

Artenreichtum von  
Herbivoren-Parasitoiden-Gesellschaften an Leguminosen:  
Ein Vergleich tropischer und gemäßigter Breiten



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# 1 Einleitung

Tropische Lebensräume sind gegenüber solchen gemäßigter Breiten durch eine größere Artenvielfalt gekennzeichnet. Der Großteil der Biodiversität unseres Planeten konzentriert sich auf die Tropen (Myers et al. 2000). Entsprechende geographische Gradienten der Artenvielfalt sind bereits seit den Naturforschern des 19. Jahrhunderts bekannt (z. B. Wallace 1878). Die Frage nach der Ursache solcher Muster gehört zu den zentralen Anliegen der Ökologie (Huston 1994, Rosenzweig 1995, Begon et al. 1996) und es existieren zahlreiche, oft widersprüchliche, Erklärungsansätze für die höhere Artenvielfalt in den Tropen (Rohde 1992).

Insekten kommt bei der Betrachtung von Diversitätsmustern besondere Bedeutung zu, da sie den überwiegenden Teil aller auf der Erde vorkommenden Organismen ausmachen (Strong et al. 1984, Greenwood 1987). Etwa ein Viertel aller Insektengruppen ist in den Tropen nicht artenreicher als in gemäßigten Breiten (Hawkins 1990). Dies gilt sowohl für einige Herbivore (Eastop 1978, Dixon et al. 1987) als auch für Parasitoide (Owen & Owen 1974, Janzen & Pond 1975, Gauld 1986). Die Artenvielfalt der meisten Taxa nimmt dagegen mit abnehmender geographischer Breite zu (Kusnezov 1957, Fischer 1960, Pianka 1966, Schoener and Janzen 1968, Price 1997), und einige kommen fast ausschließlich in den Tropen vor (Samways 1992).

Pflanzen, Herbivore und Parasitoide können dabei nicht separat betrachtet werden, da sie über multitrophische Interaktionen in Verbindung stehen (Tscharntke 1992, Kruess & Tscharntke 1994, 2000b). Pflanze-Insekt-Beziehungen kommt eine zentrale Bedeutung bei der Strukturierung von Lebensgemeinschaften zu, denn Pflanzen und Insekten machen zusammen etwa vier Fünftel aller weltweit vorkommenden Arten aus (Strong et al. 1984). Insekten nutzen Pflanzen vorwiegend als Nahrungsressource. Die Vorhersagbarkeit dieser Ressource fördert die Artenvielfalt (Strong et al. 1984, Hawkins & Lawton 1987, Tscharntke & Greiler 1995, Kelly & Southwood 1999). Entsprechend haben große, häufige, langlebige Pflanzen mit komplexer Architektur artenreichere Insektenlebensgemeinschaften als kleine, seltene, kurzlebige und architektonisch einfachere (Lawton & Schröder 1977, Moran 1980, Lawton 1983). Die relative Seltenheit einzelner Pflanzenarten in den Tropen entspricht einer größeren Fragmentierung von Ressourcen als sie in gemäßigten Breiten vorherrscht. Diese sollte

generell eine geringere Spezialisierung nach sich ziehen (Beaver 1979, Basset 1992). Allerdings sind unterschiedliche Auswirkungen auf Herbivore und Parasitoide denkbar.

Herbivore werden durch Ressourcenfragmentierung vergleichsweise wenig beeinträchtigt (Kruess & Tschardtke 1994, 2000b). Es wird vermutet, daß ihr großer tropischer Artenreichtum daher rührt, daß die pflanzlichen Ressourcen durch mehr Arten von Herbivoren genutzt werden. Tropische Lebensräume haben demnach im Vergleich zu gemäßigten engere Nischen und begünstigen die Koexistenz von mehr Arten (MacArthur & Wilson 1967, MacArthur 1969). Damit würde eine höhere Spezialisierung von Herbivoren als in gemäßigten Breiten einhergehen.

Mehr als auf Herbivoren wirkt sich Ressourcenfragmentierung auf höhere trophische Ebenen aus (Kareiva 1987, Pimm 1991, Kruess & Tschardtke 1994, 2000a, 2000b, Didham et al. 1996, Holt et al. 1999). Außerdem übersteigt die relative Seltenheit der Wirte noch die von Pflanzen. Es wird angenommen, daß viele Wirte daher zu selten sind, um von Parasitoiden gefunden zu werden. Entsprechend sollten Parasitoidenkomplexe in den Tropen nicht artenreicher sein als in gemäßigten Breiten (Janzen & Pond, 1975, Janzen, 1981, Hawkins, 1990, Hawkins, 1994). Die höhere Anfälligkeit der Parasitoide gegenüber der Fragmentierung von Ressourcen sollte außerdem eine geringere Spezialisierung nach sich ziehen als sie in gemäßigten Breiten vorherrscht (Askew & Shaw, 1986).

Artenreichtum und Ökosystemfunktionen sind in vielen Fällen miteinander gekoppelt. So steigt nicht nur der Artenreichtum sondern auch das Ausmaß der Herbivorie mit abnehmender geographischer Breite an (Lowman 1984). Die effiziente biologische Kontrolle phytophager Insekten durch Parasitoide ist positiv mit deren Artenreichtum korreliert (Hawkins et al. 1993). Artenärmere Parasitoidenkomplexe sollten daher auch mit geringeren Parasitierungsraten einhergehen.

Viele Schlußfolgerungen zur Charakterisierung tropischer Lebensgemeinschaften basieren auf örtlich begrenzten Studien (Owen and Owen 1974, Janzen and Pond 1975, Askew 1990). Bislang ist kaum bekannt, inwieweit sie sich generalisieren lassen. Es stellt sich die Frage, ob sich tropische Insektenlebensgemeinschaften derselben Pflanzenfamilie in verschiedenen Regionen ähneln. Aus gemäßigten Breiten sind deutliche Unterschiede zwischen Insektenlebensgemeinschaften verschiedener geographischer Lage bekannt (Tschardtke et al., 2000).

Folgende Hypothesen standen bei der vorliegenden Arbeit im Vordergrund:

(1) Die Anzahl der Herbivorenarten pro Pflanzenart ist in tropischen Lebensgemeinschaften größer als in gemäßigten. Dieses Verbreitungsmuster liegt in engeren Nischen (bzw. einem höheren Spezialisierungsgrad) und einer besseren Handhabung der in den Tropen größeren Ressourcenfragmentierung begründet.

(2) Die Anzahl der Parasitoidenarten pro Wirtsart ist geringer in tropischen Lebensgemeinschaften verglichen mit nicht tropischen. Dazu trägt die höhere Anfälligkeit von Parasitoiden gegenüber Ressourcenfragmentierung bei, die mit breiten Nischen (bzw. einem niedrigeren Spezialisierungsgrad) einhergehen sollte.

(3) Ökosystemfunktionen sind an den Artenreichtum gekoppelt. Als Folge von mehr Herbivorenarten pro Pflanze ist auch die Befallsrate in den Tropen größer als in den gemäßigten Breiten. Weniger Parasitoidenarten pro Wirt resultieren in einer geringeren Parasitierungsrate.

(4) Tropische Lebensgemeinschaften unterschiedlicher geographischer Lage ähneln sich in ihren Mustern und ihrer Struktur.

## **2 Material und Methoden**

In der vorliegenden Untersuchung wurden die genannten Hypothesen anhand von Herbivoren-Parasitoid-Lebensgemeinschaften an Leguminosen (Fabaceae) untersucht. Für eine Analyse von Diversitätsmustern erscheinen Klein-Lebensgemeinschaften, die sich um Arten der selben Pflanzenfamilie gruppieren, besonders geeignet. Sie weisen eine überschaubare Artenzahl auf und umfassen mehrere trophische Ebenen. Sie können leicht mit meßbaren Parametern charakterisiert werden. Leguminosen sind eine der größten Pflanzenfamilien mit ca. 18.000 Arten und weltweit verbreitet (Polhill et al., 1981). Die Hülsen von Leguminosen werden von einer Vielzahl samenfressender Insekten und deren Parasitoiden genutzt. Unabhängig von der geographischen Lage beherbergen sie Insekten gleicher Familien (v. a. Bruchidae, Curculionidae und Apionidae als Herbivore sowie Ichneumonidae, Braconidae und mehrere Familien der Chalcidoidea als Parasitoide). Dies macht sie zu geeigneten Objekten für vergleichende Untersuchungen. Durch die Analyse von Lebensgemeinschaften, die sich auf eine Nahrungsnische beschränken, sind am ehesten generalisierbare Muster zu erwarten. Die

Konzentration auf die endophage Insektengemeinschaft von Leguminosenhülsen repräsentiert daher eine standardisierte Methode zur Erfassung vorliegender Muster.

Im Mittelpunkt der Arbeit stand die Untersuchung der Insektenlebensgemeinschaft von 15 Arten von Leguminosen in Madagaskar. Zu diesem Zweck wurden insgesamt 8170 Hülsen gesammelt und auf die in ihnen lebenden Insektenarten untersucht. Diese wurden gezählt und (als Morphospezies) bestimmt. Die Anzahl der Herbivoren pro Pflanzenart und die Anzahl der Parasitoide pro Wirtsart spiegelte dabei jeweils die Artendichte wider. Die Individuendichte der Herbivoren pro Hülse bestimmte die Befallsrate, das Individuenverhältnis von Parasitoiden zu allen Insekten pro Hülse die Parasitierungsrate. Die Anzahl der von den jeweiligen Insektenarten genutzten Wirtspflanzen charakterisierte ihre Spezifität. Merkmale der Wirtspflanzen (Höhe, Seltenheit, Architektur) wurden ebenso erfaßt wie (für Bäume) die Abstände zum nächsten Individuum der gleichen Art. Die Auswirkung von Ressourcenfragmentierung auf die Insektenlebensgemeinschaft wurde auch experimentell untersucht. Dazu wurden 6 Populationen von *Tephrosia purpurea* ausgewählt, von denen jeweils 25 Individuen entfernt wurden. Jeweils 5 von ihnen wurden in 5 Plastiktöpfe gepflanzt, die in Abständen von 0, 10, 20, 30 und 50m zur Ausgangspopulation eingegraben wurden.

Die in Madagaskar analysierte Lebensgemeinschaft endophager Herbivoren und Parasitoide wurde mit bekannten Mustern entsprechender Lebensgemeinschaften in Deutschland verglichen. Dabei konnte auf die Daten von Garbe (1996) zurückgegriffen werden. Da diese mit der gleichen Methodik erhoben wurden, ergaben sich wesentlich bessere Möglichkeiten eines direkten Vergleiches als anhand von in der Methodik ihrer Erhebung oft differierender Literaturdaten.

Für einen innertropischen Vergleich wurden insgesamt 51 botanische Institutionen in Afrika mit der Bitte um Zusendung von jeweils 200 Hülsen von 4 Leguminosenarten angeschrieben, doch lediglich 6 waren zur Kooperation bereit (siehe Danksagung). Die Anzahl der aus diesen Proben geschlüpften Insekten (vgl. Anhang) reichte daher leider nicht für einen Vergleich mit den madagassischen Daten aus. Trotz der o. g. Problematik einer Literaturswertung war es daher notwendig, Literaturdaten miteinzubeziehen. Eine der umfangreichsten Arbeiten über tropische Insektenlebensgemeinschaften von Leguminosen stammt aus der Elfenbeinküste von

Rasplus (1988, 1994), dessen Daten mit denen aus Madagaskar in Beziehung gesetzt wurden.

Weitere Details zu Material und Methoden sind den nachfolgenden Kapiteln zu entnehmen. Tabellen der Originaldaten finden sich im Anhang.

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#### **4 Artenreichtum von Herbivoren-Parasitoiden-Gesellschaften an Leguminosen: Ein Vergleich tropischer und gemäßigter Breiten**

[1] DOLCH, R., TSCHARNTKE, T. (2000) Species packing of herbivores and parasitoids on legume host plants: comparing tropical and temperate communities. *Journal of Animal Ecology* (to be submitted).

[2] DOLCH, R., TSCHARNTKE, T. (2000) Tropical herbivores and their parasitoids: a comparison of insect communities on Fabaceae in Madagascar and the Ivory Coast. *Ecological Entomology* (to be submitted).

## **Species packing of herbivores and parasitoids on legume host plants: comparing tropical and temperate communities**

### **Abstract**

1.) Species richness and species packing was assessed for endophagous insects of 15 species of wild legumes (Fabaceae) from Madagascar and 27 species from Germany. Degrees of specificity, herbivore load, and percent parasitism were also compared between sites.

2.) Within Madagascar, herbivore species richness could be explained by plant traits and increased with the plants' height, life span and pod length, whereas parasitoid species richness was best predicted by species richness of herbivores.

3.) Species packing and specificity of herbivores were higher in Madagascar, supporting the idea of narrower niches in the tropics. Herbivores appeared to cope well with resource fragmentation in Madagascar. Higher species packing in Madagascar did not result in higher herbivore load.

4.) Species packing of parasitoids was lower in Madagascar, although parasitoid species were more specific than in Germany. Within Madagascar, species richness of parasitoids but not herbivores declined with increasing distance between host trees, supporting the idea of resource fragmentation being more severe for higher trophic levels. Although parasitoid complexes were smaller in Madagascar, percent parasitism did not differ between study sites.

5.) The results indicate that the man-made and large-scale fragmentation process currently under way in Madagascar is likely to particularly threaten biodiversity of higher trophic levels and possible biological control of phytophagous insects.

Key Words: resource fragmentation, niche compression, latitudinal patterns, species richness, trophic position, Madagascar, Fabaceae

## Introduction

The tendency of species richness to increase with decreasing latitude has long been known (Kusnezov, 1957; Fischer, 1960; Pianka, 1966; Price et al., 1991; Huston, 1994; Rosenzweig, 1995). Global biodiversity hotspots are strikingly concentrated in tropical countries (Myers et al., 2000). Numerous hypotheses exist to explain those latitudinal gradients of species richness (e. g. Rohde, 1992). Insects may provide the key for understanding patterns, since they contribute a major part to biodiversity. Arthropods account for more than half of global species richness (Stork, 1991), most of them being herbivorous insects and their parasitoids (Strong *et al.* 1984). Diversity of plants may trigger species richness of insects in the tropics (Gentry, 1986). In general, more predictable resources favour speciation (Strong et al., 1984; Hawkins & Lawton, 1987; Tschamntke & Greiler, 1995; Kelly & Southwood 1999). Abundant, large, long-lived, and architecturally complex plants should therefore have the most species of insects (Lawton & Schröder, 1977; Moran, 1980; Lawton, 1983). Most insect taxa do indeed increase in species richness towards lower latitudes (e. g. Huston 1994; Stevens, 1989 and references therein), although there are exceptions (Owen & Owen 1974; Janzen & Pond, 1975, Dixon et al., 1987; Kouki et al., 1994). It has been hypothesized, that tropical organisms have narrower niches, permitting more species to coexist compared to temperate regions, and that tropical species richness is accompanied by greater species packing (MacArthur, 1969). Examination of tropical and temperate insects exploiting similar resources allows direct comparisons of species packing. While focusing on the number of herbivore species per species of host plant and the number of parasitoid species per species of host, different patterns for herbivores and parasitoids seem plausible.

Tropical-temperate differences in herbivore species packing may be derived from host plant specificity. A higher degree of resource specificity in tropical versus temperate phytophagous insects would indicate narrower niches than outside the tropics. These narrower niches would permit more herbivore species packed per host plant. Greater chemical diversity of tropical plants is thought to be linked to higher specialization in tropical herbivores (Basset, 1994; Coley & Barone, 1996). Since host plants represent islands for colonizing herbivores (Janzen, 1968, 1973; Brown & Kodric-Brown, 1977; Southwood & Kennedy, 1983), species richness should decrease

with increasing isolation (= distances between individuals) of particular species of host plants (sensu MacArthur & Wilson, 1967). This is likely to occur in the tropics, where relative rarity of plant species is naturally high. A possible adaptation of herbivores to that natural fragmentation of resources in tropical regions is the exploitation a wide range of resources (Beaver, 1979; Basset, 1992). This would be synonymous with lower specificity of tropical herbivores. Thus, plant chemistry and resource fragmentation exert opposing selection pressures. Yet, tropical herbivores may be better at handling fragmentation of resources than temperate ones (e. g. by being better dispersers), so that the selection pressure for becoming a generalist may be low (Coley & Barone, 1996).

Parasitoids may be adversely affected by high concentrations of toxic secondary compounds ingested by their 'nasty' hosts. This has been proposed as possible cause for lower species richness of parasitoids in the tropics (Gauld et al. 1992, Gauld & Gaston, 1994). Due to different detoxification systems or metabolism parasitoids may be even more vulnerable to plant chemistry (e. g. Mullin 1985) than herbivores. Coping with specific chemical traits of the host should require a higher degree of specialization (Sime & Brower 1998). However, taxa of higher trophic position are also known to be more susceptible to fragmentation of resources than herbivores (Kareiva, 1987; Pimm, 1991; Kruess & Tschamtker, 1994, 2000a, 2000b; Schoener & Spiller, 1995; Zabel & Tschamtker 1998; Holt et al., 1999). Thus, higher fragmentation of resources in the tropics is likely to exercise more influence on tropical parasitoids than on tropical herbivores. Increasing herbivore species richness in the tropics may render hosts a too fragmented resource for parasitoids to be exploited. As a consequence, tropical parasitoid complexes may not be more speciose than non-tropical ones (Janzen & Pond, 1975; Janzen, 1981; Hawkins, 1990; Hawkins, 1994). This has been hypothesized as cause for lower tropical species richness of the Ichneumonoidea, which constitute one of the most debated exceptions from latitudinal patterns of species richness (Owen & Owen 1974; Janzen & Pond, 1975; Gauld, 1986; Hawkins 1990; Price 1991). As in herbivores, resource fragmentation implies different patterns of parasitoid specificity than chemical diversity of hosts. Lower host specificity would increase a parasitoid's effectivity in finding its fragmented host population (Askew & Shaw, 1986).

Here we addressed two main hypotheses: (1) Species packing of herbivorous insects per species of host plant is higher in tropical versus temperate regions. This latitudinal

pattern is based on two hypothesized mechanisms: (i) narrow feeding niches or higher resource specificity, respectively, and (ii) the species' better handling of resource fragmentation, i.e. of the naturally larger distances between host plants. (2) Species packing of parasitoids per herbivorous host is lower in tropical versus temperate communities (Hawkins, 1994). The supposed mechanisms include: (i) susceptibility to resource fragmentation increases with trophic rank, and (ii) adaptive strategy of parasitoids to resource fragmentation involves broad feeding niches or lower resource (host) specificity, respectively.

Despite its priority in global conservation, Madagascar is nearly virgin of systematic research on terrestrial insect communities, although these are presumed to predominantly contribute to the country's extraordinary biodiversity. Although considerable taxonomic work has been done on Malagasy arthropods - Gaston (1994) reports, that some remarkable 7% of all recently described beetle species were from Madagascar - disappointingly little is published on their ecology. Ecological research has mainly been focusing on vertebrates (e. g. Langrand & Wilmé, 1997; Vallan, 1999; Ganzhorn et al., 2000; Goodman & Rakotondravony, 2000), but rarely on insects (e. g. Fisher, 1999). Hawkins (1994) lists only 3 published parasitoid-host interactions from Madagascar, having accomplished an extensive literature survey on global host records for parasitoids.

Madagascar is suspected to be a centre of origin of Fabaceae (Labat, 1996). Their worldwide distribution makes them ideal organisms for comparisons of their insect communities at different latitudes. Fabaceae (legumes) produce pods, which are used by a variety of seed-feeding insects and their parasitoids in the tropics (Rasplus, 1994; Dolch & Tschamtkke, 2000). Investigation of species richness of insects stretching over more than one feeding type may lead to dilution of the results (Hawkins & Lawton, 1987; Hawkins; 1990, 1994). Thus, we focused on legume pods as one particular feeding type, representing a standardized method to examine patterns of species packing.



## **Material and methods**

### *Tropical and temperate sample sites*

We sampled legume pods in Central Western Madagascar, approximately 60-70km north of Morondava. The original vegetation of that area, which is commonly known as the Menabe, is dry deciduous forest. Slash-and-burn agriculture and a general lightheartedness towards fire have contributed to the vast deforestation of the region (Genini 1996). One of the largest forest blocks remaining is a 10.000 ha forestry concession of the Centre de Formation Professionnelle Forestière (CFPF) at Kirindy. Continuity of the forest is interrupted by patches of grassland, either natural savannah or (more likely) of anthropogenic origin. Further information on the Kirindy forest can be found in Ganzhorn & Sorg (1996). Both forest and grassland areas were surveyed for legumes (Fabaceae), focusing on Kirindy and extending sampling northwards and southwards to the villages of Beroboka and Marofandilia, respectively. In total, 15 species of legumes were chosen for sampling of pods (Table 1). Field work was done during two consecutive 5-months periods in the dry season (April to August) in 1996 and 1997. Identification of plants was based on former research by CFPF (e. g. Abraham & Schroff 1991). Plants included trees, shrubs, as well as perennial and annual herbs. Additional information on the life cycle of certain herbaceous species was taken from Gillett *et al.* (1971). Legumes were characterized by their architecture (trees, shrubs, herbs) as a measure of both longevity and structural complexity. They were also classified as either being rare or not. Besides personal observation, assistance by foresters C. Rakotondrasoana and R. Randriamarosoa was indispensable in doing so. Sampling comprised at least 160 pods of each species (>8.000 pods in total), and we always took pods from at least 10 individuals per species (Table 1). For each individual plant sampled, we measured height and circumference at its base. We also counted the number of pods and measured their mean length and width, based on a subsample of 10 of the pods collected. Plant individuals other than trees were growing too close to one another to test for resource fragmentation, represented by distance between conspecifics. Therefore, distance to the nearest conspecific was only estimated for individual trees. Extension of the canopy was estimated as planar area for each. Data on temperate insect communities of Fabaceae were available from Garbe (1996), who collected 200 pods of each of 27 species of legumes in southwestern Germany. He

reared herbivores and parasitoids from the pods and assessed height, abundance and life cycle for each plant species. His sampling area near Karlsruhe, commonly known as Kraichgau, is characterized by orchard meadows (grassland with interspersed trees), making it sufficiently comparable to Kirindy.

**Table 1.** Fabaceae species sampled in Kirindy. Plant abundance, plant life cycle, number of plant individuals and the number of pods sampled for each species are shown.

<b>Scientific name</b>	<b>plant abundance</b>	<b>plant life cycle</b>	<b>number of plant individuals</b>	<b>number of pods sampled</b>
<i>Crotalaria retusa</i>	abundant	annual herb	30	375
<i>Cassia laevigata</i>	rare	annual herb	10	170
<i>Tephrosia purpurea</i>	rare	annual herb	30	380
<i>Indigofera stenosephala</i>	abundant	perennial herb	35	1090
<i>Indigofera hirsuta</i>	rare	perennial herb	15	545
<i>Sesbania madagascariensis</i>	rare	perennial herb	15	550
<i>Tephrosia reptans</i>	rare	perennial herb	20	435
<i>Mimosa delicatula</i>	abundant	shrub	14	770
<i>Albizia sp.</i>	rare	shrub	20	905
<i>Albizia masikororum</i>	abundant	tree	16	680
<i>Chadsia grevei</i>	abundant	tree	10	500
<i>Delonix boiviniana</i>	abundant	tree	15	160
<i>Colvillea racemosa</i>	rare	tree	10	160
<i>Cordyla madagascariensis</i>	rare	tree	12	545
<i>Dalbergia sp.</i>	rare	tree	18	905
<b>Σ</b>			<b>270</b>	<b>8170</b>

### *Fragmentation experiment*

The effects of resource fragmentation on the insect community of Malagasy legumes were examined experimentally. We chose 6 different patches grown with *Tephrosia purpurea* in the "Cirque" area in the northern part of Kirindy. We removed 25 individuals of each population, planting always 5 of them in each of 5 plastic pots. One of the pots was placed in the center of the original population, the others were put in distances of 10, 20, 30 and 50m to the original population, respectively. Longer isolation distances could not be tested, since populations grew too close to each other. For standardization, each pot was dug in at ground level and supplied with a water depot, connected to the plants by a hygrophilous wick. Pots were planted in June 1996 and harvesting of pods was hoped to happen in the following season. However, in 1997 most of the pots planted (25 out of 30) were found to have been removed by people entering the area illegally. Fortunately, many of the plants potted in the previous year disseminated and germinated. Patches of plants of the new generation grew conspicuously close to (or even in) the pits which marked the position of the removed pots. We could therefore reasonably treat them as isolated sub-populations, as intended originally. Height, circumference and average pod length were measured for each plant. Number of plants and number of pods was counted and all pods were collected within each sub-population.

### *Sample treatment and statistics*

All pods collected during the sampling periods were put into glass vials and closed with gauze. Insects inhabiting the pods and their seeds were reared and given (at least three months) time to hatch. Individual insects that did not manage to hatch were retrieved by dissecting the pods, a method also used to assess the number of seeds for each pod.

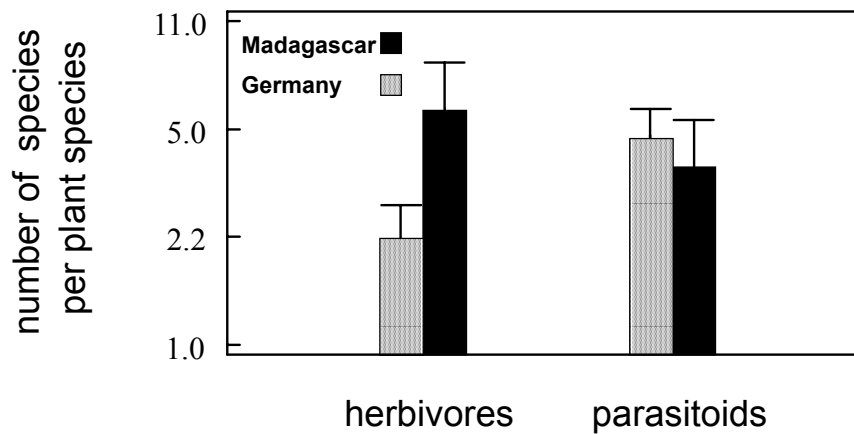
Insect specimens were counted and both herbivore load and percent parasitism were assessed. Herbivore load was defined as the mean number of herbivore specimens per pod and plant species. Percent parasitism was calculated as the ratio of the mean number of parasitoid specimens per pod to the mean number of all insect specimen per pod for each plant species. Both herbivores and parasitoids were sorted and grouped into morphospecies (hereafter referred to as species). Herbivores other than Coleoptera were solely distinguished morphologically. Given the worldwide distribution of

Coleoptera families, we could rely on taxonomic literature for Europe (Freude et al., 1965) to also identify Malagasy beetles on family level. Parasitoids were at least identified to superfamilies (Gauld & Bolton, 1988; Goulet & Huber, 1993). Species packing of the communities was measured as the mean number of herbivore species per plant species and the mean number of parasitoid species per species of herbivores, respectively. Since niche breadth is best reflected by diet breadth, herbivores and parasitoids were also separated in monophagous ('specialist') and polyphagous ('generalist') species. Per definition, monophagous species were those reared from one species of host plant only, whereas species reared from more than one host plant species were characterized as polyphagous.

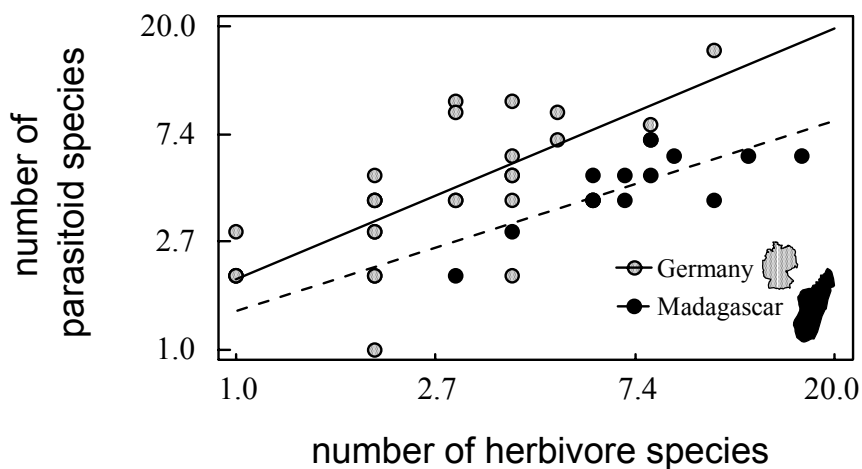
Statistical analyses included simple and multiple regression, ANOVA and ANCOVA. Data that were not normally distributed were log-transformed and percentages were arcsine-transformed prior to analysis. Statgraphics Plus for Windows 3.0 (Manguistics, 1996) was used for calculating statistics.

## **Results**

Higher numbers of pods were collected in Germany than in Madagascar (ANOVA;  $F = 51.01$ ;  $P < 0.0001$ ;  $n = 42$  plant species) and sampled plant species were significantly taller in Madagascar compared to Germany (ANOVA;  $F = 18.39$ ;  $P = 0.0001$ ;  $n = 42$  plant species). Therefore, we used both plant height and number of collected pods as covariates in subsequent analyses. Species richness of temperate insect communities on legumes was lower than that of tropical ones. Different patterns were found for different trophic levels. Malagasy insect communities on Fabaceae had more herbivore species than those in Germany, whereas there were no differences in the number of parasitoids per plant (Fig. 1). Yet, we found lower numbers of parasitoid species per host species in Madagascar versus Germany (Fig. 2). Parasitoid species richness could best be explained by herbivore species richness in both Germany and Madagascar. Comparison of regression lines shows no significant differences between slopes, but between intercepts (Fig. 2). Similar insect families dominated at both sites (Table 2).



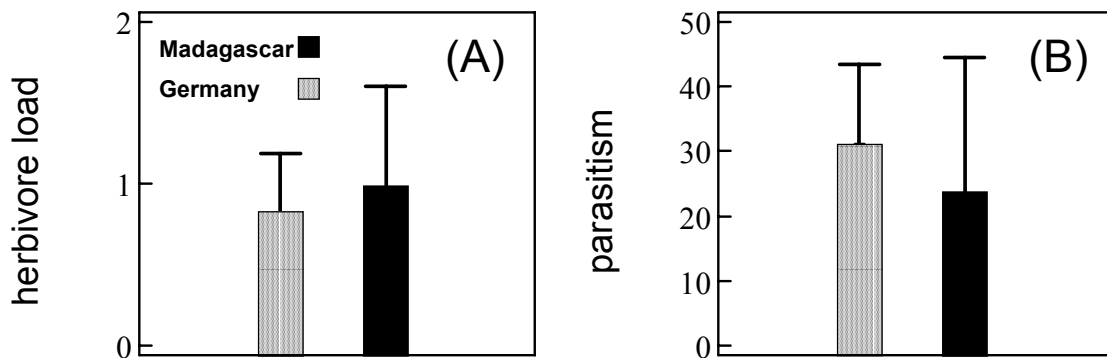
**Fig. 1.** Mean number of herbivore and parasitoid species per plant species in Madagascar and Germany. ANCOVA,  $n = 42$  plant species, standard errors are shown. Herbivores:  $F = 5.73$ ;  $P = 0.0217$ . Parasitoids:  $F = 0.36$ ;  $P = 0.5543$ ).



**Fig. 2.** Mean number of parasitoid species per plant species in relation to mean number of herbivore species. Madagascar:  $\log y = 0.35 + 0.59 * \log x$ ;  $F = 17.67$ ;  $r^2 = 0.576$ ;  $P = 0.0010$ ,  $n = 15$  plant species. Germany:  $\log y = 0.65 + 0.77 * \log x$ ;  $F = 14.13$ ;  $r^2 = 0.520$ ;  $P < 0.0001$ ,  $n = 27$  plant species. The intercepts of these regression lines are significantly different ( $F = 13.43$ ;  $P < 0.0001$ ), whereas the slopes are not ( $F = 0.44$ ;  $P = 0.51$ ).

**Table 2.** Number of insect species per plant species. Means and standard errors are shown.

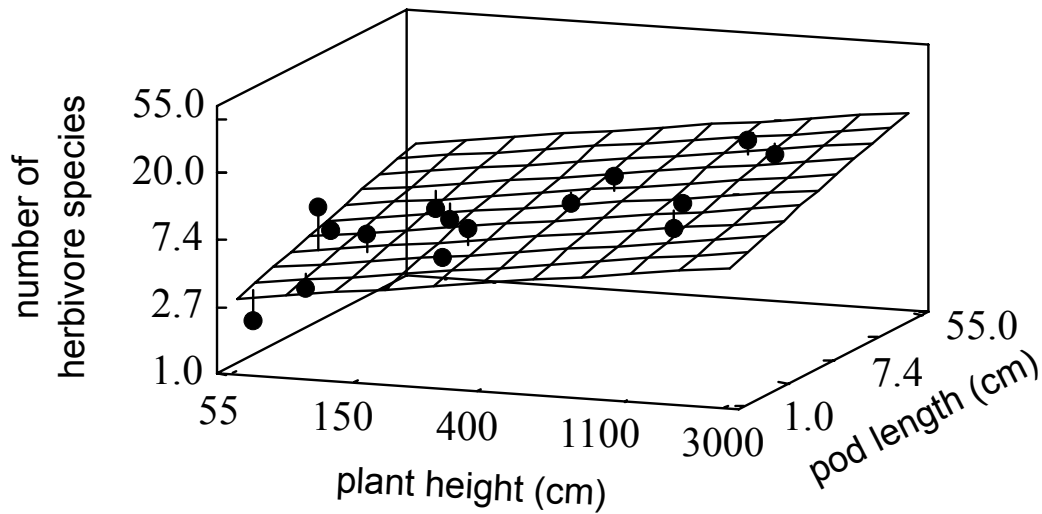
	Madagascar	Germany
<b>Coleoptera</b>	5.33 ± 0.62	1.81 ± 0.35
Curculionidae	1.33 ± 0.27	1.37 ± 0.31
Bruchidae & Apionidae	1.80 ± 0.39	0.44 ± 0.10
<b>Lepidoptera</b>	1.60 ± 0.47	0.30 ± 0.09
<b>Hymenoptera (phytophagous)</b>	0.00 ± 0.00	0.19 ± 0.08
<b>Hymenoptera (parasitic)</b>	3.93 ± 0.38	3.63 ± 0.59
Ichneumonoidea	0.07 ± 0.07	0.88 ± 0.17
Chalcidoidea	3.87 ± 0.39	2.74 ± 0.49



**Fig. 3.** Plant-herbivore and host-parasitoid interactions in insect communities of Madagascar and Germany. ANCOVA,  $n = 42$  plant species, standard errors are shown. (A) Herbivore load (mean number of herbivore specimens per pod);  $F = 0.05$ ;  $P = 0.8178$ . (B) Percent parasitism (ratio of mean number of parasitoid specimens to the mean number of all insect specimens per pod);  $F = 0.12$ ;  $P = 0.7299$ .

Examining the parasitoid community in more detail, the proportion of chalcidoids to ichneumonoids was significantly elevated in the samples from Madagascar compared to those from Germany (ANCOVA;  $F = 24.00$ ;  $n = 42$  plant species;  $P < 0.0001$ ). In Germany, there were 35 species of herbivores (62.9% specialists) and 52 species of parasitoids (57.7% specialists). The tropical insect community in Madagascar was found to be considerably more species rich and to have a higher degree of specialization. Here, we identified 165 insect species. Only a minute proportion of the herbivores could be found on more than one plant species (96.1% specialists), whereas not a single parasitoid species was found on different plant species (100% specialists). The number of herbivore specimens per pod (the herbivore load) did not differ between Germany and Madagascar (Fig. 3a). Likewise, there were no differences of percent parasitism between sites (Fig. 3b).

In the Madagascar dataset several plant characteristics were found to be intercorrelated. Plant height was positively correlated with plant circumference ( $F = 196.5$ ;  $r^2 = 0.938$ ;  $P < 0.0001$ ;  $n = 15$  plant species) and extension of the canopy ( $F = 52.0$ ;  $r^2 = 0.800$ ;  $P < 0.0001$ ;  $n = 15$  plant species). Likewise, pod length was strongly correlated with pod width ( $F = 13.94$ ;  $r^2 = 0.517$ ;  $P = 0.0025$ ;  $n = 15$  plant species). Therefore we did not include circumference, canopy extension and pod width as variables in multiple regression analyses. In the Malagasy insect community, insect species richness rose with the number of specimens sampled ( $\log$  number of species =  $1.93 + 0.21 \log$  number of specimens;  $F = 83.51$ ;  $r^2 = 23.76$ ;  $P < 0.0001$ ). In order to correct for that, we included the number of individuals as covariate in all analyses (sensu Hawkins, 1994). Several plant traits correlated significantly with insect species richness in simple regressions. Using multiple stepwise regression, plant height turned out to be the best and sole predictor of overall insect species richness ( $\log$  insect species =  $0.91 + 0.27 \log$  plant height;  $F = 15.78$ ;  $r^2 = 0.514$ ;  $P = 0.0016$ ;  $n = 15$  plant species). Herbivores and parasitoids showed different patterns and their species richness was explained by different factors. Herbivore species richness was best explained by plant height and length of the pods in the multiple model (Fig. 4). Parasitoid species richness could not be explained by plant traits at all. Instead, the number of parasitoid species was best predicted by the number of herbivore species (Fig. 2).



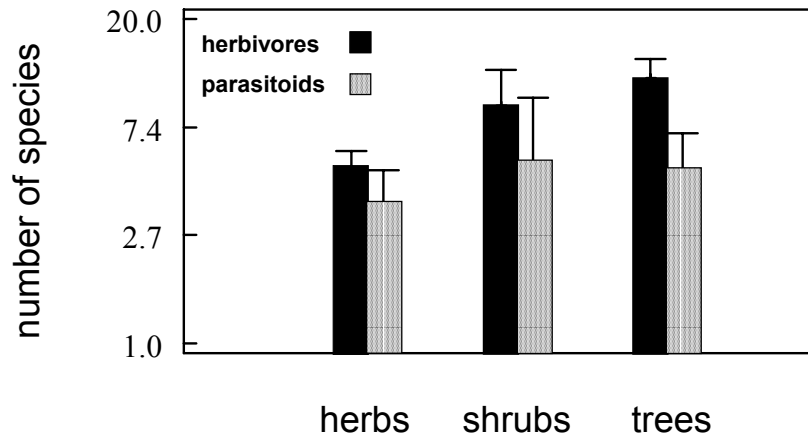
**Fig. 4.** Mean number of herbivore species per plant species in Madagascar in relation to plant height and pod length.  $\log y = 0.13 + 0.24 \log x + 0.24 \log z$ ;  $F = 14.47$ ;  $r^2 = 65.81$ ;  $P = 0.0006$ ;  $n = 15$  plant species.

The herbivore load in Madagascar depended on only plant architecture (ANCOVA;  $F = 6.56$ ;  $P = 0.0100$ ;  $n = 15$  plant species) and abundance of the plant (ANCOVA;  $F = 14.73$ ;  $P = 0.0033$ ;  $n = 15$  plant species). Trees had more individuals than shrubs, shrubs had more than herbs, and abundant plants had more than rare ones. The number of parasitoid specimens was independent of all those traits ( $F = 0.09$ ;  $P = 0.978$  and  $F = 0.00$ ;  $P = 0.965$ , respectively). Plant architecture also affected species richness, but only in the case of herbivores, which showed a significant increase in species richness with increasing architectural complexity of the plants (Fig. 5).

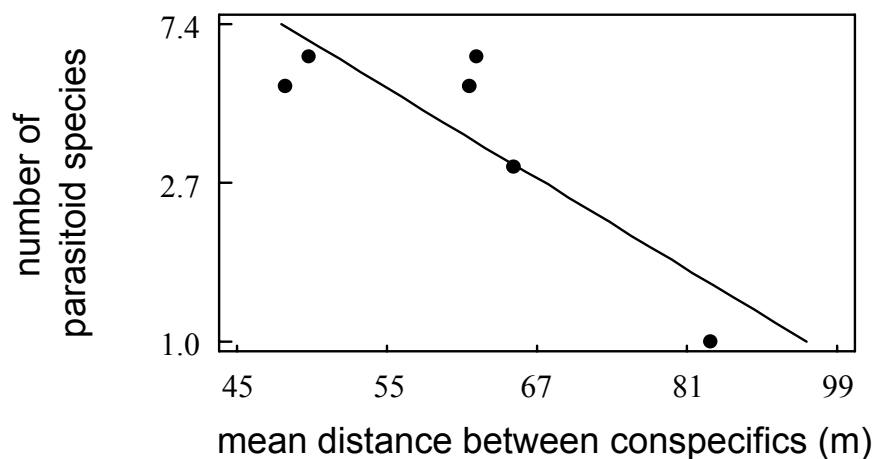
In the fragmentation experiment using the herb *Tephrosia purpurea*, we found plant traits such as the number of plants within each sub-population, plant height, as well as number and length of the pods to be positively correlated with insect species richness in simple regressions. In multiple analyses, herbivore species richness could only be explained by the number of pods collected ( $\log \text{herbivore species} = -0.51 + 0.55 \log \text{pods collected}$ ;  $F = 43.71$ ;  $r^2 = 0.715$ ;  $P < 0.0001$ ;  $n = 30$  plant populations), whereas parasitoid species richness was again positively correlated with the number of herbivore species ( $\log \text{parasitoid species} = 0.07 + 1.04 \log \text{herbivore species}$ ;  $F = 23.25$ ;  $r^2 =$



0.567;  $P = 0.0002$ ;  $n = 30$  plant populations). Distance between the different sub-populations had no effect on insect species richness, herbivore load, or percent parasitism at all, neither in the multiple, nor in the simple analyses.



**Fig. 5.** Mean number of herbivore and parasitoid species per plant species on plants of different architecture in Madagascar. ANCOVA,  $n = 15$  plant species, standard errors are shown. Herbivores:  $F = 21.44$ ;  $P = 0.0002$ . Parasitoids:  $F = 1.19$ ;  $P = 0.3396$ .



**Fig. 6.** Mean number of parasitoid species per tree species in relation to mean distance to the nearest conspecific tree in Madagascar.  $\log y = 12.99 - 2.85 * \log x$ ;  $F = 10.16$ ;  $r^2 = 0.717$ ;  $P = 0.0333$ ;  $n = 6$  tree species.

Total insect species richness could not be explained by distance between conspecific trees. Herbivore species richness could not be explained by mean distance of the nearest tree of the same species, but parasitoid species richness depended on the proximity of conspecifics (Fig. 6). Percent parasitism also decreased with distance to the next conspecific tree in a multiple model (percent parasitism =  $47.66 - 3.39 * \log \text{ distance} - 3.67 * \log \text{ number of herbivore specimens}$ ;  $F = 23.55$ ;  $r^2 = 0.763$ ;  $P = 0.0001$ ;  $n = 6$  tree species).

## **Discussion**

Species packing of herbivores per plant species was higher in Madagascar than in Germany (Fig. 1). Resource specificity (diet breadth) was also higher in the Malagasy communities, supporting our initial assumption on narrower feeding niches. Although some tropical herbivores seem to be fairly generalistic (Basset, 1992, 1999; Fiedler, 1998), high degrees of specialization have been found in many phytophagous insects in the tropics (Janzen, 1988; Hodkinson & Casson, 1991; Basset, 1994; Marquis & Braker, 1994; Coley & Barone, 1996; Barone, 1998). Maybe the most famous example are Erwin's (1982) enormously specialized canopy beetles. High host specificity of tropical herbivores feeding on legume seeds has also been documented (Rasplus, 1994). Tropical plants are supposedly better defended than temperate ones (Coley & Barone, 1996; Coley & Aide, 1991), resulting in lower palatability for herbivores. Specialization of herbivores is suspected to be an effective strategy to cope with this variety of chemical barriers (Basset, 1994). Higher specificity of tropical herbivores might enable them to occupy more niches, resulting in more herbivore species packed per plant species. Thus, our results support MacArthur's (1969) niche compression hypothesis when considering herbivores of similar feeding type. A further selection pressure on herbivores is exerted by the fact that most plant species in tropical forests are rare per unit area and may be difficult for insect species to locate (Beaver, 1979). Marquis (1991) found abundant plants to have more insect species than closely related rare plants in tropical Central America. Generally, abundant hostplants are more reliable resources that are easier to find, which should result in more species rich herbivore communities (Kelly & Southwood, 1999). However, this was not the case for the phytophagous insects in Madagascar. We therefore assume, that susceptibility of

Malagasy herbivores to resource fragmentation is low. Taller host plants are generally easier to find. In Madagascar, large hostplants attracted more herbivore species than smaller ones, leading to higher species richness. Additionally, herbivore species richness gradually increased from herbs to shrubs and trees (Fig. 5). Similar patterns have been found by Lawton & Schröder (1977) for temperate communities. Increasing plant height and architectural complexity appeared to increase the spatial predictability of the resource (as did the length of the pods, obviously crucial after having reached a particular plant, Fig. 4). More species of architecturally complex (arborescent) Fabaceae in Madagascar versus Germany and the fact that Malagasy legumes are taller on average may promote the herbivores' reduced susceptibility to resource fragmentation, and thereby the high herbivore species richness. Thus, the outcome of opposing selection pressures appeared to be in favour of specialization. This is additionally supported by the results from the fragmentation experiment with *Tephrosia purpurea*. We did not find the isolation of plant populations to affect herbivore species richness. Neither size of the population nor distance from the source population did have any effect on herbivore species richness. Moreover, distance between conspecific trees had no effect on herbivore species richness, indicating that Malagasy herbivores are capable of coping with fragmentation of resources.

Despite higher species packing of herbivores, herbivore load was not higher in Madagascar than in Germany, indicating a similar impact of herbivores on plants. Rates of herbivory have been found to be slightly greater in the tropics than in temperate regions (Coley & Barone, 1996). However, these results are based on folivorous insects. Leaves of tropical plants have a greater diversity of defenses compared to their temperate counterparts (Coley & Aide, 1991), whereas seeds may be a fairly similar resource in both the tropics and extra-tropics.

Although the number of parasitoid species per plant did not differ between sites (Fig. 1), species packing of parasitoids per species of herbivore host was lower in Madagascar versus Germany (Fig. 2), confirming our initial expectation. Like herbivores, Malagasy parasitoids were much more specialized than temperate ones in our study. In Costa Rica, none of the parasitoid species reared from an extensive collection effort of more than 54.000 caterpillar specimens is considered a generalist (Janzen & Gauld, 1997). This could indicate tropical parasitoid communities to be

structured by plant chemistry (sensu Gauld et al, 1992), which via cascade effects might restrict tropical parasitoids to a narrower host spectrum than non-tropical ones. (Gauld & Gaston, 1994; Hawkins, 1994; Sime & Brower 1998). Smaller sized parasitoids like chalcidoids, might be favoured in exploiting small undefended host stages such as small larvae or eggs (Noyes, 1989). Chalcidoidea are generally known to be more species rich in the tropics than outside (Hespenheide, 1979; Noyes, 1989; Askew, 1990) and the proportion of chalcidoids to ichneumonoids typically rises towards the tropics, especially among parasitoids of boring insects (Hawkins, 1994). The higher ratio of chalcidoids to ichneumonoids in Madagascar compared to Germany appears to support this hypothesis. On the other hand (notwithstanding the high degree of specificity and thus contradicting the predictions of Askew & Shaw (1986)), Malagasy parasitoids appear to be clearly affected by resource fragmentation. Indeed we did not find the isolation of plant populations to affect parasitoid richness in our fragmentation experiment using *Tephrosia purpurea*, but the results were considerably blurred by theft of the pots. Moreover, we suspect that distances between sub-populations (50m and less) might have been too small to detect any effects. In a similar experiment, Kruess & Tschardtke (1994) found pronounced effects on the insect community, after having potted legumes in distances of at least 50m to a source population (with 500m maximum distance). Similar distances only existed between conspecific trees in Kirindy. Unlike that of herbivores, the number of parasitoid species decreased with increasing distance of conspecific trees, indicating a strong influence of resource fragmentation on the parasitoid community. Taxa of higher trophic position are known to be more affected by isolation, which may dramatically disturb herbivore-parasitoid interactions (Kruess & Tschardtke, 1994). Since parasitoids in our study showed an enormous degree of specialization, the negative impact of isolation on their species richness seems plausible. Not only species richness, but also percent parasitism decreased with distance to the next conspecific tree in our study, so species richness (of parasitoids) and ecological function (parasitism) covaried.

Percent parasitism did not differ between Madagascar and Germany, despite the fact that Malagasy parasitoid complexes were smaller. We assume parasitoid species to more effectively control host populations when exploiting only one species of host than when dispersed among many host species. When a parasitoid manages to overcome the

chemical barrier of a 'nasty' host, the impact on that species of host is likely to increase. Although predators may be contributing more to control of tropical herbivores than parasitoids (Hawkins et al., 1997), our data suggest that parasitism may still be an important mortality factor for herbivore populations in tropical regions.

Based on the insect communities of the same plant family and feeding type, we conclude that higher species richness of herbivores in the tropics is caused by higher species packing, whereas, despite higher degrees of specialization, resource fragmentation may contribute to lower species packing of tropical parasitoids. Thus, our results indicate the importance of unfragmented vegetation within Madagascar. The large-scale deforestation of Madagascar (e. g. Green & Sussman, 1990) resulting in enormous degrees of fragmentation is likely to threaten biodiversity and to especially be detrimental to higher trophic levels, hampering possible biological control of phytophagous insects.

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# **Tropical herbivores and their parasitoids: a comparison of insect communities on Fabaceae in Madagascar and the Ivory Coast**

## **Abstract**

1.) We compared tropical insect communities associated with Fabaceae in Madagascar and the Ivory Coast to examine geographical consistency in species richness, species packing, and specificity. We tested if host plant traits exert the same influence on the insect communities in both countries.

2.) Herbivore communities in the Ivory Coast appeared to be undersaturated, since species packing of herbivores was lower than in Madagascar. Specificity of Malagasy herbivores was higher than that of Ivorian ones and appeared to be linked to more tightly packed niches.

3.) The higher specificity and higher species packing of herbivores may be related to the fact that local diversity of host plants was smaller in Madagascar than in the Ivory Coast, possibly indicating a stronger influence of resource fragmentation in the latter.

4.) Parasitoid species richness in the Ivory Coast did not differ from that in Madagascar. Species packing of Ivorian parasitoids was higher than that of Malagasy ones, but parasitoid specificity was lower, possibly due to the area effect of the African mainland and the additional colonization of polyphagous parasitoids.

5.) Herbivore species richness increased with plant height in both Madagascar and the Ivory Coast. Parasitoid species richness could also be explained by plant height in the Ivory Coast, whereas it was independent of plant traits in Madagascar.

6.) Most conclusions drawn from patterns in Madagascar do not hold for the Ivory Coast, emphasizing the need to repeat analyses in different geographical regions in order to find general patterns.

Key Words: species richness, species packing, community saturation, latitudinal patterns, trophic position, Bruchidae, Chalcidoidea

## Introduction

More than a century ago (e.g. Wallace, 1878), it has been recognized that species richness varies greatly between temperate and tropical regions. The major part of the earth's biodiversity is concentrated in tropical regions (Huston, 1994; Rosenzweig, 1995; Myers et al., 2000). This pattern especially holds for insects (Kusnezov, 1957; Fischer, 1960; Pianka, 1966; Schoener & Janzen, 1968; Price, 1997 and references therein), which constitute the bulk of global species richness (Strong et al., 1984; Stork, 1991; Samways, 1992). Since herbivores and parasitoids account for a major part of that diversity (Strong et al., 1984), studies of their communities are likely to reflect general patterns. However, many general conclusions drawn from the study of tropical insect communities and interactions rely on only local analyses (Owen & Owen, 1974; Janzen & Pond, 1975; Askew, 1990). Many of them may not hold at a larger scale, since insect communities may differ largely within a small latitudinal band (Tscharntke et al., 2000).

In an earlier study (Dolch & Tscharntke, 2000), we investigated patterns of species richness and species packing in plant-herbivore-parasitoid communities of legumes (Fabaceae) in Madagascar. High numbers of herbivore species packed per plant and high degree of specificity let us conclude that herbivores occupied narrow niches but were not affected by fragmentation of resources. On the other hand, resource fragmentation (which is generally high in tropical regions due to the relative rarity of hosts) appeared to have a strong influence on parasitoids. Here, we test the hypothesis that similar patterns exist on the African mainland and that tropical plant-herbivore-parasitoid communities are geographically consistent. Since insect communities are largely influenced by plant characteristics (Askew, 1980; Strong et al., 1984; Askew & Shaw, 1986; Leather, 1986; Hawkins & Lawton, 1987), we also examined traits of host plants in order to determine if they exert the same influence on the insect communities in both Madagascar and West Africa.

Endophagous insect communities of Fabaceae represent a proper study object for studies applying to both ecology and geography (Kruess & Tscharntke, 1994, 2000; Rasplus, 1994; Dolch & Tscharntke, 2000). Fabaceae are one of the world's largest plant families (Polhill et al., 1981) and have a worldwide distribution. Taxonomically, they are very homogeneous and therefore support insect species of similar families, irrespective of latitude. This similarity is especially given when focusing on the pods of

Fabaceae. This resource is mainly exploited by seed-feeding beetles (Bruchidae, Curculionidae, Apionidae, among others) and some moths. Parasitoid complexes contain species of Ichneumonidae, Braconidae and several families of Chalcidoidea. Plant taxonomy (Hawkins et al., 1990) and insect feeding niche (Hawkins, 1994) are known to considerably determine patterns of species richness. Focusing on insect communities exploiting taxonomically related plants (Fabaceae) in identical feeding niches (pods) is likely to involve less sources of variation.

### **Materials and methods**

Fabaceae were sampled in the Menabe region in Western Madagascar (Dolch & Tschardtke, 2000). The sampling site was located in the Kirindy area (see Ganzhorn & Sorg, 1996), about 60km north of the city of Morondava. The results are based on a collection of 8170 pods representing 15 species (out of a total of 39) during a 2-yr period (concentrating on the dry season, respectively, Table 1). Collection effort differed between plants and comprised between 160 and 1090 pods per species. Data on insect communities of Fabaceae in West Africa were taken from Rasplus (1988, 1994). He sampled Fabaceae pods at the Lamto Ecological Station in the Ivory Coast, about 160km north of Abidjan. Out of a total of 178 species of Fabaceae sampled at Lamto during a 4-yr period (1983-1986), an array of the 40 principal species attacked by herbivores (excluding lianas) was included in Rasplus (1994) and analysed here (Table 1). Between 500 and 3000 pods were collected for each species. The main vegetation in Kirindy is a dry forest, interrupted by patches of (natural or anthropogenic) grassland. Since the vegetation of Lamto is characterized as that of an arboreal savanna (Rasplus, 1988), both study sites appear to be adequately comparable.

After having hatched from the pods, Malagasy insects were sorted into morphospecies (hereafter referred to as species) and identified to (super)family level. Numbers of herbivore and parasitoid species were counted for each plant species. Species numbers of Ivorian insects were taken from Rasplus (1988, 1994). Species packing of herbivores is reflected by the number of species per species of plant. Species packing of parasitoids was determined by calculating the ratio of parasitoid species per herbivore species on each species of plant. Degree of host specificity was defined by the number of host plant species on which a certain species of herbivore or parasitoid was found. Logically,

polyphagy increases with the number of used plant species, whereas monophagous insects used only one species of plant.

Each plant species was characterized by three different traits: (1) height, (2) architecture (defining a plant species as a herb, shrub or tree); (3) abundance (defining a plant as either abundant or rare). For Madagascar, plant height was measured for each species. Plant architecture and abundance were determined by personal observation and with assistance of Malagasy foresters (see Dolch & Tschardtke, 2000 for more detail). For the Ivory Coast, we again relied on Rasplus (1988) for data on plant height and architecture, but compiled supplemental information from Gillett et al. (1971). Abundance of a plant was defined by its range size. Species that are restricted to either the Ivory Coast or the West African region were characterized as rare, whereas species with continent-wide or even pantropical distribution were defined as abundant.

Data were statistically analysed using simple and multiple analyses of variance and regression. Data that were not normally distributed were log-transformed prior to analysis. Statistics were calculated by using Statgraphics Plus for Windows 3.0 (Manguistics 1996).

## **Results**

The mean height of Fabaceae species did not differ between the Ivory Coast and Madagascar (ANOVA;  $F = 0.93$ ;  $P = 0.3404$ ;  $n = 55$  plant species). Since the number of pods collected for each plant did not only differ within but also between sites (ANOVA;  $F = 13.56$ ;  $P = 0.0005$ ;  $n = 55$  plant species), we used it as a covariate in subsequent analyses.

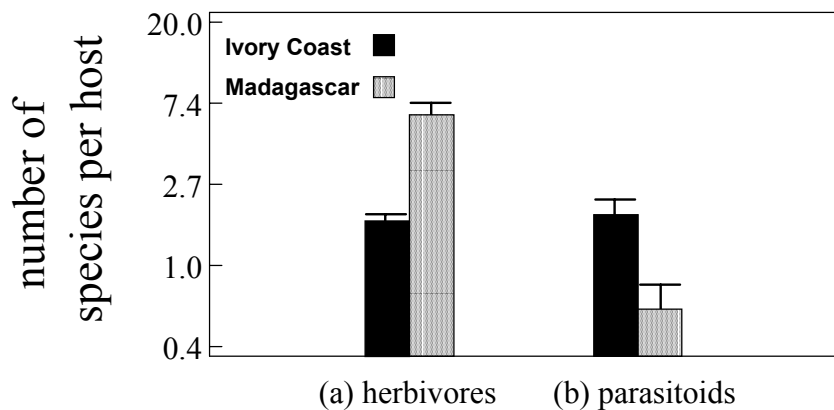
The number of herbivore species per plant (i. e. herbivore species packing) was higher in Madagascar than in the Ivory Coast (Fig. 1a). The number of parasitoid species per plant species did not differ (ANCOVA;  $F = 0.24$ ;  $P = 0.6268$ ;  $n = 55$  plant species), but the number of parasitoid species per host (i. e. parasitoid species packing) was lower in Madagascar than in the Ivory Coast (Fig. 1b).

On average, herbivores exploited less species of host plants in Madagascar than in the Ivory Coast (Fig. 2a). A similar pattern arose for parasitoids (Fig. 2b), indicating a



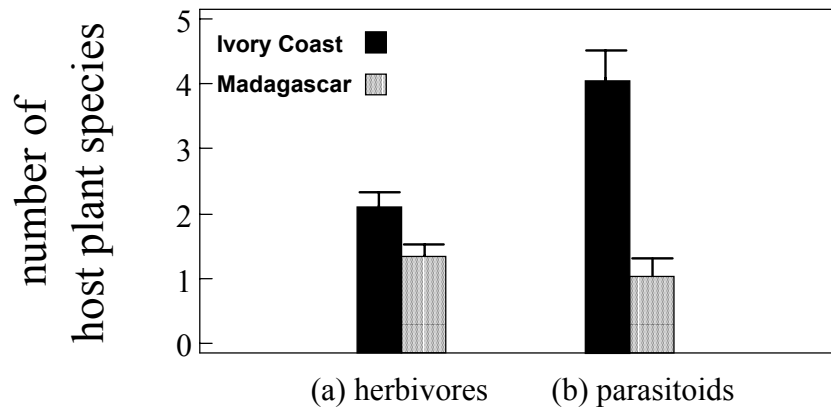
**Table 1.** Fabaceae species from Madagascar and the Ivory Coast considered for analysis. Plant architecture and mean height are given for each species.

<b>Fabaceae species</b>	<b>plant architecture</b>	<b>mean plant height (m)</b>
<b>MADAGASCAR</b>		
<i>Albizia masikororum</i>	tree	5,0
<i>Albizia sp.</i>	shrub	2,2
<i>Cassia laevigata</i>	annual herb	1,4
<i>Chadsia grevei</i>	tree	3,5
<i>Colvillea racemosa</i>	tree	11,0
<i>Cordyla madagascariensis</i>	tree	0,6
<i>Crotalaria retusa</i>	annual herb	1,1
<i>Dalbergia sp.</i>	tree	10,5
<i>Delonix boiviniana</i>	tree	12,7
<i>Indigofera hirsuta</i>	perennial herb	11,1
<i>Indigofera stenosephala</i>	perennial herb	0,8
<i>Mimosa delicatula</i>	shrub	2,2
<i>Sesbania madagascariensis</i>	perennial herb	1,1
<i>Tephrosia purpurea</i>	annual herb	0,7
<i>Tephrosia reptans</i>	perennial herb	0,7
<b>IVORY COAST</b>		
<i>Acacia nilotica</i>	tree	25,0
<i>Albizia adianthifolia</i>	tree	40,0
<i>Albizia ferruginea</i>	tree	40,0
<i>Albizia zygia</i>	tree	25,0
<i>Alysicarpus ovalifolius</i>	annual herb	0,6
<i>Cathormion altissimum</i>	tree	35,0
<i>Crotalaria atrorubens</i>	annual herb	0,9
<i>Crotalaria calycina</i>	annual herb	0,6
<i>Crotalaria glauca</i>	annual herb	0,8
<i>Crotalaria goreensis</i>	annual herb	0,9
<i>Crotalaria lathyroides</i>	annual herb	0,5
<i>Crotalaria ochroleuca</i>	annual herb	1,0
<i>Crotalaria retusa</i>	annual herb	0,8
<i>Desmodium salicifolium</i>	annual herb	1,0
<i>Dialium guineense</i>	tree	20,0
<i>Dichrostachys cinerea</i>	shrub	5,0
<i>Eriosema molle</i>	perennial herb	1,8
<i>Eriosema psoraleoides</i>	perennial herb	1,5
<i>Indigofera bracteolata</i>	annual herb	0,5
<i>Indigofera dendroides</i>	annual herb	0,8
<i>Indigofera hirsuta</i>	annual herb	0,8
<i>Indigofera macrophylla</i>	perennial herb	0,5
<i>Indigofera nigrifolia</i>	annual herb	1,5
<i>Indigofera paniculata</i>	annual herb	1,5
<i>Indigofera polysphaera</i>	annual herb	0,9
<i>Indigofera pulchra</i>	annual herb	1,5
<i>Indigofera simplicifolia</i>	annual herb	0,8
<i>Indigofera suffruticosa</i>	annual herb	1,6
<i>Lonchocarpus cyanescens</i>	tree	20,0
<i>Mimosa pigra</i>	perennial herb	2,0
<i>Parkinsonia aculeata</i>	shrub	8,0
<i>Pericopsis laxiflora</i>	tree	10,0
<i>Pseudarthria hookeri</i>	annual herb	3,0
<i>Psophocarpus palustris</i>	perennial herb	0,5
<i>Tephrosia elegans</i>	annual herb	0,6
<i>Teramnus buettneri</i>	perennial herb	1,5
<i>Vigna ambacensis</i>	annual herb	0,5
<i>Vigna multinervis</i>	annual herb	0,5
<i>Vigna racemosa</i>	annual herb	0,5
<i>Vigna reticulata</i>	annual herb	0,5

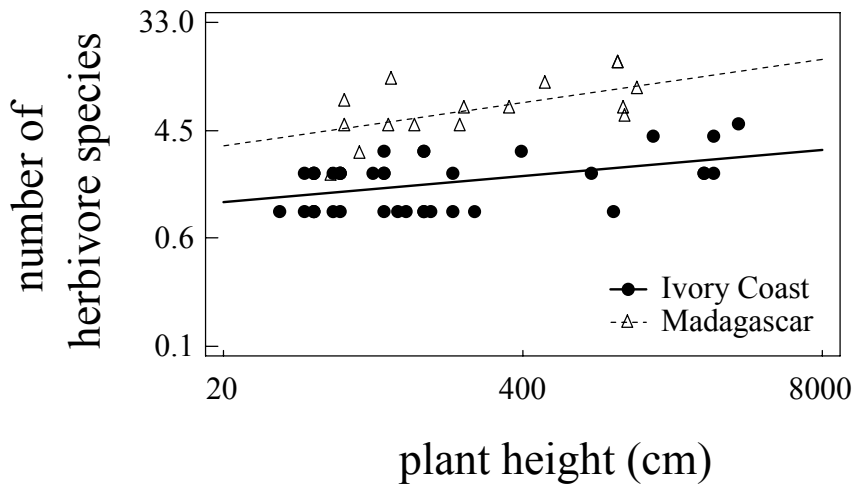


**Fig. 1.** Mean number of insect species per species of host. ANCOVA, n = 55 plant species. (a) number of herbivore species per species of plant;  $F = 75.12$ ;  $P < 0.0001$ . (b) number of parasitoid species per species of herbivore;  $F = 18.46$ ;  $P = 0.0001$ .

higher degree of specificity of both Malagasy herbivores and parasitoids. In Madagascar, species richness of herbivores turned out to be best explained by plant height alone in a stepwise multiple regression ( $\log$  herbivore species =  $0.39 + 0.27 \log$  plant height;  $F = 6.50$ ;  $r^2 = 0.282$ ;  $P = 0.0242$ ;  $n = 15$  plant species). Plant architecture, plant rarity and the number of collected pods did not contribute to the model. Similarly, species richness of herbivores in the Ivory Coast was only predicted by plant height ( $\log$  herbivore species =  $-0.30 + 0.16 \log$  plant height;  $F = 9.67$ ;  $r^2 = 0.186$ ;  $P = 0.0036$ ;  $n = 40$  plant species). When comparing regression lines for both countries, we found no differences between slopes, but between intercepts (Fig. 3). In Madagascar, parasitoid species richness could not explained by plant traits at all. In the Ivory Coast, multiple stepwise regression produced plant height as the only predictive variable of parasitoid species richness ( $\log$  parasitoid species =  $-0.55 + 0.34 \log$  plant height;  $F = 11.85$ ;  $r^2 = 0.253$ ;  $P < 0.0017$ ;  $n = 40$  plant species).



**Fig. 2.** Mean number of plant species used by insect species. ANCOVA. (a) Mean number of plant species per herbivore species;  $F = 7.72$ ;  $P = 0.0061$ ;  $n = 160$  species of herbivores. (b) Mean number of plant species per parasitoid species;  $F = 53.78$ ;  $P < 0.0001$ ;  $n = 148$  species of parasitoids.



**Fig. 3.** Mean number of herbivore species per plant species in relation to plant height. Ivory Coast:  $\log y = -0,30 + 0,16 \log x$ ;  $F = 9.67$ ;  $P = 0.0036$ ;  $r^2 = 0.186$ ;  $n = 40$  plant species. Madagascar:  $\log y = 0,39 + 0,27 \log x$ ;  $F = 6.50$ ;  $P = 0.0242$ ;  $r^2 = 0.333$ ;  $n = 15$  plant species. The intercepts of the regression lines are significantly different ( $F = 91.73$ ;  $P < 0.0001$ ), whereas the slopes are not ( $F = 0.92$ ;  $P = 0.3422$ ).

In Madagascar, simple analysis showed that species richness of herbivores increased with increasing architectural complexity of the plants (ANCOVA;  $F = 21.44$ ;  $P = 0.0002$ ;  $n = 15$  plant species), although this had no influence in the multiple model (see above). Plant architecture also had no influence on herbivore species richness in the Ivory Coast (ANCOVA;  $F = 0.92$ ;  $P = 0.4099$ ;  $n = 40$  plant species). Neither in Madagascar (ANCOVA;  $F = 1.19$ ;  $P = 0.3396$ ;  $n = 15$  plant species), nor in the Ivory Coast (ANCOVA;  $F = 0.90$ ;  $P = 0.4166$ ;  $n = 40$  plant species) did parasitoid species richness depend on plant architecture in simple or multiple analyses.

## **Discussion**

The comparison of insect communities in Madagascar and the Ivory Coast indicates that conclusions based on patterns found in the one location may not be valid in the other. Since communities may considerably differ between sites (e. g. Tschardt et al., 2000), studies should therefore be repeated in many different geographical locations order to find general patterns. "Perhaps the major weakness of traditional community ecology (...) is its overwhelming emphasis on localness. By assuming that most of the key drivers determining community structure happen internally, within the system, the discipline could be missing major parts of the action" (Lawton, 1999, p. 183).

Species packing of herbivores was lower in the Ivory Coast versus Madagascar (Fig. 1a). This suggests that niches are not tightly packed and that Ivorian herbivore communities are not at equilibrium. Although MacArthur (1969) hypothesized that tropical communities have smaller niches, permitting more species of insects to be packed per host (plant) species, tropical insect communities are known to be often undersaturated (Lawton, 1982; Price, 1991; Hawkins & Compton, 1992). The different patterns in Madagascar and the Ivory Coast could lead to premature conclusions on niche breadth (as indicated by species packing) in tropical communities, using only either of both for generalization. This difference cannot be explained by differences in sample size, since herbivore species packing was higher in Madagascar despite lower sample size. Madagascar's smaller size compared to the African mainland would also suggest a smaller species pool, and less species of Malagasy insects should be expected to colonize host plants in a particular location. The greater proximity of the Ivory Coast to the equator should result in even higher species packing compared to Madagascar.

We are not able to explain the causes of lower species packing of herbivores in the Ivory Coast versus Madagascar without more extensive data from the African mainland. A different pattern emerged for parasitoids. There were more parasitoid species packed per host in the Ivory Coast (Fig. 1b). Since these parasitoids are rather polyphagous, the higher species richness may be due to the larger area of the African mainland and corresponding colonization of the large species pool of less specific parasitoids. Such an area effect was also assumed by Tscharrntke et al. (2000), since parasitoid complexes in continental Europe (Germany) were found to be larger than in Britain due to many polyphagous species.

Specificity of both herbivores and parasitoids also differed greatly between Madagascar and the Ivory Coast (Fig. 2). Differences in specificity of tropical herbivores have also been found by others. Some data suggest high levels of specialization (Janzen, 1988; Basset, 1994; Barone, 1998), others do not (Janzen, 1980; Lawton, 1991; Marquis, 1991; Price, 1991; Basset, 1992; Fiedler, 1995, 1998). As our results indicate, these differences may at least be partly due to the locality chosen. Tropical species of seed-feeding beetles appear to be highly host specific (Janzen, 1977) and many afrotropical legumes have a specialized herbivore community (Chemengich, 1993; Delobel et al., 1994; Rasplus, 1994; Krüger & McGavin 1998; Dolch & Tscharrntke, 2000). This may not be a general feature, since specificity of Ivorian herbivores was significantly lower than that of Malagasy ones (Fig. 2a). This appears to be directly linked to their lower species packing (*sensu* MacArthur, 1969). Higher degrees of herbivore specificity are also suspected to coincide with greater diversity of secondary compounds in tropical plants, since specialization is one way to overcome this diverse array of chemical defenses (Coley & Aide, 1991; Basset, 1994; Coley & Barone, 1996). Yet, tropical dry forests such as in Kirindy are generally expected to have lower levels of toxic chemicals compared to plants of the wet tropics such as near Lamto (Coley & Aide 1991, Coley & Barone 1996). Being less specialized might be an adaptation to resource fragmentation in the tropics, since relative rarity of resources should select for polyphagy. Herbivore species that cannot cope with fragmentation of their resources are likely to become extinct, failing to establish minimum viable populations (e. g. Dixon et al., 1987). This must finally lead to lower species packing, as reflected by the Ivorian herbivore communities at Lamto. Thus, resource fragmentation

may be of greater importance in the Ivory Coast than in Madagascar. Lower host specificity is likely to discriminate against those herbivore species that have to deal with lower abundance of their host plants. In an area of similar extent, legume diversity in Lamto was found to be higher (178 species) than in Kirindy (39 species), indicating lower plant abundance in the Ivory Coast. While lacking a higher degree of specificity, Ivorian herbivores might be prevented from occupying more niches, concurrently limiting the number of herbivore species per plant species.

The scarcity of herbivores exacerbates problems of host finding for parasitoids. As in herbivores, resource fragmentation should therefore select for higher degrees of generalization to overcome scarcity of hosts (Janzen, 1981; Hawkins 1990; Gauld & Gaston, 1994). Accordingly, tropical communities are suspected to have more species of less specialized parasitoids (Askew & Shaw, 1986; Gauld, 1987; Hawkins, 1990; Gauld & Gaston, 1994; Quicke & Kruft, 1995). Moreover, parasitoids of endophytic hosts are often dominated by generalists (Hawkins, 1990). These assumptions are supported by relatively low specificity of Ivorian but contradicted by high specificity of Malagasy parasitoids (Fig. 2b). Diversity of plant chemistry should lead to higher degrees of specialization to cope with specific chemical host plant traits, mediated by herbivore hosts via trophic cascading (Gauld et al., 1992). Herbivores might become unpalatable for parasitoids, restricting the number of parasitoid species per herbivore. The result would be lower species packing of parasitoids per host species, leading to a pattern similar to the one that we found in Madagascar.

Herbivore species richness appeared to be similarly affected by plant height in Madagascar and the Ivory Coast (Fig. 3). Taller plants usually have more insect species, since they offer more stable resources, are more apparent and are easier to find (Strong, 1979; Lawton, 1983). The same is valid for more complex plants (Lawton & Schröder, 1977). Yet, herbivore species richness could only be predicted by plant architecture in Madagascar. Parasitoid species richness increased with plant height in the Ivory Coast. Increasing parasitoid species richness with increasing size of the host plant was first predicted by Askew (1980), since location of the host plant has to precede location of the host itself (e.g. Hawkins & Lawton, 1987). Nevertheless, species richness of Malagasy parasitoids was independent of plant traits and the number of parasitoid species only depended on the number of herbivore species (Dolch & Tschardtke, 2000).

Although some plant traits affect insect species richness similarly in both Madagascar and the Ivory Coast, the results suggest that tropical insect communities are more heterogeneous than often expected. General conclusions drawn from single localities may be premature (Tscharrntke et al., 2000). Whereas Malagasy herbivore communities appeared to have tightly packed niches, Ivorian ones are likely to be undersaturated. Parasitoid communities showed a reverse pattern. We also found evidence for tropical insect communities to be more specific in one location versus the other. This may possibly be linked to different mechanisms structuring tropical communities, such as resource fragmentation, higher plant diversity or plant chemistry, depending on geography. In short, small scale analyses of tropical communities may be too punctual to draw general conclusions. Sime and Brower (1998) argue for a better understanding of many case histories to better define general patterns. According to Lawton (1999), we believe that a large-scale study involving many localities (preferably standardized by focusing on insect communities feeding in identical niches of the same plant family) is most likely to yield general patterns.

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## 5 Zusammenfassung

Die hohe Artenvielfalt tropischer gegenüber nicht tropischen Lebensräumen charakterisiert eines der augenscheinlichsten biogeographischen Muster. Die Beantwortung der Frage nach den Ursachen tropischer Artenvielfalt gehört zu den zentralen Anliegen der Ökologie.

In der vorliegenden Dissertation stand die Betrachtung tropischer Pflanze-Herbivor-Parasitoid-Systeme im Vordergrund. Dabei wurden 15 Arten von Leguminosen (Fabaceae) in Madagaskar untersucht, von denen mehr als 8000 Hülsen gesammelt wurden. Die Lebensgemeinschaft endophager Herbivore und Parasitoide wurde analysiert und mit bekannten Mustern entsprechender Lebensgemeinschaften in den gemäßigten Breiten (Deutschland) und anderen tropischen Regionen (Elfenbeinküste) verglichen.

Insgesamt fanden sich in Madagaskar 55 Arten von Herbivoren und 109 Arten von Parasitoiden. Zur Bestimmung der Nischenbreite wurde die Artendichte ermittelt, d. h. die Anzahl der Herbivorenarten je Pflanzenart bzw. die Anzahl der Parasitoidenarten je Wirtsart. Daneben wurde die Befallsrate durch die Individuendichte der Herbivoren pro Hülse und die Parasitierungsrate (Verhältnis der Parasitoiden-Individuen zur Gesamtzahl aller Insekten-Individuen je Hülse) bestimmt. Die Spezifität von Herbivoren und Parasitoiden wurde über die Anzahl der von ihnen genutzten Wirtspflanzen ermittelt. Diese die Insektenlebensgemeinschaft charakterisierenden Parameter wurden mit Merkmalen der Wirtspflanzen in Beziehung gesetzt.

Außer mit Hilfe der empirisch gewonnenen Daten wurde auch experimentell untersucht, welche Auswirkung die Fragmentierung von Ressourcen auf die Insektenlebensgemeinschaft hat. Die Distanz zwischen Individuen wurde erfaßt und die zwischen Populationen einer gleichen Pflanzenart experimentell variiert, um die Ressourcenfragmentierung zu ermitteln.

Entsprechend der Erwartung hing der Artenreichtum der Herbivoren in Madagaskar von mehreren Pflanzenparametern ab. So stieg die Artenzahl mit zunehmender Höhe der Wirtspflanze. Auch die Pflanzenarchitektur übte einen Einfluß auf die Artenvielfalt aus. Bäume hatten mehr Herbivoren-Arten als Sträucher, die wiederum artenreicher waren als krautige Pflanzen. Der Artenreichtum der Parasitoide konnte nicht mit

Pflanzenparametern in Beziehung gebracht werden. Die Artenzahl parasitischer Insekten stieg vielmehr mit der Artenzahl ihrer phytophagen Wirte.

Im Vergleich zu gemäßigten Lebensgemeinschaften zeigten sich wichtige Unterschiede. In Madagaskar fanden sich mehr Arten von Herbivoren pro Pflanzenart als in Deutschland. Dadurch wird die Annahme gestützt, daß tropische Lebensgemeinschaften engere Nischen aufweisen. Dies ging mit einer höheren Spezialisierung madagassischer Herbivoren einher, was darauf hindeutet, daß sie gut mit der natürlichen Fragmentierung in den Tropen zurechtkommen. Entsprechend konnte kein Einfluß von Ressourcenfragmentierung (Distanz zwischen Wirtspflanzen) auf die Herbivoren festgestellt werden. Die größere Artendichte pro Pflanzenart in Madagaskar war nicht mit einer größeren Befallsrate der Herbivoren als in Deutschland verbunden.

In Madagaskar fanden sich weniger Arten von Parasitoiden pro Wirtsart als in Deutschland. Madagassische Parasitoide waren spezialisierter als solche in Deutschland. Entsprechend wurden sie stark durch die Fragmentierung ihrer Ressourcen beeinflusst. Entgegen der Situation bei den Herbivoren nahm der Artenreichtum der Parasitoide mit zunehmender Entfernung zwischen Pflanzen der gleichen Art ab. Dies führte gleichzeitig zu einer Abnahme der Parasitierungsrate, so daß der Rückgang der Artenvielfalt mit einer Verminderung der Ökosystemfunktion gekoppelt war. Damit wird auch die Hypothese unterstützt, daß Organismen höherer trophischer Ebenen anfälliger für Fragmentierung sind. Die Parasitierungsrate unterschied sich nicht zwischen Madagaskar und Deutschland, obwohl die Parasitenkomplexe in Madagaskar kleiner waren. Dadurch wird die Bedeutung der Parasitoide in tropischen Lebensgemeinschaften unterstrichen.

Vergleiche der madagassischen Lebensgemeinschaften mit denen der Elfenbeinküste zeigten, daß tropische Lebensgemeinschaften in vielen Merkmalen nicht übereinstimmen. Von einer tropischen Lokalität kann daher nicht notwendigerweise auf generelle Muster geschlossen werden. Es fanden sich mehr Arten von Herbivoren pro Pflanzenart in Madagaskar, allerdings kamen in der Untersuchungsregion in der Elfenbeinküste mehr Leguminosenarten vor als in der Madagaskars. In Madagaskar gab es weniger Arten von Parasitoiden pro Wirtsart als in der Elfenbeinküste. Unterschiede gab es auch im Spezialisierungsgrad. Während madagassische Herbivoren spezifischer

waren als solche aus der Elfenbeinküste, galt für Parasitoide der umgekehrte Fall.

Schlußfolgerungen aus der Analyse von Herbivor-Parasitoid-Systemen in Madagaskar können daher nicht zwangsläufig auf andere tropische Regionen übertragen werden. Wegen der hohen Variabilität innerhalb tropischer Lebensgemeinschaften verspricht deshalb die Betrachtung möglichst vieler verschiedener Regionen in den Tropen am ehesten die Entdeckung allgemeingültiger Muster.

Für Madagaskar lassen sich anhand der Ergebnisse Schlußfolgerungen ziehen, die die Konsequenzen weiter fortschreitender Fragmentierungsprozesse betreffen. Deren negative Auswirkungen bedrohen nicht nur die Artenvielfalt sondern insbesondere die ökologische Funktion höherer trophischer Ebenen, wodurch eine Reduktion der Effektivität der biologischen Kontrolle phytophager Insekten wahrscheinlich erscheint.

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Ny faniriam-potsiny ihany tsy mahatanteraka ny zavatra nokasaina  
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## **8 Anhang**

Tabelle 1. Leguminosenarten und ihre Insekten in Madagaskar

Tabelle 2. Pflanzenparameter von Leguminosen in Madagaskar

Tabelle 3. Experimentelle Isolation von Populationen von *T. purpurea* in Madagaskar

Tabelle 4. Afrikanische Leguminosen aus Zusendungen botanischer Institute

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