THE INFLUENCE OF EPIPHYTES ON ARTHROPODS IN THE TROPICAL FOREST CANOPY

Dissertation zur Erlangung des
naturwissenschaftlichen Doktorgrades der
Bayerischen Julius-Maximilians-Universität Würzburg

vorgelegt von
Sabine Stuntz
aus München

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For my loving mother
and in loving memory of my father

"As earnestly men may seek to understand the workings of the universe, they must remember that God is not hampered by their limited logic – that all observed effects may have been wrought by Him in any one of an infinite number of omnipotent ways, and these must ever evade mortal comprehension."

from *Galileo's Daughter* by Dava Sobel

CONTENTS

1 THE INFLUENCE OF EPIPHYTES ON CANOPY ARTHROPODS – SUMMARIZING INTRODUCTION 1
Setting the scene – the role of epiphytes for arthropod diversity 1
Choosing a feasible system – *Annona glabra* and its epiphytes 2
Aim of the dissertation 3
Synopsis 3
2 TRAPPING TECHNIQUES – MONITORING BIODIVERSITY IN THE CANOPY 5
ABSTRACT 5
INTRODUCTION 5
STUDY SITE 6
TRAPPING PROTOCOL 6
RESULTS 7
DISCUSSION 8
3 EPIPHYTES MODERATE CLIMATIC EXTREMES IN TROPICAL TREE CROWNS 9
ABSTRACT 9
INTRODUCTION 9
STUDY SITE 10
METHODS 10
Temperature 11
Evaporative drying rate 12
Evapotranspiration 12
RESULTS 12
Temperature 12
Evaporative drying rate 15
Evapotranspiration 15
DISCUSSION 15
Epiphytic airconditioning 15
Host tree effects 16
The arthropod perspective 16
Conclusion 17
4 EPIPHYTES AS MICROHABITATS: THE ARTHROPOD FAUNA INHABITING THREE EPIPHYTE SPECIES 18
ABSTRACT 18
INTRODUCTION 18
STUDY SITE 19
METHODS 19
Study organisms 19
Sampling the fauna 20
Statistics 21
RESULTS 21
Faunistic composition 21
The influence of host plant biomass 23
Differences in species composition (β-diversity) 23

Guild composition: feeding and hunting strategies 24
DISCUSSION 26
A simple relationship? 26
Microclimate 26
Differences in feeding guild composition and the importance of litter 27
Differences in spider composition 27
Conclusion 28
5 ORDINAL COMPOSITION AND SEASONALITY OF THE ARTHROPOD FAUNA IN TREE CROWNS WITH DIFFERENT EPIPHYTES 29
ABSTRACT 29
INTRODUCTION 29
STUDY SITE 31
METHODS 31
Study trees and epiphytes 31
Sampling protocol 32
Epiphyte biomass and tree phenology 32
Statistics 32
RESULTS 33
Composition of the fauna 33
Seasonality and Phenology 34
Host tree traits 36
Differences among trees with different epiphyte loads 36
DISCUSSION 38
Faunal composition 38
Seasonality 39
Do epiphytes influence arboreal arthropods? 41
6 DO NON-MYRMECOPHILIC EPIPHYTES INFLUENCE COMMUNITY STRUCTURE OF ARBOREAL ANTS? 42
ABSTRACT 42
INTRODUCTION 42
STUDY SITE 43
METHODS 43
Study trees and epiphytes 43
Trapping and processing the ants 44
Epiphyte biomass and tree phenology 44
Statistics 44
RESULTS 45
Composition of the fauna 45
Comparison of tree/epiphyte categories 47
DISCUSSION 50
Annona glabra as model system for tropical canopies? 50
Dominants, submissives and mosaics 50
Epiphytes and ants 52
Conclusion 52
7 THE BEETLE FAUNA OF TROPICAL TREE CROWNS WITH DIFFERENT EPIPHYTES 53
ABSTRACT 53
INTRODUCTION 53

STUDY SITE 54
METHODS 54
Study trees and epiphytes 54
Sampling protocol 55
Epiphyte biomass and tree phenology 55
Statistics 55
RESULTS 56
Composition of the fauna 56
Comparison of trees with different epiphyte loads 57
Guild composition 60
Phytophagous beetles 61
DISCUSSION 62
Faunal similarity among trees 62
Seasonal rhythms 63
Herbivory and Epiphytes 64
Conclusion 64

8 EPIPHYTES AS STRUCTURAL ELEMENTS OF THE CANOPY - SPIDER RESPONSES TO EPIPHYTE LOAD 65

ABSTRACT 65
INTRODUCTION 65
STUDY SITE 66
METHODS 66
Study trees and epiphytes 66
Trapping and processing the spiders 67
Statistics 67
RESULTS 67
Composition of the fauna 67
Comparison of tree/epiphyte categories 68
β-diversity 70
Guild structure 71
Comparison of epiphyte-free and epiphyte-laden trees 71
DISCUSSION 72
Is the spider fauna of *Annona* comparable to those of other tropical canopies? 72
Epiphytes as structural elements of the canopy 73
Microclimate 74
The influence of epiphytes on spiders – a question of scale? 75
Conclusion 75

9 SUMMARY 76

10 ZUSAMMENFASSUNG 78

11 REFERENCES 80

12 APPENDIX 91

ACKNOWLEDGEMENTS 106

LEBENSLAUF 108

PUBLICATIONS 109

ERKLÄRUNG 111

FIGURES

FIGURE 1.1: Study area. 2
FIGURE 1.2: *Annona* with epiphytes..... 3
FIGURE 2.1: Illustration of the four trap types. 6
FIGURE 3.1: Microsites of the temperature measurements. 11
FIGURE 3.2: Temperature gradients in tree crowns with different epiphytes. 14
FIGURE 4.1: The three epiphyte species growing on a branch of *Annona glabra*. 20
FIGURE 4.2: Two-dimensional scaling of the arthropod faunas of three epiphyte species. 24
FIGURE 4.3: Guild composition of the inhabiting faunas of the three epiphytes. 25
FIGURE 4.4: Proportion of web building versus hunting spiders. 25
FIGURE 5.1: Sketches of the four categories of study trees (*Annona glabra*). 31
FIGURE 5.2: Illustration of the study epiphytes..... 31
FIGURE 5.3: Composition of the arthropod fauna collected in *Annona glabra*. 33
FIGURE 5.4: Box plot of total numbers of arthropods in the study trees. 34
FIGURE 5.5: Box plot of the abundances of herbivorous taxa (Homoptera, Thysanoptera). 35
FIGURE 5.6: Phenology of *Annona glabra* and arthropod abundance during the survey year. . 36
FIGURE 5.7: Epiphyte biomass plotted against arthropod abundance in the study trees. 38
FIGURE 6.1: Rank-abundance plot of ant species..... 45
FIGURE 6.2: Two-dimensional scaling of the ant assemblages of the four tree categories. 48
FIGURE 7.1: Epiphyte biomass plotted against the number of beetle species. 58
FIGURE 7.2: Two-dimensional scaling of the beetle assemblages of the four tree categories. . 59
FIGURE 7.3: Pie charts depicting the distribution of beetles among categories. 60
FIGURE 7.4: Guild composition of beetles. 61
FIGURE 7.5: Seasonal abundance of herbivorous beetles throughout the study year. 62
FIGURE 8.1: Box plot of Sørensen indices of the spider assemblages. 69
FIGURE 8.2: Two-dimensional scaling analysis of the spider assemblages (data set 1). 70
FIGURE 8.3: Two-dimensional scaling analysis of the spider assemblages (data set 2). 71
FIGURE 8.4: Abundances of four of the most common spider species in epiphyte-laden versus epiphyte-free trees. 72

TABLES

TABLE 2.1: Trap yields. 7
TABLE 3.1: Temperatures at different locations (see Figure 3.1) within tree crowns..... 13
TABLE 3.2: Evaporative drying rate at different microsites within tree crowns..... 15
TABLE 4.1: Faunistic characteristics and analyses results of the arthropod assemblages inhabiting the three investigated epiphytes..... 22
TABLE 4.2: Results of correlation analyses between epiphyte biomass and faunal traits. 23
TABLE 5.1: Host tree traits (leaf area of host foliage; biomass and leaf area of its epiphyte load), numbers of arthropods and analyses results, detailed by tree category..... 37
TABLE 6.1: Species (morphospecies) list of ants..... 46
TABLE 6.2: Numbers of ant individuals and species in the 25 study trees. 47
TABLE 6.3: Average Sørensen values (mean ± SD) and statistics of 300 pair wise comparisons among study trees. 49
TABLE 6.4: Rank order and abundance (n = median) of the most abundant species in the four tree categories. 49
TABLE 7.1: Numbers of beetle individuals and species in the 25 study trees. 56
TABLE 7.2: Family composition and guild assignment. 57
TABLE 7.3: Comparison of the four tree/epiphyte categories..... 58
TABLE 8.1: Spider composition at the familial level. 68
TABLE 8.2: Numbers of spider individuals and species in the 25 study trees. 69

1 THE INFLUENCE OF EPIPHYTES ON CANOPY ARTHROPODS – SUMMARIZING INTRODUCTION

> *"The diversity of life forms, so numerous that we have yet to identify most of them, is the greatest wonder of this planet."*
>
> (Edward O. Wilson, in the preface of his book 'The current state of biological diversity', 1990.)

The astonishing species richness of tropical rainforests has provoked many such enthusiastic comments. But not only is this diversity one of the 'greatest wonders' of our planet, as stated here by Wilson (1990), it is also still one of its great mysteries. The challenge of a complete inventory has always fascinated biologists. Probably the first account of global species richness comes from Linnaeus (1758): he presented a record of 4400 animal species and presumed that this figure quite closely approximated the number of species on earth. As of now, biologists have encountered and described about 1.5 millions of species (Stork, 1997). Until the 1980s, the general belief was that the actual number of the world's species would double or maybe triple that number (Stork, 1997). However, the evaluation of the first spot samples from tropical rainforest canopies boosted these figures by an order of magnitude (Erwin, 1983), and simultaneously started a vivid debate about global species richness (Adis, 1990, Basset *et al.*, 1996, Erwin, 1990, May, 1986, Ødegaard, 2000a, Stork, 1988).

Not only the sheer scope of biodiversity still remains a sort of mystery, but also its causes and consequences. It has been the goal of many researchers during the past two decades to unravel the processes and mechanisms underlying the spectacular species richness of tropical ecosystems (Linsenmair, 1990, Nadkarni, 1999, Stork *et al.*, 1997). One of the many potential factors, that could contribute to high diversity in forest canopies, shall be investigated here.

Setting the scene – the role of epiphytes for arthropod diversity

Arthropods are responsible for most of the biotic diversity that make humid tropical forests the most complex of the world's terrestrial ecosystems. For the establishment and maintenance of arthropod species richness, epiphytes have been credited a major importance, e.g., by Benzing (1990):

> "The prime contribution made by canopy [epiphyte] flora to animal welfare lies in provision of safe harbor in a world of abundant predators and climatic extremes. [...] Uncounted thousands of animal populations (mostly insects) regularly associate with these plants, sometimes because there are no alternatives for lodging, food, or other critical resources. [...] Epiphytic vegetation of all types promotes carrying capacity simply by humidifying the forest canopy and roughening and expanding its surface."

The assumption concerning the benefiting effect of epiphytes on 'animal welfare' has been made without baseline data, and although reiterated by several researchers (Kitching *et al.*, 1997, Nadkarni, 1994, Richards, 1996, Rodgers & Kitching, 1998), evidence is still missing.

The influence of epiphytes on arthropod diversity and abundance has not been studied thoroughly (e.g., Ødegaard, 2000a), which inspired this dissertation.

Certainly, epiphytic vegetation greatly increases the available space for animal life by adding substantial amounts of biomass and a great variety of plant architecture to the tree crowns they dwell in (e.g., Gentry & Dodson, 1987). Moreover, epiphytes could render as harsh a habitat as the high canopy a more habitable place for arthropods by providing nesting sites and shelter from predators, by moderating climatic extremes, and by adding habitat types that are otherwise rather rare in the upper forest strata, e.g., litter deposits and soil-like microsites.

The subsequent chapters will address these factors and their potential influence on the fauna extensively. Hereafter, I will briefly explain how I intended to examine some fundamental aspects of the relationship between arthropods and epiphytes, and will outline the most important results of this study.

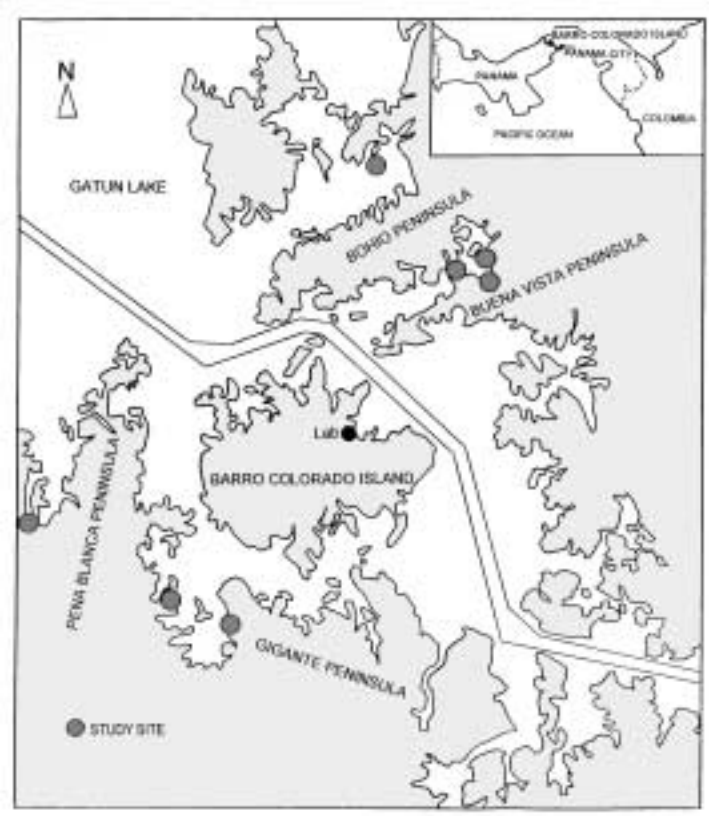

FIGURE 1.1: Study area.
The map shows Barro Colorado Island (BCI) and the peninsulas of the Barro Colorado Nature Monument (BCNM), where the study trees of the one-year survey were located. The seven sites are indicated with gray circles. The inlay illustrates the position of the study area within the Republic of Panama.

Choosing a feasible system – Annona glabra *and its epiphytes*

Considering the complexity of tropical forest canopies, ecological patterns might be tracked more easily in appropriate model systems, with less confounding variables than in whole forest ecosystems (Linsenmair, 1995). I found a feasible study system in *Annona glabra* L., a small tree occurring abundantly on the lake shores of the Barro Colorado Nature Monument in Panama (Figure 1.1). Many of these trees bear dense, distinct epiphyte assemblages, often dominated by a single species of epiphyte (Zotz *et al.*, 1999). These formed suitable units for a comparison between tree crowns with different traits related to their epiphyte load, for example structural heterogeneity, resources available for herbivores, or microclimatic conditions.

Although *Annona glabra* does not have the stature of an emergent rainforest tree, its crown microclimate is similar to the conditions in the upper strata of the forest due to its openness and exposure to sun and wind along the lake shore (Zotz *et al.*, 1999). The trees are inundated up to their lower stem portions during the rainy season and during most of the dry season (Figure 1.2). Access of terrestrial arthropods is therefore impeded, leaving primarily the arboreal species. In 25 of those trees, I conducted a one-year survey of the arthropod fauna, using a combination of different trap types. The methods are addressed in full detail in Chapter 2.

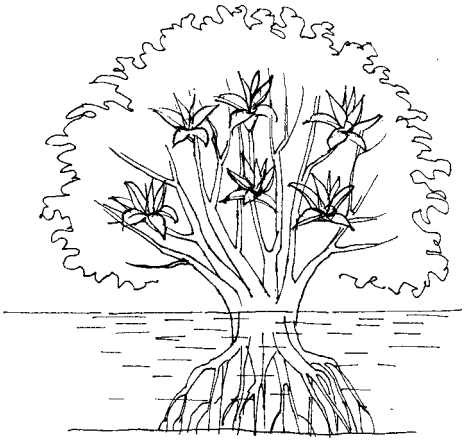

FIGURE 1.2: *Annona* with epiphytes.

The extent to which the arthropod communities in *Annona glabra* would be comparable to the fauna of the high canopy was an open question at the beginning of my project. I will show in the following, that major faunal characteristics (arthropod abundance, species richness and composition) were reasonably similar to communities sampled in high-diversity rainforests (as reported by, e.g., Adis *et al.*, 1998, Harada & Adis, 1998, Höfer, 1990, Stork, 1991). Thus, my rather modest array of one small species of host tree and three different species of epiphytes seemed to be a feasible surrogate for more intricate forest canopies.

Aim of the dissertation

I sought answers to two main questions:
(1) Do epiphytes affect arthropod abundance and diversity in tropical tree crowns?
(2) What might be the driving forces behind this potential influence?

In addition to the long-term survey of entire *Annona glabra* tree crowns (Chapter 5 - 8), I assessed the fauna inhabiting individual epiphytes quantitatively (Chapter 4), and investigated the mitigating influence of epiphytes on canopy microclimate (Chapter 3). To obtain a more comprehensive understanding of the communities I was studying, and to help elucidate the causes for the patterns found, I recorded various traits of the host trees (leaf area, phenology of leaf flush, fruiting and flowering) and its epiphyte assemblage (biomass and leaf area).

Before addressing these topics at length in the subsequent chapters, the principal results shall be briefly anticipated in the last paragraphs of this introduction.

Synopsis

At the microhabitat level of individual epiphytes, the inhabitant fauna was strongly influenced by their host plants (Chapter 4). Arthropod abundance was a function of epiphyte biomass, and different epiphyte species fostered very distinct arthropod assemblages, both taxonomically and ecologically. In the chapters 5 - 8 I investigated if this pronounced effect scaled up to the level of entire tree crowns. On a higher taxonomic level, there were no detectable effects of epiphytes on the fauna: the ordinal composition was indistinguishable between trees with different epiphyte assemblages (Chapter 5).

Three focal taxa (ants, beetles and spiders) were examined at species level. The diversity and abundance of ants was not influenced by the epiphytes of the study trees (Chapter 6). Species richness and distribution of beetles were also entirely unaffected by the presence of epiphytes in *Annona glabra* (Chapter 7). Spiders, however, were strongly influenced by the epiphyte assemblages of the host trees (Chapter 8). Both abundance of individual spider families and guild composition differed among trees with different epiphyte loads. Most remarkably, trees with different epiphytes supported spider assemblages with clearly distinct species compositions.

Thus, the prevalent notion that epiphytes positively influence arthropod diversity in tropical canopies seems justified, but not without reservation. Two most obvious trends are derived from these results. Whether an influence of epiphytes on the fauna is discernible depends greatly on

1) the scale of the investigated system: clear faunal distinctions at the microhabitat level might be blurred or absent at a higher habitat level, for instance in entire tree crowns, let alone forests or even larger areas.
2) the focal taxa: the present study confirmed that the selection of focal taxa affects the outcome of ecological studies considerably, and how misleading it may be to generalize biological patterns from results of one group alone (see, e.g., Lawton *et al.* 1998; Bartlett *et al.* 1999). A multi-taxon approach is therefore imperative to elucidate large-scale ecological questions.

In conclusion, I resume that epiphytes are associated with a species-specific inhabiting fauna, and that epiphytes impose an influence on certain, but not all, taxa even at the level of entire tree crowns. The mechanisms behind these patterns remain obscure, experimental evidence is lacking, and several questions requiring further research emerge from my results and hypotheses. Still, this study provides the first comprehensive investigation of the role of epiphytes in determining arthropod abundance and diversity in tropical tree crowns.

2 TRAPPING TECHNIQUES – MONITORING BIODIVERSITY IN THE CANOPY

ABSTRACT

The sampling techniques used for a long-term survey of arboreal arthropod faunas are presented. Animals were collected with a combination of three different trap types: composite flight interception traps, branch traps and yellow color traps, which remained in the study tree crowns throughout one year. The traps are described and illustrated, and their yields presented. The three trap types were selective towards different taxa and complemented each other well. In conclusion, traps proved to be feasible devices to monitor long-term abundance of arboreal arthropods and yielded sufficient but workable numbers of animals.

INTRODUCTION

The most frequently used method to sample arboreal arthropods in tropical tree crowns is still insecticide knock-down, or 'fogging' (e.g., Erwin, 1983, Floren & Linsenmair, 2000, Stork, 1987b). The advantages of this technique are obvious: it allows for nearly quantitative collections of the fauna of whole tree crowns, and the high canopy can be sampled conveniently from the forest floor. Moreover, fogging is unsurpassed in yielding vast amounts of arboreal arthropods in a minimum amount of time spent in the field (Erwin, 1995). For large inventories, knock-down techniques are therefore certainly the superior method, because all other methods are limited in providing a complete sample (Erwin, 1995).

However, it is hardly possible to monitor mid- and long-term changes of arthropod communities with fogging, and impossible to address seasonal fluctuations. Moreover, the consequences of those destructive methods for the fauna, especially for less mobile arthropods, are rather poorly studied (but see Floren & Linsenmair, 1997, Höfer *et al.*, 1994). Less invasive sampling of arthropods by means of insect traps has proved to be an efficient alternative to sample arboreal arthropods. Trapping techniques have been successfully used to reveal ecological patterns of the arboreal fauna, e.g., differences between forest types (Schubert, 1998), stratification and spatial distribution (Simon & Linsenmair, 2001, Sutton & Hudson, 1980), or large-scale biodiversity (Bartlett *et al.*, 1999). Capturing the fauna with traps usually involves large numbers of spatial as well as temporal replicates, and thus allows to address seasonal fluctuations and between-site heterogeneity. However, different trap types are selective towards certain taxa (Schubert 1998; Simon & Linsenmair 2001, this Chapter). It is therefore recommendable to use a variety of traps to obtain a reasonably broad spectrum of the arboreal fauna.

In this chapter I will present the sampling techniques for the long-term survey of the fauna in the 25 study trees (see Chapter 1). Arthropods were collected continuously with three different trap types throughout one year, in order to obtain a comprehensive sample of the arboreal arthropod communities.

STUDY SITE

The investigations were conducted in the Barro Colorado Nature Monument (BCNM, 9°10'N, 79°51'W) in the Republic of Panama. Focal trees were located along mainland peninsulas of Lake Gatún (Figure 1.1). The vegetation of this biological reserve has been classified as 'tropical moist forest' (Holdridge *et al.* 1971). The area receives approximately 2600mm of annual precipitation with a pronounced dry season from late December to April. Detailed descriptions of climate, vegetation and ecology are reported by Croat (1978), Leigh *et al.* (1982) and Windsor (1990).

TRAPPING PROTOCOL

In order to sample arthropods continuously throughout one year, I designed a setup of traps that would remain in the tree crowns with minimal maintenance. Three different trap types were used to sample the arboreal arthropod fauna (Figure 2.1): (1) composite flight interception traps with a central cross-panel of transparent plexiglas. The funnels above and beneath the 'windows' were of dark plastic sheeting, each leading to a collecting jar. Trap size is 30cm x 80cm, corresponding to the rather small tree crowns of the study trees (Chapter 1). (2) branch traps, as described by Koponen *et al.* (1997): a flexible PVC tube (e.g., an ordinary gardening hose) was winded around a branch and sealed against the bark (Figure 2.1). It was painted with Fluon (Klüver & Schulz, Hamburg, Germany), so that arthropods attempting to crawl across would slip and fall and be funneled into the vessel underneath. (3) yellow color traps, for which I used yellow sand-buckets (diameter 15cm), roofed with an aluminum sheet (Figure 2.1). All capture vessels were provided with overflow holes.

We installed two flight interception traps, two branch traps and one yellow color trap per tree. A 1% copper sulfate solution was used as killing and preservation liquid. It kills arthropods quickly and prevents destruction of sampled animals by fungi but is non-toxic to vertebrates at this concentration. Traps were emptied every two weeks and arthropods transferred into 70% ethanol.

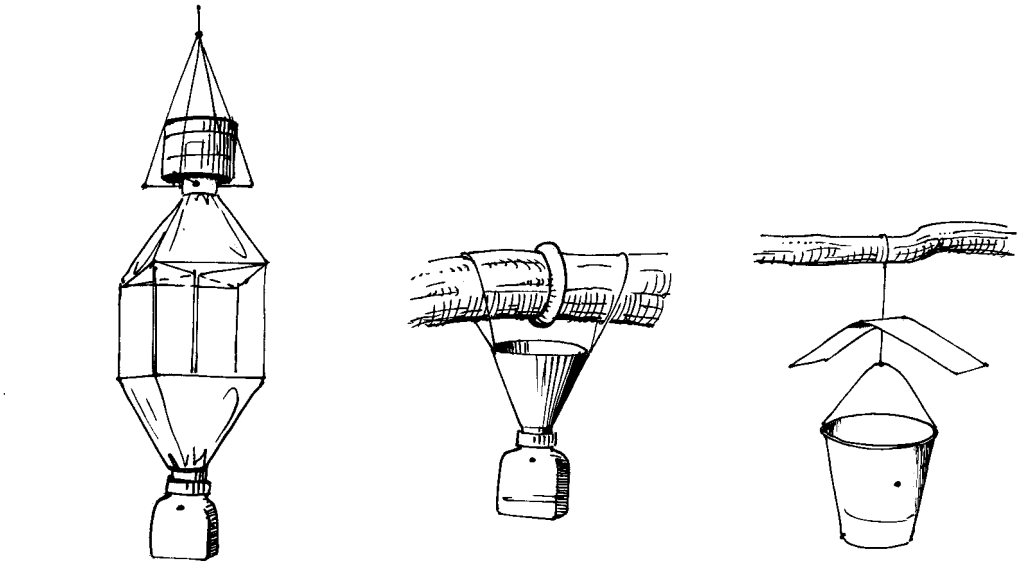

FIGURE 2.1: Illustration of the four trap types.
From left to right: Flight interception trap, branch trap, yellow color trap.

RESULTS

A total of 273,490 arthropods from 29 orders was caught throughout the study period. The distribution of taxa among trap types was clearly heterogeneous (Table 2.1). This was expected from the diverse ways arthropods move about and the many microsites they occupy in tree crowns. Table 2.1 also shows that branch traps not only captured arthropods foraging on branches, but also flying insects. Correspondingly, flight traps collected not only flying insects, but also many unwinged arthropods. The highest overall yield was attained by yellow color traps. Each of them caught an average number of 156 ± 150 (mean ± SD) individuals in a two-week trapping period. This was mainly due to a large proportion of Diptera, which are considered 'tourists' (sensu Stork 1987a). The high standard deviations reflect large seasonal fluctuations in arthropod abundances (Chapter 5).

TABLE 2.1: Trap yields.
Data are average numbers of individuals per trap per two weeks (mean ± SD). Arthropods were collected with 50 flight interception traps, 50 branch traps and 25 yellow color traps during 27 capture intervals (54 weeks). Numbers in bold script indicate the trap type which sampled the largest proportion of specimens within each taxon.

Taxon	Flight interception trap	Branch trap	Yellow color trap
Araneae	**4.3** ± 6.2	2.5 ± 2.8	3.1 ± 2.2
Coleoptera	**5.7** ± 5.9	4.0 ± 4.0	3.9 ± 3.2
Formicidae	4.8 ± 5.8	**10.2** ± 19.3	3.8 ± 6.7
Diptera	22.0 ± 22.9	10.3 ± 12.2	**44.9** ± 31.0
Hydroptilidae, Trichoptera	**38.3** ± 47.4	12.2 ± 15.0	35.8 ± 35.3
Homoptera	2.0 ± 2.3	2.2 ± 2.5	**3.5** ± 3.6
Psocoptera	**3.8** ± 5.6	3.2 ± 5.5	2.2 ± 1.8
Hymenoptera (excl. ants)	2.3 ± 2.9	2.2 ± 2.8	**6.1** ± 5.7
Collembola	14.8 ± 21.4	**21.3** ± 37.2	10.6 ± 14.5
Acari	6.6 ± 9.7	**13.7** ± 22.9	5.2 ± 5.3
Others*)	**39.9** ± 49.3	47.6 ± 56.5	37.0 ± 41.3
Total	144.4 ± 179.5	129.5 ± 180.7	**156.1** ± 150.6

*) In order of decreasing abundance: Diplopoda, Lepidoptera, Thysanoptera, Hemiptera, Isopoda, Chilopoda, Blattodea, Orthoptera, Ephemeroptera, Trichoptera other than Hydroptilidae, Neuroptera, Odonata, Embioptera, Pseudoscorpiones, Dermaptera, Scorpiones, Strepsiptera, Mantodea.

The orders that were mainly caught by flight interception traps were beetles, psocids (Psocoptera), micro-caddisflies (Hydroptilidae, Trichoptera) and, somewhat unexpected, spiders. Many of the captured spiders were clearly too large to balloon (i.e. drift by their silk strand). Web-building spiders frequently used the traps for web attachment, and hunting spiders were often caught in the top vessels of the flight interception traps, which they probably mistook as shelter (Stuntz, personal observation). Once, I also found a large tarantula (Mygalomorphae), which had accomodated itself in the lower funnel of a flight trap, constructing a retreat with silk and leaf litter. Ants were also well represented in flight traps, due to the preponderance of winged reproductives. Ant workers were trapped abundantly in branch traps, together with very high numbers of springtails (Collembola) and mites (Acari). Diptera, Hymenoptera other than ants and Homoptera were mainly caught in yellow color traps.

DISCUSSION

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

However, the results of a study where arthropods are obtained by trapping will always be dependent on the setup. Table 2.1 displays the selectivity of different trap types. Using one kind of trap exclusively will undoubtedly bias the results toward certain taxa. For example, estimates of faunal composition obtained by sampling with flight interception traps only would have considerably underestimated the contribution of Formicidae to the total arthropod assemblage in the study trees in terms of both abundance and species richness. A combination of various trap types is likely to reduce the capture bias and allows to sample a broader spectrum of the canopy fauna.

In conclusion, the trapping techniques selected for this study proved feasible to sample a broad spectrum of the arboreal arthropod fauna and yielded sufficient but workable numbers of individuals.

3 EPIPHYTES MODERATE CLIMATIC EXTREMES IN TROPICAL TREE CROWNS

ABSTRACT

Epiphytes are often assumed to influence microclimatic conditions of the tree crowns that they dwell in. In order to quantify this notion, I measured the parameters temperature (of the substrate surface and the boundary layer of air above it), evaporative drying rate and evapotranspiration at various locations within tree crowns with differing epiphyte assemblages. The host tree species was *Annona glabra*, which was either populated by one of three epiphyte species (*Dimerandra emarginata*, *Tillandsia fasciculata*, or *Vriesea sanguinolenta*) or devoid of epiphytes. I found that during the hottest and driest times of day, microsites in the immediate proximity of epiphytes had significantly lower temperatures than epiphyte-bare locations within the same tree crown, even though the latter were also shaded by host tree foliage or branches. Moreover, water loss through evaporative drying at microsites adjacent to epiphytes was reduced by almost 20% compared to exposed microsites. I also found that over the course of several weeks, the evapotranspiration in tree crowns bearing epiphytes was significantly lower than in trees without epiphytes. Although the influence of epiphytes on the temperature extremes and evaporation rates is relatively subtle, their mitigating effect is significant and may be of substantial importance for small animals like arthropods inhabiting an environment as harsh and extreme as the tropical forest canopy.

INTRODUCTION

The tropical forest canopy is the home of a multitude of plant and animal species and probably harbors the greatest portion of global biodiversity, providing living space for some tens of millions of arthropod species (Erwin, 1983, Erwin, 1990). Survival conditions in tree crowns are diverse and sometimes similar to those on the ground (Benzing, 1990, Freiberg, 1997). However, the climate of the upper canopy is also often extremely harsh and the fluctuations of environmental parameters substantial (Buckley *et al.*, 1980, Freiberg, 1997, Nadkarni & Longino, 1990, Tobin, 1995). Brusque changes in temperature and relative humidity are typical and are mainly due to the lack of the climatic buffering of an absorptive soil beneath and the reduced shade by tree crowns overhead.

It is well established that canopy-dwelling flora, especially in the uppermost strata of forests, is adapted in manifold and elaborate ways to overcome these ecoclimatic constraints (Benzing, 1990). Less is known about such adaptations of the arboreal fauna. Researchers still struggle to cope with the baffling biotic diversity of tropical canopy arthropods (Erwin, 1983, Floren & Linsenmair, 1997, Stork, 1991, Wilson, 1986). The primary focus is on counting the species (Leigh, 1999), and little has been done to unravel details of the biology of particular taxa, let alone their responses and adaptations to canopy climate. However - although experimental evidence is rare - a number of studies have attributed distribution patterns of arthropods in tropical forests to microclimatic parameters (Didham *et al.*, 1998, Kaspari, 1993, Nadkarni & Longino, 1990, Nicolai, 1986, Rodgers & Kitching, 1998). For small

animals like most arthropods, microclimatic conditions in their environment can be extremely limiting factors, e.g. by restraining their behavior and distribution to niches in which desiccation and overheating can be avoided.

In this context, epiphytes may be of considerable ecological importance. They are assumed to exert a moderating influence on climatic conditions in the canopy (Benzing, 1990). Freiberg (1997) comprehensively measured climatic parameters in a tree top, and found that on branches surrounded by humus mats and non-vascular epiphytes (mosses), the climatic gradients were substantially mitigated. However, I am not aware of any study in which climatic parameters in direct proximity of vascular epiphytes were quantified and compared to those of more exposed, epiphyte-free sites within the same tree crown. Moreover, I intended to clarify if a mitigating influence is already exerted by epiphytes growing on bare bark, without a thick layer of organic matter ('canopy soil'). In this chapter I suggest answers to the questions 1) How strong do epiphytes moderate climatic extremes in tree crowns and 2) Are there species-specific differences between epiphytes in this context? In order to address these questions, I investigated the parameters temperature, evaporative drying rate and evapo-transpiration both at different microsites within tree crowns as well as among several tree crowns with different epiphyte assemblages.

STUDY SITE

The study was conducted in the Barro Colorado Nature Monument (BCNM, 9°10’ N, 79°51’ W) in Panama. The vegetation of this biological reserve has been classified as tropical moist forest (Holdridge *et al.*, 1971) and receives approximately 2600mm of annual rainfall. The movement of the Intertropical Convergence Zone (Lauer, 1989) causes a quite severe dry season from late December to April, during which only about eight percent of the yearly precipitation occur (Windsor, 1990). Detailed descriptions of climate, vegetation and ecology can be found in Croat (1978), Leigh (1999) and Windsor (1990).

METHODS

Microclimatic parameters were measured in the late dry season of 1999. It has been shown that 'extreme' climatic events are most important to life in the canopy (Buckley *et al.*, 1980, Freiberg, 1997). In order to obtain data from situations as 'extreme' as possible, I took measurements exclusively on bright and cloudless days during midday hours, the hottest and driest times of the day (Leigh, 1999, Windsor, 1990). I classified four different categories of the host tree *Annona glabra* L., in order to compare epiphyte-free with epiphyte-laden trees as well as trees with different epiphytes among each other: one control group of trees without epiphytes, a group of trees dominated by the large tank bromeliad *Vriesea sanguinolenta* Cogn. & Marchal (Figure 3.1), one dominated by the smaller bromeliad *Tillandsia fasciculata* Sw. var. *fasciculata*, and another tree group bearing populations of the orchid *Dimerandra emarginata* (G. Meyer) Hoehne. Species names follow D'Arcy (1987). The epiphytes, hereafter addressed by generic names, are illustrated are illustrated in Figure 4.1 and Figure 5.2. Statistical analysis was done with STATISTICA 5.0 (StatSoft Inc., Oklahoma, USA). Data were normally distributed and thus allowed for parametric tests (one-way and two-way ANOVA, t-tests for dependent samples).

Temperature

Temperature was measured with a thermocouple sensor attached to a control unit (TH 65, Wescor, Logan, USA). Within a tree crown, ten series of temperature measurements at different locations were taken, five of which were fully exposed to penetrating sunlight, and five that were partially shaded by host tree foliage. In epiphyte trees, each series included four different microsites in the vicinity of an epiphyte (Figure 3.1): 1) on exposed bark on the upper side of a branch, 2) at the underside of the same branch, 3) on substrate adjacent to an epiphyte, i.e. on the outside of a bromeliad rosette or an orchid stand and 4) inside the epiphyte (i.e. between the leaves of a bromeliad rosette or the stems of an orchid stand). All microsites except the first were usually shaded either by the branch or the respective epiphyte. For control, I measured temperature at microsites 1) and 2) in epiphyte-free trees. When necessary, the sensor tip was shaded during the measurements to avoid heating by direct insolation. At each microsite, I measured both surface temperature and the temperature of the boundary layer, which I defined as the air temperature one millimeter above the respective branch or epiphyte surface.

In each tree crown, the mean values of the ten measuring series were computed for further evaluation. I obtained measurements for 20 trees in total, i.e. five replicates of each of the four tree categories.

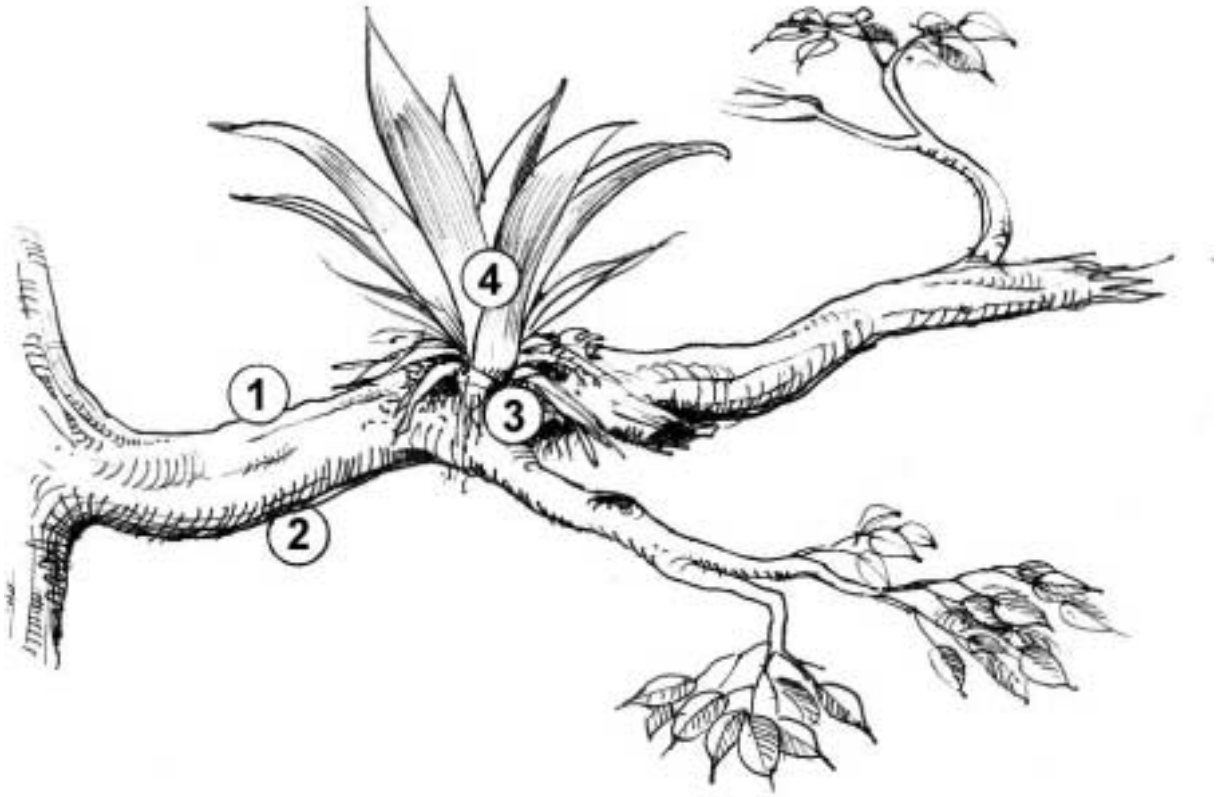

FIGURE 3.1: Microsites of the temperature measurements.
A branch of *Annona glabra* carrying a large specimen of *Vriesea sanguinolenta*. The four microsites for the temperature measurements are indicated with encircled numbers: 1) branch top side, 2) branch underside, 2) adjacent to epiphyte 4) inside epiphyte.

Evaporative drying rate

This term was introduced by Didham (1999), who described a simple but effective field device to measure evaporative drying rate (EDR), consisting of a water-filled test tube with a milliliter volume scale. A filter paper wick of standardized size was put into the tubes to increase surface area and thus speed up evaporation. The rate of water loss is expressed as milliliter per hour and is a combination of the effects of air temperature, relative humidity and wind speed (Didham, 1999). The measurements were taken in the same tree crowns and simultaneous to the temperature measurements described above. I suspended eight measuring tubes in each tree crown from branches, four at sites far from epiphytes, and four in direct proximity of epiphytes (except in the control trees free of epiphytes, where only four tubes were fixed at haphazard sites on branches). The tubes were installed on measuring days around 11:00 am and remained in the tree crown for three hours. The water level inside the tubes was recorded every 30 minutes. After the final reading, the tubes were collected and returned to the laboratory. As for the temperature measurements, I selected sites within the tree crown that were both fully exposed or partially shaded by host tree foliage. For data evaluation, the mean values of, respectively, the four exposed and the four epiphyte-near sites within a tree crown were used.

Evapotranspiration

In order to compare tree crowns with different epiphyte assemblages among each other, I measured evapotranspiration in the tops of 36 *Annona* tree crowns, using four ETgages (ETgage Company, Loveland, CO 80537, USA). At the beginning of a measuring period, they were placed in the approximate crown centers of four trees, each of a different category, but at a comparable location. The ETgages remained in the trees for seven days and were then moved to the next four tree crowns at a different location. Hence, in contrast to the measurements of temperature and evaporative drying rate, these were not instantaneous measurements during midday hours of hot and sunny days only, but instead integral recordings over the course of entire weeks.

RESULTS

Temperature

Gradients within tree crowns

Table 3.1 shows the results of the temperature measurements. A two-way ANOVA revealed that both the tree category as well as the microsite within the tree crown had a significant influence on temperature (2-way-ANOVA, $p<0.001$ for both factors tree category and microsite) and that there was no interaction between these factors ($p=0.221$). Figure 3.2 illustrates the rankings: the trees differ from each other in that the temperatures next to and inside epiphytes in the *Dimerandra* category are on average higher than in the *Tillandsia* or *Vriesea* category (factor one of the two-way ANOVA; post-hoc LSD-test; $p<0.001$). The latter two categories were almost identical in their thermal properties (LSD-test; $p=0.93$). The second factor, the microsite within the tree crown (Figure 3.1), also influenced temperatures significantly: there was a strong gradient, with temperatures being highest at the top of a

branch, intermediate at its underside and lowest at microsites near or inside epiphytes (Figure 3.2). In all trees, throughout all categories, the temperatures of the exposed upper side of a branch was significantly higher than the epiphyte-associated microsites (LSD-test; $p<0.001$). The temperature of the shaded branch underside was intermediate: it was significantly lower that the branch top side (LSD-test; $p<0.001$) and – although this was not the case when *Dimerandra* trees were considered separately (see below) – significantly higher than the microsites next to or within epiphytes (LSD-test; $p<0.001$). Similarly conforming across all study trees, I never found a significant difference between the temperature *next to* an epiphyte and the temperature *inside* it (LSD test; $p=0.66$). As expected, the temperature gradients of the irradiation absorbing surfaces were steeper and the differences between microsites larger than the respective gradients and differences in boundary layer temperatures. However, the statistical results were similar (Table 3.1).

TABLE 3.1: Temperatures at different locations (see Figure 3.1) within tree crowns.
Given are means and SDs of temperatures at the four microsites and differences between hottest and coolest microsites (n=5 for each category; n=15 for all epiphyte trees), and significance levels of ANOVA or, if marked with an asterisk, t-tests for dependent samples. Significant differences between microsites (post hoc LSD-test; $p<0.05$) are indicated by different letters in superscript.

Tree category	Branch top side [°C]		Branch underside [°C]		Next to epiphyte [°C]		Inside epiphyte [°C]		Difference (max-min) [°C]		p-level
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	
SURFACE											
Control trees	**33.7^{a}**	0.6	**31.6^{b}**	0.9	-	-	-	-	**1.8**	0.6	<0.001*
Trees with *Dimerandra*	33.7^{a}	1.0	31.4^{b}	0.5	31.0^{b}	0.6	30.8^{b}	0.8	2.9	0.9	<0.001
Trees with *Tillandsia*	33.0^{a}	1.0	31.2^{b}	0.6	29.3^{c}	0.7	29.4^{c}	0.8	3.9	0.8	<0.001
Trees with *Vriesea*	33.3^{a}	1.2	31.2^{b}	1.1	29.3^{c}	0.8	29.0^{c}	0.9	4.3	0.8	<0.001
All epiphyte trees	**33.3^{a}**	1.0	**31.2^{b}**	0.7	**29.9^{c}**	1.0	**29.7^{c}**	1.1	**3.7**	1.0	<0.001
BOUNDARY LAYER											
Control trees	**32.1^{a}**	0.7	**31.1^{b}**	0.7	-	-	-	-	**0.7**	0.3	0.003*
Trees with *Dimerandra*	32.7^{a}	0.8	31.5^{b}	0.7	31.5^{b}	0.3	31.3^{b}	0.7	1.5	0.7	0.017
Trees with *Tillandsia*	32.0^{a}	0.8	31.4^{b}	0.7	30.4^{c}	0.6	30.0^{c}	0.5	1.9	0.6	<0.001
Trees with *Vriesea*	32.1^{a}	0.9	31.2^{a}	0.8	30.3^{b}	1.0	30.0^{b}	0.9	2.1	0.5	0.011
All epiphyte trees	**32.2^{a}**	0.8	**31.4^{b}**	0.7	**30.8^{c}**	0.9	**30.4^{c}**	0.9	**1.8**	0.6	<0.001

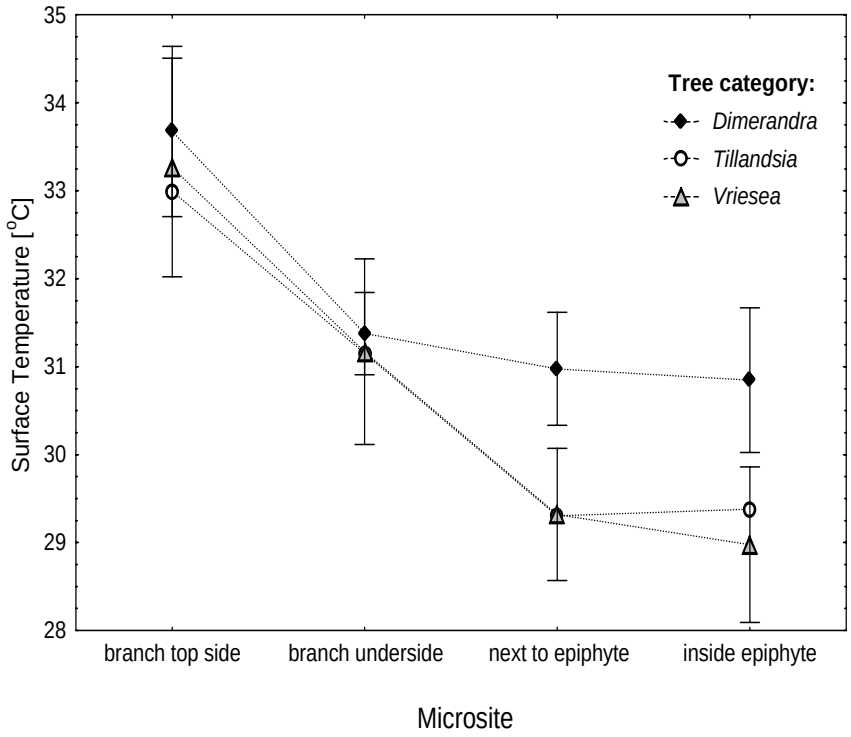

FIGURE 3.2: Temperature gradients in tree crowns with different epiphytes.
Given are surface temperatures (symbols: means, error bars: SDs) at four different microsites within tree crowns of three different tree/epiphyte categories. The factor 'Microsite' influenced the temperatures significantly (two-way-ANOVA; $F(3.48) = 56.65$; $p<0.001$), as did the factor 'Tree category' ($F(2.48) = 9.56$; $p<0.001$). There was no significant interaction between these two factors ($F(6.48)=1.43$; $p<0.2214$).

When considering the tree categories separately (with a one-way ANOVA), I found that only in the bromeliad trees the surface at the shaded branch underside was significantly warmer than the substrate close to or inside an epiphyte (LSD-test, $p<0.01$). In trees with *Dimerandra*, however, the temperatures of the branch underside did not differ from the temperatures near or within an orchid stand (LSD test, $p>0.05$). As for boundary layer temperatures, the trends were similar, but the only significant difference between branch underside and epiphyte-near microsites was found in trees with *Tillandsia* (LSD, test $p<0.05$).

Comparison with control trees

The highest temperatures measured in epiphyte trees, which were invariably measured at the branch top side, were not significantly different from temperatures in control trees (surface: 33.4°C ± 1.0 (SD); boundary layer: 32.2°C ± 0.8; ANOVA, $p>0.5$) (Table 3.1). As expected, there was a significant difference in the temperatures of the coolest microsite among trees (ANOVA, $p<0.02$). However, control trees and trees with the orchid *Dimerandra* did not differ significantly from each other, neither was there a difference between trees with *Vriesea* and trees with *Tillandsia* (LSD test, $p>0.1$), leaving the significant difference between the first and the latter pair of tree categories (LSD test, $p<0.05$). The coolest microsite in control trees and in trees with *Dimerandra* had mean surface temperatures of, respectively, 31.6°C ± 0.4 (SD) and 30.8°C ± 0.7, while the lowest temperatures in trees with *Tillandsia* or *Vriesea* were 29.1°C ± 0.7 and 29.0°C ± 0.9.

The mean surface temperature difference between the hottest and coolest microsite in the tree crowns without epiphytes was only 1.8°C ± 0.6 (SD), compared to 3.7°C ± 1.0 in tree crowns with epiphytes (Table 3.1). In the boundary layer, this difference was 0.7°C ± 0.6 in control trees, and 1.8°C ± 0.6 in epiphyte-laden trees. The maximum measured difference was found in a tree with *Tillandsia*: the site next to the bromeliads was 8.1°C cooler than the exposed branch upper side.

Evaporative drying rate

The EDR (expressed as water loss in milliliters per hour) was significantly higher at exposed sites within a tree crown than at sites in direct proximity of epiphytes (Table 3.2; t-test for dependent samples, $p<0.05$). On average, epiphytes reduced the water loss in their immediate surrounding by almost 20%, compared to the exposed locations in the same tree crown. The EDR in the epiphyte-free trees of the control group was not different from the EDR of similarly exposed sites in epiphyte-laden study trees (ANOVA, $p>0.5$). In contrast to the temperature data, there were no differences in the water loss rates of epiphyte-associated microsites when comparing the three different tree/epiphyte categories (ANOVA, $p>0.5$).

Evapotranspiration

In contrast to the data presented above (Table 3.2), evapotranspiration was measured only in the crown center (for logistic reasons), allowing comparisons among the four tree categories. Similar to data of Zotz and Thomas (1999), evaporation in trees without epiphytes was c. 70% of that measured above the canopy. In tree with epiphytes I observed significantly lower evaporation rates compared to epiphyte-free controls (ANOVA, $p<0.03$). Although there seemed to be a trend from decreasing evapotranspiration in trees with *Dimerandra* to trees with *Tillandsia*, being lowest in trees with *Vriesea*, these differences were not significant (LSD-test, $p>0.05$). Relative to control trees, the mean evapotranspiration in *Dimerandra* trees amounted to 75%, in trees with *Tillandsia* to 64% and in trees with *Vriesea* only to 58%.

TABLE 3.2: Evaporative drying rate at different microsites within tree crowns.
Given are means and SDs (n=5 for each category; n=15 for all epiphyte trees), absolute differences between exposed microsites and those adjacent to epiphytes, and significance levels of t-tests for dependent samples.

Tree category	(1) EDR at exposed microsites [mlh^{-1}]		(2) EDR at microsites near epiphytes [mlh^{-1}]		Difference between (1) and (2)	p-level
	mean	SD	mean	SD		
Control trees	1.53	0.17	-	-	-	
Trees with *Dimerandra*	1.54	0.22	1.30	0.15	0.24	0.032
Trees with *Tillandsia*	1.54	0.19	1.19	0.16	0.35	0.010
Trees with *Vriesea*	1.45	0.19	1.21	0.21	0.24	0.004
All epiphyte trees	**1.51**	0.19	**1.23**	0.17	**0.28**	**<0.001**

DISCUSSION

Epiphytic airconditioning

It is general knowledge that a forest diminishes the desiccation and overheating of the soil beneath it (e.g., Otto, 1994). For example, Selleck (1957) found that soil water loss in open grassland was four times higher than under pine forest. Leigh (1999), compiling data from numerous climate studies, compared the rainforest with a giant air conditioner, maintaining the glasshouse-like wet warmth which is most suitable for plant growth. Moreover, it is widely recognized that heat becomes harsher when tropical forests are cleared (Leigh, 1999). In a similar manner, canopy vegetation may moderate climatic extremes of the tree crowns that they colonize. I showed that epiphytes significantly lower the temperature of their

immediate surrounding (Table 3.1) and reduce water loss through evaporation by almost 20% (Table 3.2). These effects were often already exerted by a single plant (as in FIGURE 3.1), irrespective of the partial shading by host tree foliage. Only in the case of *Dimerandra* there was no decrease in temperature close to the orchid as opposed to a shaded branch underside. This is certainly due to the open structure of this orchid, the limited self-shading of its leaves and the lack of water-impounding tanks as found in the bromeliads. A similar mitigating influence on microclimatic parameters in tree crowns has been reported for humus mats that had accumulated around branches (Freiberg, 1997). Although many epiphytes grow on such aerial soils (Benzing, 1990), I chose epiphytes that grow on bare bark to show that the plants themselves also exert this influence, despite the absence of an absorptive substrate of organic matter.

Although the two bromeliads are of quite distinct size and architecture, there were no detectable differences between these two species concerning their influence on microclimatic parameters. *Dimerandra*, while not significantly lowering temperatures, had a similarly mitigating effect on evaporative drying rate and evapotranspiration. The species identity of epiphytes thus seems to be rather unimportant for the reduction of water loss through evaporative drying. Apparently, the mere presence of a plant as shade-provider, windbreaker and water reservoir serves as shelter from climatic extremes, irrespective of its structure. Moreover, all plants transpire to avoid overheating. Leigh (1999) suspected the plants' transpiration to be responsible to help maintain the climate for the forest as a whole. It would be intriguing to test, e.g. by using artificial structures, how much of this airconditioning effect is due to plants' transpiration, and how much is merely an effect of reducing incident radiation and wind speed, both factors that are mathematically related to evapotranspiration (Leigh, 1999, Penman, 1948).

Host tree effects

Naturally, the host tree foliage also has a buffering effect on its own crown microclimate. Zotz and Thomas (1999) reported that the evapotranspiration in *Annona glabra* amounted to only 70% percent of the evapotranspiration measured above the forest canopy. The airconditioning effect of the epiphytes adds to this moderation: according to the results of this study, an average epiphyte-laden *Annona* crown experiences thus only c. 45% of that out in the open.

The sunlight absorbing branch surfaces in the *Annona* tree crowns were considerably warmer (33.4°C) than the air above the canopy (30.1°C mean monthly maximum; Paton, unpublished data), despite the partial shading by host tree foliage. Even at the branch undersides, which were never exposed to direct insolation, the mean temperatures were higher (31.3°C). Only in trees with the bromeliads *Vriesea* or *Tillandsia*, the substrate temperatures were reduced relative to the air temperature above the canopy (29.3°C). For comparison, Paton recorded an average of 28°C in the deeply shaded understory of primary forest on Barro Colorado Island (Paton, unpublished data).

The arthropod perspective

For small and, moreover, poikilothermic animals like arthropods, the microclimatic conditions of their habitat must be crucial determinants of their distribution and behavior (Almquist, 1970, Kaspari, 1993, Nicolai, 1986, Rodgers & Kitching, 1998, Tobin, 1995). In the canopy, where the bulk of arthropod diversity is expected (Erwin 1983; Stork et al. 1997),

the climatic conditions are often extremely harsh and characterized by brusque changes in temperature and relative humidity. Canopy-dwelling plants, such as vascular epiphytes, have evolved a multitude of effective adaptations to withstand drought and high insolation (Benzing, 1990). Much less is known about specific adaptations of arboreal arthropods to endure the hostile conditions of the high canopy. Instead, it has often been assumed that arthropods show a certain behavioral adaptation, in that they search for sites with more favorable microclimata where desiccation and overheating can be successfully avoided (Almquist, 1970, Didham *et al.*, 1998, Kaspari, 1993, Lowrie, 1948, Nicolai, 1986, Riechert & Tracy, 1975).

In general, these constraints apply to all canopy-dwelling animals. However, with decreasing body size, the surface-volume ratio increases and with it the organism's vulnerability to desiccation and heat. As the vast majority of tropical arthropods is minute, rarely exceeding 3mm body length (Erwin & Scott, 1980, Morse *et al.*, 1988, Nentwig, 1983, Nentwig, 1985), it is very likely that they are especially sensitive to harsh climatic conditions. Kaspari (1993) hypothesized that "given that desiccation is a major risk to small arthropods, and smaller species can maintain larger populations and subdivide the environment better, then wet sites (even in the wet tropics) may be local centers of arthropod diversity and critical refugia during dry episodes". In this context, epiphytes may be of great ecological importance for the canopy arthropod fauna, providing shelter from climatic extremes.

The results of the next chapter lend support to this presumption: in a comparative assessment of the arthropod fauna inhabiting the three studied epiphyte species, I found a diverse and abundant arthropod fauna inhabiting *Vriesea* and *Tillandsia*, and a much less species- and individual-rich assemblage in *Dimerandra* (Chapter 4). This finding is partially explained by differences in plant size and structure, and the bromeliads' ability to impound leaf litter in their tanks. However, it is also likely that the greater faunal richness of the bromeliads is to some extent an effect of more favorable microclimatic conditions compared to the orchid (Table 3.1). Experiments on temperature and humidity preferences of the bromeliad inhabiting taxa could give valuable insight to test the relevance of this assumption.

Conclusion

Epiphytes have a significant influence on the microclimate in tropical tree crowns, both at various microsites *within* a tree crown and *among* tree crowns with different epiphyte growth. On hot and cloudless days, they provide microsites with lower temperatures and reduced water loss through evapotranspiration compared to epiphyte-free spaces within the same tree crown. Moreover, I found significantly lower evapotranspiration in tree crowns bearing epiphytes in comparison with epiphyte-free control trees over the course of several weeks. Without having experimental evidence, I suggest that this mitigating influence might positively affect the diversity and abundance of the arboreal arthropod fauna. The results of the subsequent chapter (Chapter 4) are consistent with this notion.

4 EPIPHYTES AS MICROHABITATS: THE ARTHROPOD FAUNA INHABITING THREE EPIPHYTE SPECIES

ABSTRACT

It has been proposed repeatedly that vascular epiphytes are important for the establishment and maintenance of high arthropod diversity in tropical forest canopies. The arthropod fauna inhabiting 90 individuals of three different species of epiphytes was investigated in the moist lowland forest of the Barro Colorado Nature Monument in Panama. In total, 3,688 arthropods belonging to 89 morphospecies 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 the ability to impound leaf litter is discussed. In conclusion, epiphytes constituted microhabitats for a diverse and numerous fauna, and different species of epiphytes fostered both taxonomically and ecologically very distinct arthropod assemblages. Whether epiphytes influence local and between-habitat diversity at the level of entire tree crowns remains the subject of subsequent chapters.

INTRODUCTION

Ever since Terry Erwin's often-cited, much applauded, criticized and re-assessed estimates of global species richness (Erwin, 1983), researchers have been trying to unravel the mechanisms behind the bewildering biotic diversity of tropical forest canopies. In this chapter I investigate the 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 & Matheson, 1989, Stork, 1987a). 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 & Matheson, 1989), and thus enrich the variety of microhabitats available for arthropods in tropical tree crowns.

Much of what is known about tropical arthropod diversity in forest canopies comes from insecticide knockdown studies on relatively large sampling units, mostly entire tree crowns (e.g., Adis *et al.*, 1998, Erwin, 1983, Floren & Linsenmair, 2000, Höfer *et al.*, 1994, Stork & Brendell, 1993). It is difficult if not impossible to characterize and quantify all relevant parameters potentially influencing patterns in community structure and species composition of arthropods in these large assemblages. It may be advantageous to choose more manageable, smaller model systems. Vascular epiphytes are not only conspicuous elements of tropical forests, they are discrete microcosms fostering a diverse and probably characteristically

structured arthropod community (Benzing 1990, Cotgreave *et al.* 1993, Dejean *et al.* 1995, Nadkarni 1994). Richardson (1999) found that diversity within bromeliads reflected relationships between diversity, productivity and habitat complexity known from larger study systems and suggested using these epiphytes as subsamples for entire forest ecosystems. I investigated the macro-arthropod fauna of three species of canopy epiphytes.

It is well established that plant architecture plays a major role in determining the diversity and abundance of insects (Lawton, 1986), and structural parameters of the environment strongly influence many animal assemblages (Cherrett, 1964, Duffey, 1966, Gunnarson, 1990, Halaj *et al.*, 1998, Hatley & MacMahon, 1980, Pianka, 1967, Rypstra, 1983). I chose three locally abundant epiphyte species, all growing in the same study area and under quite similar conditions on the same host tree species, *Annona glabra* L. At least for human perception, these three species feature very different structural characteristics. I addressed the questions: 1) Are there consistent differences in species richness, species composition and guild arrangement 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 Nature Monument (9°10’ N, 79°51’ W) in Panama. The area receives approximately 2600mm 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). Epiphytes were collected in the dry seasons of 1998, 1999 and 2000.

METHODS

Study organisms

I selected three epiphyte species (thereafter addressed by their generic names) for this study, each featuring a different microhabitat structure according to its plant architecture (Figure 4.1): *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 liters 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) Höhne is an orchid with a rather simple structure. It grows in clusters of erect, slender stems with linear distichous leaves. *Dimerandra* does neither impound leaf litter nor water. I 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 by different host-associated faunas. The host was *Annona glabra* L., a small flood-resistant tree (mean height 4,9m ± 0.9 SD) which grows along the shores of Lake Gatún (Figure 1.2). 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).

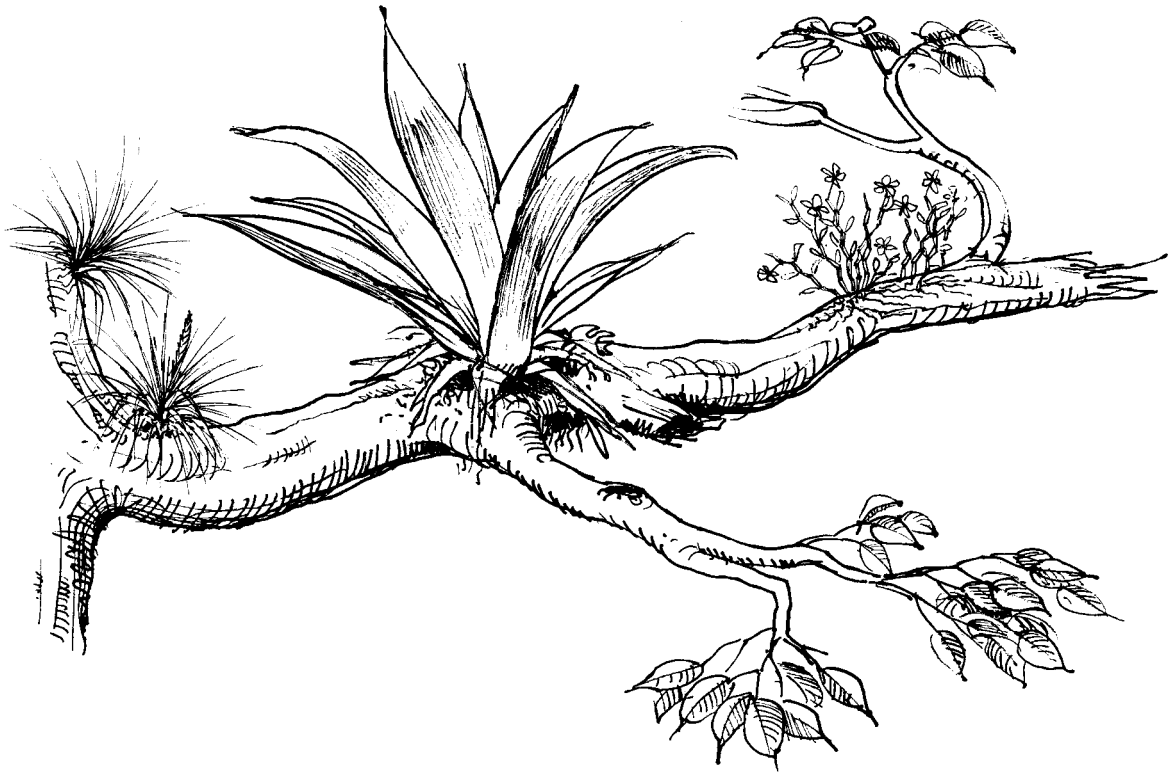

FIGURE 4.1: The three epiphyte species growing on a branch of *Annona glabra*.
From left to right: *Tillandsia fasciculata*, *Vriesea sanguinolenta*, *Dimerandra emarginata*.

Sampling the fauna

Epiphyte harvests. Entire plants were harvested in the field and brought to the laboratory for further study. Before an epiphyte was removed from the host tree, it was enclosed 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 for *Dimerandra*. Its open structure was much less shut-off towards the immediately surrounding area (Figure 4.1). Here, all animals that were found on or between the stems and leaves of an orchid stand were sampled. In doing so, I 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 (Klüver & Schulz, Hamburg, Germany) lining on the rim, whereas large epiphytes were examined on a modified table with a coarse grid surface roofed with mosquito netting. Underneath the table I 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.

Identification of arthropods. Monitoring arthropod diversity in a tropical rainforest is an extremely time- and money-consuming endeavor and is thwarted by the existence of many millions of yet undiscovered and undescribed species (Erwin 1983, 1995, Wilson 1990).

However, it may not be imperative to determine species to reveal diversity patterns (Didham *et al.*, 1998, Erwin, 1995). Oliver and Beattie (1996a) showed that the outcome of a comparative invertebrate survey was affected very little, regardless of whether animals were identified to species level by specialists or sorted to morphospecies without the use of any keys.

I sorted the collected arthropods 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 appended at the end of this chapter (Appendix 1). All animals were cross-referenced with a voucher collection to ensure singularity of assigned species. I collected only individuals over 1-2mm 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), so I 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 his 'scavengers, dead wood and fungal feeders' were replaced for 'detritivores'. Ants were excluded 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. Also excluded was a single case of an aggregation of ant-tended Homopterans with 123 individuals on a *Tillandsia* plant. Animals were assigned to either predators, detritivores, herbivores, tourists, ants, or arthropods with unknown feeding behavior (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). Statistical analysis was done 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 I used species richness, i.e. the absolute number of species that were found in one sampling unit, and the Sørensen index as a measure of β-diversity (Magurran, 1988). To test for differences in the species compositions of the faunas among the epiphyte species, I ran multidimensional 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 I collected 3,688 arthropods belonging to 89 species, of which almost one third (29%) were singletons (Table 4.1, Appendix 1). Nearly 10% of the 90 harvested epiphytes (six *Dimerandras*, three *Vrieseas* and one *Tillandsia*) yielded no animals at all. Those were consistently plants of small size. The results for the different epiphyte species are summarized

in Table 4.1. 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 ($p<0.001$), again reflecting the size difference of the three epiphyte species. Indeed, when I 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 ($p=0.68$). This indicates that abundance of inhabiting arthropods is a function of plant size rather than of plant species.

TABLE 4.1: Faunistic characteristics and analyses results of the arthropod assemblages inhabiting the three investigated epiphytes.
Results from quantitative destructive sampling of 30 plants per species.

	Vriesea	*Tillandsia*	*Dimerandra*	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 have zero minima (not shown).
**) with host plant biomass as covariate

Species richness, which I used as a measure of α-diversity, showed a different pattern (Table 4.1). 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 taxa in all three epiphytes were the ants, comprising almost three quarters of the total fauna (73%). Similarly consistent, the second most numerous taxon were the spiders, accounting for nine percent 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 4.2). When pooling the 90 study plants, all relationships were highly significant ($p<0.001$). However, analyzing the epiphyte species separately, the correlations with plant biomass were insignificant 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 4.2). This was not the case in *Dimerandra*.

TABLE 4.2: Results of correlation analyses between epiphyte biomass and faunal traits.

Correlation of host plant biomass with	n	r^2	p
(1) Numbers of species per plant			
all study plants	90	0.73	>0.001
Vriesea sanguinolenta	30	0.72	>0.001
Tillandsia fasciculata	30	0.55	>0.001
Dimerandra emarginata	30	(0.015)	0.530, n.s.
(2) Numbers of individuals (including ants)			
all study plants	90	0.51	>0.001
Vriesea sanguinolenta	30	0.58	>0.001
Tillandsia fasciculata	30	0.15	0.034
Dimerandra emarginata	30	(0.003)	0.780, n.s.
(3) Numbers of individuals (excluding ants)			
all study plants	90	0.82	>0.001
Vriesea sanguinolenta	30	0.80	>0.001
Tillandsia fasciculata	30	0.60	>0.001
Dimerandra emarginata	30	(0.001)	0.860, n.s.

n.s.= not significant

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 very common throughout the Neotropics (Longino & Nadkarni, 1990) and very abundant in the study area (Berghoff *et al.* 2001; Stuntz, unpublished data). *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, the latter one being a common element of the litter fauna in the study area (Zotz and Ziegler, unpublished data).

As a measure of faunistic similarity, I 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* (Sør=0.08) and *Tillandsia* (Sør=0.06), and a slightly higher index between *Vriesea* and *Tillandsia* (Sør=0.24). A multidimensional scaling analysis,

comparing the dissimilarities between the arthropod assemblages of individual plants (Southwood, 1978), divided the fauna clearly into three distinct clusters along the x-axis, corresponding to the three epiphyte species: Figure 4.2 conspicuously illustrates both the similarity of the arthropod assemblages *within* the epiphyte species as well as the faunistic dissimilarities *between* them.

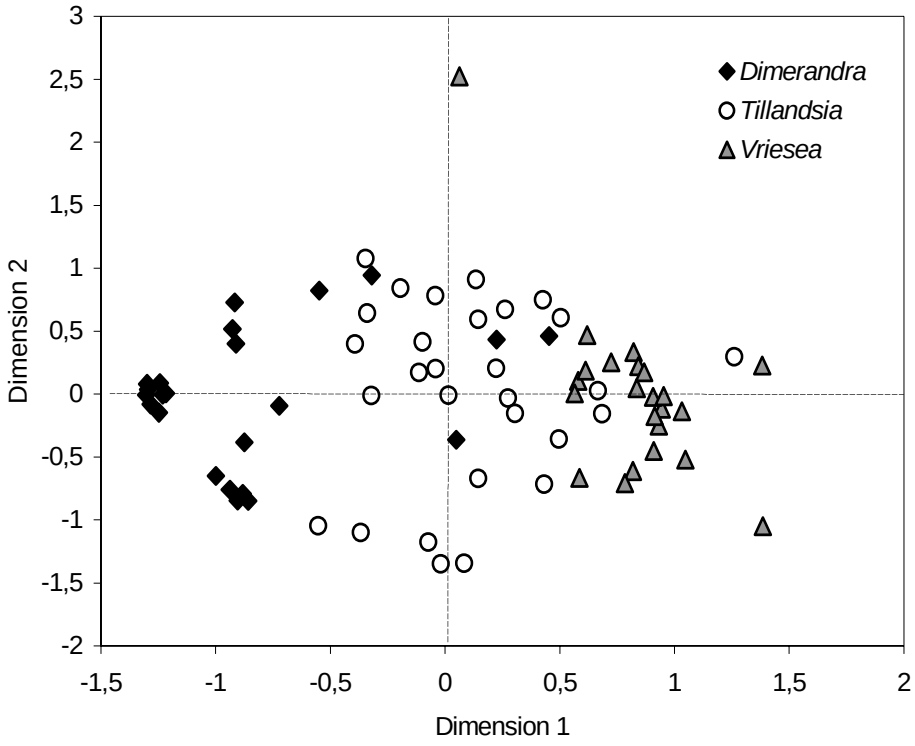

FIGURE 4.2: Two-dimensional scaling of the arthropod faunas of three epiphyte species.
The two outliers of *Vriesea sanguinolenta* (gray triangles) represent plants of small size with very few individuals.

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 4.3). 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* (Heteroptera sp. 1 and Thysanoptera sp. 1, see Appendix 1), 0.4% in *Tillandsia* (Heteroptera sp. 2), and lacked entirely in *Vriesea*. All phytophagous species were sap-suckers, there were no chewing herbivores.

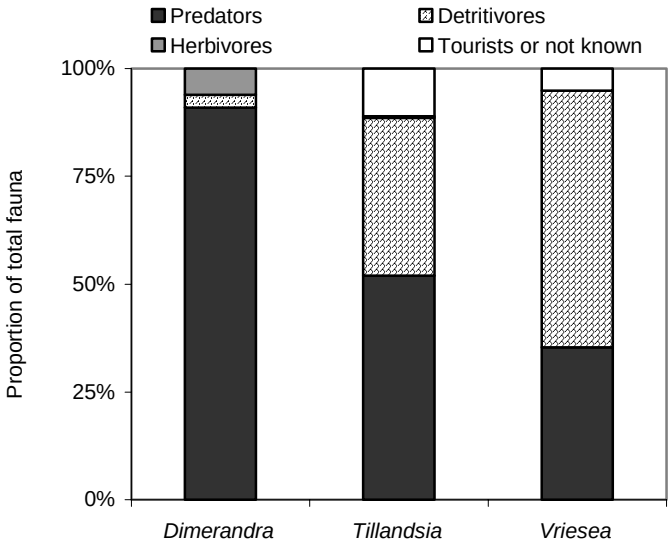

FIGURE 4.3: Guild composition of the inhabiting faunas of the three epiphytes. For guild assignment see Appendix 1.

Even within a given feeding guild I detected further differences. Spiders, the numerically most abundant group after the ants in all three study species (Table 4.1), can conveniently be divided into two major hunting guilds: web-builders and active hunters (Figure 4.4). Again, there were very distinct differences among the three epiphytes. 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.

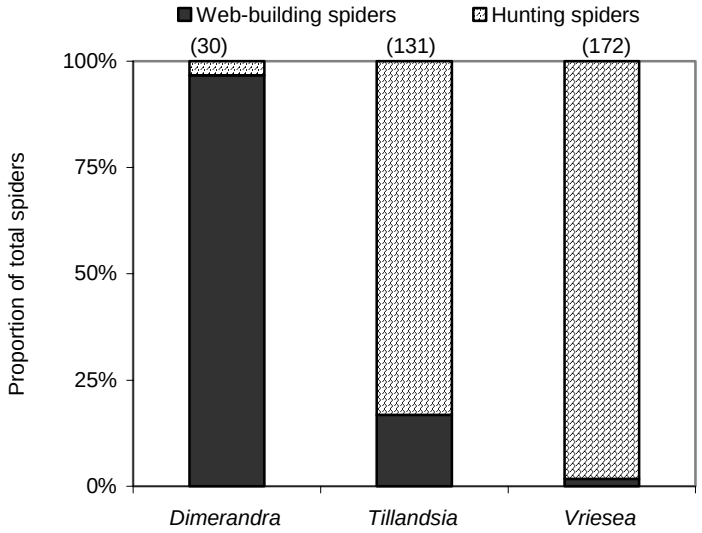

FIGURE 4.4: Proportion of web building versus hunting spiders.
Given are percentages of total spider assemblages. The absolute numbers of the spider totals are indicated in parentheses above the columns.

DISCUSSION

A simple relationship?

The largest epiphyte species, *Vriesea*, held the most numerous arthropod assemblage and, correspondingly, *Dimerandra*, the smallest species, harbored the fewest animals (Table 4.1). Within epiphyte species, arthropod diversity and abundance also increased with plant size (Table 4.2). This is consistent with Lawton's (1983) 'size *per se*' hypothesis, derived from the theory of island biogeography (MacArthur & Wilson, 1967), 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 with neither species richness nor abundance (Table 4.2). Its rather open structure may be less suited for arthropods compared to the set of interconnected, litter- and moisture-filled tanks featured by the 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. Southwood and Kennedy (1983) applied the island biogeography theory (MacArthur & Wilson, 1967) to their study trees (Southwood & Kennedy, 1983,) *'Trees as islands'*). Richardson (1999) quoted that bromeliads behaved as islands in that the species richness and abundance of their faunal communities were correlated with plant size. Furthermore, several authors demonstrated a relationship between structural habitat parameters and animal diversity (e.g., Halaj *et al.*, 1998, Lawton, 1986, MacArthur & MacArthur, 1961, Terborgh, 1977, Uetz, 1991).

However, 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 4.1). 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, is clearly not the case. The three epiphyte species fostered strikingly distinct arthropod faunas, both taxonomically (Figure 4.2, Appendix 1) and ecologically (Figure 4.3, Figure 4.4), even though they grew in close vicinity on the same host tree species.

Microclimate

Invertebrates dwelling in as harsh an environment as the 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 the preceding chapter, I showed that epiphytes influence temperature and humidity conditions in their immediate surrounding significantly (Chapter 3). 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 4.3) probably reflect the distinct features 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 are being decomposed, thus creating soil-like microsites, an important prerequisite for detritivorous inhabitants (Benzing, 1990, Richardson, 1999). *Dimerandra*, with its simpler structure, lacked this essential resource of decaying substrate, and had consequently barely 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, Gradwohl & Greenberg, 1982); 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 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, unpublished data). Fragoso and 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 this study do 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 throughout the three epiphyte species was remarkable (Figure 4.3). No single phytophagous species was found in *Vriesea*, the epiphyte with the greatest biomass (Table 4.1) and consequently, largest leaf area (see Chapter 5, Table 5.1). Only three singletons could be assigned as sap-suckers, and none as leaf chewers. Herbivory in epiphytes has not been studied thoroughly (Benzing, 1990, Schmidt & Zotz, 2000), although it has been stated that extensive defoliation is rare in neotropical epiphytes, and that many bromeliads and xeromorphic orchids are remarkably immune to herbivores (Benzing, 1990). Bromeliad leaves contain very little nitrogen (Stuntz & Zotz, 2001), and might thus be unattractive to herbivores. Schmidt and Zotz (2000) reported that *Vriesea* had only one main herbivore (*Napaea eucharilla* Bates, a lepidopteran larvae), but occasionally suffered extensive foliage damage. Zotz (1998) found that, of over 300 individuals of *Dimerandra*, only three had been chewed at, and found also only one lepidopteran herbivore (*Cremna thasus* Stichel). The scarcity of phytophagous insects in this study lends further support to the assumption that epiphytes are rather unattractive as hosts for herbivores.

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). As the strong predominance of web-building spiders on *Dimerandra* suggests, this orchid provides suitable web attachment sites

with its numerous erect and densely clustered stems and leaves. *Vriesea*, on the other hand, with its widely spaced and arching leaves, probably seems much less attractive to web builders (Figure 4.4). Litter depth and complexity has been shown to increase the diversity of hunting and web-building 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 retreat (Stuntz, personal observation). 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'). In *Dimerandra*, where few arthropods other than spiders or ants live (see Table 4.1 and Appendix 1), both of which are not preferred spider prey, this peculiarity allows the web-builders to survive. In contrast, hunting spiders forage in their habitat for other more or less mobile arthropods, and cannot rely on aerial prey. The rich fauna in the debris-filled tanks of *Vriesea* and, to a lesser extent, *Tillandsia*, apparently harbors 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 influence spider composition, it is possible that they indirectly influence the arthropod faunas of tropical canopies. It would be intriguing to test this conception on the level of entire tree crowns.

Conclusion

The arthropod faunas inhabiting three different species of vascular epiphytes displayed pronounced differences in species richness, species composition and guild arrangement. 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. The results confirm the importance of plant size and structure, in particular the ability to hold leaf litter and debris. In conclusion, epiphytes constituted important microhabitats for a diverse and numerous fauna, and different epiphytes fostered taxonomically and ecologically very distinct arthropod assemblages. Whether epiphytes influence local and between-habitat diversity at the level of entire tree crowns will be the subject of the following chapters.

5 ORDINAL COMPOSITION AND SEASONALITY OF THE ARTHROPOD FAUNA IN TREE CROWNS WITH DIFFERENT EPIPHYTES

ABSTRACT

It has been proposed that epiphytes influence the composition of arthropod communities in tropical tree crowns. To test this assumption, I conducted a one-year survey of 25 *Annona glabra* trees within the Barro Colorado Nature Monument in Panama. Selected trees supported distinct epiphyte assemblages and were assigned to four different categories; three with different species of epiphytes, and an epiphyte-free control group. I collected arthropods continuously with three different types of traps. Tree phenology was monitored throughout the study year. In total, I collected 273,490 arthropods from 29 orders. All taxa exhibited a strong seasonality, with highest abundances at the end of the dry season of 1998. Both total abundance of arthropods and herbivore abundance were not synchronized with neither the phenology of the host trees, nor with epiphyte phenologies. There were no significant differences in arthropod abundances among the different tree/epiphyte categories, neither in total numbers nor for any particular taxon (except of Diptera, who were slightly less abundant in trees with the large bromeliad *Vriesea sanguinolenta*). The relative proportions of the taxa were similar among categories. The number of arthropods was independent of total epiphyte leaf area and biomass in a particular tree, although the latter varied by almost two orders of magnitude. In conclusion, there was no clear effect of epiphytes on the ordinal composition of the arthropod fauna on the level of entire tree crowns.

INTRODUCTION

Most of global biodiversity occurs in the canopy systems of tropical forests. Arthropods probably constitute the largest fraction of this species pool, but how large remains yet to be determined. This prompted a vivid debate during the past two decades (Erwin, 1983, Gaston & Williams, 1993, Mawdsley & Stork, 1997, May, 1986, Ødegaard, 2000a, Stork, 1988). Still, the primary focus is on inventorying species (Leigh, 1999), while the mechanisms underlying the establishment and maintenance of arthropod diversity in tropical forest canopies are rather unclear. In this respect, vascular epiphytes have been proposed to be of considerable significance (Benzing, 1990, Nadkarni, 1994, Rodgers & Kitching, 1998). Aside from increasing the structural heterogeneity of the canopy and mitigating climatic extremes, epiphytes could profoundly affect the occurrence and abundance of arboreal invertebrate species by supplying resources for herbivorous species. For instance, Ødegaard (2000a) estimated a total of ten thousand species of phytophagous beetles to be specialized solely on epiphytes.

The effect of epiphytes on arthropod diversity and abundance in tree crowns has not been thoroughly studied. Hereafter, I present the outcome of a one-year survey of arthropods that

was carried out in a tropical moist forest in Panama. I sought to answer the questions: 1) Do vascular epiphytes affect arthropod assemblages in terms of relative abundance and faunal composition at the scale of entire tree crowns? and 2) how does arthropod abundance fluctuate seasonally, and are these fluctuations synchronized with the phenology of the host tree and/or its epiphytes?

Considering the complexity of most tree crowns, I chose a relatively simple study system consisting of a small tree species and three species of epiphytes (Chapter 1). The tree *Annona glabra* L. occurs abundantly along peninsular shorelines in the Barro Colorado Nature Monument (BCNM), and is often dominated by only one epiphyte species (Zotz *et al.*, 1999). Thus, tree crowns bearing distinct plant assemblages could be selected for a comparison of the respective arthropod faunas. I collected the arthropods with three different trap types to obtain an ample spectrum of the canopy fauna (Chapter 2). To account for seasonal variation, I sampled arthropods continuously throughout one year.

Our study area experiences a quite severe dry season from late December until May (Leigh *et al.*, 1982, Windsor, 1990), which has profound consequences for a multitude of plant and animal species (e.g., Foster, 1982, Leigh, 1999, Leigh & Smythe, 1978, Smythe, 1982, Wolda, 1978). Arthropods have been shown to synchronize their fluctuating abundances with the phenology of their host trees (e.g., Aide, 1993, Basset, 1991, Coley, 1983, Lowman, 1982, Wolda, 1978). I monitored flowering, leaf flush and fruit fall in *Annona glabra*, in order to investigate whether the arthropod fauna adjusts to the seasonal rhythms of their host trees. The epiphytes I studied provide new leaves continuously over the year, (*Vriesea sanguinolenta* and *Tillandsia fasciculata*; Schmidt and Zotz, unpublished data), or during most of the rainy season (*Dimerandra emarginata*; Zotz, 1998). Herbivory in epiphytes remains a poorly studied issue (Benzing, 1990), although it has been shown that one of the study epiphytes, *Vriesea sanguinolenta*, suffers regularly and considerably from leaf damage through lepidopteran larvae (Schmidt & Zotz, 2000). If phytophagous arthropods generally benefit from the continuous supply of young bromeliad leaves, their abundance might fluctuate less in epiphyte-laden trees compared to trees devoid of them. In the same context, the abundance of herbivores could be increased, because epiphytes substantially add to the green biomass in the canopy.

I will present here the results at ordinal level. If there is a significant effect of epiphytes on the fauna, I expect to evidence it already at higher taxonomic levels. For instance, epiphytes indirectly increase the amount of organic matter ('suspended soil') in the canopy by impounding leaf litter between their leaves or stems (Benzing, 2000, Nadkarni, 1994, Richardson, 1999, Rodgers & Kitching, 1998), and could therefore promote the occurrence of taxa that would otherwise be rather restricted to terrestrial habitats, such as, e.g., Diplopoda, Chilopoda or Isopoda. The presence of ants could also be positively influenced by epiphytes: many ant species nest inside epiphytes (Blüthgen *et al.*, 2000, Dejean *et al.*, 1992, Richards, 1996, Schimper, 1888), or in the litter they suspend (Longino & Nadkarni, 1990). Spiders often respond to the physical structure of environments (Cherrett, 1964, Duffey, 1966, Gunnarson, 1990, Halaj *et al.*, 1998, Hatley & MacMahon, 1980, Rypstra, 1983). For example, Stevenson and Dindal (1982) and Uetz (1979) demonstrated that habitat complexity correlated with the diversity of hunting and web-building spiders. By increasing the structural heterogeneity of the canopy habitat (Benzing, 1990, Nadkarni, 1994), epiphytes might also influence spider species richness and abundance. Epiphytes moderate climatic extremes in the canopy (Chapter 3). It is possible that the presence of epiphytes acts as a buffer for the activity of arthropods during the harsher dry season.

STUDY SITE

The study was conducted from April 1998 until April 1999 in the Barro Colorado Nature Monument (BCNM), in which center Barro Colorado Island (BCI) is located (9°10' N, 79°51' W) in the Republic of Panama. Study trees were selected along the shores of mainland peninsulas of Lake Gatún. The annual rainfall in this 'tropical moist forest' (Holdridge *et al.*, 1971) amounts to approximately 2600mm. Detailed descriptions of climate, vegetation and ecology are reported by Croat (1978), Leigh *et al.* (1982) and Windsor (1990).

METHODS

Study trees and epiphytes

The small tree *Annona glabra* L. (Annonaceae), which grows along the lake shore, was appropriately suited for my research goals. Roots and lower stem portions are inundated, impeding the access of terrestrial arthropods. The low canopy of *A. glabra* (mean height of the study trees: 4,9m ± 0.9 (SD), n=25) is easily accessible by boat but climatic conditions are similar to the upper forest canopy (Zotz *et al.*, 1999) due to its exposure to sun and wind along the shore. Moreover, Zotz *et al.* (1999) found that *A. glabra* is often dominated by a single epiphyte species.

This peculiarity allowed me to define distinct tree categories with rather uniform epiphyte assemblages. I defined four categories (Figure 5.1, Figure 5.2): trees without epiphytes as control group, trees with *Dimerandra emarginata* (Orchidaceae), trees with the large tank bromeliad *Vriesea sanguinolenta* (Bromeliaceae) and trees dominated by *Tillandsia fasciculata* (Bromeliaceae, often occurs in dense clusters of several individuals).

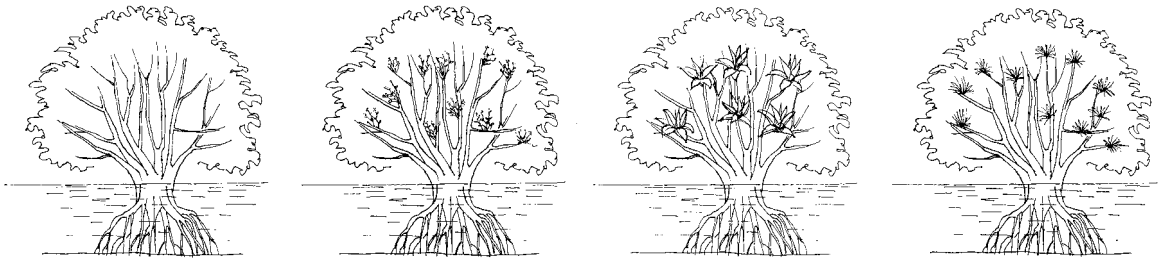

FIGURE 5.1: Sketches of the four categories of study trees (*Annona glabra*).
From left to right: control tree, tree with *Dimerandra emarginata* (Orchidaceae), tree with *Vriesea sanguinolenta* (Bromeliaceae), tree with *Tillandsia fasciculata* (Bromeliaceae).

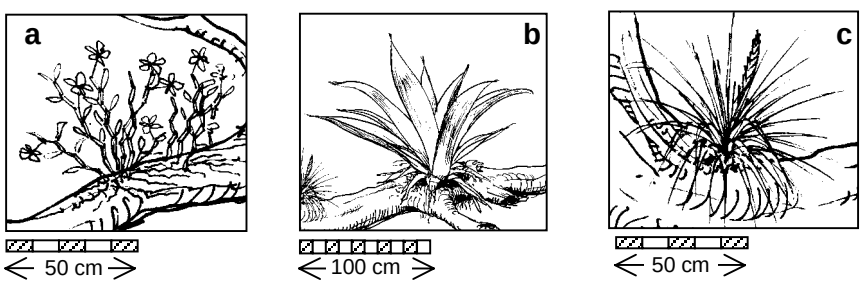

FIGURE 5.2: Illustration of the study epiphytes. *Dimerandra* (a), *Vriesea* (b) and *Tillandsia* (c). Please note the different scales. For comparison, see the specimen of *Tillandsia* in the lower left corner of (b).

These epiphyte species (thereafter addressed by their generic names) are adapted to the harsh conditions of the upper canopy and were locally abundant in the study area. Three of the four categories were replicated at seven sites distributed all over BCNM, where I could find trees of all categories in close vicinity (Figure 1.1). However, *Tillandsia*-trees were found only in the proximity of four of those sites. I chose to sample those trees only when arthropod abundance was expected to be high, and closed the traps during the second half of the rainy season, i.e. from July to November 1998.

Sampling protocol

Different trapping techniques may yield very different animal assemblages and hence strongly influence the outcome of faunal studies (Basset *et al.*, 1997; Stuntz *et al.*, 1999; Simon & Linsenmair, 2001, Chapter 2). In order to obtain a reasonably broad spectrum of the arboreal fauna, I used three different types of traps: flight interception traps (two per tree), branch traps (two per tree) and yellow color traps (one per tree). They are illustrated and described in Chapter 2. The traps remained in the tree crowns for an entire year and were emptied every two weeks. I transferred the captured arthropods to 70% ethanol until further treatment in the laboratory. All animals were identified and counted at the ordinal level with the help of trained assistants.

Epiphyte biomass and tree phenology

To estimate non-destructively the total biomass of epiphytes on a tree, I measured the maximum leaf length of all the bromeliads on a study tree or, respectively, the length of the latest stem of each orchid stand. These parameters are strongly correlated with total plant biomass (Schmidt & Zotz, 2001). Using their regressions, I estimated the epiphyte load of each tree. Total leaf area of *Annona* was estimated from crown diameter and leaf area index (Zotz *et al.*, 1999). Leaf area estimates for the epiphytic vegetation were also obtained non-destructively from published correlations of plant size and leaf area (Schmidt & Zotz, 2001, Zotz & Andrade, 1998, Zotz & Tyree, 1996).

When surveying the traps, I recorded the phenological state of the host trees. I estimated the flushing of new leaves and the presence of flowers or fruit at a scale from zero to three (0–no new leaves/flowers/fruits; 1–very few; 2–present and 3–many). Because the performance of the twenty-eight trees at a particular point in time was quite coherent, I believe that the estimates are solid, despite the rather coarse scale. The dates for the beginning and end of the dry seasons 1998 and 1999 (in Figure 5.4) were provided by the Panama Canal Commission.

Statistics

Statistical analyses were performed with STATISTICA (StatSoft Inc., Oklahoma, USA). I compared the faunal assemblages of the four tree categories with Kruskal-Wallis-ANOVA (KW-ANOVA), Mann-Whitney-U-Tests and repeated-measures ANOVA (RM-ANOVA), and used the Spearman rank coefficient to test for significant correlations between tree parameters and abundance of arthropods. Seasonal rhythms were analyzed with circular statistics (Watson's U^2) according to Zar (1999), using the program Rayleigh & Co. 3.1 (oxalis GmbH, 33335 Gütersloh, Germany).

RESULTS

Composition of the fauna

In total I collected 273,490 arthropods belonging to 29 orders (Figure 5.3). Micro-caddisflies (Hydroptilidae, Trichoptera) constituted the majority of the captured arthropods, contributing nearly a third (29%) to the total. This group was represented by a few species of the genus *Oxyethira*, which probably breed in the Lake Gatún (O. Flint, personal communication). Two species, *O. circaverna* Kelley and *O. maya* Denning, were especially abundant. The second and third most abundant orders were flies (Diptera, 21%) and springtails (Collembola, 13%). Sixteen taxa were represented by less than 1% of the total fauna (in order of decreasing abundance): Lepidoptera, Thysanoptera, Hemiptera, Isopoda, Chilopoda, Blattodea, Orthoptera, Ephemeroptera, Trichoptera other than Hydroptilidae, Neuroptera, Odonata, Embioptera, Pseudoscorpiones, Dermaptera, Scorpiones, Strepsiptera, Mantodea. The latter nine taxa constituted even less than 0.1% of the catch.

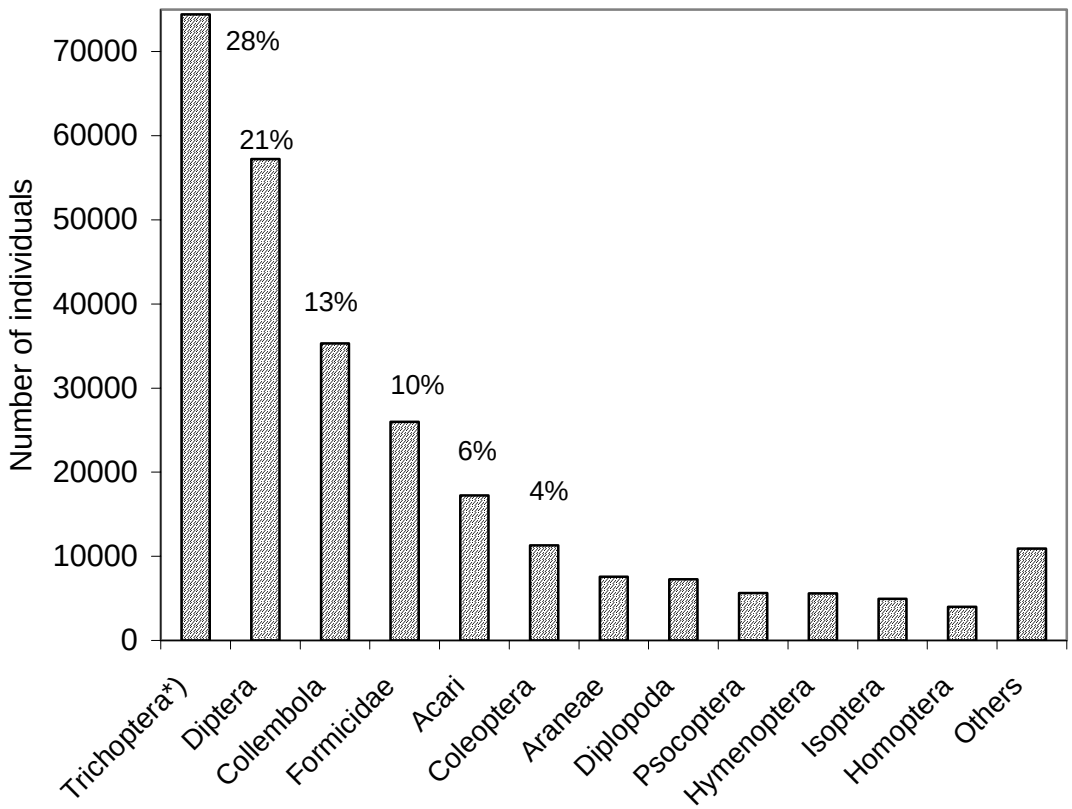

FIGURE 5.3: Composition of the arthropod fauna collected in *Annona glabra*.
In total, I collected 273,490 animals during the course of a year in 25 tree crowns. Trichoptera*) means Hydroptilidae, micro-caddisflies. 'Others' comprises seventeen taxa that contributed less than 1% to the entire fauna.

Seasonality and Phenology

As expected, all arthropod taxa exhibited strong annual fluctuations in their abundances (Figure 5.4). Trees with *Tillandsia* were not included in the following analysis, because they were not sampled continuously. On average, I caught 7,232 individuals every two weeks (median, n=27, range 3,450-21,733). There was one common peak shortly after the beginning of the trapping period, which coincided with the end of the dry season (FIGURE 5.4): in May and June 1998, nearly a third of the catch of the entire year was collected (30.3%). This pattern was observed in all taxa (data not shown), with few exceptions: in Homoptera, this initial peak was even sharper and lasted only one month (Figure 5.5). The same was true for termites (Isoptera) the vast majority of which were winged specimens, which are known to fly almost exclusively after the first heavy rains following the dry season (Smythe, 1982). Conversely, Diplopoda, Chilpoda and Isopoda were quite abundant until August 1998 and dropped by September to almost zero for the rest of the sampling period.

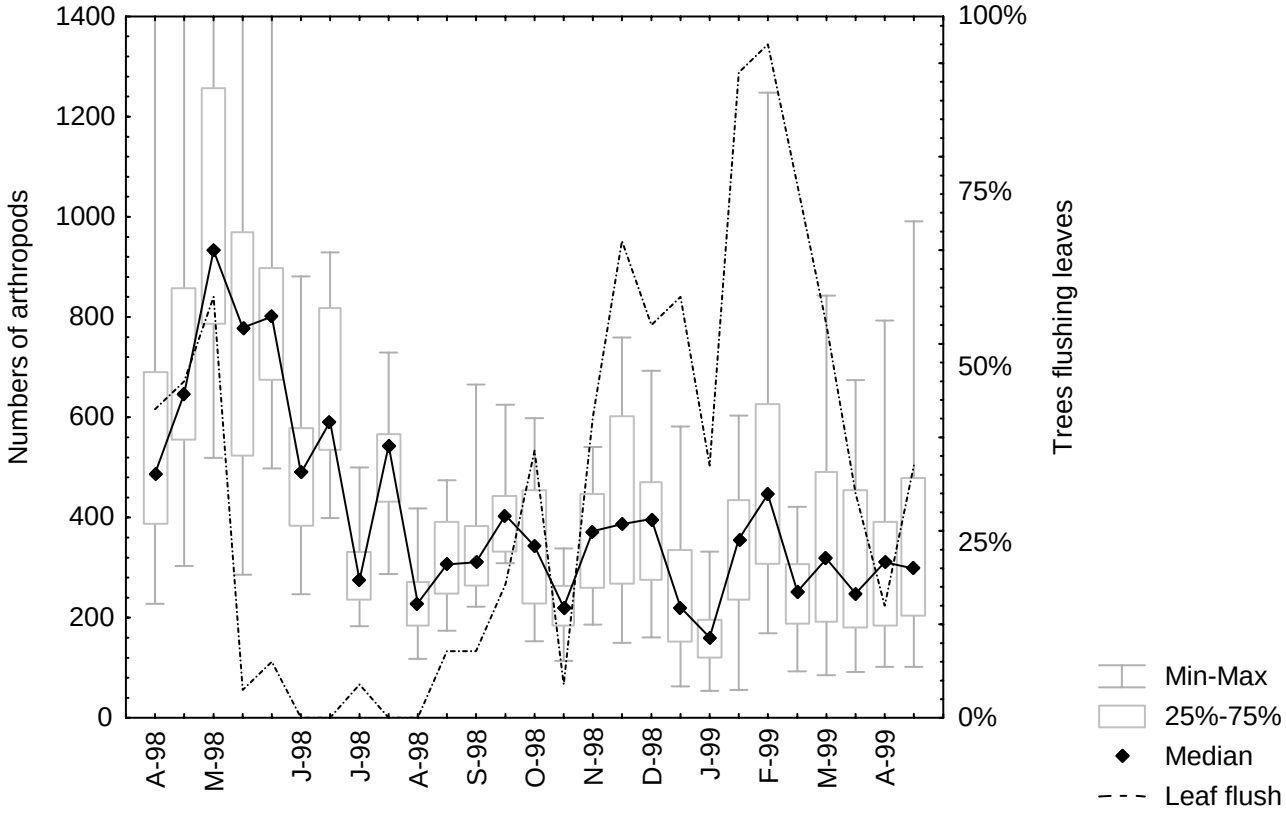

FIGURE 5.4: Box plot of total numbers of arthropods in the study trees.
The proportion of trees which were flushing new leaves is given as dashed line.

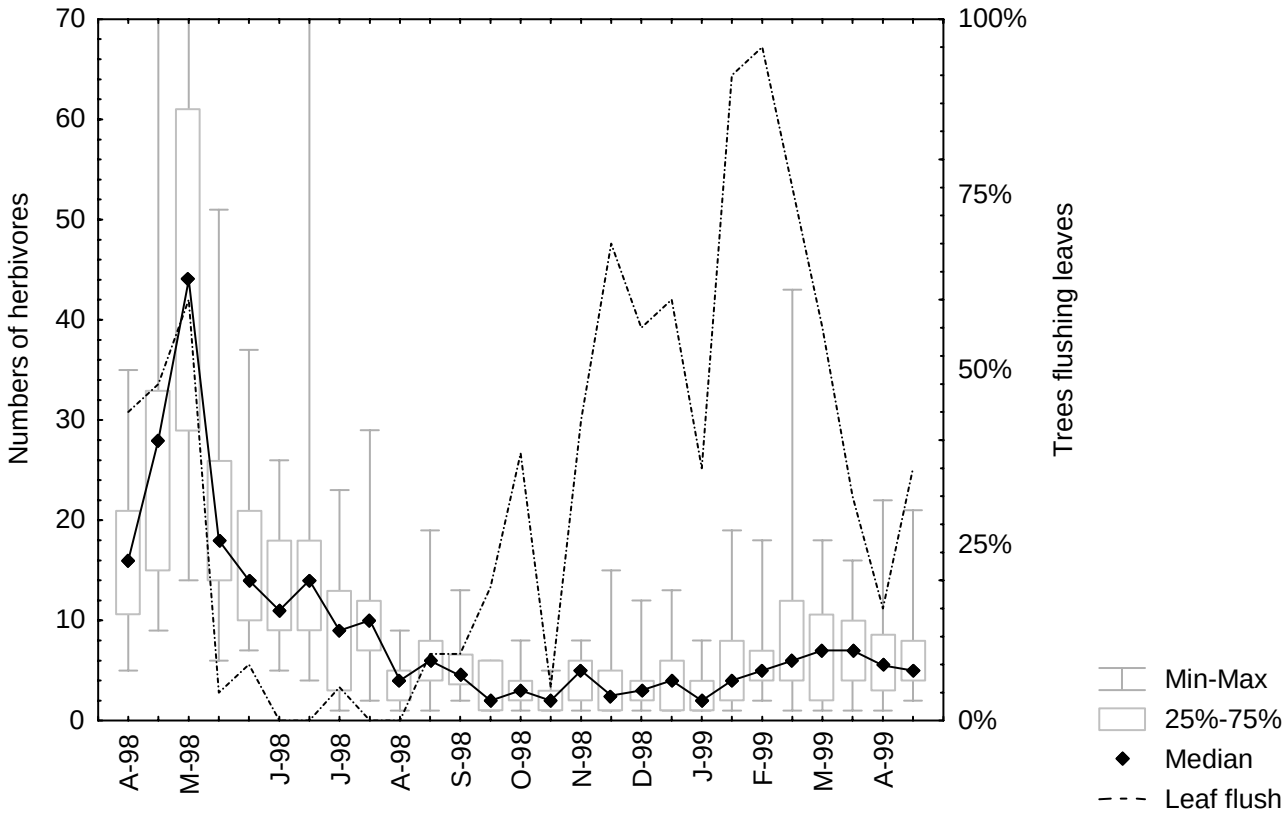

FIGURE 5.5: Box plot of the abundances of herbivorous taxa (Homoptera, Thysanoptera). The proportion of trees which were flushing new leaves is given as dashed line.

The results of the phenological survey of the host trees is displayed in Figure 5.6. Flowering and fruiting in *Annona* followed quite similar patterns. After a peak in April and May 1998, almost no flowers and fruit were observed until February 1999. Leaf flushes occurred several times during the study period, peaking in late January 1999, just at the onset of the dry season.

Abundance fluctuations of arthropods were not synchronized with the leaf flushes of the host trees (Watson's U^2; $p>0.05$; Figure 5.4). This was also true when considering only phytophagous taxa (Homoptera and Thysanoptera; Watson's U^2; $p>0.05$; Figure 5.5).

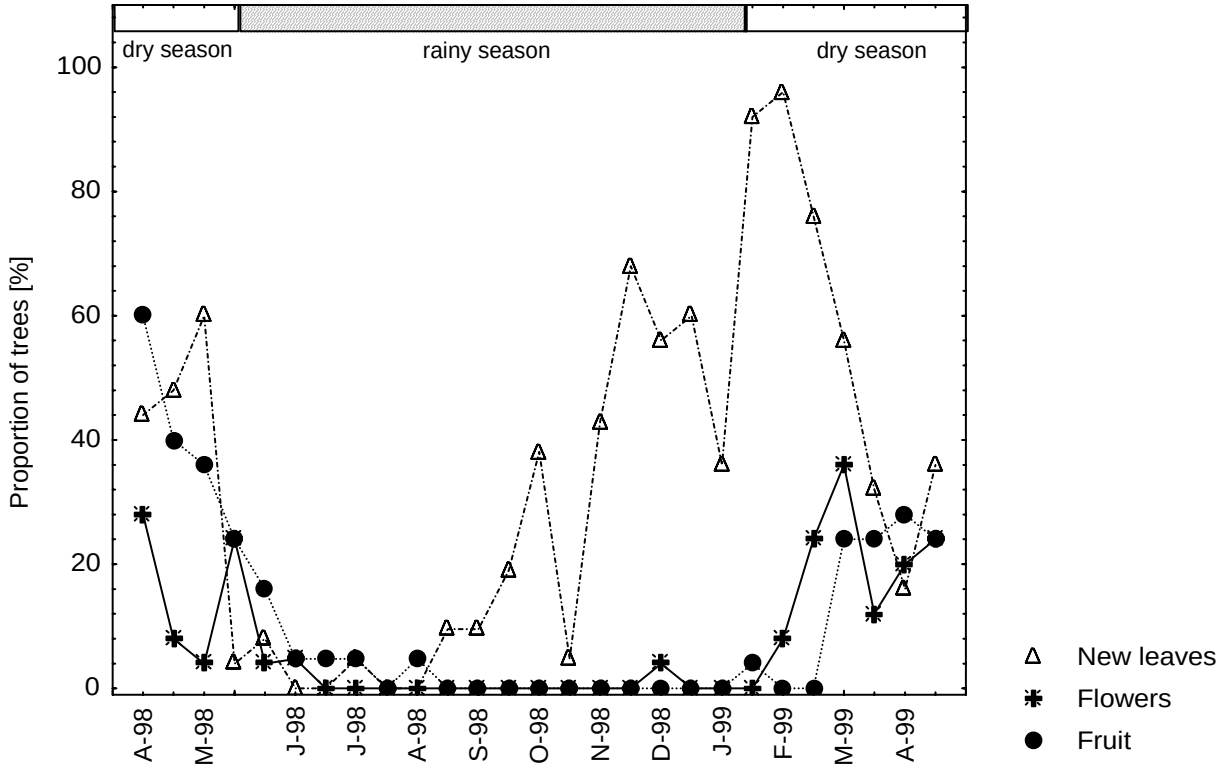

FIGURE 5.6: Phenology of *Annona glabra* and arthropod abundance during the survey year.
Proportion of study trees in which new leaves (open triangles), flowers (closed circles) or fruit (asterisks) were observed. In this chart, trees were included that were valued at a minimum score of 2, i.e. trees within which a fair amount of leaves/flowers/fruit were visible. The horizontal bars indicate rainy and dry seasons.

Host tree traits

The median leaf area of the host trees was $30m^2$ (range: 16 – 60) and did not differ among categories (KW-ANOVA, p=0.123, n=25; Table 5.1). The median leaf area of all epiphytes in one tree was $8m^2$ (range: 0.2 – 28, n=18, excluding control trees). Host tree leaf area was weakly correlated with epiphyte leaf area, although this was due to two trees with very high values of both tree leaf area and epiphyte leaf area (Spearman rank correlation, p=0.045; r^2=0.23; Appendix 2, Appendix 3). Without those outliers, there was no such correlation (Spearman rank, p=0.77).

Both total biomass and leaf area of the epiphyte load of the trees varied greatly and ranged from 90g dry weight (and $0.21m^2$ leaf area) in a tree with a rather sparse *Dimerandra* population to 3,853g dry weight in a tree abundantly laden with *Tillandsia.* The highest epiphyte leaf area was found in a tree with *Vriesea* ($27.9m^2$; Table 5.1). Both parameters were significantly different across categories (KW-ANOVA, p=0.002): trees with *Dimerandra* had lower epiphyte biomass and leaf area than trees with *Vriesea* or *Tillandsia* (U-test, p<0.01). The latter two categories did not differ among each other (U-Test, p=0.12; Table 5.1).

Differences among trees with different epiphyte loads

Epiphyte species identity. To account for seasonal fluctuations in animal abundance, I ran RM-ANOVA, considering the samples in their temporal sequence separately. There were no significant differences in numbers of individuals among the categories of trees: the analysis

only confirmed a strong seasonality by yielding significant p-levels for the temporal factor ($p<0.001$ for all taxa, Table 5.1), but the epiphyte load of the trees had no significant influence on the abundance of any of the taxa – with one exception: among all taxa representing at least 1% of the total fauna, only Diptera occurred in significantly lower numbers in trees with the large bromeliad *Vriesea* than in control trees and in trees with *Dimerandra* (RM-ANOVA, $p<0.007$; post-hoc LSD test $p<0.01$). The compositions of the arthropod assemblages were consistent among the four categories.

TABLE 5.1: Host tree traits (leaf area of host foliage; biomass and leaf area of its epiphyte load), numbers of arthropods and analyses results, detailed by tree category.
Given are median values, minima and maxima. Arthropods were collected in 25 trees with 125 traps during a period of eight months. Significant differences among categories are indicated in superscript.

Variable	Control trees	Trees with *Dimerandra*	Trees with *Vriesea*	Trees with *Tillandsia*	p-level
Host tree leaf area [m^2]	28.6 (16.7-30.9)	25.3 (15.9-53.9)	33.3 (27.5-60.2)	32.1 (21.3-39.6)	KW-ANOVA, p=0.12
Epiphyte leaf area [m^2]	0 -	0.6[a] (0.21-0.99)	12.6[b] (6.34-27.9)	10.9[b] (6.67-16.1)	KW-ANOVA, p<0.001
Epiphyte biomass [g dry weight]	0 -	318[a] (90-912)	1,670[b] (879-3,853)	3,207[b] (2,740-3,828)	KW-ANOVA, p<0.001
Numbers of arthropods per 2 wks	370 (54-1,621)	371 (92-2,137)	303 (85-1,317)	461 (113-1,758)	RM-ANOVA, p<0.001 (time), p>0.05 (categ.)
Totals of arthropods (8 months, n trees)	53,718	56,325	45,054	30,569	-
replicates (n)	7	7	7	4	-

Epiphyte quantity. Considering the large variation in epiphyte load (Table 5.1), I investigated whether the quantity of epiphytes irrespective of species identity in an *Annona* crown had an influence on arthropod abundance, but found no correlation. Both the total arthropod yield of the study trees at the end of the trapping period and the median values of the bi-weekly captures in each tree were independent of epiphyte biomass (Spearman rank correlation, $p>0.1$; Figure 5.7). This was also true for individual taxa ($p>0,1$). Only the abundance of Diptera was weakly negatively correlated with epiphyte leaf area (Spearman rank correlation, $p=0.038$, $r^2=0.177$), but not with epiphyte biomass ($p>0.1$). Arthropod abundance was independent of host tree leaf area (Spearman rank correlation, $p>0.1$).

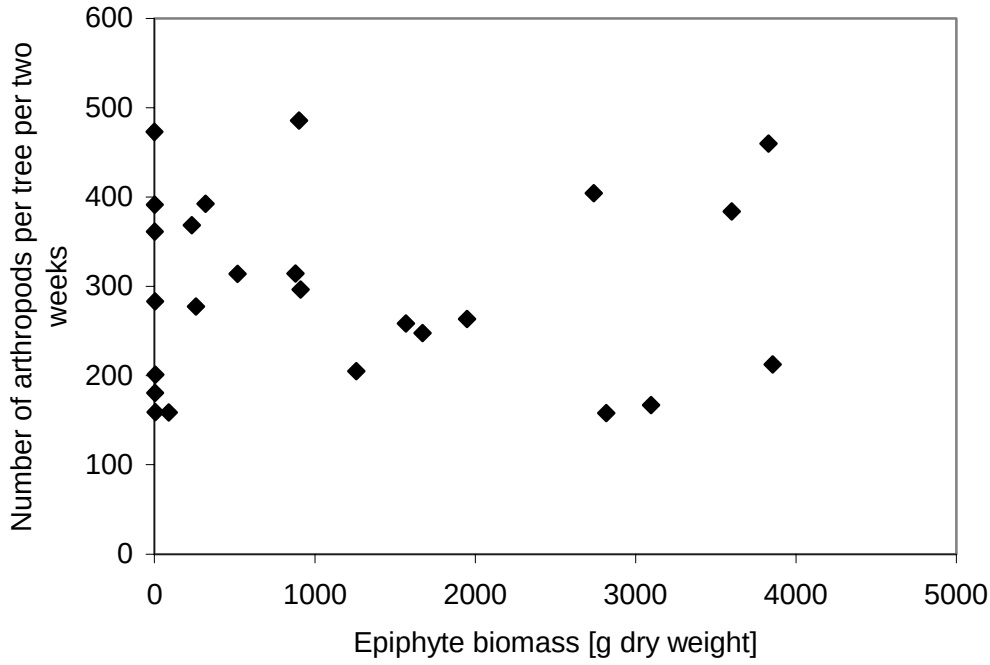

FIGURE 5.7: Epiphyte biomass plotted against arthropod abundance in the study trees.
Each symbol represents the median value of individuals caught per study tree in two weeks from April 1998 until June 1998 and December 1998 until April1999 (Spearman rank, $p>0.72$).

DISCUSSION

Faunal composition

The relative proportions of some taxa in the present study differ from other samples of arthropod faunas of tropical tree canopies (e.g., Adis *et al.*, 1998, Erwin, 1983, Floren & Linsenmair, 1997, Guilbert *et al.*, 1995, Hijii, 1983, Höfer *et al.*, 1994, Kitching *et al.*, 1993, Stork, 1991, Stork & Brendell, 1993, Wagner, 1997). This probably results from simple factors. The first and probably most prominent peculiarity is the high abundance of micro-caddisflies (Trichoptera, Hydroptilidae), which contributed almost 30% to the arthropod community in the study trees (Figure 5.7). Trichoptera in most canopy fogging studies are rare enough to be to included in 'other arthropods' (Floren & Linsenmair, 1997, Stork, 1991, Wagner, 1997), or not to be mentioned at all (Adis *et al.*, 1997). Abundant Trichoptera are certainly a consequence of the location of the focal trees along the shore of Lake Gatún, whereas the mentioned fogging surveys were carried out within rainforests. As the majority of caddisfly larvae are aquatic, and most adults are weak fliers, they are restricted to areas in the vicinity of aquatic habitats. The exceedingly abundant species *Oxyethira circaverna* and *O. maya* also dominated the caddisfly fractions in light trap samples on Barro Colorado Island (O. Flint, personal communication). Lake Gatún apparently represents a very suitable habitat especially for these two species.

The proportion of ants in the samples was relatively low (10%, Figure 5.3) compared to the percentages reported by other authors: (Adis *et al.*, 1998: 45%, Floren & Linsenmair, 1997: 58% , Stork, 1991: 18.2%, Stork & Brendell, 1993: 48%, Tobin, 1995: 32%, Wagner, 1997: 36-49%). Methodological reasons partly explain this discrepancy: insecticide fog used in these studies causes the majority of ants to abandon their nests and attempt to escape by dropping from the canopy (Floren, personal comment). Thus, ant colonies are sampled nearly quantitatively, while traps capture only a small fraction of each colony, i.e. workers that are active outside the nest. Considering the sizes of canopy ant colonies, these differences can cause marked deviations in relative abundance of ants, depending on the sampling method. Another reason for the poor numerical contribution of ants in my study is the relatively high proportion of springtails (13%) and mites (6%). These groups are probably underrepresented in fogging studies due to their minute size: while falling from the canopy, they might drift away before reaching the sampling trays (Simon & Linsenmair, 2001). Disregarding these taxa, as has been done by other authors (e.g., Basset, 1990), and omitting the micro-caddisflies, which are no common element of rainforest canopies elsewhere, the ant proportion of my samples would increase to 19%, thus approaching the results of previous studies in tropical forests.

However, despite the differences in methodology, the relative proportions and rankings of other taxa were quite consistent with those found by canopy fogging: the contribution of spiders and beetles, for example, were similar to those reported by Wagner (1997) and Höfer *et al.* (1994). Diptera were among the most abundant taxa in other studies as well (Adis *et al.*, 1998, Kitching *et al.*, 1993, Wagner, 1997). Diptera are considered as 'tourists' or 'transient species' that are not tightly associated with the trees in which they have been collected (e.g., Stork, 1987a). In fact, they were the only taxon in the present study that was significantly influenced by the epiphyte load of the host trees, albeit negatively. They decreased in numbers with increasing epiphyte leaf area, and were less abundant in the category with the largest epiphyte, *Vriesea*. This might result from a certain reluctance of these flying insects to navigate through densely epiphyte-laden tree crowns, which might appear as obstacles in the flight path. This argument is of course highly speculative and moreover not supported by similar phenomena in other fast-flying orders, such as the Hydroptilidae (micro-caddisflies) or Hymenoptera.

Seasonality

The movement of the Intertropical Convergence Zone causes a quite severe dry season in Panama. Leigh (1999) emphasized the importance of this cyclic alternation of seasons for the timing of tree phenologies on BCI remarking that it can "cause feast and famine in successive years". The host tree, *Annona glabra*, exhibits a pronounced seasonality (Figure 5.4) similar to most trees in the forest of the study area, approximately synchronizing with their major peaks of fruit fall, flowering and leaf flush (Foster, 1982, Leigh & Smythe, 1978, Leigh & Windsor, 1982). In contrast to a previous study in Brazil, where several *Annona* species flowered during the rainy season (Gottsberger, 1989a), the trees studied here flowered only in the dry season (Figure 5.4). Fluctuations of animal abundances, especially in phytophagous taxa, are sometimes correlated with host tree phenology. For instance, abundances of herbivores frequently rise simultaneously with the production of new leaves, which are the preferred diet of most phytophagous insects (e.g., Aide, 1993, Basset, 1991, Coley, 1983, Lowman, 1982, Wolda, 1978). In my study system, however, abundance of arthropods did not correlate with the flushing of new leaves in the tree crowns (Figure 5.4). This was also true for phytophagous taxa (Figure 5.5).

The studied bromeliads produce new leaves continuously throughout the year (Zotz, unpublished data), but arthropod abundance did change significantly over time in all tree categories (Figure 5.4, Table 5.1). If herbivorous taxa were positively influenced by this predictable resource of young leaves in the bromeliad trees, then trees with *Vriesea* and *Tillandsia* should have smaller abundance fluctuations, or greater abundance of phytophagous taxa, or both. Neither was the case. In a similar manner, arthropod abundance appeared not to coincide with the phenology of *Dimerandra*, which flushes leaves approximately from April until August (Zotz, 1998): most taxa declined in abundance during this period. The implication that herbivorous arthropods were not influenced by epiphyte leaf flushes is further supported by the finding that the studied epiphyte species are attacked by very few herbivorous species, which moreover occur in rather low numbers (Schmidt & Zotz, 2000, Zotz, 1998; see also Chapter 6).

Host tree leaf area had no influence on the phytophagous taxa Homoptera and Thysanoptera, nor did the latter synchronize their seasonal rhythms in abundance with the phenology of their hosts. This might indicate that phytophagous arthropods in the study system were rather weakly associated with their host tree. However, this notion must be regarded as merely hypothetical until data on species composition and ecology of the respective organisms are available. Recent studies have also reported a rather low host specifity of phytophagous taxa in tropical canopies (Mawdsley & Stork, 1997, Stork, 1987a). For example, Ødegaard (2000a), summarizing results of large arthropod inventories (Basset *et al.*, 1996, Mawdsley & Stork, 1997, Ødegaard, 2000b) calculated a median of only four species of phytophagous beetles effectively specialized on a particular tree species.

It is also possible that the chosen method underestimated phytophagous insects, that are often more or less sessile on the leaves they feed on. A prerequisite of being captured in traps in sufficient number is a reasonably high activity of arboreal or aerial movement. Trapping thus monitors animals more on the basis of their activity (or 'intensity of activity', see Adis, 1979). For less mobile organisms, other methods, such as hand collecting or branch clipping, might be more useful for investigating small faunal distinctions (Köhler, 1997). Nevertheless, I consider it very unlikely that arthropod catches were biased only toward species with little tendency to associate with the host tree.

I recorded a pronounced peak of arthropod abundance at the beginning of the rainy season, and lower numbers during the dry season (Figure 5.4). This is consistent with earlier findings of Wolda (1978) and Smythe (1982) for the BCI forest. Leigh (1999) assumed that insects are generally most abundant in the early rainy season and much less so during the dry months. One could interpret this as an indication that arthropods are somewhat constrained by climatic conditions, apparently decreasing in abundance during the harsher dry season. However, the reduction in numbers during the second half of the rainy season (Figure 5.4) is certainly not consistent with this argument. Moreover, if mitigation of microclimatic extremes increased arthropod abundance, I would expect to find more arthropods in trees with epiphytes. Epiphytes substantially moderate the microclimate in tree crowns by reducing evaporation as well as air and surface temperatures in their immediate surrounding (Chapter 3). Nevertheless, arthropod abundances during the dry season in tree crowns heavily laden with epiphytes were similar to those in trees devoid of them.

Do epiphytes influence arboreal arthropods?

Do epiphytes influence the arthropod assemblages of entire tree crowns? At the ordinal level I did not find such an effect. In fact, the four tree categories that were defined *a priori* (Figure 5.1) had rather similar arthropod faunas in terms of relative and absolute abundance, although their epiphyte load differed significantly (Table 5.1). Furthermore, arthropod abundance did not correlate with epiphyte biomass (Figure 5.6) or leaf area. My initial hypothesis that epiphytes might act as a buffer for harsh climatic conditions during the dry season could not be confirmed (Table 5.1). However, I do not suggest that epiphytes have no influence at all on canopy arthropods, but that these considerations may be scale-dependent. At the level of individual epiphytes, I found clearly defined arthropod assemblages as a function of both host plant species and biomass (Chapter 4). Among epiphyte species, arthropod abundance increased with plant size, and feeding and hunting guild composition was almost completely turned over (Chapter 4). At the level of entire tree crowns, such an effect was not detectable.

In conclusion, these results do not support the notion that epiphytes impose a significant effect on the arthropod assemblages of entire tree crowns, even in this rather simple study system. However, a closer examination of the fauna at species level may modify this conclusion, and will be the aim of three subsequent chapters.

6 DO NON-MYRMECOPHILIC EPIPHYTES INFLUENCE COMMUNITY STRUCTURE OF ARBOREAL ANTS?

ABSTRACT

In a one-year-survey in Panama I examined the potential influence of a tree crown's epiphyte assemblage on its ant fauna. Ants were collected with various types of insect traps in 25 tree crowns of Annona glabra. The study trees were assigned to three different categories according to their epiphyte load, and to an epiphyte-free control group. I collected 22,335 specimens of 91 morphospecies, 32 genera and six subfamilies. By far the most abundant species was *Solenopsis zeteki*, a minute Myrmecinae which was found in each of the 25 study trees. Many other species were also rather common and evenly distributed throughout the study area. Only six species were singletons. Measures of α- and β-diversity, species abundance and species composition were not influenced by the epiphyte load of a tree. The lack of association between ant species indicated that the ant assemblages were not mosaic-like structured. The relevance of the mosaic theory in species-rich rainforest canopies is discussed briefly. I conclude that in the studied tree crowns, epiphytes do not influence the composition of ant assemblages, because ants are probably highly opportunistic with respect to their host plants.

INTRODUCTION

Due to their extraordinary abundance, ants are a most remarkable component of the tropical arboreal arthropod fauna (Erwin, 1983, Floren & Linsenmair, 1997, Hölldobler & Wilson, 1990, Stork, 1988, Tobin, 1991). According to Tobin (1995), ants comprise approximately 30% of the arthropod biomass in the forest canopy on Barro Colorado Island. They have proved to be a useful indicator taxon in a multitude of ecological studies, for example in order to assess overall biodiversity (Andersen, 1995, Longino & Colwell, 1997), altitudinal gradients (Brühl *et al.*, 1998, Brühl *et al.*, 1999), forest edge effects (Dejean & Gibernau, 2000), or differences between understory and canopy (Kaspari & Yanoviak, 2001, Longino & Nadkarni, 1990, Yanoviak & Kaspari, 2000). Ants may be of major importance for the structure of arboreal arthropod communities, because they exert a constant, high predation pressure (Floren & Linsenmair, 1997, Stork, 1987b, Tobin, 1995), and have even been given the superlative 'most important invertebrate predators' in the tropics (Hölldobler & Wilson, 1990, Linsenmair, 1990).

For more than a century, ant-plant interactions have been a favorite topic in tropical ecology (e.g., Dejean *et al.*, 1992, Dejean *et al.*, 1995, Fiala *et al.*, 1994, Janzen, 1974, Schimper, 1888, Whalen & Mackay, 1988, Wheeler, 1942, Yu, 1994). Epiphytes are frequent partners of such mutualisms (Benzing, 1990, Davidson & Epstein, 1989), providing living space for ant colonies (domatia), or nutrition from extrafloral nectaries, or both. In return, the plants benefit from nutrients they retrieve from the ants' waste, or enjoy rigorous protection from herbivores (reviewed in Hölldobler & Wilson, 1990).

In this chapter, however, I investigate whether *non-myrmecophilic* epiphytes influence ant diversity and abundance in the tropical forest canopy. Apart from increasing the structural heterogeneity of the canopy habitat and providing shelter from climatic extremes, epiphytes could promote ant occurrence by impounding large amounts of leaf litter (e.g., Benzing, 1990, Richards, 1996, Richardson, 1999), which is an important prerequisite for many canopy-nesting ants (Longino & Nadkarni, 1990). Many ant species also nest inside non-myrmecophilic epiphytes (Blüthgen *et al.*, 2000, Dejean *et al.*, 1992, Richards, 1996, Schimper, 1888). Epiphytes sometimes foster a rich arthropod fauna (Cotgreave *et al.* 1993, Paoletti *et al.* 1991, Richardson 1999, Chapter 4), a potential resource for predatory ants. Thus, it is conceivable that epiphytes positively influence ant diversity. However, it might as well be that ants are rather independent of the epiphytes in their environment: ants have been declared successful opportunist in many ways (e.g., Blüthgen *et al.*, 2000, Hölldobler & Wilson, 1990, Stork, 1987b). At present, our understanding of the role of non-myrmecophilic epiphytes for ant community composition is clearly quite poor, which motivated the present study. I compared the ant faunas of tree crowns bearing different sets of epiphyte assemblages, and trees free of epiphytes.

The present study also contributes to the ongoing discussion on the occurrence and importance of ant mosaics in the tropics. Recently, existence of well-organized ant mosaics was refuted for high-diversity rainforests (Floren & Linsenmair, 2000). Most of what is known of ant mosaics comes from orchards, mangroves or other areas with rather small faunas (Adams, 1994, Cole, 1983, Fowler *et al.*, 1998, Fox & Fox, 1982, Leston, 1973b, Leston, 1973a, Majer, 1976, Majer, 1982, Room, 1971). Thus, I wanted to find out whether in my model system of small trees on the forest edge, the ant fauna is mosaic-like structured, or if it is rather heterogeneous and unpredictable like the one investigated by Floren and Linsenmair (2000).

STUDY SITE

The study was conducted in the tropical moist forest of the Barro Colorado Nature Monument (BCNM, 9°10’ N, 79°51’ W) in Panama. The area receives approximately 2600mm 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).

METHODS

Study trees and epiphytes

The chosen host tree, *Annona glabra* L., grows abundantly along the shore of Lake Gatún. Despite its rather small stature (mean height of the study trees 4,9m ± 0.9 SD, n=25), the climatic conditions in its tree crowns are similar to the upper forest canopy (Zotz *et al.*, 1999) due to its exposure to sun and wind along the shore. *A. glabra* is often dominated by a single epiphyte species (Zotz *et al.*, 1999), which allowed us to define distinct tree categories with rather uniform epiphyte assemblages: 1) trees free of epiphytes as control group, 2) trees with the orchid *Dimerandra emarginata*, 3) trees with the large tank bromeliad *Vriesea sanguinolenta*, and 4) trees dominated by the medium-sized bromeliad *Tillandsia fasciculata*. Hereafter, the study species are addressed by their generic names. In order to account for

spatial heterogeneity across different locations, I chose sites where I could find trees of all categories in close vicinity. *Tillandsia*-trees were found only at four of the seven study sites (distributed all over BCNM, see Figure 1.1), and were sampled only when arthropod abundance was expected to be high, and thus closed the traps during the second half of the rainy season, i.e. from July to November 1998. Thus, for comparisons among categories, two different data sets were regarded: when the entire sampling period of thirteen months was included, I compared only the categories 1-3, and when all four categories were taken into account, I analyzed data from eight months with active traps in all trees and disregarded the captures between July and November 1998.

Trapping and processing the ants

I collected arthropods with three different types of traps: flight interception traps, branch traps and yellow color traps, which remained in the tree crowns for an entire year and were emptied every two weeks. They are illustrated and described in (Chapter 2). The captured arthropods were transferred to 70% ethanol until further treatment in the laboratory. Ants were separated from the rest of the catch, mounted and subsequently assigned to morphospecies based on external morphology. The reference collection was sent to specialists (Philip S. Ward for the *Pseudomyrmecinae* and John T. Longino for all other subfamilies), for species identification. Vouchers are deposited at the Smithsonian Tropical Research Institute in Panama, and at the Technische Universität München (Freising, Germany).

Epiphyte biomass and tree phenology

I estimated epiphyte biomass by measuring either the maximum leaf length of each bromeliad or the length of the latest stem of each orchid stand, respectively. Biomass was computed from known correlations with those parameters (Schmidt & Zotz, 2001).

Statistics

Statistical analysis was done with STATISTICA (StatSoft Inc., Oklahoma, USA). Numbers of species and individuals of the four tree categories were compared with Kruskal-Wallis-ANOVA (KW-ANOVA) and repeated-measures ANOVA (RM-ANOVA), and the Spearman rank analysis was used to test for significant correlations between epiphyte load and ant abundance. The Sørensen values in Table 6.3 were normally distributed and thus allowed the use of parametric one-way ANOVA among categories. As a measure for α-diversity I used species richness, i.e. the absolute number of species that were found in one sampling unit, and the Sørensen index as a measure of β-diversity (Magurran, 1988). To test for differences in the species compositions of the faunas among the epiphyte species, I ran multidimensional scaling analyses based on a dissimilarity matrix of 1-Sørensen values (Southwood, 1978). I also ran three-dimensional scaling analyses with the same matrices, and the outcome was always similar (not shown). Association analyses were computed following the protocol of Ludwig and Reynolds (1988).

RESULTS

Composition of the fauna

In total, I collected 22,335 specimens and identified 91 species in 32 genera and six subfamilies (Table 6.1). Many species were rather widespread throughout the study area (Figure 6.1): 26 species (29%) were found in more than half of all study trees, eight species occurred in over 90% of the trees, and three of those, *Solenopsis zeteki, Pheidole* cf. *flavens* and *Camponotus (Myrmobrachys)* sp. 4 (cf. *auricomas*) were even found in every single study tree. *Solenopsis zeteki* was by far the most abundant species (4,632 specimens) and contributed fully one fifth to the total of individuals. Five more species were represented by over a thousand individuals. Forty-one species were collected with less than ten representatives, and six species were singletons. The Myrmicinae were the most diverse and numerous subfamily (40 species and 15,222 individuals) (Table 6.1). The most species-rich genera were *Camponotus* (Formicinae), *Pheidole* (Myrmicinae) and *Pseudomyrmex* (Pseudomyrmecinae), which were represented by ten species each.

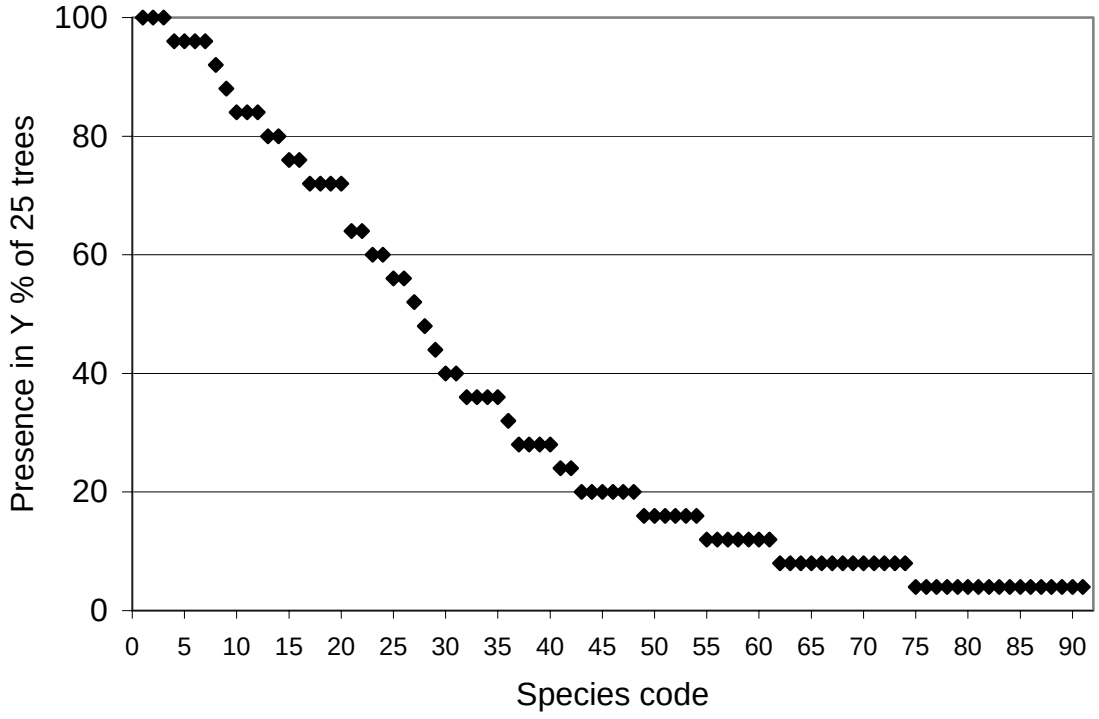

FIGURE 6.1: Rank-abundance plot of ant species.
Abundance is defined as the proportion of study trees (n=25), in which a certain species was collected during a trapping period of one year. For lack of space, the species ranked along the x-axis have been given numbers (see Table 6.1).

TABLE 6.1: Species (morphospecies) list of ants.
Given are totals of specimens (n) trapped in 25 study trees during 13 months. The totals of individuals within one subfamily are given in italics, the number of species within a subfamily in parentheses behind the family names. The species codes ('code') are referred to in Figure 6.1. Morphospecies names (genus + sp.1, sp.2 etc) relate to my voucher collection or to the collection of J. T. Longino (JTL-001).

Species or morphospecies name	n	code	Species or morphospecies name	n	code
Myrmicinae (40)	*15,222*		**Formicinae (15)**	*1,952*	
Solenopsis zeteki	4,678	1	*Paratrechina sp.2*	602	27
Wasmannia rochai	2,293	15	*Camponotus (Myrmobrachys) sp.4 (*cf.	344	3
Pheidole cf. *flavens*	1,893	2	*Camponotus atriceps*	301	6
Solenopsis sp.1	1,631	10	*Paratrechina sp.1*	220	7
Monomorium floricola	928	21	*Paratrechina sp.3*	181	19
Solenopsis sp.4	918	13	*Camponotus sexguttatus*	154	12
Pheidole punctatisssima	857	17	*Camponotus novogranadensis*	52	25
Cyphomyrmex rimosus complex	567	5	*Paratrechina sp.4*	32	32
Crematogaster carinata and	472	14	*Camponotus (Myrmeurynota) sp.7*	20	37
Pheidole radoszkowskii pugnax	417	28	*Camponotus mucronatus*	14	35
Pheidole cocciphaga	344	16	*Camponotus senex*	10	51
Pheidole sp.7	29	75	*Brachymyrmex sp.1*	8	53
Pheidole radoszkowski luteola	29	44	*Camponotus planatus*	8	52
Leptothorax echinatinodis	19	38	*Camponotus (Tanaemyrmex) sp.1*	5	57
Xenomyrmex JTL-001	17	62	*Camponotus sericeiventris*	1	82
Pheidole sp.6	17	34			
Pheidole sp.10	14	55	**Dolichoderinae (9)**	*3,619*	
Crematogaster brevispinosus crucis	11	45	*Azteca* cf. *velox*	1,410	4
Pyramica cf. *epinotalis*	10	76	*Azteca cf. trigona*	1,336	8
Pheidole pubiventris	10	63	*Dolichoderus bispinosus*	429	23
Pheidole decem	8	77	*Dolichoderus diversus*	407	18
Cephalotes grandinosus	7	54	*Dolichoderus debilis*	15	41
Xenomyrmex panamanus	6	66	*Azteca forelii*	10	46
Atta cephalotes	6	64	*Tapinoma melanocephalum*	7	40
Strumigenys borgmeieri	6	48	*Dolichoderus lutosus*	3	70
Cephalotes umbraculatus	4	68	*Dolichoderus laminatus*	2	72
Cephalotes atratus	4	67			
Cephalotes minutus	4	58	**Pseudomyrmecinae**	*543*	
Acromyrmex octospinosus	3	69	*Pseudomyrmex elongatus* (Mayr)	241	9
Strumigenys emmae	3	61	*Pseudomyrmex gracilis* (Fabricius)	121	24
Crematogaster crinosa	3	60	*Pseudomyrmex simplex* (F. Smith)	85	20
Cardiocondyla wroughtonii	3	59	*Pseudomyrmex ita* (Forel)	39	31
Strumigenys elongata	2	80	*Pseudomyrmex filiformis* (Fabricius)	34	43
Rogeria foreli	2	74	*Pseudomyrmex oculatus* (F. Smith)	12	56
Cephalotes setulifer	2	71	*Pseudomyrmex tenuissimus* (Emery)	7	54
Wasmannia auropunctata	1	92	*Pseudomyrmex euryblemma* (Forel)	2	79
Solenopsis sp.6	1	91	*Pseudomyrmex boopis* (Roger)	1	88
Solenopsis sp.5	1	90	*Pseudomyrmex browni* (Kempf)	1	89
Megalomyrmex silvestrii	1	84			
Leptothorax antoniensis	1	83	**Ecitoninae (10)**	*572*	
			Labidus praedator	358	30
Ponerinae (7)	*427*		*Labidus coecus*	149	36
Odontomachus bauri	225	11	*Neivamyrmex sp.1*	36	29
Odontomachus ruginodis	116	22	*Neivamyrmex sp.2*	11	42
Pachycondyla harpax	31	49	*Eciton hamatum*	10	50
Hypoponera opaciceps	30	33	*Neivamyrmex pilosus*	3	78
Pachycondyla villosa	18	39	*Eciton burchelli*	2	73
Ectatomma ruidum	6	65	*Neivamyrmex sp.3*	1	86
Anochetus inermis group	1	81	*Neivamyrmex sp.4*	1	85
			Nomamyrmex esenbeckii	1	87

*) These two species were lumped and assigned to one morphospecies

Comparison of tree/epiphyte categories

α-diversity

During a trapping period of eight months, I collected a median number of 26 (range: 15-38) species and 510 (88-1,039) individuals per tree (n=25). Medians, minima and maxima of the numbers of ant species and individuals in trees of the four different categories are given in Table 6.2. There were no significant differences among categories (KW-ANOVA n=25, numbers of species: p=0.62; numbers of individuals: p=0.39). To account for seasonal fluctuations, I tested for differences between tree groups over time with RM-ANOVA: during the course of the study year, the temporal factor significantly influenced both numbers of individuals and species (p<0.001). Confirming the results of the previous analysis, the tree/epiphyte category proved to be insignificant for both numbers of individuals (p=0.30) and species (p=0.29). There was no interaction between the factors time and tree category (p>0.55).

TABLE 6.2: Numbers of ant individuals and species in the 25 study trees.
Given are median values, minima and maxima of n trees collected during a period of eight months.

	Control trees	Trees with *Dimerandra*	Trees with *Tillandsia*	Trees with *Vriesea*
Individuals per tree				
Median	272	376	679	510
Min	88	297	436	269
Max	1,039	955	1,014	913
Species per tree				
Median	26	27	22	29
Min	17	15	19	21
Max	38	35	30	35
n	7	7	4	7

On the subfamilial level, one taxon showed differences in abundance across tree categories: Dolichoderinae were more numerous in *Tillandsia* trees compared to the remaining three categories (KW-ANOVA; n=25; p=0.049). In trees with *Tillandsia*, I collected a median number of Dolichoderinae of 139 (range: 42-278, n=4), whereas in trees of other categories, the median values were only 37 (13-166, n=7) in control trees, 34 (15-91, n=7) in trees with *Dimerandra* and even only 10 (0-115; n=7) in trees with *Vriesea*, respectively. In three of the four trees with *Tillandsia*, hundreds of ants of the genus *Azteca* could be readily observed inhabiting (and vigorously defending) most bromeliads, each probably being an outpost of a polydomous colony (Stuntz, Linder, personal observation). The abundance of the other subfamilies was independent of the tree category, both in terms of numbers of species and individuals (KW-ANOVA, p>0.1).

The category assignment was based merely on the species identity of the prevalent epiphyte in a tree, irrespective of the quantity of epiphytes in its crown. To investigate whether varying amounts of epiphytes partially explained the parameters ant abundance and diversity, I tested for correlations between epiphyte biomass and numbers of species and individuals. In both cases, there was no significant relationship (Spearman rank correlation, numbers of species:

p=0.81; numbers of individuals: p=0.18). This was also the case when analyzing the subfamilies separately (Spearman rank correlation, p>0.1).

ß-diversity

By means of two-dimensional scaling analyses, I tested whether the ant assemblages in the four tree/epiphyte categories differed in their species composition, using a matrix of dissimilarities (1-Sørensen) among all study trees (Figure 6.2). The symbols were obviously not grouped corresponding to the four tree categories, but rather evenly distributed throughout the plot. Consequently, the Sørensen indices of the ant communities in the four categories were quite high and ranged from 0.69 (between trees with *Tillandsia* and control trees) to even 0.83 between trees with *Vriesea* and control trees.

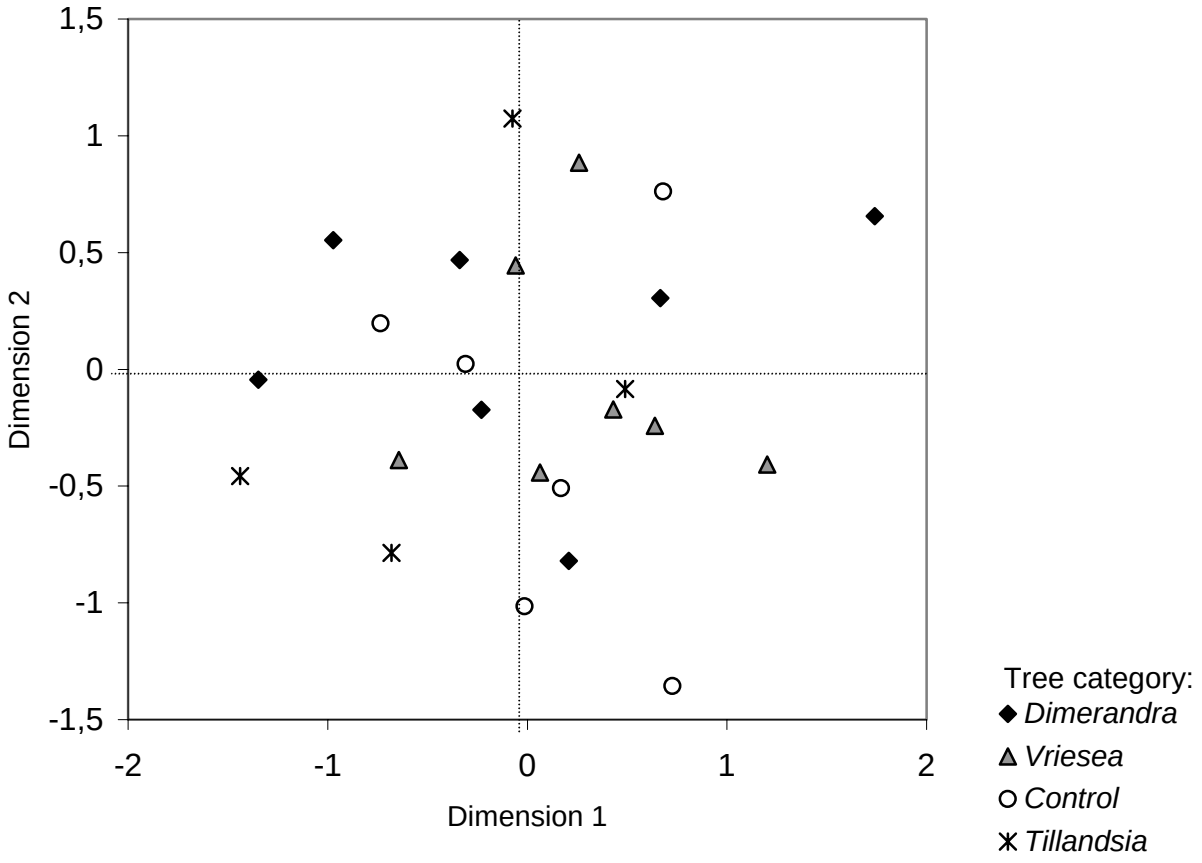

FIGURE 6.2: Two-dimensional scaling of the ant assemblages of the four tree categories.
Each symbol represents one study tree (n=25). Ants were collected with 125 traps during eight months.

Comparing the species assemblages of the individual study trees did not yield significant differences either (Table 6.3). The Sørensen indices between pairs of epiphyte-laden trees among each other, of control trees among each other and of epiphyte-laden trees paired with control trees did not differ (ANOVA, p=0.75). Similar results were obtained when including only those species that were present on a minimum of three study trees (to reduce chance effects by the occurrence of rare species; one-way ANOVA, p=0.87), or when excluding the

most abundant species, reasoning that their 'generalist' appearance might blur subtle differences in the composition of less abundant species (one-way ANOVA, p=0.10; Table 6.3).

TABLE 6.3: Average Sørensen values (mean ± SD) and statistics of 300 pair wise comparisons among study trees.
'Only abundant species' includes only species that were present on at least three trees, and 'only rare species' excludes species that were present on more than twenty study trees.

Comparison	Epiphyte-laden trees among each other	Epiphyte-laden trees with control trees	Control trees among each other	ANOVA p-level
All species	0.56 ± 0.08	0.55 ± 0.08	0.54 ± 0.08	0.75
Only abundant species	0.59 ± 0.09	0.58 ± 0.09	0.57 ± 0.09	0.87
Only rare species	0.44 ± 0.11	0.42 ± 0.11	0.39 ± 0.12	0.10
n pair wise comparisons	153	126	21	

Table 6.4 shows the ranking of the most abundant species within the four tree categories. The omnipresent *Solenopsis zeteki* was first-ranked throughout all categories. Of the 19 species that were represented by a minimum of five specimens (median) per tree (during eight months of trapping), three occurred throughout all categories and another three were abundant in three of the four categories. Nine of these 19 species were ranked among the most abundant species in one category only.

TABLE 6.4: Rank order and abundance (n = median) of the most abundant species in the four tree categories.
Included are species of which at least five individuals (median) per tree were trapped during eight months. Species present in all four categories are displayed in bold script, and species occurring in three of the four categories are underlined.

Control trees	n	Trees with *Dimerandra*	n	Trees with *Tillandsia*	n	Trees with *Vriesea*	n
Solenopsis zeteki	96	***Solenopsis zeteki***	64	***Solenopsis zeteki***	221	***Solenopsis zeteki***	55
*Camponotus sp.4**)	18	*Monomorium floricola*	53	*Azteca* cf. *velox*	139	***Pheidole*** cf. ***flavens***	52
Azteca cf. *velox*	13	*Solenopsis sp.4*	47	***Azteca*** cf. ***trigona***	37	*Solenopsis sp.1*	22
Dolichoderus diversus	12	*Pheidole punctatisssima*	36	***Pheidole*** cf. ***flavens***	19	***Azteca*** cf. ***trigona***	9
Camponotus atriceps	11	*Pheidole radosz. pugnax*	29	*Paratrechina sp.1*	11	*Odontomachus bauri*	8
Pheidole cf. ***flavens***	11	***Pheidole*** cf. ***flavens***	14	*Camponotus sp.4**	7	*Pheidole punctatisssima*	8
Azteca cf. ***trigona***	10	*Dolichoderus diversus*	13	*Cyphomyrmex rim. compl.*	6	*Camponotus atriceps*	7
*Crematogaster carinata and brasiliensis***)	10	*Dolichoderus bispinosus*	11	*Solenopsis sp.1*	6	*Cyphomyrmex rim. compl.*	5
Pseudomyrmex elongatus	6	*Pseudomyrmex gracilis*	10	*Pseudomyrmex elongatus*	6		
		*Camponotus sp.4**	9	*Camponotus atriceps*	5		
		Solenopsis sp.1	7				
		Azteca cf. ***trigona***	6				

*) *Camponotus (Myrmobrachys) sp.4 (*cf. *auricomus)*
**) These two species were lumped and assigned to one morphospecies

Association calculations for 903 species pairs revealed that no species in the study was significantly associated with another, neither positively nor negatively (p>0.05). This suggests that a structured ant mosaic did not exist in my study system.

DISCUSSION

Annona glabra *as model system for tropical canopies?*

At the beginning of this study, I claimed that despite the simplicity of the study system, it is feasible as model system for the high canopy. This assumption seemed to apply for the ant faunas. Both overall diversity (91 species) and diversity per individual tree (26 species) was within the scope of the species richness reported in previous studies of tropical canopies (Wilson 1986: 43 species per tree in the Amazon; Longino & Nadkarni 1990: 21 species nesting in canopy litter in Costa Rica; Floren & Linsenmair 1994: 30-40 species per tree in Malaysia; Majer 1994: 91 species in total from a Brazilian coca plantation; Adis *et al.* 1998: 124 species in total from the Amazon; Harada & Adis 1998: 52 species per tree in the Amazon). *Annona* is probably much smaller (4.9m) than the trees investigated in those studies, so the lower species diversity per tree seems justified. In the canopy of *Luehea seemanii* on Barro Colorado Island, a tall and persistent tree (Croat, 1978), Montgomery (1985) found 22-35 species of ants per tree. A recent study in the same study area strongly supports the presumption that the ant fauna in *Annona* is comparable to the one in the high canopy: Yanoviak and Kaspari (2000) found 32 ant species on baits in the crowns of four emergent tree species on Barro Colorado Island, 27 of which could be identified to species level and thus compared to the assemblage I collected. Sixty-three percent of their species were also common in my samples. Thus, I am confident that the ant fauna of *Annona glabra* is comparable to those of other undisturbed tropical forest canopies.

Dominants, submissives and mosaics

Methodological considerations. Many ant communities have clear hierarchies, featuring a few dominant species (so-called 'large-scale-conquerors' sensu Rosengren & Pamilo, 1983), and several subordinate species (e.g., Adams, 1994, Dejean & Gibernau, 2000, Hölldobler & Wilson, 1990, Leston, 1973a, Majer, 1990). The dominance of an ant species cannot necessarily be deduced from its massive occurrence in insect traps, but rather involves a characteristic behavior towards co-occurring species. Other workers have defined an ant species as dominant because of its ability to monopolize a bait, i.e. to defend food resources successfully from other, submissive species, while excluding other dominants (Yanoviak & Kaspari, 2000). Hölldobler and Wilson (1990) characterized dominants as consistently aggressive to workers of all other species, whereas those of the subordinate species almost invariably run from enemies. The discrepancy between high abundance (in my traps) and true 'dominance' sensu Leston (1973a) is best illustrated by the following example. *Solenopsis zeteki* was by far the most abundant species in the study area (Table 6.1), present on each of the 25 trees (Figure 6.1), and first-ranked in all tree categories (Table 6.4). It would be misleading, however, to derive from this omnipresence that *S. zeteki* is dominant in the study system. This tiny species (with less than 1.5mm body length; Stuntz, unpublished data) is a typical 'insinuator' (sensu Wilson, 1971): it moves in minute bark cracks and exploits food resources without alarming other species (C. Linder, unpublished data). *Solenopsis zeteki* was never observed to be involved in aggressive interactions with other species in order to defend territories or food resources (C. Linder, unpublished data), but workers exploited the baits in great numbers from underneath.

Nevertheless, apart from similar exceptions, abundance data usually give reasonable hints regarding dominance hierarchies. Dominants have large colonies and quickly recruit great

amounts of workers to food resources (e.g., Hölldobler & Wilson, 1990, Leston, 1973a, Yanoviak & Kaspari, 2000). This higher activity is reflected by greater abundance in the trap yields. Supporting this assumption, the twelve most abundant species of this study (except *S. zeteki*) were observed to show typical dominant behavior on baits (C. Linder, unpublished data). Some of the species have also been reported as dominants in other studies (*Azteca trigona, A.velox, Wasmannia rochai:* Adams, 1990, Adams, 1994, Fisher & Zimmerman, 1988, Fowler et al., 1998, Yanoviak & Kaspari, 2000).

Ant mosaics. Since Leston (1973a) originally described the phenomenon of an 'ant mosaic', there have been numerous accounts of mosaic-structured ant communities (reviewed in Hölldobler & Wilson, 1990). In such systems, dominant species form the core of the local community, each being the center of a positive association of other, non-dominant ants and of a negative association with other dominants (Leston, 1973a). However, most of the information on those highly deterministic and predictable communities comes from locations with a somehow impoverished fauna, e.g., African and Brazilian cocoa farms (Fowler *et al.*, 1998, Leston, 1973b, Majer, 1976, Room, 1971), mangroves (Adams, 1994, Cole, 1983), or tropical Australia (Fox & Fox, 1982, Majer, 1982), which is known for its little diverse ant fauna (Majer, 1990).

In my study system, I found no such mosaic. There were certainly dominant species (see also Figure 6.1, Table 6.1 and Table 6.4), the presence of which was often painfully apparent when they were fiercely defending their territory against any intruder. But they neither had a set of favored subordinates typical for a mosaic, nor did they consistently exclude other dominants: I found no significant association, negative or positive alike, between ant species. Moreover, on most trees I found three or more species which were present with more than 100 individuals. Correspondingly, Linder (unpublished data) found no negative correlations between dominants and no specific aggregation of submissives around dominants. These findings coincide with the outcome of a recent study in Malaysia: Floren and Linsenmair (2000) concluded, after an extensive fogging study in a pristine, highly diverse rain forest canopy, that the ant communities were very heterogeneous and unpredictable in their species composition. Finding neither negative nor positive species associations, they ruled out the existence of an ant mosaic in this mature lowland rainforest.

Contrastingly, Berghoff *et al.* (2001) reported mosaic-like structured ant assemblages in *Annona glabra* trees bearing the epiphytic orchid *Caularthron bilamellatum* (Rich.f.) Schult. However, this orchid is a true myrmecophyte, providing nesting space in its hollow pseudobulbs and nutrition from extrafloral nectaries. According to Jackson (1984), ant mosaics are often established around a predictable food source. While none of my study epiphytes supplied extrafloral nectar, *C. bilamellatum* guaranteed a year-round supply of nourishing exudates (Berghoff *et al.*, 2001). Carbohydrate-rich nectar is the main diet of most canopy dominants (Kaspari & Yanoviak, 2001, Leston, 1973a, Tobin, 1991). Thus, it seems likely that the orchid's nectaries provoke vital interspecific competition. Consequently, the absence of such predictable and attractive food resources might allow for a less hierarchic, more haphazardly array of ant species.

Hölldobler and Wilson (1990) noted the worldwide tendency that true dominants occur only in regions where faunas as a whole are small (boreal Europe, small islands, orchards) and proposed the 'dominance-impoverishment rule'. They reasoned that it is more likely for large-scale conquerors to originate in species-poor areas than for ant faunas to become impoverished by the suppressing effect of such dominant species. The fact that most of what

is known of ant mosaics, which are shaped by such true dominants, comes from similarly low-diversity areas supports this hypothesis. If species poorness is a prerequisite for the establishment and maintenance of ant mosaics, it is well conceivable that in very species-rich ecosystems like the Malayan rainforest canopy (Floren & Linsenmair, 2000) or the one I studied, a well-organized mosaic is not likely to occur.

Epiphytes and ants

In synopsis, the results of this chapter converged in that the epiphytes dwelling in the crowns of the study trees had no effect on the latter's arboreal ant fauna. Measures of α- and β-diversity were not influenced by the type or amount of epiphytes in the respective crown, neither was abundance (Table 6.2, Table 6.3); nor the species composition of the ant assemblages (Figure 6.2, Table 6.4).

These findings do not agree with the results of a previous study in the same area (Berghoff *et al.*, 2001). Berghoff *et al.* found that the ant fauna associated with the epiphytic orchid *Caularthron bilamellatum* growing on *Annona* was significantly influenced by the epiphyte. In trees with *C. bilamellatum*, both α- and β-diversity were higher than in trees without epiphytes. As mentioned earlier, this orchid is a myrmecophyte, which supplies domatia and nutrition for ants. There is a wealth of information about positive (although often facultative) interactions between ants and ant-plants in the tropics (e.g., Davidson & Epstein 1989; Dejean *et al.* 1992; Dejean *et al.* 1995; Fiala *et al.* 1994; Janzen 1974; Koptur, Rico-Gray & Palacios-Rios 1998; Schimper 1888; Wheeler 1942; Yu 1994). It was the aim of the present study to investigate whether non-myrmecophilic epiphytes also contribute to ant diversity by increasing the structural heterogeneity of the canopy habitat and providing shelter from climatic extremes and predators. Many epiphytes can impound large amounts of leaf litter (e.g., Benzing, 1990, Richards, 1996, Richardson, 1999), which is an important microhabitat for canopy-nesting ants (Longino & Nadkarni, 1990). Moreover, ants frequently nest inside (non-myrmecophilic) epiphytes (Blüthgen *et al.*, 2000, Dejean *et al.*, 1992, Schimper, 1888). Richards (1996) even remarked that epiphytes provide the chief nesting sites for arboreal ants in tropical rainforests. In a companion study, Linder (unpublished data) collected 40 ant species on tuna baits in *Annona*, 42% of which nested inside *Tillandsia*, *Vriesea* and *C. bilamellatum*. Thus, ants readily use the available infrastructure provided by epiphytes in tropical canopies. In spite of this, I could not detect any positive influence of the epiphytes on the ant fauna. Conformingly, Longino and Colwell (1997), after an extensive inventory of a lowland rainforest in Costa Rica, reported that ants were not specific towards their host trees. Blüthgen *et al.* (2000), who investigated the ant fauna inhabiting different species of tank bromeliads and found 13 species nesting within, found that these were haphazardly distributed among epiphyte species and concluded that ants are probably highly opportunistic with respect to host plants. My results support this hypothesis.

Conclusion

The epiphytes on the study trees had no significant influence on neither α-diversity nor β-diversity of ants. Some ant species were numerically dominant on certain trees, but the lack of associations – neither positive nor negative – indicated that the species community was not arranged in a well-organized ant mosaic. I conclude that non-myrmecophilic epiphytes in tropical tree crowns, although readily used as nesting sites and shelter, do not influence local or between-habitat diversity of ants. Instead, ants seem to be highly opportunistic with respect to their host plants.

7 THE BEETLE FAUNA OF TROPICAL TREE CROWNS WITH DIFFERENT EPIPHYTES

ABSTRACT

In order to examine the potential influence of a tree crown's epiphyte assemblage on its beetle fauna I conducted a one-year-survey in Panama. Beetles were collected with various types of insect traps in 25 tree crowns of *Annona glabra*. The study trees were assigned to three different categories according to their epiphyte load, and to an epiphyte-free control group. I collected 7,681 specimens of 352 morphospecies and 43 families. The most numerous and species-rich family was Curculionidae. By far the most abundant species was a small bark beetle (Curculionidae: Scolytinae), which contributed 16% to the specimens total. The proportion of rare species was relatively low (10% singletons, 30% doubletons). Species richness and abundance neither differed significantly between the tree/epiphyte categories, nor did it correlate with epiphyte biomass. I could not detect differences in species composition between categories by means of Sørensen indices and multidimensional scaling analyses. The guild composition was remarkably similar across categories: the most numerous guilds were scavengers, dead wood and fungal feeders, and herbivores tended to be the most diverse guild. The abundance of phytophagous beetles was not correlated with host tree leaf area, epiphyte leaf area, nor epiphyte biomass. It did neither synchronize with the tree's leaf flushes. The importance of herbivory in epiphytes is discussed. I conclude that epiphytes do not exert an ecologically significant influence on the beetle fauna in the investigated tree crowns.

INTRODUCTION

In this chapter I will present the species level results of the most diverse of the focal groups, the beetles. I chose this taxon for several reasons: beetles are both taxonomically and ecologically very diverse and can be found in most habitats and in all important feeding guilds. Many beetle species in all strata of the forest are strict specialists (Köhler, 1996). A wealth of data on canopy beetle diversity, guild composition and host specifity has been accumulated (Ødegaard, 2000a). For these and other reasons, beetles have been repeatedly advocated as excellent indicator organisms for a variety of ecological questions (e.g., Lawton *et al.*, 1998, Oliver & Beattie, 1996a, Pearson & Cassola, 1992). Not surprisingly, many estimates of global species richness are based on this group (Erwin, 1983, Ødegaard, 2000a).

Chapter 4 provided compelling evidence that different epiphyte species foster very distinct arthropod faunas. There were pronounced differences in faunal diversity and guild composition across host plants. Ten percent of the inhabiting arthropod species were beetles, and there was almost no species overlap among the three investigated epiphyte taxa. To test whether this effect scales up to the level of entire tree crowns, I analyzed the beetle fauna of 25 study trees with different epiphyte assemblages.

It has been reported repeatedly that the largest proportion of the species pool of arboreal beetles is phytophagous (reviewed in Ødegaard, 2000a). Epiphytes contribute substantially to the green biomass in tropical tree crowns (Benzing, 1990). In several of the study trees, the leaf area of the epiphytes in a tree constituted more than 25% of the total crown leaf area (see Appendix 2 and Chapter 5). It might be possible that this additional food supply exerts a positive influence on the abundance and diversity of herbivorous beetles. However, herbivory in epiphytes has received little attention and remains a rather poorly studied topic (Benzing, 1990). One of the study epiphytes, *Vriesea sanguinolenta*, suffers regularly and considerably from leaf damage through phytophagous insects, but most of this damage could be attributed to lepidopteran larvae (Schmidt & Zotz, 2000). Ødegaard (2000a) remarked that as yet, epiphytes have been virtually overlooked as hosts for arboreal beetles, although they are a major component of the tropical canopy flora. Without having baseline data, he estimated an average of 0.5 species of phytophagous beetles specialized on every species of epiphyte, resulting in a total of 10,000 epiphyte-specialized beetles worldwide. If epiphyte leaves constitute a valuable resource for arboreal phytophagous beetles, I would expect an increase of herbivores in epiphyte-laden trees compared to trees devoid of them.

STUDY SITE

The study was conducted in the tropical moist forest of the Barro Colorado Nature Monument (BCNM, 9°10’ N, 79°51’ W) in Panama. The area receives approximately 2600mm 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).

METHODS

Study trees and epiphytes

The chosen host tree, *Annona glabra* L., grows abundantly along the shore of Lake Gatún. Despite its rather small stature (mean height of the study trees 4,9m ± 0.9 SD, n=25), the climatic conditions in its tree crowns are rather similar to the upper forest canopy (Zotz *et al.*, 1999) due to its exposure to sun and wind along the shore. This tree is often dominated by a single epiphyte species (Zotz *et al.*, 1999), which allowed to classify distinct tree categories with rather uniform epiphyte assemblages: 1) trees free of epiphytes as control group, 2) trees with the orchid *Dimerandra emarginata*, 3) trees with the large tank bromeliad *Vriesea sanguinolenta* and 4) trees dominated by the medium-sized bromeliad *Tillandsia fasciculata*. Three of the four categories were replicated at seven sites distributed all over BCNM, where I could find trees of all categories in close vicinity (Figure 1.1). However, *Tillandsia*-trees were found only in the proximity of four of those sites. I chose to sample those trees only when arthropod abundance was expected to be high, and closed the traps during the second half of the rainy season, i.e. from July to November 1998. Thus, for comparisons among categories, there were two different data sets: when the entire sampling period of thirteen months was included, I compared only the categories 1-3, and when all four categories were taken into account, I analyzed data from eight months with active traps in all trees and disregarded the captures between July and November 1998. Hereafter, I will address the study plants by genus names.

Sampling protocol

I collected arthropods with three different types of traps (flight interception traps, branch traps and yellow color traps, see Chapter 2), which remained in the tree crowns for an entire year and were emptied every two weeks. They are illustrated and described in (Chapter 2). The captured arthropods were transferred to 70% ethanol until further treatment in the laboratory. Beetles were counted and separated from the rest of the catch with the help of trained assistants, then identified to family (subfamily) level, mounted and assigned to morphospecies (in the following referred to as species) based on external morphology. Subsequently, I assigned the species to feeding guilds, mainly following the guild classification of Stork (1987b). A reference collection with vouchers of all species is kept at the Department of Entomology at the University of Panama.

The beetle family Scolytidae (bark beetles) has recently been assigned to Curculionidae (weevils, subfamily Scolytinae). Here, it was convenient to treat them nevertheless as separate taxa, due to their distinct biology (e.g., for guild analyses: Scolytinae are wood eaters, whereas the remainder of Curculionidae classifies as herbivores; see Table 7.3). Subsequently (if not indicated otherwise), 'Scolytinae' and 'Curculionidae excluding Scolytinae' will be addressed independently. Other beetles were not further identified to subfamilial level.

Epiphyte biomass and tree phenology

I estimated the biomass of epiphytes on a tree by measuring the maximum leaf length of each bromeliad on a given study tree or, respectively, the length of the latest stem of each orchid stand. Because those parameters are tightly correlated (Schmidt & Zotz, 2001), I could compute biomass for the entire epiphyte load of a host tree non-destructively. Total leaf area of *Annona* was estimated from crown diameter and leaf area index (Zotz *et al.*, 1999). Leaf area estimates for the epiphytic vegetation were also obtained non-destructively from published correlations of plant size and leaf area (Schmidt & Zotz, 2001, Zotz & Andrade, 1998, Zotz & Tyree, 1996).

I recorded the phenological state of the host trees every two weeks. The production of new leaves was observed and valued at a scale from zero to three (0–no new leaves/flowers/fruits; 1–very few; 2–obviously present and 3–many). The data on host tree phenology are presented in more detail in (Chapter 5). In Figure 5.6, I display the proportion of study trees that were scored at least 2, i.e. trees with a substantial proportion of new leaves.

Statistics

Statistical analysis was done with STATISTICA (StatSoft Inc., Oklahoma, USA). I compared the faunal assemblages of the four tree categories with Kruskal-Wallis-ANOVA (KW-ANOVA) and repeated-measures ANOVA (RM-ANOVA), and used the Spearman rank coefficient to test for significant correlations between epiphyte load and beetle abundance. As a measure for α-diversity I used species richness, i.e. the absolute number of species that were found in one sampling unit, and the Sørensen index as a measure of β-diversity (Magurran, 1988). For the two-dimensional scaling analysis in Figure 6.2 I used a matrix of dissimilarities (1-Sørensen values) between the animal assemblages of the respective host trees (Southwood, 1978). I also ran three-dimensional scaling analyses with the same data sets, but the outcome was always similar (not shown). Seasonal rhythms were analyzed with circular statistics (Watson's U^2) according to Zar (1999), using the program Rayleigh & Co. 3.1 (oxalis GmbH, 33335 Gütersloh, Germany).

RESULTS

Composition of the fauna

I collected 7,681 beetle specimens and assigned them to 352 species in 43 families (Table 7.1, Table 7.2). Ten percent of the species were singletons, and almost a third (30%) were doubletons, the majority (81%) of which were sampled as pairs at a single occasion. Ninety-four species (27% of all species) were represented by ten individuals or more, and accounted for fully 89% of all specimens. The five most abundant species belonged to the families Curculionidae (Scolytinae), Alleculidae, Anthicidae, Staphylinidae and Buprestidae, and contributed 44% to the total number of individuals (Table 7.1). A small bark beetle (Curculionidae, Scolytinae) was by far the most abundant species (1,258 individuals). The most diverse families were Curculionidae (54 species; without Scolytinae: 45 species), Chrysomelidae (31) and Cerambycidae (29), and the most individual-rich families were Curculionidae (due to the predominance of the mentioned most abundant Scolytinae species; 1,528 individuals), followed by Staphylinidae (1,116) and Anthicidae (1,073) (Table 7.2). On average, I collected 330 beetle specimens and 72 species in each study tree (median values, n=21).

TABLE 7.1: Numbers of beetle individuals and species in the 25 study trees.
Species and specimen numbers are given in absolute figures (n) and relative to the total (%). The first two columns include all beetles captured in 25 study trees throughout one year (April 1998-April 1999; 13 months), the latter two columns are based on the months with active traps in all four categories (April-June 1998 and December 1998-April 1999; 8 months).

	Trapping time: 13 months		Trapping time: 8 months	
	n	%	n	%
Number of species				
Total	352	100	278	100
Singletons	35	10	35	13
Doubletons	105	30	88	32
Species with ≥ 10 individuals	94	27	68	24
Number of individuals				
Total	7,681	100	5,072	100
Most abundant species *(Scolytinae 1)*	1,258	16	763	15
The five most abundant species	3,404	44	2,268	45
The ten most abundant species	4,059	53	2,716	54
Species with ≥ 10 individuals	6,866	89	4,433	87

TABLE 7.2: Family composition and guild assignment.
Guild abbreviations are h (herbivores), p (predators), and s (scavengers, dead wood and fungal feeders). Shown are only families represented by at least three species. Families with two species were (in order of decreasing species richness) Languriidae, Erotilidae, Haliplidae, Lycidae, Notoeridae, Bruchidae and Phengodidae, and the families Ptilodactylidae, Cryptophagidae, Byrrhidae, Phalacridae, Cantharidae, Cicindelidae, Platypodidae, Salpingidae and Xylophaga were represented by one species each.

Family	Number of species	Number of individuals	Feeding guild
Curculionidae (excluding Scolytinae)	45	230	h
Chrysomelidae	31	152	h
Cerambycidae	29	121	h
Staphylinidae	23	1,116	p
Elateridae	18	299	h
Coccinellidae	16	240	p
Anthicidae	15	1,073	s
Endomychidae	15	168	s
Scarabaeidae	15	62	s
Nitidulidae	13	200	p
Carabidae	10	40	p
Dermestidae	10	98	h
Anthribidae	9	50	s
Scolytinae (Curculionidae)	9	1,298	s
Cucucjidae	8	129	p
Mordellidae	7	28	h
Pselaphidae	7	265	s
Helodidae	6	207	h
Ptilidae	6	97	s
Elmidae	5	149	p
Lampyridae	5	23	s
Tenebrionidae	5	14	p
Colydiidae	5	117	s
Alleculidae	4	963	s
Buprestidae	4	191	h
Histeridae	3	6	p
Mycetophagidae	3	33	s
Ostomidae	3	14	p

Comparison of trees with different epiphyte loads

alpha-diversity

Total numbers of individuals and species in the study trees did not differ significantly across the categories (KW-ANOVA, $p>0.1$). This was also the case when analyzing the families separately (KW-ANOVA, $p>0.1$). The median values and analyses results are given in Table 7.3. Because seasonal fluctuations in beetle abundance were high, I analyzed the samples with RM-ANOVA. The results confirmed a strong seasonality by yielding significant p-levels for the temporal factor ($p<0.001$), but both number of species and individuals were independent of tree category ($p>0.1$).

TABLE 7.3: Comparison of the four tree/epiphyte categories.
The faunistic data are from eight months of trapping in 25 study trees (with n replicates per category). Given are median values, minima and maxima.

	Control trees	Trees with *Dimerandra*	Trees with *Vriesea*	Trees with *Tillandsia*	p-level*)
individuals per tree	232 (115-303)	184 (131-346)	202 (117-338)	211 (134-292)	p=0,93
species per tree	50 (33-67)	46 (38-76)	47 (28-62)	50 (41-58)	p=0,84
replicates (n)	7	7	7	4	

*) KW-ANOVA

The epiphyte load of the study trees varied considerably: total epiphyte biomass was significantly different among categories and ranged from 90 g dry weight to ca. 3900 g (Chapter 5). In order to account for this variation, I examined whether the faunistic parameters were correlated with epiphyte biomass, irrespective of category assignment, but this was not the case. Neither beetle species richness nor abundance were correlated with the biomass of epiphytes in a tree (Spearman Rank test, p>0.90; Figure 7.1), nor with epiphyte leaf area (Spearman rank test, p=0.15). In fact, the highest number of species per tree (75) was found in a tree with the fourth-lowest epiphyte biomass.

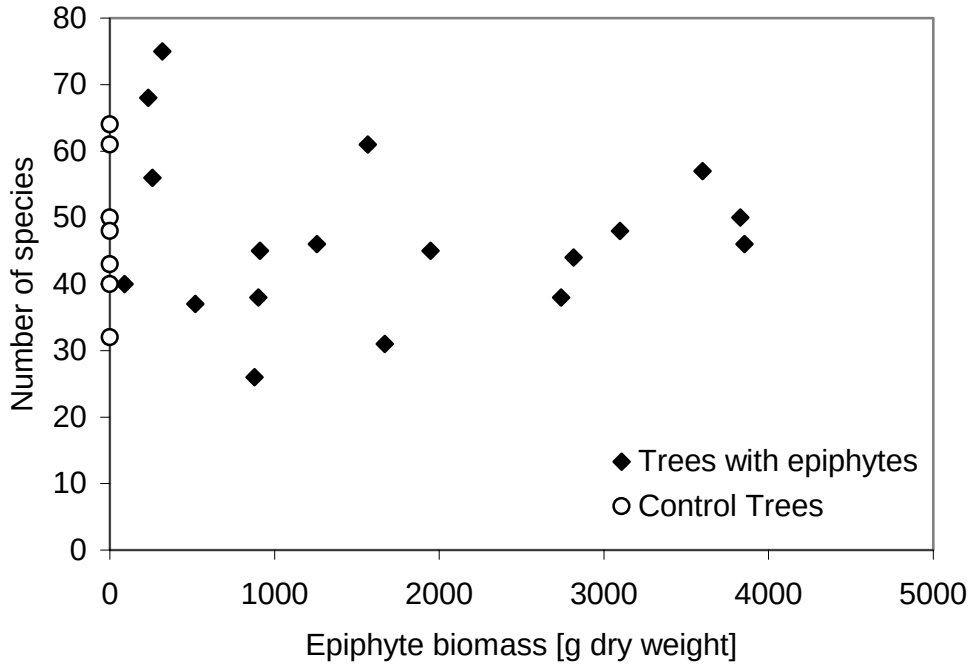

FIGURE 7.1: Epiphyte biomass plotted against the number of beetle species.
Each symbol represents the total values of one study tree. The two parameters are not correlated (Spearman Rank, p=0.90). The symbols on the very left (epiphyte biomass = zero) are the control trees.

Total beetle species richness and abundance was also independent of the leaf area of the host trees (KW-ANOVA, p=0.25). Seasonal fluctuations of beetle diversity and abundance did not correlate with the leaf flushing or flowering rhythms of the host trees (Watson's U^2, p>0.1).

beta-diversity

To investigate whether the beetle assemblages in the four tree/epiphyte categories differed in their species composition, I ran two-dimensional scaling analyses based on dissimilarities (1-Sørensen) among all study trees (Figure 7.2). There was no clustering of tree categories, rather an even distribution.

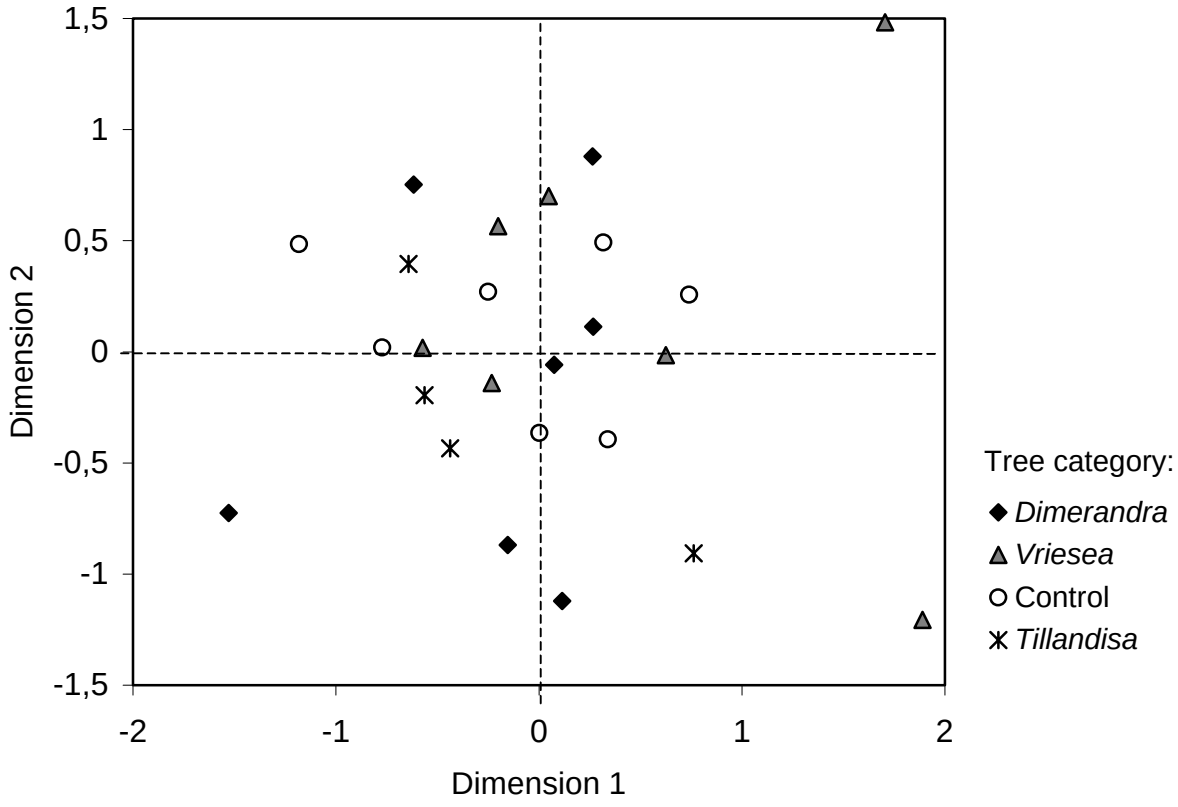

FIGURE 7.2: Two-dimensional scaling of the beetle assemblages of the four tree categories. Each symbol represents one study tree. Data are from 8 months of trapping in 25 trees.

I computed the Sørensen index for the beetle communities of the four categories as a measure for faunal similarity. The values occupied a narrow range and indicated quite high similarities across the categories: the greatest resemblance occurred between control trees and trees with *Dimerandra* (Sør=0.65), and the lowest similarity between control trees and trees with *Tillandsia* (Sør=0.54).

Figure 7.3 shows the distribution of species and individuals across the four categories. Almost half of all species occurred in only one of the four categories. While only one fifth of the species were found in all of the four categories (Figure 7.3a), these represented the vast majority of the specimens (82%; Figure 7.3b). For instance, the twenty most abundant species

(represented by 50 individuals or more) were collected in study trees of all categories. Excluding those 'generalist' species did not alter the outcome of the two-dimensional scaling analysis (Figure 7.2) in any obvious way (data not shown).

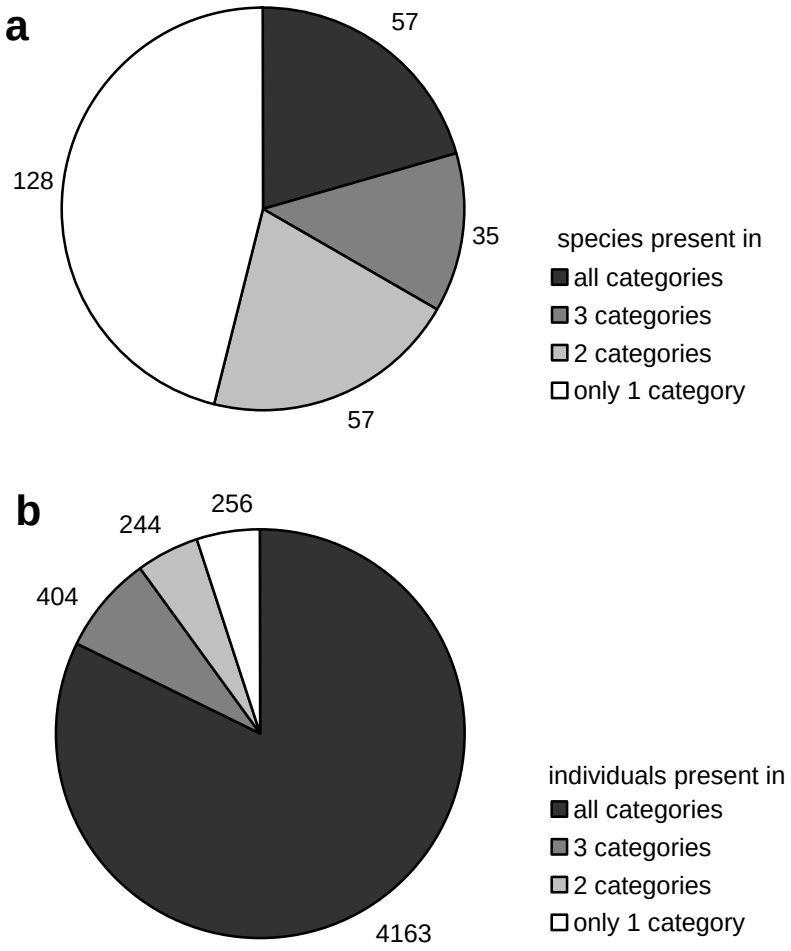

FIGURE 7.3: Pie charts depicting the distribution of beetles among categories.
Proportion of species (a) and individuals (b). Included are data from the months with active traps in all trees.

Guild composition

I showed that the faunas of the four tree categories did not differ significantly on a taxonomic level. To test whether the beetle assemblages differed with respect to ecological traits, I assigned the families to three different feeding guilds (Table 7.2). Figure 7.4 displays the guild composition. The proportions of individuals in the different guilds were strikingly constant across the four tree categories (Figure 7.4b): throughout all study trees, the majority of specimens belonged to the guild scavengers, dead wood and fungal feeders (KW-ANOVA, $p<0.03$). This was mainly due to the presence of two very abundant taxa, Scolytinae (Curculionidae) and Alleculidae. The species richness did not differ significantly among guilds (KW-Anova, $p>0.05$), although there was a trend that herbivores constituted the most diverse guild. This trend was consistent across most categories (except in *Tillandsia* trees, see Figure 7.4a). The guild composition was similar across tree categories: number of species and

individuals within guilds did not differ between categories (KW-ANOVA, p>0.8 for numbers of individuals, p>0.7 for numbers of species).

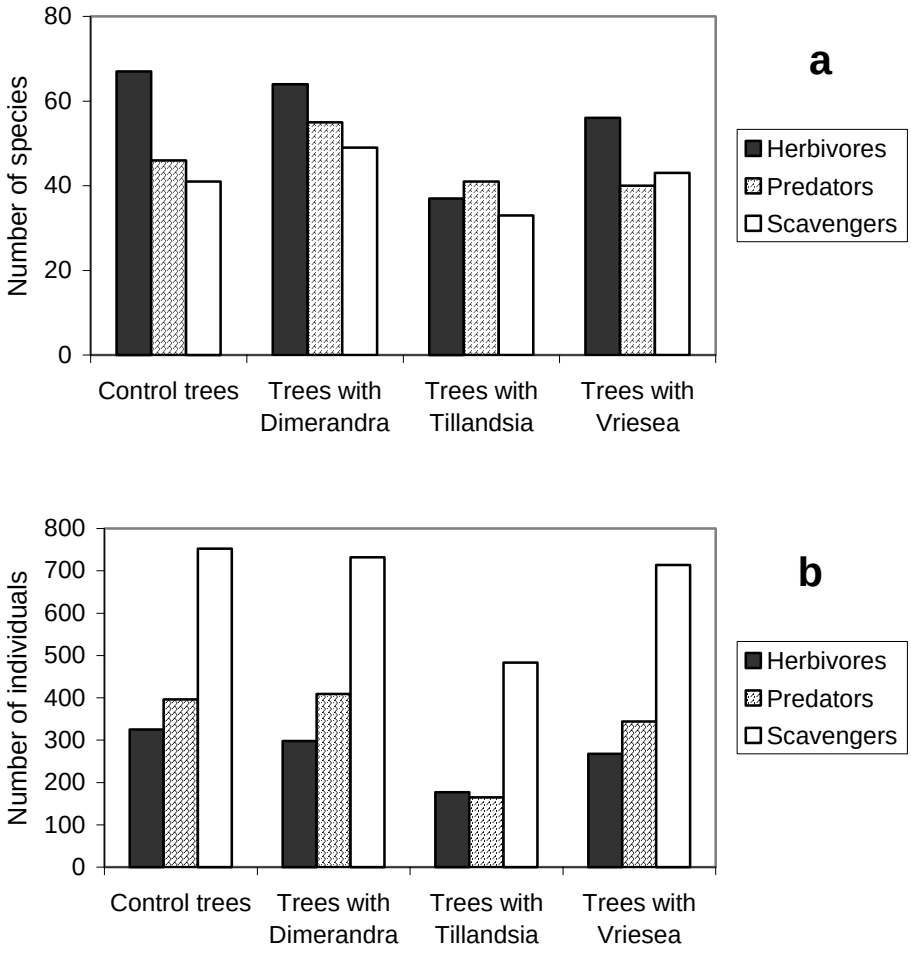

FIGURE 7.4: Guild composition of beetles.
Given are numbers of species (a) and individuals (b). Guild assignment was done family-wise according to Stork (1987, see Appendix 4). The guild 'scavengers' also includes dead wood and fungal feeders.

Phytophagous beetles

I observed the production of new leaves in the host trees in order to test whether the abundance of phytophagous beetles synchronized with leaf flush, but found no correlation (Circular statistics, Watson's U^2, p>0.05; Figure 7.5). Although the simultaneous peaks of leaf flush and numbers of herbivores at the beginning of the study period seemed to suggest a relationship between these factors, herbivore numbers continued low when the major leaf flush in *Annona* occurred later in the year.

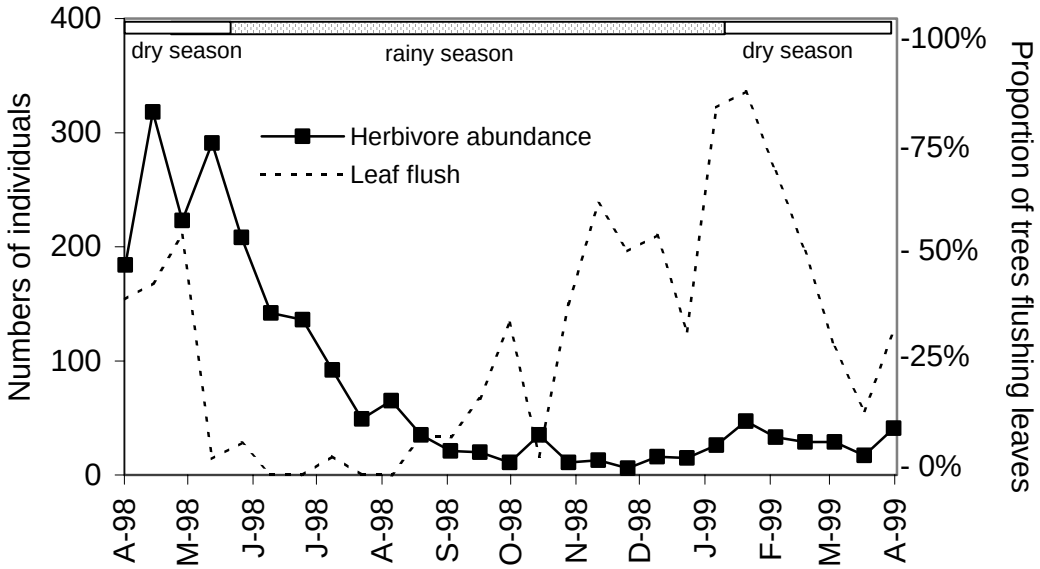

FIGURE 7.5: Seasonal abundance of herbivorous beetles throughout the study year.
Given are totals of individuals of 21 study trees (the *Tillandsia* trees were excluded, because they were not sampled continuously). The horizontal bars indicate rainy and dry seasons. The proportion of study trees flushing new leaves is shown as dotted line.

Phytophagous beetles might be more closely linked to their host tree and its epiphytes than other guilds that do not rely on green biomass for nutrition. Therefore I ran two-scaling analyses with purely herbivorous beetle assemblages. The results did not differ from the outcome of the analysis of the entire beetle fauna (data not shown). Again, the scatter of individual tree symbols was substantial with no obvious clusters corresponding to tree category.

I also tested whether the beetles within the guild 'herbivores' responded to increasing epiphyte biomass of the host trees with greater diversity and abundance. This was not the case: both species richness and abundance of purely phytophagous beetle families were independent from epiphyte biomass (Spearman rank correlation; $p=0.62$) and epiphyte leaf area (Spearman rank correlation; $p=0.30$). Furthermore, diversity and abundance of herbivorous beetles were independent of the leaf area of the host trees (Spearman rank correlation, $p=0.53$).

DISCUSSION

Faunal similarity among trees

The beetle fauna of the investigated 25 tree crowns was quite similar with no clear effect of the co-occurring epiphyte flora. I could not detect any significant faunistic differences between trees with differing epiphyte load, neither in terms of epiphyte species (i.e. the defined categories), nor of epiphyte quantity (biomass and leaf area). The beetle assemblages were quite similar with respect to measures of α-diversity (Table 7.3), β-diversity (Figure 7.2)

and feeding guild composition (Figure 7.4), and moreover did not respond to greater epiphyte biomass with increasing species richness or abundance (Figure 7.1).

A typical trait of tropical canopy insect communities is the large proportion of rare species (e.g., Horstmann *et al.*, 1999). Many studies report that singletons account for approximately half of all species (Allison *et al.*, 1997: 48%, Didham *et al.*, 1998: 45%, Morse *et al.*, 1988: 58%, Novotny, 1993: 45%). Thus, the percentage of singletons of only ten percent in the study (Table 7.1) seems quite low. However, almost a third of the species was represented by two individuals ('doubletons'), and in most cases, these two occurred as a pair in one trap vessel. Still, even if I add singletons and doubletons to a total of 40% of rare species, this number is at the lower end of published results. On the other hand, several beetle species were very abundant and, moreover, quite evenly distributed. Figure 7.3 clearly illustrates the 'generalist' appearance of the highly abundant species: although only a fifth of the species were found in each of the four categories (Figure 7.3a), they represented the vast majority of the specimens (82%; Figure 7.3b). The twenty most abundant species (with 50 individuals or more) were collected in study trees of all categories.

Host trees were selected for similarity in terms of height, crown size, exposure, or distance from other trees. The leaf areas of the trees were similar (Chapter 5). Moreover, all shared the peculiarity of a habitat at the forest edge, bordering the lake. Didham *et al.* (1998), who surveyed beetle communities at forest edges and compared them to within-forest communities, suggested that the extreme microclimatic conditions at the forest edge may be near the upper tolerance limits for many species, and that several species might be edge specialists. Possibly, these common characteristics of the study trees with respect to their environmental and intrinsic parameters are partially responsible for the similarity of the beetle faunas, or that even a very subtle effect of epiphytes on faunal patterns is outweighed by the superimposed unifying host tree and habitat characteristics.

Seasonal rhythms

The seasonal fluctuations of the beetle fauna I studied were consistent with previous studies in the same area: the highest abundance of arthropods in general has been recorded towards the end of the dry season and the beginning of the rainy season (Chapter 5,Leigh, 1999, Smythe, 1982, Wolda, 1978). Barrios (1997), investigating the beetle fauna on Barro Colorado Island collected in light traps, also found the greatest abundance in May and June, and much lower quantities of beetles towards the end of the year until April.

Seasonal rhythms of tree phenologies can have substantial consequences for the fauna (e.g., Leigh, 1999). For instance, abundance fluctuations of phytophagous taxa have been shown to correlate with host tree phenology, especially with the production of new leaves, which are the preferred diet of most phytophagous insects (e.g., Aide, 1993, Basset, 1991, Coley, 1983, Lowman, 1982, Wolda, 1978). However, I found that herbivorous beetles did not synchronize their abundance fluctuations with the seasonal rhythm of leaf flushing in *Annona*. Trees of the genus *Annona* are pollinated by beetles, which feed on the fleshy petals and seek shelter and find mates in the floral chamber (Gottsberger, 1989a, Gottsberger, 1989b). In the trees studied here, beetle diversity and abundance did not correlate with the flowering rhythm of my host tree species. However, *Annona glabra* is also capable of self-pollination, contrasting its congeners (Gottsberger, 1989b).

Herbivory and Epiphytes

The occurrence of phytophagous beetles in this study were independent of green epiphyte biomass (Figure 7.1) and epiphyte leaf area (not shown). There was neither an increase in species richness or abundance of phytophagous beetles in trees with epiphytes compared to control trees (Table 7.3), nor did the proportion of herbivores increase relative to other guilds (Figure 7.4). This may lead to the assumption that the phytophagous beetles were rather indifferent to the epiphytes in their surrounding, or in other words, that epiphytes are probably an unattractive resource for most herbivorous beetles. In sharp contrast to the wealth of data available on specific associations of phytophagous beetles with rainforest trees and lianas (Allison *et al.*, 1997, Basset *et al.*, 1996, Erwin & Scott, 1980, Ødegaard, 2000b, Wagner, 1997), epiphytes have been neglected almost completely as potential hosts (Ødegaard, 2000a). Indeed, previous studies addressing herbivory in epiphytes indicate that the majority of foliage feeders on epiphytes is of non-coleopteran origin (Dejean *et al.*, 1992, García-Franco & Rico-Gray, 1992, Koptur *et al.*, 1998, Rauh, 1990, Zotz & Andrade, 2001). This seemed also to apply to the study epiphytes: in an extensive survey of herbivory on *Vriesea sanguinolenta*, Schmidt and Zotz (2000) found that 95% of the leaf damage through herbivores could be attributed to one single lepidopteran species, the larvae of *Napaea eucharilla* Bates. *Tillandsia fasciculata* is rather well defended against herbivory due to its highly sclerotized leaves, and has only been observed to be attacked by occasional leaf miners (M. Matzat, personal comm.). Zotz (1998) recorded only three plants of *Dimerandra emarginata* out of over 300 to be chewed at by another lepidopteran larva (*Cremna thasus* Stichel). In synopsis, these findings may be interpreted as indications that herbivorous beetles are rather weakly or not associated with epiphytic hosts. This argument, however, remains purely hypothetical, until data on ecology, especially the feeding preferences of the respective taxa are available.

Conclusion

While on the level of individual epiphytes I found clear distinctions of the inhabiting fauna, (Chapter 4), I could not detect an effect of epiphytes on beetle fauna of entire tree crowns, even in this rather simple study system. I can only hypothesize that this might in part be due to the fact that epiphytes are rather unattractive to herbivorous beetles, which constitute the largest fraction of the beetle fauna in tropical canopies. I conclude that a tree's epiphyte assemblage does not influence the composition of its beetle fauna in an ecologically significant way, at least not on the level of entire tree crowns.

8 EPIPHYTES AS STRUCTURAL ELEMENTS OF THE CANOPY - SPIDER RESPONSES TO EPIPHYTE LOAD

ABSTRACT

The question whether epiphytes as structural parameters in tropical tree crowns influence the resident spider fauna was explored in a one-year-survey in a moist tropical lowland forest in Panama. Spiders were collected with various types of insect traps in 25 tree crowns of the tree *Annona glabra*. The study trees were assigned to three different categories according to their epiphyte load, and to an epiphyte-free control group. In total, 6,533 spiders were collected, of which 194 morphospecies and 29 families could be determined. Overall spider abundance and species richness did not differ among trees, but particular families (Clubionidae, Oonopidae, and Anyphaenidae) exhibited marked differences in abundance between the tree categories. Guild structure also differed significantly corresponding to the trees' epiphyte load: the proportion of 'hunters' versus 'web-builders' was higher in trees with *Vriesea* compared to other categories, and 'ambushers' clearly preferred control trees over epiphyte-laden trees. Most remarkable were the differences in species composition across tree categories, as revealed by Sørensen indices and two-dimensional scaling analyses. It is concluded that the composition of arboreal spider faunas is profoundly influenced by the epiphyte assemblages in tree crowns. This is the first account of the influence of epiphytes on spiders in tropical canopies.

INTRODUCTION

The physical structure of environments exerts an important influence on the composition of spider communities (Wise, 1993). Unlike the focal taxa treated in the preceding chapters, spiders are strict carnivores. Thus, the potential associations between tree crowns and their spider communities are not confounded by epiphyte- or host tree-specific dependences on food supply. Instead, spiders often select their habitat according to structural parameters (Cherrett, 1964, Duffey, 1966, Gunnarson, 1990, Halaj *et al.*, 1998, Hatley & MacMahon, 1980, Rypstra, 1983). In this chapter, I investigate the role of epiphytes as structural elements of the canopy.

There is abundant evidence that habitat structure governs community composition and distribution of spiders. This was extensively studied in several ecosystems (grasslands: Duffey 1966; deserts: Riechert & Tracy 1975; Lubin 1978; forest floor: Uetz 1979; shrublands: Hatley & MacMahon 1980, MacIver *et al.* 1992). Accounts on correlations between spiders and habitat structure in tree crowns come exclusively from temperate forests. For example, Stratton *et al.* (1979) studied the spider fauna in coniferous trees and attributed the differences in spider abundance and assemblage structure to differences in tree architecture. Gunnarson (1990, 1988) and Sundberg & Gunnarson (1994) found that spider distribution depended on needle density of Norway spruce branches (Picea abies). Finally, Halaj *et al.* (1998) reported increased diversity and abundance of spiders on branches of tree

species with higher structural complexity, concluding that a combination of prey availability and habitat structure may play an important role in structuring spider assemblages. The availability of prey items also influences the distribution of spiders (Greenstone, 1984, Halaj *et al.*, 1998, Rypstra, 1983, Wise, 1993). Nentwig (1985) found that 50-70% of the insects preyed upon by web-building spiders in Panama were Diptera. In the *Annona* trees investigated here, this taxon, together with the likewise small and soft-bodied micro-caddisflies (which I have observed to be attacked and killed readily by hungry spiders in feeding experiments; Stuntz, personal observation) comprised 50% of the arthropod fauna (Chapter 5). I presume therefore that the web-building spider fauna in the studied tree crowns is not prey-limited.

A most remarkable feature of tropical forest canopies is their enormous structural heterogeneity (e.g., Leigh, 1999, Linsenmair, 1990). However, the effect of this architectural diversity on the tropical spider fauna has not been studied yet. Epiphytes could be of major importance for spider communities in this context, because they substantially augment the structural heterogeneity of the canopy (Benzing, 1990, Nadkarni, 1994). Epiphytes provide a great variety of architectural traits themselves, but also increase habitat complexity indirectly by impounding leaf litter (Nadkarni, 1994; Rodgers & Kitching, 1998; Richardson, 1999). In this chapter, I will investigate this potential influence.

STUDY SITE

The study was conducted in the Barro Colorado Nature Monument (BCNM; 9°10’ N, 79°51’ W) in Panama. The vegetation in this area has been classified as 'tropical moist forest' (Holdridge *et al.*, 1971). The region receives approximately 2600mm of annual rainfall and experiences a pronounced dry season from late December to April. Detailed descriptions of climate, vegetation and ecology have been published by Croat (1978) Leigh *et al.* (1982) and Windsor (1990).

METHODS

Study trees and epiphytes

The chosen host tree, *Annona glabra* L., grows abundantly along the shore of Lake Gatún. Despite its rather small stature (mean height of the study trees 4,9m ± 0.9 SD, n=25), the climatic conditions in its tree crowns are similar to the upper forest canopy (Zotz *et al.*, 1999) due to its exposure to sun and wind along the shore. *A. glabra* is often dominated by a single epiphyte species (Zotz *et al.*, 1999), which allowed us to define distinct tree categories with rather uniform epiphyte assemblages (Figure 5.1): 1) trees free of epiphytes as control group, 2) trees with the orchid *Dimerandra emarginata*, 3) trees with the large tank bromeliad *Vriesea sanguinolenta* and 4) trees dominated by the medium-sized bromeliad *Tillandsia fasciculata*. Hereafter, I address the study species by their generic names. In order to account for spatial heterogeneity across different locations, I chose sites where I could find trees of all categories in close vicinity. *Tillandsia*-trees were found only at four of the seven study sites (distributed all over BCNM, see Figure 1.1), and were sampled only when arthropod abundance was expected to be high, and closed the traps during the second half of the rainy season, i.e. from July to November 1998. Thus, for comparisons among categories, there were two different data sets: when the entire sampling period of thirteen months was included, I

compared only the categories 1-3 (data set 1), and when all four categories were taken into account, I analyzed data from eight months with active traps in all trees and disregarded the captures between July and November 1998 (data set 2). If not indicated otherwise, I refer to the latter data set for category comparisons.

Trapping and processing the spiders

I collected arthropods with three different types of traps: flight interception traps, branch traps and yellow color traps, which remained in the tree crowns for an entire year and were emptied every two weeks. They are illustrated and described in Chapter 2. The captured arthropods were transferred to 70% ethanol until further treatment in the laboratory. Spiders were separated from the rest of the catch and identified to family or genus level using an identification key provided by Nentwig (1993). Adult spiders were sorted to morphospecies (hereafter referred to as species) based on external morphology. Vouchers are deposited at the Technische Universität München (Freising, Germany).

Guild assignment. The spider families were assigned to five prey-capture guilds according to Hatley and MacMahon (1980): web-builders, nocturnal hunters, day-active (agile) hunters, ambushers, and runners (Appendix 5). Because runners were represented by two specimens only, I omitted them from the analyses. For some analyses I summed up 'nocturnal hunters' and 'day-active hunters' to the meta-guild 'hunters'.

Statistics

Statistical analysis was done with STATISTICA (StatSoft Inc., Oklahoma, USA). For the multiple comparison of data sets we used a Kruskal-Wallis ANOVA (KW-ANOVA). As post-hoc-tests we performed Nemenyi tests for balanced data sets (Köhler *et al.*, 1996), and Schaich-Hamerle-tests for unbalanced data sets (Boltz *et al.*, 2000). We compared control trees with epiphyte-laden trees using Mann-Whitney-U-tests, and where appropriate, Spearman rank coefficients. A sign-test was applied for the comparisons of guild composition within tree categories. As a measure for α-diversity we used species richness, i.e. the absolute number of species that were found in one sampling unit, and the Sørensen index as a measure of β-diversity (Magurran, 1988). To test for differences in the species compositions of the faunas among the epiphyte species, we ran two-dimensional scaling analyses based on a dissimilarity matrix of 1-Sørensen values (Southwood, 1978).

RESULTS

Composition of the fauna

In total, I collected 6,533 spiders in 194 species and 29 families (Table 8.1, Appendix 6). Fully 60% (3,917) of the total were juveniles and were only sorted to family level. The most numerous (411 individuals, 17% of the total) and diverse (48 species, 25% of all species) family were Salticidae. The most diverse families thereafter were Theridiidae (30 species), Linyphiidae (30) and Corinnidae (19). Including juveniles, Araneidae were the most abundant family, of which I collected large amounts of early instars (Table 8.1). Two families were very numerous, but species-poor. Scytodidae constituted 15% of the total, but were represented by only two species. Symphytognathidae (15%) were represented by only one

species, *Anapistula* cf. *secreta*, a tiny four-eyed spider occurring abundantly throughout all study trees.

TABLE 8.1: Spider composition at the familial level.
Data are from 13 months of trapping in 25 tree crowns. Proportions of the totals are given in italics. Included were families which were represented by four specimen or more. Families with three or less individuals were (in order of decreasing abundance) Anapidae, Miturgidae, Pholcidae, Segestridae, Thomisidae, Heteropodidae, Oxyopidae, Idiopidae, Selenopidae, Philodromidae, Trechaleidae, Deinopidae.

Family	Number of individuals (adults)		Number of species (adults)		Number of individuals (including juveniles)	
	n	%	n	%	n	%
Salticidae	411	*16.5*	48	*24.5*	825	*15.0*
Symphytognathidae	379	*15.2*	1	*0.5*	379	*6.9*
Scytodidae	364	*14.6*	2	*1.0*	364	*6.6*
Linyphiidae	348	*14.0*	30	*15.3*	539	*9.8*
Clubionidae	246	*9.9*	7	*3.6*	255	*4.6*
Oonopidae	175	*7.0*	4	*2.0*	419	*7.6*
Araneidae	162	*6.5*	12	*6.1*	1245	*22.6*
Corinnidae	85	*3.4*	19	*9.7*	120	*2.2*
Theridiidae	79	*3.2*	30	*15.3*	249	*4.5*
Gnaphosidae	57	*2.3*	8	*4.1*	106	*1.9*
Lycosidae	3	*0.1*	1	*0.5*	54	*1.0*
Anyphaenidae	50	*2.0*	3	*1.5*	78	*1.4*
Ctenidae	38	*1.5*	3	*1.5*	353	*6.4*
Caponiidae	34	*1.4*	1	*0.5*	34	*0.6*
Palpimanidae	18	*0.7*	1	*0.5*	18	*0.3*
Tetragnathidae	14	*0.6*	5	*2.6*	31	*0.6*
Pisauridae	6	*0.2*	4	*2.0*	373	*6.8*

Comparison of tree/epiphyte categories

α-diversity

During a trapping period of eight months, I collected a median number of 21 (range: 13-29) species and 142 (74-334) individuals per tree (n=25). Medians, minima and maxima of the numbers of spider species and individuals in trees of the four different categories are given in Table 8.2. There were no significant differences among categories (KW-ANOVA, numbers of species: $p=0.56$; numbers of individuals: $p=0.41$). Family composition was very similar (Spearman rank correlation, $p<0.001$) among categories, and the relative proportions of families within a category did not differ significantly (KW-ANOVA, $p>0.05$), although some strong trends could be detected: Clubionidae tended to occur more frequently in control trees compared to trees with *Vriesea* (KW-ANOVA, $p=0.068$; Schaich-Hamerle-post-hoc-test, $0.1<p<0.05$), and Anyphaenidae were more numerous in trees with *Dimerandra* compared to trees with *Vriesea* (KW-ANOVA, $p=0.047$; Nemenyi-post-hoc-test, $p<0.05$ (this applied only to data set 1, see methods)). Oonopidae were more abundant in trees with *Dimerandra* (KW-ANOVA, $p=0.052$; Schaich-Hamerle-post-hoc-test $0.05<p<0.1$).

TABLE 8.2: Numbers of spider individuals and species in the 25 study trees.
Given are median values, minima and maxima of n trees collected during a period of eight months (data set 2).

	Control trees	Trees with *Dimerandra*	Trees with *Tillandsia*	Trees with *Vriesea*
Individuals per tree				
Median	137	164	151	122
Min	74	170	108	91
Max	265	266	202	334
Species per tree				
Median	21	23	25	18
Min	15	13	17	14
Max	29	25	25	27
N	7	7	4	7

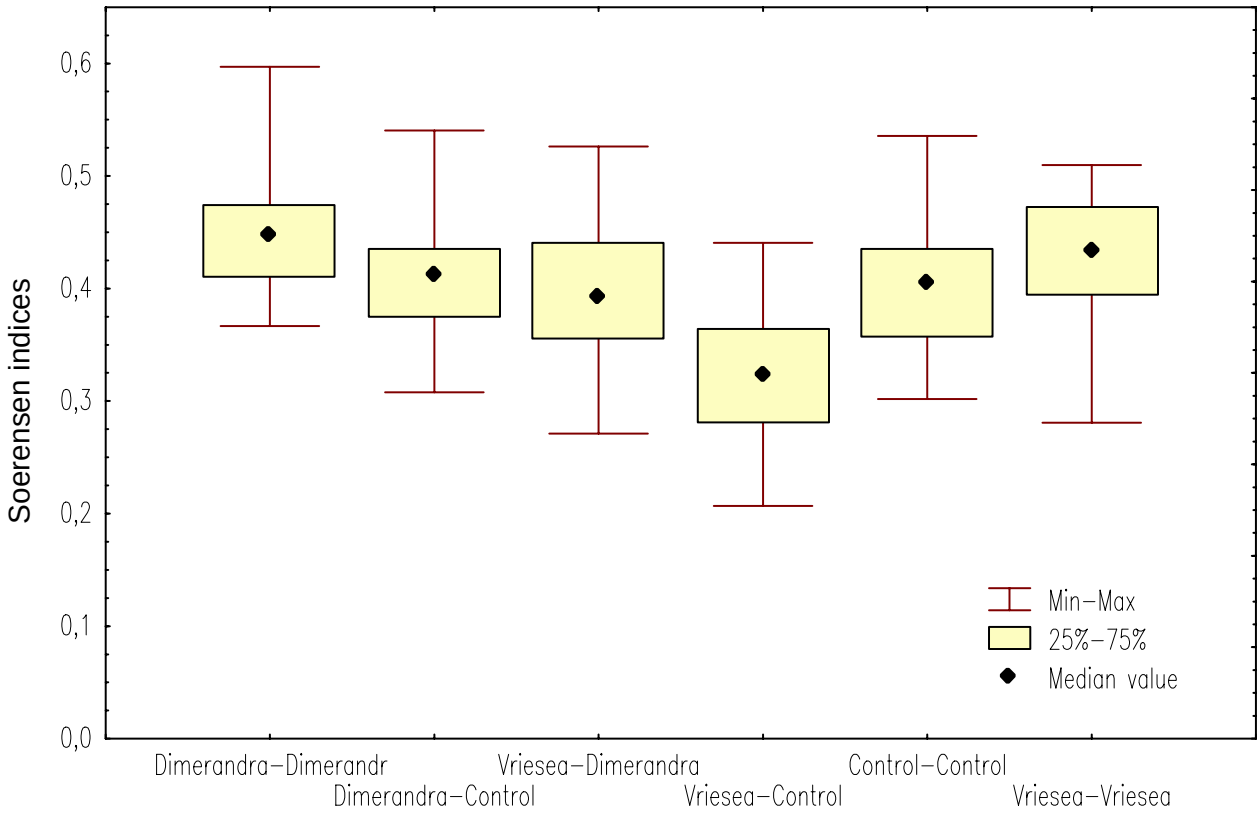

FIGURE 8.1: Box plot of Sørensen indices of the spider assemblages.
The indices between the pair *Vriesea*-Control is significantly lower than the Sørensen values of all other pairs of study trees (see text; data set 1).

β-diversity

The similarities of spider faunas between pairs of study trees yielded highly significant differences: the comparison of the spider assemblages of control trees and *Vriesea* trees had significantly lower Sørensen-values than all other category pairs (Figure 8.1; data set 1: KW-ANOVA, $p<0.001$; Schaich-Hamerle-post-hoc-test, $p<0.05$), i.e. the largest faunal dissimilarities (as indicated by low Sørensen indices) existed between those two categories. Other categories did not differ in their faunal similarities (KW-ANOVA, $p>0.05$). These results were consistent for both data sets (data set 2: KW-ANOVA, $p<0.001$; Schaich-Hamerle-post-hoc-test, $p<0.05$ for the comparisons control trees-trees with *Vriesea*; KW-ANOVA, $p>0.05$ for all other pair wise comparisons).

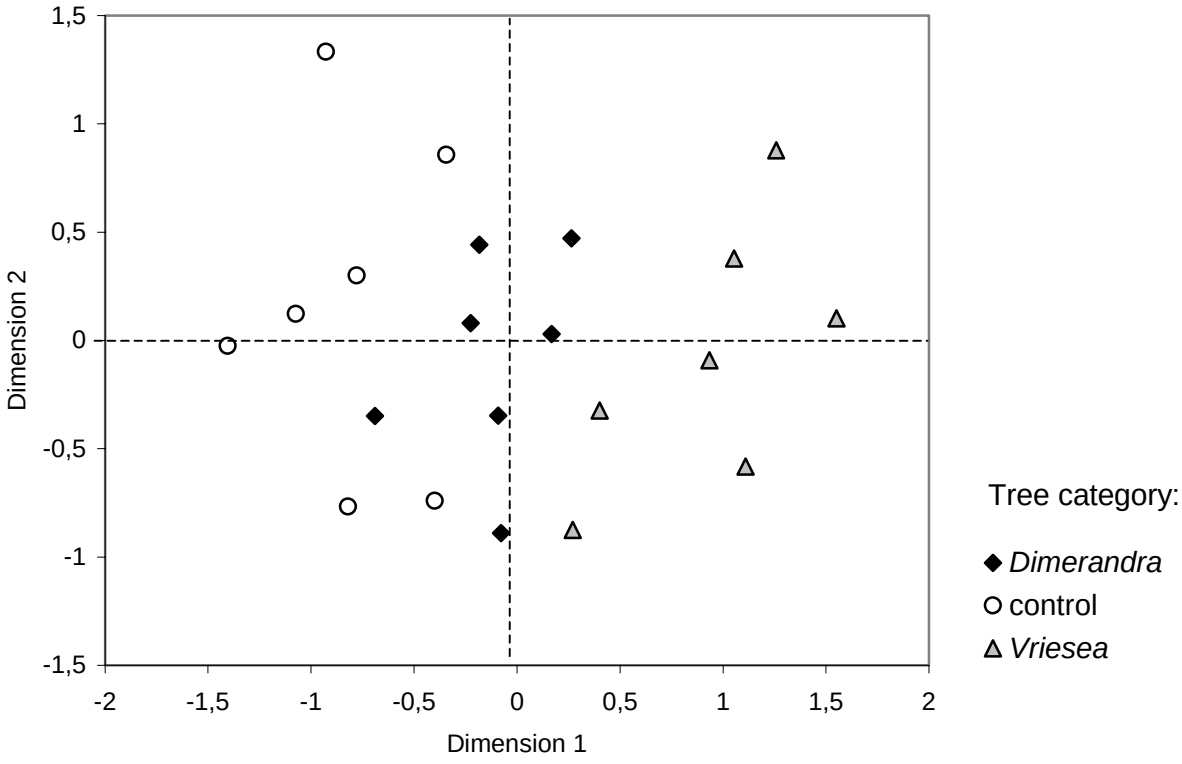

FIGURE 8.2: Two-dimensional scaling analysis of the spider assemblages (data set 1).
The fauna was sampled in 21 study trees throughout 13 months. Each symbol represents one study tree.

A multidimensional scaling analysis based on dissimilarities between the individual study trees (1 - Sørensen) revealed a remarkably clear clustering according to categories (Figure 8.2). The most conspicuous results were obtained analyzing data set 1 (3 categories, 12 months of sampling). Confirming the previous analyses, the *Vriesea*-trees were separated as a coherent group from all other trees. The clustering of trees with *Dimerandra* and control trees was slightly less distinct, but still apparent. Repeating the scaling analysis with data set 2 (all categories, 8 months of sampling), the symbols were more interspersed, but still distinctly clustered along the x-axis according to categories (Figure 8.3). However, *Tillandsia* trees were widely scattered throughout the plot. This might also be an artifact of the lower number of replicates (4 instead of 7) in this category.

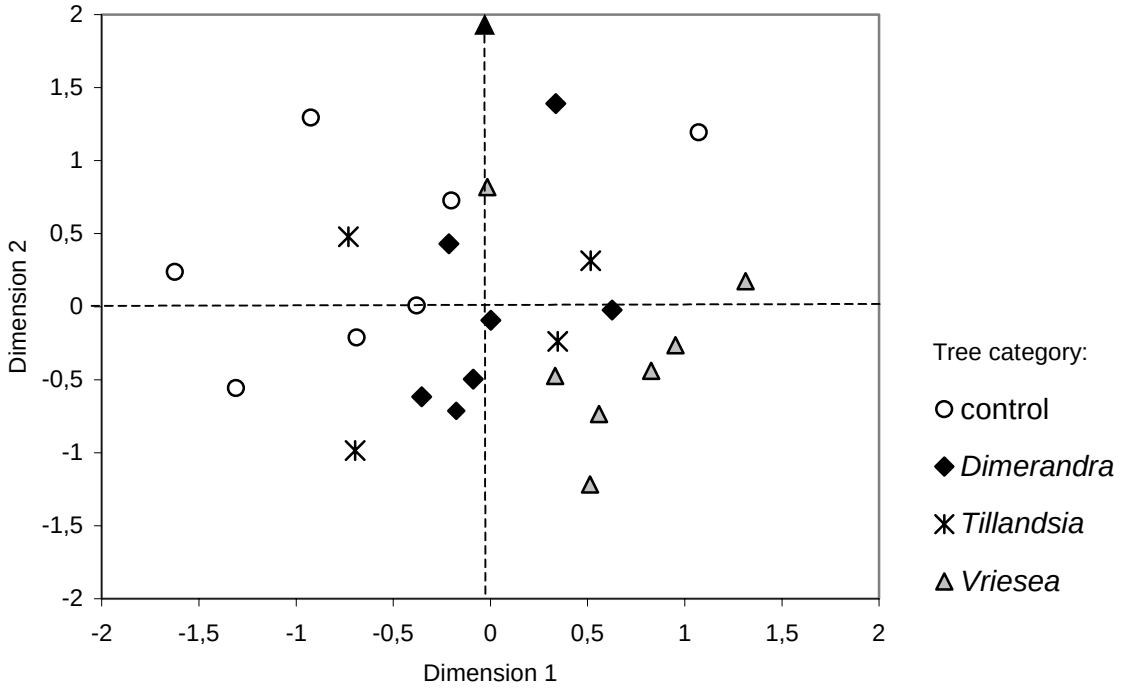

FIGURE 8.3: Two-dimensional scaling analysis of the spider assemblages (data set 2).
The fauna was sampled in 25 study trees throughout 8 months. Each symbol represents one study tree.

Guild structure

Compared to control trees, ambushers were significantly less abundant in *Dimerandra* trees (KW-ANOVA, $p=0.036$; Nemenyi-post-hoc-test, $p<0.05$, data set 1) and in *Vriesea* trees, although only marginally significant (Nemenyi-post-hoc-test, $p<0.1$). The proportions of web-builders, nocturnal hunters and day-active hunters were similar among categories (KW-ANOVA, $p>0.3$). Adding up 'nocturnal hunters' and 'day-active hunters' to the meta-guild 'hunters' yielded significant differences among categories: in trees with *Vriesea*, 'hunters' were significantly more numerous than web-builders (sign-test, $p=0.023$). The proportions of those guilds in trees with *Dimerandra* as well as in control trees were not significantly different (sign-test, $p>0.05$).

Comparison of epiphyte-free and epiphyte-laden trees

Comparing epiphyte-free trees (n=7) with epiphyte-laden trees by pooling the three epiphyte categories (n=7+7+4=18) revealed the following differences: at family level, Clubionidae tended to occur more frequently in trees without epiphytes (Mann-Whitney-U-test, $p=0.056$), and Oonopidae were significantly more numerous in epiphyte-laden trees than in control trees (U-test, $p=0.013$). Guild composition also differed between study trees: 'ambushers' were significantly less abundant in epiphyte trees (U-test, $p=0.025$), while 'day-active hunters' tended to be less numerous in trees devoid of epiphytes (U-test, $p=0.093$).

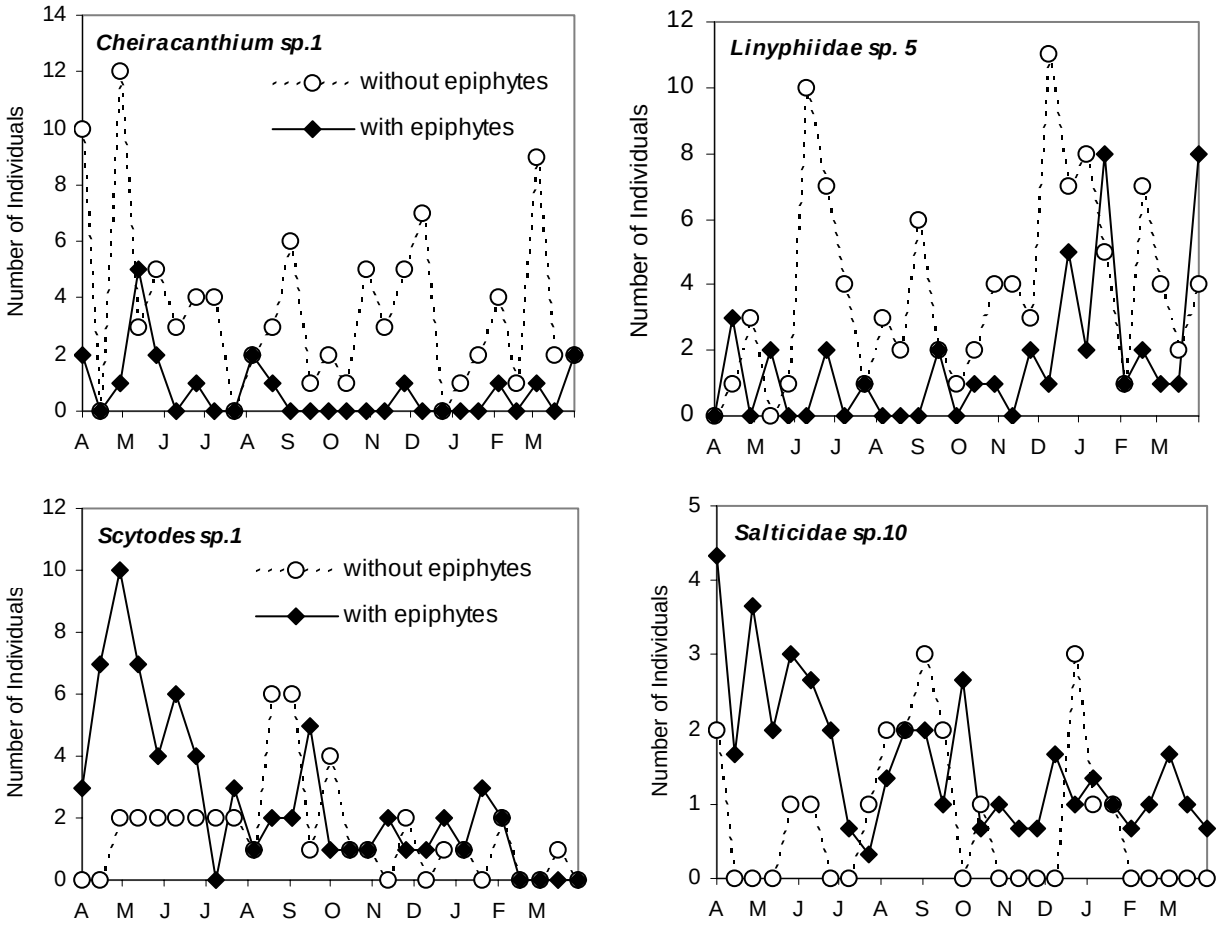

FIGURE 8.4: Abundances of four of the most common spider species in epiphyte-laden versus epiphyte-free trees. The symbols depict the sum of specimens caught in seven epiphyte-free trees (open circles), and the median value of the sums of specimens caught in the tree categories with epiphytes, respectively (closed diamonds). *Cheiracanthium sp. 1* is a Clubionid spider and accounts for 92% of the individuals of this family.

Distinct preferences for either epiphyte-laden or epiphyte-free trees could also be persuaded on species level. Figure 8.4 illustrates the conspicuous differences in abundance of four of the most common spider species.

DISCUSSION

Is the spider fauna of Annona *comparable to those of other tropical canopies?*

At the beginning of this study, it was questionable whether the fauna of one small tree species at the forest edge would be representative for those of other tropical canopies. Because morphospecies assignment is still the prevalent identification technique to assess diversity of large arthropod samples from the tropics (Erwin, 1995, Oliver & Beattie, 1996b), faunal lists can only be compared at higher taxonomic levels. Major characteristics of the spider assemblages collected here were quite similar to those reported by other authors from tropical forest canopies. The samples from *Annona* yielded 194 spider species, while 190 species were collected in a Bornean rainforest (Russel-Smith & Stork, 1995, Stork, 1991), and 140 species

in Amazonian tree crowns (Höfer, 1990, Höfer *et al.*, 1994) by insecticide knock-down. I found 13-29 species per individual study tree, whereas Russel-Smith and Stork (1995) collected 16-62 spider species in ten rainforest trees in Borneo. They reported also a similar proportion of juveniles (68%, this study: 60%). Furthermore, the high species richness of Theridiiae and the high abundance of Salticidae and Araneidae in my samples seem to be unifying traits of tropical forest canopies (Basset, 1990, Höfer *et al.*, 1994, Russel-Smith & Stork, 1995, Stork, 1991). Thus, the simple model system investigated here proved to be a feasible surrogate for tropical tree crowns in high-diversity rainforests, at least with respect to the spider fauna. A remarkable deviation from the mentioned studies was the high abundance of Symphytognathidae. These were minute spiders (body size: 0.65mm ± 0.1 (mean ± SD); Stuntz, unpublished data) which might not be sampled well with insecticide fogging.

Epiphytes as structural elements of the canopy

It is widely acknowledged that the physiognomy or physical structure of environments has an important influence on the habitat preferences of spider species, and ultimately on the composition of spider communities (Uetz, 1979, Wise, 1993). This has frequently been confirmed, but mostly in habitats other than forests (Duffey, 1966, Lowrie, 1948, Lubin, 1978, MacIver *et al.*, 1992, Riechert & Tracy, 1975, Uetz, 1979), or in the forest understory (Uetz 1979). However, there are some accounts on the relationship between canopy-dwelling spiders and structural traits of tree crowns, although exclusively for temperate forests. Spider diversity differed with respect to structural complexity within tree species (needle density on spruce: Gunnarson 1988, 1990) as well as among different tree species (architectural differences among coniferous trees: Stratton *et al.* 1979; complexity and biomass of foliage: Halaj *et al.* 1998). Halaj *et al.* (1998) also described differences in guild composition: trees with a more complex branch structure harbored increased amounts of web-building spiders. Envisaging epiphytes as structural elements of the canopy, some of the differences in spider composition presented above can be explained accordingly.

The most prominent effect of epiphyte load in this study was the high β-diversity (i.e. low similarity in species compositions) between categories (Figures 8.2, 8.3). In particular, trees with *Vriesea* were responsible for most of this phenomenon: the spider faunas in those trees showed significantly lower Sørensen-values in comparison with control trees than other epiphyte categories (Figure 8.1). Moreover, the proportion of hunting spiders versus web-builders was significantly increased in *Vriesea* trees. The different architectural traits of the three epiphyte species might explain part of these distinctions: *Vriesea* provides voluminous litter-filled tanks that foster diverse microcosms (Chapter 4). *Tillandsia* bears only small tanks that intercept little leaf litter, and *Dimerandra* features no such structures at all (Figure 4.1). This outstanding characteristic of *Vriesea* might partially explain the preponderance of hunting spiders in trees of this category. Litter depth and complexity has been shown to positively correlate with the diversity of hunting spiders (Stippich, 1989, Uetz, 1979, Waldorf, 1976). These authors emphasized the importance of litter for hunting spiders as shelter during times of rest. In fact, I frequently observed both Gnaphosidae and Salticidae using dead curled leaves suspended in the bromeliad tanks as retreat (Stuntz, personal observation).

Moreover, the debris-filled tanks of *Vriesea* harbor a rich arthropod fauna, which may be an essential resource for hunting spiders (Chapter 4). In contrast, web-building spiders mainly feed on flying insects (Nentwig, 1985), and rest in their webs. Thus, both increased prey abundance and litter complexity via bromeliad tanks in trees with *Vriesea* might be

responsible for the prevalence of hunting spiders over web-builders, and probably also the distinctions in species composition. The results of Chapter 4 support this presumption compellingly: the inhabitant fauna of *Vriesea* was almost exclusively comprised of hunting spiders, whereas web-builders strongly prevailed in *Dimerandra* (Figure 4.4). Cotgreave *et al.* (1993), who found a diverse spider fauna inhabiting bromeliads, remarked that tank litter probably accounted for high spider abundance and species richness in those epiphytes.

Other, mostly fast-moving spider families clearly prefer open, flat surfaces to forage (e.g., Lycosidae: Duffey, 1966, Uetz, 1979). In this study this seemed to apply for the family Clubionidae, the majority of which was represented by the abundant species *Cheiracanthium 1*. This family was significantly more frequent in trees without epiphytes (Fig. 8.4, Appendix 6). Correspondingly, *Cheiracanthium 1* was not found inhabiting epiphytes (Chapter 4, Appendix 1).

Microclimate

Spiders, as most other organisms, are sensitive to the microclimatic conditions of their environment. Their activity and distribution are often constrained by the risk of overheating and desiccation (Almquist, 1970, Lowrie, 1948, Riechert & Tracy, 1975). The microclimate in tropical forest canopies can be quite extreme and challenge the tolerance limits of many arthropods (Buckley *et al.*, 1980, Nadkarni & Longino, 1990, Tobin, 1995). I showed that epiphytes significantly reduced both temperature and evaporative water loss in their immediate surrounding (Chapter 3, Figure 3.1, Tables 3.1 and 3.2). It is conceivable that epiphytes indirectly influence spider distribution in *Annona* crowns due to this mitigating effect.

The following observations support this hypothesis: Clubionidae were significantly more abundant in control trees whereas Oonopidae clearly preferred epiphyte-laden trees (Figure 8.4, Appendix 6). Clubionidae exceeded Oonopidae in body size by a factor of five (body size of Clubionidae: 6.4mm ± 1.0 (mean ± SD); Oonopidae: 1.2mm ± 0.2; Stuntz, unpublished data). Smaller arthropods are more severely affected than larger ones by microclimatic extremes due to their increased surface/volume ratio (Chapter 3). Thus, it seems likely that the distribution of Clubionidae and Oonopidae is in part explainable by differences in body size and the resulting vulnerability to overheating and desiccation. Moreover, Clubioniade are nocturnal hunters, while Oonopidae are day-active. During the day, I sometimes observed *Cheiracanthium 1* (which constituted 92% of Clubionidae) resting in shelters made of folded-up *Annona* leaves and silk. They avoided the harshest climatic conditions during daytime and hunted by night, when desiccation and overheating was not likely to occur. In contrast, Oonopidae are agile, day-active hunters. Considering their small body size, they may often need to seek shelter from climatic extremes during times of activity. Thus, they might prefer epiphyte-laden trees which offer microsites with cooler and moister air during hot and dry midday hours (see Tables 3.1 and 3.2). However, these considerations remain purely hypothetical until data on temperature preferences and hunting behavior are available. Nentwig (1993) investigated Panamanian spiders associated with bromeliads and reported that Oonopidae were the most frequent family. The lack of this taxon in the epiphyte-inhabiting faunas (Chapter 4) is an effect of sampling technique: I collected only arthropods larger than approximately 2mm and thereby probably omitted the tiny Oonopidae.

The influence of epiphytes on spiders – a question of scale?

In Chapter 4 I investigated the arthropod fauna inhabiting the study epiphytes. Of the 20 adult spider species that were collected inside the epiphytes, 18 (90%) appeared as well in the traps, although sometimes in very different abundances. For instance, of *Corinna 4* I found 21 individuals inside epiphytes, but only four in the tree crowns. Of the ten most abundant species collected in the tree crowns, three were quite abundant inside epiphytes as well (*Araneidae 2, Salticidae 10* and *Scytodes 1)*, but seven were not found inhabiting the epiphytes, e.g. *Cheiracanthium 1*. This is certainly also an effect of the substantially higher sampling effort during the long-term survey.

The spider faunas dwelling inside the epiphytes showed pronounced differences in both numbers of individuals (KW-ANOVA, $p=0.017$) and species ($p=0.006$), with *Dimerandra* fostering significantly poorer spider assemblages than the two bromeliads (Nemenyi-post-hoc-test, $p<0.05$). Such strong differences were not found at the level of entire tree crowns. Overall spider species richness and abundance were unaffected by the epiphyte load of the host trees. On a high taxonomic level, only three families tended to prefer certain tree categories (Clubionidae, Oonopidae and Anyphaenidae). In individual epiphytes, guild composition of spiders differed dramatically (Figure 4.4). There was almost a complete turnover of the prevailing guilds among the epiphyte species: *Dimerandra* harbored almost exclusively web-builders, while *Vriesea* fostered mainly hunters. In tree crowns carrying those epiphytes, certain trends for differing preferences of hunters and ambushers were detectable, and a predominance of hunters over web-builders in trees with *Vriesea*. But again, those differences were much more subtle than at the level of individual epiphytes.

Conclusion

The composition of the spider fauna was significantly influenced by the epiphyte load of the trees. Preferences for certain tree categories were detectable in three families and within particular guilds. Between-tree diversity (β-diversity) was high, indicating clear distinctions in species composition between the tree categories. This probably reflected differences in structural heterogeneity among study trees resulting from the different epiphyte architectures. Especially the voluminous litter-filled tanks of *Vriesea* seemed to be important for spider distribution. The moderation of microclimatic extremes in the vicinity of epiphytes might have been another potential factor explaining differences in spider distribution. The distinctions between the faunas inhabiting trees with differing epiphyte loads were much less pronounced than the distinctions between the spider assemblages inhabiting individual epiphytes.

9 SUMMARY

The understanding of the mechanisms underlying the establishment and maintenance of the extraordinary biodiversity in tropical forests is a major challenge for modern biology. In this context, epiphytes are presumed to play an important role. To investigate the biological reality of this persistent yet insufficiently investigated notion, I conducted the present study. The main questions I intended to clarify were: (1) do epiphytes affect arthropod abundance and diversity in tropical tree crowns? and (2) what might be the driving forces behind this potential influence? I studied the arthropod fauna of 25 tree crowns bearing different epiphyte assemblages, and the resident fauna of 90 individual epiphytes. I also quantified the mitigating influence of epiphytes on the microclimate in tree crowns. In total, more than 277,000 arthropods were collected and about 700 morphospecies determined.

Epiphytes had a significant moderating influence on canopy microclimate (Chapter 3), both at various microsites *within* a tree crown and *among* tree crowns with different epiphyte growth. On hot dry season days, they provided microsites with lower temperatures and reduced evaporative water loss compared to epiphyte-free spaces within the same tree crown.

Quantitative sampling of the arthropods inhabiting three different epiphyte species provided compelling evidence for the specificity of epiphyte-associated faunas (Chapter 4). Epiphytes proved to be microhabitats for a diverse and numerous arthropod fauna, and different epiphyte species fostered both taxonomically and ecologically very distinct arthropod assemblages: among epiphyte hosts, the inhabitant faunas showed remarkably little species overlap, and guild composition differed strongly.

In the subsequent chapters I investigated if this pronounced effect scaled up to the level of entire tree crowns. Arthropods were captured with three different trap types to obtain an ample spectrum of the canopy fauna (Chapter 2). Four tree categories were classified, three of which were dominated by a different species of epiphyte, and an epiphyte-free control group. On a higher taxonomic level, there were no detectable effects of epiphytes on the fauna: the ordinal composition was similar among tree categories and indifferent of the amount of epiphytes in a tree crown (Chapter 5). I examined three focal groups (ants, beetles and spiders) on species level. The diversity and abundance of ants was not influenced by the epiphyte load of the study trees (Chapter 6). Although many species readily used the epiphytes as nesting site and shelter, they seemed to be highly opportunistic with respect to their host plants. Likewise, the species richness and abundance of beetles, as well as their guild composition were entirely unaffected by the presence of epiphytes in the study trees (Chapter 7). Focusing on herbivorous beetles did not alter these results. Spiders, however, were strongly influenced by the epiphyte assemblages of the host trees (Chapter 8). Overall spider abundance and species richness did not differ among trees, but particular families and guilds exhibited marked differences in abundance between the tree categories. Most remarkable were the substantial differences in spider species composition across trees with different epiphyte assemblages.

Conclusion

Thus, the prevalent notion that epiphytes positively influence arthropod diversity in tropical canopies seems justified, but not without reservation. Whether an influence of epiphytes on the fauna was discernible depended greatly on

(1) the scale of the investigated system: clear faunal distinctions at the microhabitat level were absent or much more subtle at the level of tree crowns.
(2) the focal taxa: different arthropod orders allowed for completely different statements concerning the importance of epiphytes for canopy fauna. I therefore recommend a multi-taxon approach for the investigation of large-scale ecological questions.

In conclusion, I resume that epiphytes are associated with a species-specific inhabiting fauna, and that epiphytes impose an influence on certain, but not all, taxa even at the level of entire tree crowns. Although I could only hypothesize about the potential causes for this influence, this study provided the first comprehensive investigation of the role of epiphytes in determining arthropod abundance and diversity in tropical tree crowns.

10 ZUSAMMENFASSUNG

Eines der zentralen Themen der modernen Biologie ist die Erforschung der Ursachen für die außerordentlich hohe Biodiversität tropischer Regenwälder. In diesem Zusammenhang wird den Epiphyten häufig eine bedeutsame Rolle zugeschrieben. In der vorliegenden Studie sollte diese gängige aber unzulänglich belegte Vorstellung erforscht werden. Zwei Fragen standen dabei im Mittelpunkt:

(1) Beeinflussen Epiphyten den Arten- und Individuenreichtum in tropischen Baumkronen?
(2) Was könnten die treibenden Kräfte für diesen potentiellen Einfluss sein?

Um diesen Fragen auf den Grund zu gehen, erforschte ich die Arthropodenfaunen von 25 Baumkronen mit verschiedenem Epiphytenbewuchs, sowie die Zönosen im Inneren von 90 einzelnen Epiphyten. Darüber hinaus quantifizierte ich den mildernden Einfluss von Epiphyten auf das Mikroklima in Baumkronen. Insgesamt wurden mehr als 277.000 Arthropoden gesammelt und ca. 700 Arten (Morphospezies) bestimmt.

Die Untersuchungen bestätigten den mäßigenden Einfluss von Epiphyten auf die extremen mikroklimatischen Verhältnisse der Baumkronen (Kapitel 3). An heißen Tagen der Trockenzeit waren in der unmittelbaren Umgebung von Epiphyten deutlich niedrigere Temperaturen sowie geringerer evaporativer Wasserverlust zu verzeichnen, verglichen mit exponierten Mikro-Standorten in derselben Baumkrone .

Die quantitative Erfassung der Arthropoden, die verschiedene Epiphyten bewohnten, belegte klar die Spezifität der epiphyten-assoziierten Fauna (Kapitel 4). Epiphyten erwiesen sich als Mikrohabitate für eine diverse und individuenreiche Arthropodengesellschaft. Die Zönosen verschiedener Arten von Epiphyten unterschieden sich erheblich in ihrer Arten- und Gildenzusammensetzung.

Parallel dazu erforschte ich, ob sich solchermaßen starke Effekte der epiphytischen Flora auch auf dem Niveau ganzer Baumkronen weiterverfolgen ließen. Arthropoden wurden mittels verschiedener Fallentypen gesammelt, um ein möglichst breites Spektrum der Kronenfauna zu erhalten (Kapitel 2). Ich teilte die Untersuchungsbäume in drei Kategorien mit jeweils unterschiedlichem Epiphytenbewuchs ein und in eine vierte, epiphyten-freie Kontrollgruppe. Auf höherem taxonomischen Niveau ließen sich keinerlei Effekte der Epiphyten auf die Fauna nachweisen (Kapitel 5): die ordinale Zusammensetzung der Arthropoden zeigte sich unabhängig vom Epiphytenbewuchs.

Drei Tiergruppen (Ameisen, Käfer und Spinnen) wurden des Weiteren auf Artebene untersucht. Diversität und Abundanz der Ameisen blieben unbeeinflusst vom Epiphyten-bewuchs der Bäume (Kapitel 6). Obwohl viele Ameisenarten die Epiphyten als Niststandort und Rückzugsort beanspruchten, schienen sie in Bezug auf ihre Wirtspflanzen eher opportunistisch zu sein. Ebenso waren Diversität, Häufigkeit und Gildenzusammensetzung der Käfer unabhängig von den Epiphyten in den untersuchten Baumkronen (Kapitel 7). Die gesonderte Betrachtung der phytophagen Käfer änderte nichts an diesen Resultaten. Spinnen jedoch wurden deutlich beeinflusst vom Epiphytenbewuchs der Bäume (Kapitel 8). Sowohl auf der Ebene einzelner Familien als auch auf Gilden- und Artniveau waren signifikante Unterschiede zwischen den Kategorien zu verzeichnen. Bemerkenswert war vor allem die

unterschiedliche Artenzusammensetzung der Spinnengemeinschaften in Bäumen mit verschiedenem Epiphytenbewuchs.

Fazit

Die Hypothese, Epiphyten würden die Arthropodendiversität tropischer Baumkronen positiv beeinflussen, scheint gerechtfertigt, allerdings nicht ohne Vorbehalt. Die genannten Ergebnisse ließen zwei Haupttendenzen feststellen. Ob ein Effekt der Epiphyten auf die Fauna erkennbar ist hing ab von

1) dem Maßstab des Untersuchungssystems. Der klare Einfluss der Epiphyten auf Mikrohabitat-Niveau war auf dem Niveau ganzer Baumkronen nicht mehr nachweisbar oder wesentlich schwächer ausgeprägt.
2) den untersuchten Tiergruppen. Verschiedene Tiergruppen ließen sehr unterschiedliche Schlussfolgerungen in bezug auf den Einfluss der Epiphyten auf die Kronenfauna zu. Dies bestätigte, wie irreführend es sein kann, von den Ergebnissen einzelner Taxa ausgehend auf generelle ökologische Zusammenhänge zu schließen. Die Erforschung von biologischen Mustern sollte deshalb stets mehrere Tiergruppen umfassen, wie z.B. in dieser Studie.

Zusammenfassend möchte ich Folgendes festhalten: Epiphyten sind mit einer artspezifischen Arthropodenfauna assoziiert, und beeinflussen darüber hinaus einige Tiergruppen auch auf der Ebene ganzer Baumkronen. Die Mechanismen dieser Wirkungen blieben weitgehend unerklärt, und aus meinen Ergebnissen und Hypothesen ergaben sich viele Fragen, die näher erforscht werden müssten. Dennoch ist durch diese Studie zum ersten Mal die Bedeutung von Epiphyten für den Arten- und Individuenreichtum von Arthropoden in tropischen Baumkronen umfassend untersucht worden.

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12 APPENDIX

APPENDIX 1: Species list and guild assignment of arthropods inhabiting epiphytes. 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

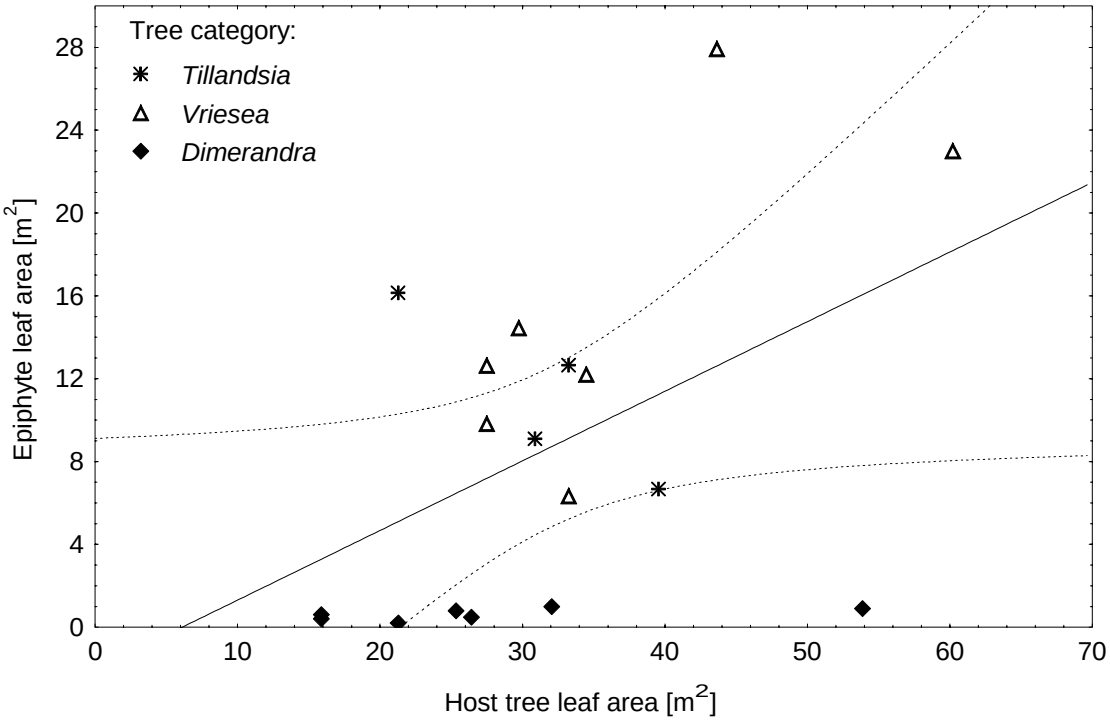
Morphospecies name	*Vriesea*	*Tillandsia*	*Dimerandra*	Feeding guild	Hunting guild (spiders)
SPIDERS (ARANEAE)					
Araneidae sp. 2	-	-	17	p	w
Araneidae sp. 21	2	-	-	p	w
Araneidae sp. 23	-	2	-	p	w
Corinna sp. 4	18	3	-	p	h
Ctenidae sp. 1	79	10	-	p	h
Gnaphosidae sp. 1	8	-	-	p	h
Gertschosa sp. 4	-	1	-	p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

Wasmannia rochai	-	125	49	a
OTHERS				
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

APPENDIX 2: Leaf area of the host trees and their epiphytes,
and the latter's contribution to the total crown leaf area, which is the sum of host tree and epiphyte foliage.

Tree code	Host tree leaf area [m^2]	Epiphyte leaf area [m^2]	Contribution of epiphyte leaf area to total crown leaf area [%]
Control trees:			
n1	20.33	-	-
n2	29.73	-	-
n3	30.89	-	-
n5	28.6	-	-
n7	27.49	-	-
n8	29.73	-	-
n9	16.72	-	-
Trees with *Dimerandra:*			
d1	25.33	0.79	3.0
d2	32.06	0.99	3.0
d3	53.88	0.9	1.6
d5	21.29	0.21	1.0
d7	26.4	0.49	1.8
d8	15.88	0.4	2.5
d9	15.88	0.6	3.6
Trees with *Tillandsia:*			
t1	33.26	12.64	27.5
t2	21.29	16.14	43.1
t3	39.58	6.67	14.4
t5	30.89	9.09	22.7
Trees with *Vriesea:*			
v1	33.26	6.34	16.0
v2	43.64	27.94	39.0
v3	29.73	14.46	32.7
v5	60.21	23	27.6
v7	27.49	9.83	26.3
v8	27.49	12.64	31.5
v9	34.48	12.21	26.2

APPENDIX 3: Correlation between host tree leaf area and leaf area of the epiphytes in its crown.
The lines depict the regression and a 95% confidence interval (p=0.045; r^2=0.23, n=21; Epiphyte leaf area=-2.1+0.34*Host tree leaf area). The significance is caused by the two outliers on the upper right of the plot, i.e. two *Vriesea* trees with very high values of both tree and epiphyte leaf area. Omitting those two trees renders the correlation non-significant (p=0.78).



APPENDIX 4: Species list of beetle morphospecies and their distribution among the four tree/epiphyte categories. Data are not to be compared among all four tree categories, because trees with *Tillandsia* were replicated with four individuals instead of seven as for other trees, and moreover were not sampled continuously (see methods sections of Chapters 5 - 9).

Morphospecies code	Control trees	Trees with *Dimerandra*	Trees with *Tillandsia*	Trees with *Vriesea*	Family
All 1	238	243	169	301	Alleculidae
all 2	1	3		4	Alleculidae
All 4		1		2	Alleculidae
all 3				1	Alleculidae
Ant 1	210	212	53	201	Anthicidae
Ant 9	32	39	22	43	Anthicidae
Ant 5	22	28	1	24	Anthicidae
Ant 6	4	40	3	15	Anthicidae
Ant 11	2	30	1		Anthicidae
Ant 12	4	6	7	1	Anthicidae
Ant 4	5	2		11	Anthicidae
Ant 3	6	6	1	1	Anthicidae
Ant 10	2	10		1	Anthicidae
ant 2	8	3		1	Anthicidae
ant 7	7			2	Anthicidae
ant 13	2	2			Anthicidae
Ant 14	1		1		Anthicidae
ant 8	1				Anthicidae
anth 4	5	6	4	11	Anthribidae
Anth 5	2	4	3		Anthribidae
anth 6	1	1	3		Anthribidae
Anth 7	2			2	Anthribidae
anth 1		2			Anthribidae
Anth 10	1				Anthribidae
Anth 17				1	Anthribidae
anth 2		1			Anthribidae
anth 3		1			Anthribidae
Bru 2	2				Bruchidae
Bru 1				1	Bruchidae
bup 1	54	49	32	50	Buprestidae
bup 2	2				Buprestidae
bup 3			2		Buprestidae
Bup 4			2		Buprestidae
byr 1	2	5	3	3	Byrrhidae
can 1	3	1		1	Cantharidae
car 7	1	11			Carabidae
car 6	4	2	1	3	Carabidae
car 4	4			1	Carabidae
car 1	1	1		1	Carabidae
car 10		2			Carabidae
car 2		1	1		Carabidae
car 8				2	Carabidae
car 9		2			Carabidae
car 3	1				Carabidae
car 5		1			Carabidae
cer 6	12	2		4	Cerambycidae
Cer 8	10	1		3	Cerambycidae
Cer 10	4	5		3	Cerambycidae
Cer 7	6	3			Cerambycidae
Cer 26	5	2			Cerambycidae

cer 14	5				Cerambycidae
cer 16		4		1	Cerambycidae
cer 9		1	2	2	Cerambycidae
cer 15			4		Cerambycidae
Cer 11	2			1	Cerambycidae
Cer 17		1		2	Cerambycidae
Cer 19			3		Cerambycidae
cer 3	1	2			Cerambycidae
cer 1	1	1			Cerambycidae
cer 12			2		Cerambycidae
cer 13				2	Cerambycidae
cer 18				2	Cerambycidae
Cer 20			2		Cerambycidae
cer 21	2				Cerambycidae
cer 22	2				Cerambycidae
cer 23				2	Cerambycidae
Cer 24	2				Cerambycidae
Cer 25		2			Cerambycidae
cer 27	2				Cerambycidae
cer 28			2		Cerambycidae
cer 29		2			Cerambycidae
Cer 4	1	1			Cerambycidae
cer 2				1	Cerambycidae
cer 5		1			Cerambycidae
Chr 12	6	11		8	Chrysomelidae
Chr 14	10	5	2	1	Chrysomelidae
Chr 11	5	7		3	Chrysomelidae
chr 1	3	7		1	Chrysomelidae
chr 13		1	1	9	Chrysomelidae
chr 4	3	1		5	Chrysomelidae
Chr 6	3	1		4	Chrysomelidae
chr 17	1	3			Chrysomelidae
chr 18	1	2	1		Chrysomelidae
chr 23	2			2	Chrysomelidae
chr 16	1	2			Chrysomelidae
Chr 22		1		2	Chrysomelidae
chr 31		3			Chrysomelidae
Chr 15	1	1			Chrysomelidae
chr 19		2			Chrysomelidae
chr 2		2			Chrysomelidae
chr 20	2				Chrysomelidae
chr 21				2	Chrysomelidae
chr 24		2			Chrysomelidae
Chr 25				2	Chrysomelidae
Chr 26			2		Chrysomelidae
Chr 27		2			Chrysomelidae
Chr 28		2			Chrysomelidae
chr 29				2	Chrysomelidae
chr 30	2				Chrysomelidae
chr 32				2	Chrysomelidae
chr 8		1		1	Chrysomelidae
Chr 9	2				Chrysomelidae
chr 10	1				Chrysomelidae
chr 3	1				Chrysomelidae
chr 5				1	Chrysomelidae
chr 7		1			Chrysomelidae

cic 3		5			Cicindelidae
coc 14	28	25	1	1	Coccinellidae
coc 10	14	2	6	15	Coccinellidae
Coc 9	5	12	1	18	Coccinellidae
Coc 1	4	4	7	14	Coccinellidae
Coc 13	8	15	1		Coccinellidae
coc 7	1	11		1	Coccinellidae
Coc 2	4	1		6	Coccinellidae
coc 11		4	3	3	Coccinellidae
Coc 8	3	3	1		Coccinellidae
Coc 3	3	2		1	Coccinellidae
coc 4	2	2			Coccinellidae
coc 12	1	2			Coccinellidae
Coc 15	2				Coccinellidae
Coc 5			1	1	Coccinellidae
coc 6		1			Coccinellidae
col 1				2	Colydiidae
cry 1	14	19	20	19	Cryptophagidae
cuc 3	22	19	13	11	Cucucjidae
Cuc 1	8	9	4	3	Cucucjidae
Cuc 2	5	2	3	3	Cucucjidae
cuc 4	2	5			Cucucjidae
Cuc 9		3	4		Cucucjidae
Cuc 6	2	1		3	Cucucjidae
Cuc 7	4	1		1	Cucucjidae
cuc 5	1				Cucucjidae
Cur 1	20	8	14	17	Curculionidae
Cur 3	7	10			Curculionidae
Cur 17		3		10	Curculionidae
Cur 7	3	7		3	Curculionidae
Cur 5	3	3	1	4	Curculionidae
Cur 29	2	2	3	1	Curculionidae
Cur 25		4	1	1	Curculionidae
cur 16	2	1		2	Curculionidae
Cur 23	1	2		2	Curculionidae
cur 34	3			2	Curculionidae
Cur 6	3	2			Curculionidae
cur 9	1	3		1	Curculionidae
Cur 12	3	1			Curculionidae
Cur 19	2	2			Curculionidae
cur 2	2	2			Curculionidae
Cur 22	1	3			Curculionidae
cur 18			2	1	Curculionidae
Cur 27	3				Curculionidae
Cur 32	1	2			Curculionidae
cur 33		2	1		Curculionidae
Cur 4	1			2	Curculionidae
Cur 47	2	1			Curculionidae
cur 13	1	1			Curculionidae
cur 20				2	Curculionidae
cur 21	2				Curculionidae
cur 24	2				Curculionidae
cur 26				2	Curculionidae
Cur 28			2		Curculionidae
cur 30		2			Curculionidae
cur 31	2				Curculionidae

Cur 35	1	1			Curculionidae
cur 36	2				Curculionidae
cur 37				2	Curculionidae
cur 38		2			Curculionidae
cur 39	2				Curculionidae
Cur 40			2		Curculionidae
Cur 41				2	Curculionidae
cur 42				2	Curculionidae
cur 43		2			Curculionidae
Cur 44	2				Curculionidae
cur 45	2				Curculionidae
cur 46	2				Curculionidae
cur 14		1			Curculionidae
cur 48		1			Curculionidae
cur 49	1				Curculionidae
cur 8		1			Curculionidae
der 4	19	24	1	1	Dermestidae
Der 3	11	15	1	4	Dermestidae
Der 6		2		5	Dermestidae
der 9	2			2	Dermestidae
der 10			2		Dermestidae
der 2	2				Dermestidae
Der 5			1	1	Dermestidae
der 7		2			Dermestidae
der 8	2				Dermestidae
der 1				1	Dermestidae
Ela 1	30	26	26	23	Elateridae
Ela 4	16	25	3	24	Elateridae
Ela 2	5	28	5	12	Elateridae
Ela 13	1	2	13	2	Elateridae
Ela 11	1	5	4	4	Elateridae
Ela 3	3	3	1	4	Elateridae
Ela 10	2	4			Elateridae
Ela 6	1	1		3	Elateridae
ela 15	2		1		Elateridae
Ela 18		1		2	Elateridae
ela 7	2			1	Elateridae
ela 12	2				Elateridae
Ela 14				2	Elateridae
ela 16				2	Elateridae
ela 17				2	Elateridae
ela 8				2	Elateridae
ela 9				2	Elateridae
ela 5				1	Elateridae
Elm 1	59	27	16	19	Elmidae
Elm 2	3	6	2	5	Elmidae
elm 3	2	5		1	Elmidae
Elm 6				3	Elmidae
Elm 4		1			Elmidae
end 6	33	30	4	25	Endomychidae
End 2	3	11	1	3	Endomychidae
end 1	3	4	4	6	Endomychidae
End 4	5	1		1	Endomychidae
End 5	3	3			Endomychidae
End 7		4	1	1	Endomychidae
End 10		4		1	Endomychidae

end 9		4			Endomychidae
End 11		1	1		Endomychidae
End 12		1	1		Endomychidae
End 13	2				Endomychidae
end 14			2		Endomychidae
end 15				2	Endomychidae
End 3		1		1	Endomychidae
end 8	1				Endomychidae
Ero 1				3	Erotilidae
Ero 2			1	1	Erotilidae
hal 1	2			1	Haliplidae
Hal 2		1		1	Haliplidae
Hel 2	33	22	10	30	Helodidae
Hel 1	32	19	7	24	Helodidae
Hel 3	2	4		6	Helodidae
Hel 4	4	7			Helodidae
Hel 5				5	Helodidae
Hel 6				2	Helodidae
his 1	1		2		Histeridae
His 2		2			Histeridae
His 4	1				Histeridae
Lam 1	6	5	2	2	Lampyridae
Lam 2			2		Lampyridae
lam 3		2			Lampyridae
lam 4	2				Lampyridae
lam 5		2			Lampyridae
lan 1	11	6			Languriidae
lan 2	2				Languriidae
Lyc 1		2			Lycidae
Lyc 2		2			Lycidae
mon 2	28	11	2	18	Monomidae
mon 3	30	10		14	Monomidae
mon 4	1	1			Monomidae
mor 2	3	1	1	3	Mordellidae
Mor 1	3	2		1	Mordellidae
mor 4		4		2	Mordellidae
Mor 5		2		1	Mordellidae
Mor 6	2				Mordellidae
Mor 7	2				Mordellidae
mor 3		1			Mordellidae
myc 3	8	9		10	Mycetophagidae
myc 1	2	1			Mycetophagidae
myc 4		2			Mycetophagidae
myc 2	1				Mycetophagidae
nit 5	31	43	2	33	Nitidulidae
Nit 2	6	8		6	Nitidulidae
Nit 7	3	6	2	5	Nitidulidae
nit 1	1	2	2	5	Nitidulidae
nit 3	1	2	1	6	Nitidulidae
Nit 11	6	1		2	Nitidulidae
nit 4	1	2	1	3	Nitidulidae
Nit 6	3	2		1	Nitidulidae
nit 8	1	2	2		Nitidulidae
nit 12		3			Nitidulidae
Nit 13	1		2		Nitidulidae
nit 9	2				Nitidulidae

not 1				2	Notoeridae
not 2	2				Notoeridae
ost 1	4	2	1		Ostomidae
ost 3	4				Ostomidae
ost 2	2		1		Ostomidae
pha 1	4	5	5	7	Phalacridae
phe 2		2			Phengodidae
phe 1	1				Phengodidae
Pla 1		1		2	Platypodidae
Pse 1	66	44	18	56	Pselaphidae
Pse 4	8	16	4	12	Pselaphidae
Pse 2	7	11		1	Pselaphidae
pse 6	3	6	1	6	Pselaphidae
pse 3		4		1	Pselaphidae
pse 5				1	Pselaphidae
Ptil 1	27	34	7	29	Ptilidae
Pti 1	27	22	16	37	Ptilodactylidae
Pti 3	5	3		9	Ptilodactylidae
Pti 4	3		3	3	Ptilodactylidae
pti 2	4				Ptilodactylidae
Pti 6		1			Ptilodactylidae
Pti 8		1			Ptilodactylidae
sal 1		1			Salpingidae
sca 8		7		3	Scarabaeidae
sca 1	2		2	4	Scarabaeidae
Sca 9	4	3		1	Scarabaeidae
sca 7	2	1		2	Scarabaeidae
Sca 10				4	Scarabaeidae
Sca 2	3	1			Scarabaeidae
sca 4	1			3	Scarabaeidae
sca 5	2	1		1	Scarabaeidae
sca 13	1	2			Scarabaeidae
sca 3	1		1	1	Scarabaeidae
Sca 11			2		Scarabaeidae
sca 12		2			Scarabaeidae
sca 14		2			Scarabaeidae
sca 15				2	Scarabaeidae
sca 6	1				Scarabaeidae
Sco 1	386	351	123	398	Scolytinae
Sco 5	2	1	5	3	Scolytinae
Sco 6	5	2		1	Scolytinae
Sco 4	1	1		3	Scolytinae
Sco 3	3	1			Scolytinae
sco 8	2			2	Scolytinae
sco 2	2			1	Scolytinae
sco 9	2			1	Scolytinae
Sco 7		2			Scolytinae
Sta 1	127	99	35	73	Staphylinidae
Sta 3	18	35	13	26	Staphylinidae
Sta 2	30	21	7	31	Staphylinidae
sta 13	24	11	5	36	Staphylinidae
Sta 15	21	24	9	17	Staphylinidae
sta 11	16	23	6	25	Staphylinidae
Sta 8	20	16	5	20	Staphylinidae
Sta 9	13	12	4	29	Staphylinidae
sta 12	22	16	3	11	Staphylinidae

Sta 10	14	21	2	12	Staphylinidae
sta 4	9	17	4	11	Staphylinidae
sta 6	11	11		5	Staphylinidae
sta 14	11	3		9	Staphylinidae
Sta 7	9	2		3	Staphylinidae
sta 16	2	3	4	2	Staphylinidae
sta 17		6		3	Staphylinidae
sta 18				7	Staphylinidae
Sta 21	1	2		4	Staphylinidae
Sta 23	2	1		4	Staphylinidae
sta 20		2	1	2	Staphylinidae
sta 19	4				Staphylinidae
Sta 5	1	3			Staphylinidae
Sta 24			3		Staphylinidae
sta 22	2				Staphylinidae
ten 4		4	1		Tenebrionidae
Ten 1	2			1	Tenebrionidae
Ten 3		3			Tenebrionidae
Ten 5		1		1	Tenebrionidae
ten 2	1				Tenebrionidae
Xyl 1	1				Xylophaga

APPENDIX 5: Guild assignment of spider families, following Hatley and MacMahon (1980).

Prey capture guild	Spider family	Prey capture guild	Spider family
day-active hunters	Lycosidae	runners	Philodromidae
day-active hunters	Oonopidae	web-builders	Araneidae
day-active hunters	Pisauridae	web-builders	Linyphiidae
day-active hunters	Salticidae	web-builders	Pholcidae
day-active hunters	Scytodidae	web-builders	Symphytognathidae
ambushers	Idiopidae	web-builders	Tetragnathidae
ambushers	Thomisidae	web-builders	Theridiidae
nocturnal hunters	Anyphaenidae	unknown	Anapidae
nocturnal hunters	Clubionidae	unknown	Caponiidae
nocturnal hunters	Corinnidae	unknown	Deinopidae
nocturnal hunters	Ctenidae	unknown	Miturgidae
nocturnal hunters	Gnaphosidae	unknown	Oxyopidae
nocturnal hunters	Heteropodidae	unknown	Palpimanidae
nocturnal hunters	Segestridae	unknown	Selenopidae
		unknown	Trechaleidae

APPENDIX 6: List of spider morphospecies.

1) Adult spiders, 2) Juvenile or undetermined spiders.

Data are not to be compared among all four tree categories, because trees with *Tillandsia* were replicated with four individuals instead of seven as for other trees, and moreover were not sampled continuously (see methods sections of Chapters 5 - 9).

Morphospecies	Family	Control trees	Trees with *Dimerandra*	Trees with *Tillandsia*	Trees with *Vriesea*
1) Adult spiders					
Anapidae 1	Anapidae	1	1	-	-
Anapidae 2	Anapidae	-	-	-	1
Aysha 1	Anyphaenidae	9	26	2	9
Aysha 2	Anyphaenidae	3	-	-	-
Teudis 1	Anyphaenidae	-	-	-	1
Araneidae 1	Araneidae	5	1	2	1
Araneidae 14	Araneidae	-	4	-	3
Araneidae 2	Araneidae	30	23	8	8
Araneidae 21	Araneidae	1	-	-	-
Araneidae 26	Araneidae	-	-	-	1
Araneidae 28	Araneidae	-	-	-	1
Araneidae 29	Araneidae	1	-	-	-
Araneidae 3	Araneidae	4	4	-	-
Araneidae 30	Araneidae	1	-	-	-
Araneidae 31	Araneidae	-	1	-	1
Araneidae 8	Araneidae	11	17	5	8
Araneidae 9	Araneidae	6	12	1	2
Nops 1	Caponiidae	8	13	2	11
Cheiracanthium 1	Clubionidae	149	50	8	26
Clubiona 1	Clubionidae	-	-	3	-
Clubiona 2	Clubionidae	4	-	-	-
Clubiona 3	Clubionidae	-	1	-	-
Clubiona 4	Clubionidae	-	-	-	2
Clubiona 5	Clubionidae	-	-	-	2
Clubiona 6	Clubionidae	-	1	-	-
Castaneira 2	Corinnidae	1	-	-	-
Castaneira 3	Corinnidae	1	-	-	-
Corinna 2	Corinnidae	1	-	1	-
Corinna 3	Corinnidae	1	1	-	-
Corinna 4	Corinnidae	2	-	-	2
Corinna 5	Corinnidae	1	-	-	-
Corinna 6	Corinnidae	1	2	-	2
Corinna 7	Corinnidae	-	-	-	1
Corinna 8	Corinnidae	-	-	-	1
Corinna 9	Corinnidae	1	-	-	-
Mazax 1	Corinnidae	1	2	6	17
Mazax 2	Corinnidae	4	-	15	6
Mazax 4	Corinnidae	-	1	-	-
Myrmecotypus 1	Corinnidae	1	1	-	-
Myrmecotypus 2	Corinnidae	-	1	-	7
Myrmecotypus 3	Corinnidae	2	-	-	-
Myrmecotypus 4	Corinnidae	1	-	-	-
Trachelas 1	Corinnidae	1	-	-	-
Ctenidae 2	Ctenidae	-	-	-	1
Ctenidae 3	Ctenidae	1	-	-	6
Cupiennus 1	Ctenidae	2	8	6	14
Gertschosa 2	Gnaphosidae	-	-	-	1
Gertschosa 3	Gnaphosidae	1	-	-	-
Gertschosa 4	Gnaphosidae	5	-	10	-
Gertschosa 5	Gnaphosidae	2	-	-	-
Gertschosa 6	Gnaphosidae	-	-	1	-

Gertschosa 7	Gnaphosidae	1	-	-	-
Zimiromus 1	Gnaphosidae	1	14	2	18
Zimiromus 2	Gnaphosidae	-	-	-	1
Heteropodidae 1	Heteropodidae	-	1	-	1
Idiops 1	Idiopidae	15	-	-	1
Linyphiidae 1	Linyphiidae	3	6	2	4
Linyphiidae 11	Linyphiidae	-	2	-	-
Linyphiidae 12	Linyphiidae	-	1	-	-
Linyphiidae 13	Linyphiidae	-	-	-	1
Linyphiidae 14	Linyphiidae	1	-	-	-
Linyphiidae 15	Linyphiidae	-	1	-	-
Linyphiidae 16	Linyphiidae	-	-	-	1
Linyphiidae 17	Linyphiidae	-	1	-	-
Linyphiidae 18	Linyphiidae	3	1	2	-
Linyphiidae 19	Linyphiidae	-	-	-	1
Linyphiidae 2	Linyphiidae	-	7	1	4
Linyphiidae 20	Linyphiidae	-	2	-	-
Linyphiidae 21	Linyphiidae	-	-	-	1
Linyphiidae 22	Linyphiidae	3	1	-	1
Linyphiidae 23	Linyphiidae	1	-	-	-
Linyphiidae 24	Linyphiidae	1	1	-	-
Linyphiidae 25	Linyphiidae	-	3	1	-
Linyphiidae 26	Linyphiidae	1	1	1	-
Linyphiidae 27	Linyphiidae	2	-	-	1
Linyphiidae 28	Linyphiidae	-	-	1	-
Linyphiidae 29	Linyphiidae	2	-	-	-
Linyphiidae 3	Linyphiidae	1	1	-	-
Linyphiidae 30	Linyphiidae	-	1	-	-
Linyphiidae 31	Linyphiidae	-	1	-	-
Linyphiidae 32	Linyphiidae	-	-	-	1
Linyphiidae 33	Linyphiidae	-	-	-	1
Linyphiidae 4	Linyphiidae	1	1	1	1
Linyphiidae 5	Linyphiidae	103	92	29	46
Linyphiidae 6	Linyphiidae	-	-	-	1
Linyphiidae 8	Linyphiidae	-	1	-	-
Lycosidae 1	Lycosidae	21	19	5	9
Eutichurus 1	Miturgidae	1	1	1	-
Oonopidae 1	Oonopidae	1	-	-	-
Oonopidae 2	Oonopidae	1	-	-	1
Oonops 1	Oonopidae	-	10	2	14
Triaeris 1	Oonopidae	28	50	1	67
Oxyopidae 1	Oxyopidae	1	1	-	-
Othiotops 1	Palpimanidae	-	3	3	12
Thanatus 1	Philodromidae	-	-	-	1
Pholcidae 1	Pholcidae	1	-	1	-
Pholcidae 3	Pholcidae	-	-	-	1
Pisauridae 1	Pisauridae	1	-	-	-
Pisauridae 2	Pisauridae	1	-	-	1
Pisauridae 3	Pisauridae	-	2	-	-
Pisauridae 4	Pisauridae	-	-	-	1
Fluda princeps	Salticidae	1	1	-	2
Myrmarachne 1	Salticidae	5	3	6	6
Salticidae 1	Salticidae	-	-	-	2
Salticidae 10	Salticidae	20	37	27	63
Salticidae 11	Salticidae	1	1	-	2
Salticidae 12	Salticidae	-	-	-	2
Salticidae 13	Salticidae	2	-	-	-
Salticidae 14	Salticidae	2	-	-	-
Salticidae 15	Salticidae	1	-	-	-
Salticidae 16	Salticidae	1	-	-	1

Salticidae 17	Salticidae	1	1	-	-
Salticidae 18	Salticidae	3	2	12	7
Salticidae 19	Salticidae	3	4	2	1
Salticidae 2	Salticidae	-	2	-	-
Salticidae 20	Salticidae	8	11	2	2
Salticidae 21	Salticidae	15	19	2	4
Salticidae 22	Salticidae	-	2	-	-
Salticidae 23	Salticidae	-	1	-	-
Salticidae 24	Salticidae	-	1	-	-
Salticidae 25	Salticidae	-	-	-	1
Salticidae 26	Salticidae	4	1	-	2
Salticidae 27	Salticidae	4	3	1	5
Salticidae 28	Salticidae	1	1	1	3
Salticidae 29	Salticidae	-	-	-	1
Salticidae 3	Salticidae	4	5	2	-
Salticidae 30	Salticidae	-	-	-	4
Salticidae 31	Salticidae	2	-	-	3
Salticidae 32	Salticidae	-	1	-	-
Salticidae 33	Salticidae	-	1	-	-
Salticidae 34	Salticidae	7	5	1	3
Salticidae 35	Salticidae	1	-	-	-
Salticidae 37	Salticidae	-	1	-	1
Salticidae 38	Salticidae	-	1	1	1
Salticidae 39	Salticidae	-	2	1	-
Salticidae 4	Salticidae	4	4	1	3
Salticidae 40	Salticidae	-	-	1	-
Salticidae 41	Salticidae	1	-	-	-
Salticidae 42	Salticidae	-	-	1	-
Salticidae 43	Salticidae	-	1	-	-
Salticidae 44	Salticidae	-	1	-	1
Salticidae 45	Salticidae	-	1	-	-
Salticidae 46	Salticidae	1	-	-	-
Salticidae 47	Salticidae	1	-	-	-
Salticidae 5	Salticidae	-	-	2	8
Salticidae 6	Salticidae	-	2	-	-
Salticidae 7	Salticidae	1	-	-	-
Salticidae 8	Salticidae	2	1	1	-
Salticidae 9	Salticidae	7	-	-	-
Scytodes 1	Scytodidae	41	139	28	87
Scytodes 3	Scytodidae	27	16	1	25
Ariadna 1	Segestridae	-	-	-	1
Ariadna 2	Segestridae	-	1	-	-
Ariadna 3	Segestridae	-	1	-	-
Selenops 1	Selenopidae	1	-	1	-
Anapistula 1	Symphytognathidae	84	130	37	128
Tetragnatha 1	Tetragnathidae	2	3	3	-
Tetragnatha 2	Tetragnathidae	-	1	-	1
Tetragnatha 3	Tetragnathidae	1	-	-	1
Tetragnatha 4	Tetragnathidae	-	-	1	-
Tetragnatha 5	Tetragnathidae	-	1	-	-
Theridiidae 1	Theridiidae	-	-	2	-
Theridiidae 11	Theridiidae	-	-	1	4
Theridiidae 13	Theridiidae	4	1	-	-
theridiidae 15	Theridiidae	-	-	-	1
theridiidae 16	Theridiidae	2	5	-	-
Theridiidae 17	Theridiidae	2	2	1	-
Theridiidae 18	Theridiidae	1	-	1	-
Theridiidae 19	Theridiidae	1	-	-	-
Theridiidae 2	Theridiidae	-	1	-	-
Theridiidae 20	Theridiidae	-	3	2	1

Theridiidae 21	Theridiidae	1	2	-	-
Theridiidae 22	Theridiidae	-	1	-	1
Theridiidae 23	Theridiidae	1	-	-	1
Theridiidae 25	Theridiidae	-	1	-	-
Theridiidae 26	Theridiidae	1	-	1	1
Theridiidae 27	Theridiidae	-	1	-	-
Theridiidae 28	Theridiidae	-	-	1	-
Theridiidae 29	Theridiidae	1	1	-	-
Theridiidae 3	Theridiidae	-	1	-	1
Theridiidae 30	Theridiidae	2	-	-	-
Theridiidae 31	Theridiidae	-	1	-	-
Theridiidae 32	Theridiidae	-	-	1	-
Theridiidae 33	Theridiidae	-	1	-	1
Theridiidae 34	Theridiidae	-	-	-	1
Theridiidae 35	Theridiidae	-	1	-	1
Theridiidae 36	Theridiidae	1	-	-	-
Theridiidae 4	Theridiidae	-	1	-	-
Theridiidae 7	Theridiidae	4	2	-	3
Theridiidae 8	Theridiidae	3	-	1	-
Theridiidae 9	Theridiidae	1	-	-	2
Thomisidae 1	Thomisidae	1	1	-	-
Thomisidae 2	Thomisidae	1	-	-	-
Trechaleidae	Trechaleidae	-	1	-	-
2) Juvenile or undetermined spiders					
Anyphaenidae juv	Anyphaenidae	3	14	3	5
Aysha sp.	Anyphaenidae	2	1	-	-
Araneidae juv	Araneidae	344	303	82	346
Araneidae sp.	Araneidae	2	4	-	2
Clubiona sp.	Clubionidae	-	-	1	4
Clubionidae juv	Clubionidae	2	-	-	2
Corinna sp.	Corinnidae	-	1	-	1
Corinnidae juv	Corinnidae	5	8	5	9
Mazax sp.	Corinnidae	1	1	3	-
Sphecotypus 1	Corinnidae	-	-	-	1
CCML juv	Corinn.-Clubion.-Liocran.-Miturg.-complex	37	78	9	36
Ctenidae juv	Ctenidae	90	93	44	84
Cupiennus sp.	Ctenidae	-	1	-	3
Deinopidae juv	Deinopidae	1	3	-	1
Gertschosa sp.	Gnaphosidae	5	11	3	3
Gnaphosidae juv	Gnaphosidae	4	3	3	5
Zimiromus sp.	Gnaphosidae	1	4	1	6
'Hunter' juv	Hunter	41	29	7	23
Linyphiidae juv	Linyphiidae	59	72	16	41
Linyphiidae sp.	Linyphiidae	-	1	-	2
Miturgidae juv	Miturgidae	2	1	-	1
'Web-builder' juv	Web-builder	232	302	51	126
Oonopidae juv	Oonopidae	67	22	3	152
Philodromidae juv	Philodromidae	-	1	-	-
Pisauridae juv	Pisauridae	121	103	47	96
Salticidae juv	Salticidae	84	111	38	177
Salticidae sp.	Salticidae	3	1	-	-
Segestridae juv	Segestridae	-	-	2	-
Tetragnathidae juv	Tetragnathidae	5	8	2	2
Theridiidae juv	Theridiidae	55	51	16	46
Theridiidae sp.	Theridiidae	-	1	-	1
Thomisidae juv	Thomisidae	3	1	3	5
not determined	-	21	24	3	9

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I fully had to consent with Egbert G. Leigh Jr. when I read in the preface of his book:

> *"Tropical forest has provided me with a large share of that experience of beauty without which any life would be sadly incomplete."*

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Stuntz, S., Simon, U. & Zotz, G. 1999. Assessing potential influences of vascular epiphytes on arthropod diversity in tropical tree crowns. *Selbyana* 20:276-283.

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Stuntz, S., Simon, U. & Zotz, G. 2001. Seasonality and abundance of arthropods in tree crowns with different epiphyte loads. In Basset, Y., Novotny, V., Miller, S. E. & Kitching, R. (ed.) *Arthropods of Tropical Forests - Spatio-Temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge: submitted.

MEETING PARTICIPATION

Stuntz, Simon, Zotz 1999. *The potential influence of epiphytes on arthropod diversity in tropical tree crowns - First results of a one-year-survey in Panama.* Annual Meeting of the British Ecological Society. Leeds, UK

Stuntz, Simon, Zotz 1999. *Assessing potential influences of vascular epiphytes on arthropod diversity in tropical tree crowns.* Jahrestagung der Gesellschaft für Tropenökologie. Ulm

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ERKLÄRUNG

Die vorliegende Dissertation habe ich in allen Teilen selbständig angefertigt. Es wurden keine anderen Quellen und Hilfsmittel verwendet als die angegebenen. Ich habe diese Arbeit weder in gleicher noch in ähnlicher Form zu einem anderen Prüfungsverfahren vorgelegt.

Ort, Datum Unterschrift