77.

Chao, A., R. L. Chazdon, R. K. Colwell, and T.-J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8: 148–159.

Clark, K. L., and N. M. Nadkarni. 2000. Epiphytic histosols. *In* N. M. Nadkarni and N. T. Wheelwright (Eds.). Monteverde: Ecology and conservation of a tropical cloud forest, pp. 34. Oxford University Press, New York, New York.

Clark, K. L., R. O. Lawton, and P. R. Butler. 2000. The physical environment. *In* N. M. Nadkarni and N. T. Wheelwright (Eds.). Monteverde: Ecology and conservation of a tropical cloud forest, pp. 15–38. Oxford University Press, New York, New York.

Colwell, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at http://purl.oclc.org/estimates.

Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biol. J. Linn. Soc. 61: 153–181.

Davidson, D. W., S. C. Cook, R. R. Snelling, and T. H. Chua. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. Science 300: 969–972.

Ellwood, M. D. F., and W. A. Foster. 2004. Doubling the estimate of invertebrate biomass in a rainforest canopy. Nature 429: 549–551.

Ellwood, M. D. F., D. T. Jones, and W. A. Foster. 2002. Canopy ferns in lowland dipterocarp forest support a prolific abundance of ants, termites, and other invertebrates. Biotropica 34: 575–583.

Erwin, T. L. 1982. Tropical forests: Their richness in Coleoptera and other arthropod species. Coleopt. Bull. 36: 74–75.

Estrada, A., R. Coates-Estrada, and D. Merritt, Jr. 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. Ecography 17: 229–241.

Fittkau, E. J., and H. Klinge. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. Biotropica 5: 2–14.

Floren, A., and K. E. Linsenmair. 1999. Changes in arboreal arthropod communities along a disturbance gradient. Selbyana 20: 284–289.

Floren, A., and K. E. Linsenmair. 2003. How do beetle assemblages respond to anthropogenic disturbance? *In* Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching (Eds.). Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy, pp. 190–197. Cambridge University Press, Cambridge, UK.

Gentry, A. H., and C. Dodson. 1987. Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19: 149–156.

Gerson, U. 1982. Bryophytes and invertebrates. *In* A. J. E. Smith (Ed.). Bryophyte ecology, pp. 291–332. Chapman and Hall, London, UK.

Gradstein, S. R., S. P. Churchill, and N. Salazar-Allen. 2001. Guide to the bryophytes of tropical America. Memoirs of the New York Botanical Garden, vol. 86. New York Botanical Garden Press, New York, New York.

Haber, W. A., W. Zuchowski, and E. Bello. 1996. An introduction to cloud forest trees: Monteverde, Costa Rica. La Nación, San José, Costa Rica.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391: 72–76.

Lawton, R. O., U. S. Nair, R. A. Pielke, Sr., and R. M. Welch. 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. Science 294: 584–587.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Inc., Cary, North Carolina.

Longino, J. T. 2000. The ants of Monteverde. *In* N. M. Nadkarni and N. T. Wheelwright (Eds.). Monteverde: Ecology and conservation of a tropical cloud forest, pp. 132–136. Oxford University Press, New York, New York.

Malcolm, B., and N. Malcolm. 2000. Mosses and other bryophytes: An illustrated glossary. Micro-Optics Press, Nelson, New Zealand.

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.

Nadkarni, N. M., and N. T. Wheelwright (Eds.). 2000. Monteverde: Ecology and conservation of a tropical cloud forest. Oxford University Press, New York, New York.

Nadkarni, N. M., T. J. Matelson, and W. A. Haber. 1995. Structural characteristics and floristic composition of a Neotropical cloud forest, Monteverde, Costa Rica. J. Trop. Ecol. 11: 481–495.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: A case study. Conserv. Biol. 10: 99–109.

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.

Perry, D. R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155–157.

Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 398: 611–615.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. Bioscience 46: 609–620.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Rodgers, D. J., and R. L. Kitching. 1998. Vertical stratification of rainforest collembolan (Collembola: Insecta) assemblages: Description of ecological patterns and hypotheses concerning their generation. Ecography 21: 392–400.

Saavedra, F., and L. Douglass. 2002. Using mixed models in SAS for ecological analyses. Bull. Ecol. Soc. Am. 83: 180–182.

SAS Institute. 2002. SAS/STAT user's guide, version 9. SAS Institute Inc., Cary, North Carolina.

Schonberg, L., J. T. Longino, N. M. Nadkarni, S. P. Yanoviak, and J. C. Gering. 2004. Arboreal ant species richness in primary forest, secondary forest, and pasture habitats of a tropical montane landscape. Biotropica 36: 402–409.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd edition. W. H. Freeman, New York, New York.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L.

Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427: 145–148.

United Nations Development Programme, United Nations Environmental Programme, World Bank, and World Resources Institute. 2000. World resources 2000–2001: People and ecosystems: The fraying web of life. World Resources Inst., Washington DC.

Wagner, T. 2000. Influence of forest type and tree species on canopy-dwelling beetles in Budongo Forest, Uganda. Biotropica 32: 502–514.

Whitmore, T. C., and J. A. Sayer (Eds.). 1992. Tropical deforestation and species extinction. Chapman and Hall, London, UK.

Yanoviak, S. P., and M. E. Kaspari. 2000. Community structure and the habitat templet: Ant assemblages in the tropical canopy and litter. Oikos 89: 259–266.

Yanoviak, S. P., G. Kragh, and N. M. Nadkarni. 2003a. Spider assemblages in Costa Rican cloud forests: Effects of forest level and forest age. Stud. Neotrop. Fauna Environ. 38: 145–154.

Yanoviak, S. P., N. M. Nadkarni, and J. C. Gering. 2003b. Arthropods in epiphytes: A diversity component that is not effectively sampled by canopy fogging. Biodivers. Conserv. 12: 731–741.

Yanoviak, S. P., H. Walker, and N. M. Nadkarni. 2004. Arthropod diversity in vegetative vs. humic portions of nonvascular epiphytes in a Neotropical cloud forest. Pedobiologia 48: 51–58.