

Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama

SABINE STUNTZ*, CHRISTIAN ZIEGLER*, ULRICH SIMON† and GERHARD ZOTZ*‡¹

**Lehrstuhl für Botanik II der Universität Würzburg, Julius-von-Sachs-Platz 3, 97082 Würzburg, Germany*

†*Technische Universität München, Forstwissenschaftliche Fakultät, Am Hochanger 13, 85354 Freising, Germany*

‡*Smithsonian Tropical Research Institute, Apdo 2072, Balboa, Panama*

(Accepted 26th May 2001)

ABSTRACT. The arthropod fauna inhabiting 90 individuals of three different species of epiphyte was investigated in the moist lowland forest of the Barro Colorado National Monument in Panama. In total, 3694 arthropods belonging to 89 morpho-species and 19 orders were collected. While arthropod abundance was primarily a function of host plant biomass irrespective of epiphyte species, there were pronounced differences in species richness, species composition and guild structure of the arthropod faunas of the three epiphyte species. Although all study plants were growing in close proximity on the same host tree species, there was remarkably little overlap in the species assemblages across epiphyte taxa. The inhabitant species also differed dramatically in their ecological functions, as feeding guild and hunting guild analyses indicated. The influence of plant size, structure and impounded leaf litter on arthropod diversity is discussed. We conclude that epiphytes are microhabitats for a diverse and numerous fauna, and that different species of epiphytes foster both taxonomically and ecologically very distinct arthropod assemblages.

KEY WORDS: Barro Colorado Island, bromeliads, guild structure, leaf litter, microclimate, orchids, plant size, spiders

INTRODUCTION

Ever since Erwin (1983) published his estimates of global species richness, researchers have been trying to unravel the mechanisms behind the extraordinary biotic diversity of tropical forest canopies. In this paper we investigate the

¹ Address for correspondence: Botanisches Institut der Universität Basel, Schönbeinstrasse 6, CH - 4056 Basel, Switzerland. Email: gerhard.zotz@unibas.ch

role of vascular epiphytes, which are frequently described as important for the establishment and the maintenance of high arthropod diversity in tropical forest canopies (Benzing 1990, Nadkarni 1994, Nadkarni & Matelson 1989, Stork 1987a,b). The reasoning behind this assumption, which has rarely been addressed thoroughly, is as follows: epiphytes are highly diverse (Benzing 1990), they contribute to the structural complexity of tree crowns, add food and energy resources missing in epiphyte-free forests (Nadkarni 1994, Nadkarni & Matelson 1989), and thus potentially expand the variety of microhabitats for arthropods in tropical tree crowns.

The investigation of the possible influence of epiphytes on canopy arthropods faces a problem of scale, because it can be studied from the level of individual epiphytes up to the level of entire tree crowns. Although Richardson (1999) reasoned that diversity within epiphytic bromeliads reflects relationships between diversity, productivity and habitat complexity known from larger study systems and suggested the use of epiphyte subsamples for entire forest ecosystems, it seems unlikely that results from individual epiphytes can simply be scaled up to trees or entire forest canopies. The present communication, which reports the results of a study on the macro-arthropod fauna directly associated with three species of canopy epiphyte, is part of a larger study, which follows the influence of canopy-dwelling flora on arthropods from single epiphyte to tree crown within the same study system (Stuntz *et al.* 1999).

Considering that plant architecture and other structural parameters of the environment play a major role in determining the diversity and abundance of arthropods (Cherrett 1964, Duffey 1966, Gunnarson 1990, Halaj *et al.* 1998, Hatley & MacMahon 1980, Lawton 1986, Pianka 1967, Rypstra 1983), we chose three locally abundant epiphyte species that feature very different structural characteristics, and included the entire range of plant sizes. In contrast, we standardized the remaining environment as much as possible by conducting the study in a rather small study area with all plants growing under quite similar conditions on the same host tree species, *Annona glabra* L. This setup was utilized to address two main questions: (1) Are there consistent differences in arthropod species richness, species composition and guild structure between epiphyte species? (2) If so, what might be the driving forces for these differences?

STUDY SITE

The study was conducted in the tropical moist forest of the Barro Colorado National Monument ($9^{\circ}10' N$, $79^{\circ}51' W$) in Panama. The area receives approximately 2600 mm of annual precipitation with a pronounced dry season from late December to April. Detailed descriptions of climate, vegetation and ecology can be found in Croat (1978), Leigh *et al.* (1982) and Windsor (1990). We collected arthropods in the dry seasons of 1998, 1999 and 2000.

METHODS

Study organisms

We selected three epiphyte species (hereafter addressed by their generic names) for this study, each featuring a different microhabitat structure according to its plant architecture (Figure 1): *Tillandsia fasciculata* Sw. var. *fasciculata* is a medium-sized tank bromeliad with numerous lanceolate and stiff leaves. The tanks impound water and debris. It often occurs in dense clusters of several individuals. *Vriesea sanguinolenta* Cogn. & Marchal is much larger and features broad, somewhat arching leaves. Its tanks can store several litres of rain water and considerable amounts of leaf litter. Organic matter decomposes between the basal portions of the leaves, thus creating soil-like microsites. *Dimerandra emarginata* (G. Meyer) Hoehne is an orchid with a rather simple structure. It grows in clusters of erect, slender stems with linear distichous leaves. *Dimerandra* impounds neither leaf litter nor water. We collected 30 individuals of each species of varying size. All three epiphyte species are locally very abundant in the study area (Croat 1978, Zotz *et al.* 1999). The study plants were taken from one tree species to avoid confounding effects of different host-associated faunas. The host was *Annona glabra*, a small flood-resistant tree (mean height c. 5 m) which grows along the shores of Lake Gatún. Due to its exposure to sun and wind, the microclimatic conditions in this habitat are similar to the conditions in the upper canopy (Zotz *et al.* 1999).

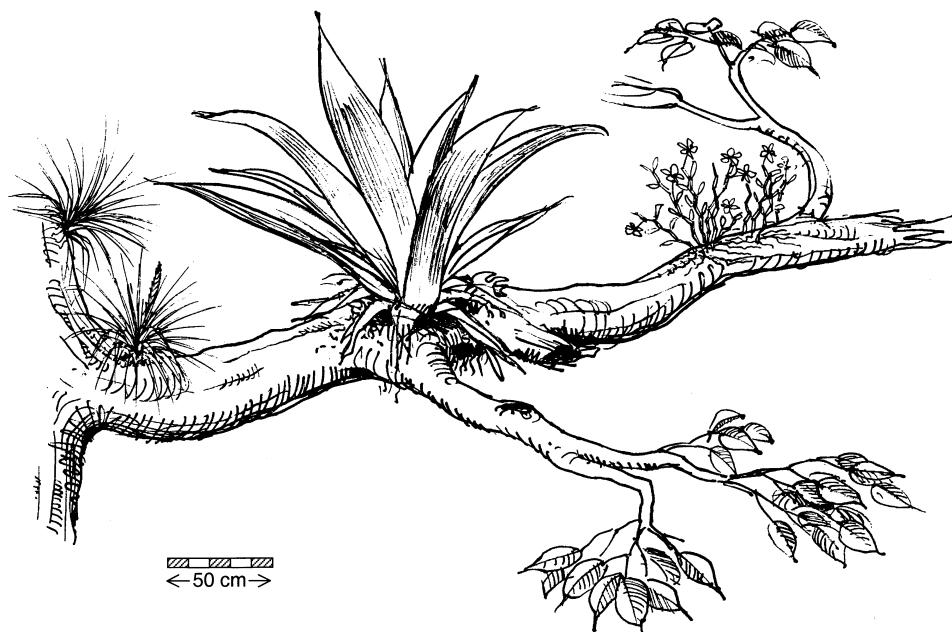


Figure 1. The three epiphyte species growing on a branch of *Annona glabra*. From left to right: *Tillandsia fasciculata* var. *fasciculata*, *Vriesea sanguinolenta*, *Dimerandra emarginata*.

Sampling the fauna

Epiphyte harvests. We harvested entire plants in the field and brought them to the laboratory for further study. Before an epiphyte was removed from the host tree, we enclosed it in a plastic bag to prevent highly mobile animals from escaping. While it was easy to define an ‘inhabitant’ fauna for the bromeliads, whose funnel-like structure actually enclosed arthropods, and resident organisms usually sought refuge between the leaf bases after disturbance rather than attempting to escape (see also Richardson 1999), it was more difficult in the case of *Dimerandra*. Its open structure was much less shut-off from the immediate surroundings (Figure 1). Here, we sampled all animals that were found on or between the stems and leaves of an orchid stand. In doing so, we probably caused a certain bias in the data by collecting some arthropods (e.g., ants) that were not genuinely associated with the orchid, so-called ‘tourists’ or ‘transient species’.

Laboratory treatment. Small and medium-sized epiphytes were dismantled leaf by leaf in plastic bins with fluon lining (Klüver & Schulz, Hamburg, Germany) on the rim, whereas large epiphytes were examined on a modified table with a coarse grid surface roofed with mosquito netting. Underneath the table we attached a large funnel of plastic sheeting ending in a capture vessel in which arthropods that had fallen through the grid were collected. Arthropods were then transferred into 70% ethanol and sorted to morphospecies based on external morphology (in the following referred to as species). Immatures were recorded as species only if presence of the respective adult could be excluded (e.g., several lepidopteran larvae were collected, but no mature moths or butterflies). A complete record of species is given in Appendix 1.

All animals were cross-referenced with a voucher collection to ensure singularity of assigned species. We collected only individuals over 1–2 mm body size and thereby omitted Collembola and Acari from the survey. Another small-sized group, the Psocopterans, were collected only occasionally in *Vriesea* and were not cross-referenced (although relatively species-rich as the quantitative *Tillandsia* collection indicated). We excluded Psocopterans from the analyses. Vouchers were deposited at the Forstwissenschaftliche Fakultät, Technische Universität München, Germany.

Guild assignment. Species were assigned to feeding guilds, mainly following Stork (1987b), except that we replaced his ‘scavengers, dead wood and fungal feeders’ by ‘detritivores’. We excluded ants from the analysis for the following reasons. Firstly, a majority of ants are probably opportunist feeders (Hölldobler & Wilson 1990, Stork 1987b). Secondly, when comparing numbers of individuals, social insects pose a problem due to their clumped occurrence. We also excluded a single case of an aggregation of ant-tended homopterans with 123 individuals on a *Tillandsia* plant. Animals were assigned to either predators,

detrivores, herbivores, tourists, ants, or arthropods with unknown feeding behaviour (Appendix 1).

Statistics

The maximum leaf length (or stem length, respectively) of every harvested epiphyte was measured in order to estimate total plant biomass from known regressions (Schmidt & Zotz 2001, Zotz, unpubl.). Statistical analysis was performed with STATISTICA (StatSoft Inc., Oklahoma, USA). Biomass and faunal parameters across the three epiphyte species were compared with ANOVA and ANCOVA. As a measure for α -diversity we used species richness, i.e. the absolute number of species that were found in one sampling unit. The Sørensen index was used as a measure of β -diversity (Magurran 1988). To test for differences in the species composition of the faunas among the epiphyte species, we ran multi-dimensional scaling analyses based on a dissimilarity matrix of 1 – Sørensen values, following the protocol of Southwood (1978). Three-dimensional scaling yielded results similar to two-dimensional scaling (not shown).

RESULTS

Faunistic composition

In total we collected 3694 arthropods belonging to 89 species, of which 29% were singletons (Table 1, Appendix 1). Nearly 10% of the 90 harvested epiphytes (six *Dimerandra*, three *Vriesea* and one *Tillandsia*) yielded no animals at

Table 1. Faunistic characteristics and statistics of the arthropod assemblages inhabiting the three investigated epiphytes. Data are from quantitative destructive sampling of 30 plants per species.

	<i>Vriesea</i>	<i>Tillandsia</i>	<i>Dimerandra</i>	P-levels of ANOVA/ANCOVA
Individuals	2375	1075	244	
Morphospecies	41	51	11	
Singletons (% of all species)	4 (10%)	20 (39%)	5 (46%)	
Mean number of individuals per plant (max)*	79.0 (645)	35.9 (215)	7.9 (85)	ANOVA: P < 0.005 ANCOVA: P = 0.68
Mean number of morphospecies per plant (max)*	8.4 (22)	5.2 (13)	1.2 (5)	ANOVA: P < 0.001 ANCOVA: P < 0.002**
Most numerous taxon (n individuals; % of total individuals)	ants (1806; 76%)	ants (695; 65%)	ants (211; 87%)	
Most diverse taxon (n morphosp.; % of total morphosp.)	ants (13; 32%)	spiders (16; 31%)	spiders/ants, both (4; 37%)	
Mean biomass (g dry weight) (range)	63.3 (0.2–202.3)	4.5 (1.2–87.0)	3.7 (0.4–11.5)	ANOVA: P < 0.001

*Some smaller plants of each of the three epiphyte species contained no arthropods, i.e. they had zero minima (not shown).

**With host plant biomass as covariate.

all. Those were consistently plants of small size. There was a striking difference in numbers of (arthropod) individuals in the three investigated plant species. *Vriesea*, the largest epiphyte, held by far the largest number of individuals, and both mean and maximum number of individuals per plant well exceeded those of the other two plant species. *Dimerandra*, the smallest species, had the lowest values in all three measures. The differences in arthropod individuals per plant were highly significant (ANOVA, $P < 0.005$). There was a similar three-step sequence in total plant biomass (ANOVA, $P < 0.001$), again reflecting the size difference of the three epiphyte species. Indeed, when we controlled for host plant size by running analyses of covariance (ANCOVA) with biomass as covariate, the differences in numbers of individuals per plant across the epiphyte species became non-significant. This indicates that abundance of inhabiting arthropods was a function of plant size rather than of plant species.

Species richness, which we used as a measure of α -diversity, showed a different pattern (Table 1). Again, the numbers of species per plant were significantly different (ANOVA, $P < 0.001$), and both mean and maximum number of species per plant were still highest in *Vriesea* and lowest in *Dimerandra*. But in contrast to the individual counts presented above, these differences remained significant even when controlling for the increase in host plant biomass (ANCOVA, $P = 0.002$). Remarkably, overall species richness and proportion of singletons was highest in the medium-sized epiphyte *Tillandsia*, not in *Vriesea*, the largest.

The most abundant taxon in all three epiphytes was the ants, comprising almost three-quarters of the total fauna (73%). Similarly consistent, the second most numerous taxon was the spiders, accounting for nine per cent of the species pool. The remaining 18% were comprised of 17 other arthropod orders (see Appendix 1 for a complete record).

The influence of host plant biomass

Correlation analyses revealed that both numbers of species per plant and numbers of individuals per plant were a function of epiphyte biomass (Table 2). When pooling the 90 study plants, all relationships were highly significant ($P < 0.001$). However, analysing the epiphyte species separately, all correlations with plant biomass were non-significant in *Dimerandra* ($P > 0.5$). As social insects, ants were frequently found in large numbers, and therefore unevenly augmented individual counts. Indeed, excluding ants from the analyses, the correlations tightened in the two bromeliads (Table 2). This was not the case in *Dimerandra* (Table 2).

Differences in species composition (β -diversity)

Besides significant differences in species richness (α -diversity), the species composition of the arthropod assemblages associated with the three epiphyte species showed remarkably little overlap. Of all 89 species, only a single one occurred in all three epiphytes: a minute ant of the genus *Solenopsis*, which is

Table 2. Results of correlation analyses.

Correlation of host plant biomass with	n	r^2	P
(a) numbers of species per plant			
all study plants	90	0.73	<0.001
<i>Vriesea sanguinolenta</i>	30	0.72	<0.001
<i>Tillandsia fasciculata</i>	30	0.55	<0.001
<i>Dimerandra emarginata</i>	30	(0.015)	0.53, n.s.
(b) numbers of individuals (including ants)			
all study plants	90	0.51	<0.001
<i>Vriesea sanguinolenta</i>	30	0.58	<0.001
<i>Tillandsia fasciculata</i>	30	0.15	0.034
<i>Dimerandra emarginata</i>	30	(0.003)	0.78, n.s.
(c) numbers of individuals (excluding ants)			
all study plants	90	0.82	<0.001
<i>Vriesea sanguinolenta</i>	30	0.80	<0.001
<i>Tillandsia fasciculata</i>	30	0.60	<0.001
<i>Dimerandra emarginata</i>	30	(0.001)	0.86, n.s.

n.s.= not significant

very common throughout the neotropics (Longino & Nadkarni 1990) and very abundant in the study area (Stuntz, unpubl.). *Dimerandra* shared only one other species with *Tillandsia* and another one with *Vriesea*, both of which were ants. The two most common ant species in *Dimerandra* were never found in *Vriesea* and vice versa. The arthropod fauna of the two bromeliads was slightly more similar: *Tillandsia* and *Vriesea* had eleven species in common, although often in very different abundances (see Appendix 1). They shared five ant species, four spider species, one beetle and a cockroach species.

As a measure of faunistic similarity, we computed the Sørensen index for the arthropod communities of the three epiphyte species and, as expected, found very low values between *Dimerandra* and both *Vriesea* ($S_{\text{or}} = 0.08$) and *Tillandsia* ($S_{\text{or}} = 0.06$), and a slightly higher index between *Vriesea* and *Tillandsia* ($S_{\text{or}} = 0.24$). A multi-dimensional scaling analysis, comparing the dissimilarities between the arthropod assemblages of individual plants (Southwood 1978), divided the fauna into three clearly distinct clusters along the x-axis, corresponding to the three epiphyte species: Figure 2 illustrates both the similarity of the arthropod assemblages *within* the epiphyte species as well as the faunistic dissimilarities *between* them.

Guild composition: feeding and hunting strategies

Similar to the taxonomic structure of the three faunas, the guild composition differed markedly among the epiphyte species (Figure 3). The two dominant guilds were detritivores and predators, together comprising approximately 80% of the animal assemblages. While the fauna associated with *Dimerandra* consisted almost entirely of predators (mainly spiders), the contribution of the predatory guild to the total fauna decreased in *Tillandsia* and even more in *Vriesea*, coinciding with an increase in the proportion of detritivores. Remarkable was the paucity of herbivores: they constituted only 6% in *Dimerandra*

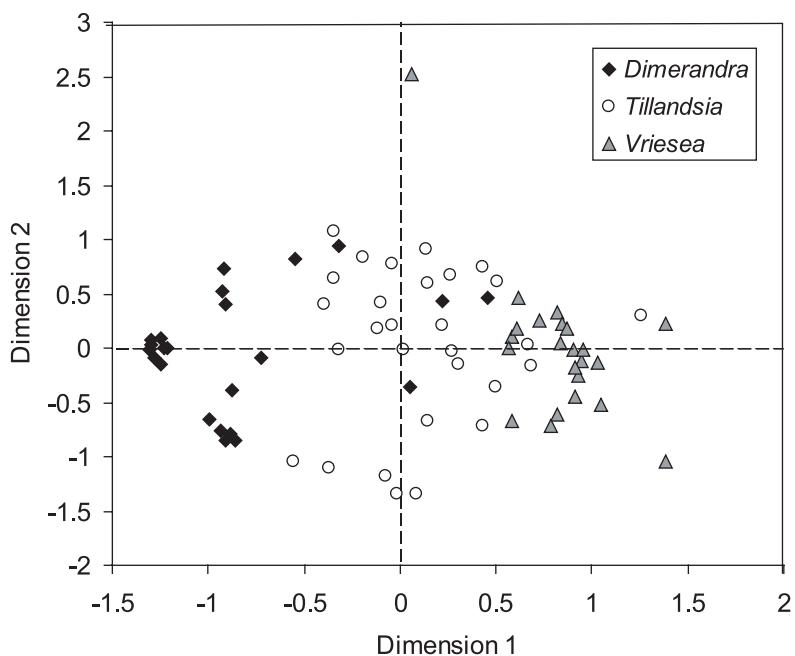


Figure 2. Two-dimensional scaling analyses of the arthropod assemblages of the three epiphyte species, based on a dissimilarity matrix ($1 - \text{Sørensen values}$). The two outliers of *Vriesea sanguinolenta* represent plants of small size with very few individuals.

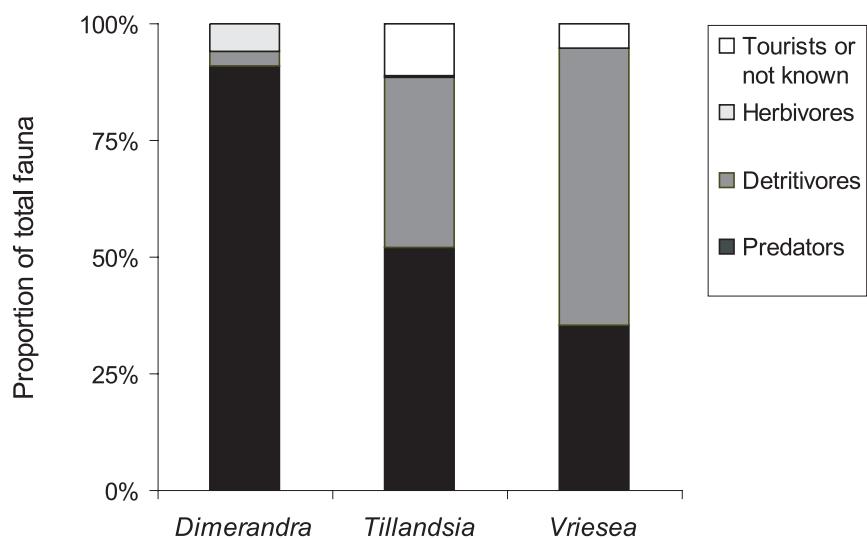


Figure 3. Guild composition of the inhabiting faunas of the three epiphytes. The first guild comprises a small percentage of tourists, and some arthropods with unknown feeding behaviour. For guild assignment see Appendix 1.

(Heteroptera sp. 1 and Thysanoptera sp. 1, see Appendix 1), 0.4% in *Tillandsia* (Heteroptera sp. 2), while none were found in *Vriesea*. All phytophagous species were sap-suckers; we found no chewing herbivores.

Even within a given feeding guild further differences were detected. Spiders, the numerically most abundant group after the ants in all three study species (Table 1), could be divided conveniently into two major hunting guilds: web-builders and active hunters (Figure 4). Again, there were distinct differences among epiphyte species. The spider fauna in *Dimerandra* consisted nearly completely of web-builders (97%), while almost all spiders in *Vriesea* were hunters (98%). *Tillandsia* was somewhat intermediate but resembled more closely the other bromeliad with 83% of hunting spiders.

DISCUSSION

A simple relationship?

The largest epiphyte species, *Vriesea*, held the most numerous arthropod assemblage and, correspondingly, *Dimerandra*, the smallest species, harboured the fewest animals (Table 1). Within epiphyte species, arthropod diversity and abundance also increased with plant size (Table 2). This is consistent with Lawton's (1983) 'size per se' hypothesis, which predicts that larger plants are more likely to be discovered and colonized by arthropods and consequently can support larger populations and a greater diversity of species. However, in *Dimerandra*, plant size correlated neither with species richness nor abundance (Table 2). Its rather open structure may be less suited for arthropods compared to the set of interconnected, litter- and moisture-filled tanks featured by the

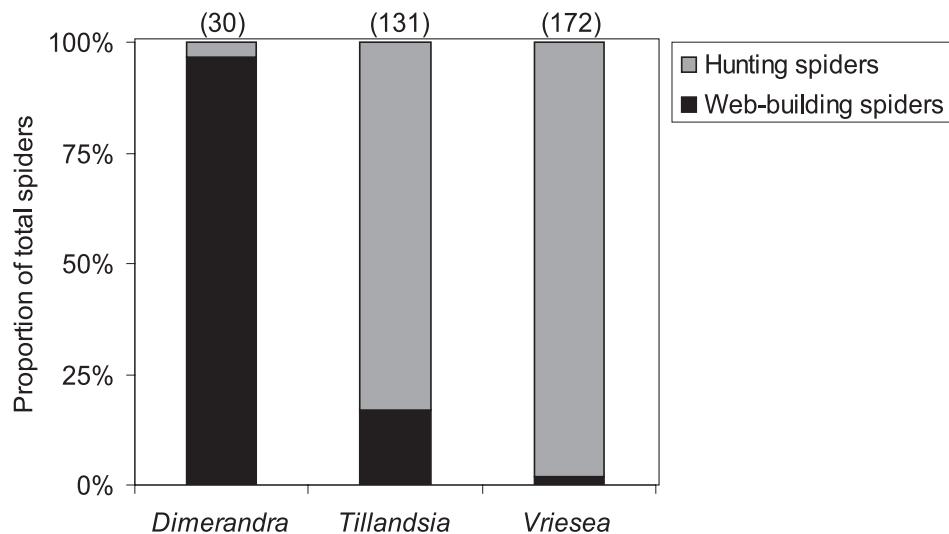


Figure 4. Proportion of web-building versus hunting spiders as percentage of total spider assemblage. The absolute numbers of the spider totals are indicated in parentheses above the columns.

bromeliads. The orchid's fauna consisted almost entirely of web-building spiders, who can rely on self-made structures for a living, and ants, which were probably foraging workers.

On a much larger scale, it has been reported decades ago that larger areas contain more species and individuals of animals than smaller ones (Arrhenius 1923, Connor *et al.* 2000, Dony 1977, Williams 1943). In a similar manner, a larger host plant with more available space, more structure and thus more niches, could sustain more numerous and diverse animal populations. For example, Richardson (1999) stated that bromeliads behaved as islands (compare MacArthur & Wilson 1967) with species richness and abundance of their faunal communities correlating with plant size. On the other hand, the differences in faunal diversity among epiphyte species could not be explained by plant size alone: species richness per plant remained significantly different across epiphyte species when controlling for host biomass (Table 1). Furthermore, if the differences in species per plant were merely a function of host size or biomass, then the species pool of a smaller plant should be a subset of the more diverse species pool of the larger epiphyte. This, however, was clearly not the case. The three epiphyte species fostered strikingly distinct arthropod faunas, both taxonomically (Figure 2, Appendix 1) and ecologically (Figure 3, Figure 4), even though growing in close vicinity on the same host tree species.

Microclimate

Invertebrates dwelling in as harsh an environment as the forest canopy are probably substantially constrained by microclimatic parameters (Almquist 1970, Basset 1992, Didham *et al.* 1998, Kaspari 1993, Nicolai 1986, Riechert & Tracy 1975), and might often need to seek shelter from climatic extremes. In a companion study, we found that epiphytes significantly influence temperature and humidity conditions in their immediate surroundings (Stuntz *et al.* 2001). In the proximity of *Vriesea* or *Tillandsia*, substrate temperatures were lower than on exposed branches of the host tree, whereas *Dimerandra* did not exert such a cooling effect. Thus, the heat-moderating influence of the two bromeliads could also contribute to the greater faunal diversity and abundance in comparison with *Dimerandra*.

Differences in feeding guild composition and the importance of litter

The pronounced differences in arthropod guild composition across plant species (Figure 3) probably reflect the distinct resources the epiphytes provide for animal life: the two bromeliads feature tanks that can hold leaf litter, debris and water. Between the leaf bases, dead leaves decompose, thus creating soil-like microsites, an important prerequisite for detritivorous species (Benzing 1990, Richardson 1999). *Dimerandra*, with its simpler structure, lacked this essential resource of decaying substrate, and had consequently hardly any detritivores.

Leaf litter is a very important microhabitat in tropical forest canopies. For

example, dead curled leaves suspended in the vegetation may contain considerably more insects than green leaves (Gradwohl & Greenberg 1980, 1982), and some insectivorous bird species even became specialist feeders searching for insects in suspended leaf litter (Gradwohl & Greenberg 1982, Nadkarni & Matelson 1989, Remsen & Parker 1984). Leaf litter is used as a nesting site by a great variety of arboreal ant species (Longino & Nadkarni 1990). Moreover, the amount of detritus in bromeliad tanks correlated with diversity and abundance of arthropods (Richardson 1999, Zotz & Ziegler, unpubl. data). Fragoso & Rojas-Fernandez (1996), who found a correlation between bromeliad size and numbers of inhabiting earthworms, also attributed this relationship to be an effect of tank litter and moisture. Thus, the lack of litter in *Dimerandra* might not only explain its deficiency of detritivores, but also its small fauna as a whole.

The resource diversity hypothesis (Lawton 1983) predicts that plants with a greater variety of structural variables or resource types support a greater diversity and abundance of arthropods. Although the bromeliads in our study barely provide the important resources leaf litter and debris themselves, their architecture allows them to supply it anyway: bromeliads impound 'external' leaf litter from canopy foliage in their tanks, thus attaining a greater structural complexity indirectly.

The extreme scarcity of herbivores associated with the three epiphyte species was remarkable (Figure 3). No phytophagous species was found in *Vriesea*, the epiphyte with the greatest biomass (Table 1) and largest leaf area (Stuntz *et al.*, unpubl.). Only three singletons could be assigned as sap-suckers. Herbivory in epiphytes has not been studied thoroughly (Benzing 1990, Schmidt & Zotz 2000). Extensive defoliation is rare in neotropical epiphytes, and many bromeliads and xeromorphic orchids seem to be remarkably immune to herbivores (Benzing 1990). Bromeliad leaves contain very little nitrogen (Stuntz & Zotz 2001), and might thus be unattractive to herbivores. Schmidt & Zotz (2000) reported that *Vriesea* had only one main herbivore (*Napaea eucharilla* Bates, a lepidopteran larva), but occasionally severe damage was observed. In *Dimerandra* very little herbivory was observed in a three-year demographic study (Zotz 1998). No comparable data are available for *Tillandsia*. Overall, the scarcity of phytophagous insects in our study is consistent with the general notion that epiphytes are rather unattractive for herbivores (Benzing 1990), but inclusion of rainy season data could well alter this conclusion.

Differences in spider composition

The physical structure of environments has an important influence on the composition of spider communities (Cherrett 1964, Duffey 1966, Gunnarson 1990, Halaj *et al.* 1998, Hatley & MacMahon 1980, Rypstra 1983, Wise 1993). Strong predominance of web-building spiders on *Dimerandra* suggests that this orchid provides suitable web attachment sites with its numerous erect and densely clustered stems and leaves. This contrasts with *Vriesea* featuring widely

spaced and arching leaves, which probably seem much less attractive to web builders (Figure 4). On the other hand, litter depth and complexity have been shown to increase the diversity of hunting spiders (Stevenson & Dindal 1982, Uetz 1979). Some spiders, e.g. Gnaphosidae and some Clubionidae, were observed to use dead, curled leaves suspended in the bromeliad tanks as retreats (Stuntz, pers. obs.). Once more, the lack of litter in *Dimerandra* could partially explain the paucity of hunting spiders in this orchid.

Another factor influencing spider distribution is prey availability (Greenstone 1984, Halaj *et al.* 1998, Rypstra 1983, Wise 1993). Web-building spiders can capture flying insects that might not even be closely associated with their direct environment (so-called 'tourists'). This peculiarity probably allows web-builders to survive in *Dimerandra*, where few arthropods other than spiders or ants live (see Table 1 and Appendix 1), both of which are not preferred spider prey. In contrast, hunting spiders forage in their habitat for other more-or-less mobile arthropods, and cannot rely on aerial prey. The debris-filled tanks of *Vriesea*, and, to a lesser extent, *Tillandsia*, apparently harbour enough arthropods to sustain a substantial population of hunting spiders, in contrast to the individual-poor fauna in *Dimerandra*.

Spiders are very important predators in tropical forests (Dial & Roughgarden 1995, Nentwig 1985, Wise 1993), sometimes even the major arboreal invertebrate predator (Pfeiffer 1996). Thus, if epiphytes strongly influence spider composition, it is possible that they indirectly influence the arthropod faunas of tropical canopies. This hypothesis will now be tested at the level of entire tree crowns.

Conclusion

We investigated the arthropod faunas inhabiting three different species of vascular epiphyte and found pronounced differences in species richness, species composition and guild structure. Total arthropod abundances were primarily a function of plant biomass irrespective of epiphyte species, while plant species identity significantly influenced both species richness and composition of the respective arthropod fauna. Our results emphasize the importance of plant size and structure, in particular the ability to hold leaf litter and debris. In conclusion, epiphytes constitute important microhabitats for a diverse and numerous fauna, and different epiphytes fostered taxonomically and ecologically distinct arthropod assemblages. Whether epiphytes influence local and between-habitat diversity at the level of entire tree crowns remains the subject of our future studies.

ACKNOWLEDGEMENTS

We thank Michael Matzat and Christoph Meyer (both Würzburg) who sampled and investigated the *Tillandsia* and *Dimerandra*. John T. Longino identified the ants. Uli Kern contributed the epiphyte drawing. The manuscript profited from

comments of Yves Basset, Timothy Schowalter and an anonymous referee. This study was funded by the German Academic Exchange Service (DAAD) and the Deutsche Forschungsgemeinschaft (Graduiertenkolleg of the Department of Botany, Universität Würzburg).

LITERATURE CITED

- ALMQVIST, S. 1970. Thermal tolerances and preferences of some dune-living spiders. *Oikos* 21:229–234.
- ARRHENIUS, O. 1923. Statistical investigations on the constitution of plant associations. *Ecology* 4:68–73.
- BASSET, Y. 1992. Influence of leaf traits on the spatial distribution of arboreal arthropods within an overstorey rainforest tree. *Ecological Entomology* 17:8–16.
- BENZING, D. H. 1990. *Vascular epiphytes*. Cambridge University Press, Cambridge. 354 pp.
- CHERRETT, M. 1964. The distribution of spiders on the Moor House National Nature Reserve, Westmoreland. *Journal of Animal Ecology* 67:27–48.
- CONNOR, E. F., COURTNEY, A. C. & YODER, J. M. 2000. Individuals-area relationships: the relationship between animal population density and area. *Ecology* 81:734–748.
- CROAT, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford. 943 pp.
- DIAL, R. & ROUGHGARDEN, J. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* 76:1821–1834.
- DIDHAM, R. K., HAMMOND, P. M., LAWTON, J. H., EGGLETON, P. & STORK, N. E. 1998. Beetle species responses to tropical forest fragmentation. *Ecological Monographs* 68:295–323.
- DONY, J. G. 1977. Species-area relationships in an area of intermediate size. *Journal of Ecology* 65:475–484.
- DUFFEY, E. 1966. Spider ecology and habitat structure. *Senckenbergiana Biologica* 47:45–49.
- ERWIN, T. L. 1983. Tropical forest canopies: the last biotic frontier. *Bulletin of the Entomological Society of America* 29:14–19.
- FRAGOSO, C. & ROJAS-FERNANDEZ, P. 1996. Earthworms inhabiting bromeliads in Mexican tropical rain forests: ecological and historical determinants. *Journal of Tropical Ecology* 12:729–734.
- GRADWOHL, J. & GREENBERG, R. 1980. The formation of antwren flocks on Barro Colorado island, Panama. *Auk* 97:385–395.
- GRADWOHL, J. & GREENBERG, R. 1982. The effect of a single species of avian predator on the arthropods of aerial leaf litter. *Ecology* 63:581–583.
- GREENSTONE, M. H. 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. *Oecologia* 62:299–304.
- GUNNARSON, B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *Journal of Animal Ecology* 59:743–752.
- HALAJ, J., ROSS, D. W. & MOLDENKE, A. R. 1998. Habitat structure and prey availability as predictors of the abundance and community organization of spiders in Western Oregon forest canopies. *Journal of Arachnology* 26:203–220.
- HATLEY, C. & MACMAHON, J. A. 1980. Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology* 9:632–639.
- HÖLLDOBLER, B. & WILSON, E. O. 1990. *The ants*. Springer Verlag, Berlin. 732 pp.
- KASPARI, M. 1993. Body size and microclimate use in Neotropical granivorous ants. *Oecologia* 96:500–507.
- LAWTON, J. H. 1983. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* 28:23–39.
- LAWTON, J. H. 1986. Surface availability and community structure: the effects of architecture and fractal dimension of plants. Pp. 317–331 in Juniper, B. E. & Southwood, T. R. E. (eds). *Insects and the plant surface*. Edward Arnold, London.
- LEIGH, E. G., RAND, A. S. & WINDSOR, D. M. 1982. *The ecology of a tropical forest. Seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington DC. 468 pp.
- 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.
- MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton. 203 pp.
- MAGURRAN, A. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton. 180 pp.
- NADKARNI, N. M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *American Zoologist* 34:70–78.
- NADKARNI, N. M. & MATELSON, T. J. 1989. Bird use of epiphyte resources in neotropical trees. *The Condor* 91:891–907.

- NENTWIG, W. 1985. Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Oecologia* 66:580–594.
- NICOLAI, V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69:148–160.
- PFEIFFER, W. J. 1996. Arboreal arachnids. Pp. 247–271 in Reagan, D. P. & Waide, R. B. (eds). *The food web of a tropical forest*. University of Chicago Press, Chicago.
- PIANKA, E. R. 1967. On lizard species diversity: North American flatland deserts. *Ecology* 48:333–351.
- REMSSEN, J. R. & PARKER, T. A. 1984. Arboreal dead-leaf searching birds of the neotropics. *The Condor* 86:36–41.
- RICHARDSON, B. A. 1999. The bromeliad microcosm and the assessment of faunal diversity in a neotropical forest. *Biotropica* 31:321–336.
- RIECHERT, S. E. & TRACY, C. R. 1975. Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. *Ecology* 56:265–284.
- RYPSTRA, A. L. 1983. The importance of food and space in limiting web-spider densities; a test using field enclosures. *Oecologia* 59:312–316.
- SCHMIDT, G. & ZOTZ, G. 2000. Herbivory in the epiphyte, *Vriesea sanguinolenta* Cogn. & Marchal (Bromeliaceae). *Journal of Tropical Ecology* 16:829–839.
- SCHMIDT, G. & ZOTZ, G. 2001. Ecophysiological consequences of differences in plant size – *in situ* carbon gain and water relations of the epiphytic bromeliad, *Vriesea sanguinolenta* Cogn. & Marchal. *Plant, Cell and Environment* 24:101–112.
- SOUTHWOOD, T. R. E. 1978. *Ecological methods*. Chapman & Hall, London. 524 pp.
- STEVENSON, B. G. & DINDAL, D. L. 1982. Effect of leaf shape in forest litter spiders: community organization and microhabitat selection of immature *Enoplognatha ovata* (Clerck) (Theridiidae). *Journal of Arachnology* 10:165–178.
- STORK, N. E. 1987a. Arthropod faunal similarity of Bornean rain forest trees. *Ecological Entomology* 12:219–226.
- STORK, N. E. 1987b. Guild structure of arthropods from Bornean rain forest trees. *Ecological Entomology* 12:69–80.
- STUNTZ, S., SIMON, U. & ZOTZ, G. 1999. Assessing potential influences of vascular epiphytes on arthropod diversity in tropical tree crowns. *Selbyana* 20:276–283.
- STUNTZ, S., SIMON, U. & ZOTZ, G. 2001. Rainforest airconditioning: the moderating influence of epiphytes on the microclimate in tropical tree crowns. *Journal of Biometeorology* submitted.
- STUNTZ, S. & ZOTZ, G. 2001. Photosynthesis in vascular epiphytes. A survey of 27 species of diverse taxonomic origin. *Flora* 196:132–141.
- UETZ, G. W. 1979. The influence of variation in litter habits on spider communities. *Oecologia* 40:29–42.
- WILLIAMS, C. B. 1943. Area and the number of species. *Nature* 152:264–267.
- WINDSOR, D. M. 1990. *Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama*. Smithsonian Institution Press, Washington DC. 145 pp.
- WISE, D. H. 1993. *Spiders in ecological webs*. Cambridge University Press, Cambridge. 328 pp.
- ZOTZ, G. 1998. Demography of the epiphytic orchid, *Dimerandra emarginata*. *Journal of Tropical Ecology* 14:725–741.
- ZOTZ, G., DIETZ, H. & BERMEJO, P. 1999. The epiphyte community of *Annona glabra* on Barro Colorado Island, Panama. *Journal of Biogeography* 26:761–776.

APPENDIX 1

Species list and guild assignment. Given are numbers of individuals collected in 30 plants per epiphyte species. The abbreviations for the guilds are as follows: p – predators; d – detritivores; t – tourists; s – sucking herbivores; a – ants; n – not known; w – web-building spider; h – actively hunting spider

Morphospecies name	<i>Vriesea</i>	<i>Tillandsia</i>	<i>Dimerandra</i>	Feeding guild	Hunting guild (spiders)
<i>SPIDERS (ARANAEAE)</i>					
Araneidae sp. 2	–	–	17	p	w
Araneidae sp. 21	2	–	–	p	w
Araneidae sp. 23	–	2	–	p	w
<i>Corinna</i> sp. 4	18	3	–	p	h
Ctenidae sp. 1	79	10	–	p	h
Gnaphosidae sp. 1	8	–	–	p	h
<i>Gertschosa</i> sp. 4	–	1	–	p	h
Linyphiidae sp. 7	–	1	–	p	w
Linyphiidae sp. 1	–	–	1	p	w
<i>Mazax</i> sp. 2	–	4	–	p	h
<i>Oonops</i> sp. 1	–	2	–	p	w
<i>Othiotops</i> cf. <i>macleayi</i>	–	1	–	p	h
Salticidae sp. 10	2	30	–	p	h
Salticidae sp. 13	–	1	–	p	h
Salticidae sp. 18	–	10	–	p	h
Salticidae sp. 2	2	–	–	p	h
Salticidae sp. 21	–	1	–	p	h
Salticidae sp. 22	–	3	–	p	h
Salticidae sp. 3	2	–	–	p	h
Salticidae sp. 31	–	1	–	p	h
Salticidae sp. 37	–	–	1	p	h
<i>Scytodes</i> sp. 1	56	35	–	p	h
Tetragnathidae sp. 1	–	–	2	p	w
<i>ANTS (FORMICIDAE)</i>					
<i>Azteca</i> cf. <i>trigona</i>	–	97	–	a	
<i>Camponotus</i> (<i>Myrmobrachys</i>) sp. (cf. <i>auricomus</i>)	256	–	2	a	
<i>Camponotus atriceps</i>	–	1	–	a	
<i>Camponotus sexguttatus</i>	60	138	–	a	
<i>Crematogaster brevispinosa crucis</i>	2	–	–	a	
<i>Crematogaster carinata</i>	594	2	–	a	
<i>Cyphomyrmex rimosus</i> complex	567	–	–	a	
<i>Dolichoderus debilis</i>	80	–	–	a	
<i>Ectatomma ruidum</i>	35	–	–	a	
<i>Odontomachus bauri</i>	–	1	–	a	
<i>Odontomachus ruginodis</i>	2	1	–	a	
<i>Pachycondyla villosa</i>	1	–	–	a	
<i>Pheidole</i> cf. <i>flavens</i>	14	61	–	a	
<i>Pheidole punctatissima</i>	2	–	–	a	
<i>Pseudomyrmex elongatus</i>	54	–	–	a	
<i>Solenopsis</i> sp. 1	–	–	145	a	
<i>Solenopsis zeteki</i>	136	257	15	a	
<i>Tapinoma melanocephalum</i>	–	10	–	a	
<i>Tetramorium bicarinatum</i>	–	2	–	a	
<i>Wasmannia rochai</i>	–	125	49	a	

Appendix 1. cont.

Morphospecies name	<i>Vriesea</i>	<i>Tillandsia</i>	<i>Dimerandra</i>	Feeding guild	Hunting guild (spiders)
<i>OTHERS</i>					
Blattodea sp. 1	104	52	—	d	
Blattodea sp. 2	2	—	—	d	
Blattodea sp. 3	—	3	—	d	
Coleoptera sp. 1	2	10	—	n	
Coleoptera sp. 2	1	—	—	n	
Coleoptera sp. 3	2	—	—	n	
Coleoptera sp. 4	—	1	—	n	
Coleoptera sp. 5	—	1	—	n	
Coleoptera sp. 6	—	1	—	n	
Coleoptera sp. 7 (Larva)	2	—	—	n	
Coleoptera sp. 8 (Larva)	3	—	—	n	
Coleoptera sp. 9 (Larva)	7	—	—	n	
Chilopoda sp. 1	17	—	—	p	
Chilopoda sp. 2	10	—	—	p	
Chilopoda sp. 3	—	1	—	p	
Diptera sp. 1	5	—	—	t	
Diptera sp. 2 (Larva)	—	13	—	d	
Diptera sp. 3 (Larva)	—	2	—	d	
Diptera sp. 4 (Larva)	—	3	—	d	
Diptera sp. 5 (Larva)	23	—	—	d	
Diptera sp. 6 (Larva)	2	—	—	d	
Diptera sp. 7 (Larva)	55	—	—	d	
Diptera sp. 8 (Larva)	13	—	—	d	
Diptera sp. 9 (Larva)	1	—	—	d	
Diptera sp. 10 (Larva)	—	7	—	d	
Diplopoda sp. 1	18	—	—	d	
Embioptera sp. 1	—	—	1	d	
Embioptera sp. 2	—	7	—	d	
Heteroptera sp. 1	—	—	1	s	
Heteroptera sp. 2	—	1	—	s	
Homoptera sp. 1	—	128	—	s	
Isopoda sp. 1	119	—	—	d	
Isoptera sp. 1	—	3	—	d	
Lepidoptera sp. 1 (Larva)	—	1	—	n	
Lepidoptera sp. 2 (Larva)	—	3	—	n	
Lepidoptera sp. 3 (Larva)	—	2	—	n	
Lepidoptera sp. 4 (Larva)	—	2	—	n	
Lepidoptera sp. 5 (Larva)	7	—	—	n	
Orthoptera sp. 2	—	1	—	n	
Orthoptera sp. 1	—	1	—	n	
Odonata sp. 1	—	1	—	t	
Pseudoscorpiones sp. 1	—	2	—	d	
Scorpiones sp. 1	3	—	—	p	
Trichoptera sp. 1	—	1	—	t	
Trichoptera sp. 2	—	3	—	t	
Thysanoptera sp. 1	—	—	1	s	