

**Patterns of arthropod distribution and determinants of arthropod
assemblage composition in a natural West African savannah**

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

vorgelegt von
Karsten Mody
aus
Mannheim

Würzburg 2003

Eingereicht am: 25.04.2003.....

Mitglieder der Promotionskommission:

Vorsitzender: Prof. Dr. Rainer Hedrich.....

Gutachter: Prof. Dr. K. Eduard Linsenmair.....

Gutachter: Prof. Dr. Bert Hölldobler.....

Tag des Promotionskolloquiums:

Doktorurkunde ausgehändigt am:



From large to small scales - and vice versa?

or

How does it affect an African caterpillar when I go to work by car?



Frontside (top): Planet Earth showing Antarctica at bottom, and Africa and Madagascar at centre (arrow indicates Côte d'Ivoire). From: Drury 1998, modified.

Frontside (bottom): *Chrysopsyche imparilis*, an African caterpillar, meeting a *Camponotus* ant on *Combretum fragrans*.

Table of Contents

I.	General Introduction.....	1
II.	Ökologische Gemeinschaften und Verständnis von Biodiversität: Welche Faktoren strukturieren artenreiche Arthropodengemeinschaften?	9
III.	Study Sites, Species and Methods.....	15
IV.	Persistent Composition of Arthropod Communities on <i>Combretum fragrans</i>	25
V.	Organisation of Arthropod Assemblages in Individual African Savannah Trees	31
VI.	Neighbouring Plants Host Different Ants: Analysis of the Ant Mosaic on a Myrmecophilic Tree	49
VII.	Plant-attracted Ants Affect Arthropod Community Structure but not Necessarily Herbivory	65
VIII.	Finding its Place in a Competitive Ant Community: Leaf Fidelity of <i>Camponotus sericeus</i>	77
IX.	Persistent Aggregation of Herbivorous Beetles on Conspecific Host Plant Individuals: What are the Causes?	89
X.	Intraspecific Host-Plant Change Affects Growth and Fecundity in a Specialist Caterpillar: Roaming for Fitness?	107
XI.	General Discussion.....	117
XII.	Summary.....	123
XIII.	Zusammenfassung	127
XIV.	References.....	131
XV.	Danksagung.....	145

I. General Introduction

Human activities alter global, regional and local processes (Vitousek et al. 1997, Chapin et al. 2000). They affect biogeochemical cycles, habitats, ecosystems, biotic communities and the distribution of species. Although they may locally increase species numbers by introduction of nonindigenous species, human activities result in a world-wide decline in species diversity, a homogenisation of species communities and a loss of genetic information (Ehrlich and Ehrlich 1981, Meffe and Carroll 1997, Lodge and Shrader-Frechette 2003). Human-induced environmental changes thereby reduce opportunities for future use and evolution of species (Western 2001), and they can negatively affect the productivity and vital functions of ecosystems (Schulze and Mooney 1993, Tilman 1999). This would not only deteriorate the quality of human life but can eventually threaten the whole functionality of Planet Earth's biosphere. Thus, the development of measures counteracting these negative impacts should be in everybody's interest whose thinking is not restricted to a present time welfare. The success of such measures will depend on the fundamental understanding of processes connected with anthropogenic alterations and with conservation and restoration efforts (Dobson et al. 1997, Symstad et al. 2003).

In order to understand biological processes and the effects of anthropogenic activities on them, an adequate knowledge of unaltered processes is essential as they have been the basis for the current and (still) working systems (Linsenmair 1990, Ewel 1999). However, this source of information is vanishing since many anthropogenic influences (e.g. climate change, rising atmospheric carbon dioxide concentrations and nitrogen deposition) are already affecting even the most remote and best protected areas (Gallagher and Carpenter 1997). If natural systems can provide unique insights into the functioning of environmental processes, it thus seems necessary to understand them as fast as possible.

Biological systems are always influenced by processes acting on very different spatial and temporal scales, regardless of whether they are strongly determined by human activities (urban landscapes, agricultural fields, plantations, etc.) or more or less natural (remote, protected areas). Consequently, they cannot be fully understood without reference to local, regional and global processes (Ricklefs 1987, Morton and Law 1997, Lawton 2000).

The studies presented here will focus on local, small-scale processes acting on coexisting and potentially interacting populations of organisms, using arthropod communities on different species of savannah trees as study system. The results of this work, however, should be considered in a broader context. They will serve to establish larger-scale studies investigating the influence of regional factors, for example comparisons of arthropod communities of the same habitat-entities (trees of the same species) in different West African countries, possibly embedded in differing habitat matrices. They will allow to test for the effects of anthropogenic land conversion and to monitor influences coming along with a continuously changing environment due to 'global change' (both in tropical and temperate regions)(Singh 2002).

The study of arthropod communities on trees and shrubs (arboricolous arthropod communities) of an unsettled West African savannah (Comoé National Park, Republic of Côte d'Ivoire) is especially informative and promising for several reasons.

- 1) The study area can be considered to be almost natural. Although changes in composition of savannah vegetation occurred in historical times as a consequence of an anthropogenically increased bushfire-frequency, it still represents the largest area of protected and unconverted savannah habitat in West Africa. At least for the studied processes (arthropod species pool, plant

population structure), it provides the basic data on natural systems mentioned above, which may be unavailable from areas more heavily altered by anthropogenic influences.

- 2) The type of habitat investigated has not been studied in detail hitherto with respect to insect-plant interrelationships. Therefore, the studies provide new information for an ecosystem which is typical for large areas of Africa between the Sahelian and the tropical forest zone and which is strongly threatened by climate change and land conversion. The studies thereby also contribute to the concerted rapid 'action plan' called for by Basset et al. (2003b) to investigate canopies in African savannahs in a concerted, immediate way.
- 3) Arboricolous arthropod communities are regarded as a model system to study the relationship between local environmental variables and the structure of speciose communities (Moran and Southwood 1982). These communities can easily be delimited (all arthropods living on one tree) and sampled in a representative, almost complete way (depending on the size of the tree and the sampling methods used). This allows to investigate the factors regulating community structure (abundance, identity and number of species) and to compare different theories that have been proposed to explain community structure (Morin 1999).

For the understanding of community organisation, two explanation-approaches are especially important (Wiens 1984, Linsenmair 1990). The first states communities to be a product of species-specific habitat requirements and interspecific competition in an environment characterised by limited resources – so called equilibrium communities or 'deterministic' community organisation. In case the specific requirements are known for the species, the composition of individual communities would then be predictable. The second approach highlights the importance of random processes (colonisation events, disturbances), which allow different species to use the same niche. In this case, the number of co-existing species would not be determined by the number of niches but by the number of species in the regional species pool – so called non-equilibrium communities or 'stochastic' community organisation. The composition of particular communities would then be much more variable and not predictable.

Tropical arboricolous arthropod communities seem to be very well suited for testing the differing 'community organisation' theories. On the one hand, the high species richness of these communities (e.g. Greenwood 1987, Erwin 1989) is difficult to explain by niche theory, as overall primary productivity of temperate and most tropical systems is almost identical and should therefore not provide opportunities for many more niches in tropical compared to temperate regions (Linsenmair 1990). If niche number is not increased, another possible mechanism explaining the much higher species richness of tropical communities could be that stochastic factors are playing a more prominent role in shaping their structure (König and Linsenmair 1996). Such stochastically structured arthropod communities have been described for some tropical rainforest trees (Floren and Linsenmair 1997, Floren and Linsenmair 2001).

On the other hand, the system 'plant with its associated arthropods' provides an immense array of deterministic factors of potentially high relevance for community organisation. These factors can be related to the tree/plant species, and can affect for example herbivores that are specialists for particular plant taxa and will therefore be restricted to these taxa at least for feeding (Basset et al. 1996a, Barone 1998, Arnold and Asquith 2002). Although the degree of specialisation is still an unknown variable for most herbivorous insects, it is generally assumed that a higher diversity and distinctiveness of plants deterministically support a higher diversity of plant-associated organisms. Important factors can also be found in characteristics of individual conspecific plants, which often vary substantially in arthropod-relevant characteristics such as phenology (Crawley and Akhteruzzaman 1988, Stork et al.

2001), architecture (Moran 1980, Lawton 1983), morphology (Basset 1991, Senn et al. 1992) or chemistry (Edwards et al. 1993, Osier et al. 2000, Staudt et al. 2001). Aside from characteristics of the plant, interactions like competition, predation and mutualism link members of the same community and can deterministically influence the distribution of species and the composition of the whole community (Begon et al. 1996, Morin 1999). Since the species number of tropical communities is much higher, a greater diversity of interspecific interactions is to be expected which affects these communities.

The highest ‘interactive potential’ in arboricolous arthropod communities is generally attributed to ants (Majer 1976, Floren et al. 2002, Dejean and Corbara 2003). They are often the most abundant insect group in the canopy of tropical forests and are well known for their competitive, predatory and mutualistic interrelationships with other ants and other arthropods. Although all ants have some of these interactive capabilities, the individual genera and species differ strongly in their resource requirements and feeding strategies and thereby also in their effects on co-occurring organisms. As a consequence, the presence or absence of *particular* ant species can be considered a major, deterministic factor affecting the composition of arthropod communities.

The most intimate interrelation with the plant hosting the community is generally found in herbivorous insects (Bernays 1989, Jolivet 1998, Schoonhoven et al. 1998). They may, like scavengers or predators, depend on plant characteristics such as phenology or architecture. In addition, they depend directly on the plant as food source, which offers many more opportunities for interaction, ranging from preference for certain host species (interspecific factors) to highly specific adaptations to certain intraspecifically variable host-parameters such as age, chemistry and morphology of leaves. According to the extraordinarily high diversity of herbivorous insects, components of life histories that influence distribution of herbivores (for example foraging tactics) are also very diverse and offer numerous ways to cope with abiotic and biotic environmental conditions. Host specificity and mobility are crucial parameters determining the local distribution of such herbivores and can therefore be considered key-elements of community organisation on the species level.

According to this considerable ‘supply’ of deterministic factors, it seems questionable whether the composition of speciose arboricolous arthropod communities of the tropics is generally and to a great part determined by stochastic factors or whether deterministic environmental parameters are actually much more important for certain habitats (e.g. for savannahs) than thought hitherto. Results of a pilot study (Mody 1998) support the hypothesis that the structure of arthropod communities on savannah trees is strongly influenced by deterministic parameters. The study demonstrated that medium-sized savannah trees (*Combretum fragrans*; formerly designated as *C. nigricans*, Combretaceae) are hosts for individual arthropod communities and that deterministic factors create a patchy mosaic of different communities and may promote small-scale β -diversity. In case these findings could be generalised, they would indicate a strong influence of deterministic processes on local biodiversity, at least in the studied savannah.

Aside from contributing to our understanding of community organisation, the interactions between herbivores and their host-plants represent a scientifically fruitful area of biological research, dealing for example with plant evolution (Ehrlich and Raven 1964), plant defence mechanisms (Gatehouse 2002), and foraging strategies of herbivores (Renwick 2001). They are also of crucial importance from applied points of view. Since insects can be considered the chief pests of crops and stored products (Dent 2000), there is an irrefutable need to better understand the factors governing the relationships between insects and plants and to unravel the causes of insect plague development, which often differs between anthropogenically altered and natural systems (Schoonhoven et al. 1998). Talking about the parameters that determine (and may suppress) a detrimental population growth of herbivorous insects,

the composition of the whole arthropod community has to be taken into consideration. Aside from pathogens, arthropods can be considered the most important biotic regulators of herbivorous insects. As long as an insect is embedded in a heterogeneous environment (providing only a limited number of suitable habitats such as plants) and a speciose community of successful (depending on variable environmental conditions) competitors and predators, it will rarely become hyper-dominant and thereby problematic for its host or co-occurring community members. Since arthropods represent a substantial part of the world's biota and are crucial for ecosystem organisation and services like decomposition or pollination and food web integrity, the knowledge about processes determining arthropod diversity can be regarded an integral part of our understanding of the worlds small- and large-scale drivers.

Box: Determinants of community structure

The structure of local communities is generally explained by a hierarchical concept, which regards community assembly as a multi-stage, multi-layered process (Schoener 1986, Morin 1999). Since the central study entities of this work are arthropod communities on individual trees, this concept of a 'hierarchical community organisation' is illustrated for plant-associated arthropod communities. Large-scale factors like evolutionary history of the biota, physiological limitations and historical events constrain the membership in the regional species pool (e.g. arthropods of the Guinea savannah). This regional species pool represents all species theoretically available for each particular local community (arthropods on an individual plant within the Guinea savannah) and thereby sets the upper limit on the species composition of this community (Zobel 1997). The assembly of individual communities can then be regarded as a stepwise filtering process (Keddy 1992), first sifting out species from the regional species pool by their dispersal and habitat selection (which arthropods reach a particular plant and accept it as host?). Plant selection may be caused by the plant's environment (e.g. forest vs. savannah), by the plant species and by intraspecifically variable plant characteristics. Depending on their specificity (is the habitat selectively or randomly approached?), these filtering factors therefore act to make communities more or less nonrandom subsets of the regional species pool. Whether arriving species will finally establish and become members of the individual community (on a plant) is, in a last step, determined by species interactions or the lack thereof (e.g. presence of ants/of a specific ant species prevents/facilitates establishment).

Thesis Outline

Based on the pilot studies' findings, the present work applies an approach which combines analyses on the level of complete communities, community sub-samples (ant assemblages) and multiple-species interrelationships, and individual species. The main objectives were to describe and analyse the patterns of composition of arthropod communities on a range of different, unrelated tree species and to understand the processes and factors structuring these communities in a natural environment.

Answers to the following questions will be given:

1) Community level

- a) What is the structure of beetle and ant assemblages on different tree species (interspecific comparison of assemblages on *Anogeissus leiocarpa*, *Burkea africana*, *Crossopteryx febrifuga*)?
- b) How similar are beetle and ant assemblages
 - (i) on heterospecific trees (interspecific comparison)?
 - (ii) on conspecific trees (interindividual comparison)?
 - (iii) on the same tree individual over time (intraindividual comparison)?
- c) Is assemblage composition on *Anogeissus leiocarpa* (arthropod orders, beetle families, beetle species and *Camponotus* species) and *Combretum fragrans* (all abundant arthropod species) rather random or predictable for conspecific, individual trees?
- d) Is species distribution on individual trees of *Anogeissus leiocarpa* (beetle and ant communities), *Combretum fragrans* (all abundant arthropod species) and *Pseudocedrela kotschy* (ant assemblages) variable or stable over time (months, years)?
- e) What are the structure and the determinants of ant assemblages on *Pseudocedrela kotschy*?

2) Multiple-species level (ant-ant, ant-plant, ant-herbivore, herbivore-plant interactions)

- a) Are extrafloral nectaries of *Pseudocedrela kotschy* attractive to ants?
- b) How similar are patterns of nectary visitation
 - (ii) on neighbouring plants (interindividual comparison)?
 - (iii) on the same plant individual over time (intraindividual comparison)?
- c) How do different ant species affect herbivory on the host plant?
- d) To what extent does ant presence influence the distribution of ants and other arthropods on *Pseudocedrela kotschy*?

3) Species level

What are the distribution patterns and their determinants for

- a) the ground nesting ant species *Camponotus sericeus* on *Pseudocedrela kotschy*?
 - (i) Are the same trees systematically used by the same forager individuals, i.e. does site fidelity to plants exist?
 - (ii) Can choice of particular host plants be explained by proximity to nest site?

- (iii) Is the distribution of ant individuals on a plant related to other ants foraging on the same plant, i.e. is there any indication of competition or any other form of resource partitioning on the level of individual plants?
- b) the mobile, generalist herbivorous beetle *Apogonia fatidica* on *Combretum fragrans*?
 - (i) Is the distribution of *A. fatidica* on its host plant *C. fragrans* random or aggregated?
 - (ii) Are the host plant visitation patterns stable or variable over time (within the same year, between years)?
 - (iii) What host characteristics may influence the beetles' distribution?
- c) the nonvolant, less mobile, generalist herbivorous beetle *Proictes curvipes* on *Combretum fragrans*?
 - (i) Is the distribution of *P. curvipes* on its host plant *C. fragrans* random or aggregated?
 - (ii) Are the host plant visitation patterns stable or variable over time (within the same year, between years?)
 - (iii) What host characteristics may influence the beetles' distribution?
- d) the little mobile, specialist caterpillars of the moth *Chrysopsyche imparilis* on *Combretum fragrans*?
 - (i) Is the distribution of *C. imparilis* caterpillars on their host plant *C. fragrans* random or aggregated?
 - (ii) What behaviour (of adults or of larval stages) governs the distribution on host plants?
 - (iii) Is the host-changing behaviour a consequence of decreasing host-quality induced by the feeding caterpillar?
 - (iv) Does dietary mixing, achieved by intraspecific host-change, increase fitness of *C. imparilis*?

In [Chapter II](#) an overview is given in German for a selection of the presented studies. Linkages of the thesis with the Convention on Biological Diversity are outlined and a short introduction to the BIOTA-project is provided. [Chapter III](#) gives additional information concerning the study sites, the study species and the methods used. This information, which could not be provided in the submitted publications (Chapters V-X) in adequate detail, may serve to better familiarise the reader with the presented work. In [Chapter IV](#) the distribution of the abundant arthropod species on the savannah tree *Combretum fragrans* is described for different years. This study represents the direct continuation of the pilot study (Mody 1998) and provides basic information on distribution patterns of insect species discussed in Chapters IX and X in more detail. [Chapter V](#) presents the first study describing the structure of arthropod communities on mature individuals of characteristic tree species of the West African savannah. The study concentrates on the characteristics of individual trees as a set of very local factors structuring arthropod assemblages, and it also compares these factors with other structuring factors acting at a larger scale.

In [Chapter VI](#) a marked small-scale patchwork of different ant assemblages on neighbouring, conspecific savannah trees is described. The question is addressed as to how the mosaic-like ant distribution is stable and predictable on a daily basis and over longer periods of time, and the factors influencing the distribution of the dominant ant species are examined. In [Chapter VII](#) the question 'what determines the effectiveness of plant protection by ants?' is investigated from several perspectives. The study covers different aspects of ant-plant and ant-arthropod interactions, which are fundamental to the understanding of inter-relationships between insects and host-plants and organisation of arthropod communities. The study reported in [Chapter VIII](#) describes for the first time leaf fidelity caused by extrafloral nectaries and micro-site fidelity within the context of species rich ant

communities. The study covers different aspects of ant biology such as individual foraging behaviour, resource partitioning and orientation capabilities.

While Chapters VI to VIII are focussed on ant distribution and their interactions with other community members and host plants, respectively, the following Chapters deal with herbivorous insects, their relations to the host plants and resulting consequences for the animals' distribution. In Chapter IX the distribution patterns of a mobile (*Apogonia fatidica*) and a less mobile herbivorous beetle (*Proictes curvipes*) on their host plant *Combretum fragrans* are described and analysed for different years. The determinants that govern host-utilisation patterns are explored as well as differences in mobility that may influence host-selection and resulting distribution of these beetles. Chapter X deals with caterpillars of the lasiocampid moth *Chrysopsyche imparilis*. Although these caterpillars are specialist herbivores with restricted mobility, they regularly change their host plants. This behaviour leads to a conspicuously dispersed distribution on the plants (cf. Chapter IV). The study presented in Chapter X asks for the reasons of this remarkable behaviour by investigating whether the changing behaviour can be explained by effects of herbivores on host-quality or by a fitness-increase caused by dietary mixing achieved by regular intraspecific host-change.

In Chapter XI (general discussion) the findings presented in Chapters IV to X are discussed with regard to the various factors that structure and organise arthropod communities on plants. It becomes evident how small scale and large scale processes are interrelated.

Publication of the results

The main chapters of this thesis have been or will be submitted for publication in peer-reviewed books or journals (with the exception of Chapter II), with the following authorship and titles:

Chapter II: Mody, K. (2002). Ökologische Gemeinschaften und Verständnis von Biodiversität: Welche Faktoren strukturieren artenreiche Arthropodengemeinschaften? In *Treffpunkt Biologische Vielfalt II. Aktuelle Forschung im Rahmen des Übereinkommens über die biologische Vielfalt* (eds H. Korn & U. Feit), pp. 171-176. Bundesamt für Naturschutz, Bonn.

Chapter IV: Mody, K. & Linsenmair, K.E. Persistent composition of arthropod communities on *Combretum fragrans* (in preparation).

Chapter V: Mody, K., Bardorz, H.A., & Linsenmair, K.E. (2003). Organization of arthropod assemblages in individual African savanna trees. In *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy* (eds Y. Basset, V. Novotny, S.E. Miller & R.L. Kitching), pp. 198-212. Cambridge University Press, Cambridge.

Chapter VI: Mody, K. & Linsenmair, K.E. Neighbouring plants host different ants: analysis of the ant mosaic on a myrmecophilic tree. (submitted to *Oecologia*).

Chapter VII: Mody, K. & Linsenmair, K.E. Plant-attracted ants affect arthropod community structure but not necessarily herbivory. (submitted to *Ecological Entomology*).

Chapter VIII: Mody, K. & Linsenmair, K.E. Finding its place in a competitive ant community: leaf fidelity of *Camponotus sericeus*. (*Insectes Sociaux*, 50, in press).

Chapter IX: Mody, K. & Linsenmair, K.E. Persistent aggregation of herbivorous beetles on conspecific host plant individuals: what are the causes? (in preparation).

Chapter X: Mody, K., Unsicker, S.B., & Linsenmair, K.E. Intraspecific host-plant change affects growth and fecundity in a specialist caterpillar: roaming for fitness? (submitted to *Proceedings of the Royal Society of London, Series B*).

II. Ökologische Gemeinschaften und Verständnis von Biodiversität: Welche Faktoren strukturieren artenreiche Arthropodengemeinschaften?

Abstract - The main objective of the Convention on Biological Diversity (CBD) is the conservation and the sustainable and fair use of biodiversity. To achieve this goal, a thorough understanding of biodiversity is needed. Therefore a subdivision of the term biodiversity into several components is proposed. These are a) origin, b) recent maintenance, and c) function and use of biodiversity. Local processes structuring species-rich communities – i.e. questions in the context of recent maintenance of biodiversity in natural and anthropogenically altered environments - were studied in arthropod communities of savannah trees in the West African Comoé National Park. Repeatedly sampled, the arthropod communities of individual shrubs and trees were distinctive even for conspecific plants growing in closest neighbourhood. Thus, each plant was inhabited by a unique, characteristic set of arthropods. This striking diversity pattern suggested a community organisation governed rather by deterministic environmental variables than by stochastic events. Focal observations on several arthropod species belonging to different guilds supported this interpretation. They demonstrated that variable plant characteristics and interactions between species were particularly influential on the animals' distribution. The results of this study stress the importance of small scale variation in environmental variables for support of arthropod diversity. In order to meet the CBD's demands for conservation and sustainable use of biodiversity this has to be considered – especially as arthropods are an integral part of ecosystems and a considerable source of global biodiversity.

Schlagwörter: Biodiversitätskonvention, BIOTA, Comoé Nationalpark, Gemeinschaftsstruktur, Arthropodengemeinschaften, lokale und regionale Prozesse, Schutz, nachhaltige Nutzung

II.1 Einleitung

In der Konvention über die Biologische Vielfalt (Convention on Biological Diversity – CBD) verpflichten sich die Unterzeichnerstaaten völkerrechtlich verbindlich zum Schutz und der nachhaltigen und gerechten Nutzung der biologischen Vielfalt (CBD, Art. 1). Biologische Vielfalt wird in der CBD sehr allgemein als die „Vielfalt innerhalb der Arten und zwischen den Arten und als die Vielfalt der Ökosysteme“ definiert (CBD, Art. 2). Durch den Anspruch und das Ziel, diese Vielfalt zu schützen und nachhaltig zu nutzen, wird die früher hauptsächlich den Biowissenschaften zufallende Beschäftigung mit der Artenvielfalt als gesellschaftliche Aufgabe anerkannt. Biologische Vielfalt oder kurz Biodiversität wird zu einem weitläufig verwendeten, mit positiv belegter Wertschätzung verbundenen Schlagwort (Diversität ist zu schützen und ist nützlich). Sie erscheint dadurch schnell als leicht verständlich und verstanden. So erfreulich die allgemeine Wertschätzung von Biodiversität aus Sicht der mit der Erhaltung der Diversität Beschäftigten erscheinen mag, so wenig hilfreich ist sie für das konkrete Verstehen der Diversität. Dieses Verstehen ist aber eine Grundvoraussetzung für die gezielte Entwicklung erfolgversprechender Schutzmaßnahmen und einer nachhaltigen, dauerhaft nicht zu Beeinträchtigungen führenden Nutzung (Meffe and Carroll 1997, Margules and Pressey 2000).

Unabhängig von der Organisationsebene der betrachteten biologischen Vielfalt (Gene, Arten, Ökosysteme), kann eine Unterscheidung einzelner Bestandteile der Diversität zu einem besseren Verständnis derselben beitragen. Zu diesen Bestandteilen gehören (a) die Entstehung der Biodiversität, (b) die aktuelle Erhaltung der (entstandenen) Biodiversität unter natürlichen **und** unter anthropogen veränderten Bedingungen und (c) die Bedeutung und Nutzung der Biodiversität. Die einzelnen

Aspekte unterliegen dabei der Expertise verschiedener Fachdisziplinen, was den holistischen Charakter des „Konzepts Biodiversität“ unterstreicht. Punkt (a) ist Gegenstand naturwissenschaftlicher Evolutionsforschung, für die Punkte (b) und (c) liefert die Ökologie grundlegendes Verständnis, das als Basis für die wissenschaftlich, gesellschaftlich und politisch zu regelnde Erhaltung und Nutzung dienen kann.

Gegenstand der im folgenden vorgestellten Arbeit sind Fragen, die zum Themenkomplex (b) gehören. Die Arbeit wird im Rahmen des vom BMBF (Bundesministerium für Bildung und Forschung) geförderten BIOTA Projekts durchgeführt. Die Untersuchungen zielen zunächst auf ein grundlegendes Verständnis von Faktoren, die unter natürlichen Umweltbedingungen die Diversität eines Gebiets beeinflussen. Von diesen Erkenntnissen ausgehend soll die Bedeutung unterschiedlicher Landnutzungsformen für die Diversität der Untersuchungseinheiten festgestellt werden. Aus der Kombination von Informationen zu natürlichen Lebensgemeinschaften und anthropogen veränderten Zönosen sollen - unter Zuhilfenahme von Computermodellen - Vorschläge für ein diversitätserhaltendes und -förderndes Management sowohl von Schutzgebieten als auch von Nutzungsgebieten erarbeitet werden.

II.2 Das BIOTA Projekt

BIOTA-Africa (Biodiversity monitoring Transect Analysis in Africa) ist ein Verbundprojekt, das von über 30 Arbeitsgruppen deutscher Hochschulen und Forschungseinrichtungen getragen wird. Das prinzipielle Ziel von BIOTA ist es, einen substantziellen partnerschaftlichen Beitrag von deutscher Seite zur Erforschung der Biodiversität des afrikanischen Kontinents zu leisten (CBD, z.B. Art. 5, 12, 16, 18, 20). Hierzu werden in den wichtigsten Biomen Afrikas der gegenwärtige Zustand und eintretende Änderungen der Biodiversität verschiedenster Organismengruppen festgestellt und analysiert. Es werden standardisierte Untersuchungsflächen (Biodiversitätsobservatorien) angelegt, die Arbeitsgruppen verschiedenster Fachrichtungen die Möglichkeit geben, vergleichbare Datensätze über die Diversität unterschiedlicher Organismengruppen zu erheben. Die Biodiversität soll in diesen Observatorien sowohl aktuell erfasst als auch langfristig beobachtet werden (Monitoring). Durch Vergleiche von Observatorien in natürlichen und anthropogen beeinflussten Bereichen soll der Einfluss menschlicher Aktivitäten auf verschiedene Diversitätsmaße sowie auf Ökosystemprozesse erkannt und Modellieransätze geschaffen werden. Die erhaltenen Informationen werden Entscheidungsträgern in Politik und Wirtschaft bereitgestellt, was ein praktikables, effizientes und nachhaltiges Management von Biodiversität unterstützen soll. Weitere Informationen zu BIOTA sind auf der BIOTA-Homepage, unter www.biota-africa.de zu finden.

II.3 Arborikole Arthropodengemeinschaften, Untersuchungsgebiete und die Erfassung von Diversität

Um zu verstehen, wie es zur Herausbildung hoher lokaler Diversität kommen kann, wurden für die vorgestellte Untersuchung tropische Arthropoden (Gliederfüßler) ausgewählt. Tropische Arthropoden gelten nach heutigem Kenntnisstand als artenreichste Organismengruppe überhaupt (Heywood and Watson 1995, König and Linsenmair 1996). Die Betrachtung „typischer Zönosen“, die bei Biodiversitätsuntersuchungen dem Fokussieren auf einzelne Arten vorzuziehen ist (Jedicke 2000), wurde durch die Beschränkung auf Arthropodengemeinschaften individueller Büsche und Bäume erreicht. Diese sogenannten arborikolen Arthropodengemeinschaften stellen ein Modell-System zur Untersuchung der Bedeutung lokaler Faktoren für die Struktur artenreicher Gemeinschaften dar

(Moran and Southwood 1982). Für diese Untersuchungseinheiten lässt sich der Artenbestand umfassend inventarisieren und das Habitat klar definieren. Außerdem können die auf die Gemeinschaft einwirkenden abiotischen und biotischen Umwelteinflüsse quantitativ erfasst und zur Klärung kausaler Zusammenhänge experimentell manipuliert werden.

Allgemein wird die Zusammensetzung ökologischer Gemeinschaften von vielen Parametern beeinflusst (Strong et al. 1984a, Belyea and Lancaster 1999). Habitateigenschaften, Interaktionen zwischen Organismen und Zufallsereignisse gelten als besonders wichtige lokale Faktoren (Begon et al. 1996). Der große Artenreichtum tropischer arborikoler Arthropodengemeinschaften legt eine Strukturierung durch stochastische Faktoren, die eine Besetzung der gleichen Nische durch mehrere Arten ermöglichen, nahe (Linsenmair 1990). Auf der anderen Seite sind gerade diese an das „Habitat Baum“ gebundenen Gemeinschaften besonders vielen deterministischen Strukturierungsfaktoren ausgesetzt. So können Habitatparameter wie Pflanzenart, Pflanzenchemie, Pflanzenphänologie, Pflanzenarchitektur, Umgebung und Mikroklima direkt auf einzelne Arten oder auf Interaktionen wie Konkurrenz, Prädation und Mutualismus einwirken und die Gemeinschaftsstruktur entscheidend mitbestimmen. Neben lokalen Faktoren wird die Diversität von Gemeinschaften vom regionalen Artenpool, d.h. von den im Gebiet aufgrund historischer und evolutiver Vorgänge vorkommenden Arten, beeinflusst (Ricklefs 1987). Nur solche Arten, die im regionalen Artenpool vorhanden sind, können auch in einzelnen Gemeinschaften anzutreffen sein. Lokale Faktoren wie Zufallsereignisse oder Umwelteinflüsse bestimmen dann, welche der potentiell vorhandenen Arten tatsächlich vorkommen. Wird der Artenbestand lokaler Gemeinschaften hauptsächlich durch Zufallsfaktoren bestimmt, so ist die Zusammensetzung des regionalen Artenpools maßgebend für die lokale Diversität. Haben hingegen lokale Umweltbedingungen einen großen Einfluss auf die Verteilung der Organismen, so hängt die Zusammensetzung der Gemeinschaften stark von der Ausprägung und Vielfalt lokaler Umweltfaktoren ab.

Die Untersuchungen zur Frage, welche der genannten Faktoren eine besonders wichtige Rolle für die Bestimmung der lokalen Diversität (tropischer) Arthropodengemeinschaften spielen, wurden im westafrikanischen Comoé-Nationalpark durchgeführt. Der im Norden der Elfenbeinküste gelegene Comoé-Nationalpark gehört mit einer Fläche von 11500 km² zu den größten Nationalparks Afrikas. Er ist durch eine Vielzahl unterschiedlicher Vegetationstypen gekennzeichnet. So kann man auf einer Fläche von wenigen Quadratkilometern ein Mosaik von dichtem Galeriewald, Inselwäldern, verschiedenen Savannenformationen und nahezu vegetationsfreien Bowal-Flächen finden (Poilecot 1991, Porembski 1991). Als Untersuchungshabitate wurden lokal häufige Savannenbaumarten gewählt, deren Arthropodenbestand sich aufgrund ihres von anderen Holzpflanzen isolierten Wuchsortes sehr genau erfassen ließ. Alle Untersuchungen beschränkten sich auf sehr kleine Abschnitte (wenige Hektar) zusammenhängender Savannenbereiche. Hierdurch war es möglich, ausschließlich lokale, von Änderungen des Klimas oder des regionalen Artenpools unabhängige Prozesse zu untersuchen.

Um die Diversität von Gemeinschaften bestimmen zu können, muss der Diversitätsbegriff geklärt sein. In Studien zur Struktur von Tier- oder Pflanzengemeinschaften verwendet man dabei üblicherweise Diversitätsmaße, die sowohl die Zahl von Arten als auch die Häufigkeitsverteilung der einzelnen Arten berücksichtigen. Das Problem, diese Dualität von Artenzahl und relativer Häufigkeit der einzelnen Arten zu berücksichtigen, führte zur Entwicklung einer großen Zahl von Heterogenitäts-Indizes als Diversitätsmaße. Da keiner dieser Indizes als Optimallösung für alle Fragestellungen verstanden werden kann, wird eine Kombination unterschiedlicher Indizes als sinnvollste Vorgehensweise betrachtet (siehe z.B. Magurran 1988). Eine solche Kombination wurde entsprechend für die vorliegende Arbeit angewandt.

Das Erkennen von Diversitätsmustern ist eine Grundlage für das Verständnis der Prozesse, die für die Verteilung von Organismen und damit für die Diversität eines Gebiets verantwortlich sind. Die Diversitätsmuster können diese Verteilung aber nicht erklären. Um ein genaueres Verständnis der Vorgänge zu gewinnen, die die Zusammensetzung der untersuchten Gemeinschaften bestimmen, wurden zusätzlich einzelne Arten unterschiedlicher trophischer Ebenen untersucht. Dabei lag der Schwerpunkt auf Arthropoden, die a) die Pflanze direkt als Nahrung nutzen (phytophage Käfer und Schmetterlingslarven), b) andere Arthropoden der Gemeinschaft fressen (Spinnen, Ameisen) oder Pflanzenabscheidungen bzw. Abscheidungen von Pflanzensaftsaugern nutzen (Ameisen).

II.4 Ergebnisse und Diskussion: Diversitätsmuster, Verteilung ausgewählter Arthropodentaxa, Bedeutung für die lokale Artenvielfalt

Zur Präsentation der für Fragen zur Biodiversität relevanten Ergebnisse dieser Arbeit wird eine hierarchische Vorgehensweise gewählt. Es wird mit der Betrachtung allgemeiner Diversitätsmuster ganzer Gemeinschaften begonnen. Diese dienen dann als Ausgangspunkt für detailliertere Einzelartenbetrachtungen.

Bei wiederholten, sich bisher über fünf Jahre erstreckenden Erfassungen des Arthropodenbestandes zeigte es sich, dass viele der häufigen Arthropodenarten immer wieder nur auf ganz bestimmten Pflanzenindividuen vorkamen. Dies bedeutete, dass jede individuelle Pflanze von einer ganz typischen Arthropodengemeinschaft besiedelt wurde, die von den Gemeinschaften anderer Pflanzen zu unterscheiden war. Dies traf selbst dann zu, wenn die Gemeinschaften von benachbarten, artgleichen Pflanzen verglichen wurden (Mody 1998).

Der Befund, dass jede Pflanze eine eigene, charakteristische Tiergemeinschaft aufweist, die über Monate und Jahre von den Gemeinschaften benachbarter Pflanzen zu unterscheiden ist, legt eine Strukturierung der Gemeinschaften durch sehr kleinräumig wirkende Umweltfaktoren nahe. Zufallsfaktoren, die eine stärkere Artendurchmischung und damit unscharfe Gemeinschaftsgrenzen bedingen würden, scheinen dementsprechend von untergeordneter Bedeutung zu sein. Da sich für die untersuchten Zönosen lediglich die individuellen Wirtspflanzen, nicht aber der regionale Artenpool oder generelle Standortbedingungen unterschieden, muss davon ausgegangen werden, dass die Arthropoden bereits auf geringfügige Umweltvariationen reagierten. Diese Umweltfaktoren können variierende Pflanzeigenschaften sein. Bei Untersuchungen einzelner Arthropodenarten konnte gezeigt werden, dass die Tiere tatsächlich zwischen einzelnen Pflanzen unterscheiden können und sich ihre Verteilung z.B. nach der Nahrungsattraktivität der Pflanze ausrichtet. Wodurch die Unterschiede zwischen Pflanzenindividuen hervorgerufen wurden, ob durch genetische Unterschiede oder kleinräumige Variationen z.B. des Bodens, konnte bisher noch nicht geklärt werden. Fest steht aber, dass Tiere sehr empfindlich auf die Variabilität von Wirtspflanzen reagieren können und diese damit eine entscheidende Bedeutung für die Verteilung der Tiere hat.

Neben Pflanzeigenschaften können auch Interaktionen zwischen verschiedenen Tierarten einen Einfluss auf die Gemeinschaftsstruktur ausüben. Als besonders wichtiger Bestandteil von Arthropodengemeinschaften sind in diesem Zusammenhang Ameisen zu betrachten. Ameisen können eine aggressiv-abwehrende oder räuberische Lebensweise führen und die Anwesenheit vieler Arten dadurch verhindern. Auf der anderen Seite zeigen Ameisen häufig auch förderliche Beziehungen zu anderen Arthropodenarten und ermöglichen hierdurch erst deren Vorkommen. Diese diversitätsbeeinflussenden Interaktionen können sowohl zwischen verschiedenen Ameisenarten als auch zwischen Ameisen und anderen Arthropodengruppen auftreten. Die Ameisengemeinschaften einzelner Pflanzen weisen beispielsweise feste Artenkombinationen auf, die man auch als Ameisen-Mosaik bezeichnet. In diesen sind bestimmte dominante Arten in vorhersagbarer Weise mit anderen

Ameisenarten vergesellschaftet. Da sich die einzelnen Ameisenarten zum Teil stark in ihrer Häufigkeit und ihrem Verhalten unterscheiden, kann von einem starken Einfluss des spezifischen Ameisenbestandes auf die Zusammensetzung der übrigen Arthropodengemeinschaft ausgegangen werden. Dieser vorläufig angenommene Zusammenhang zwischen der Verteilung bestimmter Ameisenarten und der Diversität anderer Arthropodengruppen muss aber noch durch weitergehende Analysen und gezielte Experimente bestätigt werden.

Das Nebeneinander unterschiedlicher Gemeinschaften führt zu einer hohen lokalen Diversität. Diese wird in starkem Maße von kleinräumiger Umweltheterogenität beeinflusst, wie die charakteristische, nicht-zufällige Zusammensetzung der Gemeinschaften zeigt. Welche Art der Umweltheterogenität dabei besonders bedeutsam ist, wie sie durch gezielte Managementmaßnahmen beeinflusst werden kann, und wie sie sich durch anthropogene Einflüsse - seien sie lokal durch z.B. Landnutzung oder Schadstoffeintrag, oder global durch eine allgemeine Klimaveränderung - verändert, ist noch im Detail zu klären. Hierzu sollen zum einen Untersuchungen ausgewählter Gemeinschaften auf den Dauerbeobachtungsflächen (Biodiversitätsobservatorien) in natürlichen und gestörten Bereichen beitragen. Zum anderen soll überprüft werden, wie stark die festgestellte Umweltheterogenität in anderen Klimazonen ausgeprägt ist und ob ähnliche Zusammenhänge auch für die Diversität z.B. gemäßiger Breiten gelten. Sind die Ergebnisse auf andere Systeme zu übertragen, so ist ein Ansatzpunkt zur Beurteilung unterschiedlicher Landnutzungsformen und für ein diversitätsförderndes Management gegeben. Da - zumindest auf der Ebene der Arthropoden - bereits geringfügige Unterschiede (z.B. genetisch variable Wirtspflanzenpopulationen, uneinheitliche Vegetationsstruktur und lokale Boden- und Mikroklima-Vielfalt) eine große Wirkung haben können, müssen diese Maßnahmen nicht zwingend aufwändig sein. Sie müssen nur ergriffen werden und sind z.B. bei der Pflege von Dauergrünland oder Wäldern leicht zu realisieren.

II.5 Ausblick

Arthropoden sind zentrale Bestandteile von Ökosystemen und stellen einen beträchtlichen Anteil der globalen Biodiversität dar. Aus der vorgestellten Arbeit lässt sich ableiten, dass Arthropoden sehr empfindlich auf kleinräumige Umweltheterogenität reagieren und diese daher einen großen Einfluss auf die lokale (Arthropoden) Diversität haben kann. Um Konzepte zum Schutz und der nachhaltigen Nutzung biologischer Vielfalt zu entwickeln, ist dieses Wissen um lokale Prozesse zu vertiefen und mit der Erforschung regionaler Prozesse zu kombinieren. Ein umfassendes Verständnis der Biodiversität kann dabei nur erreicht werden, wenn von unterschiedlichen regionalen und lokalen Prozessen beeinflusste Gebiete in die Untersuchungen einbezogen werden. Besonders aufschlussreich sind aber sicher Untersuchungen hochdiverser Systeme, die noch in ihrer natürlichen, nicht vom Menschen dominierten Form vorliegen. Solche Bereiche sind vornehmlich in den Tropen zu finden. Da die meisten tropischen Länder (noch) nicht über das Wissen, die Technologien und die finanziellen Mittel verfügen, diese grundlegenden Diversitätsuntersuchungen durchzuführen, ist eine enge Kooperation von Industrie- und Entwicklungsländern nötig (CBD, Art. 5, 12, 16, 18, 20). Diese kann über ein umfassenderes Biodiversitätsverständnis hinaus zu weiterreichenden partnerschaftlichen Beziehungen zwischen den Ländern führen und so u.a. neue Wege zur Bewältigung der Biodiversitätskrise eröffnen.

Danksagung. Diese Studie wurde durch ein DAAD Doktorandenstipendium (Nr. 332 4 04 101), ein Stipendium des DFG-Graduiertenkollegs 200 und durch das BMBF BIOTA-Projekt (Teilprojekt W06, 01LC0017) finanziert.

III. Study Sites, Species and Methods

In the following, the study site, the main study species and a selection of the methods applied in the following chapters is described in order to complement and illustrate the respective sections of the subsequent chapters.

III.1 Study Site

The presented studies were conducted in Comoé National Park (CNP) between April 1999 and September 2002. A pilot study was conducted from May through August 1997 (Mody 1998). The information given on CNP in the following is mainly based on excerpts from Poilecot (1991), Porembski (1991) and Rödel (2000). Comoé National Park is located in the north-east of the Republic of Côte d'Ivoire, and covers 11,500 km² of Guinea- and Sudan-zone savannah. The maximal north-south diameter of the park is about 110 km, whereas the east-west extent totals about 130 km (Figure III.1a,b). Most of CNP is occupied by a more or less flat plateau at altitudes of 220 – 300 metres above sea level, which also forms the watershed between the Comoé and the Volta river systems.

Most of the soils found in CNP are formed of granite. In the western and north-western parts, tropical ferruginous soils are covering strata containing considerable portions of iron and aluminium. In the central area between the Iringou and Comoé rivers and in a narrow patch of land west of the Comoé, ferruginous soils are covering a basic layer of slate. Alongside the rivers and rivulets, hydromorphic soils prevail. Besides, there are 'insular' patches of soils showing a rather complex composition, being a mixture of ferruginous or iron, aluminium and tropical brown soils. At some parts of the surface, these predominantly ferralitic soils form a solid crust. Regions where such crust covers vast areas are called 'bowal'.

The climate of CNP is characterised by a long dry season from about November to March/April, a mean annual precipitation of 950 mm and an annual average temperature of 25 °C to 28 °C (Linsenmair 1998). The highest amount of rainfall regularly occur in August/September and a minor dry season is likely to be in June/July. While in the dry season the average level of rainfall rarely exceeds 50 mm, precipitation in the rainy season is highly variable, both with respect to extent (total amount ranging from 850 – 1700 mm) and to frequency in respective months.

CNP supports a wide variety of natural vegetation types including gallery forest, island forest, savannah forest, shrub and tree savannah, grass savannah and bowal areas. The proportional contribution of these different vegetation types to the total vegetation of a particular area changes from the wetter southern part (which belongs to the Guinea zone) to the drier northern part (which belongs to the Subsudan and Sudan zone). The same can be observed for many tree species, which are mainly or exclusively found in the southern or northern parts of the park. All studies presented in this thesis took place within the same area (about 5 km²) of Guinea-savannah in the southern part of the park (08°44'N, 003°49'W, c. 220 m), about 15 km apart from the southern park border (Figure III.1c,d).

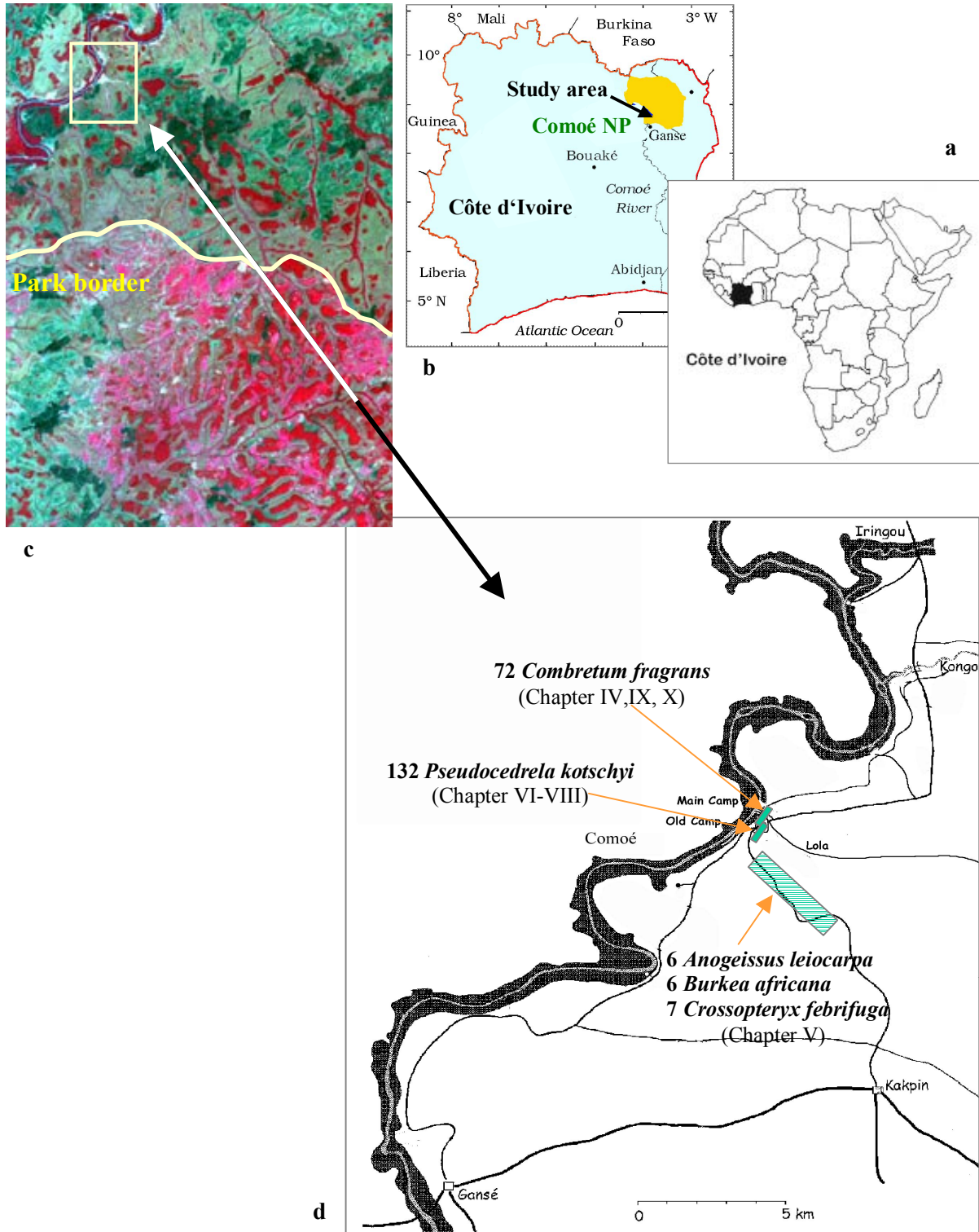


Figure III.1 Location of the study sites in Comoé National Park (Côte d'Ivoire): map of Africa (a); map of Côte d'Ivoire (b); Landsat Image of the region of southern Comoé National Park, indicating differences in vegetation cover between Comoé National Park and its surrounding (source: Biota W01/W04, D. Götze, modified) (c); specified location of the study sites (d).

III.2 Study Species

Arthropods

This study comprises distribution data of several hundred arthropod species, which are presented in some detail in the following chapters. Additionally, detailed investigations on the population and individual level have been conducted for one ant species (*Camponotus sericeus* (Formicidae), two beetle species (*Apogonia fatidica* (Scarabaeidae), and *Proictes curvipes* (Curculionidae)), and one moth species (*Chrysopsyche imparilis* (Lasiocampidae), (Figure III.2), (see Chapter VIII for *C. sericeus*, Chapter IX for *A. fatidica* and *P. curvipes*, and Chapter X for *C. imparilis*).

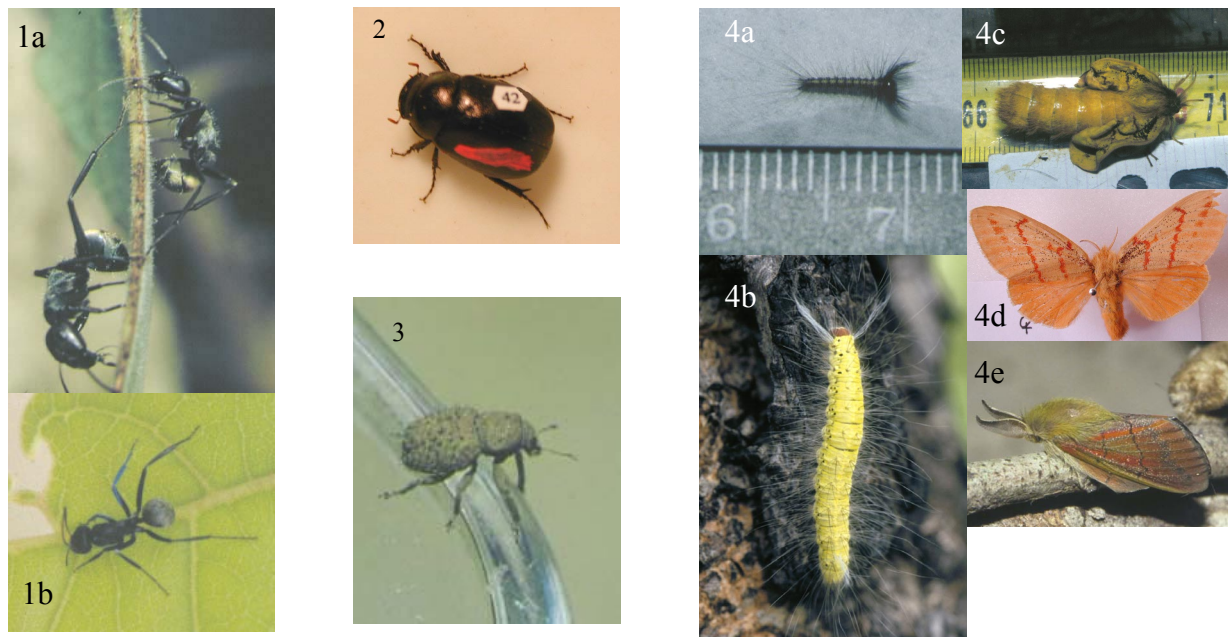


Figure III.2 Study species: *Camponotus sericeus* foragers, lateral view (1a); *C. sericeus* forager feeding at an extrafloral nectary (1b); *Apogonia fatidica* with individual marking (2); *Proictes curvipes* (3); *Chrysopsyche imparilis*: first instar larva (a); sixth instar larva (b); freshly eclosed female moth (c); female moth (d); male moth (e).

Trees

Five species of typical savannah trees were chosen as main hosts to study plant-associated arthropod communities (Figure III.3). In the following, these species will be presented in more detail, using information provided by Aubréville (1950), Steentoft (1988), von Maydell (1990), Mabberley (1997), and Arbonnier (2002).

Anogeissus leiocarpa (DC.) Guillemin et Perrottet (Combretaceae)

Synonyms: *Anogeissus leiocarpus* (DC.) Guill. et Perr., *Anogeissus schimperi* Hochst. ex Hutch. et Dalz., *A. leiocarpus* var. *schimperi* (Hochst. ex Hutch. et Dalz.) Aubrév., *Conocarpus leiocarpus* (DC.).

Description: *A. leiocarpa* is the only West African species of the genus *Anogeissus*. Its distribution lies on the extreme western edge of the area of distribution of the genus (tropical Africa-Southeast Asia). It is a tall deciduous tree, up to 30 m high, attaining a stem diameter of 70 cm. The bark is grey,

yellowish, scaly, and turns black with age. The slash is yellow, flamed, secreting dark coloured gum. The twigs are fine and weeping, brown, pubescent. The leaves are solitary or alternate and typically arranged two on one side, two on the opposite side, ovate, 4-7 cm long, short petioled, base acute, tip mucronate, 4-8 lateral nerves. The underside of the leaves is slightly pubescent. *A. leiocarpa* flowers during the rainy season. The fruits are small, conelike, dark brown heads, breaking up easily into numerous two winged seeds.

Distribution: Africa between the isohyet of about 200 mm and the rainforest, from Senegal to Sudan and Ethiopia, in the south to Zaire. *A. leiocarpa* is particularly prominent on forest-savannah boundaries, but occurs wherever there is protection from fire. In the study region, it occurred in 90 % of island forests and 33 % of savannah transects studied by Hovestadt et al. (1999).

Site requirements: Very large ecological amplitude, permitting a range from the southern limit of the Sahara to the northern limit of the rainforest. Prefers fresh soils, such as near seasonal lakes, in river valleys, often forming gallery forest, occasionally dense, closed stands. Originally widespread but strongly reduced and limited to 'relict' sites.

Combretum fragrans Hoffmann F. (Combretaceae)

Synonyms: *Combretum multispicatum* Engl. et Diels, *C. ghasalense* Engl. et Diels.

Description: *C. fragrans* is a small shrub or tree, up to 12 m high. The bark appears beige-brownish-reddish and warty. The slash is reddish at the surface and yellowish underneath. The leaves are opposite or rarely alternate, elliptic to oval, 5-20 x 2.5-10 cm. They are glabrous on the adaxial site and dark green when fully expanded. Leaves and twigs are very elastic. *C. fragrans* flowers at the end of the dry or at the beginning of the rainy season. The fruit is an elliptic, four-winged and glabrous samara.

Distribution: *C. fragrans* is widespread from Senegal to Sudan and Cameroun, and in southern Africa. It occurs in different types of savannahs and open forests. Its local abundance may reach from common to scattered. In the study region, *C. fragrans* (designated as *C. nigricans*) occurred in 8 % of island forests and 56 % of savannah transects studied by Hovestadt et al. (1999). In the local study area, it reached densities of 400 plants ha⁻¹ (K. Mody, pers. obs.).

Site requirements: *C. fragrans* grows on all types of soil. It is frequently found on clayey, loamy or lateritic soils.

Burkea africana Hooker (Leguminosae (Caesalpinaceae))

Synonyms: -

Description: *B. africana* is the only species of the genus *Burkea*. It is a deciduous tree, usually 10-12 m (rarely up to 20 m) high, attaining a stem diameter of up to 60 cm. The bark appears dark grey, rough and flaking. The slash is brown-violaceous and secretes gluey exudates. The young shoots and the tips of young branches are velvety and rusty-red to maroon. Leaves are crowded at the ends of branchlets and 10-35 cm long. They are bipinnate, with two pairs of pinnae and 5-9 (18) leaflets per pinna. The leaflets are elliptic, 3-5 cm, grey-green to dark green, with silvery oppressed hairs when very young. Twigs rigid, grey to brown. *B. africana* flowers at the end of the dry season, usually before or during appearance of first leaves. The fruit, a thin, flat pod of about 5 cm, is pale brown and hangs down in conspicuous clusters from the end of the branches. It remains on the trees for months, often until after the leaves have fallen at the end of the season.

Distribution: South of the Sahara, *B. africana* has a panafrikan distribution. It is a characteristic tree of Guinea- and Sudan-savannahs. It is common and locally abundant but usually not aggregated. In the study region, it occurred in 6 % of island forests and 100 % of savannah transects studied by Hovestadt et al. (1999).

Site requirements: *B. africana* prefers sandy, well-drained soils but may also occur on rocky and ferruginous soils.

Pseudocedrela kotschy (Schweinf.) Harms (Meliaceae)

Synonyms: *Cedrela kotschy* Schweinf., *Pseudocedrela chevaleri* C. DC.

Description: *P. kotschy* is the only species of the genus *Pseudocedrela*. It is a small to medium sized (4-5 m, maximally 12 m), monoecious, deciduous savannah tree. The slash is red and flamed. The bark is grey and deeply longitudinally fissured. The leaves are impari- or paripinnate, with up to 19 alternate asymmetrical leaflets with wavy edges. The leaflets are lanceolate to elliptic, 5-15 x 2-6 cm. *P. kotschy* bears inconspicuous leaf-EFNs which occur mainly along the nerves of the leaflets and are distributed over all leaves of the whole plant. EFNs are so unproductive that nectar neither accumulated to visually detectable amounts nor could it be tasted by humans (even after exclusion of nectar-collecting animals; K. Mody, pers. obs.). *P. kotschy* flowers in the middle of the dry season. The fruit is an erect, woody capsule, about 10 x 3 cm in size.

Distribution: *P. kotschy* is widespread in Sudan- and Guinea-savannahs from Senegal to Sudan and Cameroun. Its local abundance may reach from scattered to highly aggregated. In the study region, *P. kotschy* occurred in 6 % of island forests and 50 % of savannah transects studied by Hovestadt et al. (1999).

Site requirements: *P. kotschy* is found specially on heavy soils and in swampy areas. It is able to spread into eroded and bowal areas by root suckers, thereby forming *Pseudocedrela*-dominated stands of woody vegetation.

Crossopteryx febrifuga (Afzel. ex G. Don) Bentham (Rubiaceae)

Synonyms: *Rondeletia febrifuga* Afzel. ex G. Don, *Crossopteryx kotschyana* Fenzl, *Rondeletia africana* T. Winterb.

Description: *C. febrifuga* is the only species of the genus *Crossopteryx*. It is a small shrub or tree, up to 9 m high. The bark appears greyish to pale-brownish, with fine fissures and scales. The slash is brownish at the surface and salmon to orange underneath. The leaves are opposite, elliptic to oval, 6-10 x 3.5-7 cm. They are tomentose to glabrous and dark green when fully expanded. *C. febrifuga* flowers mainly at the end of the dry season. The fruit is a globose capsule, about 1 cm in diameter.

Distribution: *C. febrifuga* is widespread in Sudan- and Guinea-savannahs from Senegal to Sudan and Cameroun, in East and in southern Africa. Its local abundance may reach from common to scattered. In the study region, *C. febrifuga* occurred in 12 % of island forests and 94 % of savannah transects studied by Hovestadt et al. (1999).

Site requirements: *C. febrifuga* is frequently found on drained, rocky and incrustated soils.

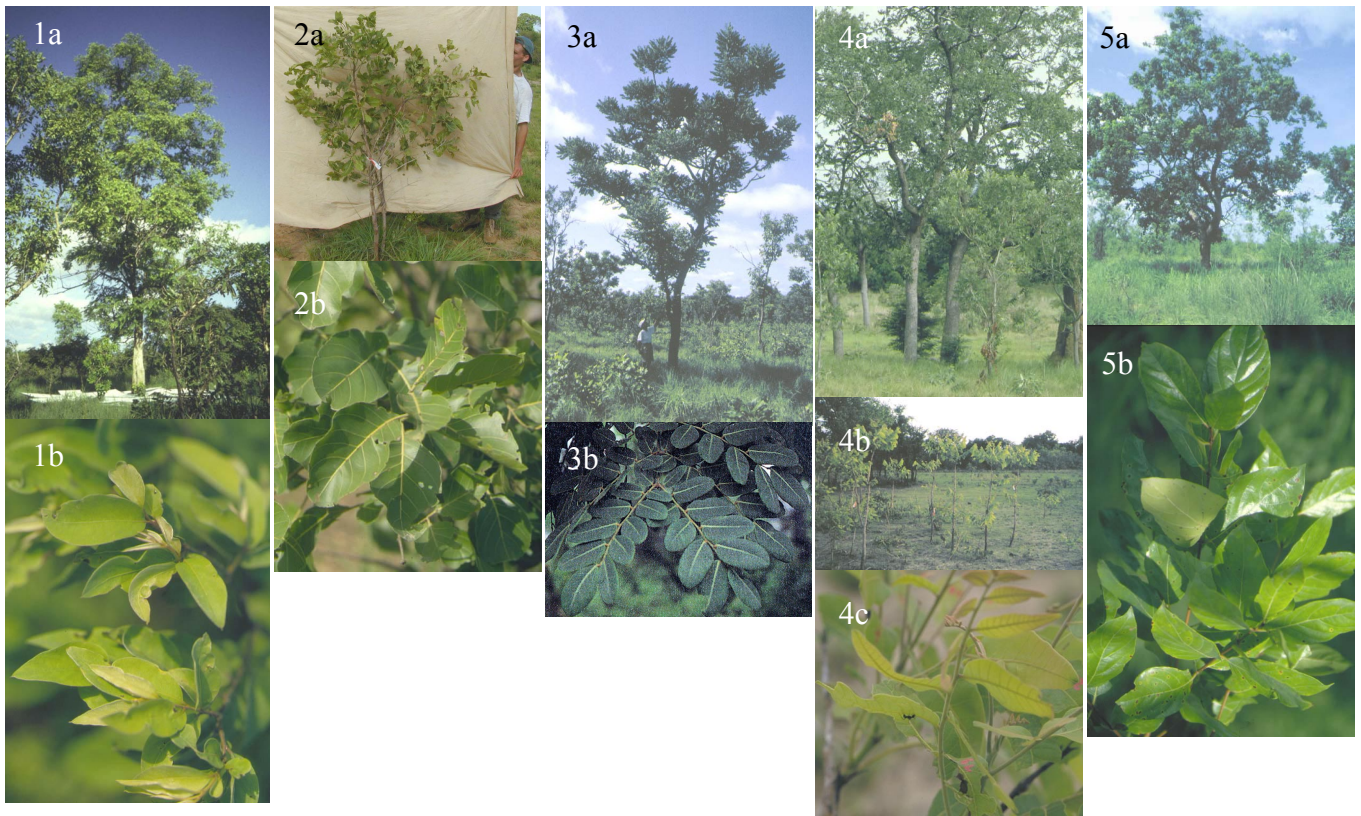


Figure III.3 Study Trees: *Anogeissus leiocarpa* habitus, study tree with collecting trays (1a); leaves (1b); *Combretum fragrans* habitus, study tree (2a) (Cf13, Chapter IX); leaves (2b); *Burkea africana* habitus (3a); leaves (3b; from Arbonnier 2002, modified); *Pseudocedrela kotschyi* habitus, mature tree (4a); habitus, study trees (4b); leaves with foraging ant (4c); *Crossopteryx febrifuga* habitus (5a); leaves (5b).

III.3 Methods

The brief method descriptions given below are intended to complement the method sections of the respective chapters. They are ordered according to their first appearance in Chapters IV-X.

The differential GPS (Chapter IV, VI-IX)

The Global Positioning System (GPS) is a worldwide radio-navigation system formed from a constellation of 24 satellites and their ground stations. GPS uses the satellites and ground stations as reference points to calculate positions accurate to a matter of metres and, with advanced forms of GPS, to a matter of centimetres. One such advanced form is the so-called differential GPS or ‘DGPS’. DGPS involves the co-operation of two receivers, one that is stationary (Figure III.4a and b) and another that is roving around (Figure III.4c) making position measurements. Using the DGPS-technique (Leica SR530, Leica Geosystems AG, Switzerland), it was possible to obtain the exact vertical and horizontal position of each study plant with an accuracy of 1-5 cm.

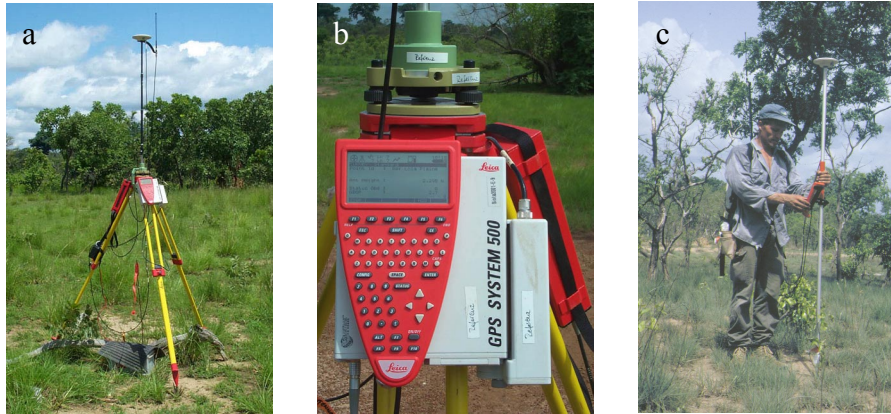


Figure III.4 Differential GPS. stationary receiver (a, b; photo: N. Ebigbo); roving receiver (c).

The ‘beating’ method (Chapter IV, IX)

Beating is considered to be a relatively simple, fast technique for sampling a range of insects. Usually, a beating tray is held under a few branches which are then struck with a stick, and the fallen arthropods are then sampled with aspirators (Basset et al. 1997). Using the beating method this way, certain insect groups of low mobility which drop readily from branches are well sampled, while other groups may quickly escape or remain on the plant. In order to circumvent most of the problems linked with the common beating technique, the method was modified in this study. (i) The design of the beating tray was specified (Figure III.5a). The tray had a large opening (60 x 40 cm) and very steep tray sides (62 cm), made of smooth balloon-silk. The collecting pot, a 500 ml polyethylene bottle, was directly fitted underneath in a screw thread. The weight of the pot automatically tightened the tray sides, thereby greatly improving the catching efficiency of the tray. The fixing by a screw thread allowed to easily transfer the collected arthropods to storage containers, without risking to loose any arthropods (which inevitably happens with interposed techniques like aspirators). (ii) The sampling unit was not a part of a plant but the *whole* plant. In combination with visual controls before and after the beating procedure, the complete arthropod community of the particular plant could be sampled.

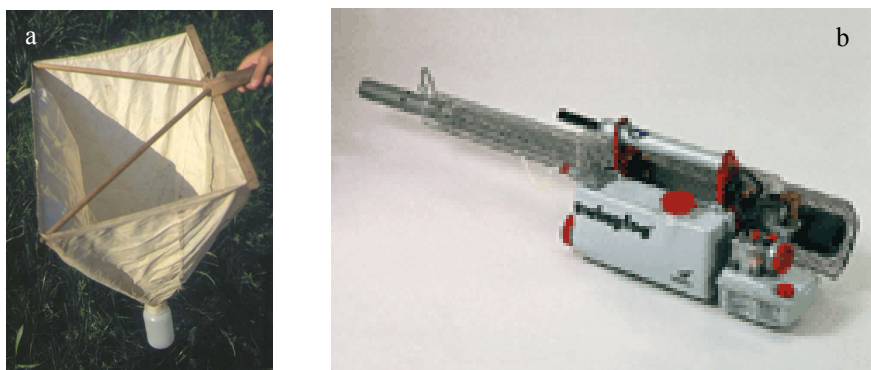


Figure III.5 Beating tray (a) and the fog generator Swingfog™ SN-50 (b; photo: Swingtec).

The ‘canopy fogging’ technique (Chapter V)

Canopy fogging is an insecticide knockdown technique, using a thermal aerosol fog generator (SwingfogTM SN-50, Figure III.5b). A fuel/air mixture from the carburetor is ignited in the combustion chamber, and the resulting deflagrations oscillate a column of gas in the resonator pipe between 80 and 110 times per second. The insecticide solution is injected into the hot air stream at the end of the fogging tube and is dispersed into the finest aerosol droplets and distributed into an extensive, dense fog. This insecticidal fog can be relatively precisely applied to individual tree crowns (in the case of isolated savannah trees) and the arthropods can be quantitatively collected if the crown projection is completely covered by collecting trays (see Figure III.3, *Anogeissus leiocarpa* with collecting trays) .

Canopy fogging has been used in many studies (see Stork et al. 1997, Basset et al. 2003a). The main advantages of this technique are its relatively quick implementation, high productivity, and ‘clean’ samples. Disadvantages are susceptibility to weather conditions (needs dry leaves and calm air conditions), the difficulty to determine arthropod densities (even if the tray area is quantified it is usually very difficult to also quantify the amount of foliage above the tray), and the difficulty to assign the collected arthropod to specific habitats within the tree (Basset et al. 1997). Natural pyrethrum as an insecticide is very efficient for arthropods and biodegrades within hours. Thus, it can at least reduce the detrimental site effects on arthropods of neighbouring communities and on re-colonising arthropods (few hours after fogging, many ants were found foraging again on the fogged trees; K. Mody, pers. obs.).

The determination of herbivory (Chapter VII, IX, X)

Several methods were applied to determine the degree of herbivory or the amount of leaf material consumed by herbivores in feeding trials. All methods were oriented towards determining the area of a leaf before a feeding event (either observational by free ranging herbivores in the field or experimentally by herbivores kept in the laboratory) and after a feeding event (after experiments in the field or in the laboratory). In the first year of the study, the leaves’ contours were exactly copied to drawing paper before and after the experiment, the drawings were scanned and the areas of the untreated leaf and of the missing leaf parts were quantified (Figure III.6a, Chapter IX). In the following years, the leaves were photographed with a digital camera (on the plant, Figure III.6b, and removed from the plant, Figure III.6c) in a standardised procedure. They were spread out on a board of white Plexiglas and tightly covered with a hinged lid of non-reflecting glass. Leaves were photographed with a reference square (1 cm²) from a fixed distance, with the same resolution, and without flash. Digital photographs were analysed using the graphics package ‘Adobe PhotoShop’. By referring to the ‘pixel number’ of the reference square, the leaves’ area could be computed. Leaf area was also determined for leaf-remainings after the feeding experiment. From differences in leaf area before and after the experiment, consumed leaf area was computed.

To quantify pre-experimental herbivory (PLD), the area of the leaf was determined as collected (untreated leaf; Figure III.6d), using the same procedure as described above. After the area of the untreated leaf had been determined, the leaf parts missing due to herbivory were added to the digitised leaf, using the undamaged portion of the leaves as a template when leaves were damaged along their margin (Figure III.6e). Leaf area was again determined for this ‘restored leaf’. PLD was then quantified as the difference between area of the untreated and the restored leaf.



Figure III.6 Determination of herbivory: exact leaf copy, experimental leaf damage is shaded (arrows) (a); digitising leaves remaining on the plant (b); digitising leaves removed from the plant (c); quantification of original leaf area (d); quantification of restored leaf area (e).

The marking of individual ants (Chapter VIII)

Workers of *Camponotus sericeus* were caught in a marking tube (Figure III.7a) when leaving their nests and individually marked with four colours of fast drying enamel paint applied to thorax and leg segments. They were set free after 3 minutes when the paint had dried.



Figure III.7 Individual marking of ant foragers. (a) the marking tube; (b) an ant during marking.

The feeding choice experiments (Chapter IX, X)

Three species of insect herbivores (*Apogonia fatidica*, *Proictes curvipes* and *Chrysopsyche imparilis*) were tested in pairwise feeding choice experiments, offering leaves or leaf pieces of two different plants simultaneously to the herbivores (Figure III.8a). *A. fatidica* was additionally tested in a Cafeteria experiment, offering leaf pieces of 12 different plants simultaneously to 24 beetles (Figure III.8b).

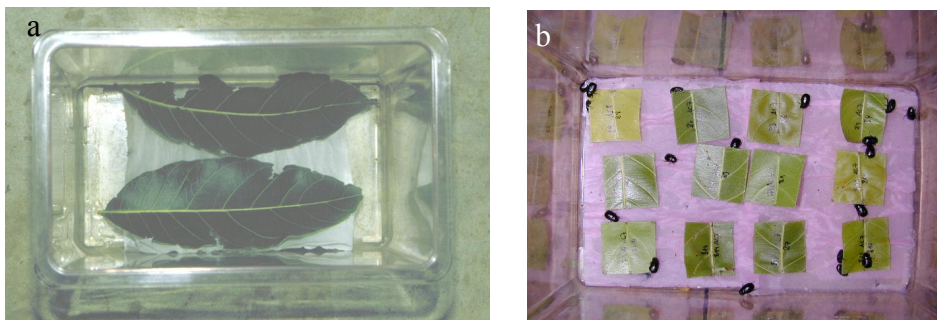


Figure III.8 Feeding choice experiments. (a) pairwise test; (b) Cafeteria test.

IV. Persistent Composition of Arthropod Communities on *Combretum fragrans*

Abstract - *Combretum fragrans* trees host speciose arthropod communities. With very few exceptions, the more abundant arthropod species were not randomly distributed on conspecific, neighbouring *C. fragrans* trees but aggregated on particular individuals. The same plant individuals were consistently recolonised by particular arthropod species after complete removal of arthropods. This resulted in a persistent distribution of species-specific, very similar aggregations on individual plants. The preference of arthropod species for particular plant individuals was persistent within the same year (over a 3 months period) and between two different years. It is concluded that *C. fragrans* trees vary with respect to arthropod relevant plant characteristics. These characteristics are stable over time and lead to a persistent distribution of arthropods in a deterministic way.

IV.1 Introduction

Many aspects of the structure of ecological communities can be investigated on the basis of the equilibrium theory of island biogeography (Preston 1962, Mac Arthur and Wilson 1967). The basic premise of this theory ‘that the biota of any island is in dynamic equilibrium between immigration of species new to the island and local extinction of those already present’ can be easily applied to other communities which are, like an island, easy to delimit. Plant associated arthropod communities represent such a type of community. The habitat of the community (the plant) can be easily delimited and characterised (species, size, leaf characteristics, distance to other plants, etc) and the community can, in many cases, be completely sampled, allowing to determine the composition of the original community and of thereupon repeatedly established communities (cf. Simberloff and Wilson 1969, Sanchez and Parmenter 2002).

In 1997, an investigation was conducted on arthropod communities associated with the savannah tree *Combretum fragrans*, applying a complete defaunation approach as used by studies concerned with the equilibrium theory of island biogeography (e.g. Simberloff and Wilson 1969, Brown and Kodric-Brown 1977, Rey 1981). *C. fragrans* and its associated arthropod community represented a model system which was very well suited to investigate the structure and structuring processes of speciose communities in a natural environment (Mody 1998). This study demonstrated that individual *C. fragrans* plants hosted very distinctive arthropod communities. By regularly repeating the complete defaunations, the study could additionally show that the distinctive structure was stable over time (within a 3 months period and also between successive years), indicating that every plant hosted its ‘own, characteristic’ arthropod community. Although the study could not quantify the underlying causes, it is hypothesised that (i) differences in the individual plants’ characteristics were relevant for the arthropods and were causing the arthropods to selectively colonise individual plants and (ii) that these arthropod-relevant plant attributes should be stable to explain the persistent distribution patterns of the arthropods. If stable plant characteristics existed and if these varied among conspecific plants, then one should expect to find an arthropod distribution reflecting these interindividually variable but intraindividually stable plant attributes.

The present study represents a direct continuation of the 1997-study. It analyses arthropod distribution on *C. fragrans* plants in two different years and asks whether arthropod-relevant plant characteristics – as reflected by arthropod presence or absence - are variable or stable over time. The study also provides basic information on occurrence patterns of insect species discussed in more detail in Chapters IX and X (*Proictes curvipes* and *Chrysopsycha imparilis*).

IV.2 Methods

Study site and tree species. The study was conducted in Comoé National Park, Republic of Côte d'Ivoire, from June through August 1997 and from April through July 1999. Comoé National Park is located in the north-east of the Republic of Côte d'Ivoire, and covers 11,500 km² of Guinea- and Sudan-zone savannah. The climate of Comoé National Park is characterised by a long dry season from about November to March/April, a mean annual precipitation of 950 mm and an annual average temperature between 25 °C and 28 °C (Linsenmair 1998). More information on Comoé National Park is provided in chapter III of this thesis and by Poilecot (1991) and Rödel (2000). The study area was situated within the Guinea-savannah in the southern part of the Park (08°44'N, 003°49'W, c. 215 m a.s.l.).

The studied host plant species, *Combretum fragrans* F. Hoffm. (Combretaceae) is a medium-sized (maximum height 12 m), deciduous savannah tree that is widespread in West African savannahs (Aubréville 1950, Arbonnier 2002) and reaches densities of 400 plants per ha in the studied area (K. Mody, pers. obs.). *Combretum fragrans* was chosen as study plant since it (i) forms local aggregations which provide repeated sampling opportunities under comparable site conditions, (ii) it is used by a diverse arthropod community (K. Mody, pers. obs.), and (iii) it is characterised by a high degree of physical resilience which allows intensive and repeated sampling by mechanical methods.

Host plant characterisation. The host plants were characterised by several variables. Plant size was determined as plant height, plant width (maximum diameter), plant depth (maximum diameter perpendicular to plant width), and leaf number. Spatial information was obtained by recording the exact position of each plant with a portable Differential GPS (Leica SR530, Leica Geosystems AG, Switzerland), providing exact information on vertical and horizontal position with a precision of 1-5 cm. All studied plants were syntopically growing within a marginally sloping (maximum orthometrical height difference 4.2 m on a distance of 106 m) section of shrub savannah which was located between gallery forest and open grass-land. The maximum distance between two study plants was 134 m, the minimum distance was 2.5 m.

Arthropod sampling. The sampling of the complete arthropod communities of 14 individual *C. fragrans* trees was conducted in the daytime, using a specified beating tray (Mody 1998): a deep tray of the dimension 60 x 40 x 62 cm, made of smooth balloon-silk, fitted underneath with a 500 ml polyethylene bottle simultaneously acting as collecting pot and weight to tighten the steep tray sides (see Figure III.5a). Before using the beating tray, the plant was carefully inspected for visible arthropods, which were directly transferred into the beating tray. After this, the whole plant was inserted into the tray and intensively shaken. The whole procedure was repeated three times, with three-minutes interruptions prompting arthropods latching onto the twigs to loosen their grip. Finally, the plant was again visually checked for remaining arthropods and the ground under the plant was checked for fallen arthropods. Sampling of complete communities was repeated at 10 day intervals for all *C. fragrans* plants. The communities were collected 8 times in 1997 and 6 times in 1999.

The arthropods were transferred to storage bottles containing 70 % ethanol directly after sampling. They were first sorted to orders (all arthropods), families (beetles, spiders, Heteroptera) or genera (ants) using the keys provided by Freude et al. (1965-1983), Delvare and Aberlenc (1989), Scholtz and Holm (1989) and Bolton (1994). They were then assigned to morphospecies (RTUs: recognisable taxonomic units), or determined to known species by specialists (see Danksagung).

Data analysis. The dispersion patterns of ‘regularly sampled’ arthropod species were analysed in this contribution. A species was recorded as ‘regularly sampled’ if it was sampled at least at six independent occasions within one year (on different trees at the same sampling date, or on the same tree at different sampling dates). This sampling incidence was used to consider a particular species as typical member of the *C. fragrans* community and to distinguish it from transient or ‘tourist’ species. The distribution of the individual arthropod species on the study trees was described by the index of dispersion (I_D) (Southwood and Henderson 2000), with $I_D = s^2(v - 1) / m$, where m and s^2 are the sample mean and variance, respectively, and v is the sample size. This index has been widely used (e.g. Morris et al. 1992) and provides satisfactory results for a small value of v . I_D values significantly greater than the chi-square statistic for the 0.025 probability level with $(v - 1)$ degrees of freedom indicate an aggregated distribution of the taxa considered (Ludwig and Reynolds 1988). I_D values were computed for the sum of individuals of a particular species sampled on the individual trees for each year. I_D values were also computed for the pooled sums of the two years (d.f. = 13 for the single-year and the pooled-year analyses).

IV.3 Results

The total number of arthropods collected from the 14 *C. fragrans* plants in 8 complete defaunations was 5424 for 1997. In 1999, 4607 arthropods were sampled in 6 complete defaunations. Of these arthropods, 21 species turned out to be regularly sampled according to the definition given above (for total numbers see Table IV.1). Four of these species fulfilled the criteria to be recorded as a ‘regular species’ only in one year (the ant Le2, the leaf beetle Ch4, the weevil Cu2 and the grasshopper Cl1; see Table IV.1 for all data presented and discussed in this Chapter). All other species were regularly found in both years, which indicated that they can be considered as typical members of the studied communities and that their population size did not strongly vary between the years. The most striking feature of the distribution of most of the species was their pronounced aggregation on particular plant individuals. Only three species, an eumolpine leaf beetle (Ch4), a lasiocampid caterpillar (Ci, i.e. *Chrysopsyche imparilis*; cf. Chapter X) and a salticid spider (Sa2) turned out to be never aggregated. Most of the other species were highly significantly aggregated in both years and in the combined analysis.

Table IV.1 Dispersion of most abundant arthropod (morpho)species on 14 *Combretum fragrans* trees.

Taxa	MS	1997				1999				1997 & 1999			
		N	TN	SI	Dis.	N	TN	SI	Dis.	N	TN	SI	Dis.
Formicidae													
<i>Crematogaster</i>	Cr1	1746	11	61	A***	938	11	37	A***	2684	12	98	A***
<i>Camponotus</i>	Ca1	124	9	24	A***	60	2	7	A***	184	9	31	A***
<i>Camponotus</i>	Ca2	40	9	24	A***	47	9	29	A***	87	10	53	A***
<i>Lepisiota</i>	Le1	58	11	30	A***	35	8	19	A***	93	13	49	A***
<i>Lepisiota</i>	Le2	27	7	11	A***	4	3	3	R	31	7	14	A***
<i>Pheidole</i>	Ph1	209	5	23	A***	48	2	6	A***	257	5	29	A***
Coleoptera													
Chrysomelidae	Ch1	352	14	78	A***	199	14	58	A***	551	14	136	A***
Chrysomelidae	Ch2	51	11	20	A***	20	9	16	R	71	13	36	A***
Chrysomelidae	Ch3	42	6	18	A***	18	6	13	A**	60	8	31	A***
Chrysomelidae	Ch4	21	8	11	A***	5	4	4	R	26	8	15	A***
Chrysomelidae	Ch5	18	9	17	R	6	5	6	R	24	10	23	R
Curculionidae	Cu1	56	8	23	A***	37	11	20	A***	93	11	43	A***
Curculionidae	Pc	79	5	20	A***	122	6	22	A***	201	6	42	A***
Curculionidae	Cu2	3	3	3	R	41	6	17	A***	44	6	20	A***
Coccinellidae	Co1	11	6	9	R	22	9	15	A***	33	9	24	A***
'Homoptera'													
Cicadellidae	Ci1	55	11	37	A***	11	6	10	R	66	12	47	A***
Araneae													
Salticidae	Sa1	61	11	37	A***	8	5	7	R	69	12	44	A***
Salticidae	Sa2	16	9	16	R	7	5	6	R	23	10	22	R
Lepidoptera													
Lepidoptera-larv.	Ll	13	6	9	A*	7	5	6	R	20	10	15	R
Lepidoptera-larv.	Ci	32	12	23	R	14	8	11	R	46	13	34	R
Orthoptera													
Caelifera	Cl1	15	7	13	A***	2	2	2	R	17	7	15	A***
Miscellaneous													
Cicadoidea juv.	Cij	569	14	101	A***	255	14	68	A***	824	14	169	A***
Araneae juv.	Arj	765	14	106	A***	211	14	71	A**	976	14	177	A***
Collembola	Coc	-	-	-	-	1112	14	75	A***	1112	14	75	A***
Thysanoptera	Thc	-	-	-	-	88	14	53	A***	88	14	53	A***

N = total number of individuals; MS: morphospecies code; N: total number of individuals of a particular species sampled; TN: number of trees on which the particular species was found; SI: sampling incidence of a particular species; Dis.: pattern of distribution: A: aggregated, R: random; larv.: larvae; juv.: juveniles not sorted to morphospecies; level of probability: **: $p < 0.01$, ***: $p < 0.001$. The values for the weevil *Proictes curvipes* (Pc; cf. Chapter IX) and the caterpillars of the lasiocampid moth *Chrysopsyche imparilis* (Ci; cf. Chapter X) are bold.

IV.4 Discussion

The study demonstrated that most of the arthropods considered as typical members of the studied *C. fragrans* arthropod communities occurred significantly aggregated on particular plant individuals. The aggregated distribution was observed within and between the study years. Especially the finding that aggregations persisted in the pooled-years analysis is striking. It clearly demonstrated that species did not only prefer particular plant individuals in the same year, but also in different years.

The repeated recolonisation of the same plant individual within the same year already indicates that arthropod-relevant plant attributes (distribution determining characteristics) should be persistent over time. The communities were studied over a three months period, ranging from the early to the late rainy season. During this time span, many characteristics of the plants changed pronouncedly, for example, the availability of young leaves and the plants' architecture (leaf chemistry was not recorded). Individual variation in the phenology of the study trees was substantial, with a difference of about three weeks in starting leaf flushing after the dry season (K. Mody, pers. obs.; cf. Crawley and Akhteruzzaman (1988) for reports on individual variation in phenology of trees and consequences on arthropods). Thus, the amount of young foliage available on individual plants was highly variable at the start of the investigation. At later recording events, no differences with regard to this parameter were detectable, as the leaves matured within two weeks and rate of new leaf production was negligible in the later rainy season. A comparable change in plant characteristics was observed for some variables of plant architecture. Plants differed greatly in the number and growth of new shoots produced after the dry season, which resulted in variable changes, for example, in size parameters and leaf density. Therefore, individual plants varied greatly in some characteristics. If these variable factors had primarily affected the distribution of the arthropods, their distribution should have changed according to these parameters and should have been variable for individual plants. The finding that arthropod distribution on individual plants was stable over time hence clearly indicates that stable plant characteristics were more important. Those stable characteristics could be caused by specific site conditions (Lightfoot and Whitford 1989, Ylioja and Rousi 2001, De Bruyn et al. 2002; e.g. nutrient, water availability), or they could also have an invariable genetic basis (Fritz and Price 1988, Orians and Fritz 1996, Osier et al. 2000).

A stable distribution within the same year could be explained in parts by plant independent variables, too. For species using permanent scent markers or orienting towards plants formerly damaged by conspecifics, such variables related to conspecifics could help to explain a continuous, repeated recolonisation of the same plant individuals. Although it is not known whether any of the studied species is able to use such attractants, it would at least be conceivable, for example, for herbivorous beetles (Bach and Carr 1990, Wan and Harris 1996, Kalberer et al. 2001).

This argument is, however, certainly not sufficient to explain the finding that the same plants were preferably used by the same arthropod species in different years. The two study periods were separated by two dry seasons, which means that the arthropods were confronted twice with total leaf shedding and direct contact to bushfire. Since neither individual arthropods nor species-specific markings will have persisted these interruptions, only intraindividually stable plant characteristics seem to be a plausible explanation of the arthropods' persistent distribution patterns (see also Chapter IX and X).

The random distribution of the salticid spider Sa2 corresponds to expectations for a cursorial hunter which needs to find prey and has to avoid predators independently of a particular site (Dippenaar-Schoeman and Jocqué 1997). In this context, the highly aggregated distribution of the second salticid spider (Sa1) seems more remarkable. Sa1 was an ant-mimicking salticid (probably of the genus *Myrmarachne*), which was usually found on the same plants like the ant Ca1 (not only on

the 14 *C. fragrans* plants reported here, but also on other plants, K. Mody, pers. obs.). Therefore, the aggregated distribution of Sa1 is probably attributable to the distribution of Ca1 (although it is not known hitherto which interrelationships link the two species). While the random distribution of the eumolpine leaf beetle Ch4 is not explainable with our current knowledge, the distribution of the lasiocampid caterpillar *C. imparilis* initiated a more intensive investigation on this species (see Chapter X) and seems now explainable.

In combination with another study presented in this thesis (Chapter IX, distribution of *Apogonia fatidica*) this study emphasises the need to consider daytime dependent changes in arthropod community structure. *Apogonia fatidica* was one of the most important and most abundant herbivores on *C. fragrans*. However, due to its completely nocturnal lifestyle, it was never collected during the diurnal defaunations presented in this study. If a complete understanding of community processes is the objective aimed at by a study, the day and the night perspectives have to be considered (see also Chapter VI and, for example, Costa and Crossley 1991).

V. Organisation of Arthropod Assemblages in Individual African Savannah Trees

Abstract - This study describes and compares arthropod assemblages collected by insecticide knockdown in Comoé National Park, Côte d'Ivoire, and occurring on three savannah tree species, *Anogeissus leiocarpa* (Combretaceae), *Burkea africana* (Leguminosae), and *Crossopteryx febrifuga* (Rubiaceae). Differences between beetle assemblages indicate an effect of tree species on assemblage composition. Beetle density and species richness was highest on *Anogeissus* (maximum density: 113.7 beetles m⁻², maximum species number: 145 per tree) whereas *Burkea* and *Crossopteryx* assemblages were not distinguishable on this basis. Mean species similarity of beetles was higher for conspecific (22-28 %) than for heterospecific trees (13-17 %). Principal component analysis of the distribution of abundant beetle species clearly separated *Crossopteryx* assemblages and demonstrated highest variability for *Anogeissus* assemblages. Differences between tree species were not pronounced in terms of ant density and diversity, and mean species similarity of ant assemblages was comparable between conspecific (36-40 %) and heterospecific host-tree species (30-39 %). Density and diversity measures such as species richness, log-series index, Berger-Parker dominance index, rarefaction and Shannon-Wiener index varied considerably among individuals of all three tree species for Coleoptera and Formicidae. Only the Berger-Parker index for ants showed little variation. A marked variation was also observed in the dominance of certain beetle families on single trees, and for the regularly aggregated distribution of beetle and ant species. These results were analysed with respect to (i) the hypothesis that conspecific trees provide similar habitats and are, therefore, inhabited by similar sets of arthropods, and (ii) the question whether stochastic colonisation events and/or deterministic tree characteristics are more important in determining the assemblage structure of individual trees. Resampling the assemblages of the same trees (*Anogeissus*) at 2 months and at 1 year later indicated a high congruence of assemblage composition. At both high and low taxonomic levels (arthropod orders, beetle families, beetle species and *Camponotus* species) the assemblage structure of refogged trees correlated most strongly with those of the same tree in the previous year. Permutation of correlation matrices revealed that this finding was significant for arthropod orders, beetle families and beetle species. The results of this study, therefore, tend to reject the hypothesis that conspecific trees are very similar habitats: rather they stress the importance of individual tree characteristics for arthropod assemblage composition.

V.1 Introduction

Studies on assemblages of canopy arthropods have become a prominent part of taxonomic and ecological research since the 1980s (see contributions in Stork et al. 1997). Facilitated by new canopy-access techniques (Moffett and Lowman 1995, Barker 1997) and by effective arthropod sampling methods, including 'restricted and selective fogging' (Basset et al. 1997, Floren and Linsenmair 1997), these investigations have influenced fundamentally our perspectives upon global, regional or local patterns of biodiversity (Erwin 1982, Stork 1988, Basset 1996, König and Linsenmair 1996, Stork et al. 1997). However, they do not cover all terrestrial biomes evenly, and those of Africa are least explored (Erwin 1995), (but see, for example, Brown 1961, Majer 1973, Moran and Southwood 1982, Samways et al. 1982, Southwood et al. 1982b, Jackson 1984, Coe and Collins 1986, Grant and Moran 1986, West 1986, Basset et al. 1992, Dejean et al. 1994, Moran et al. 1994, Wagner 1997, Krüger and McGavin 1998, Mercier et al. 1998, McGavin 1999, Wagner 1999, Dejean et al. 2000c, Basset et al. 2001). For West Africa, quantitative investigations of arthropods in pristine habitats are generally scarce, and information obtained by canopy fogging is virtually nonexistent. This lack of information, together with the continuing but hardly recognized disappearance of natural lands in the forest-

savannah mosaic of West Africa, prompted us in 1997 to start a canopy fogging study on the arthropod assemblages of savannah trees in the Comoé National Park, Republic of Côte d'Ivoire.

Research on arboreal arthropods has covered a wide range of topics from investigations on the general composition of arthropod assemblages to studies aiming at understanding the observed assemblage patterns. Many factors influencing the composition of arboreal arthropod assemblages, including intraindividual variation of plant characteristics to effects of season, disturbances, forest types and host-plant species, have been investigated to date. Considering this wealth of information, studies explicitly taking the individual tree as the study unit seem to be noticeably rare. This becomes especially evident in comparison with a related field of ecological research, that of animal-plant interactions. Such studies have shown that, for example, a great number of plant characteristics vary across individual conspecific plants (Marquis 1992) and that these influence deterministically the distribution of herbivorous insects (Fritz 1992). With regard to studies on arthropod assemblages on trees, the question arises whether particular findings are applicable to systems of (a few) herbivore species and their (often nonwoody) host plants or whether they apply to species-rich arthropod assemblages as a whole. On the one hand it could be argued that an individual tree presents a much wider spectrum of characteristics than a small herb and that conspecific trees, therefore, provide very similar habitats for arthropods (Southwood and Kennedy 1983). On the other hand, it is well known that even conspecific, syntopically growing trees are variable in arthropod-relevant parameters like phenology (Crawley and Akhteruzzaman 1988, Mapongmetsem et al. 1998, Stork et al. 2001), architecture (Strong et al. 1984b), morphology (Basset 1991, Senn et al. 1992, Schmidt 1999) or chemistry (Edwards et al. 1993, Barnola et al. 1994, Butcher et al. 1994, Hemming and Lindroth 1995, Staudt et al. 2001). Such differences could be taken to suggest that individual tree characteristics might be of more importance for the structure of arthropod assemblages than is reflected in the attention that has been paid to this topic hitherto.

In this study, we have investigated the structure of arthropod assemblages on three representative species of West African savannah trees, explicitly considering assemblage structure on tree individuals. Our specific objectives were (i) to compare assemblages on conspecific and heterospecific tree individuals for among-tree similarity; (ii) to test the hypothesis that conspecific trees are inhabited by similar arthropod assemblages as they provide similar habitats; and (iii) to identify the relative importance of deterministic tree characteristics versus stochastic events as factors structuring these assemblages.

V.2 Methods

Study area and host trees. The study was conducted in Comoé National Park from June to August 1999 and from June to July 2000 during the rainy season. Comoé National Park is located in the north-east of the Republic of Côte d'Ivoire, and covers 11500 km² of Guinea- and Sudan-zone savannah. It supports a wide variety of vegetation types including gallery forest, island forest, savannah forest, shrub and tree savannah, grass savannah and areas almost free of vegetation. Porembski (1991), Poilecot (1991) and Rödel (2000) provide more detailed descriptions of the Comoé National Park. The study area was situated within the Guinea-savannah in the southern part of the park (3°49' W, 8°44' N, c. 220 m).

The three tree species studied, *Anogeissus leiocarpa* Guillemin & Perrottet (Combretaceae), *Burkea africana* Hook (Leguminosae, Caesalpinieae *sensu* Mabberley 1997), and *Crossopteryx febrifuga* Benth (Rubiaceae), are widespread in West African savannahs (Aubréville 1950) and locally abundant in the study area (Hovestadt 1997): we designate them by their generic names hereafter. In this contribution, data on the arthropod assemblages on six *Anogeissus*, six *Burkea* and

seven *Crossopteryx* individuals are presented. The size of the trees was characterised by several parameters such as tree height (TH), crown width (CW; maximum crown diameter), crown depth (CD; maximum crown diameter perpendicular to CW), crown projection area (CPA; $CPA = CW \times (CD / 4) \times \pi$) and tree volume (TV; roughly estimated as: $TV = (CPA \times TH)$). In order to study the structure of the arthropod assemblages, evaluate the sampling efficiency and observe changes in assemblage structure over time, the *Anogeissus* trees were fogged twice in 1999 (in June/July and in August) and once in 2000 (in June/July). One *Anogeissus* tree was excluded from sampling in 2000 since a colony of weaverbirds had established on this tree in the meantime. The *Burkea* and *Crossopteryx* trees were fogged once in 1999 (June/July). Trees selected for fogging seemed healthy, carried no epiphytes and were free of woody plant undergrowth. None of the trees bore ripe fruits or open flowers at the time of sampling. Details of the 19 trees are given in Table V.1. To ensure that the arthropods collected were most likely associated with the target tree, only trees completely isolated from other canopies by several metres distance were used as study units. All studied trees were syntopically growing within a section of tree savannah 3 km² in area.

Table V.1 Data on the 19 savannah trees studied including six *Anogeissus leiocarpa* (*An.*), six *Burkea africana* (*Bu.*) and seven *Crossopteryx febrifuga* (*Cr.*) individuals.

Tree code	TH (m)	CPA (m ²)	TV (m ³)	TVc (m ³)		Tray area (m ²)	
				1999	2000	1999	2000
<i>An.1</i>	10	67	670	220	310	22	31
<i>An.2</i>	15	113	1695	660	720	44	48
<i>An.3</i> ^a	12	10	120	120	-	16	-
<i>An.4</i>	15	99	1485	420	480	28	32
<i>An.5</i>	15	94	1410	690	690	46	46
<i>An.6</i>	12	133	1596	552	552	46	46
<i>Bu.1</i>	9.5	28	266	209	-	22	-
<i>Bu.2</i>	7	49	343	182	-	26	-
<i>Bu.3</i>	9	33	297	144	-	16	-
<i>Bu.4</i>	7	41	287	140	-	20	-
<i>Bu.5</i>	6.5	46	299	182	-	28	-
<i>Bu.6</i>	9	33	297	180	-	20	-
<i>Cr.1</i>	8	16	128	112	-	14	-
<i>Cr.2</i>	7	24	168	126	-	18	-
<i>Cr.3</i>	5	12	60	50	-	10	-
<i>Cr.4</i> ^a	9	18	162	180	-	20	-
<i>Cr.5</i>	7.5	16	120	90	-	12	-
<i>Cr.6</i>	8	22	176	128	-	16	-
<i>Cr.7</i>	8.5	16	136	136	-	16	-

TH: tree height; CPA: crown projection area; TV: tree volume; TVc: tree volume covered by collecting trays.

^a crown projection area is used instead of tray area for calculation of TVc.

Sampling protocol. Canopy fogging of trees 8-15 m in height was carried out from the ground for about 5 minutes with natural pyrethrum (1 % active ingredient), using a Swingfog™ SN-50. Natural pyrethrum is an insecticide that is very efficient for arthropods and that biodegrades within hours. In order to make the fog visible, a nontoxic highly refined white oil (Essobayol™ 82) was used as a carrier for the insecticide (Floren and Linsenmair 1997). Thus, fogging of the complete crown could be ensured. Sampling was performed 2 hours after sunset, the only time windless conditions and dry leaves could be expected on a regular basis. Falling arthropods were collected on 2 m² funnel-shaped trays made of smooth balloon-silk, fitted underneath with a collecting pot containing a detergent solution. The trays were arranged approximately 80 cm above the ground beneath each tree (the grass layer under the trees had been cut previously to a height of 10 cm). To ascertain that the crown projection area was representatively covered by trays, the number of used trays varied in relation to tree size (Table V.1). A strong correlation between tray area and the physical parameters of tree size indicated that coupling tray area and tree size was effective (correlation between tray area and both crown projection area and tree volume: $r_s = 0.9$, $N = 19$, $p < 0.0001$). In order to incorporate tree size into the analyses of assemblage composition, number of individuals and species of arthropods sampled were related to number of trays used per tree (that is, ‘samples per unit tray area’) and tree volume covered by collecting trays (that is, ‘sampled crown volume’). The latter was roughly estimated as: (tray area × TH). All arthropods falling during a drop time of 2 hours were sampled in the collecting pots, quickly washed with ethanol and transferred to storage bottles containing 70 % ethanol. The beetle and ant assemblages were analysed for all three tree species. They were first sorted to families (beetles) or genera (ants) using the keys provided by Freude et al. (1965-1983), Delvare and Aberlenc (1989), Scholtz and Holm (1989) and Bolton (1994). They were assigned then to morphospecies (RTUs: recognizable taxonomic units), or determined to known species by specialists (see Acknowledgements). As *Crematogaster* spp., to date, have not been cross-checked for the samples of 1999 and 2000, only *Camponotus* spp. have been used for the interyear analysis. Additionally, all specimens collected on *Anogeissus* were sorted to higher taxonomic units, and the individuals were counted. Voucher specimens were deposited at the entomological collection of the Department of Animal Ecology and Tropical Biology, Würzburg, and will be transferred to public museums after completion of analyses. For description of assemblage composition two general abundance definitions are used. These are (i) ‘dominant’, referring to beetle families contributing at least 5 % to the total numbers on a single tree; and (ii) ‘abundant’, defined as species represented by at least 12 individuals found in 1 year on the same tree.

Data analysis. For the characterisation of the arthropod assemblages, several diversity indices were calculated. Following recommendations given in Magurran (1988) and Southwood and Henderson (2000), α -diversity was described by a suite of measures such as species richness (S), the log-series index (α) (Fisher et al. 1943), the Berger-Parker dominance index (d) (Berger and Parker 1970), and rarefaction (Hurlbert 1971). Since the Shannon-Wiener index (H' , \log_{10}) is widely used, it was calculated to increase comparability with other studies, despite the well-known difficulties in its interpretation (May 1975). Differences between several diversity measures of the three host-tree species were tested using one-way analyses of variance (ANOVA). Where necessary, data were transformed to meet the assumptions of homogeneity of variances and normal distribution (Sokal and Rohlf 1995). In instances where an ANOVA was not applicable, the Kruskal-Wallis test was employed (Zar 1999).

Beta-diversity was expressed by the Jaccard index (C_j) (Magurran 1988). A comparison with the qualitative Sørensen index favored by some other authors (Smith 1986) showed no differences in the present study; therefore, C_j was used as it is the simplest, easiest to interpret and yet useful similarity coefficient. Faunal similarity was also investigated using correlation analyses (Spearman’s rank

correlation, Sachs 1997) and principal component analysis (Ludwig and Reynolds 1988, Legendre and Legendre 1998). These analyses were based on number of individuals within different taxonomic categories, such as orders, families and species (Basset et al. 1996b). To detect relevant differences between groups of correlation coefficients, permutations of correlation matrices were conducted and all possible combinations were evaluated.

The distribution of individual beetle and ant species on the study trees was described by the index of dispersion (I_D) (Southwood and Henderson 2000), with $I_D = s^2(v - 1) / m$, where m and s^2 are the sample mean and variance, respectively, and v is the sample size. This index has been widely used (e.g. Morris et al. 1992) and provides satisfactory results for a small value of v . I_D values significantly greater than the chi-square statistic for the 0.025 probability level with $(v - 1)$ degrees of freedom indicate an aggregated distribution of the taxa considered (Ludwig and Reynolds 1988). The minimum number of individuals that are required to distinguish between a random and a nonrandom distribution varies with v . For this reason, I_D values were not calculated when less than three individuals were encountered when evaluating a particular tree species ($v =$ six for *Anogeissus* and *Burkea* and $v =$ seven for *Crossopteryx*) and when less than two individuals were encountered for a consideration of all trees ($v = 19$). In addition to I_D , Green's Index (GI) was computed as $(s^2 / m - 1) / (N - 1)$, where N is the number of individuals in the sample (Ludwig and Reynolds 1988). The value of GI varies between 0 (for random) and 1 (for maximum clumping). It is considered to be independent of N and can be used to compare samples that vary in the total number of individuals, their sample means and the number of sampling units.

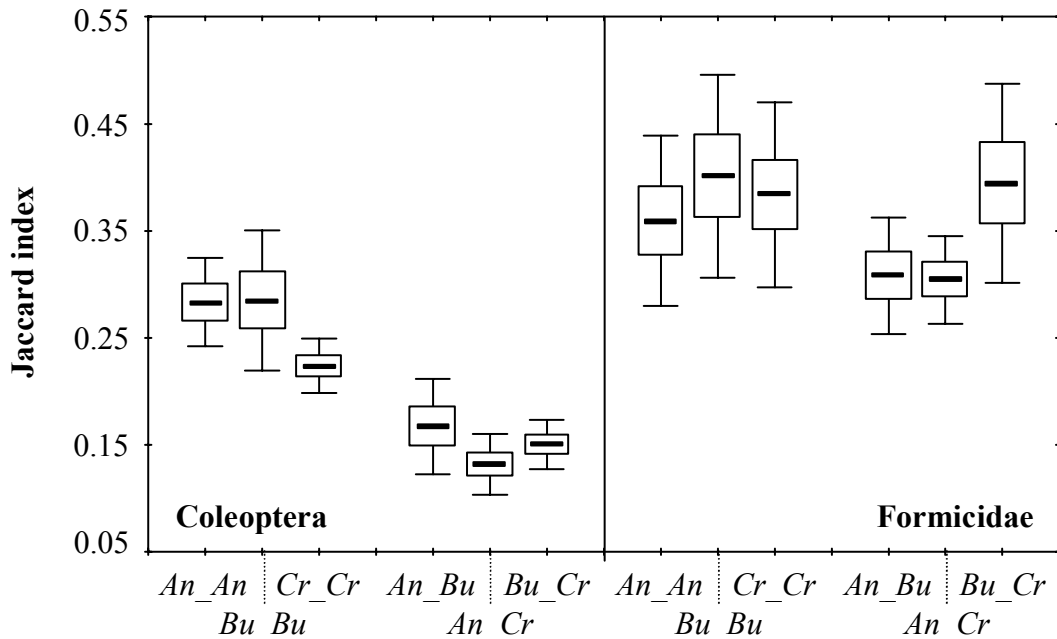


Figure V.1 Jaccard indices (mean, standard error and standard deviation) obtained for comparisons of beetle and ant assemblages of *Anogeissus* (*An*), *Burkea* (*Bu*) and *Crossopteryx* (*Cr*) trees.

Table V.2 Diversity measures for beetles and ants sampled from the 19 trees fogged in 1999.

Code for sampled trees	Total		Per tray area (m ²)		Per tree volume (m ³)		α	d	Rf ^a	H'
	N	S	N	S	N	S				
Coleoptera (beetles)										
<i>An.1</i>	322	46	14.6	2.09	1.46	0.21	14.69	0.36	12.56	1.66
<i>An.2</i>	3221	145	73.2	3.30	4.88	0.22	31.23	0.53	10.18	2.16
<i>An.3</i> ^b	100	29	10.0	2.90	0.83	0.24	13.70	0.42	13.02	1.46
<i>An.4</i>	2445	83	87.3	2.96	5.82	0.20	16.62	0.77	6.40	1.92
<i>An.5</i>	1783	93	38.8	2.02	2.58	0.13	20.86	0.24	14.30	1.97
<i>An.6</i>	5228	142	113.7	3.09	9.47	0.26	26.95	0.26	12.44	2.15
<i>Bu.1</i>	69	27	3.1	1.23	0.33	0.13	16.32	0.17	15.44	1.43
<i>Bu.2</i>	104	27	4.0	1.04	0.57	0.15	11.84	0.18	13.89	1.43
<i>Bu.3</i>	222	32	13.9	2.0	1.54	0.22	10.26	0.66	7.87	1.51
<i>Bu.4</i>	360	39	18.0	1.95	2.57	0.28	11.12	0.55	9.45	1.59
<i>Bu.5</i>	250	37	8.9	1.32	1.37	0.20	12.00	0.18	12.39	1.57
<i>Bu.6</i>	215	33	10.8	1.65	1.19	0.18	10.88	0.46	11.36	1.52
<i>Cr.1</i>	109	28	7.8	2.0	0.97	0.25	12.19	0.19	13.35	1.45
<i>Cr.2</i>	133	44	7.4	2.44	1.06	0.35	22.97	0.18	16.43	1.64
<i>Cr.3</i>	27	12	2.7	1.20	0.54	0.24	8.28	0.19	12.00	1.08
<i>Cr.4</i> ^b	73	26	4.1	1.44	0.45	0.16	14.43	0.21	14.40	1.42
<i>Cr.5</i>	33	17	2.8	1.42	0.37	0.19	14.09	0.18	14.94	1.23
<i>Cr.6</i>	77	39	4.8	2.44	0.60	0.30	31.57	0.18	18.51	1.59
<i>Cr.7</i>	329	45	20.6	2.81	2.42	0.33	14.10	0.52	10.22	1.65
Formicidae (ants)										
<i>An.1</i>	302	11	13.7	0.50	1.37	0.05	2.33	0.49	6.49	1.11
<i>An.2</i>	3358	15	76.3	0.34	5.09	0.02	2.11	0.50	5.19	1.23
<i>An.3</i> ^b	1330	6	133.0	0.60	11.08	0.05	1.02	0.50	1.81	0.90
<i>An.4</i>	3334	12	119.1	0.43	7.94	0.03	1.70	0.50	3.57	1.15
<i>An.5</i>	266	9	5.8	0.20	0.39	0.01	1.96	0.49	6.97	1.04
<i>An.6</i>	1196	20	26.0	0.43	2.17	0.04	3.35	0.50	6.19	1.34
<i>Bu.1</i>	93	9	4.2	0.41	0.44	0.04	2.52	0.48	7.81	1.04
<i>Bu.2</i>	229	6	8.8	0.23	1.26	0.03	1.38	0.49	3.96	0.90
<i>Bu.3</i>	1403	8	87.7	0.50	9.74	0.06	1.31	0.50	2.86	1.00
<i>Bu.4</i>	218	6	10.9	0.30	1.56	0.04	1.39	0.49	4.24	0.90
<i>Bu.5</i>	324	8	11.6	0.29	1.78	0.04	1.68	0.49	3.61	1.00
<i>Bu.6</i>	177	11	8.9	0.55	0.98	0.06	2.63	0.49	7.05	1.11
<i>Cr.1</i>	401	7	28.6	0.50	3.58	0.06	1.42	0.50	5.17	0.95
<i>Cr.2</i>	415	9	23.1	0.50	3.29	0.07	1.79	0.50	6.59	1.04
<i>Cr.3</i>	54	7	5.4	0.70	1.08	0.14	2.29	0.47	7.00	0.95
<i>Cr.4</i> ^b	355	10	19.7	0.56	2.19	0.06	2.05	0.49	6.23	1.08
<i>Cr.5</i>	133	9	11.1	0.75	1.48	0.10	2.30	0.48	6.70	1.04
<i>Cr.6</i>	1430	7	89.4	0.44	11.17	0.05	1.16	0.50	1.81	0.95
<i>Cr.7</i>	555	14	34.7	0.88	4.08	0.10	2.65	0.49	4.47	1.20

An.: *Anogeissus*, *Bu.*: *Burkea*, *Cr.*: *Crossopteryx*; N: number of individuals; S: number of (morpho)species
 α : Fisher's alpha; d: Berger-Parker index; Rf: Rarefaction; H': Shannon-Wiener index (log₁₀ base)

^a sample size of rarefaction (individuals) 27 for Coleoptera and 54 for Formicidae

^b crown projection area is used instead of tray area for calculation of values considering area and volume

V.3 Results

Beetle and ant assemblages on *Anogeissus*, *Burkea* and *Crossopteryx*. In total, 15 100 beetles and 15 573 ants were obtained from the sampling carried out in 1999 from trees fogged for the first time. The specimen number per tree varied clearly between conspecific and between heterospecific tree individuals (Table V.2). In general, most beetles and ants were found on *Anogeissus*. Out of 322 beetle species sampled, *Anogeissus* hosted 78 %, *Burkea* 29 %, and *Crossopteryx* 34 % of species (one-way ANOVA, log-transformed, $F_{2,16} = 8.50$; $p < 0.01$). Relative beetle abundance was even higher on *Anogeissus*. Of all beetle individuals sampled, 87 % came from *Anogeissus*, 8 % from *Burkea* and 5 % from *Crossopteryx* (one-way ANOVA, log-transformed, $F_{2,16} = 10.51$; $p < 0.01$). Differences between tree species for ants were not as distinct as for beetles. Out of 36 ant species sampled in total, 78 % were collected on *Anogeissus*, 47 % on *Burkea*, and 58 % on *Crossopteryx* (one-way ANOVA, $F_{2,16} = 2.62$; $p > 0.05$). Ant abundance was also not significantly different between tree species. 63 % of all ants were obtained from *Anogeissus*, 16 % from *Burkea* and 21 % from *Crossopteryx* (one-way ANOVA, log-transformed, $F_{2,16} = 3.23$; $p > 0.05$). Species similarity of assemblages was quite low for beetles and much higher for ants (Figure V.1). Mean species similarity of beetle assemblages on conspecific trees ranged from 22 to 28 %, and mean similarity on heterospecific trees from 13 to 17 %. For ants, mean similarity was 36-40 % for conspecific and 30-39 % for heterospecific host-tree species.

When incorporating tree size into the analyses by use of ‘samples per unit tray area’ or ‘sampled crown volume’, significant interspecific differences were detected for beetle abundance, beetle species richness on a per tray area basis, and ant species richness. No significant interspecific differences could be detected for beetle species richness on a crown volume basis and for ant abundance (Table V.2). Beetle densities were highest on *Anogeissus* (one-way ANOVA, log-transformed, $F_{2,16} = 10.45$; $p < 0.01$ for beetles per tray area, and $F_{2,16} = 5.86$; $p < 0.05$ for beetles per crown volume). Beetle species richness was also highest on *Anogeissus* though only for tray area (one-way ANOVA, $F_{2,16} = 7.73$; $p < 0.01$ for beetles per tray area, and $F_{2,16} = 2.35$; $p > 0.05$ for beetles per crown volume). For other measures of beetle α -diversity the pattern was less clear. For indices influenced by evenness in species abundance (d and rarefaction), beetle α -diversity was highest on *Crossopteryx* but the differences were not significant (one-way ANOVA, $F_{2,16} = 1.94$; $p > 0.1$ for d , and $F_{2,16} = 2.01$; $p > 0.1$ for rarefaction). Indices more strongly influenced by species-richness, such as the α and H' indices, indicated highest beetle diversity for *Anogeissus*, which was only significant for H' (one-way ANOVA, $F_{2,16} = 8.50$; $p < 0.01$ for H' , and $F_{2,16} = 2.76$; $p > 0.05$ for α). *Anogeissus* hosted the highest ant densities per tray area or crown volume but there was no significant difference detectable (one-way ANOVA, log-transformed, $F_{2,16} = 1.58$; $p > 0.1$ for tray area and, not transformed, $F_{2,16} = 0.46$; $p > 0.5$ for crown volume). Ant species richness was highest for *Crossopteryx* for both, tray area and crown volume data (one-way ANOVA, $F_{2,16} = 5.21$; $p < 0.05$ for tray area and, log transformed, $F_{2,16} = 11.01$; $p < 0.01$ for crown volume). Ant α -diversities were not different between the tree species (one-way ANOVA, $F_{2,16} = 1.11$, $p > 0.3$ for d , $F_{2,16} = 0.12$, $p > 0.8$ for rarefaction, $F_{2,16} = 2.38$, $p > 0.1$ for H' , and $F_{2,16} = 0.25$, $p > 0.7$ for α).

All three tree species showed a high variability in most assemblage parameters between assemblages on conspecific trees (with the exception of d for ants; Table V.2). Most pronounced differences could be found for beetle densities, with variation by orders of magnitude of 5.7 ($s^2 = 32.7$) on *Burkea* and 11.4 ($s^2 = 1745$) on *Anogeissus* for beetle density per tray area and 6.6 ($s^2 = 0.5$) on *Crossopteryx* and 11.4 ($s^2 = 10.5$) on *Anogeissus* for beetle density per crown volume. Data not corrected for tree size showed the highest variation for beetle density on *Anogeissus* (factor = 52, $s^2 = 3\ 676\ 064$) and the smallest variation for beetle density on *Burkea* (factor = 5.2, $s^2 = 11\ 023$).

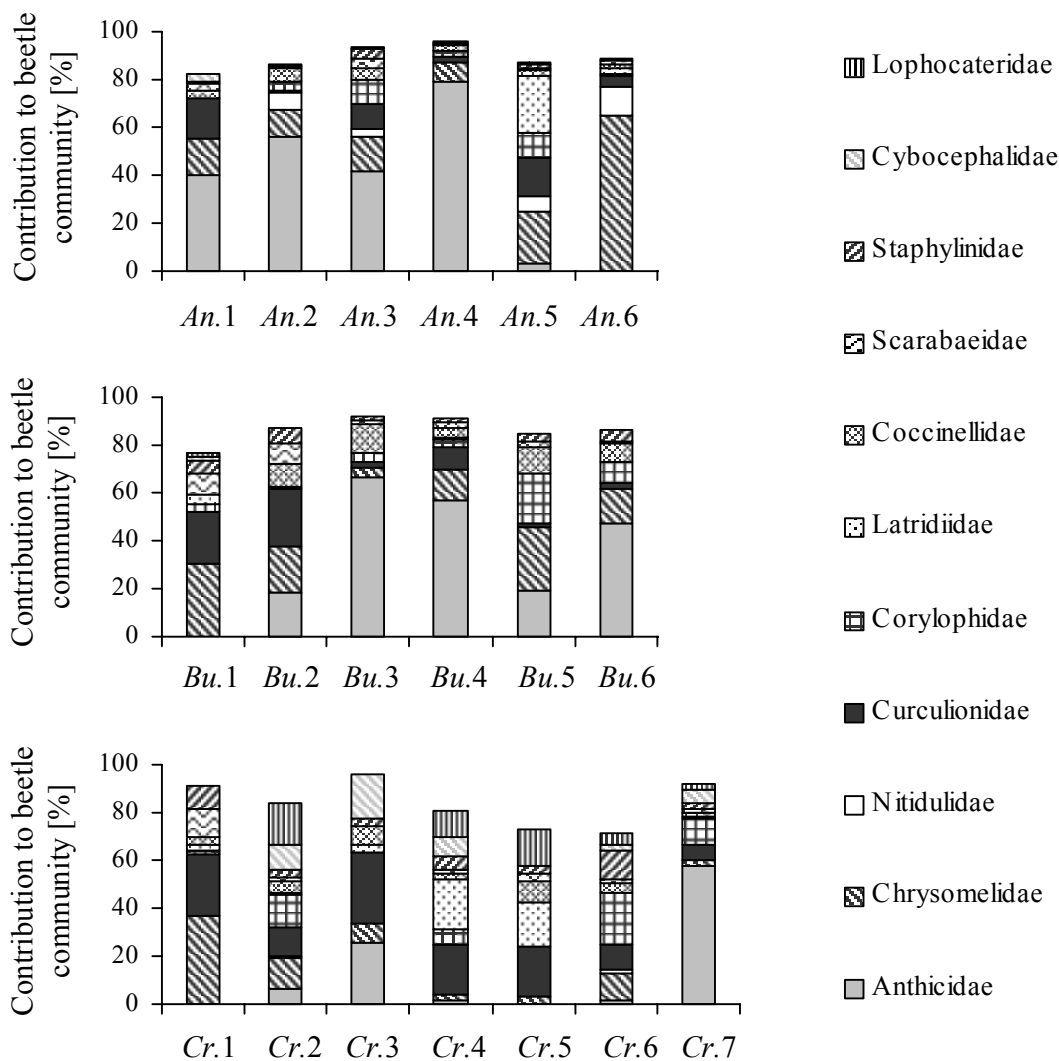


Figure V.2 Contribution of single beetle families to the entire beetle assemblage of individual *Anogeissus* (An), *Burkea* (Bu), and *Crossopteryx* (Cr) trees. Beetle families were included when they contributed at least 10 % to the beetle assemblage of an individual tree.

This marked variation was observed for assemblage parameters as well as for the dominance of certain beetle families on single trees, and for the distribution of particular beetle and ant species. The contribution of particular beetle families to the entire beetle assemblage was highly variable (Table V.3, Figure V.2). However, this was not because of the dominance of single species of the families considered in this evaluation. Specimen number and species number were always highly correlated with the exception of Corylophidae (all beetle families indicated in Table V.3: $r_s \geq 0.71$, $N = 19$, $p < 0.001$; for Corylophidae: $r_s = 0.4$, $N = 19$, $p = 0.07$). Although some beetle groups were very abundant and some differences between the tree species existed, it was not possible to rank the most abundant beetle families universally. *Anogeissus* assemblages were regularly dominated by Anthicidae. However, this beetle family was almost absent on two trees which were dominated by Latridiidae and Chrysomelidae, respectively (Figure V.2). In addition to Chrysomelidae, which were always an important group (contributing between 8-64 % of specimens), beetles of five other families contributed at least 10 % to the whole beetle assemblage of individual trees (Figure V.2). A similar pattern was observed for *Burkea* and *Crossopteryx* assemblages. *Burkea* assemblages were dominated

by beetles of seven families, of which only Chrysomelidae showed a relatively stable contribution across all tree individuals. Beetle assemblages on *Crossopteryx* were dominated by beetles of 14 families. Out of these beetles, only Curculionidae were found regularly at higher densities. Anthicidae were again very abundant on some trees while completely lacking on others (Figure V.2).

Table V.3 Abundance of beetle families, listed in decreasing order. Absolute number of beetles per family and their contribution to beetle assemblages of the single tree species are given.

Family	Total no. (%)		Median contribution to beetle communities (minimum-maximum)		
			<i>Anogeissus</i> sp.	<i>Burkea</i> sp.	<i>Crossopteryx</i> sp.
Anthicidae	4703	(31.1)	41.1 (0.3/79.0)	33.5 (0.0/66.7)	1.4 (0.0/57.8)
Chrysomelidae	4634	(30.7)	14.6 (8.3/64.1)	16.8 (4.1/30.4)	7.4 (2.4/36.7)
Nitidulidae	1020	(6.8)	4.8 (0.0/12.4)	0.0 (0.0/0.3)	0.0 (0.0/1.3)
Curculionidae	857	(5.7)	7.9 (0.9/16.5)	5.6 (1.6/24.0)	20.5 (6.1/29.6)
Corylophidae	625	(4.1)	3.4 (0.3/10.4)	3.7 (1.0/20.8)	6.8 (0.0/22.1)
Elateridae	577	(3.8)	4.1 (1.0/6.3)	1.0 (0.0/2.0)	1.8 (0.0/3.7)
Latridiidae	569	(3.8)	0.2 (0.0/24.0)	0.0 (0.0/4.3)	1.8 (0.0/20.5)
Coccinellidae	490	(3.2)	2.8 (1.6/5.5)	8.8 (0.0/11.7)	3.9 (1.5/9.1)
Scarabaeidae	203	(1.3)	1.3 (0.3/4.0)	2.7 (0.5/8.7)	1.5 (0.0/11.9)
Tenebrionidae	202	(1.3)	0.7 (0.4/6.2)	2.9 (0.0/4.2)	0.3 (0.0/6.8)
Staphylinidae	165	(1.1)	0.7 (0.2/4.0)	3.9 (1.1/6.7)	3.8 (2.4/11.7)
Alleculidae	102	(0.7)	0.5 (0.0/0.8)	0.6 (0.0/2.3)	1.8 (0.0/7.8)
Cybocephalidae	95	(0.6)	0.6 (0.1/3.1)	0.0 (0.0/1.4)	5.2 (0.0/18.5)
Cleridae	82	(0.5)	0.5 (0.1/1.0)	2.1 (0.6/7.2)	0.0 (0.0/1.4)
Lophocateridae	59	(0.4)	0.0 (0.0/0.2)	0.1 (0.0/1.4)	5.2 (0.0/18.0)
Silvanidae	48	(0.3)	0.1 (0.0/0.6)	0.0 (0.0/0.0)	1.5 (0.0/6.1)
Colydiidae	12	(0.1)	0.0 (0.0/0.1)	0.0 (0.0/0.0)	0.6 (0.0/9.1)

Many beetle species showed an aggregated distribution (Figure V.3), that is, they were restricted to particular tree individuals while being absent from others, or they occurred in very different densities on individual trees. Taking into account all beetle species that could be used for calculation of I_D values, 74.1 % of beetles were aggregated on individual *Anogeissus* trees, 35.1 % were aggregated on individual *Burkea* trees, and 60.5 % were aggregated on individual *Crossopteryx* trees. When I_D values were calculated over all 19 trees, 72.3 % of beetles turned out to be aggregated (Figure V.3d). Almost all ant species showed an aggregated distribution. When all ant species were considered, the proportion of aggregated ant species was lowest for assemblages on *Burkea* trees (66.6 % for *Burkea*, 95 % for *Anogeissus*, and 100 % for *Crossopteryx* versus 93.8 % for the all-tree comparison; Figure V.3) as was the case for the beetles (see above). Computation of Green's index confirmed these findings. For both, beetles and ants, Green's index varied significantly between tree species, with the lowest degree of clumping on *Burkea* trees: median Green's index for beetles: all trees, 0.30, *Anogeissus*, 0.35, *Burkea*, 0.12, *Crossopteryx*, 0.26 (Kruskal-Wallis test: $H = 30.56$, $p < 0.0001$ and for ants: all trees, 0.52, *Anogeissus*, 0.53, *Burkea*, 0.31, *Crossopteryx*, 0.68 (one-way ANOVA, $F_{3,78} = 3.59$, $p < 0.05$).

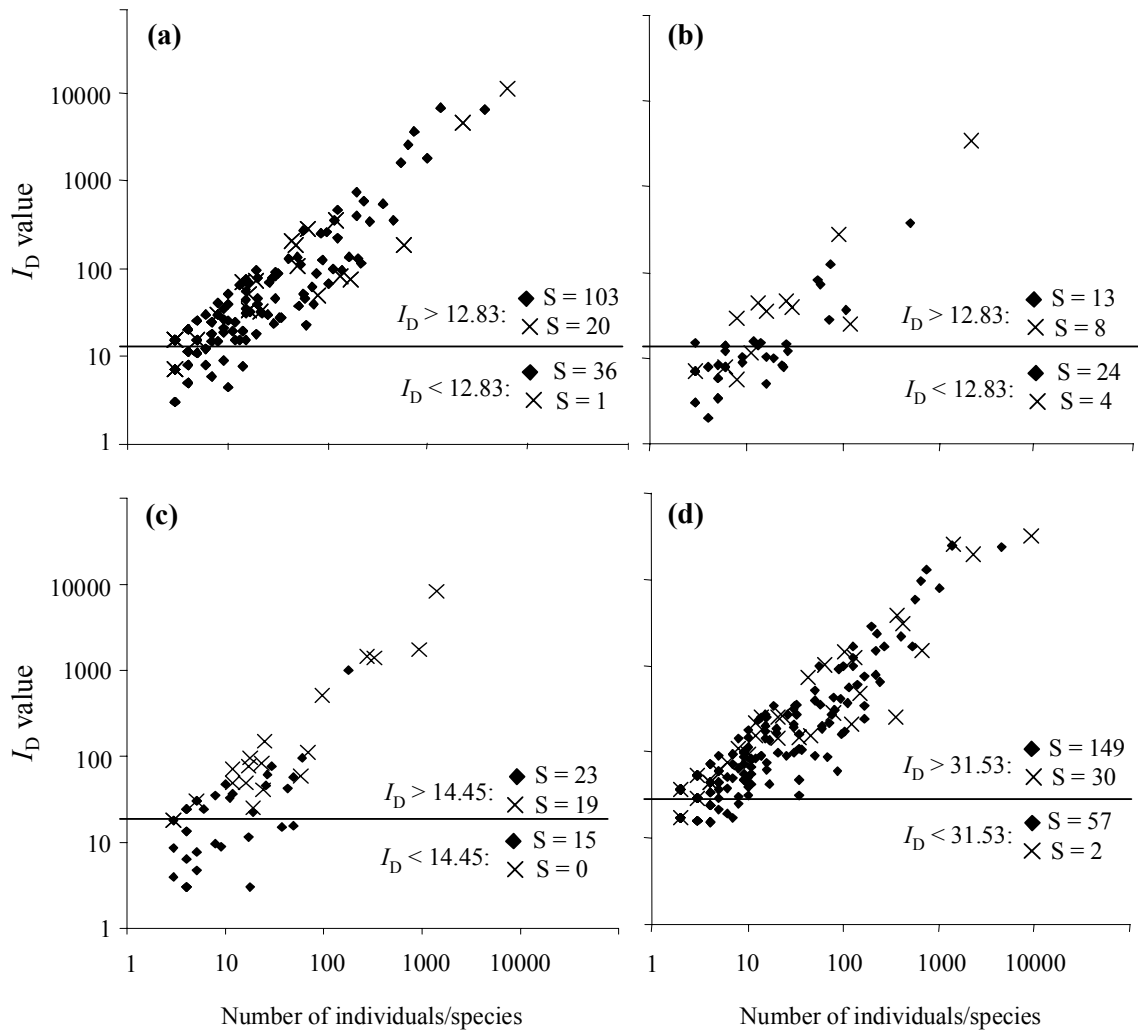


Figure V.3 Tendency of beetle (♦) and ant (X) species to occur aggregated on individual trees, indicated by I_D values greater than the chi-square statistic with sample size (v) – 1 degrees of freedom. Distribution of I_D values is given for *Anogeissus* (a; $v = 6$), *Burkea* (b; $v = 6$), *Crossopteryx* (c; $v = 7$), and for all trees combined (d; $v = 19$). I_D values were not calculated when fewer than three individuals were encountered for a-c, and when fewer than two individuals were encountered for d. S is the number of morphospecies showing an aggregated or a random distribution among trees (aggregated: above horizontal line separating I_D values greater or smaller than the critical chi-square statistic; random: below horizontal line).

Characteristics of resampled arthropod assemblages on *Anogeissus*. Beetle, and to a lesser extent ant, assemblages have turned out to be remarkably different among individual conspecific trees that were fogged in the same period. Resampling the assemblages of the same trees (*Anogeissus*) at 2 months and at 1 year later indicated a high congruence of assemblage composition with the results of the first fogging event. The data from the subsequent fogging in 1999 were quantified at the ordinal level. Comparing the first and the second fog, densities of many arthropod orders were rather similar for individual trees, or quantitative changes occurred while the relative position remained constant (Table V.4). Densities and numbers per tray area or crown volume of Coleoptera, Formicidae, Hymenoptera (excluding Formicidae), Thysanoptera, and Orthoptera were significantly correlated for the first and the second fog. For Araneae and Lepidoptera larvae, correlation coefficients obtained for densities and numbers per tray area or crown volume were considerably different and only the latter

were correlated. No significant correlation between the first and the second fogging event could be detected for Heteroptera, Diptera, Homoptera, Blattodea, Psocoptera and Thysanura. Though not significant, the negative correlation coefficients for Mantodea indicated a marked change of Mantodea densities on individual trees.

Table V.4 Correlation coefficients for comparisons of arthropod densities on individual trees between different fogging events at the ordinal level.

Taxa	Correlation coefficient for F1 versus F2 (N=6)		Correlation coefficient for F1 versus F3 (N=5)	
	Density per tray area (m ²)	Density per crown volume (m ³)	Density per tray area (m ²)	Density per crown volume (m ³)
Coleoptera	0.94 **	0.94 **	0.9 *	0.9 *
Formicidae	0.89 *	0.94 **	0.7	0.5
Araneae	0.77	0.94 **	0.3	0.6
Heteroptera	0.54	0.54	0.7	0.7
Diptera	0.31	-0.35	0.1	-0.2
Hymenoptera ^a	0.94 **	0.94 **	0.9 *	0.9 *
Homoptera	0.64	0.54	0.87	0.9 *
Blattodea	0.6	0.6	0.9 *	0.9*
Lepidoptera (larvae)	0.77	0.89 *	0.3	0.5
Neuroptera	0.66	0.77	0.2	0.2
Thysanoptera	0.93 **	0.99 ***	0.6	0.9 *
Orthoptera	0.94 **	0.99 ***	0.8	0.56
Mantodea	-0.77	-0.77	-0.5	-0.5
Psocoptera	0.31	0.09	0.11	0.11
Thysanura	0.59	0.59	0.82	0.97 **

F1: first fogging event June/July 1999; F2: second fogging event August 1999; F3: third fogging event June/July 2000; N: number of compared trees

^a Excluding Formicidae

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Comparisons of samples obtained in 1999 and 2000 indicated that the composition of assemblages on individual trees was stable over time. At both high and low taxonomic levels (arthropod orders, beetle families, beetle species and *Camponotus* spp.) the assemblage structure of trees refogged in 2000 was most strongly correlated with the structure of the same tree in the previous year (Table V.5). Permutation of correlation matrices revealed that this finding was significant for arthropod orders, beetle families and beetle species. Out of 120 possible combinations, mean correlation coefficients between assemblages of arthropod orders and beetle species on the same trees were higher than all other possible combinations ($p < 0.01$). For beetle families, only one other combination of correlation coefficients was higher than the correlation coefficients obtained for the same trees ($p < 0.01$). In contrast, the distribution of *Camponotus* spp. was less predictable on the basis of the assemblage structure in the previous year: Twenty-two combinations calculated by permutation of the correlation matrix were higher than the correlation coefficients found for the comparison of the same trees ($p = 0.18$).

These results can be evaluated more precisely when considering the examined groups separately. At the ordinal level, a very high degree of constancy in specimen number of the respective orders was observed between years (median abundance 1999 versus 2000: $r_s = 0.9$, $N = 14$, $p < 0.0001$).

Arthropod densities on individual trees were significantly correlated for Coleoptera, Hymenoptera (excluding Formicidae), Homoptera, Blattodea, Thysanoptera and Thysanura (Table V.4). For Thysanoptera and Thysanura, correlation coefficients of densities on a square metre of tray and cubic metre of crown volume were considerably different and only r_s values on the former basis were correlated. Lowest r_s values between the 1999 and the 2000 foggings could be detected for Diptera, Psocoptera, Neuroptera, Lepidoptera larvae and Araneae. This result corresponds with the findings of the within-year comparisons for Diptera, Psocoptera and Neuroptera. In contrast, densities of Araneae and Lepidoptera larvae were significantly correlated for tree volume-related values in 1999.

The species composition of ant assemblages was relatively similar for conspecific and heterospecific tree individuals (Figure V.1). Ant assemblages were dominated by *Crematogaster* and by *Camponotus* spp. in 1999 and in 2000. The composition of the *Camponotus* fauna was less distinct than that of the beetle fauna for individual trees. Although the composition of ant assemblages was significantly correlated over years for four out of five trees, the examination of median correlation coefficients supports the results of the permutation comparisons: similarities between the assemblages of the same trees were not higher than comparisons of different trees (Table V.5).

The ranking of beetle families according to abundance on single trees was very stable for most of the dominant beetle families. The strongest correlation ($r_s \geq 0.9$, $p < 0.05$) could be found for Anthicidae, Coccinellidae, Corylophidae and Tenebrionidae. No correlation existed for Elateridae ($r_s = 0.5$, $p = 0.4$), Scarabaeidae ($r_s = 0.3$, $p = 0.6$) and Carabidae ($r_s = 0.1$, $p = 0.9$), which were, however, not included in the previous analysis as they were never abundant. Comparisons at the level of 'abundant' beetle species revealed an even higher relationship between assemblages of the same tree during consecutive years. For four trees, the abundance of these common beetles, belonging to nine different beetle families, was most strongly correlated with their abundance in the previous year. This resulted in beetle assemblages on the individual trees showing a high degree of constancy over time. Principal component analysis supported the results of the correlation analyses. Ordination position of beetle assemblages of resampled *Anogeissus* trees was very similar for four tree individuals (Figure V.4a). In addition to the consistent composition of beetle assemblages on individual trees, ordination results indicated a noticeable influence of tree species on assemblage composition. In particular assemblages on *Crossopteryx* were clearly separated from those on *Anogeissus* and *Burkea*. *Burkea* assemblages were not completely separated from those on *Anogeissus* but intraspecific groupings were, on average, much closer than interspecific groupings (Figure V.4a). The correlation analyses (Table V.5) showed that *Camponotus* assemblages were not characteristic for individual trees (Figure V.4b). However, there appeared to exist an influence of the sampling date as intrayear samples were more closely grouped than interyear samples. In addition, *Camponotus* assemblages seemed to differ least among *Anogeissus* and *Burkea* trees while *Crossopteryx* assemblages were more variable.

Table V.5 Correlation coefficients for comparisons between relative arthropod abundance of the same and different *Anogeissus* trees in 1999 and 2000 at different taxonomic levels.

Tree code	<i>An.1_00</i>	<i>An.2_00</i>	<i>An.4_00</i>	<i>An.5_00</i>	<i>An.6_00</i>	Median correlation coefficient (a.v.) other trees
Arthropod orders (N=14)						
<i>An.1_99</i>	^a0.79***	0.77	0.81	0.69	0.57	0.73**
<i>An.2_99</i>	0.69	0.72**	0.71	0.56	0.48	0.62*
<i>An.4_99</i>	0.85	0.94	0.94***	0.84	0.75	0.84***
<i>An.5_99</i>	0.55	0.83	0.73	0.81***	0.79	0.76**
<i>An.6_99</i>	0.74	0.88	0.90	0.82	0.86***	0.85***
Beetle families (N=9)						
<i>An.1_99</i>	0.79*	0.70	0.73	-0.13	-0.06	0.42 ^c
<i>An.2_99</i>	0.38	0.62^c	0.30	-0.14	-0.12	0.22 ^c
<i>An.4_99</i>	0.76	0.93	0.83**	-0.08	-0.13	0.45 ^c
<i>An.5_99</i>	-0.18	-0.02	0.15	0.80**	0.88	0.17 ^c
<i>An.6_99</i>	-0.11	0.13	-0.07	0.83	0.90***	0.12 ^c
Beetle species^b (N=29)						
<i>An.1_99</i>	0.53 **	0.37	0.44	0.09	-0.30	0.34 ^c
<i>An.2_99</i>	-0.02	0.29^c	0.02	-0.09	-0.13	0.06 ^c
<i>An.4_99</i>	-0.05	0.53	0.39 *	0.12	-0.10	0.11 ^c
<i>An.5_99</i>	-0.09	0.36	0.32	0.77 ***	0.61	0.34 ^c
<i>An.6_99</i>	-0.27	0.04	-0.10	0.36	0.85 ***	0.19 ^c
<i>Camponotus</i> species (N=10)						
<i>An.1_99</i>	0.48^c	0.67	0.74	0.65	0.75	0.70*
<i>An.2_99</i>	0.54	0.68*	0.80	0.69	0.74	0.71*
<i>An.4_99</i>	0.80	0.72	0.92***	0.70	0.75	0.74*
<i>An.5_99</i>	0.66	0.77	0.76	0.79**	0.69	0.73*
<i>An.6_99</i>	0.57	0.88	0.85	0.60	0.94***	0.73*

N: number compared, a.v.: absolute value, *An.1-An.6*: *Anogeissus* tree 1-6, *_99*: sampled in 1999, *_00*: sampled in 2000

^a Values for comparison of the same tree are bold

^b At least 12 individuals found in one year

^c Not significant

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

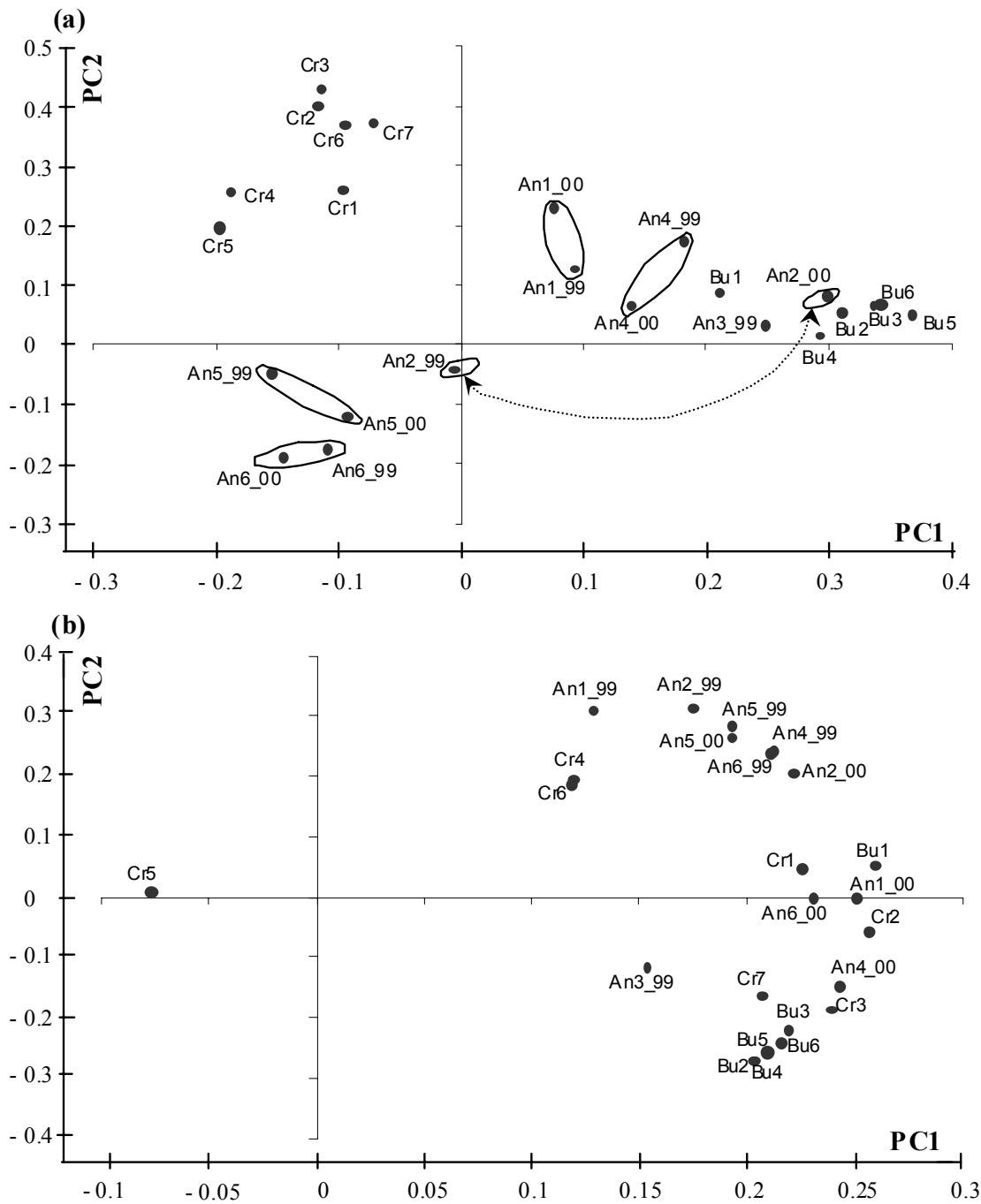


Figure V.4 Principal component (PC) analysis of relative abundance of 'abundant' beetles (a) and *Camponotus* species (b) following Table V.5. In addition to the inter-year comparison of *Anogeissus* (An), data of *Burkea* (Bu) and *Crossopteryx* (Cr) are included. The ordination position of individual *Anogeissus* trees in 1999 and 2000 is marked by ellipsoid circles for beetles. For *Camponotus* ants, communities of the same trees were not more similar than communities of different trees; they are, therefore, not marked.

V.4 Discussion

The objective of this study was to describe and compare arthropod assemblages of savannah trees and to understand aspects of the organisation of these assemblages. As several individuals of each of three different tree species were included in this analysis, the influence of traits specific to tree species as well as to tree individuals on assemblages of tree-associated arthropod assemblages can be discussed in more detail. Both groups of factors, interspecifically and intraspecifically variable tree characteristics, appeared to be of importance for the investigated arthropod assemblages. However, detailed consideration of both is beyond the scope of this contribution. Accordingly, we focus on the arthropod assemblages of individual trees, as understanding at this level of organisation can form the basis for further far-reaching comparisons of, for example, the effect of tree species or region. By so doing, we stress the potential importance of small scale variation as seen in the characteristics of individual trees. This is often indirectly reported (via the description of arthropod distribution, see below) but nonetheless is rarely accounted for directly (but see, for example, Crawley and Akhteruzzaman 1988, Winchester 1997). A more detailed analysis of interspecific differences will be presented elsewhere, taking into account the influence of guild affiliation and single species distributions (Stork 1987a, Kitching and Zalucki 1996, Basset and Novotny 1999, Wagner 2000). In order to understand the influence of individual tree characteristics, the results have been analysed with respect to the hypothesis that conspecific trees provide similar habitats and will, therefore, be inhabited by similar arthropod assemblages (Southwood and Kennedy 1983). The relative importance of stochastic colonisation events and / or deterministic tree characteristics in the determination of assemblage structure in individual trees is also discussed (Wiens 1984, Linsenmair 1990, Adis et al. 1998).

For all three tree species investigated, we have demonstrated that the composition of arthropod assemblages can differ substantially among syntopically growing individuals flogged within the same period of time. Such variation in arthropod density or diversity on individual conspecific trees seems to be a rather typical finding as it is in agreement with most studies providing arthropod assemblage data of individual trees (for example, Erwin and Scott 1980, Stork 1991, Allison et al. 1993, Floren and Linsenmair 1997, Krüger and McGavin 1997, Mawdsley and Stork 1997, Winchester 1997, Floren and Linsenmair 1998, Azarbayjani et al. 1999, Basset and Novotny 1999, Majer et al. 2000, Wagner 2000). These intraspecific differences engender variation in local arthropod density and diversity in canopy assemblages of temperate, subtropical and tropical trees. Only diversity measures obtained for beetle and ant assemblages of tropical rainforests were in general higher than the highest values of individual *Anogeissus* or *Crossopteryx* trees. This points, as do other studies, to interesting and widely discussed differences of arthropod assemblages of (pristine) tropical lowland rainforests on the one hand and tropical savannahs, dry forests, montane forests and disturbed rainforests on the other hand. Combining the result of variable assemblage composition with data obtained in other comparable studies, the hypothesis that conspecific trees can be regarded as similar habitats should be rejected in its simple form. It may apply when the comparison of distantly related tree species is the objective. But even in this case, individual variation seems worth considering not just as a sampling artefact but also as a fundamental intraspecific property of tree species. Rejecting the hypothesis that assemblages on conspecific trees are *per se* similar, potential reasons for individual variation need to be evaluated. As this and other studies demonstrate, variation is not restricted to a few particular arthropod taxa or functional groups, although herbivores appear to be generally more influenced than predacious groups (Stork 1987b). Differences were exhibited, for example, by beetles in general (Stork 1991, Allison et al. 1993, Floren and Linsenmair 1997), herbivorous beetles (Floren and Linsenmair 1998), herbivorous insects in general (Stork 1987b, Basset 1991, Basset and Novotny

1999), granivorous beetles (Miller 1996), spiders (Stork 1991, Floren and Linsenmair 1997, Azarbayjani et al. 1999), dipterans (Floren and Linsenmair 1997, Azarbayjani et al. 1999) and ants (Stork 1991, Adis et al. 1998). However, no differences were found for fungal-feeders, predators, tourists, wood-eaters, mesophyll feeders, Corylophidae, and Lepidoptera by Basset (1992). Supposing that the reported variability is not an artefact of small, unrepresentative samples, it suggests that different, intraspecific variable tree characteristics or stochastic colonisation pathways (Wiens 1984, Linsenmair 1990, Adis et al. 1998) are influencing assemblage structure.

The distribution of insect herbivores has been related to several features of their host-plants. For example, leaf nutrients, defence parameters and the proportion of young leaves have been shown to play an important role in determining food choice, abundance and distribution of herbivores (Strong et al. 1984b, Basset 1991). As these characteristics can vary among conspecific plants (Crawley and Akhteruzzaman 1988, Macedo and Langenheim 1989, Edwards et al. 1993, Barnola et al. 1994, Butcher et al. 1994, Hemming and Lindroth 1995, Mapongmetsem et al. 1998, Staudt et al. 2001, Stork et al. 2001), the high potential of individual tree characteristics to influence the distribution of herbivorous insects is clear. Aside from plant traits, arthropod behaviour probably affects arthropod distribution; for example, when movement is more likely towards plants occupied by conspecifics (Turchin 1987, Bach and Carr 1990, Morris et al. 1992, Loughrin et al. 1995). The same can apply when considering fungus-feeders or saprophages, as there is much potential variation in fungus load and dead wood content across individual trees (Bull et al. 1992, Clinton et al. 1993, Lewis 1997). Predatory arthropods may be tracking the (variable) abundance of their prey (Gagné and Martin 1968). They may also be influenced by the availability of enemy-free space or suitable sites for web construction (Halaj et al. 2000), both parameters being potentially variable among conspecific plants.

Comparisons of assemblages resampled from the same tree individuals were analysed to distinguish between individual tree characteristics and random colonisation. The results of this study suggest that the distributions of Coleoptera, Hymenoptera (excluding Formicidae) and Thysanoptera were fundamentally influenced by tree characteristics, as the highest congruence was found consistently among assemblages from the same tree individual. Other groups such as (i) Formicidae, Araneae, and Orthoptera and (ii) Homoptera, Blattodea, and Thysanura were affected, in addition, by temporal effects. Members of the first group appeared to be particularly influenced by interyear parameters, probably linked to the recolonisation of trees following the dry season. The distribution of members of the second group, however, seemed to be rather dependent on the season, showing no correlation within the same year but significant correlation between different years. For Heteroptera, Diptera, Neuroptera, Mantodea and Psocoptera, no relationship to individual trees was detectable, indicating that the distribution of these groups might be less tightly linked to individually variable tree characteristics than was the case for the other groups.

The interpretation that the distribution of many groups of arthropods is influenced by individual tree characteristics is in accordance with most studies that present resampling data, although these investigations mainly stress the random character of assemblage reorganisation (Floren and Linsenmair 1997, Adis et al. 1998, Floren and Linsenmair 1998, Azarbayjani et al. 1999). The apparent contradictions in the interpretation of results of resampling studies may point to general differences in factors structuring assemblages between savannahs and pristine rainforests (as is discussed for secondary and primary forests by Floren and Linsenmair (2000)). They may also be caused by methodological difficulties in assigning arthropod assemblages to individual trees in forests (see Erwin (1989) for 'horizontal highways'). However, these contradictions may be solved by considering different arthropod groups separately and by avoiding generalisations. (Azarbayjani et al. 1999) studied small trees that could be sampled representatively. These authors found a high turnover between original and recolonizing assemblages of the same tree individuals. Therefore, they concluded that the suites of species on these trees were not a consequence of individually variable tree

characteristics. Their interpretation appears meaningful in the framework of their data and it is, so far, in accordance with our data. Like Azarbayjani et al. (1999), we found no correlation - and, therefore, no detectable influence of individual tree characteristics - for the distribution of dipterans between different sampling events. The same can be stated for Araneae, the second taxa used in the analysis of Azarbayjani et al. (1999). Both studies indicate that Diptera and Araneae are generally weakly related to individual trees, being rather 'tourists' (Moran and Southwood 1982, West 1986, Stork 1987b, Didham 1997) or beneficiaries of structural or microclimatic properties provided by trees. However, having no close relationship to trees, these groups are not well suited for the derivation of general statements on the organisation of arboreal arthropod assemblages. They should rather be considered examples for loosely connected assemblage components and should not be mixed up with other groups that are more closely linked to the tree. Floren and Linsenmair (1997, 1998) studied understory trees of a pristine rainforest. They found a high congruence of re-established and original assemblages at the ordinal level but considerable differences at the level of ant and beetle species; they concluded that assemblages were mainly structured by stochastic factors and not by tree characteristics. Their findings for ants are in agreement with data of an other refogging study (Adis et al. 1998) and also with our study (ant abundances were not correlated with individual trees between different years and *Camponotus* assemblages showed the lowest congruence in permutation tests). Taken together, these investigations suggest that the composition of ant assemblages of trees may change rapidly in response to disturbances and stochastic recolonisation processes, no matter whether the majority of ants nest in trees (in rainforests) or soil (in savannahs). The general statement that beetle assemblages are randomly organised, however, seems not to hold true for savannah trees, where many families and species of beetles appeared to be closely linked to individual trees. The proof of individually characteristic assemblages requires a certain minimum number of individuals per species. Since densities of single arthropod species are generally very low on rainforest trees (Erwin and Scott 1980, Morse et al. 1988, Allison et al. 1993, Floren and Linsenmair 1997, Wagner 1997), it may be unreasonable to expect to detect characteristic assemblages with any reasonable sampling effort.

We conclude that individual tree characteristics are probably of greater importance in determining the structure and diversity of tree-associated arthropod assemblages than is reflected in current discussions on this topic. Whether or not the influence applies to all ecosystems and can also be demonstrated for forest trees within a closed canopy will need to be evaluated in further studies.

Acknowledgements. We thank Frank-Thorsten Krell, Thomas Wagner, and Claus Wurst for their help in beetle identification and Michael Mazat for his help in ant sorting. Thomas Hovestadt and Martin Hinsch provided theoretical background and programming experience for performing permutation tests. Permission to perform the research was granted by the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, Republic of Côte d'Ivoire. An access permit to Comoé National Park was issued by the Ministère de la Construction et de l'Environnement. The manuscript benefited from comments by Yves Basset and two anonymous referees. The study was partly supported by scholarships of the DAAD (German Academic Exchange Service, No. 332 4 04 101), and by the DFG Graduiertenkolleg 200 to K.M., and by BIOTA (Biodiversity Monitoring Transect Analysis in Africa), German Federal Ministry of Education and Research (BMBF), subproject W06, 01LC0017.

VI. Neighbouring Plants Host Different Ants: Analysis of the Ant Mosaic on a Myrmecophilic Tree

Abstract - The savannah tree *Pseudocedrela kotschyi* bears extrafloral nectaries (EFNs) and is continuously visited by foragers of many ground nesting ant species. A clear preference for certain tree individuals by colonies of different ant species could be observed, without nest site proximity being the decisive variable. The species-specific foraging patterns markedly changed during the 24 h of the day, but were highly persistent over long periods at the same day-time. Thus very different ant communities were found on closely neighbouring trees exposed to most similar environmental conditions, resulting in a mosaic-like distribution of ant species in space and in time. In order to elucidate the structural differences of neighbouring ant communities, the potential influence of tree size parameters and interspecific interactions was analysed. No significant relationship between tree size and the number of visiting ant species could be detected. The abundance of ants per plant and the distribution patterns of some ant species were, however, related to tree size parameters. Qualitative association analysis, quantitative analysis of interspecific covariation, and species co-occurrence analysis using null models suggested that competitive interactions were playing a major role in shaping the individual ant communities. All analyses revealed no positive, but many negative, relationships between different dominant ant species potentially sharing the same foraging area. The study indicates that competitive monopolisation of EFNs by dominant ants can create a small scale mosaic of different ant communities, for example on neighbouring plants. While species richness of individual communities is restricted by resource availability and is therefore low, total species number of the full-system can be much higher. It is concluded that competition for predictable resources of limited value can facilitate co-existence of different island-like ant communities and enhance diversity on the level of the entire (archipelago) system.

Key words: Community organisation, competition, interspecific association and covariation, EFNs, null models

VI.1 Introduction

Ants are a dominant taxon in most terrestrial ecosystems, directly and indirectly influencing the welfare and distribution of other organisms (Hölldobler and Wilson 1990). The influence that ants exert on their environment is dependent on the properties and abundances of the ant species involved. Ant species richness generally decreases from lower to higher latitudes and from wet to dry environments (Bentley 1977, Lévieux 1983b, Majer et al. 2001). Nevertheless, high abundances of ants may be attained under a wide variety of environmental conditions. This holds true for such different biomes as high latitude forests, tropical rainforests, temperate grass lands or tropical savannahs (Brian 1965, Fittkau and Klinge 1973, Lévieux 1983b, Stork 1988).

Ant communities (see Lawton 2000 for community definition) of West African savannahs are characterised by both, high species richness and considerable ant abundance (Lévieux 1983b). Most species are ground-nesting and many possess large foraging areas at the ground level. Additionally, a considerable portion of the ant fauna is able to expand their foraging space onto the vegetation layer (Lévieux 1983b, Mody et al. 2003). Since food resources on the soil surface are unpredictably distributed, and thus difficult to defend, foraging areas of different colonies and species generally overlap to a large extent, and patterns of foraging trails are constantly changing (Jackson 1984, Majer 1993; K. Mody, pers. obs.). As a consequence, the same area is simultaneously foraged by a diverse

ant community, even though competition occurs (Carroll and Janzen 1973, Levings and Franks 1982, Jackson 1984).

In addition to consuming unpredictable food items, such as live prey and animal derivatives, ants exploit food resources which are more stable and predictable, especially those provided by plants. Plants offer comparably stable and predictable food resources via exudates, mainly in the form of homopteran honeydew and/or extrafloral nectar (Buckley 1982, Beattie 1985, Koptur 1992). Extrafloral nectaries (EFNs) are known in more than 90 plant families (Koptur 1992). Their secretions are attractive to ants and wasps, which defend the nectary-bearing plant parts against other insects and thereby reduce herbivory (e.g. Bentley 1977, O'Dowd 1979, Beattie 1985, Barton 1986, Oliveira et al. 1987, Fiala et al. 1994, Bronstein 1998, Heil et al. 2001b). Knowledge on ant-plant interactions mediated by EFNs is scarce for West African savannahs (nectaries are not even mentioned by Lévieux (1983b) in reviews on distribution and feeding strategies of African ants, but see Lévieux 1977). There are, however, studies from comparable cerrado vegetation in the Neotropics (Oliveira and Brandao 1991), and own studies and preliminary observations (Mody and Linsenmair 2003, Mody et al., unpublished) suggest that such interactions may be important in West African savannahs as well.

Since EFNs are a valuable and defensible food resource, they may stimulate monopolisation by ants, possibly leading to areas of non-overlapping ant distributions on either a particular host plant or on a group of neighbouring plants. Such a patchwork of non-overlapping distributions of certain abundant, dominant ant species – usually associated with specific subdominant ant species – is known as ‘ant mosaic’ (Strickland 1952, Room 1971, Majer 1972, Leston 1973, Taylor 1977). Ant mosaics are reported from tropical regions around the world, mainly from plantations, but they may occur in certain primary forests as well (Majer 1993, Blüthgen et al. 2000); but see Floren and Linsenmair (2000). They may have strong effects on the plants and on other arthropods co-occurring with the ants (Wilson 1958, Majer 1976, Gilbert 1980, Majer 1993), and different ant species have been found to affect their biotic environment in differing ways (Koptur 1984, Rico-Gray and Thien 1989, Dejean et al. 2000b, Di Giusto et al. 2001). The ant mosaics that have been described to date are dominated by tree nesting ant species which are permanently present in the tree crowns. Since most savannah ants are ground nesting, they are not directly linked to certain plants. This may impede the formation of ant-mosaics.

Here we describe the activity and distribution patterns of West African, EFN-visiting savannah ants and relate them to habitat (tree size) and community (interspecific interactions) parameters in an attempt to explain the observed spatio-temporal structures. We focus on four questions concerning ant communities on the locally abundant EFN-bearing savannah tree *Pseudocedrela kotschy* (Meliaceae), namely: (1) Are EFNs of *P. kotschy* regularly used by ants? (2) Are patterns of nectary visitation similar on neighbouring plants and at different times of the day? (3) Is the composition of ant communities unpredictable or is it stable and predictable in space and time, and hence mosaic-like? and (4) Is the composition of ant communities foraging at EFNs dependent on plant size and on interactions between co-occurring ant species?

VI.2 Material and Methods

Study site and tree species. Field work was carried out in Comoé National Park from April to June 1999 and from April to May 2001 (early rainy season). Comoé National Park is located in the north-east of the Republic of Côte d'Ivoire, and covers 11,500 km² of Guinea- and Sudan-zone savannah. It supports a wide variety of vegetation types, including gallery forest, island forest, savannah forest, shrub and tree savannah, grass savannah and Bowal areas which are almost free of vegetation. A more detailed description of Comoé National Park is provided elsewhere (Poilecot 1991, Porembski 1991,

Rödel 2000). The study area was situated within the Guinea-savannah in the southern part of the Park (08°44'N, 003°49'W, c. 215 m).

The host plant species that we studied, *Pseudocedrela kotschy* (Schweinf.) Harms (Meliaceae), is widespread in West African savannahs (Aubréville 1950, Steentoft 1988), and it is locally abundant in the study area (Hovestadt 1997). Below, *Pseudocedrela kotschy* is designated by its generic name. *Pseudocedrela* is a medium-sized (4-5 m, maximally 12 m), deciduous savannah tree. It is able to spread into eroded and Bowal areas by root suckers, thereby forming *Pseudocedrela*-dominated stands of woody vegetation. Extrafloral nectar is mainly secreted along the nerves of the impari- or paripinnate leaves (K. Mody, pers. obs.).

The study trees were characterised by several parameters. Plant size was determined as plant height, crown height, crown width (maximum diameter), crown depth (maximum diameter perpendicular to crown width), and trunk girth (at 20 cm above ground). Since all size parameters were highly correlated (r_s : 0.47 - 0.75, mean \pm SD: 0.59 \pm 0.11), principal components analysis (PCA) was performed and one principal component (PC1), explaining 70.0 % of the total variance, was extracted. Height of studied trees ranged between 76 cm and 346 cm (mean \pm SD: 176 \pm 52 cm; N = 131). All of the trees were of a size that enabled them to be completely checked for foraging ants, although a ladder was used for the tallest trees.

Spatial information was obtained by recording the exact position of each plant with a portable Differential GPS (Leica SR530, Leica Geosystems AG, Switzerland), providing exact information on vertical and horizontal position with a precision of 1-5 cm. Study trees grew in three almost monospecific stands (study area (SA) -I, -II, -III). The trees within each study area were randomly chosen, except for the required condition that the selected trees should have two other trees in close proximity, and which should be similar in size to allow manipulation studies (not reported here). These two neighbouring trees were also included in the study. The closest distance between SA-I and SA-II was 270 m, between SA-II and SA-III was 250 m, and between SA-I and SA-III was 555 m. The distances between trees of the same study area ranged between 0.9 m and 33 m for SA-I (mean distance 14.9 m), 0.9 m and 57 m for SA-II (mean distance 23.9 m), and between 0.4 m and 67 m for SA-III (mean distance 29.1 m). All trees were considered to grow under similar environmental conditions: they grew on the same Bowal plain, on the same soils, and at very similar heights above sea level (mean \pm SD: SA-I: 212.5 \pm 0.4, N = 42; SA-II: 213.3 \pm 0.3, N = 45; SA-III: 213.6 \pm 0.2, N = 45). No tree was shaded by other trees, and no variations were detectable in general vegetation structure or composition in the immediate surroundings of the study trees.

Ant sampling. Voucher specimens were collected of each ant species foraging on the study trees. They were sorted to genera using the keys provided by Bolton (1994) and have been assigned provisional species designations. In the following, these provisional designations will be taken as species. The voucher specimens were deposited at the entomological collection of the Department of Animal Ecology and Tropical Biology, University of Würzburg, Germany, and will be transferred to public museums after completion of analyses. Ants were counted on every leaf of all study trees at different day and night times. Censuses were divided into 'morning census' (between 9:30 and 11:30 hours, local time), 'afternoon census' (between 15:30 and 17:30 hours), and 'night census' (between 22:00 and 02:00 hours). The 'dominance' status was assigned to ant species according to their abundance (there should be at least six individuals simultaneously on some study trees) and regularity of occurrence (on at least 18 trees) on the studied trees. Following these criteria, nine ant species, seven of the genus *Camponotus*, one of the genus *Crematogaster*, and one of the genus *Polyrhachis* were classified as dominant species (DS). In addition, the Index of Dominance (ID) was calculated to examine the validity of the classification of DS. ID was calculated following Majer et al. (1994) as:

$ID = (N-P) / (N+P)$, where N is the number of significant ($p < 0.05$) negative associations and P is the number of significant positive associations between ant species, with dominant ant species being such species with $ID > 0.8$ (for further details on association analysis see below). The computation of ID values supported the classification of dominant species, with ID values of 1 being obtained for all nine species. A rough estimate of distances regularly covered by foragers of different ant species was obtained by following ant individuals leaving *Pseudocedrela* host plants to their nests and mapping the course with a Differential GPS.

Community analysis. The ant fauna of the study trees was completely censused. Therefore species richness was chosen as the basal diversity parameter to describe the assemblages (Magurran 1988). Additionally, the estimated total species richness was obtained by applying extrapolation procedures (Colwell and Coddington 1994). Following recommendations given by Chazdon et al. (1998), Brose (2001), and Beck et al. (2002), three species richness estimators were computed using EstimateS 6.0b1 (Colwell 2000). These were the nonparametric estimators of species richness *Chao1* (abundance-based estimator of species richness, Chao 1984), *Chao2* (incidence-based estimator of species richness, Chao 1987) and *ICE*, the Incidence-based Coverage Estimator of species richness (Lee and Chao 1994).

The persistence of ant assemblage composition on individual trees was determined by analysis of species similarity (represented by the Jaccard Index JI) of ant assemblages on 48 *Pseudocedrela* trees using 1999 data. Species similarity was computed between the original assemblage (OA) and assemblages obtained in two additional ant censuses performed for each tree at the same time of the day. This provided an estimate of stability of assemblage composition at a particular time of day over several weeks. The first additional census was conducted after four days (hereafter called 'short re-census, SRC'), and the second after 10 to 30 days (hereafter called 'long re-census, LRC'). As no differences in JI were detectable between OA and both LRCs, performed 10 or 30 days after OA (Mann-Whitney U-test: $U = 226.5$, $p = 0.21$, $N = 23$ (10 days) and $N = 25$ (30 days)), all second re-censuses were pooled within one group LRC. JI was also computed between morning-, afternoon- and night-censuses of the same trees to compare assemblage composition in relation to time of day. The non-parametric Kruskal-Wallis test (Sokal and Rohlf 1995), followed by a Schaich and Hamerle multiple comparisons test (Bortz et al. 1990), was applied to compare JI values of the different censuses.

Logistic regression analysis, entering all independent variables in a single step, was performed in order to assess the influence of tree size parameters (PC1) and distribution of co-occurring ant species on the distribution of the respective dominant ant species. The distribution of co-occurring ant species was described by both, abundance and presence-absence data. Logistic regression results concerning interspecific interactions were compared to the results of interspecific association, covariation, and co-occurrence analyses (see below).

In order to assess the potential influence that interspecific interactions or overlapping habitat requirements exert on the distribution of DS, two approaches were chosen. The first approach, interspecific association analysis, expanded by interspecific covariation analysis (Ludwig and Reynolds 1988), can be considered as 'classical', as it has generally been used for the examination of ant mosaics up to date. These analyses were conservatively restricted to ant species pairs co-occurring in the same 'micro-area', thus minimising the problem of distinguishing between effects of competition and nest site position on presence of an ant species. This issue has not been previously considered in most analyses of ant mosaics. 'Micro-areas' of potential co-occurrence were defined as neighbouring trees growing at a maximum distance of 5 m to the focus-tree dominated by the particular species under consideration, or, when foraging distances were determined, as trees growing within the minimum foraging area of the respective ant species. Interspecific association describes the

affinity of two species (Ludwig and Reynolds 1988), and its calculation is based solely on the presence or absence of species in sampling units. Patterns of interspecific association may be positive, negative, or neutral, depending on whether two species select or avoid the same habitat, show some mutual attraction or repulsion, or do not interact at all. Interspecific association was tested by chi²-analysis, applying the sequential Bonferroni technique for simultaneous tests (Rice 1989). Exact *p*-values required by the sequential Bonferroni technique were calculated by logarithmic interpolation (Sachs 1997). Yates' continuity correction (e.g. Room 1971, Majer et al. 1994) was applied when the analysis turned out to be biased due to low expected frequencies (Ludwig and Reynolds 1988), but corrected values were only provided when the correction changed the outcome of the analysis.

In contrast to the qualitative analysis of interspecific association, interspecific covariation is based on quantitative species abundance data. It may have a different outcome to that from association analysis, and therefore the two terms have to be clearly distinguished from each other (Hurlbert 1969, Ludwig and Reynolds 1988). Interspecific covariation was measured by Spearman's rank correlation coupled with the sequential Bonferroni technique for simultaneous tests (Rice 1989). An independent distribution of DS on the study plants would indicate that interactions are of minor importance while significant association and covariation could point to interactions influencing the structure of the ant assemblage.

The second approach was applied to evaluate the influence interspecific interactions exert on DS distribution and was based on null model analysis (Gotelli and Graves 1996). Monte Carlo randomisations were performed to create 'pseudo communities' which could then be statistically compared with the patterns in the real data matrix using the software EcoSim (Gotelli and Entsminger 2001). This enabled us to test observed distribution data implying competitive, deterministic processes against the hypothesis of a random distribution (Floren et al. 2001). Following the procedure recently used by (Ribas and Schoereder 2002), we based the analyses of species co-occurrences on presence/absence matrices, in which columns were sites and rows were ant species. By applying the same computation settings, the obtained results could be compared to the findings of Ribas and Schoereder (2002). We computed the Stone and Roberts' (1990) C-Score co-occurrence index with the EcoSim defaults, using fixed columns and rows and 1,000 iterations. The C-Score index is negatively correlated with species co-occurrence. In a competitively structured community, the C-score should therefore be significantly higher than expected by chance. The null hypothesis is that the presence of a given ant species has no influence on the occurrence of other species (for further details see Ribas and Schoereder 2002). The analyses were run using the distribution data of the dominant species. Incorporating only these species will provide more conservative results and help to avoid confounding effects caused by rarity.

VI.3 Results

Ant distribution and community structure. In the three studied savannah areas, 23 ant species were recorded foraging on 132 *Pseudocedrela* trees. The number of ant species per area foraging on trees ranged between 12 (SA-II) and 15 (SA-I & SA-III). Extrapolation of species richness indicated that about 32 species can be expected foraging on *Pseudocedrela* in all three areas (species richness estimator \pm SD: ICE: 32.8 ± 0.01 , Chao1: 31.3 ± 17.1 , Chao2: 32.8 ± 13.2). For the single areas, expected values ranged between 13 and 23 species, with Chao2 providing the most similar values for the three areas (SA-I: ICE: 17.4 ± 0.01 , Chao1: 23.0 ± 0 , Chao2: 18.2 ± 5.3 ; SA-II: ICE: 20.2 ± 0.02 , Chao1: 13.3 ± 3.7 , Chao2: 20.0 ± 0 ; SA-III: ICE: 19.5 ± 0.01 , Chao1: 17.0 ± 0 , Chao2: 18.2 ± 5.3). Eight ant species were widely distributed and occurred in all three areas, while eight species occurred in two areas and seven species were restricted to one area. Of the 132 trees studied, all but one were

used by ants at some time of the day or night. For the separate ant counts, the percentage of trees visited by ants and the number of ants per tree varied between 90.2 % (afternoon, 1 to 37 individuals, median = 4), 92.4 % (morning, 1 to 30 individuals, median = 3), and 96.2 % (night, 1 to 40 individuals, median = 5).

The activity patterns of different ant species clearly varied with time of day. Of the 13 most commonly recorded ant species (on at least five different trees on at least seven occasions), six were exclusively or predominantly active during the day (species, % day-time recordings versus total recordings, total number of individuals recorded of respective species): *Camponotus sericeus* (100 %, 293), *C. spec.2* (100 %, 141), *C. spec.3* (95 %, 106), *C. spec.7* (100 %, 10), *C. spec.8* (100 %, 13), *Lepisiota spec.1* (100 %, 101). Three species were nocturnal: *C. spec.5* (96 %, 315), *C. spec.6* (100 %, 54), *C. spec.9* (100 %, 7). Four species were active 24h-long (% day-activity): *C. spec.1* (75 %, 220), *C. spec.4* (55 %, 591), *Crematogaster spec.1* (67 %, 439), and *Polyrhachis viscosa* (30 %, 69).

For four species, direct travel distances covered by foragers (straight line between nest and host plant) could be ascertained. These distances were (maximum distance measured, median distance, number of forager individuals investigated): *C. sericeus* (26.4m, 5.1m, 21), *C. spec.2* (66.1m, 5.5m, 11), *C. spec.1* (11.4m, 6.1m, 8), and *C. spec.4* (2.6m, 2.6m, 2).

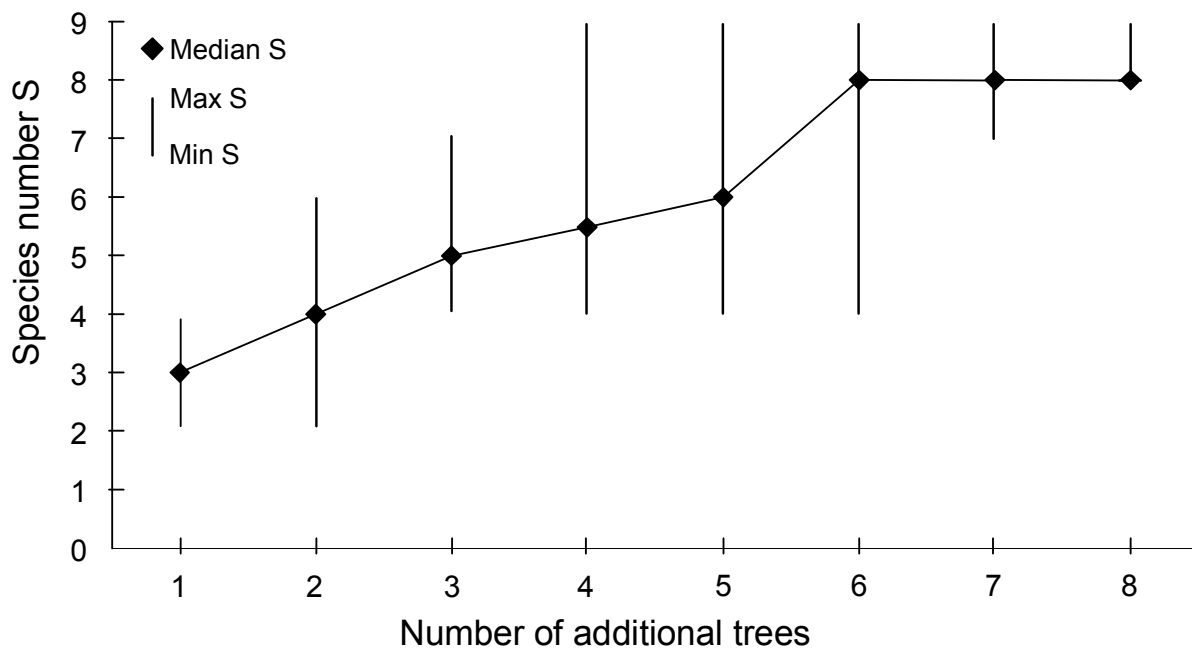


Figure VI.1 Number of trees and ant species within the 5 m radius of the study trees.

Although plants were growing close to each other, they tended to be used by a very limited set of ant species. Median species number foraging at the same time on a tree was 1 for morning and night censuses and 1.5 for the afternoon censuses ($N = 132$). The maximum species number per plant was 4 in each of the morning, afternoon, and night periods. Pooling ants recorded at different times of the day on the same plant clearly increased the species number (median: 3, maximum: 6). Ant species richness per tree was independent of the tree size parameters measured and also of the first principal component PC1 ($r_s = 0.11$, $p = 0.22$, $N = 131$, for Spearman's rank correlation between PC1 and ant species number). Ant abundance, however, was positively correlated with all single tree size parameters measured, and also with PC1 ($r_s = 0.36$, $p < 0.001$, $N = 131$, for Spearman's rank correlation between PC1 of tree size parameters and ant individual number).

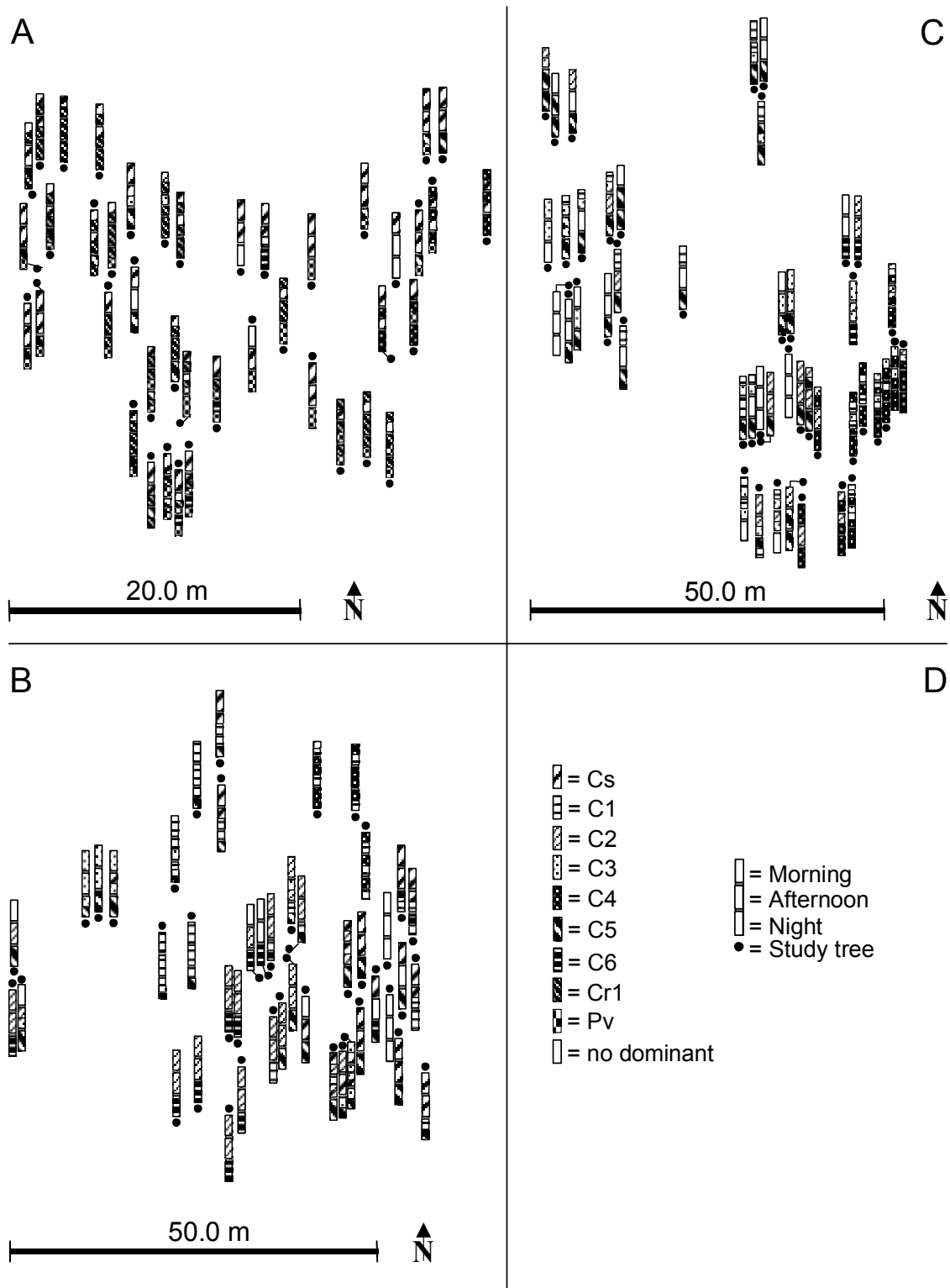


Figure VI.2 Distribution of dominant ant species in SA-I (A), -II (B), and -III (C). Differentially shaded bars describe the distribution of dominant ant species on the respective trees (D). The exact position of each study tree in the study areas is signified by ●. Cs: *Camponotus sericeus*, C1-C6: *Camponotus* spp.1-6; Cr1: *Crematogaster* spec.1; Pv: *Polyrhachis viscosa*.

The pooled number of ant species foraging on individual trees was significantly lower than the numbers on groups of neighbouring trees growing within a radius of 5 m from the study tree

(Wilcoxon's signed-ranks test: $T = 0$, $z = 8.77$, $p \ll 0.0001$, $N = 127$). Median ant species number occurring on trees within the 5 m radius was five for all trees, and it reached a maximum of eight when six or more neighbouring trees were included in the analysis (Figure VI.1). The low number of species on individual trees compared to the potential number of species occurring within their immediate vicinity, led to a small scale patchwork of ant communities (Figure VI.2A-C).

Species similarity was very high for ant communities sampled from the same trees at comparable daytimes (median JI = 1, Figure VI.3), independent of whether repeated censuses were performed 4 or 10 to 30 days after the first census (Wilcoxon's signed-ranks test: $T = 138$, $z = 0.34$, $p = 0.73$, $N = 47$). The resulting mosaic-like community composition was therefore stable when the same time of day was considered. On a 24h-basis, however, community composition was more variable (Kruskal-Wallis test: $H = 185.6$, d.f. = 10, $p < 0.0001$; Figure VI.3). Most pronounced differences could be found between morning and night and afternoon and night samples (median JI: 0 and 0.25 respectively, Figure VI.3). Species similarity values of communities sampled from the same tree in the morning and in the afternoon (median JI: 0.5, Figure VI.3) were significantly higher than those of the day-night comparisons, but were lower than those obtained at the same time of day at different sampling intervals (Figure VI.3).

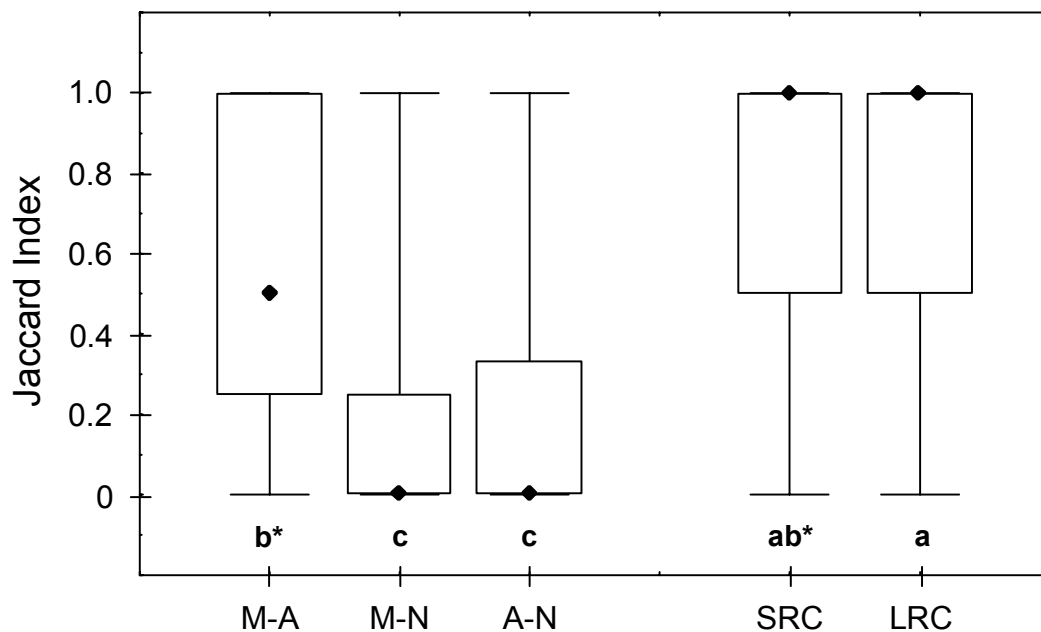


Figure VI.3 Similarity (measured as Jaccard Index, JI) between ant communities on the same trees sampled at different times of day (M-A, M-N, A-N) and in different intervals (SRC and LRC) at the same time of day. Minimum and maximum JI values are indicated by \perp , \square shows the 25-75 % percentiles of JI and \blacklozenge the median JI values. M-A: morning-afternoon, M-N: morning-night, A-N: afternoon-night comparison; SRC: short re-census, obtained four days after first census; LRC: long re-census, obtained 10 to 30 days after first census; different letters a, b, c indicate significant differences in median Jaccard index values; * indicates significant differences at the $p < 0.1$ level between a and b*, all other differences are significant at the $p < 0.05$ level at least: Kruskal-Wallis-test: $H = 168.2$, $p < 0.0001$, d.f. = 4; followed by Schaich & Hamerle multiple comparisons test.

Interrelationship analyses. Logistic regression analysis indicated that tree size parameters influence the distribution of some but not all dominant ant species. The distribution of *C. spec.1* was positively related to the tree size parameter PC1 in morning, afternoon, and night censuses (p , odds ratio, 95 % confidence interval for morning: 0.002, 3.3, 1.6-7.1; for afternoon: 0.04, 2.4, 1.1-5.3; for night: < 0.05, 2.0, 1.0-4.1). *C. spec.4* showed positive relations to PC1 in morning and afternoon samples but not at night, and *C. spec.2* and *Crematogaster spec.1* were more often present on taller plants in morning and afternoon samples respectively (*C. spec.4*, morning: 0.03, 2.2, 1.1-4.5; *C. spec.4* afternoon: 0.001, 4.4, 1.8-11.1; *C. spec.2*, morning: 0.03, 2.3, 1.1-4.6; *Crematogaster spec.1*, afternoon: 0.009, 5.7, 1.5-21.2). For all other ants, no significant relation between distribution and PC1 was detectable. Additionally, logistic regression revealed negative, time dependent relations between ant species. In the morning, negative associations between *C. sericeus* with *C. spec.2* (< 0.001, 0.03, 0.006-0.2) and *C. spec.3* (0.03; 0.07, 0.006-0.8 for presence-absence data only) could be detected. In the afternoon, negative interactions between *C. sericeus* with *C. spec.2* (0.002, 0.4, 0.2-0.7), *C. spec.1* (0.04, 0.7, 0.5-1.0), and *Crematogaster spec.1* (0.03, 0.9, 0.8-1.0) became evident. At night, negative relations were detectable between *C. spec.5* with *C. spec.6* (0.002, 0.04, 0.004-0.3) and *C. spec.5* and *Crematogaster spec.1* (0.03, 0.8, 0.7-1.0).

Examining the distribution of the dominant ant species with respect to the distribution of co-occurring species by association analysis, positive, negative and neutral relationships became evident when all trees and all ant species were considered (Table VI.1d). However, when species affinity was calculated using only ants foraging in the same 'micro-areas', no significant positive relationship could be detected (Table VI.1a-c). Analysis of both, interspecific association and covariation often resulted in negative values. The lack of positive correlation, supported by the findings of restricted association analysis, suggests that competition must be considered a major factor structuring ant communities on *Pseudocedrela*. Of 17 species combinations which showed sufficient overlap of foraging areas to be analysed, only two (*C. spec.3/C. spec.4* & *C. spec.1/C. spec.4*) seemed to be neutral in association and covariation for all different times of day.

Interspecific interactions were variable with time of day. According to differences in daily activity patterns, pairwise interactions changed between different times of day and no species pair could be found to exist during both night and day. In general, species interactions seemed to be most pronounced in the afternoon censuses, especially for the analysis of interspecific covariation. While for only 36 % of species pairs (N = 11), a significant (negative) correlation could be detected for the morning samples, 82 % of species pairs (N = 11) showed negative correlation in the afternoon samples. At night, the dominance of one species (*C. spec.5*) became especially evident, and there was absolutely no overlap detectable between this and the two other most abundant, night-active species (*C. spec.4* and 6). In total, 67 % of six species pairs showed significant negative correlations and all showed significant negative association.

Null model based C-score analysis demonstrated that co-occurrence of ant species was generally smaller (higher C-score) than expected by chance in combined ant samples and in ant samples of SA-II and SA-III (Table VI.2). In the morning and afternoon samples of SA-I, species co-occurrence lay within the 95 % limits of frequency distribution of the randomised matrices, while the observed co-occurrence was higher than expected by chance in the night samples of SA-I. C-score indices were identical for observed and randomised matrices for the SA-III night sample.

Table VI.1 Continued: Interspecific association indicated by chi-square values (lower-left triangle) and interspecific covariation indicated by Spearman correlation coefficients (r_s) (upper-right triangle).

	Cs	C1	C2	C3	Cr1	C4	C5	Pv	C6
c) Night									
Cs	-	-	-	-	-	-	-	-	-
C1	-	-	-	-	-	-	-0.08 (N=54)	-	-
C2	-	-	-	-	-	-	-	-	-
C3	-	-	-	-	-	-	-	-	-
Cr1	-	-	-	-	-	-	-0.67** (N=23)	-0.24 (N=28)	-
C4	-	-	-	-	-	-	-0.77*** (N=26)	-	-
C5	-	-17.5***	-	-	-6.2*	-26.0***	-	-0.42* (N=31)	-0.86*** (N=41)
Pv	-	-	-	-	-7.3* {-5.1*}	-	-7.5** {-5.3*}	-	-
C6	-	-	-	-	-	-	-37.2***	-	-
d) Total									
Cs	-	-	-	-	-	-	-	-	-
C1	-12.2**	-	-	-	-	-	-	-	-
C2	-28.7***	1.3	-	-	-	-	-	-	-
C3	-18.4***	9.0*	1.0	-	-	-	-	-	-
Cr1	26.8***	-11.0**	-8.6*	7.8*	-	-	-	-	-
C4	3.1	2.8	0.4	1.2	4.6	-	-	-	-
C5	0.02	0.06	0.3	3.3	4.1	-24.5***	-	-	-
Pv	35.2***	-12.2**	-13.1**	-8.9*	30.5***	0.9	2.4	-	-
C6	1.3	0.8	7.3*	6.3	0.1	3.9	-22.8***	0.3	-

Significant values are bold. Significance at the 5 % (*), 1 % (**), and 0.1 % (***) probability levels was computed applying the sequential Bonferroni technique. Chi-square values marked by ** are significant at the 1 % probability level at least. Yates' correction of chi-square values was calculated when chi-square analysis was biased. Corrected chi-square values are given in squared brackets when the level of significance of the analysis was changed by the correction. Number of trees (N), in common use of species pairs and considered in the analysis, is given with r_s for each species pair for the morning, afternoon, and night analyses. Values are given only for those species-combinations with frequencies >6 per species on neighbouring trees (maximum distance 5m) or, when foraging distances were determined, on trees growing within the minimum foraging area of the respective species. For analysis of d (total), the combined occurrence on all trees (N = 132) was considered. Cs: *Camponotus sericeus*, C1-C6: *Camponotus* spp.1-6, Cr1: *Crematogaster* spec.1, Pv: *Polyrhachis viscosa*.

Table VI.2 C-Score indices of the randomised and observed matrices for each studied mosaic. The observed values are presented in addition to minimum and maximum values of the indices calculated for 1,000 randomised matrices per sample.

Sample	Randomised matrix		Obs. matrix	<i>p</i> -values	
	Minimum	Maximum		Obs.>exp.	Obs.<exp.
Total	661.56	674.97	703.67	<0.0001	1.000
Morning a1-3	473.93	493.73	524.93	<0.0001	1.000
Morning a1	19.33	26.33	19.33	1.000	0.751
Morning a2	54.70	61.80	60.00	0.026	0.978
Morning a3	89.83	98.67	95.83	0.017	0.989
Afternoon a1-3	383.62	398.52	401.81	<0.0001	1.000
Afternoon a1	55.40	63.80	59.40	0.113	0,892
Afternoon a2	70.60	77.60	76.50	0.024	0.978
Afternoon a3	57.33	65.00	62.67	0.013	0.993
Night a1-3	348.05	376.10	372.10	0.058	0.942
Night a1	69.70	77.60	69.60	1.000	<0.0001
Night a2	73.50	82.60	80.20	0.042	0.960
Night a3	127.67	127.67	127.67	1.000	1.000

p-values are given for two-tailed tests, with the probabilities of the observed indices being larger or smaller than the expected randomised matrices. Obs. Observed, exp. expected, a: area, total: ant occurrences from all areas and times combined (table organisation follows Ribas & Schoereder 2002).

VI.4 Discussion

The investigations on interrelationships between the savannah tree *Pseudocedrela kotschy* and the ground nesting ant community foraging in the plant's catchment area revealed that (1) ants regularly use EFNs of *P. kotschy* at least during a part of the year, (2) patterns of nectary visitation vary substantially between neighbouring plant individuals and between different times of day, (3) the composition of ant communities is mosaic-like, i.e. predictable and stable over time, when time of day is considered, and (4) the composition of ant communities is partly dependent on tree size and probably strongly influenced by interspecific interactions.

The observation that EFNs are continuously used by many species of ground nesting ant species is in accordance with findings from comparable systems in other regions (Oliveira et al. 1987, Oliveira and Brandao 1991, Hossaert-McKey et al. 2001). When comparing the number of species and the identity of the dominating genera of ants, strong similarities between African savannahs and South American cerrado vegetation became evident. In both systems, more than 20 ant species could be shown to be locally attracted to the EFNs of woody plants, and in both systems large *Camponotus* species were the dominating ant genus (Oliveira and Brandao 1991). These results differ correspondingly from findings obtained from tropical forests where *Crematogaster*, *Oecophylla*, *Azteca* and *Dolichoderus* were most important members of arboricolous ant communities (e.g. Hölldobler 1979, 1983, Adis et al. 1984, Stork 1991, Majer 1993, Floren and Linsenmair 1997, Dejean et al. 2000d).

Almost all the plants under investigation were constantly used by ants. This finding indicated a permanent supply of extrafloral nectar and pointed to its nutritional value at certain periods of the year. The ant species composition was, however, not stable but turned out to be considerably variable

in the course of the day. Marked changes in daily activity patterns are well known for ant communities (for savannah and cerrado habitats see, for example, Lévieux 1983b, Oliveira and Brandao 1991, Del-Claro and Oliveira 2000). These shifts are often interpreted as effective niche separation of generalist foragers, allowing coexistence of several species competing for the same limited food resources (Lévieux 1983a, Cerdá et al. 1998). In the case of the studied savannah trees, these shifts led to daily alterations of all communities dominated by species with restricted activity phases. As two thirds of all regularly sampled ants showed clear diurnal or nocturnal activity patterns, and only four species were constantly active during day and night, these shifts in species composition were a characteristic of the studied *Pseudocedrela* communities. The variable community composition at different times of the day is in contrast to another characteristic of the studied ant communities: their stability at the same day-time. These features - changes during the 24 h of the day and persistence over long periods at the same day-time - have to be considered in combination for any analysis of ant-plant interactions. This is because ant species may differ in their effectiveness as plant defenders (Koptur 1984, Rico-Gray and Thien 1989, Dejean et al. 2000b, Di Giusto et al. 2001), and herbivores may have restricted activity periods (many chrysomelids are mainly day-active, many caterpillars and scarabaeids are nocturnal). This may present a challenge to the plant to attract the best ant-guards out of the available ant species pool at a given time, and mean that the plants could even be forced to compete for these ant species (e.g. via variable nectar supply). On the other hand, some herbivores may be stimulated to choose their host plants according to the predictability of changing ant-guards. Mobile, ant-sensitive herbivores, such as many beetles, can avoid plant individuals at the time of best defence. Less mobile herbivores, such as caterpillars, may adapt to the ants or completely avoid particular plants. The result is a small scale mosaic of differing herbivore assemblages, partly triggered by ant distribution and activity.

Differences in the distribution of foraging ants were originally expected to be mainly affected by nest site position relative to the foraging sites (Inouye and Taylor 1979, Koptur 1984, Bronstein 1998). However, since a) neighbouring trees were often used by different ant species and distances between these trees were much smaller than those covered by foraging ants, and b) no preference could be detected for plants growing closest to the nest site for *C. sericeus* studied as a model species (Mody and Linsenmair 2003), other factors than nest proximity have to be additionally considered in order to explain the ants' distribution. Trees may differ in attractiveness to ants in general and to the different species in particular. Besides proximity to nest site - which reduces costs such as time loss or exposure time to predators (Wehner et al. 1983, Denny et al. 2001) - tree attributes determining their value as food resource may vary. Differences in quality and quantity of food provided (number or productivity of EFNs) may depend on environmental or genetic factors (Heil et al. 2000). As all trees grew under similar environmental conditions, strong effects of the environment seem improbable. Genetic differences cannot yet be excluded.

However, such differences are no prerequisite to explain the observed distribution of ants. According to our analyses, two aspects, i.e. the size of the trees and competitive interactions, were strongly related to the observed distribution patterns. For some species (*C. spec.1* and *C. spec.4*, and to a lesser extent *C. spec.2*), size of trees seemed to matter. Size could increase the attractiveness in quantitative terms given the quality of the resources offered are not negatively affected and monopolisation is still possible. Both prerequisites were obviously met, since a) the abundance of ants foraging on taller trees generally increased in a linear way and showed no signs of negative relationship and b) tree size was not influential on the number of ant species foraging on a tree, indicating that variation in the size range covered by this study did not affect monopolisation. Monopolisation of taller plants may be attractive, as it allows more effective use of the greater

resources provided by these plants by intracolony resource partitioning (Acosta et al. 1995, Mody and Linsenmair 2003).

The hypothesis that competition for foraging opportunities on *Pseudocedrela* plants is an important factor influencing the structure of the ant communities is supported by the finding that simultaneous use of the same tree by different ant species was uncommon, whereas neighbouring trees were regularly foraged by different ant species. This indicates that monopolisation of trees occurs very often, suggesting that individual plants are treated as valuable and defensible resource units (Pickett and Clark 1979, Schemske 1982, Koptur 1984). The attractiveness of EFNs appeared, however, to be limited, as they were not monopolised by the most competitive ant species alone (monopolisation by these ants increased when more attractive honey-sucrose-baits were offered – K. Mody, pers. obs.). The stability of distribution patterns over time, even for species without permanent residence on plants, is remarkable in this context. It suggests that workers seem to know where to successfully forage at a particular time and where interference or exploitation (Dreisig 2000) competition is to be expected.

The influence of competitive interactions on ant distribution is also supported by association, covariation and co-occurrence analyses. These analyses revealed many significant, but always negative, relations in regard to qualitative and quantitative pairwise examinations. They also demonstrated that the distribution of the dominant species generally could not be explained by random, but rather by deterministic processes. The only exceptions were the association analysis of the combined ant samples and the C-score analyses of the SA-I communities. Positive relations between particular ant species according to the combined association analysis indicate that the same plant individuals can be used by these positively associated ant species. However, since the ants had different activity periods, positive combined association does not mean that these ants were related by positive interactions. This finding demonstrates rather, that wrong interpretations may result when temporal aspects are neglected in analyses of ant community structure. The results of the C-score analysis for SA-I showing an observed species co-occurrence within the 95 % limits of frequency distribution are the only indication found in this study that the mosaic-like distribution of the three dominant species in this area may also arise from stochastic processes. In the night sample, competition seemed not only reduced, but positive co-occurrence could also be found. However, since there was no positive relation detectable, neither by association nor covariation analysis, for the night sample, this finding seems to indicate a similar resource use by the involved species but no direct attraction. The results of the C-score analysis of the night sample of SA-III represent a special case. Since there was absolutely no overlap between the dominant species (complete avoidance, exclusion?), no differences were detectable between observed and randomised C-scores.

In conclusion, the studied *Pseudocedrela*-ant system is an example of a predictable mosaic of differing ant communities on neighbouring plants which is established by ground nesting ant species. The observed mosaic-like community patterns are, in some respects, comparable with ant mosaics maintained by tree nesting species in plantations and some forest systems. As in these, the species composition is predictable and stable, at least when the same time of day is considered. In contrast to classical ant mosaics, however, monopolisation of resources in the *Pseudocedrela*-system is restricted to considerably smaller areas (individual plants) and is achieved by more species relative to the total species pool. The limited attractiveness of the EFNs may allow competitively inferior species to monopolise resources by exploitation competition and may thereby prevent the dominance of the most competitive species alone. Thus, competition for predictable resources of limited value can facilitate co-existence of different island-like ant communities. Via effects of particular ant species on co-occurring arthropods, the characteristic distribution of ants may create a small scale patchwork of different arthropod communities and thereby enhance local arthropod diversity.

Acknowledgements. We thank Andrea Holzschuh for her very helpful research assistance in 1999, Jan Beck and Nico Blüthgen for their comments on earlier versions of this manuscript and Erhard Strohm for statistical advice. Permission to perform the research was courtesy of the ‘Ministère de l’Enseignement Supérieur et de la Recherche Scientifique’, Republic of Côte d’Ivoire. Access permit to Comoé National Park was issued by the ‘Ministère de la Construction et de l’Environnement’. The study was partly supported by scholarships of the DAAD (German Academic Exchange Service, No. 332 4 04 101), by the DFG Graduiertenkolleg 200 to K.M., and by BIOTA (Biodiversity Monitoring Transect Analysis in Africa), German Federal Ministry of Education and Research (BMBF), subproject W06, 01LC0017.

VII. Plant-attracted Ants Affect Arthropod Community Structure but not Necessarily Herbivory

Abstract - 1. The effectiveness of ants as plant defenders is equivocal for plants that attract ants via extrafloral nectaries.

2. Different aspects of ant-effects on plants and on associated arthropods were investigated using the myrmecophilic savannah tree *Pseudocedrela kotschyi* and its arthropod fauna as study system. Herbivory was determined for trees dominated by different ant species and it was compared between ant-access and ant-free trees in controlled ant exclusion experiments. Arthropod community composition was also compared between ant-access and ant-free trees.

3. Short-term ant-exclusion experiments failed to demonstrate a consistent effect of ants on herbivory.

4. Plants dominated by different ant species differed significantly in leaf damage caused by herbivorous insects. The relative ranking of herbivory levels of the trees dominated by different ant species was persistent in three consecutive years.

5. Ants significantly reduced the abundance of different arthropod groups (Araneae, Blattodea, Coleoptera, Homoptera, non-ant Hymenoptera). Other groups, among them important herbivores, seemed not to be affected (Lepidoptera, Orthoptera, Thysanoptera, Heteroptera).

6. The study suggests that ant presence only benefits plants when the 'correct' ant species is attracted and protection by these ants is not counterbalanced by their negative effect on other beneficial arthropods.

Key words: Ant mediated interactions, *Camponotus*, Comoé National Park, exclusion experiments, extrafloral nectaries, plant protection, *Pseudocedrela kotschyi*, spiders, wasps

VII.1 Introduction

A wide range of plants bear extrafloral nectaries (EFNs) which attract ants and other arthropods (Koptur 1992, Pemberton and Lee 1996). Attracting ants through EFNs is often considered an important defensive mechanism of myrmecophilic plants (e.g. Wettstein 1889, Bentley 1977, Buckley 1982). However, the data concerning the effectiveness of this mechanism is controversial. While many studies demonstrated an enhanced protection of entire plants or plant parts (Bentley 1977, Koptur 1984, Fiala et al. 1989, Oliveira et al. 1999, Heil et al. 2001b, Sobrinho et al. 2002), and references therein), other studies failed to detect any measurable preventive effects of EFN-attracted ants (O'Dowd and Catchpole 1983, Boecklen 1984, Begera 1989, Rashbrook et al. 1992).

Inefficient or lacking protection may be explained by (i) differences in defensive capabilities of different ant species (e.g. Horvitz and Schemske 1984, Koptur 1984, Dejean et al. 2000a), (ii) differences in ant foraging behaviour among habitats (Inouye and Taylor 1979, Barton 1986, Zachariades and Midgley 1999), (iii) problems of adequately assessing seasonal variation in ant-plant-herbivore interactions by short-term studies (O'Dowd and Catchpole 1983, Heil et al. 2001a), and (iv) varying susceptibility of different herbivore groups to ant predation (Fowler and MacGarvin 1985, Heads and Lawton 1985, Ito and Higashi 1991). Protective effects of ants may also be counterbalanced by their negative effects on other predatory taxa - like ants with higher defensive potential, spiders, parasitic or predatory non-ant Hymenoptera - serving plants as defenders (Janzen 1975, Heil 2002). Thus, the presence of 'wrong' ant species may result in costs rather than benefits to the plant. Such a negative impact of ants on potentially beneficial arthropods could be shown by some

studies (Halaj et al. 1997, James et al. 1999), but not by others (Grant and Moran 1986, Karhu 1998, Floren and Otto 2002).

To clarify these inconsistencies, the ants' effects on herbivory and their influence on the composition of the co-existing arthropod community have to be studied simultaneously. By using an ant-mosaic characterised by different dominant ant species on neighbouring *Pseudocedrela kotschyi*-trees (Mody and Linsenmair (a), subm.), we were able to test to what extent (i) different co-occurring ant species differentially affect herbivory, (ii) these different species influence herbivory in the short- and in the longer-term, and (iii) other arthropod groups potentially sharing the same habitat (plant individuals) are influenced by ant presence.

VII.2 Materials and Methods

Study site and species. The investigation was conducted in Comoé National Park during April through June 1999 and 2000, during April through May 2001 (early rainy season) and in September 2002 (late rainy season). Comoé National Park is located in the north-east of the Republic of Côte d'Ivoire, and covers 11,500 km² of Guinea- and Sudan-zone savannah. Its climate is characterised by a long dry season from about November to March/April, a mean annual precipitation of 950 mm and an annual average temperature between 25 °C and 28 °C (Linsenmair 1998). More information on Comoé National Park is provided by Poilecot (1991) and Rödel (2000). The study area was situated within the Guinea-savannah in the southern part of the Park (08°44'N, 003°49'W, c. 215 m a.s.l.).

The studied host plant species, *Pseudocedrela kotschyi* (Schweinf.) Harms (Meliaceae), is designated by its generic name in the following. *Pseudocedrela* is a medium-sized (4-5 m, maximally 12 m), deciduous savannah tree. The leaves are impari- or paripinnate. *Pseudocedrela* bears inconspicuous extrafloral nectaries (EFNs), which are situated mainly along the leaf nerves and occur on all leaves of the plant. Ants visited these EFNs regularly and were able to extract carbohydrates (mainly fructose and glucose as demonstrated by HPLC analyses of gut contents of ants captured when leaving their host plant; Mody & Hilpert, unpublished). During the main study period (early to mid rainy season), almost all plants (ranging in height between 76 cm and 346 cm; mean \pm s.d. = 176 \pm 52 cm; N = 131) were visited day and night by different ant species. Individual *Pseudocedrela* plants were usually dominated by a single ant species although several ant species were simultaneously foraging in the immediate surrounding of the same plants (Mody and Linsenmair, subm.).

We focused on three *Camponotus* species. *Camponotus sericeus* Fabricius was the ant species with highest incidence on the studied trees. Its numbers of foragers simultaneously using single plants ranged between 1 and 17 (median 2). The other two *Camponotus* species showed high incidence as well. Since these could not be determined yet, they are consistently called *Camponotus* spec.2 (*C. spec.2*) and *C. spec.4*. While *C. spec.4* reached highest numbers of all ants foraging on single *Pseudocedrela* (1-40, median 9), the numbers of *C. spec.2* were considerably lower (1-10, median 2). *C. sericeus* and *C. spec.2* were diurnal, with peak activity between 0800 and 1800. *C. spec.4* was equally active day and night (Mody and Linsenmair (a), subm.).

Natural ant distribution and ant-exclusion experiments. We determined the influence of ants on leaf damaging herbivorous insects by two approaches. In the first approach (*ant exclusion-experiments*), 46 *Pseudocedrela* trees, which grew in the same savannah area (0.3 ha) and were dominated by one of the three focus ant species, were selected in 1999. Trees with identical ant species were sorted to pairs whenever possible. Tree pairs had to grow closer to each other than to other neighbouring trees - distance was usually 1-3 m - and had to match in size (difference in height and

crown-width less than 15 %). One member of each pair was selected at random, and ants were excluded. These trees were banded around the trunk with a tape (10 cm in width) which was treated with AlteratTM insect-lime (Valbrenta Chemicals, Italy). Surrounding vegetation was generally low but single blades of grass had to be trimmed sometimes to prevent uncontrolled access by ants to control or treatment trees. Herbivory was measured as described below on ant-exclusion (treatment) and ant-access (control) plants prior to the experiment and three weeks later. In 2000, 29 pairs of trees dominated by one of the three focus ant species were treated as in 1999. Herbivory was quantified for treatment and control plants before the experiment and two weeks later. In 2001, measurement of herbivory accompanied the investigations of ant-effects on other arthropod groups. Sixteen pairs of *Pseudocedrela* trees dominated by one of the three focus species were chosen and treated as in 2000, with the exception that the tape was smeared with SchachtTM insect-lime (Schacht GmbH & Co. KG, Germany) and that herbivory was quantified after four weeks of ant exclusion.

The second approach (*natural experiment*) took advantage of the mosaic-like distribution of different ant species on neighbouring *Pseudocedrela* trees. After categorising trees according to their dominant ant species in each year, naturally occurring herbivory was quantified in 1999, 2000, and 2001, applying the methods for 'herbivory measurement' as described below. The *natural experiment* measured all herbivory occurring in the early rainy season when newly establishing and quickly growing leaves are especially attractive to herbivorous insects (K. Mody, pers. obs.). Since the activity of ants on *Pseudocedrela* dropped when the rainy season progressed, ants were again counted on the study trees towards the end of a rainy season, in September 2002.

Measurement of herbivory. Obtaining a representative measure of herbivory of a plant is not a trivial task (Waller and Jones 1989). In this study, we determined the leaf area removed by herbivores as measure of herbivory, although removed leaf mass could also be quantified by the methods described below for 2000 and 2001.

In 1999, the youngest leaf with fully developed leaflets and the oldest leaf of the largest twig were used to determine herbivory of a plant. The leaf area consumed by herbivores was determined for every leaflet by estimating the area of the intact leaf, using the untouched portion of the leaves as a template when leaves were damaged along the border. The missing area was then estimated with a precision of 10 %, and with a precision of 1 % when the remaining leaf area was lower than 10 % or higher than 90 % of the total leaf area. The degree of herbivory of the whole leaf was obtained by averaging (median) the values of the single leaflets (the number of leaflets ranged between 6 and 19, mean = 11.0, N = 192 leaves).

In 2000, herbivory on plants was measured by quantifying the missing area of pairs of leaflets. Sixteen leaflets were randomly chosen per plant by blindly pointing with a stick from all compass directions to the plant and assigning the leaflet first encountered as 'measure-leaflet (a)' (*MLa*). The 16 *MLa* were marked with an identification code. Then, the leaflet opposite to *MLa* at the same position of the rachis was labelled *MLb* and marked accordingly. For quantification of herbivory at the start of the experiments, all *MLa* were collected and photographed in the laboratory with a digital camera (Nikon, COOLPIX 950) by a standardised procedure. The leaflets were spread out on a board of white Plexiglas. To smooth out bulges of the leaflet which could impede determination of leaflet area, the leaflets were tightly covered with a hinged lid of transparent Plexiglas. The leaflets were photographed from a fixed distance, with the same resolution, and without flash. Digital photographs were analysed using the graphics package 'Adobe Photoshop'. By referring to the 'pixel number' of reference areas (1 cm² and 4 cm²), which were outlined on the board of white Plexiglas next to the photographed leaves, the area of every leaflet could be determined. The missing parts of the leaflets were accordingly measured after outlining them in the photograph. The percentage area removed by

herbivores was computed from missing and total area. In order to quantify changes in herbivory level due to progressing time and ant-exclusion, all *MLb* were collected two weeks later and herbivory was determined as described for *Mla*.

In 2001, effects of time and experimental design on herbivory were measured by quantifying missing leaf area repeatedly for the same leaves. Six leaflets (belonging to at least two different leaves) were randomly selected per plant. These leaflets were photographed while remaining on the plant at the beginning of the investigation. Photographs were taken using a leaf-fixing board (board of white Plexiglas with reference area and hinged lid of non-reflecting glass). The camera was mounted on a holder which ensured a standardised distance between leaf and lens. The same leaves were photographed again after four weeks and herbivory at the different times was quantified as described for the year 2000.

Herbivory measures were averaged for each plant (calculating the median as the measures of herbivory usually did not follow a normal distribution). Assumptions of parametric tests were not met by all of the resulting median degrees of herbivory after application of transformation procedures. Therefore, non-parametric analyses were used to compare herbivory (i) on the same plants at different times and on paired, different plants at the same time (Wilcoxon's signed-ranks test, *ant-exclusion experiment*), on (ii) unpaired different plants with and without ants (Mann-Whitney U-test, *ant-exclusion experiment*) and (iii) on plants dominated by different ant species (Kruskal-Wallis test, *natural experiment*), (Sokal and Rohlf 1995, Zar 1999). To account for multiple testing, *p*-values adjusted by the sequential Bonferroni correction (Hochberg 1988) are provided in addition to single test *p*-values. All analyses were computed using SPSS 11.0 and Statistica 6.0. As testing on ant-species specific effects on herbivory was an a priori goal of the study, the Kruskal-Wallis test was followed by *post hoc* comparisons (Dunn's test), to check for pairwise significant differences. The *post hoc* comparisons were computed using SsS 1.1a.

Influence of ants on other arthropods. Ants attracted to leaves by EFNs may interfere with other arthropods. To assess the influence of ants on all kinds of arthropods potentially sharing the same plant with ants, arthropod abundance was determined on plants with free ant-access (control) and on plants without ants (ant-exclusion treatment). Forty-four pairs of *Pseudocedrela* plants were selected in three neighbouring *Pseudocedrela*-stands (distances between stands were 250 m, 270 m, and 555 m). To test whether systematic differences existed between control and treatment trees, ant communities on the trees and plant size were examined before experiments. Ants were counted on every leaf of all study trees at three different times of the day (between 0930 and 1130, 1530 and 1730, and 2200 and 0200) (Mody and Linsenmair, *subm.*). Plant size was determined as plant height, crown height, crown width (maximum diameter), crown depth (maximum diameter perpendicular to crown width), and trunk girth (at 20 cm above ground). Since all size parameters were highly correlated ($r_s = 0.42-0.78$), principal components analysis (PCA) was performed and one principal component (PC1), explaining 67.3 % of the total variance, was extracted. Height of studied trees ranged between 82 cm and 332 cm (mean \pm s.d. = 176 ± 50 cm; $N = 88$). No differences were detectable between control and treatment trees for ant species number, ant abundance, and plant size (Wilcoxon's signed-ranks test: species number: $z = 0.16$, $N = 44$, $p = 0.87$; ant abundance: $z = 0.43$, $N = 44$, $p = 0.66$; plant size (PC1): paired t-test, $t = 0.82$, d.f. = 43, $p = 0.416$). Each pair member was in close proximity to the other, to ensure as far as possible that the pair members would be equally accessible to ants and other arthropods. One member of each pair was selected at random from which ants were excluded. Ant exclusion experiments were started when the foliage of the trees was fully expanded (end of April). After four weeks, the complete arthropod communities of all 88 trees were sampled. To this end, the trees were first checked for highly mobile insects like bees and wasps. These were visually

counted or caught using a collecting tube moistened with ethanol. All other arthropods were sampled by putting and shaking the whole tree in a steep-sided, funnel-shaped beating tray. The tray was made of smooth balloon-silk and fitted with a collecting pot, from which all sampled arthropods could be quickly transferred to storage bottles containing 75 % ethanol. The arthropods were sorted in the laboratory using keys and information provided by Delvare and Aberlenc (1989), Scholtz and Holm (1989), Goulet and Huber (1993) for information on the insect families and Bolton (1994) for ant genera. To analyse the effect of ants on the other arthropods, the abundance of the different groups on control and ant-exclusion trees was compared using the Wilcoxon's signed-ranks test (Sokal and Rohlf 1995). The influence of particular ant species on co-occurring arthropods was evaluated by comparing arthropod abundances on such control trees, which were dominated by one of the three focal ant species (*C. sericeus*, *C. spec.2*, *C. spec.4*). Trees dominated by other ant species were not included in the analyses. Proximity-requirements of the pairing treatment resulted in an unbalanced representation of the three ant species in these comparisons (since neighbouring trees were often dominated by different ant species).

VII.3 Results

Ant distribution and influence of ant exclusion on herbivory. All study trees were visited by ants before the exclusion experiments (early rainy season). In the late rainy season, ants could be detected on only 7 % of the trees formerly hosting the three dominant study species (N = 102 trees, five with *C. spec.2*, two with *C. spec.4* and none with *C. sericeus*). All three ant species could be observed foraging in the vicinity of the study trees, e.g. on grasses and herbaceous *Hibiscus* species.

There were no significant differences between control and prospective treatment plants before the start of the experiment in any year (Mann-Whitney U-test (*MWU*): 1999: $z = -0.178$, $N_{1,2} = 23$, $p = 0.86$; Wilcoxon's signed-ranks test (*WSR*): 2000: $z = 0.387$, $N = 29$, $p = 0.70$; 2001: $z = 0.245$, $N = 16$, $p = 0.81$; Figure VII.1). Short-term exclusion (two to four weeks) of ants from the *Pseudocedrela* trees had no consistent effects on herbivory, neither for the different years nor the different ant species considered. In 1999, herbivory significantly increased from the start to the end of the experiment, but only in the treatment plants (*WSR*: control: $z = 0.17$, $N = 23$, $p = 0.86$; treatment: $z = 2.27$, $N = 29$, $p = 0.023$; Figure VII.1). Herbivory was significantly higher for treatment- than for control-trees at the end of the experiment (*MWU*: $z = 2.65$, $N_{1,2} = 23$, $p = 0.008$; Bonferroni corrected: $p < 0.05$). When the different dominant ant species were considered separately, it became evident that herbivory increased most strongly when *C. spec.4* was excluded. No changes were detectable when *C. spec.2* or *C. sericeus* were excluded (*WSR*: *C. spec.4*: control: $z = 0.55$, $N = 5$, $p = 0.58$; treatment: $z = 2.37$, $N = 7$, $p = 0.018$ (Bonferroni corrected: $p > 0.05$); *C. spec.2*: control: $z = 0.54$, $N = 6$, $p = 0.60$; treatment: $z = 1.15$, $N = 6$, $p = 0.25$; *C. sericeus*: control: $z = 0.18$, $N = 12$, $p = 0.86$; treatment: $z = 0.47$, $N = 10$, $p = 0.64$). In 2000, no measurable changes in herbivory occurred from the start to the end of the experiment, neither for the control, nor for the treatment plants (*WSR*: control: $z = 0.60$, $N = 29$, $p = 0.55$; treatment: $z = 0.39$, $N = 29$, $p = 0.69$; Figure VII.1). No difference was detectable between control and treatment plants at the end of the experiment (*WSR*: $z = 0.22$, $N = 29$, $p = 0.83$; Figure VII.1). In 2001, new herbivory, occurring after the start of the experiment, was generally very low. It was - although higher for ant-exclusion plants - not significantly different between treatment and control plants (*WSR*: $z = 1.40$, $N = 16$, $p = 0.16$; Figure VII.1).

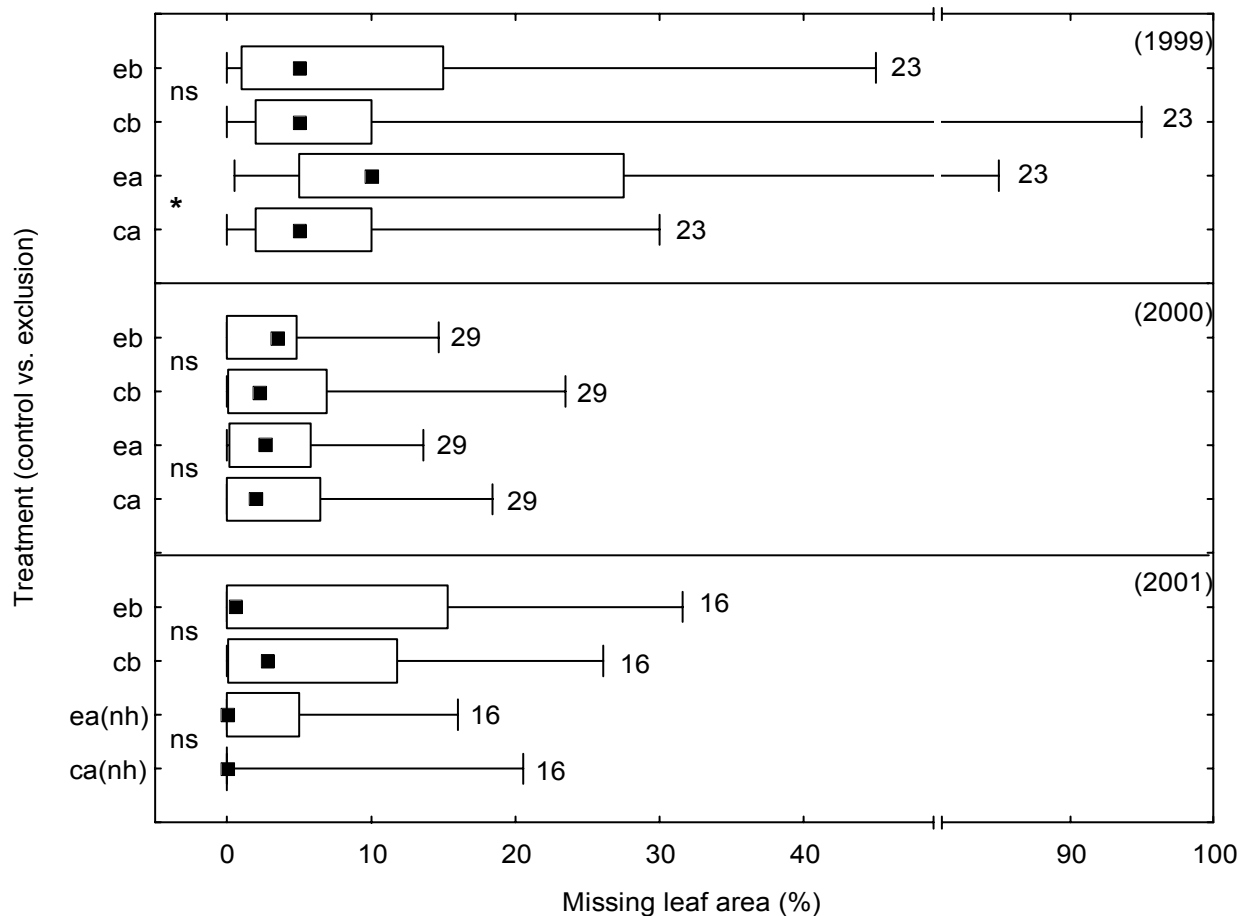


Figure VII.1 Levels of herbivory of *Pseudocedrela*-trees before (eb) and after ant exclusion (ea) and on the respective control trees (cb: control before, ca: control after) in 1999, 2000 and 2001. In 2001, new herbivory (nh, see text) occurring from the start of the experiment, was measured. Box plots display medians (black square), quartiles (box) and range (whiskers). Numbers of studied trees are given at the individual bars. Differences between control and treatment are indicated (*: $p < 0.05$; ns: not significant; Wilcoxon's signed-ranks test).

Herbivory of trees dominated by different ant species. Degrees of herbivory were consistent between different years for trees dominated by *C. sericeus* (median degree of herbivory (mh) ranged between 3.8 % and 10.0 %, Kruskal-Wallis test: $H_{2,56} = 4.02$, $p = 0.13$) and *C. spec.4* (mh between 0.2 % and 1.0 %, $H_{2,48} = 0.37$, $p = 0.16$). For trees dominated by *C. spec.2*, herbivory differed significantly between 2001 (mh = 0 %) and the other two years (mh = 3.8 and 4.0 %, $H_{2,48} = 13.17$, $p = 0.0004$; Dunn's *post hoc* $Q_{1999,2000} = 0.26$, $p > 0.05$; $Q_{1999,2001} = 3.12$, $p < 0.01$; $Q_{2000,2001} = 3.26$, $p < 0.001$; Figure VII.2).

There were significant differences in naturally occurring herbivory between plants dominated by different ant species in all three years of investigation (1999: $H_{2,46} = 9.86$, $p = 0.006$; 2000: $H_{2,58} = 7.70$, $p = 0.019$; 2001: $H_{2,48} = 13.23$, $p = 0.0006$; $p < 0.05$ for all comparisons after sequential Bonferroni correction). *Post hoc* comparisons revealed that trees dominated by *C. sericeus* showed consistently significantly higher herbivory than trees dominated by at least one of the other two species (Figure VII.2). This difference was significant at $p < 0.001$ in 2001, and at $p < 0.05$ in 1999 and 2000 (Dunn's test). No significant differences could be detected between plants dominated by *C. spec.2* and *C. spec.4*. However, herbivory was lowest in 1999 and 2000 for trees dominated by

C. spec.4. There was a significant negative correlation between median number of ant individuals on a tree and herbivory for trees dominated by *C. spec.4* (Spearman's rank correlation: $r_s = -0.76$, $p = 0.0007$; Bonferroni-corrected: $p < 0.01$). No influence of ant number on herbivory could be detected for *C. sericeus* ($r_s = -0.04$, $p = 0.88$) and *C. spec.2* ($r_s = 0.002$, $p = 0.99$).

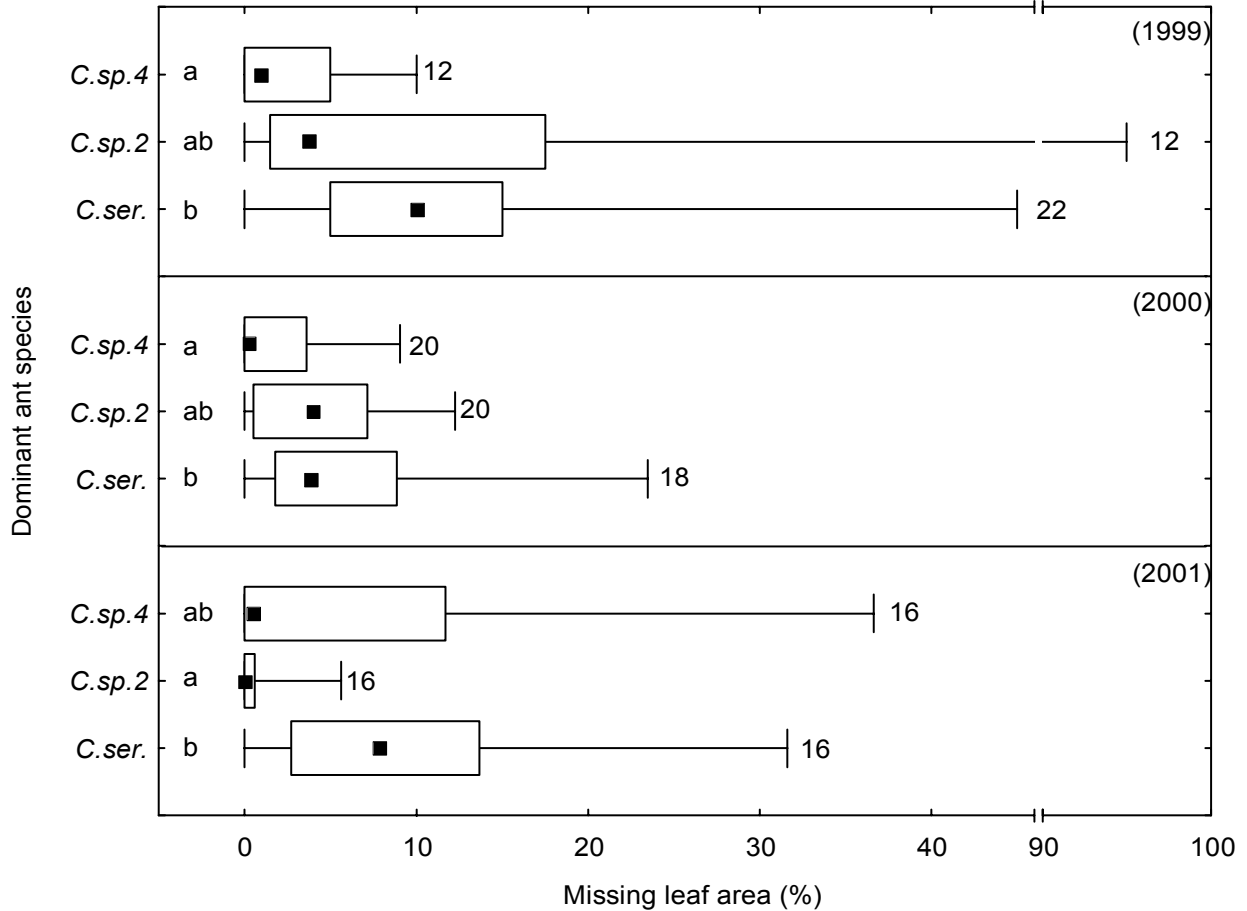


Figure VII.2 Levels of herbivory of *Pseudocedrela*-trees dominated by one of three ant species (*C.sp.4*, *C.sp.2*, *C. sericeus*) in 1999, 2000 and 2001. Explanation of box plots see Figure VII.1. Numbers of studied trees are given at the individual bars. Different letters a, b, c indicate significant differences in median herbivory ($p < 0.05$, Kruskal-Wallis test, Dunn's *post hoc* test).

Influence of ants on other plant-living arthropods. Ants numerically dominated the arthropod communities of the control trees (ants contributed 44.5 % of individuals), while they were excluded very effectively by the banding-treatment (ants then contributed only 0.7 %). With the exception of five tiny *Monomorium* and two *Crematogaster* ant individuals on two trees, no ants passed the barrier (ant numbers on control vs. treatment trees: *WSR*: $z = 5.78$, $N = 44$, $p < 0.0001$ (Bonferroni-corrected: $p < 0.0001$; Figure VII.3). Some arthropod groups showed no differences in abundance between control and treatment plants (Figure VII.3). These were Orthoptera ($z = 0.18$, $N = 44$, $p = 0.86$), Thysanoptera ($z = 0.87$, $N = 44$, $p = 0.38$), Heteroptera ($z = 1.06$, $N = 44$, $p = 0.29$), and Lepidoptera-larvae ($z = 1.26$, $N = 44$, $p = 0.21$). In the Heteroptera, marked differences occurred between one species (-group) of ant-mimetic Miridae, which contributed 53 % of total Heteroptera, and the remaining Heteroptera consisting of several families. Whereas the Miridae were found in significantly higher abundances on the control trees ($z = 3.25$, $N = 29$, $p = 0.001$), the other Heteroptera were more abundant on treatment trees ($z = 2.15$, $N = 23$, $p = 0.03$). An increase in abundance on treatment trees

could also be found for all other arthropod groups regularly occurring on the trees, with Bonferroni-corrected p -values in brackets (Araneae: $z = 5.16$, $N = 44$, $p < 0.0001$ ($p < 0.0001$); Blattodea: $z = 2.31$, $N = 44$, $p = 0.021$ ($p > 0.05$); Homoptera: $z = 2.62$, $N = 44$, $p = 0.009$ ($p > 0.05$); Coleoptera: $z = 2.90$, $N = 44$, $p = 0.004$ ($p < 0.05$); non-ant Hymenoptera (about 70 % Chalcidoidea, other groups regularly encountered were Chrysididae, Sphecidae and Vespidae): $z = 3.71$, $N = 44$, $p = 0.0002$ ($p < 0.01$); all Figure VII.3).

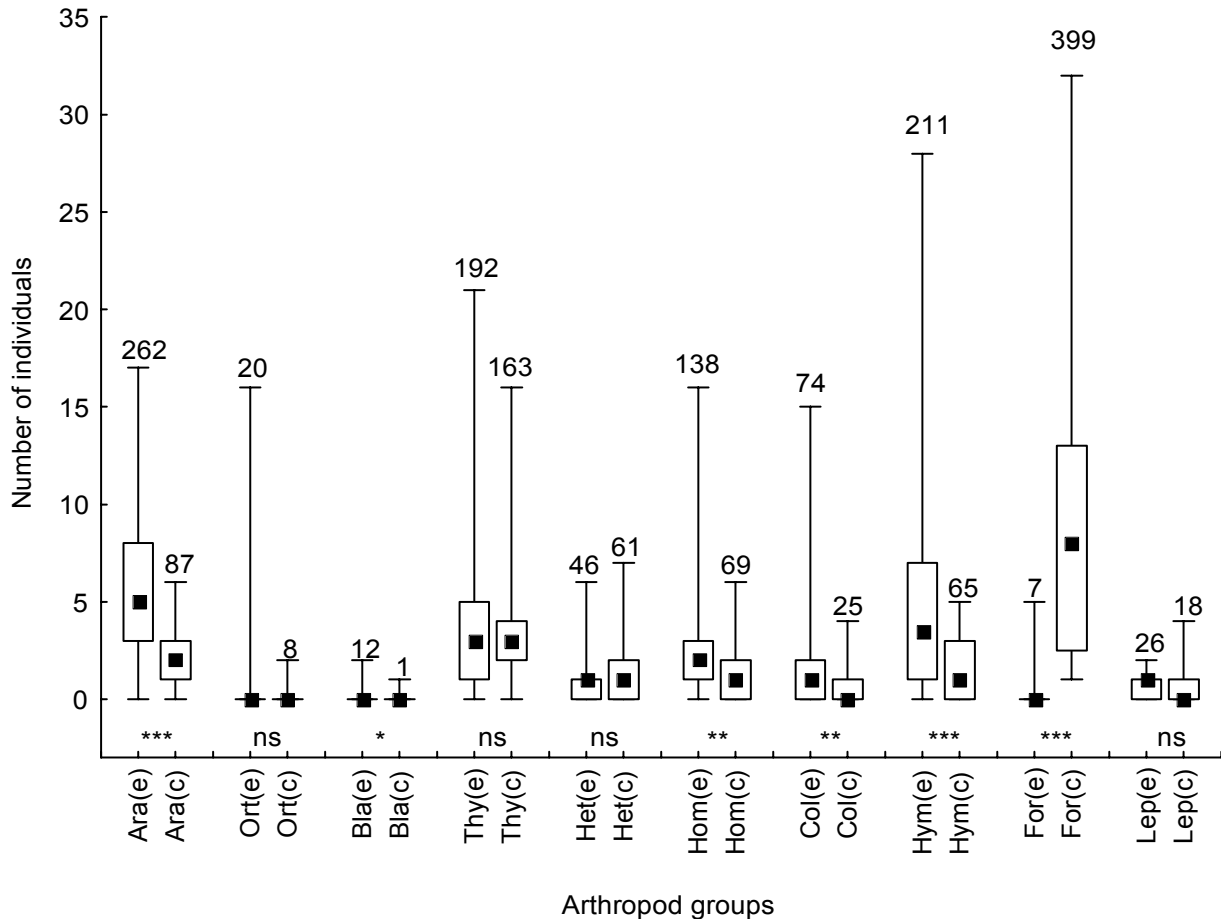


Figure VII.3 Numbers of individuals belonging to different arthropod taxa on *Pseudocedrela*-trees without ants (e) and with ants (c). Box plots see Figure VII.1 for explanation. Total number of trees sampled is given for every group at the individual bars. Ara: Araneae; Ort: Orthoptera; Bla: Blattodea; Thy: Thysanoptera; Het: Heteroptera; Hom: 'Homoptera'; Col: Coleoptera; Hym: non-ant Hymenoptera; For: Formicidae; Lep: Lepidoptera-larvae. Significant differences between exclusion- and control-trees are indicated by *, **, *** ($p < 0.05$, 0.01 , 0.001 ; ns: not significant; Wilcoxon's signed-ranks test, not Bonferroni corrected, see text).

Members of two families of Coleoptera contributed about 60 % of all Coleoptera found. These were Chrysomelidae (25 %) and Cybocephalidae (34 %). Of these, only the Cybocephalidae were - like the other Coleoptera - more abundant on treatment trees ($z = 2.49$, $N = 17$, $p = 0.013$). For the Chrysomelidae, no difference could be detected between control and treatment trees ($z = 0.97$, $N = 17$, $p = 0.33$). The individual numbers of arthropods belonging to groups regularly encountered on control trees (at least on 30 % of control trees) varied not significantly between trees dominated by different ant species (Table VII.1). A trend, however, was detectable for Homoptera (Kruskal-Wallis test: $H_{2,32} = 5.90$, $p < 0.05$, not Bonferroni corrected) with highest abundances on trees dominated by *C. sericeus*. Ant-mimetic Miridae and non-ant Hymenoptera were, in contrast, least abundant on trees dominated by *C. sericeus* (Table VII.1).

Table VII.1 Median individual numbers (minimum; maximum numbers) of arthropod taxa found on at least 30 % of control trees dominated by one of three ant species (*C. sericeus*, *C.spec.2*, *C.spec.4*).

	Ara	Thy	Mir	Hom*	Col	Hym
<i>C. ser.</i> (N = 16)	1.5 (0;6)	3.5 (0;14)	0.0 (0;1)	1.5 (0;5)	0.0 (0;2)	0.0 (0;4)
<i>C. spec.2</i> (N = 10)	2.0 (0;5)	2.5 (0;14)	1.0 (0;6)	0.0 (0;2)	0.0 (0;4)	1.5 (0;3)
<i>C. spec.4</i> (N = 6)	1.5 (1;4)	3.0 (0;16)	1.0 (0;7)	1.0 (0;6)	0.0 (0;1)	1.5 (0;2)

Ara: Araneae; Thy: Thysanoptera; Mir: ant-mimetic Miridae; Hom: 'Homoptera'; Col: Coleoptera; Hym: non-ant Hymenoptera; * indicates significant difference of arthropod numbers on trees dominated by different ant species ($p < 0.05$, Kruskal-Wallis test, not Bonferroni corrected).

VII.4 Discussion

Influence of ant exclusion and different ant species on herbivory. Contradictory effects of EFN-attracted ants on plants have been reported for various ant-plant systems (e.g. Becerra 1989, Bronstein 1998, and references therein). Different parts of our study revealed findings which could also be equivocally interpreted when regarded in isolation.

The exclusion experiments were carried out at a time of high herbivore and ant activity on the study trees (at the beginning of the rainy season, when freshly emerging leaves were heavily consumed by folivores; median herbivory of about 10 % for plants dominated by *C. sericeus*, Figure VII.2). Thereby, the problem of completely missing the period of critical ant-herbivore interactions, should be minimised (cf. O'Dowd and Catchpole 1983). However, our study failed to demonstrate a consistent effect of ants on herbivory. Ants affected herbivory in one year but no effects could be detected in two other years. As the growing season was not completely covered, we cannot say whether these differing outcomes were a consequence of variable insect-plant interactions between different years, or whether they were rather caused by within-year shifts of herbivore activity. Considering other studies, which show that short-term experiments may miss peak activities of herbivores and result in underestimation of both, herbivory and protective ant-effects (Lowman 1992, Heil et al. 2001a), our results are not suited to support or to reject the ant-protection hypothesis. They rather stress the importance of longer-term studies to understand herbivore-ant interactions, even when periods of relevant ant- and herbivore-activity can be covered by short-term studies.

While the exclusion experiments failed to demonstrate a consistent effect of ants on herbivory, the existence of such an effect is indicated by comparing leaf damage of trees dominated by different ant species. These trees obviously differed in suitability for herbivores, as their leaf damage varied in all three study years in a persistent way. Variation of conspecific plants in damage due to herbivorous insects can be caused by many factors (Schoonhoven et al. 1998). In the case of the studied *Pseudocedrela* trees, a species-specific influence of ants seems to be the most parsimonious explanation for the observed patterns of herbivory (Koptur 1984, Dejean et al. 2000a, Sobrinho et al. 2002). The trees differed systematically in the presence of the dominant ant species. For other factors, such as site or genetic effects on the plant's chemistry, no systematic differences are to be expected. Site effects seem to be no plausible explanation, since the trees dominated by different ant species often grew side by side and were exposed to most similar environmental conditions, while trees dominated by the same ant species could also be found at the most distant locations within the study

area. Variation in genetically based resistance to herbivores is a common phenomenon (Berenbaum and Zangerl 1992). However, to help explain the differences in herbivory levels between trees dominated by different ant species, individual attractiveness to herbivores and attractiveness to a particular dominant ant species must have been tightly coupled. For our study, this is an improbable explanation since the relationship between herbivory patterns and a particular ant species persisted over years although the same tree individuals could be dominated by different ant species in different years.

If herbivory is differentially affected by different ant species, this species-specific impact has to be carefully considered when evaluating plant protection by ants. Any experiment focussing on ants like *C. sericeus* will probably fail to detect relevant influences of ants on herbivory, whereas studies using ants like *C. spec.4* would more easily find detectable influences. Aside from being instructive for interpretation of ant-exclusion experiments, the finding of variable levels of herbivory on neighbouring, conspecific plants caused by different ant species means that plants might compete for the best ant-guards. Whether plants can specifically attract particular ant species (e.g. favouring ants with high forager densities like *C. spec.4* via increased nectar production) cannot be answered yet (see Apple and Feener (2001) and Hossaert-McKey et al. (2001) for interspecific variation of plants in attractiveness to ants).

Influence of ants on other plant-associated arthropods. The banding treatment significantly reduced the numbers of ants but of no other arthropod group. We therefore consider differences between arthropod communities on the treatment- and the control-trees as the result of the presence of ants. Ants clearly reduced overall arthropod density and only ant-mimetic Miridae occurred in higher densities on ant-access trees. Herbivores (Orthoptera, Thysanoptera, Lepidoptera, and the chrysomelids among the herbivorous beetles) were less affected than important predatory or parasitic groups (spiders, wasps). The only exception were Homoptera (mainly Cicadellidae, Cixiidae). This group of herbivores clearly gained from ant exclusion, which is in contrast to various studies which found a positive relationship between ants and Homoptera (reviewed in Way 1963, Buckley 1987). However, such positive relationships apply to ant-guarded Homoptera only, which could not be found on *Pseudocedrela* (K. Mody, pers. obs.). The assumption that Homoptera-density is indeed negatively affected by ant presence is additionally supported by the finding of highest Homoptera densities on trees dominated by *C. sericeus* (Table VII.1). This is in agreement with the results of the *natural experiment*, which also suggested weakest effects of *C. sericeus* on herbivores. Lepidoptera-larvae are also considered to be sensitive to ant predation. The lack of measurable reduction of caterpillar density might be explained by at least two factors. First, access of caterpillars to trees is probably hindered by the banding treatment, assuming that most caterpillars approached the trees from the ground after the trees were banded. Second, *Pseudocedrela* might be used by Lepidoptera that are adapted to live with ants. This assumption is supported by the observation that most caterpillars feeding on *Pseudocedrela* were either hairy (lasiocampid) caterpillars or leaf-rollers (K. Mody, pers. obs.). For Orthoptera, Thysanoptera and Chrysomelidae, the lack of measurable ant-effects is in accordance with other studies. Orthoptera were shown to be most strongly affected by tree nesting ants (Dejean 2000), and not by ground-nesting *Camponotus*, which were the dominant ants in our study. The influence of ants on Thysanoptera probably strongly depends on size and foraging characteristics of the ant species involved, and on the availability of sheltered sites for Thysanoptera on the plants (Del-Claro et al. 1997, De Souza et al. 1998). Chrysomelids are well known to possess different adaptations that allow co-existence with ants (Selman 1988, Jolivet 1991).

The reduction of Hymenoptera and Araneae by ants might represent a cost of ant presence to the plant. Both groups can act as plant defenders, either as parasitoids (e.g. the Chalcididae commonly

encountered on *Pseudocedrela*) or predators (Vespidae and Sphecidae, spiders) of herbivores. Hymenoptera might benefit from ant-exclusion by decreased interference and exploitation competition (O'Dowd 1979, Koptur 1985). For spiders, competition with ants and predation by ants seems to be important (cf. Halaj et al. 1997), who found competition but no predation). Ants hunted and expelled spiders from the plants (K. Mody, unpublished). Shortage of prey is considered a major problem for spiders in nature (Wise 1993). Therefore, the general rise in density of other arthropods might have additionally increased spider numbers via improved food availability. The marked reduction of spiders by ants is in contrast to some other studies, which report neutral or even positive correlation between numbers of spiders and ants (Grant and Moran 1986, Karhu 1998, Floren and Otto 2002). One reason could be the way ants are attracted by the plants in the different studies. *Pseudocedrela* attracts ants via EFNs, which are evenly distributed over the whole plant. This results in the presence of foraging ants on the whole plant (Mody and Linsenmair 2003). For the other plants, the sources of ant attractants are either clumped (Homoptera aggregations) or not specified. We suggest that foraging, which is not restricted to specific plant parts, results in more encounters between spiders and ants and thereby a larger impact of ants on spiders.

VII.5 Conclusion

The structure of plant-associated arthropod communities and the distribution of herbivores depends on a multitude of plant characters, which can vary among conspecific plants (e.g. Krischik and Denno 1983, Marquis 1992, Fritz 1995, Osier et al. 2000, Palmer et al. 2000). Our study shows that, aside from plant intrinsic characters such as morphology or chemistry, plant extrinsic factors such as the distribution of plant-attracted ants can govern the composition of arthropod communities on individual plants. This factor should increase between-diversity of communities on conspecific plants the more, the more different the ant communities on these plants are. Therefore, local ant diversity and fidelity of ants to individual plants can be considered as important parameters, affecting the distribution of arthropods on plants and arthropod-plant interactions.

Acknowledgements. The authors thank Andrea Holzschuh and Natalie Beier for research assistance in 1999 and 2000, Lars Hofmann and Cord Mikona for help with analysis of herbivory, and Martin Heil and Erhard Strohm for helpful comments on an earlier version of this manuscript. Permission to perform the research was courtesy of the 'Ministère de l'Enseignement Supérieur et de la Recherche Scientifique', Republic of Côte d'Ivoire. Access permit to Comoé National Park was issued by the 'Ministère de la Construction et de l'Environnement'. The study was partly supported by scholarships of the DAAD (German Academic Exchange Service, No. 332 4 04 101) and by the DFG Graduiertenkolleg 200 to K.M., and by BIOTA (Biodiversity Monitoring Transect Analysis in Africa), German Federal Ministry of Education and Research (BMBF), subproject W06, 01LC0017.

VIII. Finding its Place in a Competitive Ant Community: Leaf Fidelity of *Camponotus sericeus*

Abstract - Many species of ground nesting ants regularly visit extrafloral nectaries (EFNs) of the savannah tree *Pseudocedrela kotschyi*. The distribution of ants on the plants is mosaic-like, i.e. stable and predictable with different ant species dominating neighbouring trees. In order to examine whether foraging behaviour may influence the structure of these ant communities, we investigated individual foraging behaviour of *Camponotus sericeus*, the ant species with highest incidence on *P. kotschyi* trees in the study area. Foragers of *C. sericeus* continuously visited EFNs on the leaves of *P. kotschyi* during their diurnal activity period. Individually marked foragers showed a pronounced fidelity for individual plants and particular leaves. Ant individuals returned to the same plants over a three week period at least. They persistently focused foraging on the same leaves (about three per ant). Null model analysis of ant distribution revealed that ants partitioned their host plant. Co-occurrence on the same leaves was significantly lower than could be expected by chance for most trees studied. Foraging was not oriented towards the plants growing closest to the nest but more distantly growing plants were considerably used. Choice of plants could therefore be influenced by plant quality or by presence of other, competing ant species. The study is the first to show leaf fidelity caused by EFNs and micro-site fidelity within the context of species rich ant communities. It considers the resulting systematic, partitioned use of individual plants as important factor supporting the formation of a mosaic-like ant distribution on plants.

Key words: Community structure, extrafloral nectaries, foraging behaviour, resource partition, *Pseudocedrela kotschyi*

VIII.1 Introduction

Availability and monopolisation of food resources is influential on the distribution of ants and thereby on the structure of local ant communities (Carroll and Janzen 1973, Traniello 1989, Hölldobler and Wilson 1990). Food resources which are predictable in space and time, such as plant affiliated homopterans or nectaries, offer themselves for systematic use and monopolisation since they can be effectively exploited and defended (as is shown in ant mosaics on trees, for example, Strickland 1951, Jackson 1984, Blüthgen et al. 2000). The most systematic and economical resource use has probably been achieved by individual ants specialising on small and clearly defined predictable foraging sites (Lachaud et al. 1984, Fourcassié and Traniello 1993). Fidelity to such micro-sites has been mainly described for ants tending homopterans, clearly demonstrating that homopterans are a valuable and predictable food source (Rosengren 1971, Horstmann and Geisweid 1978, Ebbers and Barrows 1980, Quinet and Pasteels 1996). Micro-site fidelity of individual ants to sugar exudates derived from nectaries has less often been mentioned and has to our knowledge never been investigated systematically for extrafloral nectaries (EFNs) on leaves. It may, however, regularly occur when nectaries are sufficiently attractive, as studies on utilisation patterns of EFNs of orchid flowers (Passera et al. 1994) and nectaries of *Euphorbia* flowering structures (Fowler 1983) suggest.

Besides interference between co-occurring ant species, systematic exploitation of resources may play a major role in influencing the local distribution of ant species. This is indicated by investigations on ant species visiting the same EFN bearing plants, showing that systematic use of EFNs can be considered as a resource defence strategy determining foraging behaviour and distribution of two competing species (Dreisig 2000). For species rich ant assemblages, the potential influence of

systematic foraging behaviour on community structure has never been analysed in detail although patterns have been observed pointing to a systematic resource use as well. In ant mosaics, for example, domination of homopteran aggregations supports formation of a patchwork of different neighbouring communities (e.g. Room 1971, Leston 1978, Majer 1993, Dejean et al. 2000d). Since most ant species in these mosaics are tree nesting, both nest site and systematic resource use may influence the maintenance of the mosaic structure. There are, however, other species rich ant communities using comparable plant derived resources which neither nest in the plants nor restrict most or all foraging activity to them: ground nesting ants which regularly use plant derived carbohydrates and may cover considerable distances to get to their feeding sites on plants (Lévieux 1983b, Oliveira and Brandao 1991, Mody and Linsenmair, *subm.*). Here, a systematic use of plant resources may be also possible and may help to explain the distribution of ants.

The starting point of this study was the observation that neighbouring individuals of the savannah tree *Pseudocedrela kotschy* hosted a distinct mosaic of foragers of different ground-nesting ant species, which specifically visited the EFNs of their host plant. The distribution and abundance of ant species on individual trees was remarkably stable when the same time of the day was considered (Mody and Linsenmair, *subm.*). This finding was surprising because of at least two factors which both should impede the formation of a predictable ant distribution. First, every *P. kotschy* plant grew in the foraging area of several ant species which were able to use and to dominate the EFNs. Second, there existed marked differences in the daily activity period of the ant species, resulting in a high day-time dependent turnover in ant assemblage composition (cf. Oliveira and Brandao 1991, Del-Claro and Oliveira 2000, Hossaert-McKey et al. 2001).

Considering the important role systematic resource use can play in determining the distribution of ants (see above), we wanted to examine whether EFN-exploitation by ground nesting ants can influence the overall ant distribution on *P. kotschy* and whether it thereby helps to solve the apparent contradiction between the observed stable use pattern and the hindering circumstances such as overlapping foraging areas and day-time dependent species turnover. Choosing the ant species with highest incidence on the study plants, *Camponotus sericeus*, as the model species, we addressed the following questions regarding individual foraging behaviour and ant distribution on plants in our system: (1) Can choice of plants be explained by proximity to nest site? (2) Are the same trees systematically used by the same forager individuals, i.e. exists site fidelity to plants? (3) Is the distribution of ant individuals on a plant related to other ants foraging on the same plant, i.e. is there any indication of competition or any other form of resource partitioning on the level of individual plants?

VIII.2 Materials and Methods

Study site and species. The investigation was conducted in Comoé National Park during April through June 2000 and April through May 2001 (early rainy season). Comoé National Park is located in the north-east of the Republic of Côte d'Ivoire, and covers 11,500 km² of Guinea- and Sudan-zone savannah. It supports a wide variety of vegetation types including gallery forest, island forest, savannah forest, shrub and tree savannah, grass savannah and Bowal areas which are almost free of vegetation. A more detailed description of Comoé National Park is provided elsewhere (Poilecot 1991, Porembski 1991, Rödel 2000). The study area was situated within the Guinea-savannah in the southern part of the Park (08°44'N, 003°49'W, c. 215 m).

The studied host plant species, *Pseudocedrela kotschy* (Schweinf.) Harms (Meliaceae), is widespread in West African savannahs (Aubréville 1950, Steentoft 1988), and it is locally very abundant in the study area (Hovestadt 1997). In the following, *Pseudocedrela kotschy* is designated

only by its generic name. *Pseudocedrela* is a medium-sized (4-5 m, maximally 12 m), monoecious, deciduous savannah tree, found specially on heavy soils. It is able to spread into eroded and Bowal areas by root suckers, thereby forming *Pseudocedrela*-dominated stands of woody vegetation. The young foliage is silvery-grey, the leaves being impari- or paripinnate, with up to 12 alternate asymmetrical leaflets (Steentoft 1988). *Pseudocedrela* bears inconspicuous leaf-EFNs which occur mainly along the leaf nerves and are distributed over all leaves of the whole plant. EFNs are so unproductive that nectar neither accumulated to visually detectable amounts nor could it be tasted by humans (even after exclusion of nectar-collecting animals). Ants, however, visited these EFNs regularly and were able to extract carbohydrates (mainly fructose and glucose as demonstrated by HPLC analyses of gut contents of ants captured when leaving their host plant; Mody and Hilpert, unpublished). In the study area, almost all plants were permanently visited by different ant species. Individual *Pseudocedrela* plants were usually dominated by a single ant species at a given time, although several ant species were simultaneously foraging in the surrounding of individual *Pseudocedrela* plants. Species number of ants foraging at the same day-time on a tree ranged between 1 and 4 (median 1 for morning and night censuses and 1.5 for afternoon censuses). Since a day-time dependent species turnover was observed in the study site, species number of ants foraging on single trees increased when censuses at different day-times were combined (range between 1 and 6, median 3; N = 132 trees, Mody and Linsenmair, subm.). Ant numbers on single plants ranged between 1 and 40 (median 4). The small ant numbers on some trees probably reflected the trees' limited value as food resource rather than low density of potentially competing ants. This was indicated by a rapid increase in ant numbers and a change of species composition (in average in less than 30 minutes) when honey-sucrose-water (2:2:1) solution was provided as additional food source (K. Mody, pers. obs.). *Camponotus sericeus* Fabricius was the ant species with highest incidence on the studied *Pseudocedrela* trees (median 3, range between 1 and 28). This species was used as an example to study the influence foraging behaviour of ant species plays for community organisation. *C. sericeus* is ground nesting, strictly diurnal, with peak activity between 0800 hours (two hours after sunrise, N = 12 nests) and 1800 hours (half an hour before sunset, N = 8 nests). Its foraging radius is at least 26 m around the nest and it quickly flees to the nest when it is disturbed (K. Mody, pers. obs.).

Ant marking and tree selection. 120 *C. sericeus* workers were caught in a marking tube when leaving their nests (N = 5, nest marking experiment = NM experiment) and individually marked with four colours of fast drying enamel paint applied to thorax and leg segments. They were set free after 3 minutes when the paint had dried. In the following 14 days, *Pseudocedrela* trees in the nest's surrounding were checked twice a day for foraging ants and the marked individuals were recorded. Recordings of an ant foraging on plants were considered as 'independent' when the ant had returned to the nest between two consecutive observation events. Since the ants returned several times a day and every evening to their nest (Mody & Beier, pers. obs.), recordings obtained in the morning and in the afternoon (separated by at least five hours) as well as recordings obtained on different days, were treated as independent. Trees visited by marked foragers were numbered and distance to ant nests was determined. The tree which was most often visited by an individual ant was considered as primary, i.e. its preferred host, while other trees, more or less occasionally visited, were considered as secondary hosts. The Wilcoxon's signed-ranks test was used to test for distance differences between primary host and secondary or potential (when no secondary hosts could be detected) hosts growing closest to the nest (Sokal and Rohlf 1995).

Site partition and site fidelity. For this investigation, 12 *Pseudocedrela* trees dominated by *C. sericeus* were chosen as study plants. Spatial information was obtained for each plant by recording its exact position with a portable Differential GPS (Leica SR530, Leica Geosystems AG, Switzerland),

providing exact information on vertical and horizontal position with a precision of 1 - 5 cm. 77 *C. sericeus* workers foraging on the study plants were individually marked (tree marking experiment, TM experiment) as described above and followed back to their nests after release from the marking tube to ensure that mobility was not markedly affected by the marking procedure. The nest was defined as the always inconspicuous hole in the soil which was the starting and ending point of each foraging trip of a worker. As it could not be ascertained in this study whether different entrance holes separated from each other by only a few metres did belong to the same or to a different colony, the term nest always refers to these persistently used entrance holes and does not automatically mean 'colony'. Aggression tests revealed no differences between workers obtained from the same nest, from neighbouring nest entrances (a few metres apart from each other) and from nests separated by several hundred metres (aggression level was generally low). The position of the nests was also mapped using the Differential GPS.

Six out of the 12 study trees were selected for a more specific examination of host visitation. The leaves of every plant were numbered throughout and the foraging patterns of the 48 *C. sericeus* workers, which were foraging on these trees and which were individually marked, were recorded. These study plants were then checked for marked ants at six to 15 independent occasions in a three week period and the movements of each marked ant on the numbered leaves were recorded for an 'observation period' of three minutes by 'focal sampling' (Martin and Bateson 1993). Seven marked ants of three colonies were caught on the trees. They were kept separated from their colonies for two days. They were maintained - sorted by colonies - in '*Drosophila*'-tubes (10 cm in height, 5 cm in diameter) in open laboratory huts, protected from direct sunlight, provided with moistened filter paper, and exposed to ambient air temperature and humidity. No food was offered, but water was provided twice a day. They were released at their host trees and their behaviour was recorded.

Analysis of aggregation and co-occurrence. The distribution of individual ant foragers on the host trees was described by the index of dispersion (I_D) (Southwood and Henderson 2000), with $I_D = s^2 (v - 1) / m$, where m and s^2 are the sample mean and variance and v is the sample size. This index has been widely used and provides satisfactory results for a small v (e.g. Morris et al. 1992, Mody et al. 2003). I_D values significantly greater than the χ^2 statistic for the 0.025 probability level with $v - 1$ degrees of freedom indicate an aggregated distribution of considered taxa (Ludwig and Reynolds 1988).

Null model analysis (Gotelli and Graves 1996) was applied to examine distribution patterns of ants co-occurring on the same trees. Monte Carlo randomisations were performed to create 'pseudo distributions' which could then be statistically compared with the patterns in the real data matrix using the software EcoSim (Gotelli and Entsminger 2001). This enabled us to test observed distribution data implying resource partitioning against the hypothesis of a random distribution. We submitted presence/absence matrices in which columns are leaves and rows are forager individuals to analyses of co-occurrence, using EcoSim. We computed the Stone and Roberts' (Stone and Roberts 1990) C-Score co-occurrence index with the EcoSim defaults with fixed columns and rows and 1,000 iterations. The C-Score index is negatively correlated to co-occurrence. If resources are partitioned and overlap of foraging areas is reduced, the C-score should be significantly higher than expected by chance. The null hypothesis is that the presence of an ant forager on certain leaves is not influential on the occurrence of other foragers and that therefore no evidence is given for competition or any other form of interaction leading to site partitioning and thus influencing forager distribution. This null hypothesis is rejected - indicating that partitioning of foraging area (leaves) is taking place - if the C-Score for the original matrix is beyond the 95 % confidence limits of randomised matrices (Gotelli 2000), for further details see Ribas and Schoereder (2002).

VIII.3 Results

Tree selection. Of the 120 *C. sericeus* workers of the nest marking experiment (NM experiment), 63 (52.5 %) could be found foraging on 16 *Pseudocedrela* plants in the surrounding of the nest. Most of these ants could be repeatedly recorded at independent controls. Considering those individuals which have been found for at least six independent times (N = 22), a clear preference for certain tree individuals (primary hosts) became evident. 10 ants could be exclusively found on a single *Pseudocedrela* plant (up to 23 times!), while eight ants clearly preferred a certain tree but could also be found on other trees. Only for four ants no preference (visitation ratio of primary and secondary hosts ≥ 0.5) was detectable. No indication could be found that trees growing closest to the nest were preferred. On the contrary, distance between primary host and nest was significantly larger than distance between nest and nest-closest secondary or potential hosts (median distance primary host - nest: 4.5 m, secondary host - nest: 1.5 m, $z = 3.26$, $p = 0.001$, N = 18 foragers, Wilcoxon's matched pairs test).

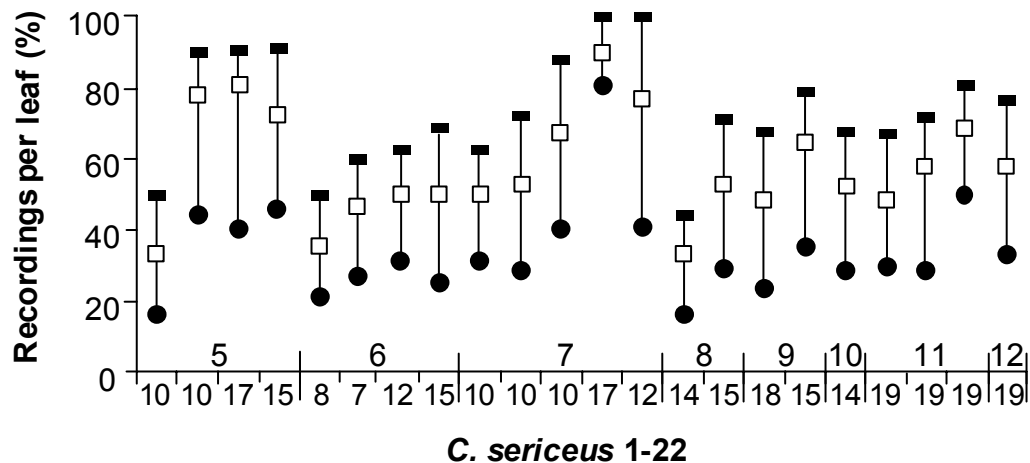


Figure VIII.1 Leaf visitation patterns of 22 *Camponotus sericeus* foragers recorded at least five independent times after individual marking. For each forager the number of independent re-sights (number above abscissa) and the total period of time (in days) with recordings of the respective forager (number below abscissa) is given. The cumulative percentage of foraging-recordings on the same leaves in proportion to total foraging movements on a plant is indicated with (●) for percent recordings on one leaf, (□) on two leaves, and (■) on three leaves.

Site partition and site fidelity. Of 77 *C. sericeus* workers foraging on the 12 study trees, 75 returned directly to their nest after release from the marking tube. This allowed to assign them to 21 nests. Individual trees were used by ants from one up to six nests with maximum distances between nests of co-occurring ants reaching 22 m (mean \pm SD: 6.9 ± 4.7 m). The 48 *C. sericeus* which were studied in more detail belonged to 10 different nests and covered distances between 1.8 m and 17.6 m between nest and host tree (direct line; median distance 3.6 m; maximum distance between nest and *P. kotschyi* host determined so far was 26.4 m for an unmarked *C. sericeus* worker). Of these 48 ants, 43 (89.6 %) returned to the tree where they were marked after their initial retreat in the nest. This fidelity to host trees was persistent as marked ants returned regularly to their original host tree in the following independent controls covering up to 19 days (Figure VIII.1; returning ants observed in (mean \pm SD) 57.9 ± 24.8 % of controls). Although all potential host trees were controlled for ants, only two marked ants could be recorded (once) on a tree different from the original host tree.

Fidelity of foragers was not only restricted to individual trees but clear preferences for small partitions of the tree could be found. Considering those ants recorded for at least six times (five re-sights), marked preferences for certain sections of a tree, usually a few leaves, became evident (when ants with fewer recording events were taken into account, preference for particular leaves was higher). The analysis of the position of individual ants on a host plant revealed that one single leaf contributed between 17 % and 80 % (mean \pm SD: 34.0 ± 13.6 %), two leaves between 33 % and 90 % (mean \pm SD: 57.4 ± 15.4 %) and three leaves between 44 % and 100 % (mean \pm SD: 73.1 ± 15.4 %) of all re-sights (Figure VIII.1). This clear preference for certain ‘target-leaves’ resulted in a significant aggregation of recorded ants on certain leaves (Figure VIII.2). This was true although all recordings per leaf obtained in one ‘observation period’ were considered only once (this is a very conservative measure of leaf visitation since preferred leaves were usually visited several times within one observation period and other leaves were only quickly passed to get to the ‘target leaves’). Fidelity to ‘target-leaves’ seemed not to be short-lived and not dependent on distance between nest and host tree. It could be demonstrated for several ants to persist at least for the whole period the study was conducted (19 days from individual marking to end of recordings, Figure VIII.1) and it could be found for both, ants nesting closely to the host tree (1.8 m), and ants nesting quite distantly from the host tree (17.6 m).

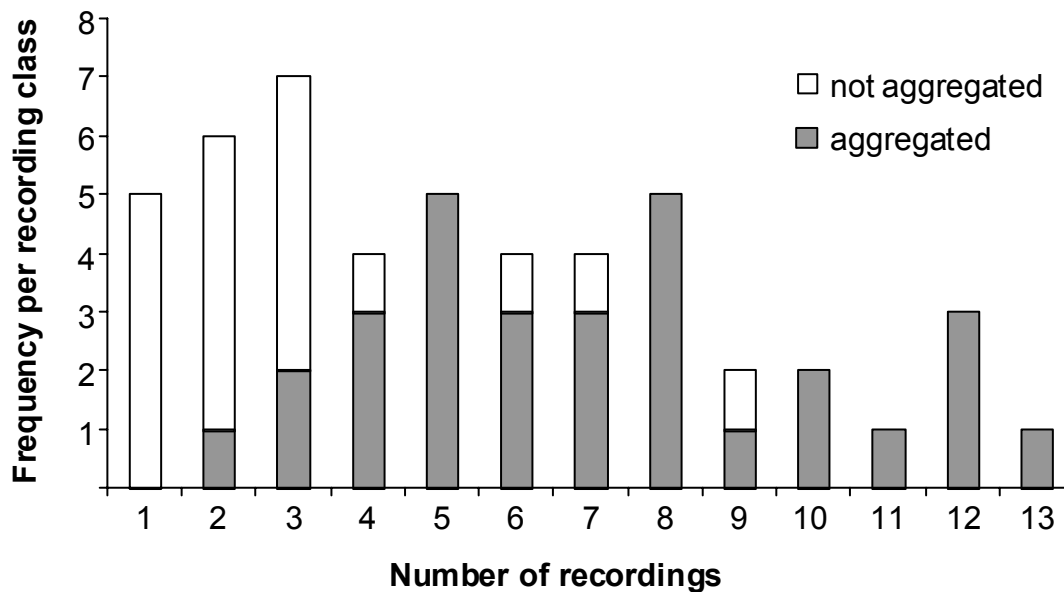


Figure VIII.2 Ant distribution on leaves of host plants as measured by the index of dispersion (I_D) in relation to number of recordings (containing initial recording and re-sights). Aggregation is indicated when certain leaves were significantly more often visited than others, i.e. when I_D values were significantly greater than the χ^2 statistic for the 0.025 probability level with $n - 1$ degrees of freedom.

Fidelity was also not interrupted by a two-day removal of foragers as four out of the seven isolated ants returned within a few hours to ‘their’ target leaves. Before visiting target leaves, all ants tried to return to their nest after their release at the base of their host tree. Three foragers returned after an acclimation-phase of 20 – 100 sec in a straight and considerably quick way to their nest. This became evident especially for the foragers covering longer distances. The forager returning to its nest 7.7 m away from the host tree needed 84 sec for its route of 8.4 m (0.36 km/h, route 9.1 % longer than direct line). The forager returning to its nest 17.7 m away from the host tree needed 227 sec for its route of 19.4 m (0.31 km/h, route 9.6 % longer than direct line). The remaining four foragers behaved

differentially after release. One forager climbed on the host tree, met a nest-mate and was carried by her after 50 seconds of intensive communication on a direct way back to the nest (adult transport). The other foragers seemed to be too weak and were not able to return to the nest. They also did not return to their host plant.

Null model analysis of ant distribution revealed that ants usually partitioned their host plant. Co-occurrence on the same leaves was significantly lower than could be expected by chance for most studied trees (Table VIII.1). An exception from this finding was a small tree with exceptionally large leaves (Pk4, Table VIII.1) visited by a relatively high number of ants of a nearby nest (distance between Pk4 and nest: 1.9 m). On this tree, the ratio of visited leaves to ants was 0.8 while it lay between 2.4 and 3.3 for the other trees. Leaf visitation patterns found for the tree Pk2 were only marginally different from a random ant distribution. Besides this deviation from ant distribution patterns found on trees of comparable size, Pk2 differed in respect to the number of nests foraging ants were belonging to. While the other trees were used by ants from one to two different nests, Pk2 was visited by ants from four different nests.

Table VIII.1 Characteristics of six *Pseudocedrela kotschy* trees (Pk1-6) and associated *Camponotus sericeus* foragers. C-Score indices of the randomised and observed matrices for ant distribution on each studied tree are shown. The observed C-score values are presented in addition to minimum and maximum values calculated for 1,000 randomised matrices per sample. *p*-values are given for two-tailed tests, with the probabilities of the observed indices being larger or smaller than the expected randomised matrices.

Tree ID	Ant number (Nest number) {Distance {m}}	Leaf number T (V)	Obs. Matrix T (V)	Randomised matrix		<i>p</i> -values	
				Minimum T (V)	Maximum T (V)	Obs.>exp. T (V)	Obs.<exp. T (V)
Pk1	13 (2) {7.6,17.6}	41 (31)	20.71 (20.71)	18.67 (18.76)	20.01 (19.94)	<0.0001 (<0.0001)	1.000 (1.000)
Pk2	12 (4) {3.5,3.7, 4.5,7.4}	39 (29)	16.82 (16.82)	15.73 (15.91)	17.08 (17.35)	0.075 (0.051)	0.934 (0.952)
Pk3	6 (1) {3.2}	38 (16)	8.53 (8.53)	6.53 (6.53)	8.80 (8.60)	0.010 (0.010)	0.992 (0.998)
Pk4	6 (1) {1.9}	9 (5)	1.40 (1.40)	1.40 (1.40)	1.93 (2.40)	1.000 (1.000)	0.365 (0.382)
Pk5	8 (2) {1.8,5.2}	32 (26)	27.61 (27.61)	25.43 (25.54)	27.12 (27.61)	<0.0001 (0.001)	1.000 (1.000)
Pk6	3 (1) {2.1}	20 (10)	13.67 (13.67)	11.00 (11.00)	13.67 (13.67)	0.022 (0.010)	1.000 (1.000)

Ant number: number of marked ants co-occurring on the same tree; Nest number: number of nests used by ants co-occurring on the same tree; Distance: distance between ant nests and host tree; T: total leaf number of a tree, or, for C-score analyses, computation related to this total leaf number; V: number of leaves visited by marked ants, or, for C-score analyses, computation related to this number of visited leaves; Obs. Observed; exp. expected.

VIII.4 Discussion

The understanding of individual foraging behaviour may help to explain the distribution of ants and thereby the composition of ant communities (Hölldobler and Wilson 1990, Crist and MacMahon 1991). Several studies have shown that individual ants concentrate their foraging on particular micro-sites of high resource concentration, creating a stable ant distribution pattern on these resource patches (Rosengren 1971, Horstmann and Geisweid 1978, Ebberts and Barrows 1980, Fowler 1983, Lachaud et al. 1984, Passera et al. 1994, Quinet and Pasteels 1996). Although such resource utilisation patterns have been described predominantly for single species in species poor ant communities, the principle of fidelity to rewarding sites could also help to explain the stable patchwork of foragers of different species observed for *Pseudocedrela* ant communities (Mody and Linsenmair, *subm.*).

The present study demonstrated that EFN-visiting foragers of *C. sericeus* showed a marked fidelity not only to individual plants but to small partitions (a few leaves) of these plants. It also became evident that this systematic EFN use was not restricted to plants growing in the immediate vicinity of the nest. It was rather found for both, plants growing closely or distantly to the nest. The first case, the preferred use of nest-near resources, can be easily explained in terms of foraging efficiency and is often described for ants (Inouye and Taylor 1979, Koptur 1984, Bronstein 1998). The other case, the systematic foraging on distant resources which are patchily distributed over a large area, is more difficult to explain. It requires well developed powers of orientation (Wehner et al. 1983, Cosens and Toussaint 1985) and additionally comprises costs such as higher time and energy effort, increased frequency of disorientation, and increased predation risk (Wehner et al. 1983, McIver 1991, Denny et al. 2001). Its occurrence may be explained by constraints exerted by a diverse ant community with many co-occurring, competing ant species. In the following, micro-site fidelity is discussed with regard to orientation capability, resource location and the distribution of other, potentially competing ant species.

Micro-site fidelity of *C. sericeus* and marking method. Fidelity to individual leaves was explicitly studied and shown by the tree marking (*TM*) experiment. A marked fidelity of individual foragers to particular trees became evident with both marking schemes, independently whether ants were marked when leaving their nest (nest marking experiment, *NM*) or when foraging on a particular tree (*TM*). The re-sight rate, however, was different between both treatments. The high re-sight rate (90 %) of *TM* foragers indicates that the marking procedure can be considered harmless for the ants in general. It also suggests that disturbance of foraging ants is not of great influence on the willingness to return to the same site, a conclusion which is also supported by the removal experiment – where an even stronger disturbance could not deter the ants from returning to their host plant. The low re-sight rate (53 %) of *NM* ants may indicate that a division of labour occurs in *C. sericeus*. This has been described for other species of ants using both, predictable food resources such as plant products and unpredictable resources such as free ranging prey and animal derivatives (Wehner et al. 1983, Schmid-Hempel 1984, Sundström 1993, Schatz et al. 1995). In this case, only the forager fraction devoted to the exploitation of stable EFN secretions would have been re-sighted and not, e.g., those searching for food on the ground or those fulfilling tasks in the nest and its immediate vicinity.

Differences between the two marking schemes could also be observed regarding the number of trees visited by individual foragers. While about one half of regularly re-sighted *NM* ants used other trees than their primary host, only two out of 48 *TM* ants could be observed using other trees. Aside from differences in foraging behaviour between specialised ‘tree foragers’ (predominantly sampled when *TM* ants were considered) and ‘all foragers’, there may be methodological reasons explaining parts of the differences. Although all trees were checked for marked ants in the *TM* experiment, the

focus was put on ant distribution on the primary hosts. In the *NM* experiment, however, all trees within a given radius around the nest were checked at least two times a day and foraging ants were more often registered when on the way between nest and target tree. For these ants, approaching their target tree, intermediate stops on trees growing by the wayside could be observed several times. Although the ants never stayed for longer than a few minutes and quickly continued their way, these intermediate stops could be easily counted as secondary tree visitation when only their momentary position and not the whole foraging course was followed.

Host choice and orientation capability of *C. sericeus*. The study could not show any preferences for trees growing closest to the nest. Trees in close proximity to the nest were regularly used but most marked ants passed several *P. kotschy* trees before reaching their target tree. As mentioned above, strong powers of orientation are required for foraging on resources which are patchily distributed over a large area. *C. sericeus* seemed to be mainly dependent on individual orientation (tandem running, explicitly described for this species (Hölldobler et al. 1974), could also be observed, but only in the context of recruitment to newly established food sources). Individual orientation is probably based on visual cues and on individual spatial memory (Rosengren and Fortelius 1986, Salo and Rosengren 2001), and it is reported to be dependent on experience and on age of foragers (e.g. Wehner et al. 1983, Harrison et al. 1989). As *C. sericeus* foragers turned out to be relatively long-lived, there would be great opportunities to improve orientation by means of learning the best way between nest and host (60 % of regularly returning ants were recorded on the same micro-site for at least two weeks and 18 % for 19 days (till the end of recordings); life expectancies reported for other ants living in comparable open habitats were six days (Schmid-Hempel 1984) and 14 days (Porter and Jorgensen 1981)).

Location, quality, and monopolisation of resources. The use of trees growing distantly from the nest indicates that the costs related to such resources are eclipsed by other constraints or compensated. The ants are probably not omniscient in respect to all available food sources. Although not critically tested in this study, observations on foragers leaving their nest suggest a directional fidelity (e.g. Fewell 1990, and citations therein), excluding from the start all trees growing in deviating directions from being used by particular foragers. Once having discovered a suitable host plant, the ants may stop to intensively search for a better one as search is costly and foraging efficiency can be optimised by learning the best way between nest and host. For fast-running ants like *C. sericeus* even longer distances may pose no relevant problem (homing *C. sericeus* ran up to 6 m/min while running *Formica aquilonia* covered 1.6 - 2.4 m/min (Cosens and Toussaint 1985), *Paraponera clavata* 2.2 - 4.6 m/min (with experienced workers running significantly faster than naive ants (Harrison et al. 1989) and foraging *Cataglyphis bicolor* on average 3 m/min (Wehner et al. 1983)). Fidelity to familiar trees may therefore be an economic way to deal with resources which are patchily distributed but predictable once discovered. This optimisation of foraging by fidelity may also help to explain the mosaic-like distribution of the ants: nothing else is to be expected, if they, in fact, focus their foraging activities on the resource patch which they first discovered and accepted as suitable. Other resource patches can then remain unused although they seem more attractive to the human eye, a phenomenon which is not restricted to *C. sericeus* as is indicated, for example, by observations on *Formica pallidefulva* (Fowler 1983) and on *F. aquilonia* (Cosens and Toussaint 1985).

Aside from the necessity to find a tree, visitation patterns can be influenced by quality of trees as food resource and by the trees' accessibility to ants. Trees of low food quality, for example as a consequence of a harsh micro-environment, genetic predisposition for producing only small amounts of nectar, or biotic interactions (Heil et al. 2000), may be disregarded when other food sources are

available. Although not explicitly studied yet, such marked differences in attractiveness of individual *Pseudocedrela* plants to nectary-visitors seem to exist. This is suggested by bee- and wasp-visitation of these plants after exclusion of ants. When ants were excluded from *P. kotschyi* trees, even neighbouring plants greatly differed in numbers of nectar-collecting bees and wasps attracted to the trees, suggesting considerable variation in attractiveness to non-ant Hymenoptera at least (Mody, pers. obs.). Accessibility of trees is probably most strongly influenced by competing ants. In a multi-species community - as is found for the described *P. kotschyi* trees with all plants being occupied by a mosaic of different ant species - a great variety of competitive interactions will occur. While exclusion of competitors by interference is restricted to ants with best fighting capabilities, resource monopolisation by exploitation can also be attained by weaker species. Assuming a mixture of interference and exploitation competition seems a most promising approach in explaining the patterns found of how a diverse set of ant species is monopolising neighbouring trees. *C. sericeus* turned out to be a non-aggressive ant species with lower fighting capabilities than at least two other co-occurring ant species (Holzschuh and Mody, unpublished results). In order to achieve the observed monopolisation of EFN bearing partitions of a tree, *C. sericeus* therefore may use both, interference against weaker competitors and exploitation against all kinds of intruders. Monopolisation of EFNs by exploitation reduces attractiveness of EFNs to intruders and may stimulate them to search for other resources without any aggressive contact between resident ants and intruders.

The observed fidelity to a few leaves suggests that systematic use may be an especially effective means of monopolisation by exploitation. As is described by (Dreisig 2000) for *Camponotus floridanus* competing with *Pseudomyrmex mexicanus* for EFNs of a perennial herb, *C. sericeus* may reduce attractiveness of *Pseudocedrela*-EFNs to any unsystematically intruding ant by systematic depletion of nectar supply, thereby preventing its accumulation to any considerable amount. The small-scale partition of a tree down to a scale of a few persistently used leaves is thereby probably a compromise between renewal-rate of nectar supply and sufficient reduction of attractiveness to any competing intruder, ensuring rewarding resource availability for longer periods of time. Partition of a tree can be optimised not only from the perspective of the individual forager but also from the colony-perspective. This can be deduced from findings obtained for the harvester ant *Messor barbarus*, where areas used by nest-mates were even more avoided than those used by alien foragers (Acosta et al. 1995). It is also suggested in this study by the clearer separation of foraging areas on trees used by several nest-mates (Pk1, 3, 5, 6; Table VIII.1) compared to those with overlapping foraging areas of alien conspecifics (Pk2; Table VIII.1). Avoiding any form of time- and energy-consuming competition and yet utilising the resources in an optimal way may only be possible via co-operation within a society.

VIII.5 Conclusion

The present study demonstrated that EFNs on the leaves of *P. kotschyi* are an attractive food resource for *C. sericeus* and that the ants are able to concentrate foraging on clearly defined partitions of particular plants. This specialisation on a few leaves can be regarded as an extreme example of micro-site fidelity. It demonstrates that micro-site fidelity is neither restricted to highly rewarding and clumped resources such as Homoptera aggregations (Horstmann and Geisweid 1978, Ebberts and Barrows 1980, Quinet and Pasteels 1996) nor to spatially concentrated resources such as nectaries of flowering structures (Fowler 1983, Passera et al. 1994). The study also demonstrated that systematic resource use can even be maintained in species rich ant communities, consisting of species with differing competitiveness and foraging skills. Whether foraging behaviour can be regarded as a generally important factor determining the structure of the diverse ant community using neighbouring

Pseudocedrela trees, has to be settled by further investigations considering foraging characteristics (e.g. orientation capabilities, mobility and life expectancy) of the other dominant ant species.

Acknowledgements. We thank Natalie Beier for her very helpful research assistance in 2000 and Brigitte Fiala for comments on an earlier version of this manuscript. This work also benefited from the constructive comments of two anonymous referees. Permission to perform the research was courtesy of the ‘Ministère de l’Enseignement Supérieur et de la Recherche Scientifique’, Republic of Côte d’Ivoire. Access permit to Comoé National Park was issued by the ‘Ministère de la Construction et de l’Environnement’. The study was partly supported by scholarships of the DAAD (German Academic Exchange Service, No. 332 4 04 101) and the DFG Graduiertenkolleg 200 to K.M., and by BIOTA (Biodiversity Monitoring Transect Analysis in Africa), German Federal Ministry of Education and Research (BMBF), subproject W06, 01LC0017.

IX. Persistent Aggregation of Herbivorous Beetles on Conspecific Host Plant Individuals: What are the Causes?

Abstract - A distinct tendency to aggregate has been reported for many herbivorous insects. It was also confirmed by this study on two herbivorous beetle species (*Apogonia fatidica* and *Proictes curvipes*), feeding on the savannah tree *Combretum fragrans*. Both species exhibited a pronounced aggregation pattern. They repeatedly (after several complete beetle removals) and persistently (within the same and between different years) colonised some *C. fragrans* trees in great quantities, while they were completely absent from other trees. Two types of feeding choice experiments (paired preference tests and Cafeteria experiments) were carried out in the laboratory to assess whether beetles differentiate between leaves of individual, conspecific plants and whether preferences expressed under experimental conditions relate to beetle distribution in the field. Besides intraspecific variation in leaf palatability, other factors can affect beetle distribution and cause aggregated distributions. Three of them were tested in the following approaches. The potential influence of variation in leaf age between individual plants was investigated in paired preference tests, in which young and old leaves of the same plant were offered simultaneously to the beetles. The influence of tree size was assessed by regression analyses, in which the relation between beetle abundance on particular plants and different size variables of the same plant was tested. The influence of volatile attractants on beetle behaviour was investigated testing *Combretum* leaves and feeding conspecifics as potential sources of volatile attractants for *A. fatidica* in an olfactometer bioassay. The experiments showed that (i) the mobile scarabaeid *A. fatidica* discriminated between conspecific plant individuals and that preferences in the laboratory were clearly linked to beetle distribution in the field, (ii) the less mobile weevil *P. curvipes* also differentiated between conspecific plant individuals but that preference was not always reflected in the beetles' distribution in the field, (iii) beetles did not discriminate between young and old leaves, (iv) beetle distribution was not correlated with tree size and (v) beetles were attracted by volatiles emitted from *Combretum* leaves and from feeding conspecifics. It is concluded that for mobile herbivorous beetles such as *A. fatidica*, intraspecifically variable host plant palatability can be an important factor in determination of aggregation. Aggregation on suitable plants can be boosted by volatiles emitted from the plants or feeding conspecifics, which may attract beetles over longer distances to the plants. Less mobile herbivores such as *P. curvipes* have more restricted choices among conspecific plants. In such cases, aggregation may therefore reflect other constraints than food suitability.

IX.1 Introduction

Understanding the distribution of herbivorous insects on conspecific host plants is of particular interest to agricultural and ecological research (Clarke et al. 1997, Schoonhoven et al. 1998, Dent 2000). It may help to predict and to counteract pest development and to develop and test ecological and evolutionary hypotheses. At the local, within-host plant population scale, different factors have been attributed to the distribution of herbivore species. These include external traits, which are not directly related to the plant (like enemy load and neighbourhood effects), structural and morphological traits (size, shoot and leaf morphology) and attractiveness of plant parts as food. The importance of these characteristics for herbivore distribution varies between different herbivore species, being influenced by resource requirements, feeding modes and mobility constraints (Stewart 1996). In order to understand which plant characteristics are particularly important for herbivore distribution, the study of conspecific, syntopically growing plants is particularly informative. These plants are comparable with respect to large scale factors (e.g. the species pool for colonisation is identical) and with respect

to plant-external factors (environment, climate is comparable). Studying those plants hence allows to directly investigate processes linked to individual plants, which are the unit of selection for both plant breeding and evolution and thereby for central insect-plant interactions.

A striking feature of most populations of insect herbivores is their tendency to aggregate on particular host plants. Aggregation of insect herbivores on individual plants or even specific zones of individual plants has been reported by many studies (e.g. Lawton 1983, Lowman 1985, Bach and Carr 1990, Morris et al. 1996, Rowe and Potter 1996). According to its commonness, many factors have been found to affect and to determine the 'phenomenon aggregation'. As important variables can be considered: plant architecture and size (Bach 1981, Rowe and Potter 1996), nutritional/defensive characteristics of leaves (Feeny 1970, Schultz 1983), enemy load (Stamp and Bowers 1988, Heinrich 1993), distribution of young leaves (Raupp and Denno 1983, Basset 1992) and the presence of feeding herbivores in general or conspecifics in particular.

Especially for herbivorous beetles, attraction by feeding conspecifics has been reported to cause aggregations in many cases (Iwabuchi and Takahashi 1983, Harari et al. 1994, Yarden and Shani 1994, Loughrin et al. 1996a, b, Harari and Landolt 1997, Harari and Landolt 1999, Ruther et al. 2000, Peacock et al. 2001, Ruther et al. 2001). The attractants may be emitted from the beetles themselves (sex or aggregation pheromones) or from the plants while being damaged by the beetles (feeding-induced plant volatiles). However, none of the mentioned studies has investigated the factors initialising the aggregation process, namely the variables determining the first beetles to stay or feed on a particular plant. Assuming that neighbouring (conspecific) plants are all passably suited as hosts, then the first beetles could be guided to the plants by random processes or by external factors like apparency (e.g. height, see Rowe and Potter 1996), start feeding and attract conspecifics. In the case of a more or less random initial colonisation, the distribution of aggregations should not be persistent over time. Instead aggregations should be variable, and different plants should be selected at different periods by varying beetle numbers. However, since different studies showed that aggregative insect distributions are persistent over time, deterministic factors have to be considered in order to understand aggregation-formation. The spatial context of the plant (visibility, accessibility), its size (persists at least for years for perennial woody plants) and some chemical/nutritional properties of consumed plant material can be considered as such deterministic factors.

A pilot study prior to this work (Mody 1998) indicated that individual *Combretum fragrans* plants hosted characteristic arthropod communities whose species composition was surprisingly stable over time. It suggested that factors resulting in a persistent aggregation of a considerable proportion of community members would be a possible explanation effecting this noteworthy community structure. Therefore, understanding the processes that (i) initiate aggregation formation, (ii) maintain aggregations and (iii) affect interspecific linkages, should be considered crucial to understand processes determining not only single species distributions, but also community composition.

Selecting two abundant beetle species from the pool of *Combretum*-associated herbivores, this study aimed at testing and understanding (1) whether the beetle distribution is in fact aggregated within the same year and between different years, (2) if beetles differentiate between leaves of individual, conspecific plants when removed from their natural environment (as a persistent distribution would require persistent determinants such as stable food quality) and, in case preferences could be detected, if these preferences would match the beetle distribution in the field. In addition, the study tested as alternative potential determinants of beetle distribution (3) the availability of foliage of different age classes and (4) tree size parameters. Bioassay experiments were (5) conducted to examine whether beetles would be able to locate food resources/conspecifics via volatile attractants.

IX.2 Materials and Methods

Study site and species. The study was conducted in Comoé National Park, Republic of Côte d'Ivoire, from June through August 1997, from April through July 1999 and 2000 and from April through May 2001. Comoé National Park is located in the north-east of the Republic of Côte d'Ivoire, and covers 11,500 km² of Guinea- and Sudan-zone savannah. The climate of Comoé National Park is characterised by a long dry season from about November to March/April, a mean annual precipitation of 950 mm and an annual average temperature between 25 °C and 28 °C (Linsenmair 1998). More information on Comoé National Park is provided in Chapter III of this thesis and by (Poilecot 1991) and (Rödel 2000). The study area was situated within the Guinea-savannah in the southern part of the Park (08°44'N, 003°49'W, c. 215 m a.s.l.).

The studied host plant species, *Combretum fragrans* F. Hoffm. (Combretaceae) is a medium-sized (maximum height 12 m), deciduous savannah tree that is widespread in West African savannahs (Aubréville 1950) and reaches densities of 400 plants per ha in the studied area (K. Mody, pers. obs.). *C. fragrans* is characterised by twigs and leaves showing a high degree of mechanical resilience. It thus can be intensively sampled without being damaged by beating methods.

The two studied beetle species, the scarabaeid *Apogonia fatidica* Kolbe (Scarabaeidae, Melolonthinae; det. F.T. Krell) and the weevil *Proictes curvipes* Hust. (Curculionidae, Entiminae; det. R. Thompson) are to be regarded polyphagous (*Apogonia* accepted eight out of nine tree species belonging to six families as food in feeding trials testing 10 beetle specimens, *Proictes* accepted 17 out of 18 tree species belonging to eight different families). The beetles can be regularly found for several weeks (*Apogonia*) or months (*Proictes*) during the rainy season, feeding on different woody-plant species. They differ in size (*Apogonia* about 0.9 cm, *Proictes* 0.4-0.5 cm in length) and in activity patterns. *Apogonia* is strictly nocturnal and emerges at dusk from its daytime shelters and flies quickly to its host plants, where it feeds for several hours. In contrast to *Apogonia*, *Proictes* can be found for 24 hours on its food plant. Being nonvolant, *Proictes* is much more limited in changing its location and in choosing particular food plants.

Below, the host plant *C. fragrans* and the two beetle species, are designated by their generic names.

Host plant characterisation. The host plants were characterised by several variables. Plant size was determined as plant height, plant width (maximum diameter), plant depth (maximum diameter perpendicular to plant width), and leaf number. Spatial information was obtained by recording the exact position of each plant with a portable Differential GPS (Leica SR530, Leica Geosystems AG, Switzerland), providing exact information on vertical and horizontal position with a precision of 1-5 cm. All studied plants were syntopically growing within a marginally sloping (maximum orthometrical height difference 4.2 m on a distance of 106 m) section of shrub savannah which was located between gallery forest and open grass-land. The maximum distance between two study plants was 430 m for the *Apogonia* study and 134 m for the *Proictes* study. The minimum distance was 2.5 m for the *Apogonia* study and 9.5 m for the *Proictes* study.

Beetle sampling. According to their differing size (*Apogonia* is more conspicuous than *Proictes*, see chapter III of this thesis) and activity patterns, the methods applied to sample the beetles from their host plants differed for the two species. Both methods aimed at collecting all beetles from the respective host, providing a very accurate estimate of abundance per plant and of rate of new recolonisation (as collected beetles were removed from the plants for further experiments). In order to

describe beetle distribution and to estimate the persistence of distribution patterns, both species were repeatedly sampled within the same year and between different years.

Sampling of *Proictes* was conducted during the day, using a beating tray specified for sampling the complete arthropod community of a respective study plant (Mody 1998): a deep tray of the dimension 60 x 40 x 62 cm, made of smooth balloon-silk, fitted underneath with a 500 ml polyethylene bottle simultaneously acting as collecting pot and weight to tighten the steep tray sides (see Figure III.5a). Before using the beating tray, the plant was carefully inspected for visible arthropods, which were directly transferred into the beating tray. After this, the whole plant was inserted into the tray and intensively shaken. The whole procedure was repeated three times. Finally, the ground under the plant was checked for fallen beetles.

Apogonia sampling was performed at night between 20:00 and 02:00 hours, depending on weather conditions. A white cotton sheet was spread out under the host plant under investigation to collect falling beetles. Then the whole plant was carefully examined for beetles using a torch and a head lamp and all beetles directly visible were manually placed in the beating tray. Finally, the whole plant was carefully put into the beating tray and shaken. Fallen beetles were collected from the sheet. *Apogonia* sampling was repeated at different time intervals. In 1999 at two different intervals, changing sampling intervals between two consecutive nights and ten days. In 2000 and 2001 sampling was performed every seven to ten days.

Feeding-choice experiments. Preference tests were carried out in the laboratory to assess whether beetles would differentiate between leaves of individual, conspecific plants when removed from natural context (surrounding vegetation, conspecifics, competitors, predators). The *a priori* hypothesis was that plants which differ in beetle densities in the field also differ in palatability, with plants hosting more beetles being more palatable. The plants were tested simultaneously either pairwise or in a 'Cafeteria experiment' (cf. Figure III.8). The beetles used in the experiments were sampled within the running survey of beetle distribution (complete sampling of beetles on particular plants, see above) and additionally on other *Combretum* plants to obtain the high number of beetles simultaneously and consecutively tested.

For pairwise comparisons, *Combretum* plants were classified according to the total beetle number they were hosting in the field as 'attractive' and 'unattractive' (after sampling all beetles on a plant at least three times). The plants then were paired with a pair consisting of an attractive and an unattractive tree. For pairwise comparisons, 12 leaves were randomly sampled from each pair member (by blindly pointing to the plant with a stick and picking the leaf first encountered), rejecting only young leaves which were not fully-grown. One leaf of each pair member was offered in parallel over night (from 19:00 till 08:00 hours) to ten *Apogonia* or six *Proictes* beetles. The beetles were kept in plastic terraria (18 x 11 x 14 cm; *Apogonia*) or Petri dishes (9 cm in diameter; *Proictes*) provided with moistened filter paper. Size of paired leaves was either standardised to square leaf pieces (16 cm²; *Apogonia*, some tests in 2000), or it was aligned by cutting the leaves and providing comparably sized parts to the beetles (*Proictes*), or it remained unchanged (*Apogonia*). The way leaves were presented did not affect the outcome of the experiments (K. Mody, unpublished; Randlkofer 2000).

In the 'Cafeteria experiment', leaves of 12 different *Combretum* individuals were simultaneously offered to the beetles. The leaves were randomly collected from the 12 trees, and a standardised square (9 cm²) was cut from each leaf. The 12 leaf-squares (one of each tree) were placed at random order in a plastic terrarium and offered over night (from 19:00 till 08:00 hours) to 24 *Apogonia* beetles. Leaf area was determined for each square after the experiment to determine consumed leaf area using the digital-camera technique described below. A reference part of each leaf was taken from the residues of each leaf.

Quantification of leaf area and consumption. Leaf area was determined before the experiment and after the experiment to assess leaf area consumed in the preference tests. Different methods were used in different study years. In 1999, the contour of each leaf was exactly copied to drawing paper. After the experiment, the remaining leaf parts were put on top of the contour-drawing and the changes in contours were copied to the drawing. In the laboratory in Würzburg, the drawings were scanned using a flat bed scanner (SNAPSCAN 1236, AGFA) and the area of the leaf before the experiment and of the consumed leaf parts was quantified using the NIH Image digitising software. In 2000 and 2001, area of the leaves and consumed leaf area was determined as follows: The leaves were photographed with a digital camera (Nikon, COOLPIX 950) in a standardised procedure. They were spread out on a board of white Plexiglas and tightly covered with a hinged lid of non-reflecting glass. Leaves were photographed with a reference square (1 cm²) from a fixed distance, with the same resolution, and without flash. Digital photographs were analysed using the graphics package 'Adobe PhotoShop'. By referring to the 'pixel number' of the reference square, the leaf's area could be computed. Leaf area was also determined for leaf-remainings after the feeding experiment. From differences in leaf area before and after the experiment, consumed leaf area was computed. For determination of fresh weight and leaf water content, leaf parts (the residue of the leaf when leaves were standardised in area) or leaf discs (1 cm diameter; when whole leaves were offered to the beetles) extracted from the freshly harvested leaves, were weighted and their area determined (as described above). The leaf pieces were then dried to weight constancy and re-weighted to determine leaf specific fresh and dry weight (mg fresh or dry weight per area) and consumed leaf mass.

Influence of leaf age on feeding preference. In order to test whether availability of young leaves could affect the attractiveness of a given plant to *Apogonia* beetles, comparisons between young and old leaves of the same plant were conducted. For each plant, 12 old and 12 young leaves were presented in a pairwise design as described above (using complete leaves with only a reference disc cut out). Young leaves were defined as the third, almost fully grown leaf, counted from the tip of a twig. The twigs were randomly selected. Old leaves were defined as the third leaf from the basal end of a twig. The third leaf was used instead of the first (the oldest) since the first two leaves counted from the basal end were often (not always) very small and atypical. At the time of the experiment, old leaves were about 1.5 months old while young leaves were still in the process of being continuously produced.

Olfactometer bioassay. The attraction responses of *Apogonia* scarabaeids to odours of *Combretum* leaves and feeding conspecifics were tested in a Y-tube olfactometer as described by Harari et al. (1994; with slight modifications, see Figure IX.1). The olfactometer was made of a Y-shaped PlexiglasTM tube. The tubing possessed a stem that was 2 cm i.d. x 14 cm long and two arms that were 2 cm i.d. x 10 cm long. Each arm led to a cubically polyethylene trap-box (10 x 10 cm), followed by the same type of box containing a source of odours. Air was pushed into the system by an aquarium pump, first through the box containing the test materials (halved leaves or beetles as treatment and empty box as control), then through the traps, then into each arm of the olfactometer, and, finally, through the stem of the olfactometer. As an assay protocol, scarabaeids were released individually at the base of the stem of the Y and their movement upwind toward an odour source or control was observed. A positive response was recorded when a scarabaeid entered one of the arms of the Y and fell into the trap box. No response was recorded and the assay was ended if a scarabaeid did not reach the trap within 10 min of release. After the testing of five beetles to a treatment and control setup, the olfactometer was turned 90° to control for any position effects and the assay was repeated with a new

beetle until beetle activity levelled off (beetles were usually tested between 20:00 till 22:00 hours). Between assay replicates, the boxes and tubes were washed with hot water followed by ethyl alcohol and again water.

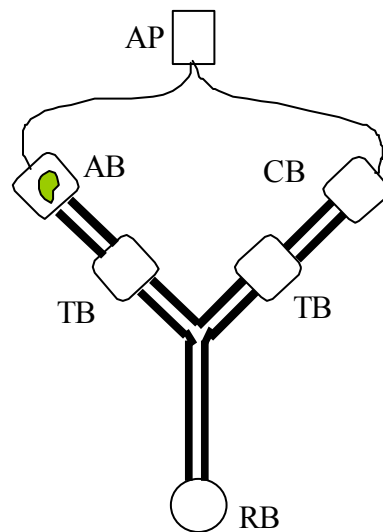


Figure IX.1 The olfactometer. AP: aquarium pump, AB: attractant box, CB: control box, TB: trap box, RB: release box.

Statistical analyses. Distribution of beetles was assessed computing the index of dispersion (I_D) (Southwood and Henderson 2000), with $I_D = s^2(v - 1) / m$, where m and s^2 are the sample mean and variance, respectively, and v is the sample size (for further information on I_D see chapter V). Before conducting statistical analyses, all data were checked for normality. In order to satisfy the assumption of normal distribution in regression analysis, beetle abundance data for 2000 were transformed to $\ln(Y + 1)$. Comparisons of leaf mass consumed in pairwise preference tests were conducted using paired t-tests. Leaf mass consumption in the Cafeteria experiments was analysed using Friedman's ANOVA and Wilcoxon-Wilcox post hoc tests. Multiple linear regression analyses were used to relate the effect of different tree size parameters to beetle distribution in the field.

IX.3 Results

Distribution of *Apogonia fatidica* scarabaeids on syntopic *Combretum fragrans* plants. Complete sampling of *Apogonia* beetles feeding on *Combretum* individuals demonstrated that beetles occurred highly aggregated on particular tree individuals (Figure IX.2 and Figure IX.3; I_D values (for total beetle number per tree): 154.4, (1999); 267.7 (2000); 346.7 (2001), all $p < 0.0001$). Repeated complete beetle removals within every year confirmed that this distribution pattern was not caused by a single colonisation event but remained stable over time (Figure IX.2 and Figure IX.3). Some trees were persistently unattractive to beetles within years (e.g. *Combretum* plant 1-12, Figure IX.1; an exact definition of 'unattractive' is not possible but less than two beetles in four complete beetle removals during the main period of activity is certainly a conservative definition of unattractive) or between years (Cf2-4, Figure IX.3). Other trees turned out to be always attractive (plant 58, Figure IX.2; Cf8 and Cf13, Figure IX.3). There were, however, also trees on which beetle abundance varied, with numbers above-average occurring only at certain times within the same year (plant 40-46 with high

beetle numbers at the first collection or 56,57 at later collections; Figure IX.2) or between years (Cf1, Figure IX.3).

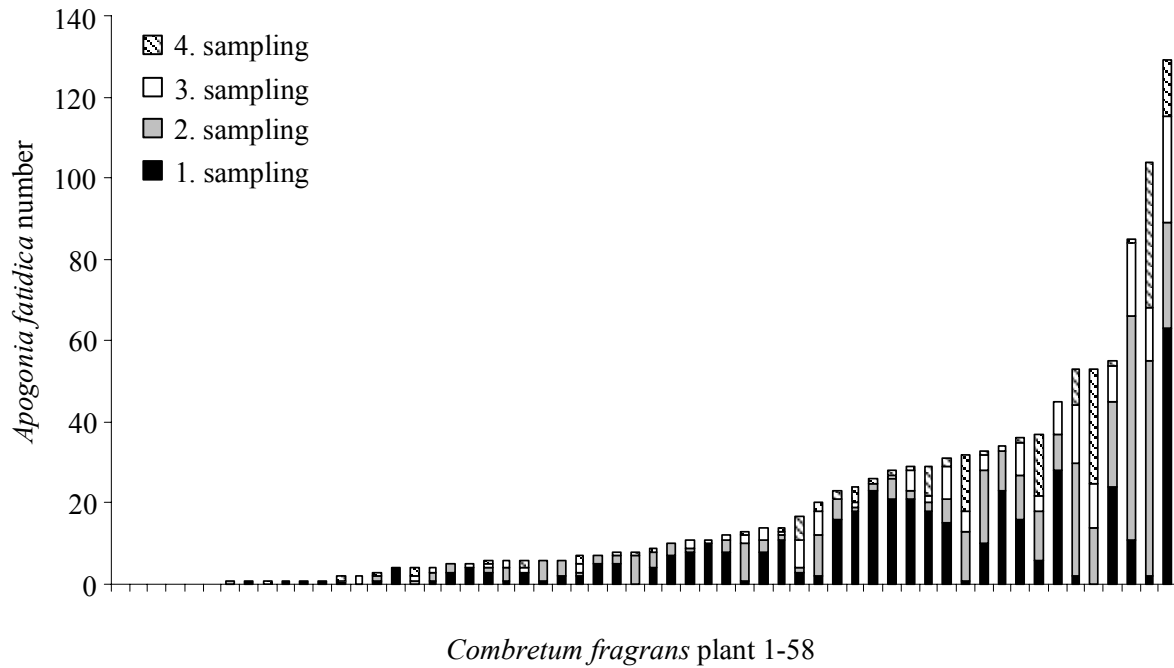


Figure IX.2 Distribution of *Apogonia fatidica* on 58 syntopically growing *Combretum fragrans* plants. Beetle survey (complete counting and removal) was conducted four times within a two-months period.

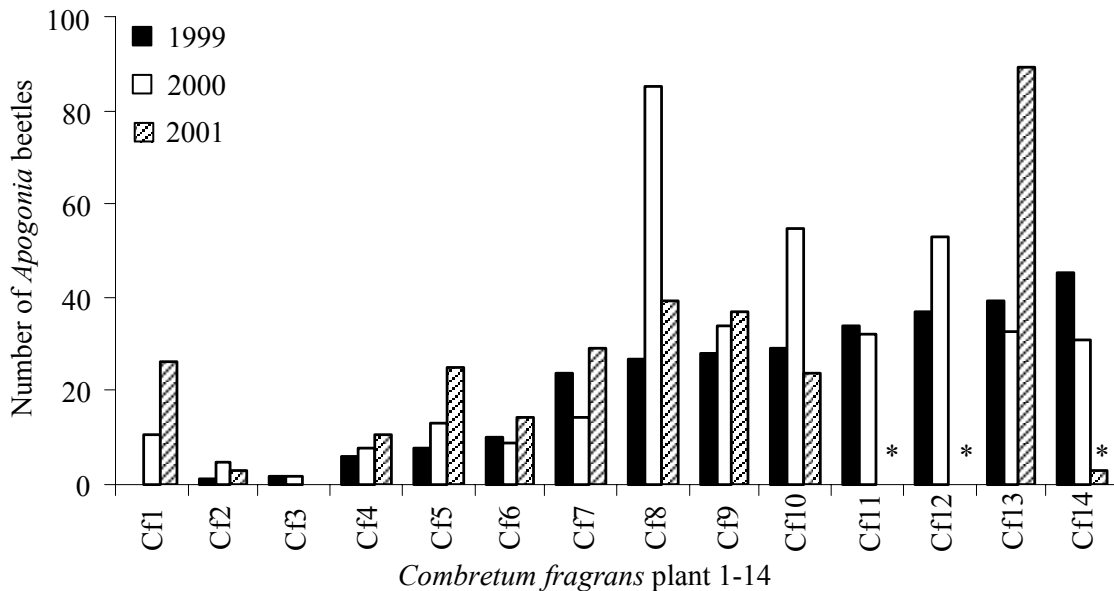


Figure IX.3 Distribution of *Apogonia fatidica* on 14 syntopically growing *Combretum fragrans* plants in three different years. Beetle survey (complete counting and removal) was conducted six times (1999, 2001) or four times (2000) within a two-months period. Cf: *Combretum fragrans* plant; *: trees destroyed by bushfire in the dry season 2000/2001.

Distribution of *Proictes curvipes* weevils on syntopic *Combretum fragrans* plants. The complete sampling of *Proictes* beetles feeding on *Combretum* individuals demonstrated that these weevils occurred highly aggregated on particular tree individuals (Figure IX.4; I_D values (for total beetle number per tree): 435.5 (1997); 589.2 (1999); both years $p < 0.0001$). Repeated complete beetle removals within both years confirmed that this distribution pattern was not caused by a single colonisation event but remained stable over time (Figure IX.4). The aggregation pattern of *Proictes* thus resembled that of *Apogonia* (Figure IX.2), but the restriction to particular trees was even more pronounced and very stable within the same year and between different years. Some trees (especially Cf8) were used by both species, while other trees had no overlap between the species. Overall, there was no correlation between the abundance patterns of the two beetle species (Spearman's rank correlation: $r_s = -0.22$, $N = 14$, $p = 0.45$).

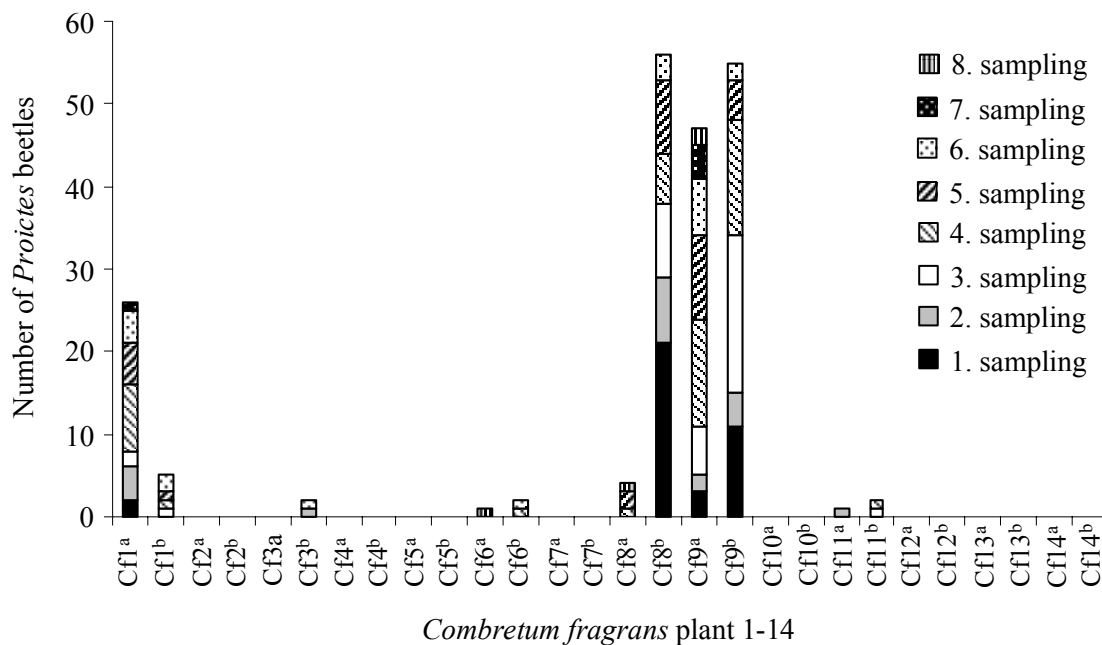


Figure IX.4 Distribution of *Proictes curvipes* on 14 syntopically growing *Combretum fragrans* plants in 1997^a and 1999^b. The beetle survey (complete counting and removal) was conducted eight times within three months (1997) or six times within a two-months period (1999).

Paired choice tests of *Apogonia fatidica* and *Proictes curvipes*. Results of paired choice tests were highly consistent with predictions based upon the pattern of distribution in the field for *Apogonia*. Of 16 plant pairs tested in feeding trials, the beetles almost consistently preferred the plant hosting higher beetle densities. Only in one plant pair, leaves with lower beetle numbers were more attractive, and for one other pair, no difference in palatability of leaves could be detected (plant pair 1 and 2, respectively; Figure IX.5). The outcome of the feeding experiments was also highly consistent for trees tested at different times within the same year (plant pair 12-16) and between different years (1999, 2001; plant pair 16). The results were not affected by the way leaves were presented to the beetles, either as complete leaf or as leaf-piece (all Figure IX.5).

For *Proictes*, consistence with the predictions based upon patterns of distribution in the field was limited (Figure IX.6). The weevils were, like *Apogonia* beetles, clearly able to differentiate between individual trees. However, feeding preferences were not always linked to beetle distribution patterns in the field. Out of five plant pairs tested, only in one a significant preference for the plant hosting higher beetle numbers in the field could be detected (plant pair 2, Figure IX.6). For two pairs no difference was detectable and for one the predictions were reversed with preference for the plant with lower beetle densities in the field (plant pair 4). The most pronounced difference in preference could be detected for a plant pair where both pair-members hosted no beetles in the field (plant pair 3, Figure IX.6).

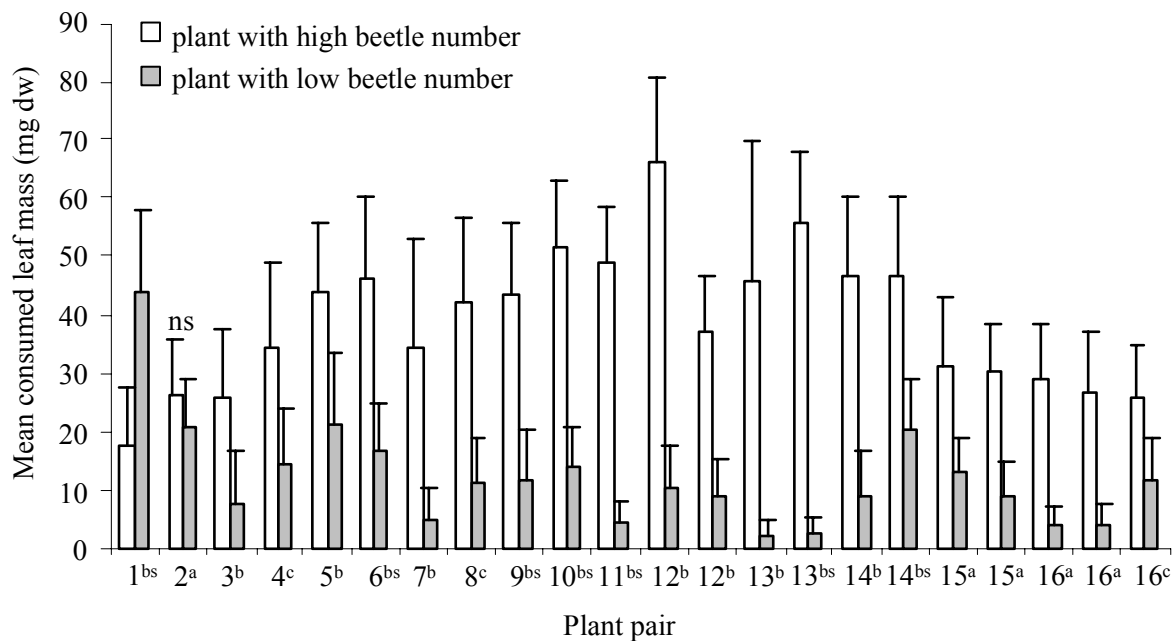


Figure IX.5 Paired feeding choice tests for *Apogonia fatidica* reporting mean (+ s.d.) consumed leaf mass. Leaves of 16 pairs of different *Combretum fragrans* plants were presented to the scarabaeids in 1999^a, 2000^b and 2001^c. Leaves were either presented as standardised leaf squares^s or as complete leaf (all pairs not marked with^s). Some of the trees used in the preference tests are also presented in Figure IX.2, 3 & 6: Plant pair (many beetles/few beetles): 2(Cf12/Cf6), 4(Cf7/Cf3), 8(Cf10/-), 12(-/Cf15), 15(Cf5/Cf1), 16(Cf13/Cf2). ns: not significant; all other comparisons significant with $p < 0.05$ (at least); paired t-test, N = 12 leaf pairs per trial; 10 *Apogonia* beetles per leaf pair.

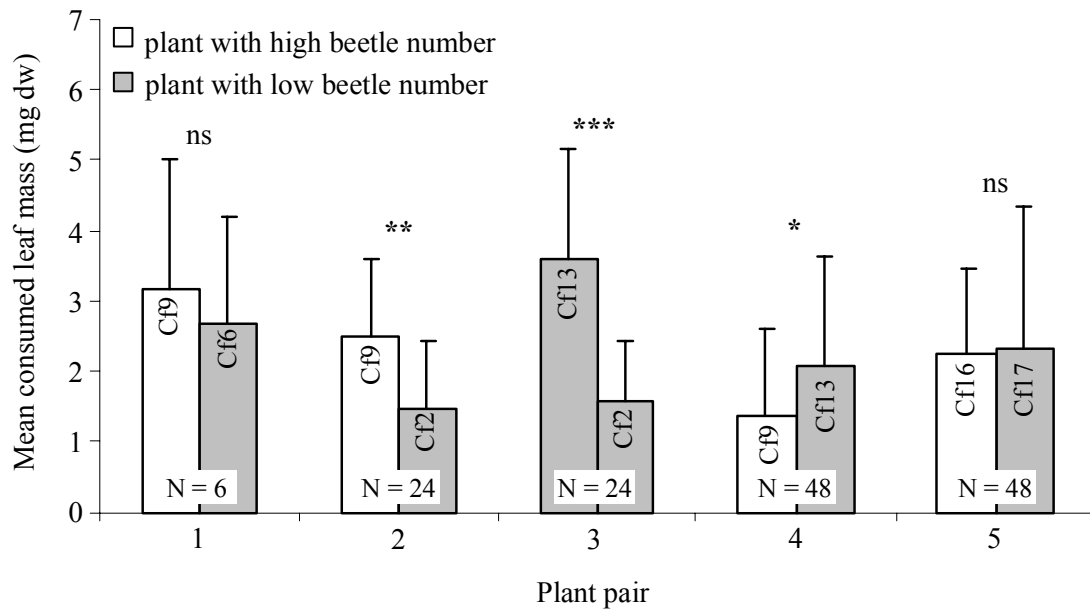


Figure IX.6 Paired feeding choice tests for *Proicetes curvipes* reporting mean (+ s.d.) consumed leaf mass. Leaves of 6 different *Combretum fragrans* plants were presented in 5 pair-combinations to the weevils in 1999. Four *Combretum* plants (Cf2, Cf6, Cf9, Cf13) were also part of the survey study (cf. Figure IX.3). Cf16 and Cf17 were additionally included as neighbouring trees hosting considerably differing beetle numbers: Cf16: 37 beetles/300 leaves; Cf17: 4 beetles/300 leaves). N: number of leaf pairs tested; significant differences in feeding preference for leaves of trees hosting high and low beetle numbers in the field are indicated by *, **, *** ($p < 0.05, 0.01, 0.001$; ns: not significant; paired t-test).

Cafeteria choice tests of *Apogonia fatidica*. The Cafeteria experiments demonstrated that beetles discriminated not only between leaves of paired plant individuals but also when leaves of several (12) plants were offered simultaneously (Figure IX.7). The beetles consumed much more leaf material of some trees than of others (Friedman's ANOVA $\text{Chi}^2 = 109.8$, d.f. = 11, $N = 24$, $p < 0.00001$). According to the Cafeteria experiment, beetles were able to discriminate between (i) highly unattractive plants (Cf2, Cf15, Cf3, Cf4), (ii) plants of intermediate attractiveness (e.g. Cf13) and (iii) highly attractive plants (especially Cf8). For most plants, palatability status did not change between years and was comparable between results from paired choice tests and the Cafeteria experiment (cf. Figure IX.5, Figure IX.7). The only exception was Cf1, which hosted no beetles in 1999, but did so in the two other years, and which was correspondingly more attractive in the Cafeteria experiment in 2001 (cf. Figure IX.3, Figure IX.7). The Cafeteria experiment demonstrated that differences in palatability of plants as found in laboratory tests and numbers of beetles occurring on the plants in the field were significantly correlated (Spearman's rank correlation: $r_s = 0.75$, $N = 12$, $p = 0.005$).

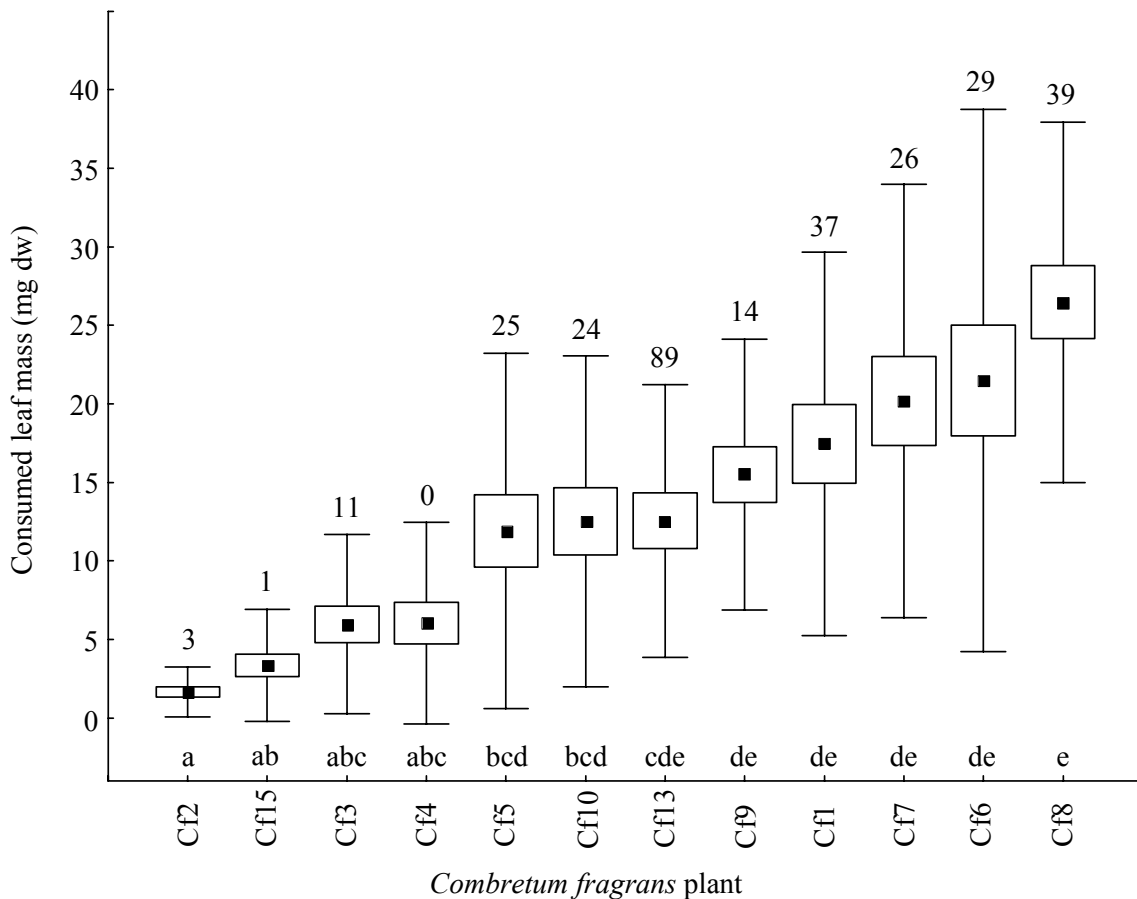


Figure IX.7 Cafeteria feeding choice tests for *Apogonia fatidica*. Leaves of 12 different *Combretum fragrans* plants (Cf) were simultaneously presented to 24 *Apogonia* beetles. Box plots display means (black square), standard error (box) and standard deviation (whiskers). Numbers of beetles found in six sampling events on the respective trees in the field are given at the individual bars. Significant differences ($p < 0.05$) in consumed leaf mass between different plants are indicated by different letters (a-e; Friedman's ANOVA, Wilcoxon-Wilcox post hoc test, $N = 24$ replicates of the experiment).

Influence of leaf age on feeding preference. Comparisons of young and old leaves of the same plant individual demonstrated no consistent preference for any of the two leaf types. In no comparison significant differences in feeding preference could be detected, and the trend was variable with older leaves being more attractive in Plant 1-3 and younger leaves being more attractive in Plant 5-6 (Figure IX.8).

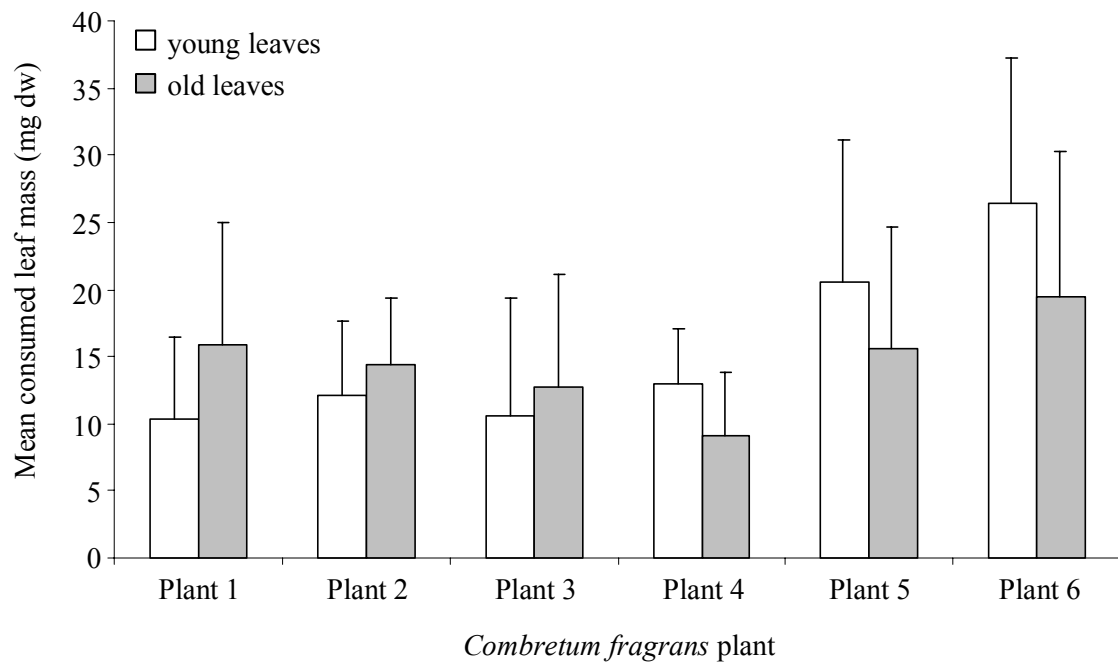


Figure IX.8 Paired feeding choice tests reporting mean (+ s.d.) consumed leaf mass of young and old leaves of six *Combretum fragrans* plants. No significant difference in preference of *Apogonia fatidica* could be detected for any of the plants tested (paired t-test, N = 12 leaf pairs per plant; 10 *Apogonia* beetles per leaf pair).

Influence of plant size on distribution of *Apogonia fatidica*. No relation between beetle distribution patterns on plants and the size of the plants could be detected in two different years. Neither any single size variable (tree height, tree width, tree depth, leaf number) nor the combination of all characteristics significantly affected beetle distribution (Table IX.1).

Table IX.1 Regression parameters ($y = a + b_1x_1 + b_2x_2 + \dots + b_px_p$) relating effect of plant size to beetle distribution on *Combretum fragrans* plants.

summary 1999						
	N	r	r ²	r ² adjusted.	F(3,10)	p
	14	0.567	0.321	0.118	1.579	0.255
source						
	β	β (s.e.)	b	b (s.e.)		p
constant	-	-	-8.708	34.675		0.807
tree height	-0.306	0.297	-0.114	0.111		0.328
tree width	0.670	0.575	0.516	0.443		0.271
tree depth	-0.234	0.604	-0.175	0.451		0.707
summary 2000						
	N	r	r ²	r ² adjusted.	F(3,53)	p
	57	0.291	0.085	0.033	1.638	0.192
source						
	β	β (s.e.)	b	b (s.e.)		p
constant			0.533	0.944		0.575
tree height	0.112	0.146	0.374	0.488		0.447
tree width	0.271	0.147	1.152	0.623		0.070
leaf number	-0.138	0.149	-0.0002	0.0002		0.358

The influence of tree size variables (x_{ip} = independent variables) on beetle numbers on individual plants (y = dependent variable) was analysed for two years (1999, 2000). r = correlation coefficient, r^2 = explained variance, F : F-value, d.f., and resulting p -value is used as an overall F-test of the relationship between the dependent variable and the set of independent variables, β = regression coefficient for standardised variables, b = raw regression coefficient.

Influence of volatile attractants on host location in *Apogonia fatidica*. The olfactometer bioassay indicated that volatile attractants emitted from the host plants (halved leaves) can attract *Apogonia* beetles. The beetles chose the treatment arm of the olfactometer (cf. Figure IX.1) more often than the control arm (Figure IX.9). There was no detectable difference in the ratio of preference for a particular olfactometer arm between the two different treatments (leaves only vs. leaves and beetles; in both treatments was the treatment arm chosen by about 60 % of beetles; Figure IX.9). Preference for the treatment arm was significant when the two experiments were pooled (due to small sample size; G (Williams corrected) = 3.864, d.f. = 1, $p < 0.05$).

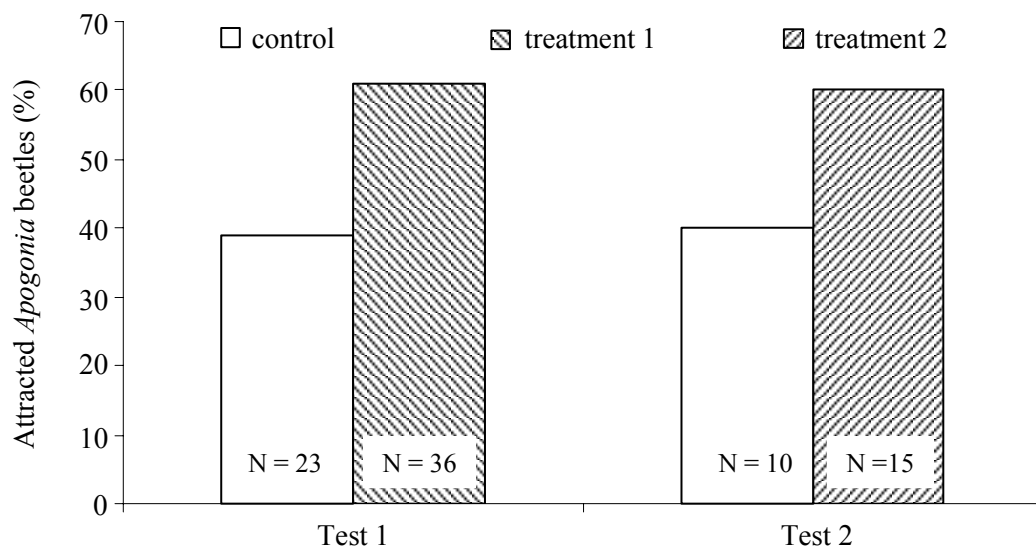


Figure IX.9 Olfactometer experiment testing the influence of odours emitted by leaves or feeding beetles on beetle orientation behaviour. Test 1: control (empty source box) vs. treatment 1 (source box containing pieces of *Combretum* leaves); Test 2: control vs. treatment 2 (source box containing 10 *Apogonia* beetles and *Combretum* leaf pieces).

IX.4 Discussion

This study demonstrated that intraspecific variability in palatability*¹ of plant leaves can act as an important determinant of insect herbivore dispersion on a local scale. Food-preference based on differentiation between conspecific plants can be a mechanism which may explain the primary step in aggregation-formation of herbivorous insects.

Both studied beetle species were clearly able to differentiate between leaves of conspecific plants as food. Therefore, the leaves' variable palatability could be an important clue for the beetles to select particular plant individuals and to cause an aggregated distribution on the most preferred plants. The pronounced preference for particular plant individuals indicated a substantial variation of the studied plants with regard to some herbivore-relevant leaf characteristics. A marked intraspecific variability in herbivore-relevant leaf attributes has been also reported for many other plant-herbivore systems. Various factors have been discussed to cause this intraspecific variability: transitory factors such as feeding events which cause induced defence reactions (Mutikainen et al. 1996, Karban and Baldwin 1997, Tscharrntke et al. 2001, Dicke and Hilker 2003), more permanent factors such as specific site conditions, as for example nutrient or water availability (Lightfoot and Whitford 1989, Ylioja and Rousi 2001, De Bruyn et al. 2002), or an invariable genetic basis (Fritz and Price 1988, Orians and Fritz 1996, Osier et al. 2000).

Since both beetle species aggregated on particular plant individuals persistently over time, only more permanent plant characteristics are likely to determine the beetles' distribution on the plants. The identification of these factors could help to explain the initialisation of herbivore resting and feeding, which is the first step in aggregation build-up. This study showed that *Apogonia* beetles differentiated between individual plants, they preferred the same plants in the laboratory and in the field, and the palatability-status of individual plants was usually relatively similar within a season and across different years. Thus, all evidences obtained in this study conclusively point to a stable, long-term variability in plant palatability as major determinant for the distribution of *Apogonia fatidica*.

In combination with the findings that beetles were not affected by two other important deterministic factors, namely tree size*² and availability of young leaves, the results of the feeding experiments suggest the following scenario for aggregation build-up in *Apogonia fatidica*: Beetles that emerge early in the season search for host plants. They will encounter plants of different species (with *Combretum fragrans* clearly being the preferred host in the area (K. Mody, pers. obs.)) and of variable palatability, which is determined by the levels of feeding stimulants such as sugars and phenolic compounds (Ladd 1986, Fulcher et al. 1998), and the levels of defensive compounds (Coley et al. 1985, Waring and Pitman 1985, Bryant et al. 1989). They may start to feed several times, but will rest for longer only if the plant's palatability is satisfying. If such a plant is finally found, the beetle continues to feed on this plant over longer periods of time. This suggestion is supported by personal observations where individually marked beetles were found to use the same plants over weeks, although they could have easily changed the tree. The feeding beetle may then serve as a directional attractant, guiding other beetles to the plant and boosting aggregation build-up.

*¹ The decisive variable determining food choice of herbivores should be rather *suitability* as food than palatability. Suitability depends on the content of nutrients and defence compounds and may affect fitness. As suitability was not quantified in this study (but compare Chapter X), palatability is used as a surrogate of suitability. Although palatability is not necessarily tantamount to suitability, there is no reason to assume the two aspects to be independent in a natural herbivore-host system.

*² Examples for tree size as important variable: Bach (1981), Lawton (1983), Rowe and Potter (1996); examples for availability of young leaves as important variable: Raupp and Denno (1983), Basset (1996), Novotny et al. (2003).

The basis for this assumption was provided by the results of the olfactometer bioassay, which confirmed that *Apogonia* beetles could generally be attracted by volatiles. However, the study could not reveal whether volatiles emitted from feeding beetles or damaged leaves alone were the stronger attractants. This might either indicate that plant volatiles emitted from damaged leaves were the main attractant, or that the study design was not precise enough to detect the relevant influence of other beetles (which can be an important factor according to many other studies on herbivorous beetles: Iwabuchi and Takahashi (1983), Harari et al. (1994), Yarden and Shani (1994), Loughrin et al. (1996a, b), Harari and Landolt (1997), Harari and Landolt (1999), Ruther et al. (2000), Peacock et al. (2001), Ruther et al. (2001)).

Proictes beetles, like *Apogonia* beetles, were able to differentiate between conspecific plants in feeding trials. However, in contrast to *Apogonia* beetles their distribution in the field did not reflect their preferences in the laboratory. These differences between *Apogonia* and *Proictes* beetles can probably be best explained by pronounced differences in mobility. Due to their ability to fly, *Apogonia* beetles are fairly mobile. Hence, they can choose between different plants and select the best plants locally available. This hypothesis is supported by personal observations of an individually marked beetle that was found the night after its release on one of the most susceptible plants, 50 m apart from the site of release (Cf8 in 2000, cf. Figure IX.3). The mobility of the nonvolant *Proictes* beetles was, however, very restricted and therefore only allowed the beetles to choose between very few plants. As these beetles, in addition, spent proportionally much more time on these plants than did *Apogonia* beetles, more characteristics of the individual plants might be important for *Proictes* beetles than for *Apogonia* beetles. While *Apogonia* approached the plants only for feeding and very rarely for mating (only five mating pairs could be observed out of many hundred beetle observations), *Proictes* was observed to stay on the plants all day and night, and both feeding and mating were observed regularly. Therefore, factors like enemy free space (Jeffries and Lawton 1984) and availability of suitable sites for egg-laying and larval development should be important habitat characteristics aside from food quality presented by individual hosts for *Proictes*.

The relative importance of plant quality for *Proictes* beetles could not be figured out by this study, as too few plants have been compared in feeding trials to allow a conclusive evaluation. However, in these feeding experiments *Proictes* beetles have proven their ability to discriminate between plant individuals. Additionally, plants which hosted many *Proictes* beetles were never very low-quality plants in the *Apogonia* feeding trials (Cf1, Cf8, Cf9; cf. Figure IX.4, Figure IX.7). Both facts suggest that to some extent plant quality is also an important factor for *Proictes* beetles.

The decisive variables that determine leaf quality for *Apogonia* and *Proictes* beetles have not been identified and quantified hitherto. However, the persistent use of the same plant individuals within the same year and across years indicates that stable leaf characteristics have to be more important than temporary characteristics in general and induced defence reactions in particular. In other studies, induced defence reactions have been identified as the most prominent temporary leaf characteristics, especially in the context of herbivore-plant interactions (e.g. Edwards and Wratten 1983, Karban and Myers 1989, Gatehouse 2002). If a plant shows strong induced defence reactions, its attractiveness should be strongly reduced by feeding insects. However, this relationship was not observed in the studied beetle-*Combretum* system. In the contrary, the most attractive and therefore most damaged plants remained attractive over time, clearly indicating that induced defence reactions are probably no decisive variable in determining the quality of *Combretum* leaves within a year or across years. Other relevant leaf characteristics can be the leaves' nitrogen or water content, the mechanical properties of the leaves, or secondary plant compounds which may act as constitutive defence chemicals or feeding stimulants (Wright et al. 2003). These factors can be relatively stable under certain conditions, i.e. if they have a strong genetic component (e.g. Gouyon et al. 1983,

Berenbaum et al. 1986, Bowers and Stamp 1992, Castells et al. 2002) or if they are caused by stable site conditions (e.g. Mihaliak et al. 1989, Waterman and Mole 1989). Additional investigations on the underlying genetic and environmental influences and the resulting specific leaf composition are necessary to further specify these factors.

X. Intraspecific Host-Plant Change Affects Growth and Fecundity in a Specialist Caterpillar: Roaming for Fitness?

Abstract - Beneficial effects of dietary mixing have been reported for herbivorous insects with wide host ranges. Since intraspecific host-plant variability is increasingly acknowledged as important factor affecting herbivore performance, the question arises whether herbivores with restricted host range may profit from mixing different conspecific hosts as well. Specialist caterpillars of the lasiocampid moth *Chrysopsyche imparilis* regularly change host plant individuals, although foliage is not considerably reduced by caterpillar feeding. Leaving the host bears the risk of predation and of failure to find new host plants. We tested two hypotheses related to host-quality to explain the host switching behaviour. First, switching hosts is set off by decreasing host-quality induced by the feeding caterpillar. Second, dietary mixing achieved by host-change is influencing fitness related parameters such as growth and fecundity. The caterpillars showed no significant preferences for leaves of different conspecific plant individuals, which significantly differed in traits such as plant-wide leaf size or previous damage by herbivores. There were, however, significant effects of food mixing on the caterpillars' performance. An experimental diet containing leaves of several plant individuals, imitating a regular intraspecific host change, resulted in increased growth compared to a diet restricted to leaves of a single host individual. Additionally, females reared on a mixed diet laid significantly more eggs than their sisters reared on a single-plant diet. We conclude that regular plant switching in *C. imparilis* is not caused by plant defences induced by caterpillar feeding, but rather by increased growth and fecundity in an environment characterised by variable host-quality.

Keywords: *Chrysopsyche imparilis*, food mixing, foraging behaviour, herbivores, host quality, intraspecific variability

X.1 Introduction

Organisms need to accumulate resources for growth and reproduction. Apart from maximising the quantity of nutritional intake, the quality of the food consumed may be crucial for developmental time and the fecundity achieved by the adult (Awmack and Leather 2002). In the case of herbivorous insects, suitable food can be obtained by specialist and generalist feeding habits (Schoonhoven et al. 1998). Using a wide range of hosts increases the availability of food and allows to mix different types of food, which may help to improve the nutrient balance (Pulliam 1975, Rapport 1980, Bernays et al. 1994). It may also help to dilute potentially poisonous allelochemicals that are unevenly distributed over different plants (Freeland and Janzen 1974, Bernays and Minkenberg 1997) or induced by the feeding herbivore itself (Karban and Baldwin 1997, van Dam et al. 2000). To achieve potential advantages via food mixing, host changes are necessary. These require mobility and some orientation capabilities to secure the timely finding of a new food source. Abandoning a proven food plant and searching for a new one, bears potential risks such as starvation, desiccation, increased exposure to predators and metabolic costs (Schultz 1983, Dethier 1988). Whether food mixing is adaptive depends on the ratio of costs and benefits involved. It should be favoured by factors increasing positive effects (such as marked differences in nutritional value or toxicity of different hosts) and reducing the risks (such as high mobility, availability of alternative hosts).

In caterpillars, regular individual switching among host species as well as feeding restricted to single host individuals, can be found (e.g. Dethier 1988, Bernays and Woods 2000). Switches have been reported for different species of generalist caterpillars (e.g. Lance and Barbosa 1982, Singer 2001). In contrast to other generalist herbivores such as Orthoptera, where food mixing positively

affected performance traits, such a relationship has been remarkably rarely reported for caterpillars (Bernays and Minkenberg 1997). Since host switching commonly occurs in some caterpillars nevertheless, the question remains whether it is mainly triggered by predator avoidance (Montllor and Bernays 1993), or whether important effects of host-characteristics (e.g. variability in nutritional or defensive compounds) remained undetected.

The caterpillars of the lasiocampid moth *Chrysopsyche imparilis* seem very suitable for an investigation into these issues. They are specialised on plants in the family Combretaceae and showed a striking host switching behaviour in a West African shrub savannah (K. Mody, pers. obs.). They changed host plant individuals on average every two to three days, although we found that foliage was never considerably reduced by caterpillar feeding. Finding a new suited host is risky for a specialist with restricted orientation capabilities, foraging in a habitat characterised by a high diversity of woody plants (Porembski 1991, Hovestadt 1997); see, for example, Dethier (1993) for information on restricted effective ranges of olfaction and vision in caterpillars). Apart from predator or parasite avoidance, two reasons related to host-quality could explain the host changing behaviour: (i) the changing behaviour is a consequence of decreasing host-quality induced by the feeding caterpillar (fitness-reduction avoidance hypothesis) and (ii) dietary mixing achieved by intraspecific host-change increases fitness (roaming for fitness hypothesis). The first hypothesis was tested by feeding-choice tests, presenting caterpillars leaves of conspecific plants differing in leaf traits and pre-experimental herbivory. The second by a rearing experiment, providing caterpillars a diet consisting either of a single or several conspecific host individuals.

X.2 Material and Methods

Study site and species. The study was conducted in Comoé National Park, Republic of Côte d'Ivoire, during June through August 2000 and during April through May 2001. More information on Comoé National Park is provided by Poilecot (1991) and Rödel (2000). The studied host plant species, *Combretum fragrans* F. Hoffm. (Combretaceae) is a medium-sized (maximum height 12 m), deciduous savannah tree that reaches densities of 400 plants per ha in the studied area (K. Mody, pers. obs.). Caterpillars of the studied moth species *Chrysopsyche imparilis* Aurivillius (Lasiocampidae) could be found in several generations throughout the whole rainy season. They are large (female larvae up to 4 g) specialists restricted to food plants in the family Combretaceae (Unsicker 2002). *C. imparilis* moths exhibit a marked sexual dimorphism: the male moths are small and very agile, while the females are much larger and clumsier. Females are poor fliers, do not feed as adults and lay eggs in clusters as is typical for many Lasiocampidae (Scholtz and Holm 1989).

Test of the fitness-reduction avoidance hypothesis. Four leaf parameters, which are suggested to influence leaf attractiveness to herbivores, were determined for every leaf used in subsequent feeding-choice tests: pre-experimental leaf damage (*PLD*), area of the complete leaf (*ACL*), leaf water content (*LWC*) and specific leaf area (*SLA*; according to Hanley and Lamont 2002). To quantify *PLD*, the area of the leaf was determined as collected (untreated leaf). For this purpose, the leaves were photographed with a digital camera (Nikon, COOLPIX 950) in a standardised procedure. The leaves were spread out on a board of white Plexiglas and tightly covered with a hinged lid of non-reflecting glass. Leaves were photographed with a reference square (1 cm²) from a fixed distance, with the same resolution, and without flash. Digital photographs were analysed using the graphics package 'Adobe PhotoShop'. By referring to the 'pixel number' of the reference square, the leaves' area could be computed. After this, leaf parts missing due to herbivory were added to the digitised leaf, using the undamaged portion of the leaves as a template when leaves were damaged along their margin. Leaf

area was again determined for this ‘restored leaf’. *PLD* was then quantified as the difference between area of the untreated and the restored leaf. *LWC* and *SLA* were determined using the remaining leaf parts, not used in the preference tests. The area of these parts was determined as described above. They were stored in airtight plastic bags. Their fresh weight was assessed within two hours after collection. The leaves were dried at 40°C to weight constancy and their dry mass determined (mg). *LWC* was computed as difference of fresh and dry mass. *SLA* was calculated by dividing leaf area by dry mass (Hanley and Lamont 2002).

Feeding-choice experiments were performed to assess whether caterpillars prefer certain plant individuals and to test whether feeding is influenced by leaf traits, in particular the degree of previous herbivory. Leaves were randomly (by blindly pointing to the plant with a stick and picking the leaf first encountered) collected from five pairs of experimental plants. The paired plants were chosen to represent, judging by appearances, one pair member with high and one with low pre-experimental herbivory. One leaf of each pair member was offered to single *C. imparilis* caterpillars for 16 hours (from 1600 till 0800, to ensure day and night-time feeding and *ad libitum* fresh leaf material to feed). The caterpillars were kept in plastic terraria (18 x 11 x 14 cm; provided with moistened filter paper) and represented all larval stadia except first instars. Size of paired leaves was either standardised to square leaf pieces (9 cm²) or was aligned by cutting the leaves and providing comparably sized apical parts to the caterpillars. If leaf area was not standardised, it was determined before the experiment following the procedure described above for leaf area determination. Leaf area was also determined for leaf-remainings after the feeding experiment. From differences in leaf area before and after the experiment, consumed leaf area was computed. Leaf specific fresh and dry weight (mg fresh or dry weight per area) was determined to derive consumed leaf mass (fresh and dry) from consumed leaf area.

Test of the roaming for fitness hypothesis. Larvae used in these feeding experiments were obtained from eggs laid by two *C. imparilis* moths (clutch 1 and 2). The female moths were reared from caterpillars collected on *C. fragrans* plants three weeks before the experiment and mated with wild-flying males attracted by the pheromones of the receptive females. The two clutches were laid with a two-day difference and the larvae hatched about 12 days after oviposition. The larvae were fed on leaves of six different *C. fragrans* individuals to control for effects of intraspecific variability in host suitability for caterpillars. Of each clutch, 96 first instar larvae (about the half of each clutch) were assigned to two experimental groups. Larvae of the first group were reared on leaves of a single plant individual (out of the six). The caterpillars of the second group were reared on leaves of all six plant individuals according to the following feeding-regime. In the first week of the experiment, larvae were continuously provided with leaves of one of the six plant individuals (main host) and additionally with leaves of one of the other five (second host). The second host was changed every day. Subsequently, larvae were reared on leaves of a single plant, changing the food plant at six-day intervals (resulting in 8 to 9 plant changes until pupation). The host-plants were changed in a fixed order, ensuring that all plants were evenly used and that caterpillars received new plant individuals until all six plants were provided to the caterpillars. After the sixth plant, the feeding scheme started anew with the main host and followed the same order as before.

For each plant individual, 8 larvae were assigned to the two treatments, resulting in 48 mixed-plant and 48 single-plant caterpillars for each clutch. For the first two instars, larvae were maintained in groups of 8 in closed Petri dishes provided with moistened filter paper. Thereafter, they were maintained in plastic terraria (23 x 17 x 15 cm) with ventilation screens inserted into the lids and provided with moistened filter paper, still at a group size of 8, while after the fourth instar their number was reduced to 4. Petri dishes and terraria were held in open laboratory huts, protected from

direct sunlight and exposed to ambient air temperature and humidity. Rearing continued until all larvae either died or pupated. Cocoons containing pupae were kept separately until eclosion.

To test if diet composition affects performance traits of *C. imparilis*, larval weight at different stadia, developmental time from hatching of larvae to eclosion, survival (number of successfully eclosing moths), sex ratio of moths, and realised fecundity of female moths was recorded. For later instars, weight turned out to be strongly biased by developmental status (feeding-, premolt- or postmolt-stage) and was therefore not used for further analyses. Female moths were unable to keep their eggs longer than about three days after eclosion. Then, they started to lay their eggs independently of whether they were mated or not and died completely exhausted a few days later. Realised fecundity was measured as number of eggs laid by these unmated females.

Data analysis. All data were checked for normality before statistical analyses. Comparisons of leaf characteristics of experimental plant pairs were conducted using paired t-tests when parametric assumptions were met and Wilcoxon's signed ranks tests when these assumptions were not fulfilled. For variables expressed as percentage, paired-sample randomisation tests were performed with 10,000 iterations (windows version of SPSS 11.0). Between-plant comparisons of single leaf characters were conducted using the Kruskal-Wallis test, since parametric assumptions were not met by these data even after application of transformation procedures (Sokal and Rohlf 1995, Zar 1999).

For analysis of growth, developmental time and realised fecundity, average values were computed for caterpillars kept in the same Petri dish or terrarium before statistical analyses to conservatively ensure independence of the data. Results were, however, identical when all caterpillars were treated as independent data. Growth parameters (weight) of second instar larvae and developmental time data were investigated with SAS statistical software by a 3-way mixed model analysis of variance, with the two clutches as blocking factor. The fixed explanatory variable was food composition (mixed-plant vs. single-plant diet), while food plant individual (six tree individuals) was considered a random effect. Growth parameters were analysed using type III sum of squares, developmental time using type IV sum of squares.

X.3 Results

Fitness-reduction avoidance hypothesis. For all leaf characteristics measured, highly significant interplant variation could be detected (Kruskal-Wallis tests for pre-experimental herbivory (*PLD*), complete leaf area (*ACL*), leaf water content (*LWC*) and specific leaf area (*SLA*), Table X.1). Leaves of paired plants differed strongly in *PLD* and *ACL* (Table X.1). *LWC* and *SLA* differed in only one plant pair. There were no differences in area of leaf pieces pairwise presented to caterpillars (*AEL*, Table X.1).

No significant difference in leaf consumption (consumed leaf fresh mass (*CLM*), Table X.1) could be detected between leaves of different plant individuals. This was also true for consumed leaf area or consumed leaf dry weight (not shown in Table X.1). Although not significant, leaves with higher pre-experimental herbivory seemed to be rather more attractive than leaves with lower pre-experimental herbivory (Table X.1).

Table X.1 Mean values (\pm s.d.) of leaf- and consumption-attributes determined for 10 *C. fragrans* plants used in paired (P1a,b-P5a,b) feeding-choice tests with *C. imparilis* caterpillars (*C.i.*).

sample	pre-experimental leaf damage (PLD) (%)	area complete leaf (ACL) (cm ²)	leaf water content (LWC) (%)	specific leaf area (SLA) (mm ² mg ⁻¹)	consumed leaf fresh mass (CLM) (mg)
P1a	0.6 (0.6)	30.7 (6.0)	69.7 (3.3)	11.7 (2.0)	28 (49)
P1b	7.2 (5.8)	40.1 (5.1)	68.1 (2.4)	10.3 (1.3)	72 (75)
<i>p</i> (1a vs. 1b)	***	***	n.s.	n.s.	n.s.
P2a	-	-	66.1 (2.8)	9.7 (0.9)	85 (63)
P2b	-	-	67.3 (3.3)	9.6 (1.4)	97 (86)
<i>p</i> (2a vs. 2b)	-	-	n.s.	n.s.	n.s.
P3a	2.8 (3.5)	39.6 (5.0)	60.3 (2.1)	8.9 (1.1)	291 (253)
P3b	8.8 (6.5)	57.2 (9.6)	61.1 (2.9)	8.6 (0.9)	317 (214)
<i>p</i> (3a vs. 3b)	**	***	n.s.	n.s.	n.s.
P4a	5.2 (3.6)	60.3 (12.8)	54.8 (3.1)	8.5 (0.6)	269 (270)
P4b	11.4 (8.9)	59.4 (15.1)	54 (2.7)	8.1 (0.7)	349 (372)
<i>p</i> (4a vs. 4b)	**	n.s.	*	*	n.s.
P5a	2.7 (3.0)	51.1 (10.0)	57.1 (0.9)	6.4 (0.8)	469 (301)
P5b	14.2 (7.8)	62.5 (17.3)	57.2 (0.9)	7.1 (1.6)	324 (366)
<i>p</i> (5a vs. 5b)	***	*	n.s.	n.s. (wsr)	n.s.
inter-plant comparison:					
$H_{(d.f.)}$:	72.5 ₍₇₎	87.3 ₍₇₎	156.1 ₍₉₎	117.1 ₍₉₎	-
<i>p</i>	***	***	***	***	-

For inter-plant variation of leaf attributes, results of Kruskal-Wallis (H) test are shown. For variation within plant-pairs, results of paired t-tests or Wilcoxon's signed-ranks test (indicated by *wsr*), or of paired sample randomisation tests (for PLD and LWC) are shown. Number of caterpillars tested: P1 = 15, P2 = 15, P3 = 20, P4 = 29, P5 = 18. n.s., non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Roaming for fitness hypothesis. The independent variables 'feeding treatment' and 'host individual' and the blocking factor 'clutch' contributed significantly to variation in weight of second instar *C. imparilis* larvae (Table X.2). Mean weight of larvae reared on mixed-plant food was generally higher than weight of larvae reared on single-plant food (paired t-test: $t = 3.66$, d.f. = 11, $p = 0.004$; see also Figure X.1). *Post-hoc* comparisons revealed that caterpillar growth differed significantly between some host individuals, indicating that plants varied in suitability (quality) as host plant (Tukey test: *C. fragrans* plant 1 (*Cf1*) vs. *Cf5*: $p = 0.003$; *Cf1* vs. *Cf6*: $p = 0.002$; *Cf2* vs. *Cf5*: $p = 0.014$; *Cf2* vs. *Cf6*: $p = 0.010$; all other pairs not significant; Figure X.1). The effect of mixing food plants for growth of second instar larvae seemed to be the more pronounced, the lower the suitability of the host plant was (Figure X.1, single- vs. mixed-plant diet, t-test: $t = 3.99$, d.f. = 14, $p = 0.001$ for *Cf1*, clutch 2 (*Cf1(2)*), $t = 1.98$, d.f. = 14, $p = 0.067$ for *Cf1(1)*, and $t = 1.94$, d.f. = 14, $p = 0.073$ for *Cf2(1)*; for all other comparisons $p > 0.1$).

No significant influence of feeding treatment or host-quality (based on single-plant diet) was detectable for survival (feeding treatment: $\chi^2 = 0.04$, d.f. = 1, $p = 0.84$; host quality: $\chi^2 = 0.82$, d.f. = 2, $p = 0.66$) and sex ratio (feeding treatment: $\chi^2 = 0.08$, d.f. = 1, $p = 0.78$; host quality: $\chi^2 = 1.0$, d.f. = 2, $p = 0.61$; Table X.3). Developmental time was also not significantly influenced by feeding treatment and host quality for both sexes (Table X.2b, Table X.3). There existed, however, a significant feeding treatment \times host quality interaction (Table X.2b), indicating that mixing foods reduces developmental time for low quality plants (cf. Table X.3). A significant difference could also be found for realised fecundity. Moths reared on a mixed-plant diet, laid in average 65 % more eggs

than moths reared on a single-plant food (mean egg number \pm s.d.: 124.0 ± 36.5 vs. 75.3 ± 53.6 ; $t = 2.22$, d.f. = 24, $p = 0.012$).

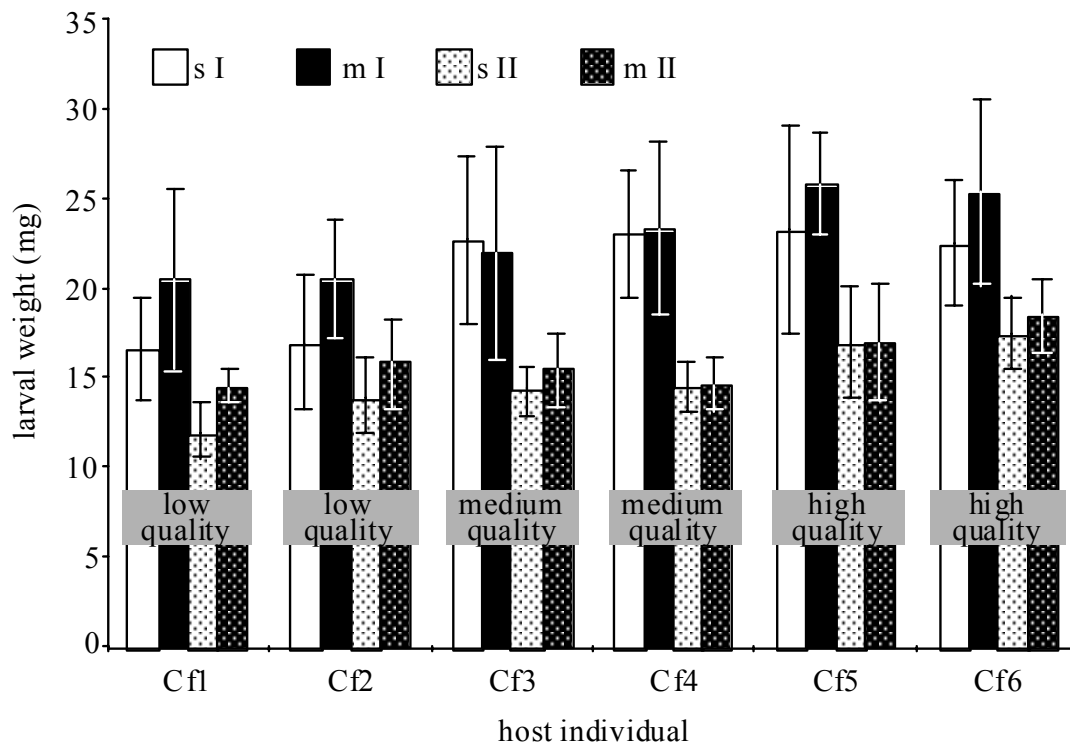


Figure X.1 Weight of second instar *C. imparilis* caterpillars of two sibling groups (I and II) with a difference in age of two days at the time of weighing. Caterpillars reared on leaves of six *Combretum fragrans* plants (Cf1 to Cf6). Leaves derived either from a single plant individual (single-plant diet: s) or from different plant individuals (mixed-plant diet: m). Weight of caterpillars reared on Cf1 and Cf2 was significantly lower (low quality host) than of larvae reared on Cf5 and Cf6 (high quality host). Weight of caterpillars reared on Cf4 and Cf5 was not distinguishable from all other groups (medium quality host). Analysed by ANOVA, Tukey *post hoc* test, see text.

Table X.2 Influence of treatment (mixed-plant vs. single-plant food) and food plant individual on weight of second instar larvae (a) and on developmental time (b). Analysed by ANOVA with clutch (different mother, different age) as blocking factor.

source	SS	d.f.	F	<i>p</i>
a) weight of second instar larvae:				
plant	16.62	5	10.83	0.010
treatment	14.98	1	9.77	0.026
plant x treatment	1.53	5	0.87	0.531
clutch	246.79	1	140.10	0.0001
b) developmental time:				
plant	20.85	5	0.46	0.792
treatment	34.62	1	0.38	0.379
plant x treatment	44.88	5	2.95	0.023
clutch	7.05	1	0.46	0.499

Table X.3 Number of eclosing *C. imparilis* moths, sex ratio and developmental times for mixed- (m) vs. single-plant (s) diet and different host qualities. Host qualities were derived from weights achieved by second instar caterpillars reared on the respective plants.

	sex ratio (female : male)	eclosed female moths	eclosed male moths	developmental time females (s.d.)	developmental time males (s.d.)
mixed-plant food	0.9	23	25	87.8 (3.8)	82.6 (3.5)
single-plant food	1.0	26	25	88.6 (4.3)	83.8 (4.4)
high quality (m)	0.8	5	6	89.8 (5.3)	83.3 (4.3)
high quality (s)	0.7	8	12	88.5 (1.9)	83.5 (4.2)
medium quality (m)	1.7	10	6	87.8 (3.5)	84.7 (3.3)
medium quality (s)	0.9	7	8	86.3 (3.9)	82.8 (5.2)
low quality (m)	0.6	8	13	86.5 (2.8)	81.3 (3.0)
low quality (s)	2.2	11	5	90.2 (5.4)	86.2 (3.3)

X.4 Discussion

Fitness-reduction avoidance hypothesis. We conducted leaf characterisation and preference tests to estimate intraspecific variability in leaf characters and to test the hypothesis that herbivory reduces the attractiveness of leaves to the caterpillars. All leaf characters determined are potentially important to herbivores (Schoonhoven et al. 1998). Since highly significant differences occurred between different plant individuals for all characters and for pairwise analysed leaves for some characters, the caterpillars should have clues to choose between plants. There were, however, no significant preferences detectable in any experiment. Contrary to expectations derived from other studies, the caterpillars neither preferred leaves from plants bearing bigger leaves (Senn et al. 1992), nor leaves with higher water content (Scriber 1977) or lower toughness (Choong 1996). They also showed no preference for leaves from plants with lower levels of pre-experimental herbivory. In contrast, if there was any trend in preference then such that leaves with higher pre-experimental herbivory were more attractive. This suggests either a generally higher attractiveness of these leaves, which is not altered by feeding (Neuvonen and Haukioja 1985), or even an increased attractiveness of the leaves as a consequence of previous herbivory (Haukioja 1990, Karban and Baldwin 1997). The caterpillars appear not to be sensitive to most of the tested leaf characters and – in the one possible exception - to be rather attracted than deterred from high-herbivory leaves. In sum, the hypothesis that herbivory reduces attractiveness of leaves and causes caterpillars to leave the plant can therefore be dismissed as a plausible explanation for host switching in *C. imparilis*.

Roaming for fitness hypothesis. Generally, findings on how dietary mixing influences performance traits of caterpillars are inconsistent. Some studies report positive effects (Merz 1959, Hägele and Rowell-Rahier 1999), while others could not find any measurable common influence (Barbosa and Capinera 1977, Bernays and Minkenberg 1997, Singer 2001). This is surprising, as host-shifting behaviour can be found in many Lepidoptera-larvae, and a diversified food turned out to be beneficial for other insects like Orthoptera (Waldbauer and Friedman 1991), and references therein). In our study, diet mixing influenced several performance traits and was most profitable when host plant quality was low. Our study also indicates that diet mixing is not restricted to switching among different plant species in polyphagous species, but may occur in monophagous species as well. Apparently, intraspecific mixing even of the same resource type (e.g. leaves) can be sufficiently

profitable that changing hosts pays off, although it is costly in terms of time and energy budgets or predation risks (cf. Waldbauer and Friedman 1991, who mention variation of used plant organs as means of self-selection).

Reasons for equivocal results in Lepidoptera species showing marked host switches naturally, might be found a) in performance traits measured, b) in caterpillar stages investigated and c) in host plants included in the studies. In our study, effects were not the same for all performance traits measured. There were significant effects on larval growth (second instar) and female fecundity, whereas survival and developmental time were almost unaffected. If performance traits respond differentially to host quality, effects of food quality - although existent - could have been missed by measuring insensitive traits. The same applies to larval stages. It is known that different caterpillar stages are differentially sensitive to environmental and food conditions (Zalucki et al. 2002). If not all stages are covered by the experiments, the results may under- or overestimate the real effect which can only be determined by measuring performance traits of the adults (Awmack and Leather 2002). The last point to be mentioned is the plants' variability in content of nutritional or toxic substances (Osier and Lindroth 2001). Dietary mixing is only effective when relevant differences exist among plants. If nutrient composition or toxin content is roughly the same, no improvement of nutrient balance or dilution of allelochemicals will be achieved by mixing plants. For cultivated plants, which are often selected for homogenous quality and low concentrations in deterrent or toxic compounds (Barbosa 1993), the requisites supporting host changes are probably not met. Wild plant populations, however, are usually characterised by high intraspecific variation in morphological and/or chemical traits (Karban 1992). For the *C. fragrans* population covered by our study, the existence of such a pronounced intraspecific variability in attractiveness to herbivorous insects is indicated by the feeding behaviour of scarabaeid beetles. These mobile herbivores only accepted certain *C. fragrans* individuals as food, while they consistently refused others in the field and in the laboratory (K. Mody, pers. obs.).

X.5 Conclusions

The importance of intraspecific plant variation for the distribution of herbivores and for animal-plant interactions is increasingly acknowledged (Fritz and Simms 1992, Mody et al. 2003). Here we show that intraspecific variability of neighbouring plants can result in effects of intraspecific food mixing on herbivore performance, which have hitherto been attributed to interspecific diet mixing at best. When herbivores are mobile and can easily select the best plants, intraspecific host variability should lead to an aggregated distribution and marked preferences for certain plant individuals in herbivores. When, however, herbivores are less mobile such as caterpillars, a regular host change may allow getting the best diet on average available (as high quality plants are only be reached by chance and comparisons are difficult for caterpillars). Therefore roaming for fitness seems to be a good explanation for host switches in *C. imparilis*. It might also apply to a multitude of herbivores with limited mobility, feeding on plants of variable - and predominantly low - quality.

Acknowledgements. The authors thank E. Strohm, Andrew Davis and W. Weisser for very helpful comments on a previous draft, and B. Pfeiffer for performing the SAS analyses. Permission to conduct the research was courtesy of the 'Ministère de l'Enseignement Supérieur et de la Recherche Scientifique', Republic of Côte d'Ivoire. Access permit to Comoé National Park was issued by the 'Ministère de la Construction et de l'Environnement'. The study was partly supported by scholarships of the DAAD (German Academic Exchange Service, No. 332 4 04 101) and by the DFG

Graduiertenkolleg 200 to K.M., and by BIOTA (Biodiversity Monitoring Transect Analysis in Africa), German Federal Ministry of Education and Research (BMBF), subproject W06, 01LC0017.

XI. General Discussion

The question raised in the subtitle of this study ‘How does it affect an African caterpillar when I go to work by car?’ may serve to explain the importance of interrelationships and of scales for the understanding of ecological processes. The awareness that processes on both large and small scales are acting in concert to shape local ecological communities has increasingly replaced the view that local communities are predominantly determined by local processes (Ricklefs 1987, Ricklefs and Schluter 1993, Lawton 2000). However, a basic knowledge of processes on lower-ranking scales is a prerequisite for understanding patterns and processes acting on larger scales. Thus, this study focussed primarily on patterns and processes whose scales ranged from the composition of individual communities down to individual organisms within the same local area. The results provide a basis and several starting points for research aiming at disentangling larger scale interrelationships, as many aspects of the different local patterns and processes presented here are clearly linked to large scale processes and are potentially affected by human activities.

In this study, the patterns of structure and similarity of **arthropod communities** on different savannah tree species represented the largest scale considered. The arthropod communities were characterised on three different levels. First, an interspecific comparison of arthropod communities on different savannah tree species was carried out. Secondly, arthropod communities on different individuals of the same tree species were described in an intraspecific, interindividual comparison. Thirdly, the analysis of arthropod communities repeatedly collected from the same tree individual lead to an intraspecific, intraindividual comparison.

The interspecific comparison of arthropod communities on different tree species was conducted for the beetle and ant assemblages of mature individuals of *Anogeissus leiocarpa*, *Burkea africana* and *Crossoteryx febrifuga*. Beetle communities on these tree species differed with respect to species richness, abundance patterns and species composition. For ant communities no such relationship between tree species and community composition was detectable. Thus, in the interspecific comparison beetles showed a more pronounced host specificity than ants. This means that certain host specific characteristics such as tree architecture, phenology, chemistry, or distribution were more relevant for beetle than for ant communities (Chapter V).

As a result of host specificity, differences in arthropod community structure on heterospecific trees should be expected *a priori*. These differences have been reported for tree-living arthropod communities of temperate zones (e.g. Southwood et al. 1982a, Ozanne 1999). However, studies reporting a pronounced influence of tree species on tropical arthropod communities are virtually lacking. Initially, it was assumed that about 20 % of phytophagous beetles are specialised on a single tropical tree species (Erwin 1982) which, however, overestimated the feeding specificity. As a response to this overestimation, many subsequent studies on tropical arthropod communities emphasised that specificity in the tropics is even lower than in temperate regions (e.g. Stork 1987a, Thomas 1990, Gaston 1991). Generally, the tree species is considered to be of minor importance for community structure of tropical trees (Wagner 1998, 2000). However, the lack of clear evidence for tree effects in tropical regions may rather be caused by the problems related with representative community sampling in tropical canopies: large sample sizes of trees that can be clearly delimited from neighbouring trees are more difficult to obtain in highly diverse forests with strongly intermingling canopies (see Chapter V for further discussion of sampling problems).

The results of this part of the presented study clearly indicate a pronounced effect of savannah tree species on the structure of tropical beetle communities (Chapter V). Consequently, a higher tree

diversity should directly be reflected in a higher beetle diversity. The question remains whether this novel observation of a pronounced tree-species effect on beetle community structure only represents the specific situation of the studied savannah region, or whether it reflects a more general finding. This question can only be answered by additional studies applying the same sampling approach used here to other tropical regions. It is, however, highly probable that this observation is as applicable to tropical regions as it is to temperate regions when taking tree relatedness into account (Kitching et al. 2003).

The finding that differences in distribution patterns were less pronounced for ant than for beetle assemblages can best be explained with a lack of host-specific resources provided by the studied trees. No food resources such as food bodies or extrafloral nectaries could be found on the trees, and none of the trees hosted larger numbers of ant-tended homopterans. Numerous studies indicate that the quantity and quality of food resources can be a decisive variable which determines the composition of ant communities (e.g. Davidson 1997, Blüthgen et al. 2000, Dejean and Corbara 2003). Thus, as long as tree species do not differ substantially with regard to these food resources, no strongly diverging patterns in ant distribution should be expected. This hypothesis could be verified by further investigations on trees like *Pseudocedrela kotschyi*, that - unlike the studied trees - provide such food resources (cf. Chapter VI-VIII).

Comparisons of arthropod communities on conspecific trees demonstrated that community composition differed considerably from one conspecific tree individual to another, even when the trees grew in close neighbourhood (Chapter IV-VI). Due to the high variability of communities on different conspecific trees, the community composition was not predictable from one conspecific tree to the other. This result extended the conclusions drawn from the interspecific tree comparisons. It showed that, in addition to species-specific tree characteristics, individual tree characteristics have a major influence on arthropod community composition and generate distinctive communities on individual plants.

The intraindividual comparison revealed that communities collected repeatedly from the same tree individual were remarkably stable over years. The community composition was considerably predictable from communities sampled previously from the same tree. For individual trees, such a predictable and stable distribution was found for *Anogeissus leiocarpa* and *Combretum fragrans* (Chapter IV, V). A predictable and stable structure was also found for ant assemblages on *Pseudocedrela kotschyi*, which turned out to be determined by competitive monopolisation of individual trees (providing carbohydrate resources via extrafloral nectaries) by different ant species (Chapter VI, VIII).

If the arthropod communities had only been sampled once, the pronounced differences in community structure of neighbouring trees could have been considered as a result of random processes. The repeated sampling revealed that each tree hosted an individual, stable arthropod community which differed from that of a neighbouring tree. Thus, deterministic rather than random processes lead to the formation of arthropod communities on individual trees. The consistent re-establishment of highly congruent communities on the same trees can only be explained by stable, arthropod-relevant attributes of the individual plant or its specific immediate environment (Chapter IV, V; IX). The community perspective can only provide limited insight into the understanding of these plant attributes, as some arthropod groups or species were shown to be closer associated with an individual plant than others. Therefore, analyses on a species level may rather serve to elucidate the major determinants for the formation of specific communities on individual plants. Specific interactions between arthropod species and habitat characteristics were further investigated as potential deterministic factors. These analyses on species interactions and influences of plant characteristics on species distribution are described in detail below.

The next lower ranking scale considered **species interactions** using ant assemblages on *Pseudocedrela kotschyi* as study system, as ants are the major interactive group in most plant-associated arthropod communities (e.g. Wettstein 1889, Majer 1976, Jeanne 1979, Porter and Savignano 1990, Cole et al. 1992, Fiala et al. 1994, Novotny et al. 1999, Floren et al. 2002). In accordance with these studies, it was found that ants exerted a strong influence on the distribution of co-occurring ants and other arthropods (Chapter VI-VIII). It was also shown that not all groups of arthropods were similarly influenced by ant presence, and that different ant species may differentially affect co-occurring arthropods and also herbivory (Chapter VII). Hence, ants may act as a deterministic local factor for some arthropod groups, which determines whether a certain species attending a tree will rest or will leave.

However, the deterministic nature of this influence is strongly dependent on the distribution of the ants: if their distribution is stable over time, they may form a stable arthropod community corresponding to the particular ant species using the plant (Chapter VI, VIII). If, however, ant community structure changes rapidly, there will be at best a general ant effect, e.g. as most ants are somehow aggressive towards many other arthropods not adapted to ants. Yet there would not be a strong ant species specific effect. Overall, ants can be considered as potentially important factors influencing the structure of local arthropod communities. Their exact effect, however, cannot be predicted in a general way. It will rather depend on the regional and local ant species pool and on the resources available within the respective community.

Aside from species interactions, plant characteristics were considered as potential deterministic factors influencing persistent arthropod community composition. The characteristic and highly predictable composition found in the intraindividual comparison of communities on *Anogeissus leiocarpa* and *Combretum fragrans* (Chapter IV, V) could not be explained by species interactions alone. As the studied trees hosted variable rather than stable ant communities, ant distribution should rather cloud than enforce patterns of predictable structure. Therefore, the reasons for stable arthropod community formation have to be sought in other arthropod groups and in the influence of habitat characteristics.

A high degree of species aggregation could be found for all communities investigated on the lowest scale considered in this study, the **species level** (Chapter IV, V, IX). This aggregated distribution of most species led to the predictable and stable arthropod composition observed on *Anogeissus leiocarpa* and *Combretum fragrans* (Chapter IV, V). Therefore, understanding the factors that determine aggregation can be very helpful in explaining the predictable composition of the studied communities.

Aggregation (in space and time) on individual plants means that some plants were more attractive for the aggregating species than other plants. Among many possible reasons that may stimulate aggregation on plants (Begon et al. 1996, Morris et al. 1996), the study showed that a stable community composition could best be explained by interindividually variable but intraindividually stable plant characteristics (Chapter IX).

The parameters that finally decide on aggregation are certainly strongly dependent on the needs of the particular species, e.g. whether it is linked to the plant via nutritional requirements like herbivores, or uses the plant as habitat or shelter. In order to obtain detailed information on these parameters, this part of the study focussed on three abundant herbivore species (the beetles *Apogonia fatidica*, *Proictes curvipes*: Chapter IX; caterpillars of the moth *Chrysopsyche imparilis*: Chapter X). They are subject to differing constraints concerning their foraging capacities and feeding requirements. According to their differing biology, these herbivores were considered to make varying demands on their host. Thus, they should represent a broad palette of host characteristics relevant for the distribution of herbivorous insects. The two beetles were typical of most arthropods as they occurred

in persistent aggregations on individual trees, whereas the caterpillars seemed to be a real exception according to their dispersed distribution (Chapter IV, IX, X).

The studies on the three herbivore species demonstrated that intraspecific variability in plant quality (measured as palatability for the two beetles and as food resource determining growth and fecundity for the caterpillars) can be considered as a very important factor affecting the distribution of different herbivores. However, the studies also demonstrated that the same factor, namely variability in plant quality, can generate very different distribution patterns and that similar distribution patterns can be caused by different factors. The two beetle species apparently exhibited the same distribution pattern, namely the persistent aggregation on individual trees. However, the combined analyses of feeding preference and distribution in the field indicated that only the mobile scarabaeid *A. fatidica* was clearly responding to plant quality. The distribution of the nonvolant weevil *P. curvipes* was yet not linked to the same degree to plant quality, though this beetle species was also able to differentiate between individual hosts. Its distribution would probably be best explained by other highly localised habitat characteristics being more influential than food quality (Chapter IX).

The difficulty to infer underlying processes from patterns of distribution is also illustrated by the last species-examination presented in this thesis. The caterpillars of *C. imparilis* were randomly distributed on individual host plants. Since the female moth lays its eggs in clusters, an aggregated distribution of caterpillars should have been expected *a priori*. The deviation from these expectations could be explained by active dispersal of the caterpillars but the reasons for the dispersal behaviour were not discernible at the start of the investigation. Consulting the findings on beetle distribution, one would not expect food quality being the major variable influencing the caterpillars' distribution. However, as caterpillars depend even more on food quality than beetles (Heinrich 1979), an apparently lower influence on the caterpillars should not be expected. And indeed, a more detailed analysis showed that the seemingly completely different distribution patterns of the caterpillars and *Apogonia* beetles were evidently determined by the same factor: by variable plant quality. As a consequence of their different ability to choose between plants, the two species adopted two different strategies to cope with variable plant quality.

Overall, the investigations on the **level of individual herbivore species** demonstrated that small scale variation in plant quality was probably a major factor determining local distribution of two out of three species. The investigations also stressed that distribution patterns can serve as an important starting point, but not as an explanation for dispersion phenomena.

Synthesis

All findings of this study point to the fundamental importance of small scale factors for arthropod distribution on plants. That includes plant characteristics such as food quality of leaves (Chapter IX, X), availability and quality of other sources of nutritional substances provided by the plant (e.g. extrafloral nectaries; Chapter VI-VIII), and probably architecture (Chapter VI). It also includes factors depending on the small-scale distribution of other organisms, affecting the distribution of organisms via interactions (Chapter VI-VIII). Overall, these factors can explain a lot of the remarkably predictable, highly heterogeneous distribution of most arthropods, and the resulting stable and characteristic composition of individual communities (Chapter IV, V). Adding the important role that species-specific attributes of tree species play for certain groups of arthropods, a clear picture of local factors influencing species distribution, species assembly and species interactions (including also plants) on the local scale is emerging.

To return to the bigger picture that unifies local, regional and global processes, the fitting of these results into the general scheme of community organisation and of hierarchical processes acting from small scale to large scale, or vice versa, seems helpful. The study started from the community perspective, which produced the remarkable pattern that arthropod communities are – in contrast to some expectations - by no means just random samples out of the regional species pool. If they had been random, it would have been easy to explain all patterns just by referring to the regional species pool. The finding that communities are not random, does not allow for ways of explanation based primarily on large scale and stochastic processes. It led, however, to a closer look on the lower-ranking scales and thereby showed that all scales down to individual behaviour (and probably genetic attributes of host plants) were involved in the shaping of the individual communities studied. If marginal factors like the individual plants' variation in attractiveness to individual beetles can affect the distribution of these beetles and thereby, on the next level, the composition of a community, then it becomes visible how small- and large-scale factors are interrelated. Small changes, for example in (i) nutritional value of plants (as a consequence of increasing CO₂ or N deposition (e.g. by car driving in Germany), (ii) the genetic heterogeneity of a plant population (by reduced size of populations, selection for some specific traits, domestication) or (iii) the species richness of a plant community (by selective harvesting, establishment of monocultures), may have significant effects on species distribution, on community structure, on viability of sensitive species, on regional species pool richness, and on ecosystem processes. Hence, small scale processes are not only influencing small scale patterns of species distribution but they are also affecting large scale processes, which in turn are the basis for many aspects of local processes.

XII. Summary

This study investigated patterns of arthropod community organisation and the processes structuring these communities on a range of different tree species in a natural West African savannah (Comoé National Park, Côte d'Ivoire). It described and analysed patterns of arthropod distribution on the level of whole communities, on the level of multiple-species interactions, and on the level of individual insect species. Community samples were obtained by applying (i) canopy fogging for mature individuals of three tree species (*Anogeissus leiocarpa*, *Burkea africana*, *Crossopteryx febrifuga*) and (ii) a modified beating technique allowing to sample the complete arthropod communities of the respective study plants for medium-sized (up to 3 m) individuals of two other species (*Combretum fragrans*, *Pseudocedrela kotschyi*). General information on ant-plant interactions was retrieved from ant community comparisons of the mature savannah trees. In addition, ant-ant, ant-plant and ant-herbivore interactions were studied in more detail considering the ant assemblages on the myrmecophilic tree *Pseudocedrela kotschyi*. Herbivore-plant interactions were investigated on a multiple-species level (interrelationships between herbivores and *Pseudocedrela* trees) and on a species level (detailed studies of interrelationships between herbivorous beetles and caterpillars and the host tree *Combretum fragrans*). The studies on individual herbivore species were complemented by a study on an abundant ant species, clarifying not only the relationship between host plant and associated animal but allowing also to look at interactive (competitive) aspects of community organisation.

Analyses on the **community level** demonstrated that communities on different tree species (interspecific comparison) showed significant differences with regard to beetle assemblage structure (abundance, diversity, species composition), which were not evident for the ant assemblage structure. The interspecific comparisons thereby emphasised that the existence of different tree species is very important for the diversity of particular arthropod groups.

An intraspecific comparison was performed both on an interindividual level (comparing communities from different conspecific tree individuals) and intraindividual level (comparing communities repeatedly collected from the same tree individual). It turned out that communities differed considerably from one conspecific tree individual to another, with the structure of beetle assemblages being again more distinct than the ant assemblage structure. Due to the high variability of communities on different conspecific trees, the community composition was not predictable from one conspecific tree to the other. In contrast to that, communities collected repeatedly from the same tree individual were remarkably stable over time, and the community composition was considerably predictable from communities sampled previously from the same tree. For individual trees, such a predictable and stable distribution was found for *Anogeissus leiocarpa* on the level of arthropod orders (primarily for Coleoptera, non-ant Hymenoptera and Thysanoptera), beetle families and beetle species, but not for *Camponotus*-ant species, and for almost all of the abundant insect species on *Combretum fragrans*. A predictable and stable structure was also found for ant assemblages on *Pseudocedrela kotschyi*, which turned out to be determined by competitive monopolisation of individual trees (providing carbohydrate resources via extrafloral nectaries) by different ant species.

Analyses on the level of **multiple-species interactions** demonstrated that extrafloral nectaries of *Pseudocedrela kotschyi* were highly attractive to ants (especially ants of the genus *Camponotus*) and to non-ant Hymenoptera (which were usually evicted by the ants from the nectaries) during the early rainy season, but less attractive during the late rainy season. When considering one individual plant, it turned out that the pattern of nectary visitation changed with time of day with regard to ant species

composition and ant numbers. However, the day-to-day pattern was highly stable and predictable. When comparing different plants, it became evident that this individual plant-specific pattern may differ substantially from the specific pattern of a neighbouring plant. Thus, ant assemblages on neighbouring plants were found to differ in ant species composition and ant numbers, resulting in a stable mosaic of different ant assemblages on neighbouring trees.

As some ant species could prevent damage of host plants by insect herbivores more effectively than others, the presence of certain ant species on neighbouring trees had a direct effect on the host tree. This differential effect on herbivory pointed to varying effects of these ant species on herbivorous insects (mainly caterpillars and beetles). Aside from this indirect evidence for the ants' influence on other co-occurring arthropods, direct evidences were supplied by ant-exclusion experiments. These experiments demonstrated that ants exert highly significant negative effects on some but not all arthropod groups. Interestingly, the most pronounced effects were detected for several groups of predatory arthropods (spiders, cybocephalid-beetles), for scavengers (Blattodea) and parasitoids (chalcidid wasps), but were less pronounced for herbivorous insects: Lepidoptera, Orthoptera, Thysanoptera, Heteroptera were not affected, only the number of Homoptera was reduced by ants.

Analyses on the **species level** were conducted for the ground nesting ant *Camponotus sericeus*, which was the ant species with the highest incidence on the *Pseudocedrela* study plants. It was shown that individually marked workers of this species exhibited a very distinct fidelity to their foraging area, by using small partitions (1-3 leaves) of the same plant in a highly systematic and persistent way. The choice of a particular plant could not be explained by its position to the nest site. It was rather determined by interactions with conspecific and heterospecific ants. The systematic use of small resource patches allowed individual *Camponotus sericeus* foragers to monopolise these resources and to defend them via exploitation competition against other ant species superior in interference competition. In case conspecific ants were using the same plant, the degree of overlap of used plant partitions was smaller with nest-mates, indicating a synchronised resource use on a colony level.

Aside from the competitive interactions pointed out for ant assemblages and *Camponotus sericeus*, herbivore-plant interactions represent an integral part in the structuring of plant-associated arthropod communities. By focussing on three herbivores which differed in mobility and degree of specialisation, several aspects of herbivore-plant interactions could be illuminated.

Both the scarabaeid beetle *Apogonia fatidica*, a mobile, generalist herbivore, and the weevil *Proictes curvipes*, a less mobile (since nonvolant) generalist herbivorous beetle, showed a highly aggregated distribution on individual *Combretum fragrans* plants. The distribution of both species was not only aggregated at a given time, but was persistent for different times within the same year and also for different years. Both species were able to differentiate between individual plants in feeding preference tests in the laboratory, thereby suggesting that plant palatability (as a surrogate of suitability) influenced the beetles distribution in the field. Correlation analyses with field distribution data confirmed this hypothesis for the mobile *Apogonia fatidica*. However, no clear link between preference and distribution could be found for the less mobile *Proictes curvipes*. It was therefore concluded that the mobile *Apogonia* beetle could easily choose between conspecific plants (it also had the means to use volatile attractants as was shown by olfactometer bioassays) and select those plants best suited as food (other factors such as tree size were not influential on the distribution of *Apogonia*). The nonvolant *Proictes* beetle, however, could not choose between conspecific plants. Thus, aggregation may rather reflect other constraints than food suitability, which were not specified in this study.

The great potential impact of the host plants' variability on the distribution of herbivorous insects became also evident in the last species examination presented in this study. The little mobile, specialist

caterpillars of the lasiocampid moth *Chrysopsyche imparilis* were exceptional in their distribution pattern on *Combretum* host plants, as they occurred dispersed and not aggregated. Since female *Chrysopsyche* moths lay their eggs in clumps, the dispersed distribution pattern has to be achieved by active dispersal of caterpillars. The caterpillars indeed changed their host plants regularly, although foliage was not considerably reduced by caterpillar feeding and leaving the host always bears the risk of predation and failure to find new host plants. Feeding and breeding experiments demonstrated that the host plant changing behaviour is probably not caused by decreasing host-quality (induced by the feeding caterpillar) but by an increased fitness when using different plants as food. Mixing host plants turned out to be most beneficial for host plants of low quality. Thus, the host changing behaviour could be regarded as an adaptation to host plants populations, which were characterised by a highly variable suitability for the herbivore and probably by an excess of low quality plants.

The study demonstrated for the first time that (i) the structure of beetle communities on tropical trees can be strongly dependent on the host tree species, (ii) individual trees can host specific arthropod communities whose characteristic structure is stable over years and is strongly determined by the individual tree's attributes, (iii) ants can express a pronounced fidelity to single leaves as foraging area and can thereby determine distribution patterns of other ants, (iv) intraspecifically variable palatability of plants for insect herbivores can be stable over years and can influence the distribution of herbivores that can distinguish between individual hosts according to palatability and (v) intraspecific host plant change can positively affect fitness of herbivores if host plant quality is variable.

In general, the present study contributes to our knowledge of anthropogenically unaltered processes affecting community assembly in a natural environment. The fundamental understanding of these processes is crucial for the identification of anthropogenic alterations and the establishment of sustainable management measures. The study points out the important role local factors can play for the distribution of organisms and thereby for community organisation. It emphasises the relevance of small scale heterogeneity of the abiotic and biotic environment to biodiversity and the need to consider these factors for development of effective conservation and restoration strategies.

XIII. Zusammenfassung

In dieser Arbeit wurden die Arthropodengemeinschaften von fünf Baumarten in einer westafrikanischen Savanne (Comoé Nationalpark, Elfenbeinküste) untersucht. Die Zusammensetzung dieser Gemeinschaften sowie verschiedene Prozesse, die zur ihrer Strukturierung beitragen, wurden dabei auf drei verschiedenen Ebenen beschrieben und analysiert: auf der Ebene von Arthropodengemeinschaften (**Gemeinschaftsniveau**), auf der Ebene von Interaktionen zwischen mehreren Arthropodenarten (**Interaktionsniveau**) und auf der Ebene individueller Insektenarten (**Artniveau**). Die Erfassung der Arthropodengemeinschaften erfolgte zum einen durch Kronenbenebelung („canopy fogging“) ausgewachsener Bäume der drei Arten *Anogeissus leiocarpa*, *Burkea africana* und *Crossopteryx febrifuga*. Zum anderen wurde eine modifizierte Klopftechnik eingesetzt, die eine Erfassung von kompletten Arthropodengemeinschaften kleiner bis mittelgroßer (bis 3 m) Individuen der Baumarten *Combretum fragrans* und *Pseudocedrela kotschyi* ermöglichte. Eine genauere Analyse von Ameisengemeinschaften der adulten Savannenbäume lieferte generelle Informationen zu Ameisen-Pflanzen-Beziehungen. Zusätzlich wurden die Interaktionen zwischen Ameisen und Pflanzen sowie zwischen Ameisen und herbivoren Insekten anhand der mit dem myrmekophilen Savannenbaum *Pseudocedrela kotschyi* assoziierten Ameisengemeinschaften genauer untersucht. Die Wechselbeziehungen zwischen Herbivoren und Pflanzen wurden sowohl auf dem Interaktionsniveau (Beziehungen zwischen Herbivoren und *Pseudocedrela*-Bäumen) als auch auf der Ebene individueller Arten analysiert (detaillierte Untersuchungen zur Wechselbeziehung zwischen herbivoren Käfern und Raupen und ihrer Futterpflanze *Combretum fragrans*). Die an individuellen Herbivorenarten gewonnenen Erkenntnisse wurden durch eine Untersuchung einer häufig auf den *Pseudocedrela*-Bäumen anzutreffenden Ameisenart ergänzt. Diese Studie führte nicht nur zu einem besseren Verständnis der Wechselbeziehungen zwischen Wirtspflanze und assoziiertem Insekt, sondern ermöglichte es auch, interaktive (konkurrenzgesteuerte) Aspekte der Organisation von Arthropodengemeinschaften zu verstehen.

Die Analysen auf dem **Gemeinschaftsniveau** zeigten, dass sich Arthropodengemeinschaften verschiedener Baumarten (interspezifischer Vergleich) signifikant in der Zusammensetzung ihrer Käfergemeinschaften unterschieden (gemessen als Abundanz, Diversität und Artenzusammensetzung). Ameisengemeinschaften auf unterschiedlichen Baumarten unterschieden sich hingegen nicht deutlich voneinander. Diese interspezifischen Vergleiche wiesen damit darauf hin, dass das Vorhandensein unterschiedlicher Baumarten eine große Bedeutung für die Diversität bestimmter Arthropodengruppen haben kann.

Vergleiche von Arthropodengemeinschaften auf artgleichen Bäumen (intraspezifische Vergleiche) wurden sowohl auf einer interindividuellen als auch einer intraindividuellen Ebene durchgeführt. Auf interindividueller Ebene wurden Gemeinschaften, die von unterschiedlichen Bäumen der gleichen Art stammten, verglichen. Auf intraindividuellen Ebene wurden Gemeinschaften verglichen, die wiederholt vom gleichen Baumindividuum abgesammelt worden waren. Der interindividuelle Vergleich zeigte, dass sich die Arthropodengemeinschaft eines Baumes sehr deutlich von der eines benachbarten artgleichen Baumes unterschied. Dies war wiederum für Käfergemeinschaften deutlicher ausgeprägt als für Ameisengemeinschaften. Da die Gemeinschaften konspezifischer Bäume so unterschiedlich waren, konnte die Zusammensetzung der Gemeinschaft eines bestimmten Baums nicht von der Zusammensetzung eines artgleichen Baums abgeleitet werden. Im Gegensatz dazu war die Zusammensetzung der vom gleichen Baumindividuum wiederholt abgesammelten Gemeinschaften auch über größere Zeiträume bemerkenswert beständig. Dementsprechend war die Gemeinschaftszusammensetzung für das gleiche Baumindividuum sehr gut

aus vorhergehenden Erfassungen ableitbar. Eine vorhersagbare, stabile Verteilung konnte für individuelle *Anogeissus leiocarpa* Bäume auf der Ebene von Insektenordnungen (vor allem für Käfer, Wespen und Bienen und Fransenflügler) und auf der Ebene von Käferfamilien und Käferarten festgestellt werden. *Camponotus*-Ameisen wiesen hingegen keine vorhersagbare Verteilung auf. Eine ebenfalls stabile, vorhersagbare Arthropodenverteilung wurde für die Gemeinschaften auf *Combretum fragrans* gefunden. In diesen Gemeinschaften waren fast alle häufigen Arten signifikant auf einzelnen Baumindividuen aggregiert. Eine vorhersagbare und stabile Zusammensetzung wiesen auch die Ameisengemeinschaften auf *Pseudocedrela kotschyi* auf. Die Monopolisierung der zuckerliefernden extrafloralen Nektarien individueller Bäume durch verschiedene Ameisenarten stellte sich für dieses System als wichtiger strukturierender Faktor heraus.

Analysen auf dem **Interaktionsniveau** zeigten, dass extraflorale Nektarien von *Pseudocedrela kotschyi* sehr attraktiv für Ameisen, v.a. der Gattung *Camponotus*, und für andere Hymenopteren (die normalerweise von den Ameisen vertrieben wurden) waren. Diese Attraktivität war zu Beginn der Regenzeit besonders ausgeprägt und ließ zu deren Ende hin stark nach. Die Nektarien individueller Pflanzen wurden zu unterschiedlichen Tageszeiten von verschiedenen Ameisenarten genutzt. Während der gleichen Tageszeit erwies sich die Zusammensetzung der Ameisengemeinschaften individueller Pflanzen jedoch als sehr stabil und vorhersagbar. Der Vergleich unterschiedlicher Pflanzen zeigte, dass sich die für die individuellen Pflanzen typischen Verteilungsmuster sehr deutlich von benachbarten, artgleichen Pflanzen unterscheiden konnten. Aus diesen Unterschieden in der Zusammensetzung und Abundanz der Ameisenarten zwischen benachbarten Pflanzen ergab sich ein stabiles Mosaik unterschiedlicher Ameisengemeinschaften auf benachbarten Bäumen.

Da einige Ameisenarten ihre Wirtspflanzen besser gegen Herbivorie schützen konnten als andere, wirkte sich die Anwesenheit bestimmter Ameisenarten direkt auf die Wirtspflanze aus. Dieser unterschiedlich ausgeprägte Schutz vor Herbivorie wies indirekt auf einen unterschiedlichen Einfluss der Ameisenarten auf herbivore Insekten hin (vor allem auf Raupen und Käfer). Neben diesem indirekten Einfluss konnte in Ameisen-Ausschlussexperimenten auch ein direkter Effekt der Ameisen auf vergesellschaftete Arthropoden nachgewiesen werden. Diese Versuche zeigten, dass die Ameisen zu einer hochsignifikanten Reduktion einiger, jedoch nicht aller Arthropodengruppen führten. Interessanterweise wurden die deutlichsten Effekte für einige Gruppen räuberischer Arthropoden (Spinnen, Cybocephalidae) sowie von Omnivoren (Blattodea) und Parasitoiden (Chalcididae) gefunden, während sie für herbivore Insekten weniger erkennbar waren: die Abundanzen der Lepidoptera, Orthoptera, Thysanoptera und Heteroptera waren nicht betroffen, und nur die Gesamtzahl der Homoptera wurde verringert.

Untersuchungen auf der Ebene von **Arten** wurden für die bodennistende Ameise *Camponotus sericeus* durchgeführt. Diese war die am häufigsten auf den untersuchten *Pseudocedrela*-Pflanzen anzutreffende Ameisenart.

Individuell markierte Arbeiterinnen dieser Art wiesen eine sehr ausgeprägte Ortstreue auf, da sie kleine Bereiche (1-3 Blätter) derselben Pflanze in sehr systematischer und beständiger Weise zur Nahrungssuche nutzten. Die Wahl einer bestimmten Pflanze konnte nicht durch deren Position zum Nest erklärt werden. Sie wurde vielmehr durch Interaktionen mit Ameisen gleicher oder anderer Arten bestimmt. Die systematische Nutzung von kleinen Nahrungsbereichen ermöglichte individuellen *Camponotus sericeus* Arbeiterinnen, diese Ressource zu monopolisieren und sie durch beständige Ausbeutung für andere Ameisenarten, die ihnen im Kampf überlegen wären, unattraktiv zu machen.

Wenn artgleiche Ameisen dieselbe Pflanze nutzten, so war der Überlappungsgrad der Fouragierbereiche mit Ameisen des gleichen Nestes geringer als mit nestfremden, was auf eine synchronisierte Ressourcennutzung innerhalb einer Kolonie hindeutete.

Neben den kompetitiven Interaktionen, die für Ameisengesellschaften im Allgemeinen und für *Camponotus sericeus* im Speziellen gezeigt werden konnten, spielten Interaktionen zwischen Herbivoren und Pflanzen eine wesentliche Rolle für die Strukturierung von pflanzenbewohnenden Arthropodengemeinschaften. Durch die Beobachtung von drei herbivoren Insektenarten, die sich im Hinblick auf Mobilität und Spezialisierungsgrad unterschieden, konnten verschiedene Aspekte dieser Herbivoren-Pflanzen-Interaktionen beleuchtet werden.

Sowohl der Blatthornkäfer *Apogonia fatidica*, ein mobiler, generalistischer Pflanzenfresser, als auch der Rüsselkäfer *Proictes curvipes*, ein weniger mobiler da flugunfähiger, generalistischer Pflanzenfresser, zeigten eine hochaggregierte Verteilung auf individuellen *Combretum fragrans* Pflanzen. Beide Arten aggregierten nicht nur zu einem Zeitpunkt auf bestimmten Pflanzenindividuen, sondern auch zu verschiedenen Zeitpunkten innerhalb eines Jahres und über mehrere Jahre hinweg. Beide Arten waren in der Lage, in Fraßwahlversuchen zwischen Blättern verschiedener artgleicher Pflanzen zu unterscheiden. Dies deutete darauf hin, dass die Attraktivität einer Pflanze als Nahrungsquelle die Verteilung der Käfer im Freiland beeinflusste. Korrelationsanalysen bestätigten einen signifikanten Zusammenhang zwischen der Verteilung des mobilen Käfers *Apogonia fatidica* im Freiland und den Ergebnissen der Fraßwahlversuche.

Für den weniger mobilen Käfer *Proictes curvipes* konnte jedoch keine deutliche Beziehung zwischen der Präferenz in Fraßwahlversuchen und der Freilandverteilung erkannt werden. Daraus wurde geschlossen, dass der mobile *Apogonia* Käfer leicht zwischen artgleichen Pflanzen auswählen konnte (unter anderem mit Hilfe von flüchtigen Lockstoffen, wie Olfaktometer-Untersuchungen zeigten), und dann die am besten als Nahrungsquelle geeignete Pflanze wählte. Der flugunfähige *Proictes* Käfer konnte hingegen nicht zwischen vielen artgleichen Pflanzen wählen. Daher spiegelte seine Aggregation eher andere Einflussfaktoren wider, die in dieser Studie nicht erfasst wurden.

Der große Einfluss der Variabilität von Wirtspflanzen auf die Verteilung herbivorer Insekten wurde auch bei der letzten Art, die im Rahmen dieser Arbeit untersucht wurde, deutlich. Die wenig mobilen, auf *Combretum* als Wirtspflanze spezialisierten Raupen der Schmetterlingsart *Chrysopsyche imparilis* (Lasiocampidae) zeigten ein besonderes Verteilungsmuster: sie aggregierten nicht auf individuellen, sondern verteilten sich gleichmäßig auf allen *Combretum*-Pflanzen.

Da weibliche *Chrysopsyche* Falter ihre Eier in großen Gelegen ablegen, konnte ein gleichmäßiges Verteilungsmuster nur durch eine aktive Verbreitung der Raupen zustande kommen. Tatsächlich wechselten die Raupen ihren Wirt regelmäßig, obwohl die vorhandene Blattmenge durch den Raupenfraß nicht deutlich reduziert wurde und ein Wirtswechsel stets das Risiko barg, gefressen zu werden oder keine neue geeignete Wirtspflanze zu finden. Fütterungs- und Aufzuchtversuche zeigten, dass das Wechseln der Wirtspflanzen wahrscheinlich nicht durch eine auf Raupenfraß zurückzuführende Qualitätsminderung der Wirtspflanze hervorgerufen wurde. Vielmehr erhöhte sich offensichtlich die Fitness der Raupen, wenn verschiedene Pflanzen der gleichen Art als Nahrungsgrundlage genutzt wurden. Dies war besonders vorteilhaft, wenn eine Wirtspflanze von geringer Nahrungsqualität war. Das Wechseln von Wirtspflanzen konnte daher als Anpassung an Wirtspflanzenpopulationen gewertet werden, die stark in ihrer Eignung als Nahrungsquelle variierten und einen großen Anteil an Pflanzen von geringer Qualität enthielten.

Die vorgestellten Untersuchungen zeigten erstmals, dass (i) die Zusammensetzung von Käfergemeinschaften auf tropischen Bäumen stark von der Art der Wirtspflanze abhängig sein kann, (ii) individuelle Bäume spezifische Arthropodengemeinschaften beherbergen können, deren charakteristische Zusammensetzung über Jahre hinweg stabil ist und stark von den individuellen Baummerkmalen beeinflusst wird, (iii) Ameisen eine deutliche Ortstreue zu einzelnen Blättern als Fouragierbereich ausbilden können, und dadurch die Verteilungsmuster anderer Ameisen bestimmen können, (iv) individuelle Unterschiede artgleicher Pflanzen in ihrer Nahrungsqualität für herbivore Insekten über Jahre stabil sind und sich die Verteilung von bestimmten Herbivoren auf den Pflanzen dieser Nahrungsqualität anpasst, (v) ein Wechsel von artgleichen Wirtspflanzen die Fitness von Herbivoren positiv beeinflussen kann, wenn die Futterqualität der Wirtspflanzen sehr variabel ist.

Insgesamt weist diese Studie besonders darauf hin, dass sehr kleinräumig wirkende, lokale Faktoren einen entscheidenden Einfluss auf die Verteilung von Organismen und die Zusammensetzung ökologischer Gemeinschaften ausüben. Sie betont die Relevanz einer kleinräumigen Umweltheterogenität für die Biodiversität eines Gebiets und verdeutlicht anhand erstmals festgestellter Zusammenhänge von Pflanzeigenschaften und Arthropodenverteilung, dass die Heterogenität abiotischer und biotischer Umweltparameter bei der Entwicklung von nachhaltigen Management-Praktiken und von Naturschutz- und Restaurationskonzepten berücksichtigt werden muss.

XIV. References

- Acosta, F. J., F. Lopez, and J. M. Serrano. 1995. Dispersed versus central place foraging: intra- and intercolonial competition in the strategy of trunk trail arrangement of a harvester ant. *American Naturalist* **145**:389-411.
- Adis, J., A. Y. Harada, C. R. V. da Fonseca, W. Paarmann, and J. A. Rafael. 1998. Arthropods obtained from the Amazonian tree species "Cupiuba" (*Goupia glabra*) by repeated canopy fogging with natural pyrethrum. *Acta Amazonica* **28**:273-283.
- Adis, J., Y. D. Lubin, and G. G. Montgomery. 1984. Arthropods from the canopy of inundated and terra firme forests near Manaus, Brazil, with critical considerations on the pyrethrum fogging technique. *Studies on Neotropical Fauna and Environment* **19**:223-236.
- Allison, A., G. A. Samuelson, and S. E. Miller. 1993. Patterns of beetle species diversity in New Guinea rainforest as revealed by canopy fogging: preliminary findings. *Selbyana* **14**:16-20.
- Apple, J. L., and D. H. Feener. 2001. Ant visitation of extrafloral nectaries of *Passiflora*: the effects of nectary attributes and ant behavior on patterns in facultative ant-plant mutualisms. *Oecologia* **127**:409-416.
- Arbonnier, M. 2002. Arbres, arbustes et lianes des zones sèches d'Afrique de l'Ouest, 2nd edition. CIRAD, MNHN, UICN, Paris.
- Arnold, A. E., and N. M. Asquith. 2002. Herbivory in a fragmented tropical forest: patterns from islands at Lago Gatun, Panama. *Biodiversity and Conservation* **11**:1663-1680.
- Aubréville, A. 1950. Flore forestière soudano-guinéenne: A.O.F. - Cameroun - A.E.F. Office de la Recherche Scientifique Outre-Mer, Paris.
- Awmack, C. S., and S. R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* **47**:817-844.
- Azarbayjani, F. F., S. S. Burgin, and B. J. Richardson. 1999. Arboreal arthropod biodiversity in woodlands. II. The pattern of recovery of diversity on *Melaleuca linariifolia* following defaunation. *Australian Journal of Ecology* **24**:655-661.
- Bach, C. E. 1981. Host plant growth form and diversity: effects on abundance and feeding preference of a specialist herbivore, *Acalymma vittata* (Coleoptera: Chrysomelidae). *Oecologia* **50**:370-375.
- Bach, C. E., and D. S. Carr. 1990. Aggregation behavior of a willow flea beetle, *Altica subplicata* (Coleoptera: Chrysomelidae). *Great Lakes Entomologist* **23**:65-76.
- Barbosa, P. 1993. Lepidopteran foraging on plants in agroecosystems: constraints and consequences. Pages 523-566 in N. E. Stamp and T. M. Casey, editors. *Caterpillars: Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York.
- Barbosa, P., and J. L. Capinera. 1977. The influence of food on the developmental characteristics of the gypsy moth, *Lymantria dispar* (L.). *Canadian Journal of Zoology* **55**:1424-1429.
- Barker, M. 1997. An update on low-tech methods for forest canopy access and on sampling a forest canopy. *Selbyana* **18**:61-71.
- Barnola, L. F., M. Hasegawa, and A. Cedeno. 1994. Mono- and sesquiterpene variation in *Pinus caribaea* needles and its relationship to *Atta laevigata* herbivory. *Biochemical Systematics and Ecology* **22**:437-445.
- Barone, J. A. 1998. Host-specificity of folivorous insects in a moist tropical forest. *Journal of Animal Ecology* **67**:400-409.
- Barton, A. M. 1986. Spatial variation in the effect of ants on an extrafloral nectary plant. *Ecology* **67**:495-504.
- Basset, Y. 1991. Influence of leaf traits on the spatial distribution of insect herbivores associated with an overstorey rainforest tree. *Oecologia* **87**:388-393.
- Basset, Y. 1992. Influence of leaf traits on the spatial distribution of arboreal arthropods within an overstorey rainforest tree. *Ecological Entomology* **17**:8-16.
- Basset, Y. 1996. Local communities of arboreal herbivores in Papua New Guinea: predictors of insect variables. *Ecology* **77**:1906-1919.
- Basset, Y., H. P. Aberlenc, H. Barrios, G. Curletti, J. M. Bérenger, J. P. Vesco, P. Causse, A. Haug, A. S. Hennion, L. Lesobre, F. Marquès, and R. O'Meara. 2001. Stratification and diel activity of arthropods in a lowland rainforest in Gabon. *Biological Journal of the Linnean Society* **72**:585-607.
- Basset, Y., H.-P. Aberlenc, and G. Delvare. 1992. Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecological Entomology* **17**:310-318.
- Basset, Y., S. E. Miller, G. A. Samuelson, and A. Allison. 1996a. How many host-specific insect species feed on a species of tropical tree? *Biological Journal of the Linnean Society* **59**:201-216.
- Basset, Y., and V. Novotny. 1999. Species richness of insect herbivore communities on *Ficus* in Papua New Guinea. *Biological Journal of the Linnean Society* **67**:477-499.
- Basset, Y., V. Novotny, S. E. Miller, and R. L. Kitching, editors. 2003a. *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge.

- Basset, Y., V. Novotny, S. E. Miller, and R. L. Kitching. 2003b. Conclusion: arthropods, canopies and interpretable patterns. Pages 394-405 in Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching, editors. *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge.
- Basset, Y., G. A. Samuelson, and S. E. Miller. 1996b. Similarities and contrasts in the local insect faunas associated with ten forest tree species of New Guinea. *Pacific Science* **50**:157-183.
- Basset, Y., N. D. Springate, H. P. Aberlenc, and G. Delvare. 1997. A review of methods for sampling arthropods in tree canopies. Pages 27-52 in N. E. Stork, J. Adis, and R. K. Didham, editors. *Canopy Arthropods*. Chapman & Hall, London.
- Beattie, A. J. 1985. *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press, New York.
- Becerra, J. X. I. 1989. Extrafloral nectaries: a defense against ant-Homoptera mutualisms? *Oikos* **55**:276-280.
- Beck, J., C. H. Schulze, K. E. Linsenmair, and K. Fiedler. 2002. From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology* **18**:33-51.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology: Individuals, Populations and Communities*, 3th edition. Blackwell Science, Cambridge.
- Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* **86**:402-416.
- Bentley, B. L. 1977. Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics* **8**:407-427.
- Berenbaum, M. R., and A. R. Zangerl. 1992. Genetics of secondary metabolism and herbivore resistance in plants. Pages 415-438 in G. A. Rosenthal and M. R. Berenbaum, editors. *Herbivores: Their Interactions with Secondary Plant Metabolites*. Academic Press, San Diego.
- Berenbaum, M. R., A. R. Zangerl, and J. K. Nitao. 1986. Constraints on the chemical coevolution: wild parsnip and the parsnip webworm. *Evolution* **40**:1215-1228.
- Berger, W. H., and F. L. Parker. 1970. Diversity of planktonic Foraminifera in deep-sea sediments. *Science* **168**:1345-1347.
- Bernays, E. A., editor. 1989. *Insect-Plant Interactions*. CRC Press, Inc., Boca Raton.
- Bernays, E. A., K. L. Bright, N. Gonzalez, and J. Angel. 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* **75**:1997-2006.
- Bernays, E. A., and O. Minkenbergl. 1997. Insect herbivores: different reasons for being a generalist. *Ecology* **78**:1157-1169.
- Bernays, E. A., and H. A. Woods. 2000. Foraging in nature by larvae of *Manduca sexta* - influenced by an endogenous oscillation. *Journal of Insect Physiology* **46**:825-836.
- Blüthgen, N., M. Verhaagh, W. Goitia, K. Jaffe, W. Morawetz, and W. Barthlott. 2000. How plants shape the ant community in the Amazonian rainforest canopy: The key role of extrafloral nectaries and homopteran honeydew. *Oecologia* **125**:229-240.
- Boecklen, W. J. 1984. The role of extrafloral nectaries in the herbivore defense of *Cassia fasciculata*. *Ecological Entomology* **9**:243-249.
- Bolton, B. 1994. *Identification Guide to the Ant Genera of the World*. Harvard University Press, Cambridge, Mass.
- Bortz, J., G. A. Lienert, and K. Boehnke. 1990. *Verteilungsfreie Methoden in der Biostatistik*. Springer Verlag, Berlin.
- Bowers, M. D., and N. E. Stamp. 1992. Chemical variation within and between individuals of *Plantago lanceolata* (Plantaginaceae). *Journal of Chemical Ecology* **18**:985-995.
- Brian, M. V. 1965. *Social insect populations*. Academic Press, London.
- Bronstein, J. L. 1998. The contribution of ant plant protection studies to our understanding of mutualism. *Biotropica* **30**:150-161.
- Brose, U. 2001. Species diversity as a measurable entity: data-analytic and sampling-theoretic methods. Pages 24 in G. Zotz and C. Körner, editors. *The functional importance of biodiversity*. Parey Buchverlag Berlin, Basel.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**:445-449.
- Brown, K. W. 1961. Entomological studies from a high tower in Mpanga Forest, Uganda. XI. Observations on Coleoptera. *Transactions of the Royal Entomological Society of London* **113**:353-355.
- Bryant, J. P., P. J. Kuropat, S. M. Cooper, K. Frisby, and N. Owen Smith. 1989. Resource availability hypothesis of plant antiherbivore defense tested in a South African savanna ecosystem. *Nature* **340**:227-229.
- Buckley, R. C. 1982. Ant-plant interactions: a world review. Pages 111-141 in R. C. Buckley, editor. *Ant-plant interactions in Australia*. W. Junk, The Hague.
- Buckley, R. C. 1987. Interactions involving plants, Homoptera, and ants. *Annual Review of Ecology and Systematics* **18**:111-135.
- Bull, E. L., R. S. Holthausen, and M. G. Henjum. 1992. Roost trees used by pileated woodpeckers in northeastern Oregon. *Journal of Wildlife Management* **56**:786-793.

- Butcher, P. A., J. C. Doran, and M. U. Slee. 1994. Intraspecific variation in leaf oils of *Melaleuca alternifolia* (Myrtaceae). *Biochemical Systematics and Ecology* **22**:419-430.
- Carroll, C. R., and D. H. Janzen. 1973. Ecology of foraging by ants. *Annual Review of Ecology and Systematics* **4**:231-257.
- Castells, E., C. Roumet, J. Penuelas, and J. Roy. 2002. Intraspecific variability of phenolic concentrations and their responses to elevated CO₂ in two mediterranean perennial grasses. *Environmental and Experimental Botany* **47**:205-216.
- Cerdá, X., J. Retana, and A. Manzaneda. 1998. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia* **117**:404-412.
- Chao, A. 1984. Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* **11**:265-270.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* **43**:783-791.
- Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* **405**:234-242.
- Chazdon, R. L., R. K. Colwell, J. S. Denslow, and M. R. Guariguata. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northeastern Costa Rica. Pages 285-309 in F. Dallmeier and J. A. Comiskey, editors. *Forest biodiversity research, monitoring and modeling: Conceptual background and Old World case studies*. Parthenon Publishing, Paris.
- Choong, M. F. 1996. What makes a leaf tough and how this affects the pattern of *Castanopsis fissa* leaf consumption by caterpillars. *Functional Ecology* **10**:668-674.
- Clarke, A. R., M. P. Zalucki, J. L. Madden, V. S. Patel, and S. C. Paterson. 1997. Local dispersion of the Eucalyptus leaf beetle *Chrysophtharta bimaculata* (Coleoptera: Chrysomelidae), and implications for forest protection. *Journal of Applied Ecology* **34**:807-816.
- Clinton, B. D., L. R. Boring, and W. T. Swank. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology* **74**:1551-1558.
- Coe, M., and N. M. Collins, editors. 1986. *Kora: An ecological inventory of the Kora National Reserve, Kenya*. Royal Geographical Society, London.
- Cole, F. R., A. C. Medeiros, L. L. Loope, and W. W. Zuehlke. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* **73**:1313-1322.
- Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. *Science* **230**:895-899.
- Colwell, R. K. 2000. EstimateS: Statistical estimation of species richness and shared species from samples. Version 6. User's Guide and application published at: <http://viceroy.eeb.uconn.edu/estimates>. in.
- Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society, (Series B)* **345**:101-118.
- Cosens, D., and N. Toussaint. 1985. An experimental study of the foraging strategy of the wood ant *Formica aquilonia*. *Animal Behaviour* **33**:541-552.
- Costa, J. T. I., and D. A. J. Crossley. 1991. Diel patterns of canopy arthropods associated with three tree species. *Environmental Entomology* **20**:1542-1548.
- Crawley, M. J., and M. Akhteruzzaman. 1988. Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology*:409-415.
- Crist, T. O., and J. A. MacMahon. 1991. Individual foraging components of harvester ants: movement patterns and seed patch fidelity. *Insectes Sociaux* **38**:379-396.
- Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of the Linnean Society* **61**:153-181.
- De Bruyn, L., J. Scheirs, and R. Verhagen. 2002. Nutrient stress, host plant quality and herbivore performance of a leaf-mining fly on grass. *Oecologia* **130**:594-599.
- De Souza, A. L. B., J. H. C. Delabie, and H. G. Fowler. 1998. *Wasmannia* spp. (Hym., Formicidae) and insect damages to cocoa in Brazilian farms. *Journal of Applied Entomology* **122**:339-341.
- Dejean, A. 2000. Ant protection (Hymenoptera : Formicidae) of two pioneer plant species against the variegated locust. *Sociobiology* **36**:217-226.
- Dejean, A., A. Akoa, C. Djieto Lordon, and A. Lenoir. 1994. Mosaic ant territories in an African secondary rain forest (Hymenoptera: Formicidae). *Sociobiology* **23**:275-292.
- Dejean, A., and B. Corbara. 2003. A review of mosaics of dominant ants in rainforests and plantations. Pages 341-347 in Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching, editors. *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge.

- Dejean, A., M. Gibernau, and J. L. Durand. 2000a. Pioneer plant protection against herbivory: impact of different ant species (Hymenoptera: Formicidae) on a proliferation of the variegated locust. *Sociobiology* **36**:227-236.
- Dejean, A., M. Gibernau, L. Durand, D. Abehassera, and J. Orivel. 2000b. Plant protection against herbivory: impact of different ant species on a proliferation of the variegated locust. *Sociobiology* **36**:227-236.
- Dejean, A., D. McKey, M. Gibernau, and M. Belin. 2000c. The arboreal ant mosaic in a Cameroonian rainforest (Hymenoptera: Formicidae). *Sociobiology* **35**:403-423.
- Dejean, A., D. McKey, M. Gibernau, and M. Belin. 2000d. The arboreal ant mosaic in a Cameroonian rainforest (Hymenoptera: Formicidae). *Sociobiology* **35**:403-423.
- Del-Claro, K., R. Marullo, and L. A. Mound. 1997. A new Brazilian species of *Heterothrips* (Insecta: Thysanoptera) co-existing with ants in the flowers of *Peixotoa tomentosa* (Malpighiaceae). *Journal of Natural History* **31**:1307-1312.
- Del-Claro, K., and P. S. Oliveira. 2000. Conditional outcomes in a neotropical treehopper-ant association: temporal and species-specific variation in ant protection and homopteran fecundity. *Oecologia* **124**:156-165.
- Delvare, G., and H. P. Aberlenc. 1989. Les Insectes d' Afrique et d' Amérique Tropicale. Clés pour la Reconnaissance des Familles. CIRAD/PRIFAS, Montpellier cedex 1, France.
- Denny, A. J., J. Wright, and B. Grief. 2001. Foraging efficiency in the wood ant, *Formica rufa*: is time of the essence in trail following? *Animal Behaviour* **62**:139-146.
- Dent, D. 2000. *Insect Pest Management*. CABI Publishing, Wallingford.
- Dethier, V. G. 1988. The feeding behavior of a polyphagous caterpillar *Diacrisia virginica* in its natural habitat. *Canadian Journal of Zoology* **66**:1280-1288.
- Dethier, V. G. 1993. Food-finding by polyphagous arctiid caterpillars lacking antennal and maxillary chemoreceptors. *Canadian Entomologist* **125**:85-92.
- Di Giusto, B., M. C. Anstett, E. Dounias, and D. B. McKey. 2001. Variation in the effectiveness of biotic defence: the case of an opportunistic ant-plant protection mutualism. *Oecologia* **129**:367-375.
- Dicke, M., and M. Hilker. 2003. Induced plant defences: from molecular biology to evolutionary ecology. *Basic and Applied Ecology* **4**:3-14.
- Didham, R. K. 1997. Dipteran tree-crown assemblages in a diverse southern temperate rainforest. Pages 320-343 in N. E. Stork, J. Adis, and R. K. Didham, editors. *Canopy Arthropods*. Chapman & Hall, London.
- Dippenaar-Schoeman, A. S., and R. Jocqué. 1997. *African Spiders. An Identification Manual*. ARC - Plant Protection Research Institute, Pretoria.
- Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* **277**:515-522.
- Dreisig, H. 2000. Defense by exploitation in the Florida carpenter ant, *Camponotus floridanus*, at an extrafloral nectar resource. *Behavioral Ecology and Sociobiology* **47**:274-279.
- Drury, S. A. 1998. *Images of the Earth. A guide to remote sensing*. Oxford University Press, Oxford.
- Ebbers, B. C., and E. M. Barrows. 1980. Individual ants specialize on particular aphid herds (Hymenoptera: Formicidae; Homoptera: Aphididae). *Proceedings of the Entomological Society of Washington* **82**:405-407.
- Edwards, P. B., W. J. Wanjura, and W. V. Brown. 1993. Selective herbivory by Christmas beetles in response to intraspecific variation in *Eucalyptus* terpenoids. *Oecologia* **95**:551-557.
- Edwards, P. J., and S. D. Wratten. 1983. Wound induced defences in plants and their consequences for patterns of insect grazing. *Oecologia* **59**:88-93.
- Ehrlich, P. R., and A. H. Ehrlich. 1981. *Extinction: The causes and consequences of the disappearance of species*. Random House, New York.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* **18**:586-608.
- Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* **36**:74-75.
- Erwin, T. L. 1989. Canopy arthropod biodiversity: a chronology of sampling techniques and results. *Revista Peruana de Entomologia* **32**:71-77.
- Erwin, T. L. 1995. Measuring arthropod biodiversity in the tropical forest canopy. Pages 109-127 in M. D. Lowman and N. M. Nadkarni, editors. *Forest Canopies*. Academic Press, San Diego.
- Erwin, T. L., and J. C. Scott. 1980. Seasonal and size patterns, trophic structure, and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the canal zone of Panama. *The Coleopterists Bulletin* **34**:305-322.
- Ewel, J. J. 1999. Natural systems as models for the design of sustainable systems of land use. *Agroforestry Systems* **45**:1-21.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* **51**:565-581.

- Fewell, J. H. 1990. Directional fidelity as a foraging constraint in the western harvester ant, *Pogonomyrmex occidentalis*. *Oecologia* **82**:45-51.
- Fiala, B., H. Grunsky, U. Maschwitz, and K. E. Linsenmair. 1994. Diversity of ant-plant interactions: protective efficacy in *Macaranga* species with different degrees of ant association. *Oecologia* **97**:186-192.
- Fiala, B., U. Maschwitz, T. Y. Pong, and A. J. Helbig. 1989. Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia* **79**:463-470.
- Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**:42-58.
- Fittkau, E. J., and H. Klinge. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* **5**:2-14.
- Floren, A., A. Biun, and K. E. Linsenmair. 2002. Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia* **131**:137-144.
- Floren, A., A. Freking, M. Biehl, and K. E. Linsenmair. 2001. Anthropogenic disturbance changes the structure of arboreal tropical ant communities. *Ecography* **24**:547-554.
- Floren, A., and K. E. Linsenmair. 1997. Diversity and recolonization dynamics of selected arthropod groups on different tree species in a lowland rainforest in Sabah, Malaysia with special reference to Formicidae. Pages 344-381 in N. E. Stork, J. Adis, and R. K. Didham, editors. *Canopy Arthropods*. Chapman & Hall, London.
- Floren, A., and K. E. Linsenmair. 1998. Non-equilibrium communities of Coleoptera in trees in a lowland rain forest of Borneo. *Ecotropica* **4**:55-67.
- Floren, A., and K. E. Linsenmair. 2000. Do ant mosaics exist in pristine lowland rain forests? *Oecologia* **123**:129-137.
- Floren, A., and K. E. Linsenmair. 2001. The influence of anthropogenic disturbances on the structure of arboreal arthropod communities. *Plant Ecology* **153**:153-167.
- Floren, A., and S. Otto. 2002. Beeinflusst die Anwesenheit der Waldameise *Formica polyctena* Foerster die Artenzusammensetzung und Struktur von Spinnengemeinschaften auf Eichen? *Arachnologische Mitteilungen* **24**:1-18.
- Fourcassié, V., and J. F. A. Traniello. 1993. Effects of experience on food-searching behavior in the ant *Formica schaufussi* (Hymenoptera: Formicidae). *Journal of Insect Behavior* **6**:287-299.
- Fowler, H. G. 1983. Individual specializations on nectaries of *Euphorbia esula* by *Formica pallidefulva* workers. *Sociobiology* **8**:99-103.
- Fowler, S. V., and M. MacGarvin. 1985. The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betula pubescens*. *Journal of Animal Ecology* **54**:847-855.
- Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* **108**:269-289.
- Freude, H., K. W. Harde, and G. A. Lohse. 1965-1983. *Die Käfer Mitteleuropas*. Goecke & Evers, Krefeld.
- Fritz, R. S. 1992. Community structure and species interactions of phytophagous insects on resistant and susceptible host plants. Pages 240-277 in R. S. Fritz and E. L. Simms, editors. *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago.
- Fritz, R. S. 1995. Direct and indirect effects of plant genetic-variation on enemy impact. *Ecological Entomology* **20**:18-26.
- Fritz, R. S., and P. W. Price. 1988. Genetic variation among plants and insect community structure: willows and saw-flies. *Ecology* **69**:845-856.
- Fritz, R. S., and E. L. Simms, editors. 1992. *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago.
- Fulcher, A. F., T. G. Ranney, J. D. Burton, J. F. Walgenbach, and D. A. Danehower. 1998. Role of foliar phenolics in host plant resistance of *Malus* taxa to adult Japanese beetles. *Hortscience* **33**:862-865.
- Gagné, W. C., and J. L. Martin. 1968. The insect ecology of Red Pine plantations in central Ontario. V. The Coccinellidae (Coleoptera). *The Canadian Entomologist* **100**:835-846.
- Gallagher, R., and B. Carpenter. 1997. Human-dominated ecosystems. *Science* **277**:485.
- Gaston, K. J. 1991. Estimates of the near-imponderable: a reply to Erwin. *Conservation Biology* **5**:564-566.
- Gatehouse, J. A. 2002. Plant resistance towards insect herbivores: A dynamic interaction. *New Phytologist* **156**:145-169.
- Gilbert, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pages 11-33 in M. E. Soulé and B. A. Wilcox, editors. *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer, Massachusetts.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606-2621.
- Gotelli, N. J., and G. L. Entsminger. 2001. EcoSim: null models software for ecology, version 7.0. Acquired Intelligence, Kesey-Bear, <http://homepages.together.net/~gentsmin/ecosim.htm>. in.
- Gotelli, N. J., and G. R. Graves. 1996. *Null Models in Ecology*. Smithsonian Institution Press, Washington, DC.

- Goulet, H., and J. T. Huber, editors. 1993. Hymenoptera of the World: An Identification Guide to Families. Centre for Land and Biological Resources Research, Ottawa, Ontario.
- Gouyon, P. H., P. H. Fort, and G. Caraux. 1983. Selection of seedlings of *Thymus vulgaris* by grazing slugs. *Journal of Ecology* **73**:299-306.
- Grant, S., and V. C. Moran. 1986. The effects of foraging ants on arboreal insect herbivores in an undisturbed woodland savanna. *Ecological Entomology* **11**:83-93.
- Greenwood, S. R. 1987. The role of insects in tropical forest food webs. *AMBIO* **16**:267-271.
- Hägele, B. F., and M. Rowell-Rahier. 1999. Dietary mixing in three generalist herbivores: nutrient complementation or toxin dilution? *Oecologia* **119**:521-533.
- Halaj, J., D. W. Ross, and A. R. Moldenke. 1997. Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia* **109**:313-322.
- Halaj, J., D. W. Ross, and A. R. Moldenke. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos* **90**:139-152.
- Hanley, M. E., and B. B. Lamont. 2002. Relationships between physical and chemical attributes of congeneric seedlings: how important is seedling defence? *Functional Ecology* **16**:216-222.
- Harari, A. R., D. Benyakir, and D. Rosen. 1994. Mechanism of aggregation behavior in *Maladera matrida* Argaman (Coleoptera, Scarabaeidae). *Journal of Chemical Ecology* **20**:361-371.
- Harari, A. R., and P. J. Landolt. 1997. Orientation of sugarcane rootstalk borer weevil, *Diaprepes abbreviatus*, to weevil, frass, and food odors. *Journal of Chemical Ecology* **23**:857-868.
- Harari, A. R., and P. J. Landolt. 1999. Feeding experience enhances attraction of female *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae) to food plant odors. *Journal of Insect Behavior* **12**:415-422.
- Harrison, J. F., J. H. Fewell, T. M. Stiller, and M. D. Breed. 1989. Effects of experience on use of orientation cues in the giant tropical ant. *Animal Behaviour* **37**:869-871.
- Haukioja, E. 1990. Induction of defenses in trees. *Annual Review of Entomology* **36**:25-42.
- Heads, P. A., and J. H. Lawton. 1985. Bracken, ants and extrafloral nectaries. III. How insect herbivores avoid ant predation. *Ecological Entomology* **10**:29-42.
- Heil, M. 2002. Ecological costs of induced resistance. *Current Opinion in Plant Biology* **5**:345-350.
- Heil, M., B. Fiala, B. Baumann, and K. E. Linsenmair. 2000. Temporal, spatial and biotic variations in extrafloral nectar secretion by *Macaranga tanarius*. *Functional Ecology* **14**:749-757.
- Heil, M., B. Fiala, U. Maschwitz, and K. E. Linsenmair. 2001a. On benefits of indirect defence: short- and long-term studies of antiherbivore protection via mutualistic ants. *Oecologia* **126**:395-403.
- Heil, M., T. Koch, A. Hilpert, B. Fiala, W. Boland, and K. E. Linsenmair. 2001b. Extrafloral nectar production of the ant-associated plant, *Macaranga tanarius*, is an induced, indirect, defensive response elicited by jasmonic acid. *Proceedings of the National Academy of Sciences of the United States of America* **98**:1083-1088.
- Heinrich, B. 1979. Foraging strategies of caterpillars. Leaf damage and possible predator avoidance strategies. *Oecologia* **42**:325-337.
- Heinrich, B. 1993. How avian predators constrain caterpillar foraging. Pages 224-247 in N. E. Stamp and T. M. Casey, editors. *Caterpillars: Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York.
- Hemming, J. D. C., and R. L. Lindroth. 1995. Intraspecific variation in aspen phytochemistry: Effects on performance of gypsy moth and forest tent caterpillars. *Oecologia* **103**:79-88.
- Heywood, V., and R. Watson, editors. 1995. *Global biodiversity assessment*. UNEP, Cambridge University Press, Cambridge.
- Hochberg, Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* **75**:800-802.
- Hölldobler, B. 1979. Territories of the African weaver ant (*Oecophylla longinoda* (Latreille)). A field study. *Zeitschrift für Tierpsychologie* **51**:201-213.
- Hölldobler, B. 1983. Territorial behavior in the green tree ant (*Oecophylla smaragdina*). *Biotropica* **15**:241-250.
- Hölldobler, B., M. Möglich, and U. Maschwitz. 1974. Communication by tandem running in the ant *Camponotus sericeus*. *Journal of Comparative Physiology* **90**:105-127.
- Hölldobler, B., and E. O. Wilson. 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Mass.
- Horstmann, K., and H. J. Geisweid. 1978. Untersuchungen zu Verhalten und Arbeitsteilung von Waldameisen an Rindenlauskolonien (*Formica rufa* L. und *polyctena* Forster; *Lachnus roboris* L.). *Waldhygiene* **12**:157-168.
- Horvitz, C. C., and D. W. Schemske. 1984. Effects of ants and an ant-tended herbivore on seed production of a neotropical herb. *Ecology* **65**:1369-1378.
- Hossaert-McKey, M., J. Orivel, E. Labeyrie, L. Pascal, J. H. C. Delabie, and A. Dejean. 2001. Differential associations with ants of three co-occurring extrafloral nectary-bearing plants. *Ecoscience* **8**:325-335.
- Hovestadt, T. 1997. Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. *Wissenschaft & Technik Verlag*, Berlin.

- Hovestadt, T., P. Yao, and K. E. Linsenmair. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* **144**:1-25.
- Hurlbert, S. H. 1969. A coefficient of interspecific association. *Ecology* **50**:1-9.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**:577-586.
- Inouye, D. W., and O. R. Taylor. 1979. A temperate region plant-ant-seed predator system: consequences of extra floral nectar secretion by *Helianthella quinquenervis*. *Ecology* **60**:1-7.
- Ito, F., and S. Higashi. 1991. Variance of ant effects on the different life forms of moth caterpillars. *Journal of Animal Ecology* **60**:327-334.
- Iwabuchi, K., and J. Takahashi. 1983. Aggregative distribution pattern of the Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), and the role of the former occupants in the formation of an aggregation. *Applied Entomology and Zoology* **18**:324-329.
- Jackson, D. A. 1984. Ant distribution patterns in a Cameroonian cocoa plantation: investigation of the ant mosaic hypothesis. *Oecologia* **62**:318-324.
- James, D. G., M. M. Stevens, K. J. O'Malley, and R. J. Faulder. 1999. Ant foraging reduces the abundance of beneficial and incidental arthropods in citrus canopies. *Biological Control* **14**:121-126.
- Janzen, D. H. 1975. *Pseudomyrmex nigropilosa*: a parasite of a mutualism. *Science* **188**:936-937.
- Jeanne, R. L. 1979. A latitudinal gradient in rates of ant predation. *Ecology* **60**:1211-1224.
- Jedicke, E. 2000. Biodiversität und Raum - Aspekte der Bewertung räumlicher Muster biotischer Vielfalt. Pages 191-195 in H. Korn and U. Feit, editors. *Treffpunkt Biologische Vielfalt - Interdisziplinärer Forschungsaustausch im Rahmen des Übereinkommens über die biologische Vielfalt*. Bundesamt für Naturschutz, Bonn.
- Jeffries, M. J., and J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society* **23**:269-286.
- Jolivet, P. 1991. Ants, plants, and beetles; a triangular relationship. Pages 397-406 in C. R. Huxley and D. F. Cutler, editors. *Ant-plant interactions*. Oxford University Press, Oxford.
- Jolivet, P. 1998. *Interrelationship between Insects and Plants*. CRC Press, Boca Raton.
- Kalberer, N. M., T. C. J. Turlings, and M. Rahier. 2001. Attraction of a leaf beetle (*Oreina cacaliae*) to damaged host plants. *Journal of Chemical Ecology* **27**:647-661.
- Karban, R. 1992. Plant variation: its effects on populations of herbivorous insects. Pages 195-215 in R. S. Fritz and E. L. Simms, editors. *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago.
- Karban, R., and I. T. Baldwin. 1997. *Induced responses to herbivory*. Univ. Chicago Press, Chicago.
- Karban, R., and J. H. Myers. 1989. Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* **20**:331-348.
- Karhu, K. J. 1998. Effects of ant exclusion during outbreaks of a defoliator and a sap-sucker on birch. *Ecological Entomology* **23**:185-194.
- Keddy, P. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**:157-164.
- Kitching, R. L., K. L. Hurlley, and L. Thalib. 2003. Tree relatedness and the similarity of insect assemblages: pushing the limits? Pages 329-340 in Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching, editors. *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge.
- Kitching, R. L., and J. Zalucki. 1996. The biodiversity of arthropods from Australian rain forest canopies: some results on the role of the tree species. Pages 21-28 in D. S. Edwards, W. E. Booth, and S. C. Choy, editors. *Tropical rainforest research - current issues: Proceedings of the conference held in Bandar Seri Begawan, April 1993*. Kluwer Academic Publishers, Dordrecht.
- König, B., and K. E. Linsenmair. 1996. Biologische Diversität - Ein Phänomen und seine Dimensionen. Pages 8-15 in B. König and K. E. Linsenmair, editors. *Biologische Vielfalt*. Spektrum, Akademischer Verlag, Heidelberg, Berlin, Oxford.
- Koptur, S. 1984. Experimental evidence for defense of *Inga* (Mimosoidae) saplings by ants. *Ecology* **65**:1787-1793.
- Koptur, S. 1985. Alternative defenses against herbivores in *Inga* (Fabaceae: Mimosoideae) over an elevation gradient. *Ecology* **66**:1639-1650.
- Koptur, S. 1992. Extrafloral nectary-mediated interactions between insects and plants. Pages 81-129 in E. Bernays, editor. *Insect-plant interactions*. CRC Press, Boca Raton, FL.
- Krischik, V. A., and R. F. Denno. 1983. Individual, population, and geographic patterns in plant defence. Pages 463-512 in R. F. Denno and M. S. McClure, editors. *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York.

- Krüger, O., and G. C. McGavin. 1997. The insect fauna of *Acacia* species in Mkomazi Game Reserve, north-east Tanzania. *Ecological Entomology* **22**:440-444.
- Krüger, O., and G. C. McGavin. 1998. Insect diversity of *Acacia* canopies in Mkomazi game reserve, north-east Tanzania. *Ecography* **21**:261-268.
- Lachaud, J. P., D. Fresneau, and J. García-Pérez. 1984. Etude des stratégies d'approvisionnement chez trois espèces de fourmis ponérines. *Folia Entomologica Mexicana* **61**:159-177.
- Ladd, T. L. J. 1986. Influence of sugars on the feeding response of Japanese beetles (Coleoptera: Scarabaeidae). *Journal of Economic Entomology* **79**:668-671.
- Lance, D., and P. Barbosa. 1982. Host tree influences on the dispersal of late instar gypsy moths, *Lymantria dispar*. *Oikos* **38**:1-7.
- Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* **28**:23-39.
- Lawton, J. H. 2000. *Community Ecology in a Changing World*. Ecology Institute, Oldendorf/Luhe.
- Lee, S. M., and A. Chao. 1994. Estimating population size via sample coverage for closed capture-recapture models. *Biometrics* **50**:88-97.
- Legendre, P., and L. Legendre. 1998. *Numerical Ecology*. Second English Edition. Elsevier, Amsterdam.
- Leston, D. 1973. The ant mosaic - tropical tree crops and the limiting of pests and diseases. *Pest Articles and News Summaries* **19**:311-341.
- Leston, D. 1978. A neotropical ant mosaic. *Annals of the Entomological Society of America* **71**:649-653.
- Lévieux, J. 1977. La nutrition des fourmis tropicales. V. Éléments de synthèse. Les modes d'exploitation de la biocoenose. *Insectes Sociaux* **24**:235-260.
- Lévieux, J. 1983a. Feeding strategies of ants in different West African Savannas. Pages 245-252 in P. Jaisson, editor. *Social Insects in the Tropics*. Presses de l'Université de Paris XIII, Paris.
- Lévieux, J. 1983b. The soil fauna of tropical savannas. IV. The ants. Pages 525-540 in F. Bourlière, editor. *Ecosystems of the world*. Elsevier, Amsterdam.
- Levings, S. C., and N. R. Franks. 1982. Patterns of nest dispersion in a tropical ground ant community. *Ecology* **63**:338-344.
- Lewis, K. J. 1997. Growth reduction in spruce infected by *Inonotus tomentosus* in central British Columbia. *Canadian Journal of Forest Research* **27**:1669-1674.
- Lightfoot, D. C., and W. G. Whitford. 1989. Interplant variation in creosotebush foliage characteristics and canopy arthropods. *Oecologia* **81**:166-175.
- Linsenmair, K. E. 1990. Tropische Biodiversität: Befunde und offene Probleme. *Verhandlungen der Deutschen Zoologischen Gesellschaft* **83**:245-261.
- Linsenmair, K. E. 1998. Risk-spreading and risk-reducing tactics of West African anurans in an unpredictably changing and stressful environment. Pages 221-242 in D. M. Newbery, H. H. T. Prins, and N. D. Brown, editors. *Dynamics of Tropical Communities*. Blackwell Science, Oxford.
- Lodge, D. M., and K. Shrader-Frechette. 2003. Nonindigenous species: ecological explanation, environmental ethics, and public policy. *Conservation Biology* **17**:31-37.
- Loughrin, J. H., D. A. Potter, and K. T. R. Hamilton. 1995. Volatile compounds induced by herbivory act as aggregation kairomones for the Japanese beetle (*Popillia japonica* Newman). *Journal of Chemical Ecology* **21**:1457-1467.
- Loughrin, J. H., D. A. Potter, T. R. Hamilton-Kemp, and M. E. Byers. 1996a. Role of feeding-induced plant volatiles in aggregative behavior of the Japanese beetle (Coleoptera: Scarabaeidae). *Environmental Entomology* **25**:1188-1191.
- Loughrin, J. H., D. A. Potter, T. R. Hamilton-Kemp, and M. E. Byers. 1996b. Volatile compounds from crabapple (*Malus spp.*) cultivars differing in susceptibility to the Japanese beetle (*Popillia japonica* Newman). *Journal of Chemical Ecology* **22**:1295-1305.
- Lowman, M. D. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rain forest tree species. *Australian Journal of Ecology* **10**:7-24.
- Lowman, M. D. 1992. Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphoras sassafras* (Monimiaceae). *Biotropica* **24**:263-272.
- Ludwig, J. A., and J. F. Reynolds. 1988. *Statistical Ecology, a Primer on Methods and Computing*. John Wiley & Sons, New York.
- Mabberley, D. J. 1997. *The Plant-book. A portable Dictionary of the Vascular Plants*, Second Edition edition. Cambridge University Press, Cambridge.
- Mac Arthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Macedo, C. A., and J. H. Langenheim. 1989. Intra- and interplant leaf sesquiterpene variability in *Copaifera langsdorfii*: relation to microlepidopteran herbivory. *Biochemical Systematics and Ecology* **17**:551-557.
- Magurran, A. E. 1988. *Ecological Diversity and its Measurement*. Chapman & Hall, London.
- Majer, J. D. 1972. The ant mosaic in Ghana cocoa farms. *Bulletin of Entomological Research* **62**:151-160.

- Majer, J. D. 1973. The nature and role of the ant complex in Ghana cocoa farms. Ph.D. thesis, University of Ghana, 553 p.
- Majer, J. D. 1976. The influence of ants and ant manipulation on the cocoa farm fauna. *Journal of Applied Ecology* **13**:157-175.
- Majer, J. D. 1993. Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia - its structure and influence on arthropod diversity. Pages 115-141 in J. LaSalle and I. D. Gauld, editors. *Hymenoptera and Biodiversity*. CAB International, Wallingford, UK.
- Majer, J. D., J. H. C. Delabie, and M. R. B. Smith. 1994. Arboreal ant community patterns in Brazilian cocoa farms. *Biotropica* **26**:73-83.
- Majer, J. D., R. L. Kitching, B. E. Heterick, K. Hurley, and K. E. C. Brennan. 2001. North-south patterns within arboreal ant assemblages from rain forests in eastern Australia. *Biotropica* **33**:643-661.
- Majer, J. D., H. F. Recher, and S. Ganesh. 2000. Diversity patterns of eucalypt canopy arthropods in eastern and western Australia. *Ecological Entomology* **25**:295-306.
- Mapongmetsem, P. M., B. Duguma, B. A. Nkongmeneck, and H. Puig. 1998. Determinisme de la defeuillaison chez quelques essences forestieres tropicales du Cameroun. *Revue d' Ecologie (Terre et Vie)* **53**:193-210.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243-253.
- Marquis, R. J. 1992. Selective impact of herbivores. Pages 301-325 in R. S. Fritz and E. L. Simms, editors. *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago.
- Martin, P., and P. Bateson. 1993. *Measuring behaviour - an introductory guide*, 2 edition. Cambridge University Press, Cambridge.
- Mawdsley, N. A., and N. E. Stork. 1997. Host-specificity and the effective specialization of tropical canopy beetles. Pages 104-130 in N. E. Stork, J. Adis, and R. K. Didham, editors. *Canopy Arthropods*. Chapman & Hall, London.
- May, R. M. 1975. Patterns of species abundance and diversity. in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts.
- McGavin, G. 1999. Arthropod diversity and the tree flora of Mkomazi. Pages 371-390 in M. J. Coe, N. C. McWilliam, G. N. Stone, and M. J. Packer, editors. *Mkomazi: the Ecology, Biodiversity and Conservation of a Tanzanian Savanna*. Royal Geographic Society and The Institute of British Geographers, London.
- McIver, J. D. 1991. Dispersed central place foraging in Australian meat ants. *Insectes Sociaux* **38**:129-137.
- Meffe, G. K., and C. R. Carroll. 1997. *Principles of Conservation Biology*, 2 edition. Sinauer, Sunderland.
- Mercier, J.-L., A. Dejean, and A. Lenoir. 1998. Limited aggressiveness among African arboreal ants (Hymenoptera: Formicidae) sharing the same territories: the result of a co-evolutionary process. *Sociobiology* **32**:139-150.
- Merz, E. 1959. Pflanzen und Raupen. Über einige Prinzipien der Futterwahl bei Großschmetterlingsraupen. *Biologisches Zentralblatt* **1**:152-188.
- Mihaliak, C. A., C. Couvet, and D. E. Lincoln. 1989. Genetic and environmental contributions to variation in leaf mono- and sesquiterpenes of *Heterotheca subaxillaris*. *Biochemical Systematics and Ecology* **17**:529-533.
- Miller, M. F. 1996. Acacia seed predation by bruchids in an African savanna ecosystem. *Journal of Applied Ecology* **33**:1137-1144.
- Mody, K. 1998. *Arborikole Arthropodengemeinschaften der westafrikanischen Baumsavanne: Untersuchungen zur Strukturierung ökologischer Gemeinschaften*. Diplomarbeit. Bayerische Julius-Maximilians-Universität, Würzburg.
- Mody, K., H. A. Bardorz, and K. E. Linsenmair. 2003. Organization of arthropod assemblages in individual African savanna trees. Pages 198-212 in Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching, editors. *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge.
- Mody, K., and K. E. Linsenmair. 2003. Finding its place in a competitive ant community: leaf fidelity of *Camponotus sericeus*. *Insectes Sociaux* **50**:in press.
- Moffett, M., and M. D. Lowman. 1995. Canopy access techniques. Pages 3-26 in M. D. Lowman and N. M. Nadkarni, editors. *Forest Canopies*. Academic Press, San Diego, USA.
- Montllor, C. B., and E. A. Bernays. 1993. Invertebrate predators and caterpillar foraging. Pages 170-202 in N. E. Stamp and T. M. Casey, editors. *Caterpillars: Ecological and Evolutionary Constraints on Foraging*. Chapman & Hall, New York.
- Moran, V. C. 1980. Interactions between phytophagous insects and their *Opuntia* hosts. *Ecological Entomology* **5**:153-164.
- Moran, V. C., J. H. Hoffmann, F. A. C. Impson, and J. F. G. Jenkins. 1994. Herbivorous insect species in the tree canopy of a relict South African forest. *Ecological Entomology* **19**:147-154.

- Moran, V. C., and T. R. E. Southwood. 1982. The guild composition of arthropod communities in trees. *Journal of Animal Ecology* **51**:289-306.
- Morin, P. J. 1999. *Community Ecology*. Blackwell Science, Malden, Mass.
- Morris, W., F. Grevstad, and A. Herzig. 1996. Mechanisms and ecological functions of spatial aggregation in chrysomelid beetles. Pages 303-322 in P. H. A. Jolivet and M. L. Cox, editors. *Chrysomelidae Biology. Volume 2. Ecological Studies*. SPB Academic Publishing, Amsterdam.
- Morris, W. F., S. D. Wiser, and B. Klepetka. 1992. Causes and consequences of spatial aggregation in the phytophagous beetle *Altica tombacina*. *Journal of Animal Ecology* **62**:49-58.
- Morse, D. R., N. E. Stork, and J. H. Lawton. 1988. Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecological Entomology* **13**:25-37.
- Morton, R. D., and R. Law. 1997. Regional species pools and the assembly of local ecological communities. *Journal of Theoretical Biology* **187**:321-331.
- Mutikainen, P., M. Walls, and J. Ovaska. 1996. Herbivore-induced resistance in *Betula pendula*: the role of plant vascular architecture. *Oecologia* **108**:723-727.
- Neuvonen, S., and E. Haukioja. 1985. How to study induced plant resistance? *Oecologia* **66**:456-457.
- Novotny, V., Y. Basset, J. Auga, W. Boen, C. Dal, P. Drozd, M. Kasbal, B. Isua, R. Kutil, M. Manumbor, and K. Molem. 1999. Predation risk for herbivorous insects on tropical vegetation: A search for enemy-free space and time. *Australian Journal of Ecology* **24**:477-483.
- Novotny, V., Y. Basset, and R. L. Kitching. 2003. Herbivore assemblages and their food resources. Pages 40-53 in Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching, editors. *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge.
- O'Dowd, D. J. 1979. Foliar nectar production and ant activity on a neotropical tree, *Ochroma pyramidale*. *Oecologia* **43**:233-248.
- O'Dowd, D. J., and E. A. Catchpole. 1983. Ants and extrafloral nectaries: no evidence for plant protection in *Helichrysum* spp. - ant interactions. *Oecologia* **59**:191-200.
- Oliveira, P. S., and R. F. Brandao. 1991. The ant community associated with extrafloral nectaries in the Brazilian cerrados. Pages 198-212 in C. R. Huxley and D. F. Cutter, editors. *Ant-Plant Interactions*. Oxford University Press, Oxford.
- Oliveira, P. S., A. F. da Silva, and A. B. Martins. 1987. Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in cerrado vegetation: ants as potential antiherbivore agents. *Oecologia* **74**:228-230.
- Oliveira, P. S., V. Rico-Gray, C. Diaz-Castelazo, and C. Castillo-Guevara. 1999. Interaction between ants, extrafloral nectaries and insect herbivores in Neotropical coastal sand dunes: herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). *Functional Ecology* **13**:623-631.
- Orians, C. M., and R. S. Fritz. 1996. Genetic and soil-nutrient effects on the abundance of herbivores on willow. *Oecologia* **105**:388-396.
- Osier, T. L., S. Y. Hwang, and R. L. Lindroth. 2000. Effects of phytochemical variation in quaking aspen *Populus tremuloides* clones on gypsy moth *Lymantria dispar* performance in the field and laboratory. *Ecological Entomology* **25**:197-207.
- Osier, T. L., and R. L. Lindroth. 2001. Effects of genotype, nutrient availability, and defoliation on aspen phytochemistry and insect performance. *Journal of Chemical Ecology* **27**:1289-1313.
- Ozanne, C. M. P. 1999. A comparison of the canopy arthropod communities of coniferous and broad-leaved trees in the United Kingdom. *Selbyana* **20**:290-298.
- Palmer, T. M., T. P. Young, M. L. Stanton, and E. Wenk. 2000. Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia* **123**:425-435.
- Passera, L., J. P. Lachaud, and L. Gomel. 1994. Individual food source fidelity in the neotropical ponerine ant *Ectatomma ruidum* Roger (Hymenoptera Formicidae). *Ethology Ecology & Evolution* **6**:13-21.
- Peacock, L., M. Lewis, and S. Herrick. 2001. Factors influencing the aggregative response of the blue willow beetle, *Phratora vulgatissima*. *Entomologia Experimentalis Et Applicata* **98**:195-201.
- Pemberon, R. W., and J. H. Lee. 1996. The influence of extrafloral nectaries on parasitism of an insect herbivore. *American Journal of Botany* **83**:1187-1194.
- Pickett, C. H., and W. D. Clark. 1979. *Function of extrafloral nectaries in Opuntia acanthocarpa* (Cactaceae). *American Journal of Botany* **66**:618-625.
- Poilecot, P. 1991. Un écosystème de savane soudanienne: Le Parc National de la Comoé (Côte d'Ivoire). UNESCO/PNUD, n°IVC/87/007; Note technique 2, Paris.
- Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* **121**:61-83.
- Porter, S. D., and C. D. Jorgensen. 1981. Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste? *Behavioral Ecology and Sociobiology* **9**:247-256.
- Porter, S. D., and D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* **71**:2095-2106.

- Preston, F. W. 1962. The canonical distribution of commonness and rarity. *Ecology* **43**:185-215; 410-432.
- Pulliam, H. R. 1975. Diet optimization with nutrient constraints. *American Naturalist* **109**:765-768.
- Quinet, Y., and J. M. Pasteels. 1996. Spatial specialization of the foragers and foraging strategy in *Lasius fuliginosus* (Latreille) (Hymenoptera, Formicidae). *Insectes Sociaux* **43**:333-346.
- Randlkofer, B. 2000. Nahrungspräferenzen bei phytophagen Käfern. Untersuchungen zur inter- und intraspezifischen Futterpflanzenwahl. F2-Praktikum. Bayerische Julius-Maximilians-Universität, Würzburg.
- Rapport, D. J. 1980. Optimal foraging for complementary resources. *American Naturalist* **116**:324-346.
- Rashbrook, V. K., S. G. Compton, and J. H. Lawton. 1992. Ant-herbivore interactions: reasons for the absence of benefits to a fern with foliar nectaries. *Ecology* **73**:2167-2174.
- Raupp, M. J., and R. F. Denno. 1983. Leaf age as a predictor of herbivore distribution and abundance. Pages 91-124 in R. F. Denno and M. S. McClure, editors. *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York.
- Renwick, J. A. A. 2001. Variable diets and changing taste in plant-insect relationships. *Journal of Chemical Ecology* **27**:1063-1076.
- Rey, J. R. 1981. Ecological biogeography of arthropods on *Spartina* islands in Northwest Florida. *Ecological Monographs* **51**:237-265.
- Ribas, C. R., and J. H. Schoederer. 2002. Are all ant mosaics caused by competition? *Oecologia* **131**:606-611.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**:223-225.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167-171.
- Ricklefs, R. E., and D. Schluter, editors. 1993. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. The University of Chicago Press, Chicago & London.
- Rico-Gray, V., and L. B. Thien. 1989. Effect of different ant species on reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae). *Oecologia* **81**:487-489.
- Rödel, M. O. 2000. Herpetofauna of West Africa. Vol. I: Amphibians of the West African Savanna. Edition Chimaira, Frankfurt/Main.
- Room, P. M. 1971. The relative distributions of ant species in Ghana's cocoa farms. *Journal of Animal Ecology* **40**:735-751.
- Rosengren, R. 1971. Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica* (Hymenoptera, Formicidae). *Acta Zoologica Fennica* **133**:1-106.
- Rosengren, R., and W. Fortelius. 1986. Ortstreue in foraging ants of the *Formica rufa* group - hierarchy of orienting cues and long-term memory. *Insectes Sociaux* **33**:306-337.
- Rowe, W. J., and D. A. Potter. 1996. Vertical stratification of feeding by Japanese beetles within linden tree canopies: selective foraging or height per se? *Oecologia* **108**:459-466.
- Ruther, J., A. Reinecke, K. Thiemann, T. Tolasch, W. Francke, and M. Hilker. 2000. Mate finding in the forest cockchafer, *Melolontha hippocastani*, mediated by volatiles from plants and females. *Physiological Entomology* **25**:172-179.
- Ruther, J., A. Reinecke, T. Tolasch, and M. Hilker. 2001. Make love not war: a common arthropod defence compound as sex pheromone in the forest cockchafer *Melolontha hippocastani*. *Oecologia* **128**:44-47.
- Sachs, L. 1997. *Angewandte Statistik. Anwendung statistischer Methoden*, 8., völlig neu bearbeitete und erweiterte Auflage edition. Springer Verlag, Berlin.
- Salo, O., and R. Rosengren. 2001. Memory of location and site recognition in the ant *Formica uralensis* (Hymenoptera: Formicidae). *Ethology* **107**:737-752.
- Samways, M. J., M. Nel, and A. J. Prins. 1982. Ants (Hymenoptera: Formicidae) foraging in citrus trees and attending honeydew-producing Homoptera. *Phytophylactica* **14**:155-157.
- Sanchez, B. C., and R. R. Parmenter. 2002. Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: a test of island biogeographic theory. *Journal of Arid Environments* **50**:247-265.
- Schatz, B., J. P. Lachaud, and G. Beugnon. 1995. Spatial fidelity and individual foraging specializations in the Neotropical ponerine ant, *Ectatomma ruidum* Roger (Hymenoptera, Formicidae). *Sociobiology* **26**:269-282.
- Schemske, D. W. 1982. Ecological correlates of a neotropical mutualism: ant assemblages at *Costus* extrafloral nectaries. *Ecology* **63**:932-941.
- Schmid-Hempel, P. 1984. Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Behavioral Ecology and Sociobiology* **14**:263-271.
- Schmidt, T. 1999. Die Arthropodengemeinschaften in der Baumkrone von Jungbirken (*Betula pendula* Roth): Welche Faktoren beeinflussen die Struktur dieser Lebensgemeinschaft? Wissenschaft und Technik Verlag, Berlin.
- Schoener, T. W. 1986. Overview: Kinds of ecological communities - ecology becomes pluralistic. Pages 467-479 in J. Diamond and T. J. Case, editors. *Community Ecology*. Harper & Row, New York.
- Scholtz, C. H., and E. Holm. 1989. *Insects of Southern Africa*. Butterworths, Durban.

- Schoonhoven, L. M., T. Jermy, and J. J. A. van Loon. 1998. Insect-plant biology. From physiology to evolution. Chapman & Hall.
- Schultz, J. C. 1983. Habitat selection and foraging tactics of caterpillars in heterogeneous trees. Pages 61-90 in R. F. Denno and M. S. McClure, editors. *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York.
- Schulze, E. D., and H. A. Mooney. 1993. *Biodiversity and ecosystem function*. Springer Verlag, Berlin.
- Scriber, J. M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). *Oecologia* **28**:269-287.
- Selman, B. J. 1988. Chrysomelids and ants. Pages 463-473 in P. Jolivet, E. Petitpierre, and T. H. Hsiao, editors. *Biology of Chrysomelidae*. Kluwer Academic Publishers, Dordrecht.
- Senn, J., S. Hanhimäki, and E. Haukioja. 1992. Among-tree variation in leaf phenology and morphology and its correlation with insect performance in the mountain birch. *Oikos* **63**:215-222.
- Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands. The colonization of empty islands. *Ecology* **50**:278-296.
- Singer, M. S. 2001. Determinants of polyphagy by a woolly bear caterpillar: a test of the physiological efficiency hypothesis. *Oikos* **93**:194-204.
- Singh, J. S. 2002. The biodiversity crisis: A multifaceted review. *Current Science* **82**:638-647.
- Smith, B. 1986. *Evaluation of Different Similarity Indices Applied to Data from the Rothamsted Insect Survey*. University of York, York.
- Sobrinho, T. G., J. H. Schoereder, L. L. Rodrigues, and R. G. Collevatti. 2002. Ant visitation (Hymenoptera: Formicidae) to extrafloral nectaries increases seed set and seed viability in the tropical weed *Triumfetta semitriloba*. *Sociobiology* **39**:353-368.
- Sokal, R. R., and F. Rohlf. 1995. *Biometry*, 3rd edition. Freeman and Company, San Francisco.
- Southwood, T. R. E., and P. A. Henderson. 2000. *Ecological Methods*. Blackwell Science, Oxford.
- Southwood, T. R. E., and C. E. J. Kennedy. 1983. Trees as islands. *Oikos* **41**:359-371.
- Southwood, T. R. E., V. C. Moran, and C. E. J. Kennedy. 1982a. The assessment of arboreal insect fauna: comparison of knockdown sampling and faunal lists. *Ecological Entomology* **7**:331-340.
- Southwood, T. R. E., V. C. Moran, and C. E. J. Kennedy. 1982b. The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology* **51**:635-649.
- Stamp, N. E., and M. D. Bowers. 1988. Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae). *Oecologia* **75**:619-624.
- Staudt, M., N. Mandl, R. Joffre, and S. Rambal. 2001. Intraspecific variability of monoterpene composition emitted by *Quercus ilex* leaves. *Canadian Journal of Forest Research* **31**:174-180.
- Steentoft, M. 1988. *Flowering plants in West Africa*. Cambridge University Press, Cambridge.
- Stewart, A. J. A. 1996. Interspecific competition reinstated as an important force structuring insect herbivore communities. *Trends in Ecology and Evolution* **11**:233-234.
- Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. *Oecologia* **85**:74-79.
- Stork, N. E. 1987a. Arthropod faunal similarity of Bornean rain forest trees. *Ecological Entomology* **12**:219-226.
- Stork, N. E. 1987b. Guild structure of arthropods from Bornean rain forest trees. *Ecological Entomology* **12**:69-80.
- Stork, N. E. 1988. Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society* **35**:321-337.
- Stork, N. E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. *Journal of Tropical Ecology* **7**:161-180.
- Stork, N. E., J. Adis, and R. K. Didham, editors. 1997. *Canopy Arthropods*. Chapman & Hall, London.
- Stork, N. E., P. M. Hammond, B. L. Russell, and W. L. Hadwen. 2001. The spatial distribution of beetles within the canopies of oak trees in Richmond Park, U.K. *Ecological Entomology* **26**:302-311.
- Strickland, A. H. 1951. The entomology of Swollen Shoot of cacao. I. - The insect species involved, with notes on their biology. *Bulletin of Entomological Research* **41**:725-748.
- Strickland, A. H. 1952. The entomology of Swollen Shoot of cacao. II. - The bionomics and ecology of the species involved. *Bulletin of Entomological Research* **42**:65-103.
- Strong, D. R., Jr., D. Simberloff, L. G. Abele, and A. B. Thistle. 1984a. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, New Jersey.
- Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984b. *Insects on Plants - Community Patterns and Mechanisms*. Blackwell, Oxford.
- Sundström, L. 1993. Foraging responses of *Formica truncorum* (Hymenoptera; Formicidae); exploiting stable vs. spatially and temporally variable resources. *Insectes Sociaux* **40**:147-161.
- Symstad, A. J., F. S. Chapin, D. H. Wall, K. L. Gross, L. F. Huenneke, G. G. Mittelbach, D. P. C. Peters, and D. Tilman. 2003. Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *Bioscience* **53**:89-98.

- Taylor, B. 1977. The ant mosaic on cocoa and other tree crops in Western Nigeria. *Ecological Entomology* **2**:245-255.
- Thomas, C. D. 1990. Fewer species. *Nature* **347**:237.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* **80**:1455-1474.
- Traniello, J. F. A. 1989. Foraging strategies of ants. *Annual Review of Entomology* **34**:191-210.
- Tscharntke, T., S. Thiessen, R. Dolch, and W. Boland. 2001. Herbivory, induced resistance, and interplant signal transfer in *Alnus glutinosa*. *Biochemical Systematics and Ecology* **29**:1025-1047.
- Turchin, P. 1987. The role of aggregation in the response of Mexican bean beetles to host-plant density. *Oecologia* **71**:577-582.
- Unsicker, S. B. 2002. Herbivore Insekten in arborikolen Systemen der westafrikanischen Savanne. Untersuchungen zum Spezialisierungsgrad blattfressender Raupen und Käfer. Diploma thesis. Wuerzburg, Wuerzburg.
- van Dam, N. M., K. Hadwich, and I. T. Baldwin. 2000. Induced responses in *Nicotiana attenuata* affect behavior and growth of the specialist herbivore *Manduca sexta*. *Oecologia* **122**:371-379.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of the Earth's ecosystems. *Science* **277**:494-499.
- von Maydell, H. J. 1990. Trees and shrubs of the sahel - their characteristics and uses. Verlag Josef Margraf, Weikersheim.
- Wagner, T. 1997. The beetle fauna of different tree species in forests of Rwanda and East Zaire. Pages 169-183 in N. E. Stork, J. Adis, and R. K. Didham, editors. *Canopy Arthropods*. Chapman & Hall, London.
- Wagner, T. 1998. Influence of tree species and forest type on the chrysomelid community in the canopy of an Ugandan tropical forest. *Mus. Reg. Sci. Nat. Torino* **1998**:253-269.
- Wagner, T. 1999. Arboreal chrysomelid community structure and faunal overlap between different types of forests in Central Africa. Pages 247-270 in M. L. Cox, editor. *Advances in Chrysomelidae Biology 1*. Backhuys Publishers, Leyden.
- Wagner, T. 2000. Influence of forest type and tree species on canopy-dwelling beetles in Budongo Forest, Uganda. *Biotropica* **32**:502-514.
- Waldbauer, G. P., and S. Friedman. 1991. Self-selection of optimal diets by insects. *Annual Review of Entomology* **36**:43-63.
- Waller, D. A., and C. G. Jones. 1989. Measuring herbivory. *Ecological Entomology* **14**:479-481.
- Wan, F. H., and P. Harris. 1996. Host finding and recognition by *Altica carduorum*, a defoliator of *Cirsium arvense*. *Entomologia Experimentalis Et Applicata* **80**:491-496.
- Waring, R. H., and G. B. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* **66**:889-897.
- Waterman, P. G., and S. Mole. 1989. Extrinsic factors influencing production of secondary metabolites in plants. Pages 107-134 in E. A. Bernays, editor. *Insect-Plant Interactions*. CRC Press, Boca Raton.
- Way, M. J. 1963. Mutualism between ants and honey-dew producing Homoptera. *Annual Review of Entomology* **8**:307-344.
- Wehner, R., R. D. Harkness, and P. Schmid-Hempel. 1983. Foraging strategies in individually searching ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). G. Fischer, Stuttgart.
- West, C. 1986. Insect communities in tree canopies. Pages 209-222 in M. Coe and N. M. Collins, editors. *Kora: An Ecological Inventory of the Kora National Reserve, Kenya*. Royal Geographical Society, London.
- Western, D. 2001. Human-modified ecosystems and future evolution. *Proceedings of the National Academy of Sciences of the United States of America* **98**:5458-5465.
- Wettstein, R. v. 1889. Über die Compositen der österreichisch-ungarischen Flora mit zuckerabscheidenden Hüllschuppen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, ser. 1* **97**:570-589.
- Wiens, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. Pages 439-457 in D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, New Jersey.
- Wilson, E. O. 1958. Patchy distributions of ant species in New Guinea rainforests. *Psyche* **65**:26-38.
- Winchester, N. N. 1997. Canopy arthropods of coastal Sitka spruce trees on Vancouver Island, British Columbia, Canada. Pages 151-168 in N. E. Stork, J. Adis, and R. K. Didham, editors. *Canopy Arthropods*. Chapman & Hall, London.
- Wise, D. H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge.
- Wright, G. A., S. J. Simpson, D. Raubenheimer, and P. C. Stevenson. 2003. The feeding behavior of the weevil, *Exophthalmus jekelianus*, with respect to the nutrients and allelochemicals in host plant leaves. *Oikos* **100**:172-184.

- Yarden, G., and A. Shani. 1994. Evidence for volatile chemical attractants in the beetle *Maladera matrida* Argaman (Coleoptera: Scarabaeidae). *Journal of Chemical Ecology* **20**:2673-2685.
- Ylioja, T., and M. Rousi. 2001. Soil fertility alters susceptibility of young clonal plantlets of birch (*Betula pendula*) to a dipteran stem miner. *Ecoscience* **8**:191-198.
- Zachariades, C., and J. J. Midgley. 1999. Extrafloral nectaries of South African Proteaceae attract insects but do not reduce herbivory. *African Entomology* **7**:67-76.
- Zalucki, M. P., A. R. Clarke, and S. B. Malcolm. 2002. Ecology and behavior of first instar larval Lepidoptera. *Annual Review of Entomology* **47**:361-393.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4 edition. Prentice-Hall, Upper Saddle River, New Jersey.
- Zobel, M. 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends in Ecology & Evolution* **12**:266-269.

XV. Danksagung

Viele Lehrer, Freunde und Bekannte leisteten einen direkten oder indirekten Beitrag zu dieser Arbeit. Ihnen allen möchte ich, namentlich erwähnt oder unerwähnt, ganz herzlich danken.

Besonders möchte ich mich bei Prof. Dr. K. Eduard Linsenmair bedanken. Er ermöglichte mir, den seit Kindertagen gehegten Wunsch „Tropenforscher“ zu werden, zu realisieren. Er ließ mir freie Hand zur Entwicklung und Bearbeitung einer eigenen Arbeit, formte diese aber auch entscheidend mit. Das von ihm geleitete tropenökologische Forschungscamp im Comoé-Nationalpark und die zusammen eingeworbene Arbeitsausrüstung bildeten den notwendigen Rahmen. Viele Ideen entsprangen seinen Lehrveranstaltungen, Publikationen sowie persönlichen Gesprächen. Durch sein großes Interesse und hilfreiche Diskussionen hat diese Arbeit durchgehend sehr profitiert.

Das Leben und Arbeiten im Comoé Nationalpark wurde durch zahlreiche Leute erleichtert, ermöglicht und in vielfacher Weise zu einer sehr schönen, bleibenden Erinnerung. Besonderer Dank gilt in dieser Hinsicht Jan Beck, Minnattallah Boutros, Njikoha Ebigbo, Jakob Fahr, Dr. Frauke Fischer, PD Dr. Ulmar Grafe, Matthias Groß, Klaus Hennenberg, Koffi Kouadio, David (Kouamé Kouassi), Britta Kunz, Lakado (Koffi Yao Maizan), Dr. Kathrin Lampert, Prof. Dr. K.E. Linsenmair, Dr. Dieter Mahsberg, Inza Ouattara, Norbert Reintjes und Sybille Unsicker.

Für die sehr gute Zusammenarbeit und Hilfe bei der Feldarbeit möchte ich mich bei Henryk Bardorz, Natalie Beier, Lars Hoffmann, Andrea Holzschuh, Katrin Maier, Burkard Pfeiffer, Barbara Randlkofer und Sybille Unsicker bedanken, die im Rahmen ihrer Diplom- und F2-Arbeiten im „Arthropoden-Pflanzen Projekt“ mitgearbeitet haben. Daneben möchte ich noch Dirk Mezger für seine Hilfe beim Sortieren und Aufarbeiten von Arthropodenproben und Cord Mikona für seine Hilfe bei der Blattflächenanalyse danken.

Einzelne Kapitel dieser Arbeit (s. auch die entsprechenden „Acknowledgements“) profitierten vom fachkundigen Rat folgender Kollegen und Freunde, denen nochmals herzlichst gedankt sei: Dr. Yves Basset, Jan Beck, Nico Blüthgen, Kathrin Dausmann, Dr. Andrew Davis, Dr. Brigitte Fiala, Julian Glos, Dr. Ulrike Gräfe, Dr. Martin Heil, Martin Hinsch, Dr. Frank-Thorsten Krell, Burkard Pfeiffer, Dr. Erhard Strohm, Dr. Thomas Hovestadt, Dr. Thomas Wagner, Prof. Dr. Wolfgang Weisser und Dr. Claus Wurst.

Für anregende Diskussionen sei neben den bereits erwähnten Personen noch Minnattallah Boutros, Dr. Carsten Brühl, Dr. Thomas Eltz, Prof. Dr. Michael Falk, Prof. Dr. Konrad Fiedler, Dr. Frauke Fischer (auch wenn wir unterschiedliche Meinungen bezüglich bestimmter Huftiere vertraten), Dr. Andreas Floren, Christian Kost, Dr. Elisabeth Obermaier, Prof. Dr. Hans Joachim Poethke, Norbert Reintjes und Dr. Mark-Oliver Rödel gedankt.

Norbert Reintjes stellte mir seinen Käfer-Markierungsstempel zur Verfügung, der sich sehr gut zum Markieren individueller Ameisen umfunktionieren ließ. Dr. Markus Voitke gab den entscheidenden Tipp, der dann zur feldtauglichen, standardisierten Erfassung von Blattflächen und Herbivorie führte: Blattflächen nicht mit einem (teuren und im Feld häufig unpraktischen) Blattflächenmessgerät, sondern mit einer Digitalkamera zu erfassen.

Das Schicksal, nur mit „Morphospezies“ arbeiten zu können, blieb mir dank der Bestimmungshilfe von Dr. Christoph Häuser (*Chrysopsyche imparilis*), Dr. Frank-Thorsten Krell (Käfer allgemein;

Apogonia fatidica), Dmitry Telnov (Anthicidae), Dr. Adjima Thiombiano (*Combretum fragrans*), Richard Thompson (*Proictes curvipes*), Dr. Thomas Wagner (Käfer allgemein; Chrysomelidae) und Dr. Claus Wurst (Käfer allgemein; Elateridae) erspart. Vielen Dank für diese sehr wichtige Hilfe!

Allen Mitgliedern des Lehrstuhls für Zoologie III danke ich für die gute Arbeitsatmosphäre. Minnattallah Boutros kann getrost die „gute Seele“ des Biota-Projekts genannt werden; auf ihre effektive organisatorische Unterstützung war jederzeit Verlass. Viel Dank gebührt auch Andrea Hilpert für ihre Hilfe bei Zucker- und Blatteinhaltsstoffanalysen (und natürlich für die Betreuung der Aubergine-Pflanzen), Thomas Igerst und Gerd Vonend für die Hilfestellung bei allen Computerproblemen, Helga Kesting für ihren unermüdlichen Einsatz gegen verdreckte Versuchsgefäße, Norbert Schneider für seine immerwährende Kreativität bei der Maß-Anfertigung von Arbeitsgeräten, Erhard Strohm für seine ständige Bereitschaft, über statistische Fragen und Probleme zu sprechen – und diese auch zu lösen, und dem Sekretariat der Zoo III unter Leitung von Birgit Bünger für die kompetente Hilfe und Beratung bei organisatorischen Problemen. Nicht zu vergessen sei auch die Mittags-Kaffeerunde und natürlich das Zoo III eigene, mit einigen Legionären verstärkte Fußballteam, die beide halfen, den von vorm Computer sitzen ermüdeten Geist wieder aufzufrischen.

Für finanzielle Unterstützung danke ich dem DAAD (Doktoranden-Auslandsstipendium), der DFG (Stipendium aus dem Graduiertenkolleg 200 „Grundlagen des Arthropodenverhaltens“) und dem BMBF (Stelle als wissenschaftlicher Mitarbeiter im Biota-Afrika Projekt).

Die Zugangsberechtigung zum Comoé Nationalpark und die Forschungserlaubnis wurden durch das „Ministère de l'Enseignement Supérieur et de la Recherche Scientifique“ und das „Ministère de la Construction et de l'Environnement“ der Elfenbeinküste gewährt. Vielen Dank.

Minnattallah Boutros, Kathrin Dausmann, Alex und Christin Froschauer und Julian Glos gaben mir das Gefühl, erreichbare Freunde für alle Fälle zu haben.

Ulrike Gräfe unterstützte mich darüber hinaus als persönliche Betreuerin und Lektorin in so vielfältiger Weise, dass sich der Dank zwar schlecht in Worte fassen lässt, ich mich aber trotzdem ganz besonders bedanken möchte.

Abschließend möchte ich meinen Eltern ganz herzlich danken. Sie haben immer an meiner Freude an der Biologie teilgenommen und mir dieses Studium ermöglicht.

Vielen Dank!

Curriculum Vitae

Name: Karsten Mody

Geburtsdatum: 25. September 1970

Geburtsort: Mannheim

Grundschule: 1977 – 1981 in Mutterstadt

Gymnasium: 1981 – 1990 Theodor-Heuss-Gymnasium, Ludwigshafen

Wehrdienst: Juni 1990 – Juli 1991

Studium: November 1991 – April 1997: Biologie Diplom
Bayerische Julius-Maximilians-Universität Würzburg
Vordiplom im November 1993
Diplomprüfung in Tierökologie und Tropenbiologie, Pharmazeutischer
Biologie sowie Ökophysiologie und Ökologie der Pflanzen im April 1997

Diplomarbeit: „Arborikole Arthropodengemeinschaften der westafrikanischen
Baumsavanne: Untersuchungen zur Strukturierung ökologischer
Gemeinschaften“ Betreuer: Prof. Dr. K. Eduard Linsenmair,
Lehrstuhl für Tierökologie und Tropenbiologie, Bayerische Julius-
Maximilians-Universität Würzburg

Promotion: 1998 - 2003 bei Prof. Dr. K. Eduard Linsenmair, Lehrstuhl für Tierökologie
und Tropenbiologie, Bayerische Julius-Maximilians-Universität Würzburg

Auslandsaufenthalte: August 1995 – Mai 1996: Duke University, North Carolina, USA
März – Mai 1994, April – August 1997, April – Juni 1999, April – Juni 2000,
Mai – Juni 2001, September 2002: Comoé-Nationalpark, Côte d'Ivoire
(Elfenbeinküste)

Würzburg, den 25. April 2003

Karsten Mody

Ehrenwörtliche Erklärung

gemäß § 4 Abs. 3 Ziff. 3, 5 und 8
der Promotionsordnung der Fakultät für Biologie der
Bayerischen Julius-Maximilians-Universität Würzburg

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation selbstständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Die Dissertation wurde bisher weder vollständig noch teilweise einer anderen Hochschule mit dem Ziel, einen akademischen Grad zu erwerben, vorgelegt.

Am 15. Juni 1998 wurde mir von der Universität Würzburg der akademische Grad "Diplom-Biologe Univ." verliehen. Weitere akademische Grade habe ich weder erworben noch versucht zu erwerben.

Würzburg, den 25. April 2003

Karsten Mody