



# Arthropod assemblages in vegetative vs. humic portions of epiphyte mats in a neotropical cloud forest

Stephen P. Yanoviak<sup>1</sup>, Hannah Walker<sup>2</sup>, Nalini M. Nadkarni\*

*The Evergreen State College, 2700 Evergreen Pkwy, Lab 1, Olympia, WA 98505, USA*

Received 8 April 2003; accepted 16 July 2003

## KEYWORDS

Canopy;  
Cloud forest;  
Detritus;  
Epiphytes;  
Microhabitat;  
Monteverde;  
Stratification;  
Tropics

## Summary

Epiphyte mats (contiguous pieces of live and dead epiphytes perched upon branches of trees) are a conspicuous component of tropical cloud forests and harbor diverse meso- and microarthropod communities. We investigated differences in arthropod assemblage structure between the vegetative (green) and humic (brown) portions of epiphyte mats in a lower montane forest in Monteverde, Costa Rica. Because of qualitative differences between the two substrates, we hypothesized that they would support different arthropod communities and that variation in community parameters would be linked to the quantity of brown material present in a mat sample. The green fraction contained twice as many individuals and species per gram dry mass than the brown fraction. Morphospecies composition was very similar between green and brown portions, but the relative abundance of several taxa differed significantly between the substrates. Contrary to our prediction, total arthropod abundance and richness in a sample were not correlated with the proportion of brown material present. In laboratory trials, the most common morphospecies of oribatid mite in this system showed a preference for brown substrates.

© 2003 Elsevier GmbH. All rights reserved.

## Introduction

The structure of tropical forest canopies comprises a heterogeneous mosaic of habitats within the three-dimensional network of tree stems. Patchy microhabitats, such as epiphyte mats, humus pockets, tree holes, and bromeliads, can add

considerable physical and biological complexity to the canopy environment (e.g., Benzing, 1983, 2000; Richards, 1996). The contribution of these microhabitats to ecological processes and biodiversity has received increasing attention (e.g., Longino and Nadkarni, 1990; Nadkarni and Longino, 1990; Paoletti et al., 1991; Benzing, 1995;

\*Corresponding author.

E-mail address: [NadkarnN@evergreen.edu](mailto:NadkarnN@evergreen.edu) (N.M. Nadkarni).

<sup>1</sup>Current address: Florida Medical Entomology Laboratory, 200 9th Street SE, Vero Beach, Florida 32962 USA.

<sup>2</sup>Current address: Glencliff Farm, P.O. Box 808, Independence, KS 67301, USA.

Yanoviak, 1999). These microhabitats presumably enhance the collective species richness of arboreal arthropods by increasing the diversity of available niches (e.g., Benzing, 1983; Erwin, 1995).

In tropical cloud forests, epiphytes, especially epiphytic bryophytes and mosses (Pócs, 1982), exist on the majority of tree surfaces. Canopy branches that support extensive epiphytic growth also tend to accumulate substantial quantities of dead organic matter. This “crown humus” (Jenik, 1973), consists of nutrients intercepted from precipitation, dry deposition, and plant- and animal-based detritus (Nadkarni and Matelson 1992; Bohlman et al., 1995; Clark and Nadkarni, 2000). Roots of resident epiphytes and the supporting tree (Nadkarni, 1981) tap this rich resource and contribute a living structural component to the humic layer. Epiphyte mats function as an important ecological niche for invertebrates; they buffer local environmental variation by retaining moisture and providing shelter against wind, and they serve as foraging and oviposition sites for a variety of arthropods (Gerson, 1982; André, 1983; Stubbs, 1989; Nadkarni, 1994; Kitching et al., 1997).

Acarina (mites), Coleoptera (beetles), Formicidae (ants), and Collembola (springtails) consistently are the most abundant arthropod taxa in epiphyte mats and crown humus (Longino and Nadkarni, 1990; Nadkarni and Longino, 1990; Paoletti et al., 1991; Yanoviak and Nadkarni, 2001; Yanoviak et al., 2003). Despite the conspicuousness of epiphyte mats in many tropical forests, relatively few studies have examined the structure of their associated arthropod assemblages, or the relationship of particular substrates or substrate characteristics to invertebrate communities (see a review by Prinzing and Woas, 2003). A comprehensive ecological assessment of an analogous system was based on the distribution of arthropods within Antarctic moss-turf habitats (e.g., Usher, 1983; Booth and Usher, 1984; Usher and Booth, 1984, 1986). Arthropods in these settings tend to form two sub-communities differing in species distributions and life stages, resulting in a “green” moss community and a “dead” moss community (Usher and Booth, 1984).

As part of a long-term project on cloud forest canopy ecology in Costa Rica, we observed that epiphyte mats in primary forest are generally thicker and contain slightly more arthropod species than secondary forest mats (Yanoviak and Nadkarni, 2001, and unpubl.). The vegetative (hereafter, “green”) portion of the mats is relatively uniform in thickness, whereas the depth of the accumulated humic (hereafter, “brown”) fraction is highly variable, and varies independently of the green

layer. Because these substrates differ in terms of nutrient content (Nadkarni et al., 2001), moisture-holding ability (Bohlman et al., 1995), and rates of productivity (Clark et al., 1998a), we hypothesized that they support different arthropod communities. We further hypothesized that the greater abundance of brown mat substrate in primary forest may be responsible for the greater species richness we observed there.

We approached these hypotheses by first determining how basic parameters of arthropod assemblages (abundance, morphospecies richness, taxonomic composition) differ between the green and brown layers of cloud forest epiphyte mats. Because the green layer is relatively less variable in thickness than the brown layer, we predicted that total arthropod morphospecies richness and abundance in a mat sample would increase with the proportional mass of brown material. The green layer borders the external environment, thereby receiving potential colonists and functioning as a zone of primary production and potentially greater energy availability per unit mass. Thus, we predicted that the green layer would contain more arthropod morphospecies and individuals per unit mass than the brown substrate. We conducted an associated laboratory study to test our prediction that the most common morphotype of saprophagous mite in epiphyte mats would show a preference for brown substrates in experimental arenas.

## Methods and materials

This study was conducted in the designated research area at the Monteverde Cloud Forest Preserve (MCFP), Cordillera de Tilarán, Costa Rica (10° 20' N, 84° 45' W). The site is on the Pacific slope very close to the Continental Divide, and falls within the lower montane wet forest life zone (Haber, 2000). The MCFP receives ca. 2500 mm of seasonal rainfall per year, plus an undetermined quantity (>1000 mm) of precipitation in the form of cloud moisture and wind-driven mist (Clark et al., 1998b). Forest at the MCFP is mostly primary (>400 years old) with embedded 1–5 ha. patches of secondary regeneration that are 30–50 years old. See Nadkarni and Wheelwright (2000) for additional details on climate and site descriptions.

## Field study

We collected 14 samples (hereafter, ‘patches’) of epiphytic bryophyte mats from the crown of each

of five trees in the primary forest of the MCFP ( $n = 70$ ). The focal trees included the most common canopy species in the MCFP (Haber et al., 1996) and represented five different families (Table 1). The majority (89%) of patches were collected in May and June 2000; the remainder were collected in February 2001. Weather conditions were similarly wet and misty during both collection periods. We accessed tree crowns with single-rope climbing techniques (Perry, 1978).

Within each tree, we examined accessible epiphyte mats and selected specific patches (ca. 10 cm × 10 cm) for collection based on two criteria: (1) the green portion of the mat was dominated by bryophytes and filmy ferns rather than by large vascular epiphytes such as bromeliads, orchids, or woody plants; and (2) the mat included >1 cm accumulation of brown material beneath the green layer. Patches collected from different points on a contiguous mat (i.e., on a single tree branch) were separated by at least 30 cm, and no more than three patches were collected from any given mat. All collections were made from live branches.

Each patch was divided into green and brown fractions in situ by cutting away and immediately placing the green layer (generally 1–2 cm thickness) into a plastic bag. We then gathered the brown material down to the branch surface and placed it in a separate bag. Green and brown fractions were transported to the lab and placed in separate Tullgren funnels for arthropod extraction (60-W incandescent light, 17 cm funnel diameter) within 2 h of collection. Tullgren funnels were run ca. 10 h d<sup>-1</sup> during daylight hours only. This was necessary to prevent contamination from nocturnal

insects attracted to the lights. The total run time for each sample was ≤25 h, depending on sample moisture content and ambient humidity. After Tullgren processing, the green and brown fractions were dried in an oven at 50°C for 24 h, and weighed to the nearest 0.001 g (Fisher Scientific® 7301A balance). Macro- and microarthropods extracted from each fraction were identified to order or family and counted. Different morphotypes within higher taxa (especially Acarina, Coleoptera, and Collembola) were assigned to morphospecies for analysis (Oliver and Beattie, 1996). Representative specimens were sent to taxonomists for identification and morphospecies verification, and a reference collection was deposited in the MCFP laboratory.

Average dry mass and arthropod assemblage parameters were compared among focal trees with analysis of variance (ANOVA) and between green and brown fractions with paired *t*-tests. We used simple linear regression to determine if total arthropod abundance and morphospecies richness in a patch vary as a function of the proportional mass of the brown fraction [brown dry mass × (green dry mass + brown dry mass)<sup>-1</sup>]. Normality was confirmed with Kolmogorov–Smirnov tests applied to ungrouped data (Sokal and Rohlf, 1995; SAS, 1999). Dry mass, abundance, and density values were log-transformed to correct variance heterogeneity, and proportional abundance data were arcsine square-root transformed before analysis. All means include ±1 standard error and were calculated from untransformed data. The 62 samples collected in June 2000 were processed solely by H.W., whereas the eight samples

**Table 1.** Mean (SE) sample mass, arthropod density, and arthropod morphospecies richness (taxa per gram dry mass of substrate) in vegetative (Green) and humic (Brown) portions of epiphyte mats of five trees

| Tree species  | Green        |              |              | Brown       |             |             |
|---|--------------|--------------|--------------|-------------|-------------|-------------|
|   | Mass (g)     | Density      | Richness     | Mass (g)    | Density     | Richness    |
| <i>Ficus crassiuscula</i> Warb. ex Standl. (Moraceae)         | 3.3 (0.56)a  | 11.4 (1.48)a | 3.9 (0.58)ab | 3.8 (0.38)a | 3.0 (0.52)a | 2.0 (0.32)a |
| <i>Matayba oppositifolia</i> (A. Rich.) Britton (Sapindaceae) | 1.5 (0.14)ab | 4.0 (0.66)b  | 3.3 (0.48)a  | 2.8 (0.42)a | 2.9 (0.81)a | 1.8 (0.41)a |
| <i>Meliosma vernicosa</i> (Liebm.) Griseb. (Sabiaceae)        | 1.1 (0.22)b  | 10.8 (1.79)a | 7.8 (1.05)c  | 3.7 (0.74)a | 4.7 (0.53)a | 2.7 (0.52)a |
| <i>Ocotea tonduzii</i> Standl. (Lauraceae)                    | 1.5 (0.21)b  | 12.5 (1.89)a | 6.4 (0.85)bc | 3.2 (0.59)a | 4.2 (0.94)a | 2.5 (0.40)a |
| <i>Pouteria fossicola</i> Cronquist (Sapotaceae)              | 1.4 (0.29)b  | 3.8 (0.54)b  | 2.4 (0.39)a  | 3.7 (0.66)a | 4.5 (1.29)a | 1.2 (0.27)a |
| Overall   | 1.8 (0.17)   | 8.5 (0.76)   | 4.7 (0.39)   | 3.5 (0.25)  | 3.9 (0.39)  | 2.0 (0.18)  |

$n = 14$  for each mean. Within a column, means followed by the same letter do not differ. Overall means differed between green and brown portions for all variables.

collected in February 2001 were processed by several people. Therefore, the June 2000 samples provided the most accurate assessment of  $\beta$ -diversity (i.e., between green and brown fractions) at the morphospecies level, and only these data were used in calculation of similarity indices and direct comparisons of morphospecies composition. The entire data set was used for arthropod abundance and richness analyses.

## Laboratory study

We used the most common morphotype of oribatid mite found in epiphytic mats to examine possible green vs. brown substrate preferences in the laboratory. Live oribatid mites were extracted from fresh epiphyte material using modified Tullgren funnels. Each funnel emptied into a plastic vial containing moist paper towel, and the rim of the vial was sealed to the funnel stem with Parafilm<sup>®</sup> to prevent escape of the mites.

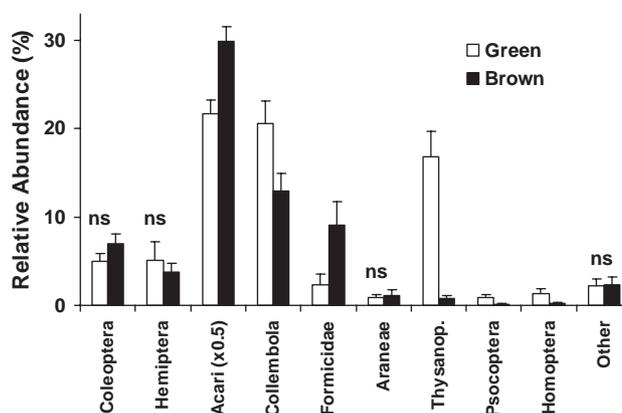
The experimental arena consisted of a black plastic film canister (5.0 cm tall and 3.3 cm diameter) half-filled with Plaster of Paris. The open area above the dried plaster substrate was evenly divided by a vertically orientated plastic screen with mesh size sufficiently large (2 mm  $\times$  2 mm) to allow unrestricted passage of mites. The space on one side of the screen was filled with green epiphyte material (ca. 0.033 g dry weight) and the other side was filled with brown material (ca. 0.170 g dry weight). Eleven individuals of the focal oribatid morphotype were placed in the center of the arena, which was then covered and set aside. After 24 h, the number of mites present in the green and brown substrates were counted under 10 $\times$  magnification. The experiment was replicated

52 times using new mites for each run. We analyzed substrate preferences using a binomial distribution to determine if mite abundance was more often greater on the brown side of the arena at the end of each run. We similarly examined the abundance of the focal mite morphospecies in the June 2000 field samples to determine if patterns observed in the lab study reflect patterns in the field.

## Results

A total of 1943 arthropods assigned to 42 different morphospecies was collected in the field portion of this study; 1054 individuals (38 morphospecies) were extracted from the green portion and 889 (35 morphospecies) from the brown material. Mites (Acarina), ants (Hymenoptera: Formicidae), and springtails (Collembola) were the most abundant groups in all samples (Fig. 1). Morphospecies assignments within mesostigmatid mites corresponded well with known genera and species, whereas our designations for oribatids more closely represented taxonomic families (V. Behan-Pelletier and E. Lindquist, pers. comm.). A preliminary list of collected mite taxa is available from SY. *Pheidole* spp., *Solenopsis* spp., and *Brachymyrmex* spp. were the most common ant genera collected. Among non-ant macrofauna, entomobryid collembolans and small weevils (Coleoptera: Curculionidae; especially *Sibinia* nr. *tenuicauda* Clark and *Coeloccephalopion* sp.) were present in almost every sample.

Mean dry mass of the brown fraction of the mat samples was significantly greater than the dry mass of the green fraction ( $t = 8.91$ ,  $df = 69$ ,  $P < 0.0001$ ; Table 1). We did not measure the volumes of the



**Figure 1.** Mean (+SE) relative abundance of major taxonomic groups in green and brown fractions of epiphyte mats.  $n = 70$  for each mean. ns = no difference between green and brown means for that taxon. All other means differ within taxa based on paired  $t$ -tests ( $\alpha = 0.05$ ). "Thysanop." = Thysanoptera. "Other" includes Isopoda, non-ant Hymenoptera, larval Diptera, and larval Lepidoptera. Acarina data were divided by 2 to save space and improve clarity.

samples; however, the brown material was consistently more dense and had a finer grain than the green layer. As with other moss-type substrates (Booth and Usher, 1984), arthropod abundance increased with sample dry mass for both the green and brown fractions (green:  $F_{1,68} = 52.80$ ,  $R^2 = 0.44$ ,  $P < 0.0001$ ; brown:  $F_{1,68} = 14.82$ ,  $R^2 = 0.18$ ,  $P < 0.0003$ ). We found similar relationships for arthropod morphospecies richness in both layers (green:  $F_{1,68} = 31.52$ ,  $R^2 = 0.32$ ,  $P < 0.0001$ ; brown:  $F_{1,68} = 10.22$ ,  $R^2 = 0.13$ ,  $P < 0.0022$ ). Therefore, we used density (number of individuals and number of morphospecies per gram of sample dry mass) as community parameters for quantitative comparisons. Sample mass, arthropod density, and arthropod morphospecies richness did not differ between the 2000 and 2001 collection periods ( $t < 1.73$ ,  $df = 68$ ,  $P > 0.087$  in all cases).

Mean density and mean morphospecies richness were consistently greater in the green fraction than in the brown fraction ( $t > 7.83$ ,  $df = 69$ ,  $P < 0.0001$  in both cases; Table 1), with 2.4 times as many morphospecies and 2.2 times as many individuals per gram in the green fraction relative to the brown fraction. When data from the green and brown layers of a given sample were combined, total morphospecies richness and total arthropod abundance did not vary predictably with the proportional mass of brown material present ( $F_{1,68} < 2.78$ ,  $R^2 < 0.04$ ,  $P > 0.10$ ).

The relative abundance of various arthropod groups also differed between the two substrate types. Mites and ants were proportionally more abundant in the brown fraction ( $t > 3.14$ ,  $P < 0.0025$ ), whereas Collembola, thrips, barklice, and Homoptera were relatively more abundant in the green fraction ( $t > 2.12$ ,  $P < 0.0371$ ; Fig. 1). Three fairly common taxa—beetles, spiders and Hemiptera—and the group “Others” (composed of miscellaneous taxa occurring in low abundance), did not differ in their proportional representation between the green and brown layers ( $t < 1.23$ ,  $P > 0.22$ ; Fig. 1).

Despite these differences in relative abundances of several groups, the presence/absence data showed the green and brown communities to be similar in terms of number of shared taxa (Sørensen index = 0.844; based on morphospecies designations from the year 2000 data,  $n = 62$  pairs). However, the probability that a pair of individuals randomly selected from the communities would be the same morphospecies was considerably lower (Morisita index = 0.603) due to the differences in the proportional abundance of taxa between the layers (Brower et al., 1998; Fig. 1). Aphids (Homoptera: Aphididae) and moth larvae (Lepidop-

tera) were found exclusively in the green material; all other higher taxa were represented by at least one morphospecies in both green and brown layers.

The green material collected from *Ficus* weighed 2–3 times as much as samples from the other trees (ANOVA:  $F_{4,65} = 6.02$ ,  $P = 0.0004$ ), and arthropod density and morphospecies richness in the green fraction differed among trees ( $F_{4,65} > 9.42$ ,  $P = 0.0001$  in both cases; Table 1). Conversely, the mean dry mass of brown material collected and arthropod assemblage parameters in the brown fraction were statistically similar among trees (ANOVA:  $F_{4,65} = < 2.04$ ,  $P > 0.10$  in all cases).

In the laboratory study, more individuals of the focal oribatid morphospecies occurred on the brown side of the arena after 24 hours in 35 of the 52 substrate choice runs. This outcome differs significantly from the null of the binomial distribution ( $P = 0.005$ ). Of the original 11 mites placed in each arena, 58% ( $\pm 0.023\%$ ) on average were found in the brown side after 24 h. Distributions of the focal morphotype were similar in the field: 33 of the 55 canopy samples containing this morphospecies had a larger number of individuals in the brown fraction (Binomial distribution  $P = 0.036$ ). Also, a larger proportion on average (61%) of the total number in each field sample was recovered from the brown fraction ( $t = 3.85$ ,  $df = 55$ ,  $P < 0.001$ ).

## Discussion

Epiphyte mats are an abundant yet poorly studied component of many tropical cloud forests (e.g., Pócs, 1982). Such habitats are dominated by meso- and microfauna, with mites, ants, springtails, and beetles as the most conspicuous representatives (Paoletti et al., 1991; Gonzalez et al., 1998; Prinzing and Woas, 2003; Yanoviak et al., 2003). Our results are consistent with those from Antarctic moss mats (e.g., Usher and Booth, 1984), and indicate that the diverse arthropod assemblages inhabiting tropical cloud forest epiphyte mats may be loosely divided into subgroups based on the distribution of vegetative (“green”) vs. detrital (“brown”) material.

Our prediction that diversity in moss mat samples is a function of the quantity of brown material present was not supported. We did not attempt to characterize morphological or nutritional aspects of the individual green and brown components; however, our results suggest that the diversity of arthropods in this system, and the differences observed among forest types in related projects (Yanoviak and Nadkarni, 2001), is a function of

qualitative variation in the green layer. Alternatively, diversity in epiphyte mats may be regulated in a more diffuse manner by complex interactions involving both layers. Some evidence for the latter comes from work in moss–turf systems, which showed that interspecific interactions were more important than environmental variables in regulating arthropod distributions at the small patch scale ( $<20\text{ cm}^2$ ), and that predators were randomly distributed at patch sizes up to  $50\text{ cm}^2$  (Usher and Booth, 1986). Given that epiphyte mats in Monteverde harbor  $10\text{--}20\times$  as many species as the Antarctic system, interspecific interactions and scale effects may be even more complex. Thus, more information pertaining to the natural history of the component species and their interactions is needed, as are studies focusing on larger scales such as whole mats and whole trees (see a review by Prinzing and Woas, 2003).

Although the overall contribution of variation in the brown fraction was smaller than expected, we did find clear differences in arthropod assemblage structure between the green and brown layers. As predicted, the green portion of epiphyte mats on average harbored larger numbers of individuals and morphospecies of arthropods per unit dry mass than the brown fraction. Bryophytes and similar plants typically are considered to be a low quality food resource. Nonetheless, a variety of insects do feed on the vegetative portions of these plants (Gerson, 1982), and part of the green/brown difference we observed can be attributed to the presence of herbivores (aphids, Lepidoptera larvae, and most of the thrips) exclusively in the green fraction. Moreover, field data and results of the lab-based substrate choice experiment indicated that the most common morphotype of oribatid mite prefers to inhabit brown substrate types. Thus, it is likely that nonrandom distributions of at least some taxa are due to active microhabitat selection.

Although several taxa occurred exclusively in the green layer, substantial overlap in morphospecies composition between green and brown layers shows that the communities inhabiting each layer are distinct in terms of relative abundances, rather than presence or absence of component taxa, a pattern that is consistent with simpler moss communities (Usher and Booth, 1984). Differences in resource availability and immigration between the green vs. brown layers probably explain many of the differences in arthropod distributions between these microhabitats. The exposed green layer is potentially subject to high rates of stochastic colonization by small aerial and crawling arthropods. Also, as a zone of insolation and net productivity, available energy per unit mass is likely

to be greater in the green layer. Thus, total consumer abundance and the persistence of rare taxa or accidental colonists should be greater than in the brown layer.

The differences we observed in green dry mass and arthropod assemblage parameters among the focal trees may be due to a variety of factors. Host-tree specificity has not been documented for most tropical epiphytic bryophytes (Pócs, 1982), but some tree characteristics such as morphology, age, location and condition may influence the species composition of epiphyte assemblages (e.g., Benzling, 2000; Merwin et al., 2003). This may be reflected in the distributions of mites and other small arthropods that are sensitive to gross epiphyte morphology and location (Martin, 1938; Gerson, 1982; André, 1984). The role of individual trees and tree species in determining the complexity of epiphyte mats and their inhabitants needs further investigation, the results of which may be particularly valuable in the context of biodiversity and forest conservation.

We provide evidence for stratification of arthropod assemblages within epiphyte mats on a microhabitat scale, based on distributions and relative abundances of component taxa. Additional studies focusing on the natural history of the system are needed before we can begin to understand the mechanisms for this pattern. Bryophyte-dominated epiphyte mats are a canopy/understory microecosystem (sensu Moffett, 2001), with the green portion analogous to forest canopy and the brown portion resembling (in an ecological context) forest understory and soil habitats. Thus, potentially scale-independent concepts already developed from studies of whole forests may provide a heuristic device for future questions focused on epiphyte mat systems. Useful starting points may include understanding the role of nutritional differences in the green vs. brown resource base, and the importance of microenvironmental (e.g., humidity, temperature) gradients as one moves from the epiphyte mat “canopy” down through its “understory” and into its “soil”.

## Acknowledgements

We thank R. Solano and C. Jandér for assistance in the field, and J. Plank for helping us in the lab. W. Haber identified the trees, V. Behan-Pelletier and E. Lindquist identified the mites, and C. O’Brien and L. Kirkendall identified selected beetles. J. T. Longino provided thoughtful advice regarding experimental design and analysis, and assisted us with ant identification. We thank the Tropical Science

Center for protecting the forest and for logistical support at the MCFP. Comments from M. Kaspari and an anonymous reviewer improved the manuscript. This research was supported by National Science Foundation Grants DEB-9615341, DEB-9974035, and DEB-9975510 to NMN.

## References

- André, H., 1983. Notes on ecology of corticolous epiphyte dwellers: 2. Collembola. *Pedobiologia* 25, 271–278.
- André, H.M., 1984. Notes on the ecology of corticolous epiphyte dwellers: 3. Oribatida. *Acarologia* 25, 385–396.
- Benzing, D.H., 1983. Vascular epiphytes: a survey with special reference to their interactions with other organisms. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), *Tropical Rain Forest: Ecology and Management*. Blackwell Scientific, Oxford, pp. 11–24.
- Benzing, D.H., 1995. Vascular epiphytes. In: Lowman, M.D., Nadkarni, N.M. (Eds.), *Forest Canopies*. Academic Press, San Diego, CA, pp. 225–254.
- Benzing, D.H., 2000. *Bromeliaceae: Profile of an Adaptive Radiation*. Cambridge University Press, Cambridge.
- Bohman, S.A., Matelson, T.J., Nadkarni, N.M., 1995. Moisture and temperature patterns of canopy humus and forest floor soil of a montane cloud forest Costa Rica. *Biotropica* 27, 13–19.
- Booth, R.G., Usher, M.B., 1984. Arthropod communities in a maritime antarctic moss-turf habitat: effects of the physical and chemical environment. *J. Anim. Ecol.* 53, 879–893.
- Brower, J.E., Zar, J.H., von Ende, C.N., 1998. *Field and Laboratory Methods for General Ecology* 4th Edition. WCB McGraw-Hill, Boston, MA.
- Clark, K.L., Nadkarni, N.M., 2000. Epiphytic histosols. In: Nadkarni, N.M., Wheelwright, N.T. (Eds.), *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, New York, pp. 34.
- Clark, K.L., Nadkarni, N.M., Gholz, H.L., 1998a. Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica* 30, 12–23.
- Clark, K.L., Nadkarni, N.M., Schaefer, D., Gholz, H.L., 1998b. Cloud water and precipitation chemistry in a tropical montane forest, Monteverde, Costa Rica. *Atmos. Environ.* 32, 1595–1603.
- Erwin, T.L., 1995. Measuring arthropod biodiversity in the tropical forest canopy. In: Lowman, M.D., Nadkarni, N.M. (Eds.), *Forest Canopies*. Academic Press, San Diego, CA, pp. 109–127.
- Gerson, U., 1982. Bryophytes and invertebrates. In: Smith, A.J.E. (Ed.), *Bryophyte Ecology*. Chapman & Hall, London, pp. 291–332.
- Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M., Evans-Freke, I., 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* 81, 2045–2047.
- Haber, W.A., 2000. Plants and vegetation. In: Nadkarni, N.M., Wheelwright, N.T. (Eds.), *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, New York, pp. 37–70.
- Haber, W.A., Zuchowski, W., Bello, E., 1996. *An Introduction to Cloud Forest Trees: Monteverde, Costa Rica*. La Nación, San José, Costa Rica.
- Jenik, J., 1973. Root systems of tropical trees. 8. Stilt-roots and allied adaptations. *Preslia* 45, 250–264.
- Kitching, R.L., Mitchell, H., Morse, G., Thebaud, C., 1997. Determinants of species richness in assemblages of canopy arthropods in rainforests. In: Stork, N.E., Adis, J., Didham, R.K. (Eds.), *Canopy Arthropods*. Chapman & Hall, London, pp. 131–150.
- Longino, J.T., Nadkarni, N.M., 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. *Psyche* 97, 81–93.
- Martin, N.M., 1938. Some observations on the epiphytic moss flora of trees in Argyll. *J. Ecol.* 26, 82–95.
- Merwin, M., Rentmeester, S., Nadkarni, N.M., 2003. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations la selva costa rica. *Biotropica* 35, 37–47.
- Moffett, M.W., 2001. The nature and limits of canopy biology. *Selbyana* 22, 155–179.
- Nadkarni, N.M., 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. *Science* 214, 1023–1024.
- Nadkarni, N.M., 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Am. Zool.* 34, 70–78.
- Nadkarni, N.M., Longino, J.T., 1990. Invertebrates in canopy and ground organic matter in a neotropical montane forest, costa rica. *Biotropica* 22, 286–289.
- Nadkarni, N.M., Matelson, T.J., 1992. Biomass and nutrient dynamics of fine litter of terrestrially rooted material in a neotropical montane forest, Costa Rica. *Biotropica* 24, 113–120.
- Nadkarni, N.M., Wheelwright, N.T. (Eds.) 2000. *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, New York.
- Nadkarni, N.M., Schaefer, D.A., Matelson, T.J., Solano, R., 2001. Comparison of arboreal and terrestrial soil characteristics in a lower montane forest, monteverde, Costa Rica. *Pedobiologia* 46, 24–33.
- Oliver, I., Beattie, A.J., 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conserv. Biol.* 10, 99–109.
- Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H., Benzing, D.H., 1991. Diversity of soil fauna in the canopy and forest floor of a venezuelan cloud forest. *J. Trop. Ecol.* 7, 373–383.
- Perry, D., 1978. A method of access into crowns of emergent and canopy trees. *Biotropica* 10, 155–157.
- Pócs, T., 1982. Tropical forest bryophytes. In: Smith, A.J.E. (Ed.), *Bryophyte Ecology*. Chapman & Hall, London, pp. 59–104.

- Prinzing, A., Woas, S., 2003. Habitat use and stratification of Collembola and oribatid mites. In: Basset, Y., Kitching, R.L., Miller, S.E., Novotny, V. (Eds.), *Arthropods of Tropical Forests—Spatio-Temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge, pp. 271–281.
- Richards, P.W., 1996. *The Tropical Rain Forest* 2nd Edition. Cambridge University Press, Cambridge.
- SAS Institute., 1999. SAS OnlineDoc, Version 8. SAS Institute Inc., Cary, NC.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry* 3rd Edition. W. H. Freeman & Co., New York.
- Stubbs, C.S., 1989. Patterns of distribution and abundance of corticolous lichens and their invertebrate associates on *Quercus rubra* in Maine. *Bryologist* 92, 453–460.
- Usher, M.B., 1983. Pattern in the simple moss-turf communities of the sub-Antarctic and maritime Antarctic. *J. Ecol.* 71, 945–958.
- Usher, M.B., Booth, R.G., 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: three-dimensional distribution of mites and collembola. *J. Anim. Ecol.* 53, 427–441.
- Usher, M.B., Booth, R.G., 1986. Arthropod communities in a maritime Antarctic moss-turf habitat: multiple scales of pattern in the mites and collembola. *J. Anim. Ecol.* 55, 155–170.
- Yanoviak, S.P., 1999. Community structure in water-filled tree holes of panama: effects of hole height and size. *Selbyana* 20, 106–115.
- Yanoviak, S.P., Nadkarni, N.M., 2001. Arthropod diversity in epiphytic bryophytes of a Neotropical cloud forest. In: Ganeshaiah, K.N., Shaanker, R.U., Bawa, K.S. (Eds.), *Tropical Ecosystems: Structure, Diversity and Human Welfare*. Proceedings of the International Conference on Tropical Ecosystems. Oxford-IBH, New Delhi, pp. 416–419.
- Yanoviak, S.P., Nadkarni, N.M., Gering, J.C., 2003. Arthropods in epiphytes: a diversity component that is not effectively sampled by canopy fogging. *Biodiver. Conserv.* 12, 731–741.