

Effects of forest fragmentation on bottom-up control in leaf-cuttings ants

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LIST OF ABBREVIATIONS

∅	diameter
%	percent
° C	degree Celsius
° N	degree North
° S	degree South
° W	degree West
a.m.	"ante meridiem" (Lat.); 'before midday'
ANOVA	Analysis of Variance
a.s.l.	above sea level
ca.	"circa" (Lat.); about
CAPES	Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
cm	centimetre
CNPq	Conselho Nacional de Desenvolvimento Científico e Tecnológico
<i>D</i>	Simpson's diversity index
DBH	diameter at breast height
df	degree of freedom
DFG	German Science Foundation
e.g.	"exempli gratia" (Lat.); 'example given' or 'for example'
<i>et al.</i>	"et alii" (Lat.); and others
<i>F</i>	<i>F</i> -value; statistical value used by ANOVA
Fig.	figure
g	gram
GC	gas chromatograph
GC/MS	gas chromatograph-mass spectrometer
h	hour
ha	hectare
HSD	Honest Significant Difference Test
i.e.	"id est" (Lat.); 'that is'
km	kilometre
l	litre
LAI	leaf area index
LCA	leaf-cutting ants
m	metre

M	molar
m ²	square metre
mg	milligram
min	minute
ml	millilitre
mm	millimetre
<i>n</i>	sample size
NE	North-East
nm	nanometre
<i>P</i>	probability
PAI	plant area index
<i>r</i>	coefficient of correlation
<i>r</i> ²	coefficient of regression
RDM	radial diffusion method
rpm	rounds per minute
RT	retention time
SE	standard error
sec.	second
SD	standard deviation
SP	sampling point
Tab.	table
TNC	total non-structural carbohydrates
vs.	“versus” (Lat.); against
v/v	volume per volume
χ^2	statistical value used by the χ^2 -test

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1. INTRODUCTION

1.1 Tropical forest fragmentation

The destruction of natural habitats, habitat loss and fragmentation have turned into the most important threat to all forested ecosystems (Gascon *et al.*, 2001). In tropical regions, this problem is especially pressing, because human interference is threatening the last large areas of tropical rainforests – the most diverse and complex of terrestrial ecosystems. Therefore, forest fragmentation is increasingly gaining importance in modern landscape management and conservation biology (Bierregaard and Gascon, 2001). Today, the rate of tropical deforestation exceeds 150 000 km² annually (Whitmore, 1997). One of the most endangered tropical forests, the Brazilian Atlantic rainforest, has been reduced to 2 % of its original area during 500 years of destruction (Ranta *et al.*, 1998).

Definition

Habitat fragmentation, by definition, involves a reduction in original area (i.e., habitat loss) and isolation of remaining patches of forest (i.e., habitat fragmentation *per se*; Gascon *et al.*, 2001; Fahrig, 2003). Both habitat loss and habitat fragmentation *per se* inevitably result in (a) smaller patches of the original habitat (i.e., area effects) and (b) an increased forest edge/interior ratio (i.e., edge effects). Additionally, fragmentation *per se* measures (c) habitat amount at the landscape scale (i.e., isolation effects; Fahrig, 2003). These measures of habitat fragmentation combine with each other in complex coherence and lead to fundamental modifications in ecosystem functioning as I will describe below.

(a) Area effects

Forest fragmentation inevitably leads to a decrease in the size of the original forest habitat. This in turn causes changes in forest ecosystem known as area effects (Hill and Curran 2001; Fahrig, 2003). Area effects cause dramatic decline in species number in the habitat patch (DeSouza *et al.*, 2001). Individual species have minimum patch size requirements, therefore smaller patches generally contain fewer species

than larger patches (DeSouza *et al.*, 2001; Fahrig, 2003). Numerous species-area curves have been modelled to predict the decline in the number of species with the loss of habitat (e.g., Hill and Curran, 2001; Scheiner, 2003; Picard *et al.*, 2004). Additionally, area effects include population-level processes, such as losses of small populations via random genetic or demographic events (Ferreira and Laurance, 1997). Similarly, community-level phenomena, such as declines in reproduction following losses of specialized pollinators or seed-dispersers have been recorded (Ferreira and Laurance, 1997).

(b) Edge effects

Creation of edges is believed to be the most important component of forest fragmentation (Saunders *et al.*, 1991; Gascon *et al.*, 2001; Köhler *et al.*, 2003). An increased forest edge/interior ratio results in numerous modifications in forest environment, structure and dynamics that are generally known as edge effects (Saunders *et al.*, 1991). Edge effects and area effects are directly linked: as the area of a forest fragment increases, edge effects decrease (Hill and Curran, 2001). Edge effects increase rapidly in importance once the fragment size falls below ca. 500 ha, depending on the shape of the fragment (Laurance *et al.*, 1998a; Laurance, 2001). Ferreira and Laurance (1997) showed that in forest fragments of 1000 ha, 22 % - 42 % of the area is actually influenced by edges. However, the changes induced by edge effects are believed to require markedly shorter time-scales than the changes caused by area effects (Ferreira and Laurance, 1997). Edge effects primarily start with the alteration of abiotic factors. The open forest edge inevitably experiences increased incident light (Saunders *et al.*, 1991; Gascon *et al.*, 2001). In continuous tropical forests, sunlight usually is restricted to vertical penetration, but in a forest fragment sunlight can penetrate laterally along the fragment's margins. This seriously affects the microclimatic conditions of the habitat. Other abiotic factors modified near forest edges include increasing temperature and wind turbulence and decreasing relative humidity or soil moisture content (reviewed in Murcia, 1995). The changes in the physical environment alter the forest structure and species composition. For example, through increased wind turbulence, edge habitats exhibit elevated tree mortality rates that in turn result in increased gap formation and light penetration in forest understory and canopy (Ferreira and Laurance, 1997; Laurance *et al.*, 1998a; Laurance, 2001; Rankin-de-Mérona and Hutchings, 2001). Moreover, once arisen,

the wind-throw induced damages expand to propagate damages further into the forest interior (Laurance, 2001; Rankin-de-Mérona and Hutchings, 2001). As a consequence, forest fragments exhibit a significant increase in recruitment rates of light-demanding plant species, pioneers and species of secondary growth (Laurance *et al.*, 1998a; Köhler *et al.*, 2003) as well as vines and lianas (Laurance *et al.*, 1998b). The changes in the plant community lead to cascading effects on insects and animals that depend on the plants for their life cycles (Gascon *et al.*, 2001).

(c) Isolation effects

The isolation of a habitat patch is defined as the measure of the amount of habitat in a landscape (Fahrig, 2003). The more isolated a patch is, the less habitat there is in the landscape that surrounds it (Fahrig, 2003). Therefore, isolation measures the lack of habitat in the landscape. The amount of habitat is the most obvious and visible effect of the process of fragmentation (Fahrig, 2003). A habitat can be removed from a landscape in many different ways, resulting in various spatial shapes and patterns. These patterns play an important role in weakening or amplifying area or edge effects of fragmentation: habitat patches of irregular shape become more vulnerable to edge effects that penetrate into the habitat interior (Ferreira and Laurance, 1997; Laurance *et al.*, 1998a). Moreover, this vulnerability is observed to depend on the size of the patch (Ferreira and Laurance, 1997; Laurance *et al.*, 1998a).

Habitat isolation is an important issue in conservation ecology. Loss of forested habitat in a landscape results in the creation of a new matrix habitat (e.g., pasture, degraded pasture, second-growth forest) around the isolated forest patches (Gascon *et al.*, 2001). The matrix habitat acts as a selective filter for the movements of species between forest patches, facilitating movements of some species and impeding others. Most commonly, disturbance-adapted species will be present in the matrix and may invade forest patches and edge habitat (Gascon *et al.*, 2001). The matrix habitat may also include human settlements. The vicinity of a human settlement increases the disturbance in a forest patch by the means of changes in land use, logging, hunting or fire risk (Cochrane *et al.*, 2002). For these reasons, dramatic changes in species composition and loss of biodiversity have been recorded in forest patches (reviewed in Brooks *et al.*, 2002; Fahrig, 2003). However, few modern management regimes could be established to control the negative effects of forest isolation. For example, faunal corridors in a matrix landscape re-

establish the connectivity between isolated forest patches and enhance movements of animals among patches (Gascon *et al.*, 2001).

The biological consequences of forest fragmentation

Historically, the effects of forest fragmentation were thought to be primarily associated with the loss of species richness (reviewed in Bierregaard and Gascon, 2001; DeSouza *et al.*, 2001). For this purpose, MacArthur and Wilson's (1967) "theory of island biogeography", originally developed to explain patterns of species numbers on oceanic islands, was transmitted into fragmentation studies to provide an approximation to the biological dynamics in habitat patches left through fragmentation (DeSouza *et al.*, 2001).

Recent studies have demonstrated that the effects of forest fragmentation on natural systems are more complex than can be predicted from simple surveys of species richness (reviewed in Gascon *et al.*, 2001; Bruna, 2004). It has been noted that species respond to fragmentation in idiosyncratic and unexpected ways, some of the latter representing novel physical and biological phenomena (Debinski and Holt, 2000). For example, specialist species are generally found to be more vulnerable to habitat fragmentation than the generalist ones (Bruna, 2004). However, specialization cannot be considered in isolation from the degree of specialization of the mutualist partners. Therefore, evaluation of both sides of the mutualistic interaction will yield insights into the mechanisms behind species' responses to habitat fragmentation. As a consequence, studies on species interactions and food web ecology are increasingly gaining importance. So far, this advanced focus includes a few studies associated with pollination (Aizen and Feinsinger, 1994), seed dispersal (Silva and Tabarelli, 2000), seedling recruitment (Bruna, 2002), or processes related to food web interactions such as predation (e.g., Fonseca and Robinson, 1990), or herbivory (e.g., Arnold and Asquith, 2002). Only few works exist which closer study interactions between plants and herbivorous insects in fragmented landscapes (but see Brown and Hutchings, 1997; Benitez-Malvido *et al.*, 1999; Rao *et al.*, 2001; Arnold and Asquith, 2002; Thies *et al.*, 2003). Yet these interactions are an auspicious area of research because they constitute an important component of almost any ecosystem (Cyr and Face, 1993; McNaughton *et al.*, 1989). Interactions between plants and insect herbivores occur at low trophic levels and as a result often influence food webs: for example, they play a crucial role in the

recycling of organic matter and hence energy and nutrient flows (Hunter, 2001; Rinker *et al.*, 2001). Furthermore, these interactions evolve and coevolve, and are therefore considered to be one of the processes and driving forces which organize ecosystems (Thompson, 1999). Moreover, insect herbivory has been shown to be one of the disturbance effects which can positively influence secondary plant succession, and thus, species diversity (Fraser and Grime, 1999). In consequence, studying insect herbivory appears to be a valuable tool that provides a better understanding of the functioning of fragmented ecosystems.

1.2 Bottom-up vs. top-down control in food webs

An important area of research during the last years in population- and community ecology has been the question on whether food webs are controlled by “bottom-up” or “top-down” forces. The bottom-up view contends that organisms on each trophic level are limited by the resources available from the level below (i.e., light, nutrients, primary productivity, prey) whereas top-down control occurs when a trophic level depends on effects of consumers (i.e., predators and parasites) from an above level (Matson and Hunter, 1992). The primary debates in this field emerged between Murdoch (1966), who asserted that an evolution of plant defenses may prevent herbivores from consuming many parts of green plant material, and Hairston and colleagues (1960), who argued that predation controls herbivore populations and thus prevents the over-consumption of plants. Since then, contradictory results have occurred in a wide range of food web model systems either supporting the bottom-up (e.g., Wratten, 1992), the top-down (e.g., Hunter *et al.*, 1997; Dyer and Letourneau, 1999) or both views (Hunter and Price, 1992; Terborgh *et al.*, 2001; Devaraj, 2004). For herbivore populations, the models developed by Fretwell (1977) and Oksanen and colleagues (1981) are most commonly accepted today. These models predict that herbivores standing on a trophic level an odd number of steps below the top level are rather predator than resource limited.

Although a lot of progress was made in this area, several complex relationships remain to be disentangled and the degree to which bottom-up and top-down forces regulate ecosystems still needs to be resolved (Terborgh *et al.*, 2001). Moreover, new debates emerged recently dealing with the facet of how the roles and importance of bottom-up and top-down effects change under varying environmental

conditions (Dyer and Letourneau, 1999; Moon and Stiling, 2002; Loeuille and Loreau, 2004) and in the areas of ecosystems and global ecology (Jackson and Hedin, 2004). Therefore, the approach of bottom-up *versus* top-down is especially suitable in the context of tropical forest fragmentation as it gives an insight into community- and ecosystem level interactions under currently changing environmental conditions. Additionally, Tscharrntke and his colleagues (Thies and Tscharrntke, 1999; Tscharrntke *et al.*, 2002; Thies *et al.*, 2003) repeatedly showed the importance of the structural complexity of a landscape to trophic interactions between herbivorous insects, their host plants and parasitoids. They emphasize the need for further research on other herbivore model systems reevaluating landscape management and conservation strategies to protect stable biological interactions and thus prevent pest outbreaks and losses of biodiversity.

1.3 Leaf-cutting ants (LCA)

LCA belong to a subgroup of the fungus-growing ants (tribe *Attini*) in the order of Hymenoptera, the family of Formicidae (subfamily Myrmicinae). Among the *Attini*, LCA represent those species with workers large and strong enough to cut pieces out of living leaves. This restricts them to the genera *Acromyrmex* with 24 known species and *Atta* with 15 species (Hölldobler and Wilson, 1990). All members of the tribe *Attini* culture fungi, whereas the substrate used to feed the fungus varies from the leaf particles cut by the LCA, to the insect faeces and rotting wood and flowers collected by some lower attine species (Cherrett, 1989; Hölldobler and Wilson, 1990). Fungus growing by ants of the tribe *Attini* probably originated in the early Tertiary and thus predates human agriculture by about 50 million years (Mueller *et al.*, 1998).

The tribe *Attini* is restricted to the New World, where members are found between ca. 40° N and 44° S of the Equator; the LCA have a narrower distribution of ca. 33° N and 44° S (Cherrett, 1989). *Atta* has still a slightly narrower latitudinal range than *Acromyrmex* (Fowler and Claver, 1991). It inhabits the whole continent of South America except Chile (reviewed in Cherrett and Peregrine, 1976). LCA are found in a wide range of habitats including deserts, swamp forests, subtropical grasslands and tropical rain forests (Cherrett, 1989; Fowler and Claver, 1991). LCA are among the most advanced and organized of all the social insects. A LCA colony is made up of one fertile queen and workers. Worker ants belong to various size

casts including the smallest workers which are required as gardeners of the symbiotic fungus, the intermediate-sized workers which are involved in the brood care, foragers with variable size which collect plant material and gigantic soldiers with powerful mandibles responsible for defending the colony. A LCA colony may contain several million ants. Members of the genus *Atta* build large nests consisting of below-ground chambers where the colony grows its symbiotic fungus. Ants grow the fungus on a newly collected fresh leaf material and feed on the hyphal tips (gongylidia) of the fungus (Hölldobler and Wilson, 1990; Wirth *et al.*, 2003b). Recent findings have shown that most cultivated fungi belong to the basidiomycete family Leptotaceae (Agaricales: Basidiomycota), and the great majority of attine fungi belong to two genera, *Leucoagaricus* and *Leucocoprinus* (Leucocoprineae) (Chapela *et al.*, 1994; Mueller *et al.*, 1998). Every year, a mature colony produces young reproductive females and males, which depart from the parental colony on mating flights. After the mating flight all males die. The fertilized queen casts off her wings and excavates a new nest in the soil. The queen carries a small wad of mycelia of her home nest's fungus to the new colony. A colony takes about five years to reach maturity (Hölldobler and Wilson, 1990; Wirth *et al.*, 2003b).

Leaf-cutting ants (LCA) are one of the most dominant herbivores in the neotropics (Wilson, 1986). Moreover, because of their huge impact on ecosystems they are considered a keystone species (Fowler *et al.*, 1989) or “physical engineers” (Wirth *et al.*, 2003b) of tropical ecosystems. LCA can have a considerable effect on vegetation: the amount of foliage cut from a mature tropical forest by *Atta colombica* has been calculated to lie between 2.5 % at a landscape level and 12.5 % within the foraging area of a colony (Wirth *et al.*, 2003b). Additionally, LCA contribute to non-trophic effects on the ecosystem. *Atta* are known to enhance soil nutrient and moisture content on the nest surface (Farji-Brener and Ghermandi, 2000; Moutinho *et al.*, 2003), disperse seeds (Dalling and Wirth, 1998), increase plant diversity at the nest sites (Farji-Brener and Ghermandi, 2000) and through cutting activity increase light intensity at the ground level within the foraging area of the colony (Wirth *et al.*, 2003b). Through the symbiotic fungus, LCA are part of the decomposer food web and have a tremendous impact on the rates of energy and nutrient transfer (reviewed in Fowler *et al.*, 1989). LCA are polyphagous herbivores foraging on a variety of host plant species, however they are also highly selective showing strong preferences for some species, whereas other species abundantly available in the foraging area are

not cut (e.g., Cherrett, 1968; Rockwood, 1976; Blanton and Ewel, 1985; Wirth *et al.*, 2003b). Due to their uniform preferences for some agricultural and horticultural crops such as eucalyptus, citrus, coffee or cocoa, LCA have earned pest status in neotropical monocultures (e.g., Cherrett and Peregrine, 1976; Vilela, 1986). Cherrett (1989) draws attention to the fact that the crops most commonly defoliated by LCA are exotic species that may not have developed defence mechanisms against LCA.

In the last decades, it has been noticed that LCA strongly respond to forest fragmentation: forest disturbance and/or clearing is known to increase the abundance of LCA colonies. LCA colony densities have been observed to increase sharply in forest edges (Wirth *et al.*, 2003a), forest remnants (Rao, 2000; Wirth *et al.*, 2003a), and early successional forests (e.g., Jaffe and Vilela, 1989; Vasconcelos and Cherrett, 1995; Moutinho *et al.*, 2003). The reasons for this increase are not yet fully understood. Both bottom-up and top-down factors have been discussed to be responsible for the phenomenon. The top-down view suggests that LCA populations are controlled by their predators such as armadillos or army ants (Rao, 2000; Terborgh *et al.*, 2001) and parasites such as phorid flies (Orr, 1992). From the bottom-up point of view, LCA have been shown to prefer pioneer plant species against late successional ones (Farji-Brener, 2001; Wirth *et al.*, 2003b). Pioneers are more abundant in early-successional, disturbed, or fragmented forests (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999). Consequently, the bottom-up school agrees in the 'palatable forage hypothesis' sensu Farji-Brener (2001), which claims that one of the reasons for the increase of LCA colony densities is the dominance of pioneer species in early successional habitats, that are highly palatable to LCA (Sheperd, 1985; Nichols-Orians, 1991; Vasconcelos and Cherrett, 1995).

In conclusion, the parameters why LCA represent an ideal model system to study the consequences of forest fragmentation on biotic interactions include: (1) LCA belong to the most dominant herbivores in the neotropics and therefore important cornerstones of ecosystem functioning; (2) as selective generalist herbivores LCA attack a wide range of plants but strongly prefer some species over others, and thus have a huge impact on vegetation; (3) LCA respond to fragmentation: LCA colony densities increase in fragmented forests.

1.4 Hypotheses and aims of the study

This study was carried out as a part of a long-term DFG- and CAPES-funded project on the bottom-up as well as top-down effects on LCA populations in fragmented forests. The present thesis deals with the bottom-up control of LCA.

So far, important knowledge referring to an impact of bottom-up factors in the control of LCA populations includes the following:

- LCA have been shown to prefer pioneer plant species in their diet against late successional ones (Farji-Brener, 2001; Wirth *et al.*, 2003b).
- Pioneer species possess less chemical defense than late successional species (Coley, 1988).
- Pioneers are dominant in early successional, disturbed, or fragmented forests (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999).

Based on this knowledge, I hypothesize that bottom-up control of LCA populations is less effective in fragmented compared to continuous forests. In order to test for less effective bottom-up control, I propose the following working hypotheses:

- (1) Decreased plant defence: The vegetation in fragmentation-related forests is more palatable to LCA.
- (2) Decreased LCA diet breadth: In fragmented habitats LCA forage on few dominant host species thus resulting in a narrower diet breadth.
- (3) Decreased LCA foraging area: LCA use smaller foraging areas in fragmented habitats.
- (4) Increased LCA herbivory rate: the herbivory rate of LCA is increased in fragmented habitats.

In this thesis, I will first introduce the study design (Chapter 2). I will then evaluate the forest structure in the study sites for some parameters known to characterize fragmentation-related and continuous forests (Chapter 3). Further, each of the four working hypotheses will be proved (Chapters 4-7, respectively). Finally, the potential role of bottom-up control for the increase in LCA colony densities will be discussed as well as the effect of forest fragmentation on trophic interactions (Chapter 8).

2. STUDY SITE AND GENERAL METHODS

2.1 Study site

The study was conducted in remnants of the Atlantic rainforest in NE Brazil, at Usina Serra Grande, a 200-km² private sugar-cane farm in the state of Alagoas (9° S, 35° 52' W; Fig. 2, 3). This area includes forest remnants that cover a total area of 11 000 ha, the majority being very fragmented with a mean fragment size of 50 ha (data provided by Usina Serra Grande). A larger forest remnant of 3500 ha served as a continuous forest (control habitat) for this study. This forest is considered to be one of the largest remnants of the Atlantic forest in NE Brazil. Extensive forest fragmentation in the area began in the 1960s, when additional forest land was cleared for increasing sugar-cane plantations. Today the fragments suffer from moderate human disturbance through logging and hunting (M. Tabarelli, personal communication). The study site is located on the low-elevation plains (500-600 m a.s.l.) of the Borborema Plateau, where prevailing soils are latosols and podzols (IBGE, 1985). The climate is highly seasonal with a steep rainfall gradient across the Borborema Plateau. Therefore, to detect seasonal patterns, I referred to local rainfall measurements during the study period (Fig. 1; data provided by Usina Serra Grande). Annual rainfall was ca. 2600 mm, with a 3-month dry season (< 110 mm month⁻¹) lasting from October to January. The vegetation has been classified as lower mountain rain forest with Leguminosae, Lauraceae, Euphorbiaceae, Melastomataceae and Sapotaceae as the dominant families (Veloso *et al.*, 1991).

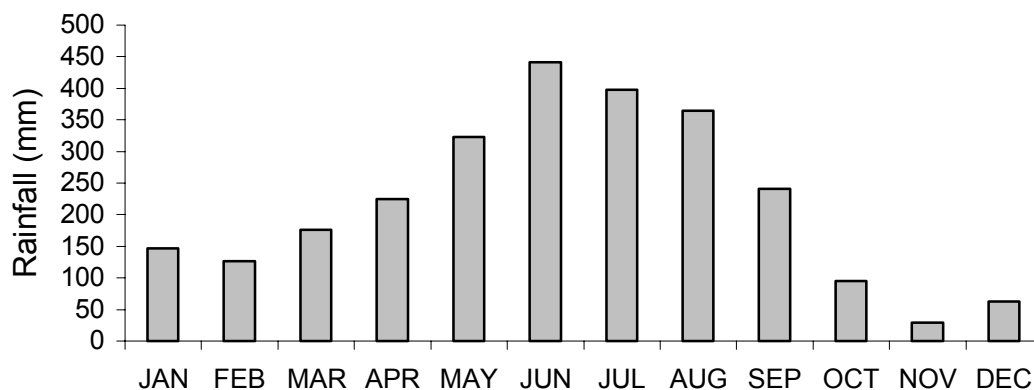


Figure 1. Mean monthly rainfall at the study site in 1997-2003. Data provided by Usina Serra Grande.

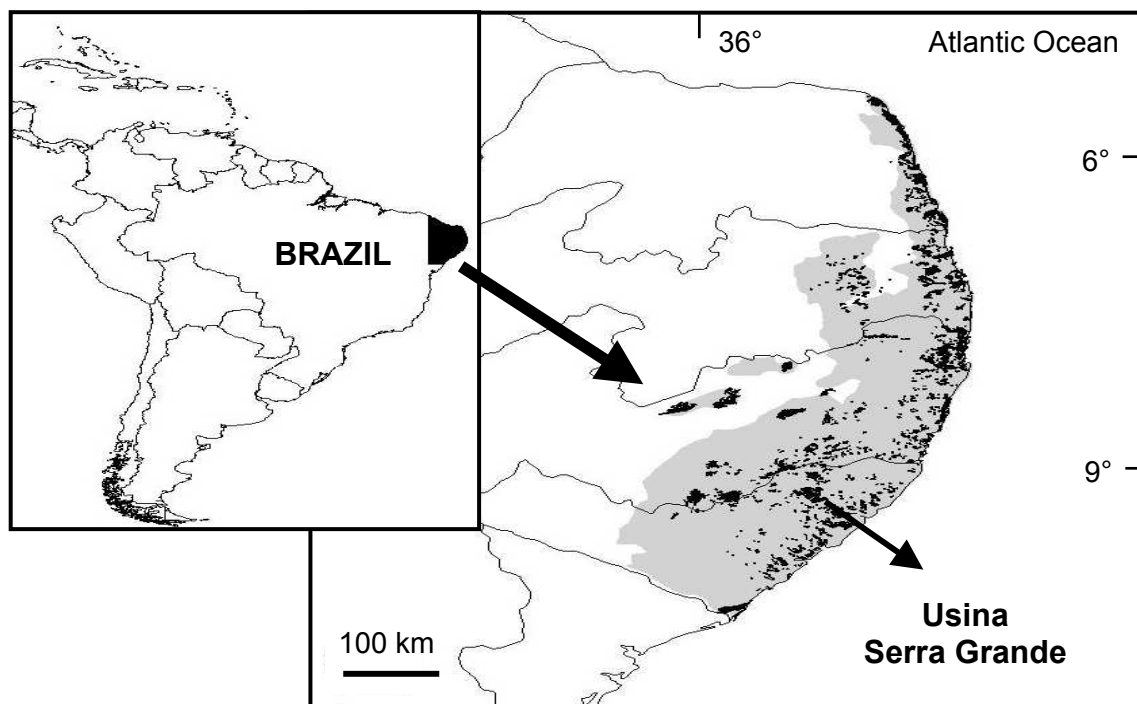


Figure 2. Geographical localization of the study site. Grey area indicates the original distribution of the Atlantic rainforest, black area indicates forest remnants. Source: Pimentel and Tabarelli (2004).



Figure 3. An example of the fragmented landscape in the study site. Forest remnants are surrounded by sugar-cane plantations. Foto: Rainer Wirth.

2.2 Study species

The most common LCA species in the region include *Atta sexdens* (L.) and *Atta cephalotes* (L.). *A. cephalotes* was chosen for the study, because it builds compact nests that are easy to define and monitor. *A. sexdens* was excluded from the study to avoid inaccurate data collection: the species builds nests with widely scattered entrance holes and subterranean foraging galleries (Vasconcelos, 1990b) This increases the risk of overlooking foraging trails and missing considerable portions of harvested plant material.

A. cephalotes is one of the most common leaf-cutting ant species in Central and South America: it has a wide distribution from Mexico to the Amazon, with an additional disjunctive occurrence in NE Brazil (Mariconi, 1970; Kempf, 1972). Unlike other *Atta* species, which prefer open and disturbed habitats, *A. cephalotes* is known as a 'woodland species' commonly found in mature or old-growth forests (Rockwood, 1973).

2.3 Sampling methods

In order to study the consequences of edge effects, I chose five distant ant colonies at the edge (< 100 m from forest border; *sensu* Laurance, 1998a) and five in the interior of the continuous forest (i.e., control habitat; Fig. 4). The studied 3500-ha continuous forest provided considerable environmental heterogeneity, so that each colony was regarded as an independent sample of the respective habitat. In order to evaluate effects of area loss (Fahrig, 2003) we included five additional colonies from the interior (> 100 m from forest border) of a nearby 50-ha forest fragment (Fig. 4). Due to the lack of *A. cephalotes* in other forest fragments in the region, this habitat type was represented by a single replication. Consequently, I am aware of the possibility of pseudoreplication and the fragment will be considered only as an additional reference in the interpretation of the results.

The 15 colonies studied in the three habitats (i.e., interior of the continuous forest, edge of the continuous forest, and interior of the forest fragment) were observed in bimonthly intervals over a period of one year (September, 2002 – July, 2003). During the study period, one colony died in the interior of the forest and was thus excluded from further analysis. Only adult colonies were chosen for the study.

For this purpose, only nests $> 30 \text{ m}^2$ and with 50 or more foraging holes were taken into consideration. The nest size and the number of foraging holes were measured in co-operation with Costa (2003).

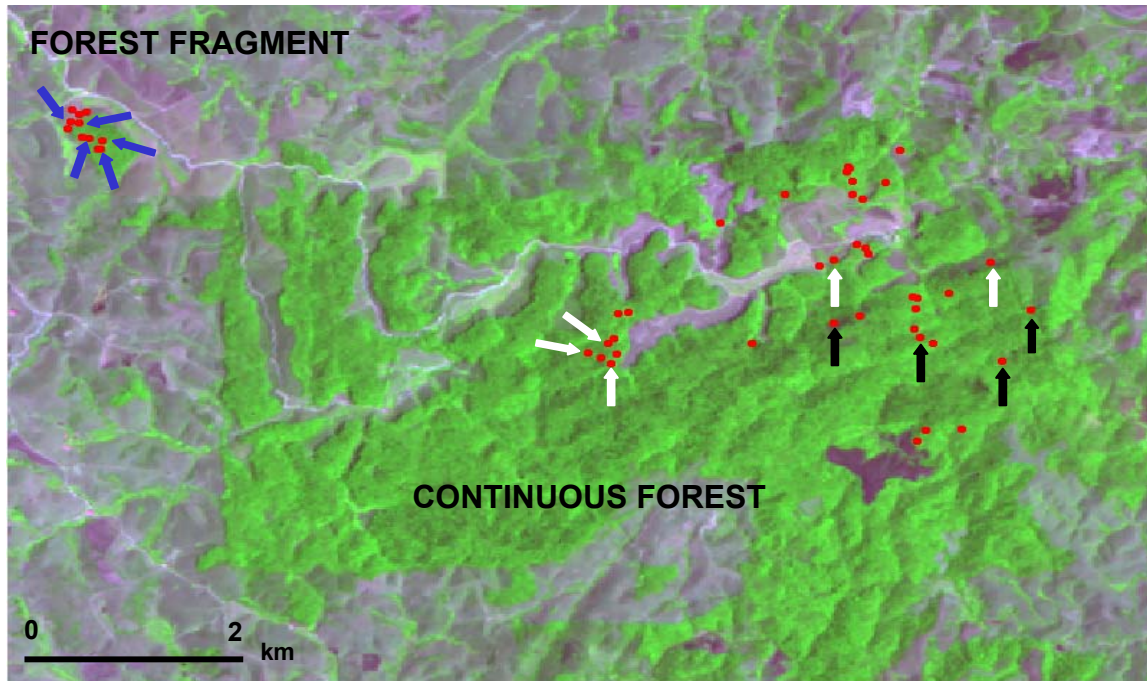


Figure 4. Localization of *Atta cephalotes* colonies in the study site. Red points indicate all *A. cephalotes* colonies found to date in co-operation with Costa (2003). Arrows indicate the colonies chosen for this study: black arrows in the interior of the continuous forest, white arrows at the edge of the continuous forest and blue arrows in the forest fragment. Image source: Shuttle Radar Topography Mission (SRTM) Elevation Dataset, 2002.

3. FRAGMENTATION-INDUCED CHANGES IN FOREST STRUCTURE

3.1 Introduction

To characterize the forest structure, several parameters like tree density, DBH (diameter at breast height), height, average crown diameter, basal area or dry biomass and attributes of canopy structure are usually studied (e.g., Veblen and Stewart, 1980; Ferreira and Prance, 1999; Asner *et al.*, 2002). The canopy structure includes the position, extent, quantity, type and connectivity of the aboveground components of vegetation (Lowman and Nadkarni, 1995). To describe the canopy structure, leaf area index (LAI) measurements are most commonly used providing an approximation of the amount of canopy foliage (e.g., Chason *et al.*, 1991; Clark *et al.*, 1996; Wirth *et al.*, 2001; Bréda, 2003).

So far, only few studies have assessed effects of habitat fragmentation on the structure of tropical forests (but see Ferreira and Laurance, 1997; Laurance *et al.*, 1997; Laurance *et al.*, 1998a; 1998b; Rankin-de Mérona and Hutchings, 2001). Fragmentation primarily results in the alterations of abiotic factors such as increasing light, temperature and wind turbulence (reviewed in Murcia, 1995). The changes in the physical environment modify the forest structure. 3-7 years after the occurrence of fragmentation, Ferreira and Laurance (1997) noted remarkable modifications in the forest stand caused by wind turbulence and microclimatic shifts: the proportion of standing dead as well as fallen or damaged trees was significantly higher near forest edges. Similarly, Rankin-de Mérona and Hutchings (2001) showed a significant decline of living trees in edge stands 3-5 years after fragmentation. 17 years after fragmentation, Laurance and colleagues (1997) reported a dramatic loss of above-ground tree biomass through wind-throw induced tree mortality in rain forest fragments in central Amazonia. These losses were largest within 100 m of the fragment edges. Furthermore, Laurance and colleagues (1998a) predicted that, in the long-term, tree mortality and damage caused by edge effects increase also in the interior of a fragment once the size of the fragment falls below 100-400 ha. On the other hand, Laurance and colleagues (1998b) observed a sharp increase in tree recruitment in forest fragments compared to the continuous forest. Moreover, recruitment depended significantly on (1) the size of the fragment, (2) the age of the fragment and (3) the distance from fragment edge. The highest recruitment rates

(244 %) were observed in 1-ha fragments and moderately high rates (35-50 %) in the fragments of 10-100 ha. In all fragments, the rates were highest within 100 m of the forest margin. Additionally, older fragments (> 5 years) had much higher recruitment than younger fragments. In consequence, the observed tree damages and losses of biomass inevitably lower the absolute tree density in a forest stand. On the other hand, increased tree recruitment in fragmentation-related forests presumably leads to an increase in the density of juvenile trees.

Few direct measurements of the mean diameter of trees have been made in tropical fragmented forests. The data is inconsistent and the results depend on how long fragmentation occurred, which particular size class of DBH was studied and how the fragmented habitat is defined (e.g., differences in defining the width of the forest edge). Schlaepfer and Gavin (2001) found no significant change in the mean DBH of large trees (DBH > 7 cm) at the edge (0-2 m from forest border) and in the center of a < 1 ha, medium-sized or > 100 ha fragment. Carvalho and Vasconcelos (1999) recorded that mean DBH of large trees (DBH > 10 cm) increased until 100 m from the edge and decreased again at the distances of > 300 m from the edge. Additionally, they noted a general increase in the density of large trees (DBH > 10 cm) with increasing distance from the forest edge.

No data exists about the changes in LAI in fragmented vs. non-fragmented forests. The LAI was firstly defined by Watson (1947) as the total one-sided area of photosynthetic tissue per unit ground surface area. The LAI drives both the within- and the below-canopy microclimate including canopy water interception, radiation extinction, water and carbon gas exchange. Therefore, the LAI is a key component of biochemical cycles in ecosystems and any change in the LAI (by storm, defoliation, drought) is accompanied by direct modifications in the forest stand productivity (Bréda, 2003). Early successional tropical forests have been reported to have a lower LAI than late successional forests, which presumably results from decreased foliage complexity in early successional habitats (Emmons and Dubois, 2003; Kalácska *et al.*, 2004). To some extent, driven by edge effects the modifications in fragmentation-related habitats resemble to those in early successional forests (Bierregaard *et al.*, 2001). For example, increased disturbance rates in fragments along with close proximity of edge habitats clearly favour early successional plant species (e.g., pioneers, vines and lianas) at the expense of late successional species adapted for the forest interior (Laurance *et al.*, 1998a; 1998b; Laurance, 2001). This indicates a

shift from a late successional to an early successional community. Consequently, one could expect lower LAI in fragmented habitats as a consequence of decreased foliage complexity of early successional vegetation and the abundance of light gaps caused by tree mortality in fragmented habitats (Saunders *et al.*, 1991; Laurance *et al.*, 1998a).

In this chapter, I will describe the forest structure in my study area. An important goal was to analyze the fragmentation-induced effects on the forest structure described in the literature and to improve the knowledge of the changes in the DBH and the LAI in fragmentation-related habitats. Additionally, LAI measurements were further used to estimate the amount of standing foliage for calculating the LCA herbivory rate (see chapter 7). I compared the structure of three forest habitats: the edge of the continuous forest, the interior of the continuous forest and the interior of a 50-ha forest fragment (see chapter 2.1).

I hypothesize that (1) due to increased tree damages and mortality, tree densities are lower at the edge of the continuous forest and in the forest fragment than in the control habitat (i.e., interior of the continuous forest); (2) due to increased tree mortality, the mean DBH of trees is smaller at the edge of the continuous forest and in the forest fragment than in the control habitat; (3) due to a presumably decreased foliage complexity in fragmentation-related forests the LAI is lower at the edge of the continuous forest and in the forest fragment than in the control habitat.

3.2 Material and methods

3.2.1 Tree density and DBH

To characterize the forest structure, I used the point-centered-quarter method (Müller-Dombois and Ellenberg, 1974). This method provides a quick way to estimate the plant density per unit area by using a series of distance measurements along transects. At the same time, the mean DBH of the forest stand can be measured. The data was collected in co-operation with Meyer (2003).

Four parallel north-south transects were established, each 60 m long and separated by 20 m distance around each ant nest in all forest habitats (Fig. 5). Around a nest the transects covered an area of at least 4800 m². The mean foraging area of a LCA colony was approximated to 10 000 m² (Wirth *et al.*, 2003b). Thus, the measurements covered an area that corresponds to the core habitat of a colony. Transects in the nearest vicinity of a nest were omitted, since LCA are known to avoid foraging close to the nest (Farji-Brener and Illes, 2000; Wirth *et al.*, 2003b). Along each transect, I placed four sampling points (SP) in 20m distance, resulting in 16 SP per colony (Fig. 5). At each SP, an imaginary line was drawn perpendicular to the transect, thus resulting in a square with four quarters. In each quarter of the square, I measured the distance to the nearest tree and its DBH. All trees > 5 cm DBH were included (see e.g., Veblen and Stewart, 1980).

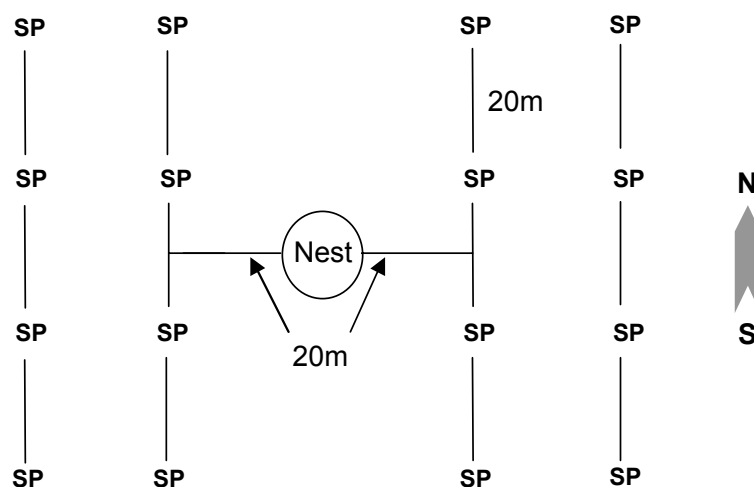


Figure 5. The layout of transects and sampling points (SP) around a LCA nest to sample the forest structure with the help of the point-centered-quarter method.

Finally, I calculated the mean DBH of the trees. The mean tree density (T) was calculated as follows:

$$T = A / D^2,$$

where A is the area covered with transects and D is the mean distance of trees from a sampling point. To statistically analyse the data I used STATISTICA 5.1 (StatSoft, 1995). The effect of the habitat (the interior of the continuous forest, the edge of the continuous forest, the forest fragment) on tree density and mean DBH was studied using one-way ANOVA. Post hoc comparisons were carried out using the Tukeys HSD test for unequal *n*.

3.2.2 Leaf area index (LAI)

To characterize the structure of the forest canopy, I estimated the cumulative LAI with digital hemispherical photographs. In the last decades, digital hemispherical photography is the most rapid, reliable and widespread indirect method for estimating LAI (e.g., Clark *et al.*, 1996; Planchais and Pontailier, 1999; Englund *et al.*, 2000; Frazer *et al.*, 2001; Jonckheere *et al.*, 2004). This method is based on the measurement of light transmission through the canopy in terms of gap fraction analysis (Jonckheere *et al.*, 2004). However, a myriad of comprehensive discussions exist about the need to adjust the LAI values gained with indirect methods to the more accurate values gained with direct measurements like litter collection and planimetric or gravimetric techniques (e.g., Chason *et al.*, 1991; Bréda, 2003; Jonckheere *et al.*, 2004). Most commonly, underestimation of the LAI through digital photography has been reported (Planchais and Pontailier, 1999; Pokorny and Marek, 2000; Soudani *et al.*, 2001). Additionally, it has been argued that indirect methods based on light interception models inevitably include woody canopy elements, thus resulting in measuring the plant area index (PAI) instead of the LAI (Gower and Norman, 1991; Chen, 1996). This leads to an overestimation of the LAI. Consequently, care has to be taken with the interpretation of the absolute values of LAI derived from indirect measurements. Therefore, it is important to note that in the present study, I am not defining the LAI *sensu stricto*, but *sensu lato* as measured by the indirect measurements. Additionally, since an important purpose of the study is a

relative comparison of various forest habitats, the absolute values are of minor importance.

For an optimal estimation of the LAI in the foraging areas of LCA colonies in fragmented vs. continuous forest habitats, four parallel north-south transects, each 80 m long and separated by 20 m distance, were established around a colony with a nest in the center (Fig. 6; see also chapter 3.2.1). Along each transect, five hemispherical photos were taken in 20-m intervals, thus resulting in a total of 20 photos per colony.

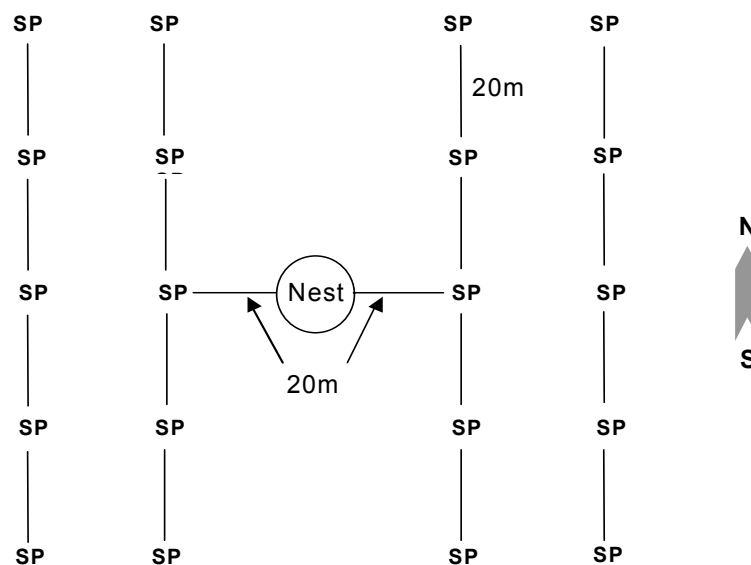


Figure 6. The layout of transects and sampling points (SP) around a LCA nest to measure the forest leaf area index (LAI) with the help of hemispherical photographs.

A Nikon Coolpix 990 camera with a 35 mm fish-eye lens was positioned below the canopy on a tripod 1 m above ground level. The camera was leveled horizontally. Photos were taken at dawn before sunrise or at dusk after sunset to avoid direct solar radiation in any part of the canopy (Chen *et al.*, 1991; Whitmore *et al.*, 1993). Based on the information in the literature (reviewed in Frazer *et al.*, 2001; Hale and Edwards, 2002), camera settings of the Nikon Coolpix 990 were standardized as follows: FISHEYE1 black and white mode, FINE image quality, aperture (f) = 2.5, automatic shutter speed, underexposure (+/-) = -0.7. Additionally, at each sample point, the topographic slope angle and aspect were estimated in order to differentiate between landscape features and vegetation on the photo for LAI calculations. To identify the north/south orientation axis on each photo, we marked the photos at the

time of exposure with a pointer protruding 5 mm above the front edge of the camera lens.

The photographs were analyzed with a “gap light analyzer” (GLA, Version 2.0), an image processing software to extract canopy structure and gap light transmission indices from fish-eye photographs (Frazer *et al.*, 2001). Each photograph was analyzed twice to compensate for the subjective aspect of the threshold adjustments, i.e., differentiating between black (canopy) and white (sky) pixels on the digitized photo. For the final LAI values the estimates of the effective LAI integrated over the zenith angles 0 to 60° (LAI 4 Ring) were used as suggested in the literature (Chason *et al.*, 1991; Frazer *et al.*, 2001; Leblanc and Chen, 2001). Finally, the mean LAI value of 20 photos was calculated per colony. The data was analyzed statistically using STATISTICA 5.1 (StatSoft, 1995). The effect of the habitat (the interior of the continuous forest, the edge of the continuous forest, the forest fragment) on the LAI was studied using one-way ANOVA. Post hoc comparisons were carried out using the Tukeys HSD test for unequal n . The data was collected and analyzed in cooperation with Araújo (2004).

3.3 Results

3.3.1 Tree density and DBH

The tree density was significantly different around the nests of *A. cephalotes* in various forest habitats (Fig. 7). Post hoc comparisons revealed that there were about twice as many trees (DBH > 5 cm) per area in the interior of the continuous forest (19.2 ± 3.3 per 100 m²) than in the forest fragment (11.2 ± 1.7 per 100 m²). However, the tree density at the edge of the continuous forest did not differ significantly from the density in the other two habitats (Fig. 7).

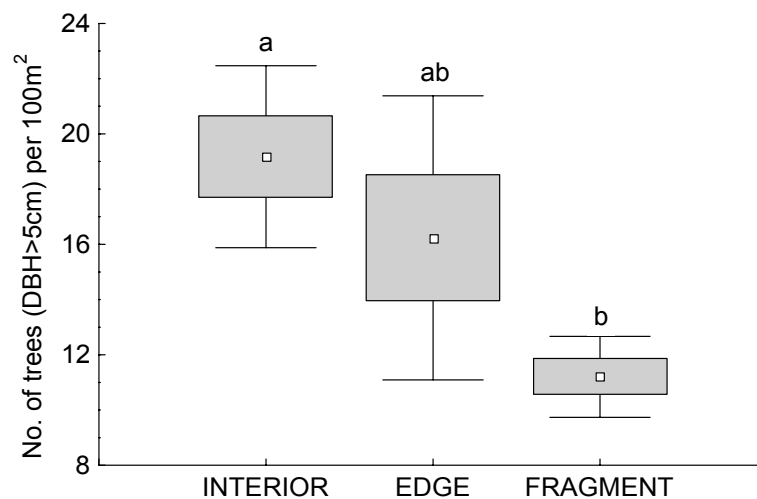


Figure 7. Mean (\pm SE, \pm SD) number of trees (DBH > 5 cm) per 100 m² around *A. cephalotes* nests in different habitats: INTERIOR = interior of the continuous forest; EDGE = edge of the continuous forest; FRAGMENT = interior of the forest fragment. Effect of HABITAT significant at $P = 0.0143$ ($df = 2$, $F = 6.182$). Different letters on the graph denote significant ($P < 0.05$) differences between habitats (Tukeys HSD post hoc test).

Similarly, the mean DBH of trees depended significantly on the forest habitat considered (Fig. 8). Post hoc comparisons showed that the mean diameter of trees around ant nests in the interior of the forest fragment (15.0 ± 2.2 cm) was significantly greater than in the interior (12.9 ± 1.1 cm) and at the edge (11.5 ± 2.3 cm) of the continuous forest. Mean DBH of trees did not differ significantly between continuous forest center and edge habitats (Fig. 8).

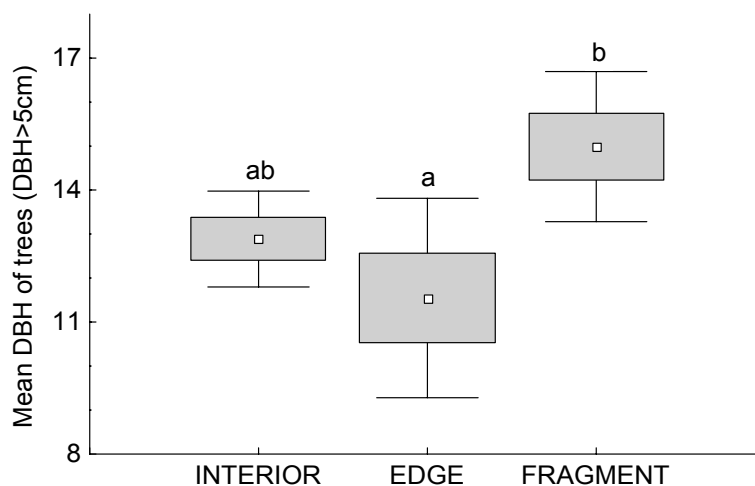


Figure 8. Mean (\pm SE, \pm SD) diameter-at-breast-height (DBH) of trees (DBH > 5 cm) around *A. cephalotes* nests in different habitats: INTERIOR = interior of the continuous forest; EDGE = edge of the continuous forest; FRAGMENT = interior of the forest fragment. Effect of HABITAT significant at $P = 0.0279$ ($df = 2$, $F = 4.895$). Different letters on the graph denote significant ($P < 0.05$) differences between habitats (Tukeys HSD post hoc test).

3.3.2 Leaf area index (LAI)

The mean LAI around ant nests was significantly influenced by the forest type (Fig. 9). The highest LAI values (4.43 ± 0.15) were measured in the interior of the continuous forest. At the edge of the continuous forest, the LAI was significantly and about 8% lower than in the interior of the continuous forest. Similarly, in the forest fragment, the LAI was significantly lower than in the interior of the continuous forest. It can be seen from figure 9 that the LAI at the edge of the continuous forest tended to be even lower than in the forest fragment, but the post hoc comparisons did not reveal a significant difference here.

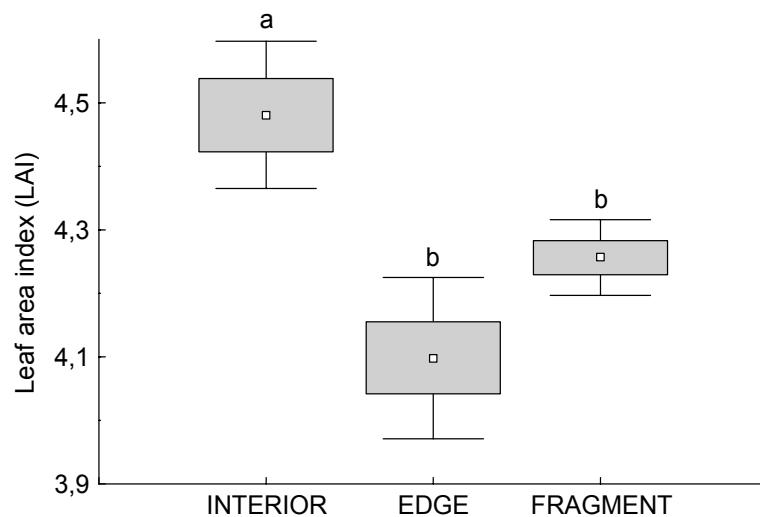


Figure 9. The mean (\pm SE, \pm SD) leaf area index (LAI) in the foraging area of *A. cephalotes* colonies in the interior of the continuous forest (INTERIOR), at the edge of the continuous forest (EDGE) and in the interior of the forest fragment (FRAGMENT). Effect of HABITAT significant at $P < 0.001$ ($df = 2$, $F = 15.0969$). Different letters on the graph denote significant ($P < 0.05$) differences between habitats (Tukeys HSD post hoc test).

3.4 Discussion

The first hypothesis of the study was partly supported. I hypothesized that fragmented habitats (i.e., the edge of the continuous forest and the interior of the forest fragment) have a lower density of trees than the control habitat (i.e., the interior of the continuous forest). According to my results, the tree density was significantly lower in the forest fragment compared to the control habitat, but only marginally lower at the edge of the continuous forest. A non-significantly lower tree density in the edge habitat is unexpected because forest edges have been repeatedly noted to experience wind-induced tree damages and increased tree mortality rates (Ferreira and Laurance, 1997; Laurance *et al.*, 1997; Laurance *et al.*, 1998a; Rankin-de-Mérona and Hutchings, 2001). Consequently, one would expect that an increased tree mortality, in the course of time, leads to a significantly lower density of trees at the forest edges. Moreover, in a long term (ca. 17 years), fragmented forest stands are reported to suffer from a considerable loss of biomass (Laurance *et al.*, 1997). Since extensive forest fragmentation in my study area began in the 1960s (see chapter 2.1), I would expect a long-term effect of tree mortality on the density of trees at the forest edge. However, an increased recruitment of early successional species observed in fragmented habitats (Laurance *et al.*, 1998b) might have accounted for a higher tree density thus mitigating the effect of high tree mortality. A low density of trees in the forest fragment may be a consequence of increasing human disturbance: the fragment is located close to an urban area and suffers from moderate logging pressure (see chapter 2.1). The absolute values of the tree densities measured by Rankin-de-Mérona and Hutchings (2001) in a newly formed forest fragment in central Amazon are lower (edge of the fragment = 6.8 ± 0.6 , interior of the fragment = 6.5 ± 0.3 per 100 m²) than in the present study (edge of the continuous forest = 16.2 ± 5.0 , interior of the continuous forest = 19.2 ± 3.3 , interior of the forest fragment = 11.2 ± 1.7 per 100m²). The differences between the data sets probably result from a different methodology used: Rankin-de-Mérona and Hutchings considered big trees with DBH > 10 cm, whereas I considered trees with DBH > 5 cm.

The second hypothesis of this study was not supported. There was no significant difference in the mean DBH of trees at the edge of the continuous forest and in the control habitat (i.e., interior of the continuous forest). Moreover, trees had the biggest DBH in the interior (i.e., > 100 m from forest margin) of the forest fragment. The phenomenon is not in line with what is reported in the literature.

Schlaepfer and Gavin (2001) found no significant changes in the mean DBH of large trees (DBH > 7 cm) at the edge and in the interior of fragments of different size (1-100 ha). Carvalho and Vasconcelos (1999) recorded that mean DBH of large trees (DBH > 10 cm) increased until 100 m from the edge and decreased again at the distances of > 300 m from the edge. However, big DBH of trees in the studied fragment might be a special characteristic of this particular forest fragment: the fragment is considered to be an old remnant of primary forest and has still large old individuals of various late successional species (M. Oliveira and M. Tabarelli, personal communications; personal observation). These trees might increase the mean DBH of the fragment.

The third hypothesis of the study was fully supported. The LAI was significantly higher in the interior of the continuous forest than in the fragmented habitats – at the edge of the continuous forest and in the forest fragment. So far, no studies exist on the variation in LAI through fragmentation-induced effects in tropical forests. However, lower LAI has been measured in early-successional forests due to decreased foliage complexity in these habitats (Emmons and Dubois, 2003; Kalácska *et al.*, 2004). Fragmented forests can be considered representatives of early-successional habitats (Bierregaard *et al.*, 2001), since they experience modifications that are characteristic for early successional forests like for example proliferation of early successional plant species (e.g., pioneers, vines and lianas; Laurance *et al.*, 1998a; 1998b; Laurance, 2001). Consequently, lower LAI in fragmented habitats could be a result of decreased foliage complexity of early successional vegetation, combined with the abundance of light gaps caused by increasing tree mortality in these habitats (Ferreira and Laurance, 1997; Laurance *et al.*, 1997; Laurance *et al.*, 1998a; Rankin-de Mérona and Hutchings, 2001). Additionally, a lower LAI in the studied forest fragment may result from light gaps caused by selective logging in this habitat (see chapter 2.1). The mean LAI of 4.1 measured at the edge of the continuous forest corresponds to an early-intermediate stage of a tropical moist forest succession in Costa Rica estimated by Kalácska and colleagues (2004), whereas the mean LAI of 4.4 measured in the interior of the continuous forest falls into the range of LAI in an intermediate-late successional stage estimated by Kalácska and colleagues (2004).

Except for the mean DBH of trees, I detected several clear effects of fragmentation on the forest structure. Fragmentation generally lowered the mean tree

density and the LAI of the forest stands at the edge of the continuous forest and in the forest fragment. The observed effects fit well the range of the effects of fragmentation known from the literature. Consequently, the observed habitats can be considered as good representatives of fragmented vs. continuous forests for my study. However, as for the mean DBH of trees, the studied forest fragment exhibited a confusing pattern. Therefore, and because of the threat of pseudoreplication (see chapter 2.3), care will be taken when interpreting the results gained from this habitat.

4. FRAGMENTATION-INDUCED CHANGES IN PLANT PALATABILITY TO LCA

4.1 Introduction

Living plants, especially the flowering plants provide food materials for about half of the species of insects (Fraenkel, 1959). However, most insects are more or less selective in their choice of host plants (Fraenkel, 1959). It has long been noticed that throughout the animal kingdom the selection of diet has become most highly developed among mobile free-living species, including insects which feed upon plants (Dethier, 1954). However, the preferences and the directing forces operating in herbivore diet selection are not yet fully understood.

The basic food requirements of insects are very similar to those of higher animals. They include the essential amino acids, most of the vitamins of the B group, a sterol, physiologically important minerals and carbohydrates (Dethier, 1954; Fraenkel, 1959). However, plants have also evolved mechanisms to defend themselves against the exploitation by herbivores. They are able to escape herbivore attack through physical and chemical, indirect and direct defence strategies (e.g., Lucas *et al.*, 2000; Theis and Ler dau, 2003; Wink, 2003). Common features of physical defence include for example toughness and hardness of the plant tissue palatable to herbivores (Lucas *et al.*, 2000). Indirect chemical defences include the release of odours that attract the natural enemies of herbivores, whereas direct defences include the production of secondary metabolites that impair herbivore development or repel herbivore attack (Theis and Ler dau, 2003).

Classical plant defence theory started to develop in 1950s, when Dethier (1954) and Fraenkel (1959) presented their ideas that plant secondary metabolites play a major role in controlling their interaction with herbivores. Fraenkel (1959) studied the insect-repellent effects of secondary metabolites in the plant families of *Cruciferae*, *Umbelliferae*, *Legaminosae*, *Solanaceae*, *Moraceae* and *Graminaceae*. Dethier (1954) hypothesized that herbivores and plants are essentially locked in a biochemical arms race. Secondary metabolites are allelochemicals that are not directly essential for basic photosynthetic or respiratory metabolism. The common groups of secondary metabolites in plants include glucosides, saponins, tannins,

alkaloids, essential oils and organic acids (Fraenkel, 1959). Today, apart from the defence against herbivores, plant secondary metabolites are known to function as defence against microbes, viruses or competing plants as well as signal compounds to attract pollinating or seed dispersing animals (Wink, 2003). Therefore, secondary metabolites are considered to be important for the plant's survival and reproductive fitness representing adaptive characters that have been subjected to natural selection during evolution (Wink, 2003). Coevolution theory predicts that plant chemistry drives herbivore specialization: specialized herbivores adopt themselves entirely to secondary compounds of some species and lose therefore the ability to feed on other species, whereas generalist herbivores feed on a wide range of species but they do so at the cost of lower feeding success on any species because of the occasional toxic effects of secondary compounds (Cornell and Hawkins, 2003). Specialization is thus a trade-off with no winners or losers: specialists pay a cost for but get the benefits of specialism; generalists pay a cost for but get the benefits of generalism (Cornell and Hawkins, 2003).

Leaf-cutting ants (LCA) are highly generalist herbivores (Cherrett, 1989). However, it has long been observed, that LCA carefully select their diet: many plant species abundant in the foraging area of the colonies escape ant attack completely (Cherrett, 1968; Rockwood, 1976; Hubbel and Wiemer, 1983; Wirth *et al.*, 2003b). The attributes that drive LCA diet choice are not yet fully understood. LCA live in a complex symbiosis with their garden fungus. Ants, especially the brood, feed basically on hyphae of the fungus, which they feed with plant material (Hölldobler and Wilson, 1990). However, Littleddyke and Cherrett (1976) found that adult ant workers also ingest nutrient-rich sap directly from plant leaves while cutting them. Quinlan and Cherrett (1979) and Silva and colleagues (2003) have shown that ant workers imbibe carbohydrates from the plant material while preparing it for the fungus, thus covering a considerable amount of their energy needs. Consequently, it has been discussed that ants and fungus have conflicting requirements for the quality of the plants to be harvested (Roces, 2002). On the one hand, ant workers may prefer resources that support maximal rates of fungus growth, irrespective of the attractiveness of the plant sap being imbibed during the harvesting process. On the other hand, workers may decide about the quality of a given resource on the immediate availability of energy to support their foraging activity. To what extent these two different demands determine LCA diet choice is not yet clear (Roces,

2002). It is generally agreed that plant secondary metabolites play a major role in host plant selection by LCA (Rockwood, 1976; Hubbel *et al.*, 1984; Howard and Wiemer, 1986). However, Howard (1987), Howard (1988) and Nichols-Orians (1991) found also that the palatability of a plant to LCA was correlated with the carbohydrate content and discuss the possibility that secondary chemistry and nutrient availability interact to determine the ant diet choice.

Even less work has been done in the ecological context of the LCA diet selection. In 1988, Coley found that fast-growing pioneer plant species that are generally preferred by LCA (Farji-Brener, 2001; Wirth *et al.*, 2003b) produce less chemical defences than slow-growing late successional species. Pioneers are more abundant in early-successional, disturbed, or fragmented forests (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999). LCA colony densities increase in fragmentation-related habitats like forest edges (Wirth *et al.*, 2003a), forest remnants (Rao, 2000; Wirth *et al.*, 2003a), and early-successional forests (e.g., Jaffe and Vilela, 1989; Vasconcelos and Cherrett, 1995; Moutinho *et al.*, 2003). Therefore, it is reasonable to suggest that apart from host plant selection secondary chemistry might also drive LCA habitat selection, i.e., the survivorship of a newly founded colony.

I hypothesized that the vegetation in fragmentation-related forest habitats is more palatable to LCA because of low contents of less secondary compounds and high contents of carbohydrates. For this, I analysed the contents of secondary compounds and carbohydrates in the LCA diet and in the surrounding forest. I did this at the forest edge (i.e., a habitat influenced by fragmentation) and in the interior of the forest which served as a control habitat. I studied two groups of secondary metabolites approved to be toxic to the ants, their fungus, or both: terpenoids and tannins (Howard and Wiemer, 1986; Howard, 1988; Nichols-Orians, 1991).

Terpenoids

Terpenoids are plant essential oils and represent one of the largest and functionally most diverse groups of natural products (Mabry and Gill, 1979). In total, more than 30000 terpenoids have been identified in plants, including both secondary and primary metabolites (Theis and Lerdau, 2003). Terpenoid secondary metabolites serve commonly as defensive chemicals and are stored in secretory structures at sites where defence is crucial such as reproductive and photosynthetic tissues (Theis and Lerdau, 2003).

Several terpenoid compounds, including mono-, sesqui-, di- and triterpenes have been isolated from plants that were avoided by LCA. Studies of Howard and colleagues (1988) suggest that ants avoid terpenoid-rich leaves rather because of the deleterious effect on the fungus than on the ants themselves. The terpenoids most commonly found to repel LCA of the *Atta* family include sesquiterpenoids caryophyllene oxide (Hubbel *et al.*, 1983; Hubbel and Wiemer, 1983; Howard *et al.*, 1988; Howard *et al.*, 1989) and caryophyllene (Hubbel *et al.*, 1983; Howard *et al.*, 1988; Howard *et al.*, 1989; Barnola *et al.*, 1994; North *et al.*, 2000). Additionally, sesquiterpenes nerolidol (Howard *et al.*, 1988), humulene (Barnola *et al.*, 1994), α -cubebene (Barnola *et al.*, 1994), α -copaene (Barnola *et al.*, 1994), diterpenes kolavenol (Howard *et al.*, 1988) and cornutin A and B (Chen *et al.*, 1992) and monoterpene trans- β -ocimene (Chen *et al.*, 1984) have been observed to exhibit repellency to LCA.

Tannins

Tannins are plant phenolic compounds (Hagerman, 2002). They are preponderant in nature: foliage and bark of some trees may contain up to 40 % of tannin which makes up a significant portion of the forest carbon pools (Kraus *et al.*, 2003). Recent findings suggest that tannins are produced by plants not for the primarily purpose of herbivore deterrence, but they play an important role in plant-plant and plant-litter-soil interactions by hindering decomposition rates, inhibiting the growth of microorganisms and affecting thereby nutrient cycles (Kraus *et al.*, 2003). However, tannins have also proved to inhibit protein digestibility in living organisms thus slowing down their developmental rates (Hagerman, 2002). Therefore, tannins are involved in herbivore repellence (e.g., Coley, 1986; Coley and Barone, 1996). Because of tannins' widespread occurrence in plants, most herbivores, and certainly all generalist herbivores, routinely encounter tannin-rich diets.

Leaf-cutting ants have been found to avoid plants with high tannin contents (Howard, 1990; Nichols-Orians, 1991). Nichols-Orians (1991) proposes that ants avoid tannins because they affect the growth of the symbiotic fungus. His idea is based on the studies of Zucker (1983) who showed that tannins, especially condensed tannins, are strong inhibitors of fungi and their enzymes. However, the repellence of tannins against LCA is not yet fully understood: there is evidence that hydrolyzable tannins play a minor role in LCA deterrence (Howard, 1987; 1988).

4.2 Material and methods

4.2.1 Selection of the species

The most dominant species in the ant diet and in the forest were studied, since it was not possible to sample the complete LCA diet and vegetation of the forest. The study was concentrated on two forest habitats – the interior and the edge of the continuous forest. Forest fragments were not included in this study, since the floristic inventory of these habitats was still in process (Oliveira, 2003).

In both habitats, the five most dominant plant species in the surrounding forest and the five top-ranked forage species in the diet of *A. cephalotes* colonies were selected to study their terpenoid, tannin, and carbohydrate content (Tab. 1, 2), resulting in a total of 20 species. The selection of the forest species based on the data gained from the floristic inventory of the study site (Tab. 1; Oliveira, 2003). For this inventory, 10 plots á 0.1 ha (100 m x 10 m) were established in each forest habitat. I chose the most dominant species per habitat by ranking the species' absolute abundance (number of individuals in the sum of the plots) and frequency (species occurrence in a plot) for each habitat.

Similarly, the top-ranked ant forage species were selected by ranking their absolute abundance (abundance of the leaf fragments of the species in the sum of samplings) and frequency (species occurrence in the sum of samplings; Tab. 2). The sampling was conducted by collecting leaf fragments carried into nest by ants during 1 minute at bimonthly intervals during one year (6 times in total) for all ant colonies per habitat (see chapter 5.2.1). In order to unmistakably identify the species in the forest, no morphospecies were considered and only taxonomically identified species were selected here. A closer look at the morphospecies concept will be taken at in chapter 5.2.1. The species were taxonomically identified in co-operation with Falcão (2004) and with the help of identified herbaceous material provided by the floristic inventory of the study site (Oliveira, 2003). In the ant diet, *Croton floribundus* and *Miconia hypoleuca* appeared on the top of the ranking list in both habitats. Therefore, in the further analysis these species were considered as representatives of both habitats. In order to be able to compare 10 different forest species vs. 10 different ant diet species, the additional sixth species was included in the ant diet for each habitat (Tab. 2).

Table 1. The most dominant species in the interior (INTERIOR) and at the edge (EDGE) of the continuous forest ranked by their absolute abundance (number of the individuals in the sum of the plots) and frequency (species occurrence in a plot) in 10 plots á 0.1 ha established in each forest habitat for the purpose of the floristic inventory of the study site (Oliveira, 2003).

Habitat	Species (Family)	Abundance	Frequency (%)
INTERIOR	<i>Mabea occidentales</i> (Euphorbiaceae)	177	80
	<i>Virola gardneri</i> (Miristicaceae)	42	70
	<i>Helicostylis tomentosa</i> (Moraceae)	33	70
	<i>Eschweilera ovata</i> (Lecythidaceae)	33	50
	<i>Tovomita mangle</i> (Guttiferae)	25	60
EDGE	<i>Byrsonima sericea</i> (Malpighiaceae)	126	100
	<i>Bowdichia virgiloides</i> (Papilionaceae)	36	100
	<i>Tapirira guianensis</i> (Anacardiaceae)	45	90
	<i>Ocotea glomerata</i> (Lauraceae)	23	80
	<i>Thyrsodium spruceanum</i> (Anacardiaceae)	54	70

Table 2. The most dominant species in the diet of *A. cephalotes* colonies in the interior (INTERIOR) and at the edge (EDGE) of the continuous forest ranked by their abundance (abundance of the leaf fragments of the species in the sum of samplings) and frequency (species occurrence in the sum of sampling). The sampling was conducted of the leaf harvest of all ant colonies per habitat. * = overlapping species (i.e., the species are abundant and frequent in both habitats).

Habitat	Species (Family)	Abundance	Frequency (%)
INTERIOR	<i>Vochysia oblongifolia</i> (Vochysiaceae)	400	50
	<i>Brosimum guianense</i> (Moraceae)	308	17
	<i>Croton floribundus</i> (Euphorbiaceae) *	241	20
	<i>Miconia hypoleuca</i> (Melastomataceae) *	146	20
	<i>Dialium guianense</i> (Caesalpinaceae)	96	14
	<i>Lecythis lurida</i> (Lecythidaceae)	85	24
EDGE	<i>Croton floribundus</i> (Euphorbiaceae) *	732	20
	<i>Inga thibaudiana</i> (Mimosaceae)	365	50
	<i>Miconia hypoleuca</i> (Melastomataceae) *	225	40
	<i>Miconia prasina</i> (Melastomataceae)	166	40
	<i>Gouanea blanchetiana</i> (Rhamaceae)	146	27
	<i>Schefflera morototoni</i> (Araliaceae)	98	17

4.2.2 Sampling and material storage

Since plants are known to exhibit a dramatic decline in the synthesis of antifungal secondary metabolites, especially terpenoids, in the dry season when the risk of fungal attack is low (Hubbel *et al.*, 1984; Howard, 1987), plant material was collected in the wet season (July, 2003) to increase the possibility of detecting the highest concentrations of secondary compounds.

Of each of the selected 20 plant species, five random individuals were marked in the forest. Of each individual, and for each type of analysis (terpenoids, tannins and carbohydrates), two random leaves were collected, thus resulting in six leaves per individual. The leaves were cut with telescopic scissors or reached by tree climbing. The leaves were collected in the morning hours (at 06-10 a.m.) in order to reduce the loss of volatile substances in the direct sunlight. Directly after collecting, for terpenoid analyses, the leaves were put into 60 ml dark glass vials closed with double tap to minimize the loss of volatile terpenoids. The vials were transported to the field station in linen bags to avoid overheating of the vials. For tannin and carbohydrate analyses, the leaves were transported to the field station loose in linen bags for further drying (Gartlan *et al.* 1980; Hagerman 1988; Ann Hagerman, personal communication).

In the field station, for terpenoid analyses, the leaves were cut into small pieces and 1 g of leaf tissue of each species was stored in 10 ml of cyclohexane (C₆H₁₂) containing 0.1 % (10 mg) anisole (C₇H₈O) in dark glass vials closed with a double tap. Cyclohexane was used as a solvent. Anisole was chosen on the bases of its similar molecular mass and boiling point as a reference substance to be able to measure the quantity of terpenoids. In the laboratory, the vials were shaken at room temperature for 1 h at 120 rpm. After shaking, the samples were kept at room temperature for further analysis.

For tannin and carbohydrate analyses, the leaves were dried in the field station in a low-temperature oven at 40° C for at least 3 days (Gartlan *et al.* 1980; Hagerman 1988; Ann Hagerman, personal communication). After drying, the samples were kept in polystyrol boxes filled with silica gel for transportation to the laboratory.

4.2.3 Chemical analyses

4.2.3.1 Identification of terpenoids

The terpenoid content of the plant samples was analysed with a gas chromatograph-mass spectrometer SHIMADZU Quadrupole QP-5050A. The chromatographic column used was a DB-5 (30 m x 0.25 mm Ø). The carrier gas used was helium at a flow rate of 1 ml / min.

The preliminary identification of the substances was carried out using the computer library `Wiley 229. LIB`. The identification of the substances was confirmed by comparing their measured retention time (RT) with the standard retention time of the authentic substances described in Adams (1995).

For this, a calibration curve with 10 randomly selected terpenoids was created between their standard (Adams 1995) and measured RT ($y = 154.43 + 0.36058 * x$; $r^2 = 0.997$, $P > 0.001$; Fig. 10). The terpenoid samples were provided by Prof. J. R. Trigo, State University of Campinas, Brazil. The standard RT of the terpenoids ranged from 319 sec. (alpha-pinene) to 2072 sec. (bisabolol), which covers the range of the RT of the terpenoids found in the plant samples by the computer library. Therefore, the model is suitable to predict the RT of the terpenoids for this study.

To confirm the identification, the measured RT of the terpenoids found in the plant samples were correlated with the RT predicted from the standard RT (Adams 1995) of these terpenoids by the calibration curve (Fig. 11). For 8 terpenoids, I found a highly significant correlation ($r = 0.9993$, $P < 0.001$) between the measured and predicted RT, which confirmed the identification of these terpenoids (Fig. 11). Germacrene-B was excluded from the analyses as an outlier.

Additionally, for caryophyllene oxide a commercial authentic sample was available (degree of purity 99 %, Sigma-Aldrich Co.), therefore it was used to verify the identification of this substance.

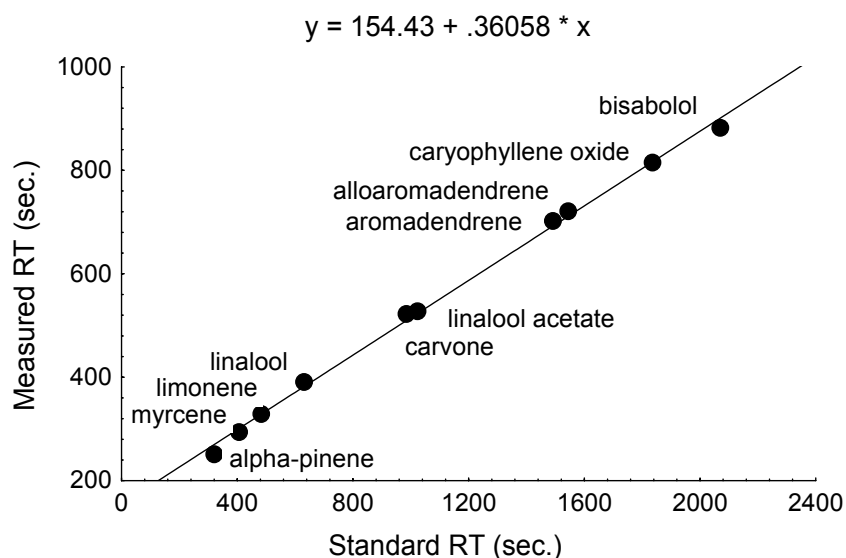


Figure 10. Relationship between the measured retention time (Measured RT) of 10 randomly selected terpenoids and their standard retention time (Standard RT; Adams, 1995). $r^2 = 0.997$, $P < 0.001$.

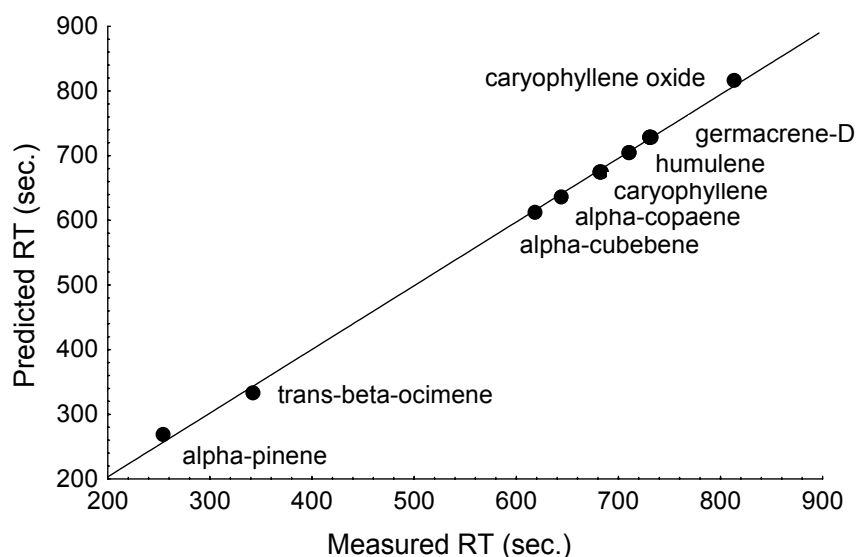


Figure 11. Relationship between the measured retention time (Measured RT) of the terpenoids found in the plant samples and the retention time (Predicted RT) predicted by the calibration curve (Fig. 10). $r = 0.9993$, $P < 0.001$.

4.2.3.2 Quantification of terpenoids

Terpenoids were quantified with a Hewlett Packard HP5890 SERIES II gas chromatograph. The column used was a HP-1 (25 min x 0.2 mm Ø).

For the quantification purpose, 10 mg of the reference substance anisol (see chapter 4.2.2) was added to each plant sample during sampling in the field. In the laboratory, a calibration curve was created between the retention time values measured in GC/MS QP-5050A (used for terpenoid identification; chapter 4.2.3.1) and in GC HP-5890 (used for terpenoid quantification; $y = -1.453 + 0.90070 * x$; $r = 0.999$, $P < 0.001$; Fig. 12). This calibration curve included 7 terpenoids from the calibration curve used for terpenoid identification (Fig. 10), that were of sufficient amount for their peaks to appear on the gas chromatograph. Also, anisol was included to the calibration curve, since its position on the gas chromatograph was clear in all plant samples.

On the bases of this calibration curve, the peaks of the terpenoids identified in GC/MS were identified on the gas chromatographs. The amount of a terpenoid in a plant sample was estimated as the relative area of its peak on the gas chromatograph compared to the area of anisol in the same sample.

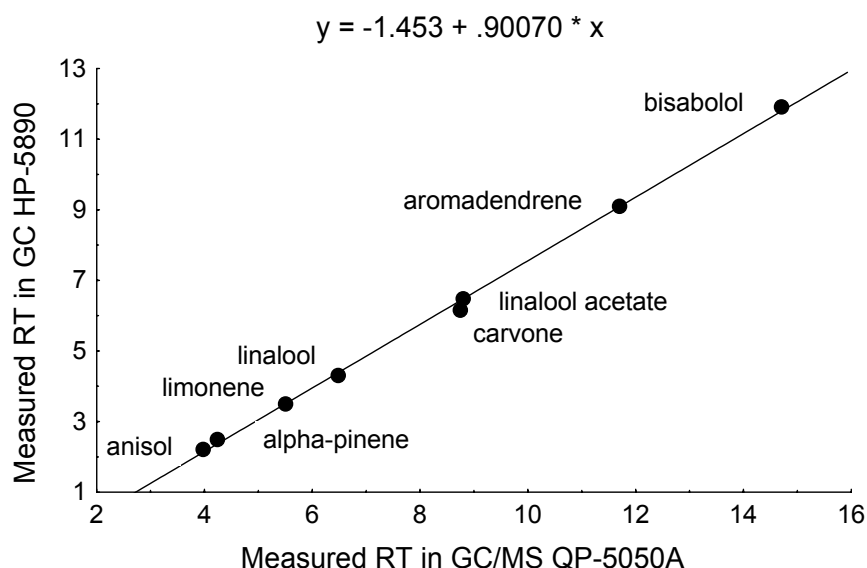


Figure 12. Calibration curve for the quantification of terpenoids. Measured retention times (RT) of 8 substances in GC/MS QP-5050A (used for terpenoid identification) in relation to the measured RT of the same substances in GC HP-5890 (used for terpenoid quantification). $r = 0.999$, $P < 0.001$.

4.2.3.3 Quantification of tannins

The tannin content of the leaf samples was quantified with the radial diffusion method (RDM; Hagerman, 1987). The method is based on tannin-protein reaction and the creation of a precipitation ring that reflects the amount of tannins. The method is especially suitable for this study since it detects both condensed and hydrolysable tannins. The advantage of the method is also that the inevitable components of plant extracts such as non-tannin phenolics or water-insoluble compounds do not interfere with the assay (Hagerman, 1987).

Dried leaves were ground and 100 mg plant tissue of each species was extracted at room temperature for some hours with 0.5 ml 50 % (v/v) methanol. For the buffer, a solution of 3 ml acetic acid, 10.5 g vitamin C and 1 l of distilled water was adjusted to pH 5.0 with 10 M NaOH. 200 ml buffer was added to 4 g agar and brought to boil. After cooling the suspension to 40° C in a water bath, 0.2 g bovine serum albumin (BSA) was added while gently stirring. The solution was dispensed in 9.5-ml aliquots in Petri dishes (8.5 cm \varnothing) and allowed to cool. After cooling, holes (5 mm \varnothing) were pierced in the agar and filled with 0.2 mg plant extracts in 3 replicas per species. Finally, the Petri dishes were covered, sealed with parafilm and incubated at 30° C for 96 h. After 96 h, the diameters of tannin precipitation rings were measured. For each ring, two diameters were measured to minimize errors caused by irregular ring development. The tannin concentration was calculated from the mean of the diameters x 3 replications per plant species as tannic acid equivalent using an appropriate calibration curve ($y = 9.7835 + 0.61666 * x$; $df = 1.3$, $n = 5$, $r^2 = 0.997$, $P < 0.001$) created with the help of commercial tannic acid.

4.2.3.4 Quantification of total non-structural carbohydrates (TNC)

The total TNC content of the plant samples was analysed with the phenol-sulfuric acid method by Dobois and colleagues (1956), modified by Ashwell (1966). The method utilizes phenol as a specific organic colour-developing agent and the amount of sugars is determined colorimetrically. Plant material was prepared for the analyses as described by Marquis and colleagues (1997). Three replicates were run per plant species.

To extract soluble sugars, 1.5 ml 80% (v/v) ethanol was added to 15 mg of dried and ground plant material. Samples were shaken overnight at 30° C. The next

day the supernatants were brought to a volume of 10 ml in volumetric flasks by adding distilled water and 2 ml of the solution were taken for further analyses. For a colour-developing reaction, 0.05 ml 80 % (by weight) phenol was added to 2 ml plant extract followed by the rapid addition of 5.0 ml concentrated sulphuric acid. The samples were incubated at room temperature for at least 30 min for the colour to stabilize. The optical density of the solutions was determined at 485 nm with a Hewlett Packard HP8453 UV-visible spectrophotometer. The samples were read against a blank containing distilled water in place of the sugar solution.

To determine the starch content of the plant samples, the solids that remained after ethanol extraction were transferred to 25 ml tubes and incubated with 2.5 ml sodium acetate buffer (0.2 M; pH 4.5) in a boiling water bath for 1 h. After cooling, 2 ml of acetate buffer and 1ml of amyloglucosidase (0.5 % by weight, Sigma A-7420) were added and the samples were incubated for 8 h at 55° C. Solutions were filtered through Whatman GF/C filters and diluted to 10 ml in volumetric flasks. The concentration of starch was determined colorimetrically as above.

The sugar concentrations of the plant samples were calculated as glucose equivalents using an appropriate calibration curve ($y = -4.046 + 106.922 * x$; $df = 1.3$, $n = 5$, $r^2 = 0.988$, $P < 0.001$). The plant TNC concentration was estimated as the sum of soluble sugars and starch measured in glucose equivalents.

4.2.3 Statistical analyses

Data was analysed using STATISTICA 5.1 (StatSoft, 1995). In the case of tannins and carbohydrates, the effects of the habitat (interior of continuous forest vs. edge of continuous forest) and the species (dominant species in the forest vs. dominant species in ant diet) were studied using two-way ANOVA. Post hoc comparisons were carried out using the Tukeys HSD test for unequal n .

4.3 Results

4.3.1 Terpenoids

The results of identification and quantification of terpenoids found in the plant samples are shown in table 3.

No terpenoids were detected in dominant plant species in the ant diet, neither in the interior nor at the edge of the forest. One can see in table 3 that of the dominant species in the forest, two tree species contained terpenoids in the forest interior (*Virola gardneri* and *Tovomita mangle*) and two at the forest edge (*Ocotea glomerata* and *Thyrsodium spruceanum*).

The species in the forest interior contained larger amounts and more different terpenoids than the species at the forest edge. *Virola gardneri*, a dominant species in the forest interior, contained the biggest number terpenoids. In this species, 6 terpenoids were detected: sesquiterpenes β -caryophyllene, caryophyllene oxid, germacrene-D, humulene and the monoterpenoids trans- β -ocimene and α -pinene. *Tovomita mangle*, a dominant tree of the forest interior contained the largest amounts of terpenoids. In this species, sesquiterpenes β -caryophyllene, α -cubebene, α -copaene, germacrene-D and humulene could be identified. The concentrations of α -copaene and β -caryophyllene were 3.976 mg and 2.698 mg / g fresh weight, respectively. Among the species at the edge of the forest, *Ocotea glomerata* contained only germacrene-D. Similarly, *Thyrsodium spruceanum* contained only germacrene-D and β -caryophyllene.

It is important to note that species in the families Moraceae, Lecythidaceae and Euphorbiaceae contained no terpenoids, neither in the forest interior nor at the edge, neither in the ant diet nor in the forest species. In the forest interior, the terpenoid-rich species were members of the families Myristicaceae (*Virola gardneri*) and Guttiferae (*Tovomita mangle*). At the edge of the forest, Lauraceae (*Ocotea glomerata*) and Anacardiaceae (*Thyrsodium spruceanum*, though not *Tapirira guianensis*) contained terpenoids.

4.3.2 Tannins

Ants preferred plant species with lower tannin concentration, independently of habitat type (main effect of FOREST vs. ANT DIET significant at $P = 0.0466$, $df = 1$, $F = 4.122$; Fig. 13). One can see from figure 13 that in the forest interior, plants contained 5.7 ± 3.9 % tannins, whereas 3.7 ± 5.5 % tannins were determined in the ant diet. Similar pattern appears at forest edge. There, in average plants contained the same amount of tannins as those in the forest interior (5.7 ± 7.7 %), however the ant diet consisted only of 2.5 ± 2.8 % tannins. One can see from figure 13 that at the forest edge, the decline of tannins in the ant diet compared to the tannins in forest plants was even bigger than in the forest interior, though this trend was not significant.

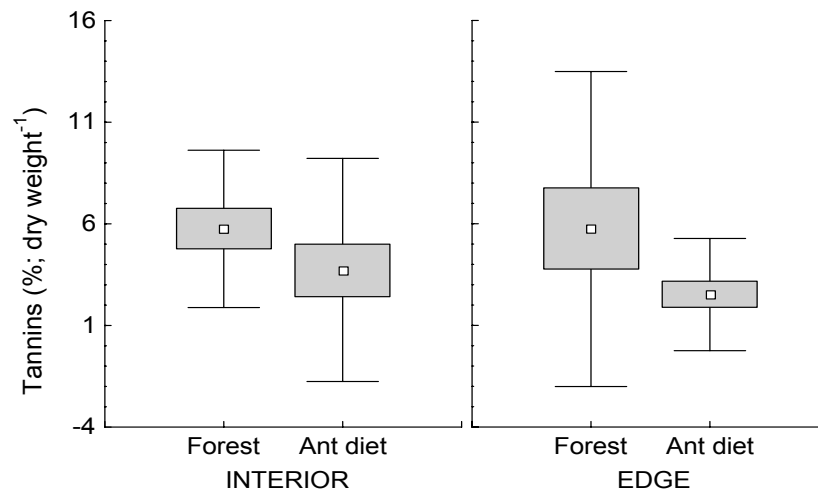


Figure 13. Mean tannin concentration (\pm SE, \pm SD) in the dominant plant species in the forest (FOREST) and in the ant diet (ANT DIET) in two habitats: the interior (INTERIOR) and the edge (EDGE) of the continuous forest. Main effect of FOREST vs. ANT DIET significant at $P = 0.0466$ ($df = 1$, $F = 4.122$). No significant post hoc effects were detected with Tukeys HSD test.

4.3.3 Carbohydrates

In figure 14, one can see a slight trend showing that the concentration of total non-structural carbohydrates (TNC) was somewhat lower in plant species preferred by ants than in those available in the forest, but this trend was not significant. In the forest interior, the dominant species contained an average of 13.6 ± 3.9 % TNC, whereas the ant diet contained only 10.5 ± 2.7 % TNC in this habitat. Similarly, at the forest edge, the species contained 15.2 ± 3.2 % TNC, but the ant diet 13.3 ± 4.8 %.

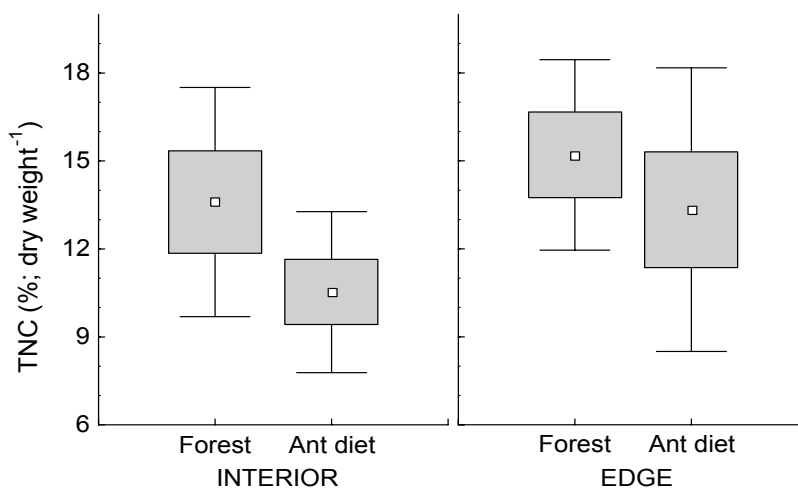


Figure 14. Mean (\pm SE, \pm SD) concentration of the total non-structural carbohydrates (TNC) in the dominant plant species in the forest (FOREST) and in the ant diet (ANT DIET) in two habitats: the interior (INTERIOR) and at the edge (EDGE) of the continuous forest. No significant effects of HABITAT or FOREST vs. ANT DIET detected.

4.4 Discussion

The hypotheses of the study can be generally accepted. In fragmentation-related forest habitats, the vegetation was probably more palatable to LCA. This mainly results from the effect of plant secondary compounds: ants clearly preferred species with lower tannin content and without terpenoids. Plant nutritional quality seemed to be of secondary importance: the carbohydrate content did not differ between the species in the ant diet and those dominant in the forest, neither in the interior nor at the edge of the forest.

All eight terpenoids identified in this study most likely repel *Atta cephalotes*: six terpenoids (caryophyllene, caryophyllene oxide, trans- β -ocimene, humulene, α -cubebene, α -copaene) have been previously shown to exhibit repellency against *Atta* species and two (α -pinene and germacrene-D) against other insect species. Caryophyllene is known to be highly deterrent and toxic to LCA even at very low concentrations (Hubbel *et al.*, 1983; Howard *et al.*, 1988; Howard *et al.*, 1989; Barnola *et al.*, 1994; North *et al.*, 2000). Similarly, caryophyllene oxide repels LCA but only at relatively high concentrations (Hubbel *et al.*, 1983; Hubbel and Wiemer, 1983; Howard *et al.*, 1988; Howard *et al.*, 1989). My results indicate that the natural concentration of caryophyllene found in plants avoided by LCA exceeded the natural concentration of caryophyllene oxide. Therefore, in my study caryophyllene and not caryophyllene oxide was probably one of the terpenoids responsible for repelling LCA. However, this can not be confirmed since I did not evaluate the amount of terpenoids to repel LCA by means of bioassays. Trans- β -ocimene has been shown in laboratory and field bioassays to be a very efficient repellent of LCA (Chen *et al.*, 1984). Barnola and colleagues (1994) found that the host selection in pine plantations by *Atta laevigata* was related to the presence of humulene. Similarly, he noted a dramatic increase in the concentrations of α -cubebene and α -copaene in pines after LCA attack which indicates a strong antiherbivore effect of these compounds. α -pinene and germacrene-D are the major compounds of the resin propolis which is produced by some stingless bee species from the plant tissue to protect their nests against insect attack (Patricio *et al.*, 2002). Because of the difficulties of quantifying the concentration of a volatile substance sampled under field conditions, the absolute concentrations of terpenoids can not be compared with the results gained under precise conditions in laboratory bioassays. However, repellent

effects of the terpenoids found in this study are supported by strong evidences from the other studies.

Terpenoids most probably influenced the LCA diet choice. According to my results, LCA were extremely selective in terms of terpenoids: the top-ranked species in their diet did not contain any terpenoids, regardless of the terpenoids found in the species abundantly available in the surrounding forest. Apart from diet choice, there is also reasonable evidence suggesting that terpenoids influence the LCA diet choice, i.e., the survivorship of LCA colonies in a habitat. One can see from table 3 that only 2 terpenoids were found in the dominant species at the forest edge, whereas ant diet consisted of species containing no terpenoids at all in this habitat. Similarly, the ant diet did not contain terpenoids in the forest interior, but in total 8 different terpenoids were detected in the dominant species here. Moreover, total terpenoid amounts were generally higher in the forest interior than at the edge. This indicates that in the interior of the forest, ants must probably have bigger foraging efforts to find a terpenoid-free diet. Additionally, I observed an interesting pattern concerning ant host plants in the forest interior. Among the dominant species in the forest, those belonging to the families of Moraceae, Lecythidaceae and Euphorbiaceae did not contain terpenoids. Interestingly, representatives of these three families were found in both, in ant diet and in the forest. The occurrence of plant secondary metabolites is known to be specific for families, subfamilies, genera, species or subspecies (Fraenkel, 1959). Therefore one could suggest that the lack of terpenoids is a general characteristic for the families Moraceae, Lecythidaceae and Euphorbiaceae. If so, this indicates that in the forest interior ants have to harvest obligatory on the few terpenoid-free plant families. This gives additional evidence suggesting that the ant diet choice is narrowed and their foraging effort is higher in the forest interior. Therefore, it is reasonable to assume that edge habitats support the survivorship of LCA colonies because of larger diet choice and lower foraging effort.

Similarly to terpenoids, tannin contents were significantly lower in the ant diet species compared to forest species, in both forest interior and edge. This is to say that ants prefer species with a lower tannin content, independently of the type of habitat. Moreover, one can see from figure 13 that at the forest edge ants harvested species with even lower tannin content than in the forest interior, though this trend was not significant. However, if true, this can be explained by the dominance of

pioneer species in edge habitats (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999): pioneers are less defended against herbivory (Coley, 1988) and growing abundantly they permit ants to select diet with low tannin amounts.

The content of carbohydrates did not differ between the plant species preferred by ants and those available in either forest habitat. This indicates that carbohydrates are probably not primarily responsible for LCA diet choice. Interestingly, one can see from figure 14 that in both habitats ants even preferred plants with somewhat lower carbohydrate content than those abundantly available in the forest, but this trend was not significant neither. However, if true, this supports the assumption that in the presence of repellent secondary compounds nutritional quality is of secondary importance to LCA. These results are inconsistent with the literature: Nicols-Orians (1991) studied the acceptability of *Inga oerstediana* seedlings to *A. cephalotes* and found that the ants preferred leaves with high carbohydrate content regardless of the tannin content. Nevertheless, it is possible that the pattern observed by Nicols-Orians (1991) for a single plant species can not be generalized.

Apart from plant physical defense which has been reported to influence LCA populations (e.g., Cherrett, 1972) my results indicate a considerable role of plant secondary metabolites, especially terpenoids, in LCA diet and habitat choice. On the bases of my results, I suggest that a terpenoid-free diet is a “must” for LCA. Furthermore, in the forest interior, at the expense of a terpenoid-free diet, ants even seem to agree with a slightly tannin-richer and carbohydrate-poorer diet than at the forest edge. Apparently, a terpenoid-free diet is more difficult to achieve in the forest interior dominated by late successional plants (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999) that generally contain more defensive compounds (Coley, 1988). Therefore, the foraging effort is bigger in the forest interior and thus ants prefer edge habitats.

5. FRAGMENTATION-INDUCED CHANGES IN LCA DIET BREADTH

5.1 Introduction

Diet breadth is a measure of diet specialization: it describes the range of the resources an organism feeds on. Diet breadth has an evolutionary background: generalist herbivores have adopted themselves to forage on a wide variety of plants whereas specialists rely on limited food resources. However, apart from the evolutionary scale, the 'optimal foraging strategy' predicts that diet breadth can be adjusted to the temporal and spatial changes in food availability (Pyke *et al.*, 1977, Pyke, 1984).

An optimal diet breadth is associated with costs and benefits. Specialized herbivores adopt themselves to a small number of highly palatable species and lose the ability to feed on other species, whereas generalist herbivores feed on a wide range of species but they do so at the cost of lower food quality (Cornell and Hawkins, 2003). Bernays and colleagues (2004) claimed that the possible temporary costs and benefits of diet breadth in phytophagous insects include factors associated with selective attention. The authors show that it may take the generalist herbivores longer than specialists to make decisions since they have potentially greater ranges of cues to evaluate the food, or they must divide attention between alternative foods. Such delays may be expected to involve reduced vigilance with respect to ecological risks such as attack by natural enemies.

LCA are generalist herbivores (Cherrett, 1989). However, they are also known to show strong preferences for some species (e.g., Cherrett, 1968; Rockwood, 1976). For example, LCA uniformly attack the neotropical silvi- and agricultural plantations such as eucalyptus, cotton and cocoa (Cherrett, 1986; Vilela, 1986). Similarly, LCA have been shown to prefer pioneer plant species against late-successional ones (Farji-Brener, 2001; Wirth *et al.*, 2003b). LCA diet breadth can vary with the availability of palatable species: Shepherd (1985) showed that in the habitats with a high density of preferred species a LCA colony specializes on these and reduces its diet breadth and foraging costs at the expense of other species. In a primary forest, Cherrett (1968) found that *Atta cephalotes* attacked ca. 50 % of the species growing in the nearest vicinity of the nest, whereas in a secondary growth forest fragment

Garcia and colleagues (2003) recorded that the diet of *Atta sexdens* consisted of ca. 40 % of the species available in the surrounding forest. On the bases of several studies, Vasconcelos and Fowler (1990) reviewed the 'optimal foraging theory' for LCA and suggested that LCA diet breadth directly depends on the absolute abundance of the "high-ranked" food items: when higher ranked food items are abundant, the diet is more specialized. LCA diet breadth can also vary with the temporal availability of palatable resources caused by the seasonal phenology of the host plants: Wirth and colleagues (1997) noted that in the dry season, *Atta colombica* collected significantly more non-green plant material such as flowers, fruits and stipules. This was in accordance with the flowering and fruiting pattern of the main host species of the colony.

Diet breadth could also drive LCA habitat selection: the survivorship of the colonies might be higher in habitats where the ants encounter a narrower diet breadth and lower foraging costs. LCA colony densities have been observed to increase in forest edges (Wirth *et al.*, 2003a), forest remnants (Rao, 2000; Wirth *et al.*, 2003a) and early-successional forests (e.g., Jaffe and Vilela, 1989; Vasconcelos and Cherrett, 1995; Moutinho *et al.*, 2003), i.e. the habitats that are generally dominated by highly palatable pioneer plant species (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999). I hypothesized that in fragmentation-related habitats like forest edges and small fragments, LCA forage on a few dominant pioneer species which results in a narrower diet breadth. I measured the diet breadth by the means of species richness and diversity (i.e., taking into account the relative proportion of each species) of the harvested plant material.

5.2 Material and methods

5.2.1 Material collection in the field

To estimate the diversity of the plant material harvested by *Atta cephalotes*, samples were collected of the plant particles carried into ant nests. The data was collected and analyzed in co-operation with Falcão (2004). To increase the possibility of encountering a representative sample of the harvested material, sampling was carried out at the time peak of colony activity. The latter was estimated by 24-h counts of the number of leaf fragments carried into nests. At the study site, all *A. cephalotes* colonies were night-active achieving a peak of colony activity around midnight. In a sampling night, the laden ants passing a fixed point close to the entrance of each foraging trail of each colony were collected during 1 min with a small rechargeable vacuum cleaner (Black & Decker V1250). After collection, the vacuum cleaner was shaken gently to induce the ants to drop their loads. Then the vacuum cleaner was opened and the ants were released. The plant material was stored in paper envelopes until reaching the field station. To encounter seasonal patterns in LCA harvest behavior, sampling was repeated in bimonthly intervals during one year, thus resulting in 6 samples per year⁻¹ * colony⁻¹. The number of the fragments of plant material collected during a sampling varied greatly between the colonies and the observed months ranging from 44 to 626 fragments (see also chapter 7.2.1).

The next day, the collected material was divided into fragments of leaves, flowers, fruits and other plant parts. Then, the material was separated into morphospecies on the bases of the surface texture, color and pubescence. Sorting of samples to morphospecies was a suitable method for this study because of the lack of appropriate literature for species identification and the incomplete floristic inventory of the study site by the time of this data collection (see Oliveira, 2003). The morphospecies concept is generally considered to be a sufficiently reliable approach in ecological biodiversity studies; however, it leads to overestimations of the number of species which must be taken into consideration when interpreting the results (e.g., Wirth *et al.*, 1997; Krell, 2004). Species were identified to the lowest taxonomic level possible on the bases of herbarium specimens collected in the study site by Oliveira

(2003). However, due to the incomplete herbarium, it was not possible to identify all species taxonomically.

5.2.2 Estimations of dietary diversity

To express the diversity of plant species in the ant diet, I used the inverse of Simpson's index D (Krebs, 1989):

$$D = \frac{1}{\sum_{i=1}^S (p_i)^2}$$

where S is the number of species, and p_i is the proportional abundance of species i in the diet. Simpson's index is commonly used in ecology as a measure of diversity taking into account the number of species present, as well as the abundance of each species. Simpson's index varies inversely with evenness of the relative abundances of species. Therefore, the inversion of the index is particularly suitable in my context since it measures the ant diet breadth in terms of equally utilized species. The higher the index value, the higher is the evenness of abundances of different species in the diet. The lower the index value, the higher is the relative dominance of the species.

In the case of the taxonomically identified species it was possible to classify them by their growth form (trees, shrubs, herbs, lianas) and regeneration strategy (pioneers vs. late successional species). This was done according to Gentry (1996), Turner (2001) and in co-operation with Oliveira (2003) and Falcão (2004).

5.2.3 Statistical analyses

In the case of species richness and diversity in the diet, data was analysed using STATISTICA 5.1 (StatSoft, 1995). The effects of the habitat (forest interior, edge, and fragment) and the observed month (Sept., Nov., Jan., March, May, July) on the species richness and diversity in the ant diet were studied using Repeated Measures ANOVA. Post hoc comparisons were carried out using Tukeys HSD test for unequal n . The frequencies of resource types, regeneration strategies and growth forms in the ant diet were compared using χ^2 -tests and BioEstat 2.0 (Ayres *et al.*, 2000).

5.3 Results

5.3.1 Species richness in LCA diet

In total, 483 morphospecies were separated in the annual diet of *Atta cephalotes* colonies. The results of ANOVA showed that the number of the monthly harvested morphospecies did not differ between the forest habitats (i.e., forest interior, edge, and fragment; Fig. 15). It turned out that in all habitats a colony forages on an average of 10.3 ± 6.0 host plant species. However, one can see from figure 15 that the number of harvested morphospecies clearly depended on the observed month: in all habitats ants harvested on more morphospecies in the dry season (Sept., Nov., Jan; main effect of MONTH significant at $P < 0.001$, $df = 5$, $F = 9.709$).

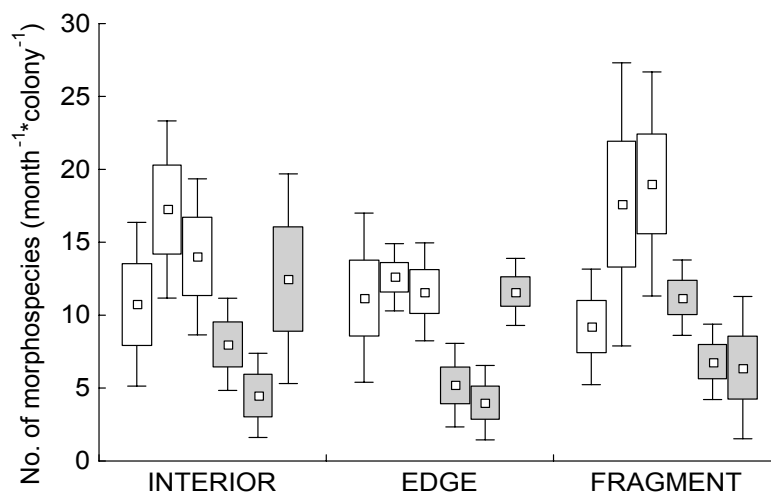


Figure 15. Estimated monthly (Sept., Nov., Jan., March, May, July, respectively) means (\pm SE, \pm SD) of the number of morphospecies harvested by *Atta cephalotes* colonies in interior of the continuous forest (INTERIOR), edge of the continuous forest (EDGE) and interior of the forest fragment (FRAGMENT). Light boxes indicate dry season, grey boxes indicate rainy season. Main effect of MONTH significant at $P < 0.001$ ($df = 5$, $F = 9.709$).

5.3.2 Species diversity in LCA diet

The plant diversity in the ant diet (i.e., taking into account the relative proportion of each species) was significantly influenced by the type of habitat (main effect of HABITAT significant at $P = 0.0453$, $df = 2$, $F = 4.155$; Fig. 16). One can see from figure 16 that the inverse of Simpson's index D was generally lower at the edge of the continuous forest than in the interior of the continuous forest (post hoc comparison marginally significant at $P = 0.0567$). This means that ant diet at the edge of the forest is less diverse, i.e., ants harvest on a few number of dominant species compared to the forest interior where the diet breadth is larger. D in the forest fragment equals to D in the other habitats. Additionally, the ant harvest was significantly influenced by the observed month ($P = 0.00151$, $df = 2$; $F = 4.556$): at the end of the dry season (Nov., Jan) the ant diet breadth was somewhat larger, i.e., ants foraged on a bigger number of dominant species, irrespective of the type of habitat (Fig. 16).

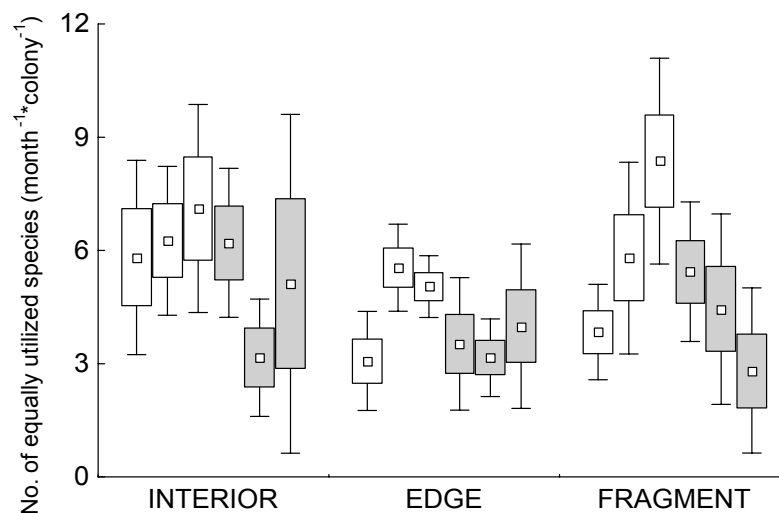


Figure 16. Estimated monthly (Sept., Nov., Jan., March, May, July, respectively) means (\pm SE, \pm SD) of the inverse of Simpson's index D expressed as equally utilized species harvested by *Atta cephalotes* colonies in interior of the continuous forest (INTERIOR), edge of the continuous forest (EDGE) and interior of the forest fragment (FRAGMENT). Light boxes indicate dry season, grey boxes indicate rainy season. main effect of HABITAT significant at $P = 0.0453$ ($df = 2$; $F = 4.155$). Main effect of MONTH significant at $P = 0.00151$ ($df = 2$; $F = 4.556$).

5.3.3 Proportion of different resource types in LCA diet

One can see from figure 17 that in all habitats the ant colonies harvested mostly leaves (total of 92.3 %) and less flowers (total of 5.6 %), fruits (total of 0.5 %) and other plant particles such as petioles or wooden debris (total of 1.6 %). The difference in the frequency of various material in the diet was highly significant ($\chi^2 = 15590.15$, $df = 3$; $P < 0.001$). This obviously results from the high proportion of leaf fragments in the diet (see Fig. 17). However, the frequency was also significantly different between forest habitats ($\chi^2 = 313.678$, $df = 6$, $P < 0.001$). This most probably results from the different harvest frequency of fruits and other plant particles. In the forest interior, the ants harvested remarkably less fruits than in the other habitats. At the edge of the forest, the colonies harvested more other plant particles than in the other habitats (Fig. 17).

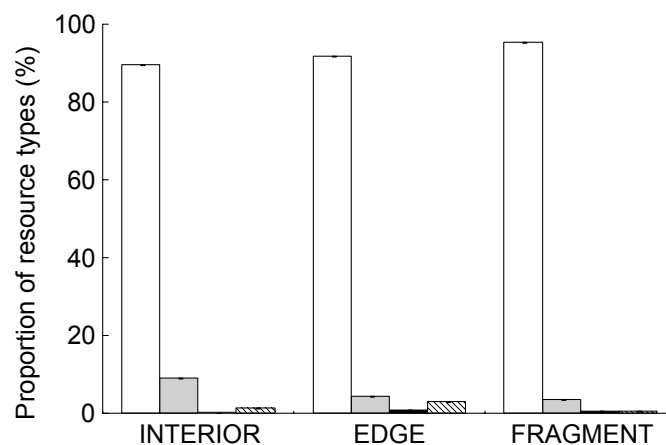


Figure 17. The proportion of leaves (white columns), flowers (grey columns), fruits (black columns) and other plant particles (striped columns) in the annual harvest of *Atta cephalotes* colonies in the interior of the continuous forest (INTERIOR), at the edge of the continuous forest (EDGE) and in the interior of the forest fragment (FRAGMENT). Difference in the relative proportion of growth-forms significant at $P < 0.001$ ($\chi^2 = 15590.15$, $df = 3$). Difference in the proportion in various habitats was not significant ($\chi^2 = 313.678$; $df = 6$; $P < 0.001$).

5.3.4 Taxonomically identified species in LCA diet, their growth form and regeneration strategy

Taxonomically, 92 species from 37 families and 66 genera were identified in the diet of *A. cephalotes* colonies (see appendix I). The most representative families in the ant diet were Melastomataceae and Rubiaceae with eight species per family. These were followed by Euphorbiaceae with seven species, Clusiaceae with five species and Lecythidaceae, Malpighiaceae, Mimosaceae and Moraceae with four species per family.

From the species where the growth form was assignable ($n = 80$), 63 % were trees (Fig. 18; Appendix I). Shrubs, herbs and lianas were less represented (18 %, 12 % and 7 %, respectively). The difference in the relative proportion of the growth forms was significant at $P < 0.001$ ($\chi^2 = 25.282$, $df = 3$). However, the forest habitats did not differ in the proportion of plant growth forms in the ant diet ($\chi^2 = 3.445$, $df = 6$; $P > 0.05$; Fig. 18).

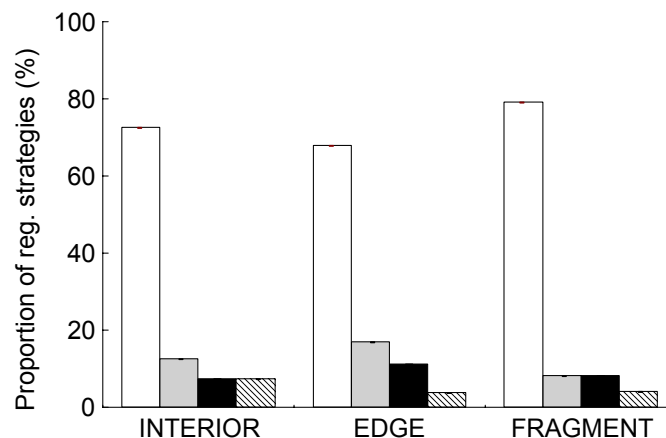


Figure 18. The proportion of trees (white columns), shrubs (grey columns), herbs (black columns) and lianas (striped columns) in the annual harvest of *Atta cephalotes* colonies in the interior of the continuous forest (INTERIOR), at the edge of the continuous forest (EDGE) and in the interior of the forest fragment (FRAGMENT). Difference in the relative proportion of growth-forms significant at $P < 0.001$ ($\chi^2 = 25.282$; $df = 3$). Difference in the proportion in various habitats was not significant ($\chi^2 = 3.445$; $df = 6$; $P > 0.05$).

From the species that could be assigned to a particular regeneration strategy ($n = 86$), most of the species in the ant diet were pioneers (70 %; Fig. 19). Shade tolerant species accounted for 30 % in the diet. This difference was significant at $P = 0.0128$ ($\chi^2 = 6.994$, $df = 1$). Similarly to the growth forms, there was no difference in the frequency of the species with various regeneration strategies in the ant diet in different habitats ($\chi^2 = 2.119$, $df = 2$, $P > 0.05$).

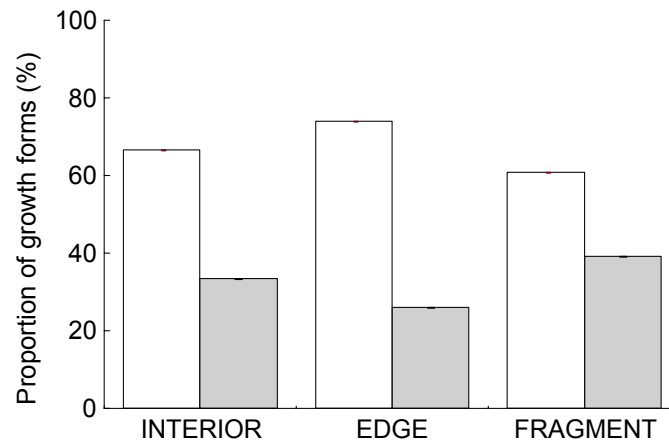


Figure 19. The proportion of pioneer species (white columns) and late successional species (grey columns) in the annual diet of *Atta cephalotes* colonies in the interior of the continuous forest (INTERIOR), at the edge of the continuous forest (EDGE) and in the interior of the forest fragment (FRAGMENT). Difference in the total proportion of pioneers vs. late-successional species significant at $P = 0.0128$ ($\chi^2 = 6.994$; $df = 1$). Difference in the proportion in various habitats was not significant ($\chi^2 = 2.119$; $df = 2$; $P > 0.05$).

5.4 Discussion

My results show that LCA preferred mostly leaves of trees that are considered pioneer species. This is in accordance with what is known so far: LCA have been shown to harvest proportionally more woody than herbaceous species (Blanton and Ewel, 1985) and cut proportionally more leaves than other plant parts (Cherrett, 1968; 1985). A big proportion of pioneer species in the ant diet is consistent with the 'palatable forage hypothesis' *sensu* Farji-Brener (2001) and the studies conducted by Wirth and colleagues (2003b). Farji-Brener (2001) showed that the proportion of pioneer species in the LCA diet is associated with their palatability to ants and not with their availability in the foraging area of the colony. Therefore, the big proportion of pioneers in the ant diet in this study could not directly result from the big abundance of pioneers in the surrounding forest. Furthermore, the proportion of pioneer species in the ant diet was equally high in the fragmentation-related habitats and in the control site, despite the pioneers being more abundant in early successional, disturbed, or fragmented forests (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999). This supports the studies of Peñaloza and Farji-Brener (2003) who found that in old-growth forests which are dominated by late successional species, LCA might predominantly forage in sites where pioneers are abundant such as treefall gaps occasionally scattered in the forest.

The results do not support my hypothesis that species richness in the diet of *Atta cephalotes* is smaller in fragmentation-related habitats like forest edges and small fragments. On the contrary, species richness in the ant diet was not influenced by the type of habitat. The lack of significant variation in dietary richness might be explained by the scouting behavior (e.g., Farji-Brener and Sierra, 1998) of these generalist herbivores. Despite definite preferences in host plants LCA seem to be permanently testing the quality of new resources, a phenomenon which can be observed by the occurrence of few leaf fragments of some species in every sample of the harvest (personal observations, Wirth *et al.*, 2003b). Shepherd (1982; 1985) suggests that LCA scouting is an attribute of optimal foraging assuring quick localization of palatable substrate patches in time and space. I suggest that irrespective of their abundance in the ant diet, leaf fragments of the species harvested during scouting inevitably count for the species richness in the ant diet thus representing a 'noisy' factor in the analyses. Therefore, species richness is not

a suitable method for estimating the diet breadth of a generalist herbivore. Additionally, the use of the morphospecies concept during data collection might play a role here, because identification is known to cause overestimations in the number of species and may thus lead to inaccuracy (Krell, 2004). The high number of inaccurate species might have concealed the possible variations in species richness.

The second hypothesis can be partly accepted. LCA dietary diversity was lower (i.e., diet breadth was narrower) at the edge of the forest than in the control habitat. Low dietary diversity indicates that ants forage on few dominant host plant species in this habitat, with few species accounting for the bulk of the total harvest. This is a feature of the selective behavior of LCA foraging (e.g., Cherrett, 1968; Rockwood, 1976): despite being generalist herbivores, the ants select resources of highest quality and concentrate on them. Low dietary diversity in the edge habitat is in accordance with the 'palatable forage hypothesis': early successional, disturbed, or fragmented forests are dominated by pioneer species (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999) and LCA prefer pioneers in their diet (Farji-Brener, 2001; Wirth *et al.*, 2003b). Therefore, high density of preferred species in the edge habitats allows ants to specialize on these species and thus results in a narrow diet breadth (reviewed in Vasconcelos and Fowler, 1990). Furthermore, foraging on abundant host species presumably decreases foraging costs of the colony compared to foraging costs in a late successional forest where pioneers are rare. Consequently, decreased foraging costs caused by narrow diet breadth might help to explain the ants' preference for edge habitats, which has been observed as an increase in LCA colony densities in forest edges (Wirth *et al.*, 2003a). However, no changes in dietary diversity were observed in the studied forest fragment compared to the control habitat. This might be a special characteristic of this particular forest fragment: the fragment is an old remnant of primary forest and thus still has a considerable proportion of late successional species (M. Oliveira and M. Tabarelli, personal communications). Moreover, LCA colonies in the forest fragment showed a considerable variation in their diet breadth (observed as big standard variations in figures 15 and 16) whereas the colonies at the edge of the continuous forest were remarkably similar in their diet. This might be another corroboration suggesting that the studied forest fragment is not uniformly dominated by LCA host plants, thus ants prefer to forage in occasional pioneer-rich sites such as treefall gaps (Peñaloza and Farji-Brener, 2003). A gap might favor the colonies located to its nearest vicinity and

be of minor importance to distant colonies, thus resulting in variations in the diet of the colonies.

Additionally, both richness and diversity in the ant diet were higher in the dry season. This could have various reasons. A narrower diet breadth in the rainy season could result from lower absolute harvest rates (see chapter 7.3.1) caused by the negative effect of rainfall on LCA harvest (Wirth *et al.*, 1997; personal observation). Alternatively, Hubbel and colleagues (1984) and Howard (1987) have suggested that the seasonality in LCA harvest might be associated with the abundance of plant secondary metabolites. They noted a dramatic decline in the synthesis of antifungal secondary metabolites in the dry season, when the risk of fungal attack is low. Consequently, one could hypothesize that, due to the low concentrations of repellent secondary compounds, LCA forage on a higher numbers of host plant species in the dry season.

6. FRAGMENTATION-INDUCED CHANGES IN LCA FORAGING AREAS

6.1 Introduction

One of the cornerstones of understanding animal foraging has been the assumption that species adopt their foraging behavior to local conditions under the pressure of natural selection. The 'optimal foraging theory' claims that animals adopt their behavior to achieve a maximum foraging efficiency and will be thus favored on an evolutionary time scale (Pyke *et al.*, 1977; Pyke, 1984). For social insects, optimal foraging is achieved by collectively adjusting their recruitment behavior and foraging trail systems to meet the needs of the superorganism (Hölldobler and Lumsden, 1980).

LCA have developed a complex foraging behavior which is understood as a long term optimization that effectively exploits palatable resources over the lifetime of the colony (Shepherd, 1982). A LCA colony uses relatively persistent foraging trails (trunk trails) to direct ant workers from the nest to patchily distributed resources. Trunk trails are accompanied by ephemeral trails which serve for searching new resources. Consequently, LCA foraging trails change in length, orientation and branching, depending on the spatial and temporal resource availability. Foraging trails are encompassed by the foraging area, thus the foraging area reflects the spatial orientation of the trails. The foraging area also serves to protect the colony's resources from competitors (Fowler and Stiles, 1980). The optimal foraging theory proposes a trade-off between costs and benefits of foraging. In case of the LCA the costs and benefits include the energy and time needed for trail construction and the quality and distance of plant resources (e.g., Howard, 1991). This allows to hypothesize that in any habitat and under any local conditions, a colony possesses an energetically optimized foraging distance, trail length and foraging area.

Several authors have estimated foraging of LCA colonies (Mintzer, 1979; Rockwood and Hubbel, 1987; Vasconcelos, 1990a; Rao *et al.*, 2001; Wirth *et al.*, 2003b) using various concepts to determine the size of the foraging area. Most commonly, the foraging area has been defined by graphically joining the ends of foraging trails and using geometrical shapes to calculate the area (Mintzer, 1979;

Rockwood and Hubbel, 1987; Rao *et al.*, 2001). Wirth and colleagues (2003b) compared three approaches to estimate the foraging area as a rectangle, ellipse or polygon around mapped foraging trails. They showed that the size of the area depends much on the used form and suggested a polygon as the most appropriate form. This idea is based on the observation that even during one year of monitoring, a LCA colony forages in four permanent foraging sectors leaving the rest of the forest untouched. Consequently, one could separately outline the foraging sectors with polygons and sum them to gain a more adequate size of the foraging area.

So far, the studies on foraging areas of LCA colonies were conducted in a single habitat type. Foraging areas have never been estimated in fragmented vs. continuous forests. It is a well-established fact that fragmented forests are dominated by pioneer plant species (e.g., Laurance *et al.*, 1998b; Hill and Curran, 2001) and that LCA prefer pioneer species against late-successional ones (Farji-Brener, 2001; Wirth *et al.*, 2003b). Consequently, I hypothesize that LCA adjust their foraging to changing environmental conditions: given there are abundantly palatable resources available in the vicinity of the nest in fragmented habitats, the ants use smaller foraging areas.

6.2 Material and methods

6.2.1 Estimations of trail length and foraging area

To estimate the foraging area of *A. cephalotes* colonies, the foraging trails of each colony were measured and mapped during one night at bimonthly intervals at the time peak of the colonies' activity (see chapter 5.2.1). Because of the LCAs habit to persistently use defined trunk trails (Wirth *et al.*, 2003b), one night of data collection every two months delivered representative information. During sampling, all active foraging trails were followed and charted by measuring the compass bearing and the length of trails until reaching the harvesting spot (e.g., standing tree or flowers and fruits lying on the ground). The trails were then digitalized with the help of the CorelDRAW software. The colony foraging area was defined as a convex polygon within 20 m distance around all digitalized trails. I used the 20 m distance as an approximation of the mean size of LCA harvesting zones along the foraging trails (see for example Wirth *et al.*, 2003b). The cumulative annual foraging area of a colony was estimated by plotting the digitalized monthly foraging areas on top of each other.

6.2.2 Statistical analyses

All data was analysed using STATISTICA 5.1 (StatSoft, 1995). The effects of the habitat and the time on the measured parameters (total length of active foraging trails, size of foraging area) were studied using Repeated Measures ANOVA. Post-hoc comparisons were carried out using the Tukeys HSD test for unequal n . Both the length of foraging trails and the size of foraging areas were adjusted to a normal distribution by natural log transformations.

6.3 Results

6.3.1 Spatial pattern and length of foraging trails

The development of the foraging trails of all *A. cephalotes* colonies at bimonthly intervals in the course of one year and the cumulative annual foraging distance are documented in appendix II. Strikingly, the figures reveal some differences in the spatial pattern of the trail system in different forest habitats. In the interior of the continuous forest, the foraging trails of the colonies are spatially more dispersed denoting various foraging directions whereas the trails at the edge of the continuous forest and in the forest fragment seem to be more clumped leading to common foraging sites.

The colonies had, in average, the longest foraging trails in the interior of the continuous forest (main effect of HABITAT significant at $P = 0.0106$, $df = 2$, $F = 7.0793$; Fig. 20). There, the foraging distance of a colony was in total 230 ± 125 m long. The mean foraging distance at the edge of the continuous forest and in the forest fragment was about half as long (108 ± 52 m, 117 ± 87 m, respectively). Additionally, the length of the trails depended on the observed month (Main effect of TIME significant at $P < 0.001$; $df = 5$; $F = 11.728$). One can see from figure 20 that the trails were longest at the end of the dry season (January - March). However, the interaction HABITAT*TIME was also highly significant ($P = 0.00175$; $df = 10$; $F = 3.370$), indicating that the pattern of yearly development of the trail length was influenced by a particular habitat.

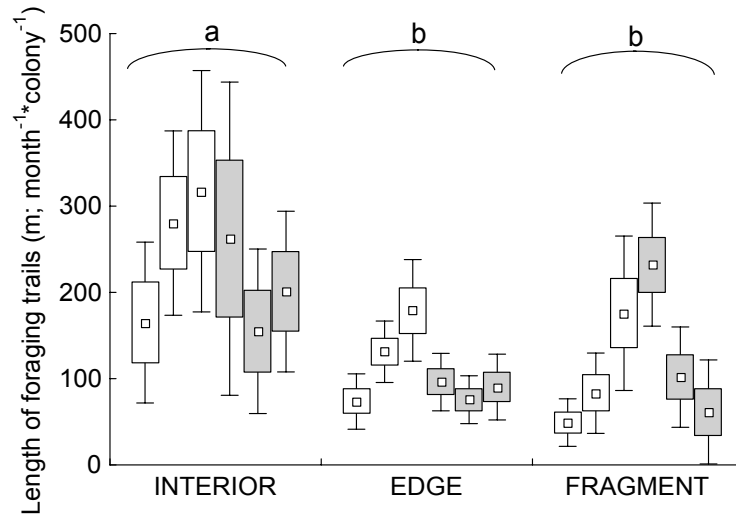


Figure 20. Mean total length (\pm SE, \pm SD) of active foraging trails of *A. cephalotes* colonies measured at bimonthly intervals (Sept., Nov., Jan., March, May, July, respectively) in the interior of the continuous forest (INTERIOR), edge of the continuous forest (EDGE) and the forest fragment (FRAGMENT). Main effect of HABITAT significant at $P = 0.0106$ ($df = 2$; $F = 6.963$). Main effect of TIME significant at $P < 0.001$ ($df = 5$, $F = 11.728$). Interaction HABITAT*TIME significant at $P = 0.00175$ ($df = 10$, $F = 3.370$). Light boxes indicate dry season, black boxes indicate rainy season. Different letters on the graph denote significant ($P < 0.05$) differences between habitats (Tukeys HSD post-hoc test).

6.3.2 Size of foraging area

The monthly development of the size of a colony foraging area followed the pattern observed for the trail length development (Fig. 20, 21). Similarly to the trail length, the size of the foraging area depended significantly on the type of habitat (main effect of HABITAT significant at $P = 0.0196$, $df = 2$, $F = 5.741$; Fig. 21). Ant colonies established largest foraging areas in the interior of the continuous forest, with an average of $9284 \pm 4046 \text{ m}^2$. At the edge of the continuous forest, foraging areas were about half as big ($5263 \pm 1347 \text{ m}^2$). However, the size of foraging areas in the forest fragment ($5979 \pm 2678 \text{ m}^2$) did not differ significantly from that in other habitats (post-hoc test; Fig. 21). The colonies used bigger foraging areas at the end of the dry season and in the beginning of the wet season (Jan.-March; main effect of TIME significant at $P < 0.001$, $df = 5$, $F = 13.353$). Nevertheless, the pattern of monthly development of foraging areas depended on the observed habitat (interaction HABITAT*TIME significant at $P = 0.00184$ ($df = 10$, $F = 3.350$)).

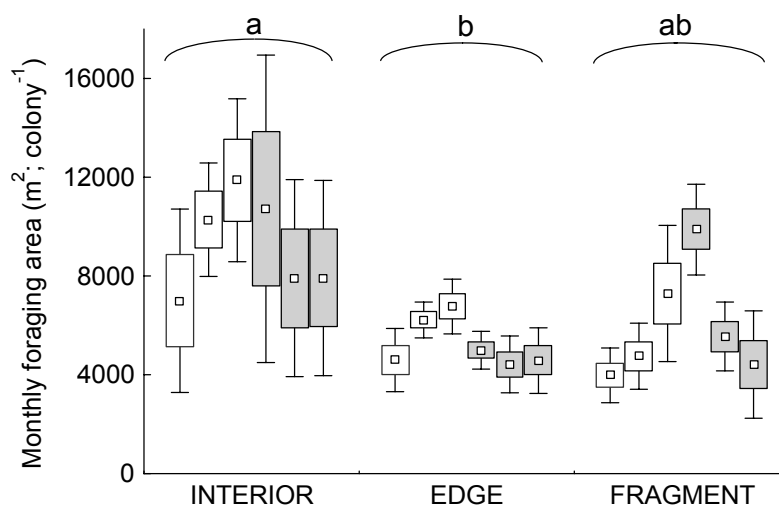


Figure 21. Mean foraging area (\pm SE, \pm SD) of *A. cephalotes* colonies measured at bimonthly intervals (Sept., Nov., Jan., March, May, July, respectively) in the interior of the continuous forest (INTERIOR), edge of the continuous forest (EDGE) and the forest fragment (FRAGMENT). Main effect of HABITAT significant at $P = 0.0196$ ($df = 2$, $F = 5.741$). Main effect of TIME significant at $P < 0.001$ ($df = 5$, $F = 13.353$). Interaction HABITAT*TIME significant at $P = 0.00184$ ($df = 10$, $F = 3.350$). Light boxes indicate dry season, black boxes indicate rainy season. Different letters on the graph denote significant ($P < 0.05$) differences between habitats (Tukeys HSD post-hoc test).

The annual foraging area of the colonies was significantly influenced by the type of habitat (main effect of HABITAT significant at $P = 0.0121$, $df = 2$, $F = 13.150$; Fig. 22). In the interior of the continuous forest, the ants annually foraged on an area of about 2.4 ± 1.0 ha, whereas at the edge of the continuous forest and in the forest fragment the foraging areas were only about half as big (1.0 ± 0.1 and 1.3 ± 0.7 ha, respectively).

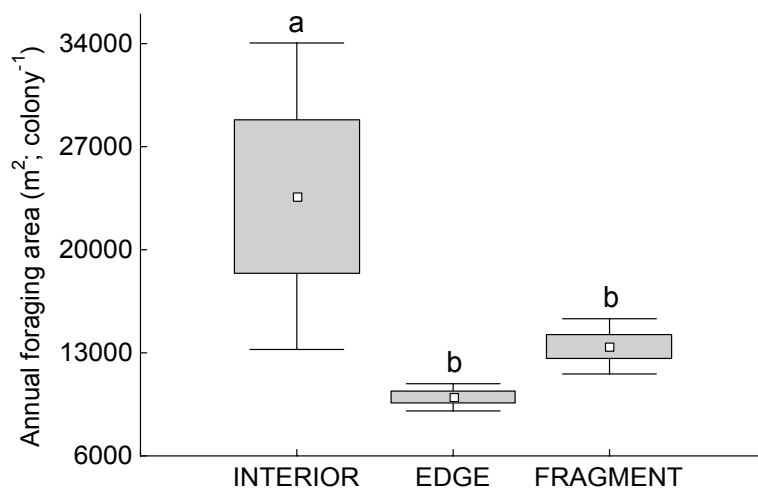


Figure 22. Mean annual foraging area (\pm SE, \pm SD) of *A. cephalotes* colonies in the interior of the continuous forest (INTERIOR), edge of the continuous forest (EDGE) and the forest fragment (FRAGMENT). Main effect of HABITAT significant at $P = 0.00121$ ($df = 2$, $F = 13.150$). Light boxes indicate dry season, black boxes indicate rainy season. Different letters on the graph denote significant ($P < 0.05$) differences between habitats (Tukeys HSD post-hoc test).

6.4 Discussion

The proposed hypothesis of this study should be accepted. The foraging distance of *A. cephalotes* colonies was clearly influenced by forest fragmentation. LCA foraging trails were significantly shorter and the corresponding foraging areas generally smaller at the edge of the continuous forest and in the forest fragment when compared to the control habitat (i.e., interior of the continuous forest). Additionally, the digitalized images of the foraging trails revealed a more dispersed spatial pattern of foraging trails in the interior of the continuous forest.

So far, foraging areas of LCA have never been estimated in fragmented vs. continuous forests. Several authors have measured LCA foraging areas (Mintzer, 1979; Vasconcelos, 1990a; Rao *et al.*, 2001; Wirth *et al.*, 2003b), however, these studies were restricted to a single habitat. Various concepts exist to determine the size of the foraging area of a LCA colony (see Wirth *et al.*, 2003b). Wirth and colleagues (2003b) observed that a colony of *A. colombica* on Barro Colorado Island, Panama, forages in defined foraging sectors, and therefore recommended an appropriate estimation of foraging area using defined sectors (polygons). However, this approach could not be used in the present study, because the colonies did not reveal defined foraging sectors (see appendix II). In this study, I defined the foraging area as a convex polygon within a distance of 20 m around all foraging trails. Wirth and colleagues (2003b) did not quantify the size of monthly foraging areas of LCA, therefore the monthly values cannot be compared with my study. Interestingly, the monthly foraging areas of the colonies observed in my study were in average only half as big as the respective annual foraging areas. This refers to a weak spatial persistence of foraging trails in the course of a year, i.e. the colonies observed in my study use less conservative foraging sectors. The annual LCA foraging area estimated by Wirth and colleagues is only about half as big (1.03 ha) as the annual foraging areas of the colonies in the interior of the continuous forest in my study (2.4 ± 1.0 ha). Nevertheless, it corresponds to the size of foraging areas in the fragmentation-related habitats of my study (1.0 ± 0.1 ha at forest edge, 1.3 ± 0.7 ha in the forest fragment). This can be a result of the relatively high abundance of pioneer plant species in the study location in Panama (see Wirth, *et al.*, 2003b) which approximates this study site to fragmentation-related forests.

Small foraging areas and shorter foraging trails in the fragmentation-related habitats can be well explained by a high availability of pioneer species in these habitats (Laurance *et al.*, 1998b; Hill and Curran, 2001), which are shown to be highly palatable to LCA (Farji-Brener, 2001). Consequently, in fragmented habitats, ants do not have to move far to find their host species and thus, they possess smaller foraging areas and shorter trails. Similarly, the dispersed spatial pattern of foraging trails in the interior of the continuous forest refers to a poor abundance of ant host plants in this habitat: instead of foraging in aggregated foraging sites close to the nest ants travel big distances in various directions to seek for suitable host plants. This is in good accordance with the optimal foraging theory: LCA plastically adjust their foraging behavior to local conditions to efficiently exploit the resources and thus meet the needs of the colony.

Small foraging areas in the fragmentation-related habitats refer to decreased foraging costs: small foraging distance inevitably saves energy for a colony. Low foraging costs caused by short foraging distance could help to explain high densities of LCA colonies in forest edges (Wirth *et al.*, 2003a), forest remnants (Rao, 2000; Wirth *et al.*, 2003a), and early successional forests (e.g., Jaffe and Vilela, 1989; Vasconcelos and Cherrett, 1995; Moutinho *et al.*, 2003). Additionally, LCA are known to avoid overlapping foraging areas of neighbouring colonies (Rockwood, 1973; Fowler, 1984) which determines a LCA colony survivorship and population density in the habitats. Therefore, I hypothesize that the reduction of LCA foraging areas in fragmentation-related forests increases the carrying capacity of these habitats to support more colonies per area.

The results indirectly support the considerable role of bottom-up forces (i.e., availability of suitable host plants) in the regulation of LCA populations. Small colony foraging areas, shorter foraging trails and clumped spatial patterns of the trails at the edge of the continuous forest and in the forest fragment refer to a high abundance of palatable host plants and thus a weak bottom-up control on LCA colonies in these habitats.

7. FRAGMENTATION-INDUCED CHANGES IN LCA HERBIVORY RATE

7.1 Introduction

Herbivores play a key role in mediating the relationship between plants and environment and thus have a huge impact on every ecosystem (Howe and Westley, 1993). In terrestrial ecosystems, they can consume a sufficiently large proportion of primary production (estimated median, 18 %) to regulate the plant biomass (Cyr and Face, 1993). Herbivores represent an important factor in energy and nutrient cycles: for example, insect herbivores in forest canopies influence soil processes (decomposition, respiration, nutrient availability) by introducing materials from the canopy to the forest floor (Rinker *et al.*, 2001).

The impact of herbivores in terrestrial systems is known to increase with increasing net primary productivity (Cyr and Face, 1993). In a major review of plant-animal interactions in 51 terrestrial ecosystems, McNaughton and colleagues (1989) found that the biomass of plant-eating animals is an increasing function of the aboveground primary production. Therefore, herbivory has a particular importance in tropical productive ecosystems. Coley and Barone (1996) estimated significantly higher rates of herbivory in tropical compared to temperate forests: in tropical forests, herbivores consume up to 11 % of the annual leaf production compared to 7 % in temperate forests. Insects are considered the most pronounced herbivores in tropical forests (Leigh, 1999), they are believed to be responsible for up to 75% of the annual herbivory damage to tropical forests (Coley and Barone, 1996).

Regrettably, despite the crucial position of herbivores in the tropical ecosystems and the increasing loss of tropical forests (Whitmore, 1997; Gascon *et al.*, 2001) there is only limited knowledge of how herbivory is affected by forest fragmentation. Few works exist which study plant-herbivore interactions in fragmented landscapes (but see Brown and Hutchings, 1997; Benitez-Malvido *et al.*, 1999; Rao *et al.*, 2001; Arnold and Asquith, 2002; Thies *et al.*, 2003). Most commonly, herbivore abundance and plant damages were found to increase in fragmented habitats (Brown and Hutchings, 1997; Rao *et al.*, 2001; Arnold and Asquith 2002).

LCA are the dominant herbivores in the neotropics (Wilson, 1986). Similarly to other herbivore groups, the abundance of LCA colonies has been reported to increase in fragmentation-related forest habitats: in forest edges (Wirth *et al.*, 2003a), forest remnants (Rao, 2000; Wirth *et al.*, 2003a), and early-successional forests (e.g., Jaffe and Vilela, 1989; Vasconcelos and Cherrett, 1995; Moutinho *et al.*, 2003). However, no information is available on how the herbivory pressure of LCA might change in these habitats compared to continuous forests. Since (1) LCA have been shown to prefer pioneer plant species against late-successional ones (i.e., the 'palatable forage hypothesis' *sensu* Farji-Brener, 2001) and (2) pioneers are more abundant in early-successional, disturbed, or fragmented forests (Laurance *et al.*, 1998b; Tabarelli *et al.*, 1999), it is reasonable to expect that the herbivory pressure by LCA increases through forest fragmentation. Quite logically, if LCA are provided with more suitable plant material in habitats created by fragmentation, they should harvest more. Similarly, the LCA herbivory rate (i.e., the relative proportion of leaves removed from the forest canopy) should increase in pioneer-dominated fragmented habitats.

Wirth and colleagues (2003b) have suggested various methodological approaches to estimate the LCA herbivory rate. Measuring herbivory at the landscape level provides an approximation of the herbivory pressure on the plant community. However, an important assumption here is the precise estimation of the density of LCA colonies in the landscape. Studies at LCA colony level provide an insight into herbivore damages in the direct foraging area of a colony.

In this study, I investigated whether both the LCA absolute leaf harvest and herbivory rate at a colony level are affected by fragmentation and habitat loss. I hypothesized that (1) the LCA leaf harvest, and (2) the herbivory rate is higher at the edge of the continuous forest and in the forest fragment compared to the interior of the continuous forest (i.e., control habitat).

7.2 Methods

7.2.1 LCA leaf harvest

The data of the LCA leaf harvest was collected and analysed in co-operation with Araújo (2004). To assess the absolute leaf harvest of *A. cephalotes* colonies, we estimated the number of leaf fragments carried into each LCA nest during one year. A regression model was created on the basis of 24-h counts of the number of leaf fragments carried into nests of seven randomly chosen colonies ($y = 672.45 * x - 14863$; $r^2 = 0.917$, $P = 0.00362$). The objective of the regression was to predict daily totals of the colony harvest from 5-min counts during the time peak of foraging activity as described by Wirth and colleagues (1997).

In the studied colonies, we counted laden ants passing a fixed point close to the entrance of each foraging trail during 5 minutes at the time peak of colony activity. The measurements were repeated at bimonthly intervals for one year, thus resulting in 6 samplings per year⁻¹ * colony⁻¹. The number of the leaf fragments collected during a sampling varied greatly between the colonies and the observed months ranging from 122 to 3038 fragments. From the harvest at the time peak of foraging, a colony daily harvest was estimated with the help of the regression model as described above. The daily harvest rates were extrapolated to achieve bimonthly values for the corresponding two months.

To calculate the harvested foliage area, the number of the leaf fragments cut by a colony was multiplied by the mean fragment area determined for each colony. For this, an area of 300 random leaf fragments per colony was measured twice a year with the help of a Li-Cor leaf area meter (model LI 3050 A).

7.2.2 LCA herbivory rate

The herbivory rate of *A. cephalotes* colonies was estimated *sensu* Wirth and colleagues (2003b) as the harvested proportion of the standing foliage (see chapter 3.2.2) in the annual foraging area of a colony (see chapter 6.2.1). The annual foraging area provides the most reliable approximation of LCA foraging because of the weak spatial persistence of the foraging trails of the studied colonies in the course of a year (see chapter 6.4). I did not account for compensatory growth as a

plant response following ant herbivory (Trumble *et al.*, 1993). Therefore, to assure conservative estimates of the herbivory rate, the proportion of the leaf area harvested was added to the standing foliage.

7.2.3 Statistical analyses

Data was analysed using STATISTICA 5.1 (StatSoft, 1995). The effect of the habitat (the interior of the continuous forest, the edge of the continuous forest, the forest fragment) and the observed month (Sept., Nov., Jan., March, May, July) on leaf harvest and herbivory rate was studied using Repeated Measures ANOVA. Post hoc comparisons were carried out using the Tukeys HSD test for unequal n .

7.3 Results

7.3.1 LCA leaf harvest

The quantity of leaf material harvested by *A. cephalotes* colonies varied almost four-fold from 283 ± 227 to $1016 \pm 299 \text{ m}^2 \cdot \text{colony}^{-1} \cdot \text{month}^{-1}$. Despite considerable variation across colonies in a given habitat, the leaf harvest of LCA colonies was not significantly different among forest interior, edge, and fragment (Fig. 23). On the other hand, the leaf harvest was significantly affected by the month of the year (main effect of MONTH significant at $P < 0.001$, $df = 5$, $F = 7.711$), showing a clear seasonal pattern with an increase during the dry season and a peak in January across all habitats (Fig. 23).

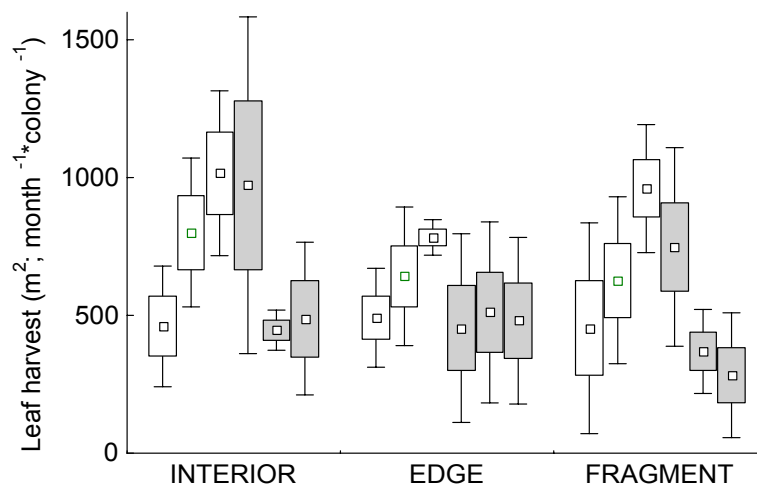


Figure 23. Estimated monthly (Sept., Nov., Jan., March, May, July, respectively) means (\pm SE, \pm SD) of leaf harvest of *Atta cephalotes* colonies in the forest interior, edge and fragment. Main effect of MONTH significant at $P < 0.001$ ($df = 5$, $F = 7.711$). Light boxes indicate dry season, grey boxes indicate rainy season.

7.3.2 LCA herbivory rate

The herbivory rate of *A. cephalotes* colonies was significantly influenced by the type of habitat (main effect of HABITAT significant at $P = 0.0221$, $df = 2$, $F = 5.50$; Fig. 24). The colonies at the edge of the continuous forest revealed the highest monthly herbivory rate. There, ant colonies removed 1.4 ± 0.7 % of leaf area from the available foliage in their annual foraging area. In the interior of the continuous forest, the herbivory rate was about half as big (0.7 ± 0.4 %) as at the edge (see post hoc comparisons; Fig. 24). In the forest fragment, the LCA herbivory rate did not differ from the herbivory rates in the other habitats (Fig. 24). Additionally, the herbivory rate depended on the observed month (main effect of MONTH significant at $P < 0.001$; $df = 5$, $F = 5.305$): one can see from figure 24 that in all habitats, the ant herbivory rate was the highest at the end of the dry season (January - March).

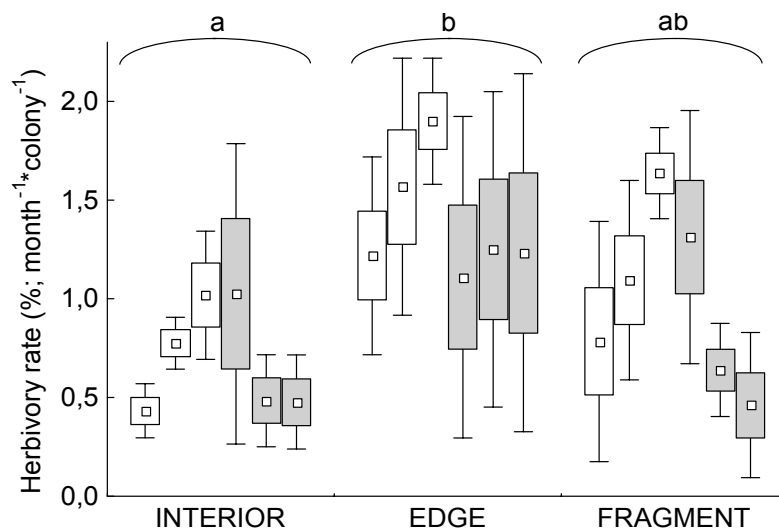


Figure 24. Estimated monthly (Sept., Nov., Jan., March, May, July, respectively) means (\pm SE, \pm SD) of herbivory rate of *Atta cephalotes* colonies in the forest interior, edge and fragment. Main effect of HABITAT significant at $P = 0.0221$ ($df = 2$, $F = 5.50$). Main effect of MONTH significant at $P < 0.001$ ($df = 5$, $F = 5.305$). Light boxes indicate dry season, grey boxes indicate rainy season. Different letters on the graph denote significant ($P < 0.05$) differences between habitats (Tukeys HSD post hoc test).

7.4 Discussion

The results do not support my first hypothesis of a reduced leaf harvest at the forest edges and fragments as compared to the control (i.e., the forest interior). Intuitively, ants could make use of the high availability of host plants and harvest greater quantities of biomass in these habitats. However, according to my findings, a colony cuts an equal amount of plant material (monthly average of $610 \pm 270 \text{ m}^2$) in all studied habitats. A possible explanation for the phenomenon is that the harvesting capacity of adult colonies has reached its limit, and hence they do not increase leaf harvest even if higher proportions of palatable resources are available. So far, the leaf harvest of LCA has never been estimated in fragmented vs. non-fragmented forest habitats. Nevertheless, the measured values of the monthly leaf harvest of a colony are consistent with the estimations done by other authors in a single habitat type. In early-successional habitats, Blanton and Ewel (1985) estimated the mean leaf harvest of *A. cephalotes* colonies of about $642 \text{ m}^2 \cdot \text{month}^{-1}$. In a relatively intact forest on BCI, Panama, Wirth and colleagues (2003b) estimated the monthly leaf harvest of two *A. colombica* colonies to reach an average of 321 m^2 and 142 m^2 , respectively. The low harvest values recorded by Wirth and colleagues might result from considering a different species of LCA. Additionally, I detected a significant seasonal variation in LCA harvest: the colonies cut significantly more vegetation in the end of the dry season (see also Araújo, 2004). A lower harvest rate in the wet season could result from the negative effect of rainfall on LCA harvest: during heavy rain showers LCA are observed to drop their loads and cease the foraging activity (Wirth *et al.*, 1997; personal observation).

The second hypothesis of the study should be accepted. The LCA herbivory rate was clearly affected by forest fragmentation. It was significantly higher at the edge compared to the interior of the continuous forest. Since the herbivory rate was determined by (1) the leaf harvest, (2) the size of the foraging area, and (3) the availability of the leaf area, the increased herbivory rate resulted from two parameters: a considerable reduction of the colony foraging area (see Fig. 22) and a slight but significant decrease of the mean LAI at the forest edge and in the fragment (see Fig. 9). Smaller LAI values reflect smaller foliage availability to LCA and thus the proportion of the removed foliage, i.e., LCA herbivory rate, inevitably increases.

Several attempts have been made to estimate LCA herbivory rates (Lugo *et al.*, 1973; Haines, 1978; Blanton and Ewel, 1985; Wirth *et al.*, 2003b). However, the results are difficult to compare because of the different scales and the methodological approaches used (e.g., measuring herbivory at plant-, colony- or landscape level). In this study, the herbivory rate was measured at the colony level and defined as the proportion of the leaf area removed from the standing foliage within the colony's foraging area (*sensu* Wirth *et al.*, 2003b). The monthly mean herbivory rates of 1.7 % - 2.6 % correspond well to the annual herbivory rate of 12.5 % measured by Wirth and colleagues (2003b) for an adult colony of *A. colombica*.

I am well aware that my findings from a single forest fragment may suffer from the lack of independent replication. However, if they represent a general pattern, the increased LCA herbivory rates in fragmentation-related habitats could help to explain the increase observed in LCA colony densities in forest edges (Wirth *et al.*, 2003a), forest remnants (Rao, 2000; Wirth *et al.*, 2003a), and early-successional forests (e.g., Jaffe and Vilela, 1989; Vasconcelos and Cherrett, 1995; Moutinho *et al.*, 2003). According to my results, a colony in a fragmentation-related habitat possesses a smaller foraging area but harvests the same amount of plant material as within a larger foraging area in a continuous forest. I further hypothesize that in fragmented habitats colonies use the surplus of energy resulting from a reduced foraging effort to increase the colony growth, the reproduction and turnover. If correct, this explains why fragmented habitats support more LCA colonies at a given time compared to continuous forest habitats. As a consequence, further studies are urgently needed to estimate LCA colony growth and turnover rates. At my study site, Costa (2003) found no significant variation in the growth rate of *A. cephalotes* colonies in fragmentation-related forest habitats (i.e., edge of the continuous forest, 50-ha forest fragment) compared to the control habitat. However, the study was carried out in the course of 12 months only. I suggest that the changes in the growth rate of LCA colonies should be observed over a longer time scale.

8. CONCLUDING REMARKS

THE IMPACT OF BOTTOM-UP CONTROL IN LCA POPULATIONS IN FRAGMENTED FORESTS

In this study, I evaluated the hypothesis that bottom-up control (i.e., availability of host plants) of LCA populations is less effective in fragmentation-related habitats (i.e., forest edges and small fragments) than in continuous forests. In order to test this, I proposed four working hypotheses. I hypothesized that LCA colonies in fragmented habitats (1) find more palatable vegetation due to low plant defences, (2) forage on few dominant species resulting in a narrow diet breadth, (3) possess small foraging areas and (4) increase the herbivory rate at the colony level. On the bases of the results, all hypotheses can be generally accepted. The results indicate that the abundance of LCA host plant species in the habitats created by forest fragmentation along with weaker chemical defense of those species (especially the lack of terpenoids) allow ants to forage predominantly on palatable species and thus reduce foraging costs on other species. This is supported by a narrower ant diet breadth in these habitats. Similarly, small foraging areas in edge habitats and in small forest fragments indicate that there ants do not have to move far to find the suitable host species and thus save foraging costs. Increased LCA herbivory rates indicate that the damages (i.e., amount of harvested foliage) caused by LCA are more important in fragmentation-related habitats which are more vulnerable to LCA herbivory due to the high availability of palatable plants and a low total amount of foliage (LAI). (1) Few plant defences, (2) a narrower ant diet breadth, (3) reduced colony foraging areas, and (4) increased herbivory rates clearly indicate a weaker bottom-up control for LCA in fragmented habitats.

I am aware that my findings from a single forest fragment may suffer from the lack of independent replication. However, in several cases the studied forest fragment revealed stronger bottom-up control on LCA populations than the edge habitat. This may indicate that edge effects of forest fragmentation are more responsible for regulating LCA populations than area or isolation effects. In the context of landscape management and conservation this would mean that in the case of LCA the creation of isolated forest patches is less destructive to trophic interactions than the increase in the proportion of forest edges. However, my results

may also support evidence that in small fragments, especially in those of irregular shape, edge effects indirectly amplify the magnitude of area effects as shown by Ferreira and Laurance (1997) and Laurance and colleagues (1998a). I suggest that a weak bottom-up control on LCA in the studied 50-ha fragment is a result of edge effects that penetrate in the interior of small fragments causing wind-induced tree damages (e.g., Laurance *et al.*, 1997), creation of light gaps (e.g., Laurance *et al.*, 1998a), increase in early-successional vegetation (e.g., Laurance *et al.*, 1998b) and thus, in LCA host plants. In the matters of conservation biology, this refers to the importance of impeding forest fragments to fall below a critical size and retaining their regular shape.

Given the studied forest fragment represents a general pattern, I find it possible to conclude that a less effective bottom-up control explains the observed increase in LCA colony densities in fragmentation-related habitats: in forest edges (Wirth *et al.*, 2003a), forest fragments (Rao, 2000; Wirth *et al.*, 2003a), and early successional forests (e.g., Jaffe and Vilela, 1989; Vasconcelos and Cherrett, 1995; Moutinho *et al.*, 2003). The attributes of bottom-up control, i.e., weak plant defence, low dietary diversity, reduced colony foraging areas, and increased herbivory rates clearly help to decrease the foraging costs of a LCA colony in the fragmentation-related habitats. I suggest that colonies use the surplus of energy resulting from reduced foraging costs to increase the colony growth, the reproduction and turnover. If correct, this explains why fragmented habitats support more LCA colonies at a given time compared to continuous forest habitats. This assumption is supported by Hunter (2002) who studied pest outbreaks in monocultures and argues that a sufficient availability of palatable resources reduces the herbivore's effort in host location. The saved energy may be allocated to reproduction. Consequently, further studies are urgently needed to estimate LCA colony growth and turnover rates.

Weak bottom-up control of LCA populations has various consequences on forested ecosystems. On the basis of my results, I suggest a loop between forest fragmentation and LCA population dynamics. On the one hand, fragmentation of tropical rain forests is pervasive (Whitmore, 1997) and the resulting habitats support more LCA colonies (e.g., Jaffe and Vilela, 1989; Vasconcelos and Cherrett, 1995). On the other hand, increased LCA colony densities, along with lower bottom-up control increase LCA herbivory pressure on the forest and thus inevitably amplify the deleterious effects of fragmentation. These effects include direct consequences of

leaf removal by ants such as mortality of plant individuals (Rao *et al.*, 2001), increased light penetration (Farji-Brener and Illes, 2000), changes in the vegetation composition in the vicinity of nests (Farji-Brener and Ghermandi, 2000) and more indirect effects on ecosystem dynamics such as increased nutrient availability and water stress on the nest surface (Moutinho *et al.*, 2003).

The degree to which bottom-up (e.g., Farji-Brener, 2001) and top-down processes (e.g., Rao, 2000; Terborgh *et al.*, 2001) regulate LCA populations has not been resolved. At my study site, several top-down effects were detected on the populations of *Atta cephalotes* by Almeida (2004) and Barbosa (2004). These findings include weak LCA parasitism by phorid flies and parasitic fungi in fragmentation-related forests. Nevertheless, my results indicate clear and significant bottom-up effects on those ant populations. This gives evidence that both top-down and bottom-up control might regulate LCA populations in fragmented habitats. I conclude that forest fragmentation leads to damages in trophic interactions in my model system and therefore results in (1) an explosion of LCA populations and (2) the cascading effects on vegetation and ecosystem. This study contributes to our understanding of how primary fragmentation effects via the alteration of trophic interactions may translate into higher order effects on ecosystem functions.

9. ABSTRACT

Fragmentation of tropical rain forests is pervasive and has a huge impact on ecosystem functioning. The colony densities of a dominant herbivore in the neotropics – the leaf-cutting ant (LCA) - increase in fragmentation-related habitats. However, the reasons for this increase are not clear. The aim of this study was to test on the hypothesis that bottom-up control (i.e., availability of host plants) of LCA populations is less effective in fragmented forests and thus explains the increase in colony densities. I hypothesized that LCA colonies in fragmented habitats (1) find more palatable vegetation due to low plant defence, (2) forage on few dominant species resulting in a narrow diet breadth, (3) possess small foraging areas and (4) increase herbivory rate. The study was conducted in the remnants of the Atlantic rainforest in NE Brazil. Two fragmentation-related forest habitats were studied: the edge of a 3500-ha continuous forest and the interior of a 50-ha forest fragment.

The results indicate a weak bottom-up control in fragmented forests. (1) The abundance of LCA host plant species in fragmented habitats along with weak chemical defense of those species (especially the lack of terpenoids) allow ants to forage predominantly on palatable species. This is supported by (2) a narrow diet breadth. Similarly, (3) small foraging areas indicate that ants do not have to walk far to find the host species. (4) Increased LCA herbivory rates indicate that the damages (i.e., amount of removed foliage) caused by LCA are more important in fragmented habitats which are more vulnerable to LCA herbivory due to the high availability of palatable plants and a low total amount of foliage (LAI).

I suggest that weak bottom-up control decreases the foraging costs of a LCA colony and the colonies use the surplus of energy to increase the colony growth, the reproduction and turnover. This may explain why fragmented habitats support more LCA colonies at a given time. From a conservation perspective, I suggest a loop between forest fragmentation and LCA population dynamics: the increased LCA colony densities, along with lower bottom-up control increase LCA herbivory pressure on the forest and thus inevitably amplify the deleterious effects of fragmentation. Edge effects of forest fragmentation seem to be more responsible in regulating LCA populations than area or isolation effects. This refers to the importance of impeding big forest fragments to fall below a critical size and remain their regular shape.

10. LITERATURE

- Adams, R.P., 1995. Identification of essential oil components by gas chromatography/mass spectroscopy. Allured Publishing Corporation. Illinois. USA.
- Aizen, M.A., Feinsinger, P., 1994. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. *Ecology* 75, 330-351.
- Almeida, W.R., 2004. Fragmentação florestal: redução no controle da formiga cortadeira *Atta laevigata* por moscas parasitóides. MSc thesis. Federal University of Pernambuco, Recife, Brazil.
- Araújo, M.V.Jr., 2004. Efeito da fragmentação florestal nas taxas de herbivoria da formiga cortadeira *Atta laevigata*. MSc thesis. Federal University of Pernambuco, Recife, Brazil.
- Arnold, A.E., Asquith, N.M., 2002. Herbivory in a fragmented tropical forest: patterns from islands at Lago Gatún, Panama. *Biodiversity and Conservation* 11, 1663-1680.
- Ashwell, G., 1966. New colorimetric methods of sugar analysis. VII. The phenol-sulfuric acid reaction for carbohydrates. *Methods in Enzymology* 8, 93-95.
- Asner, G.P., Palace, M., Keller, M., Pereira, R.Jr., Silva, J.N.M., Zweede, J.C., 2002. Estimating canopy structure in an Amazon forest from Laser Range Finder and IKONOS satellite observations. *Biotropica* 34, 483-492.
- Ayres, M., Ayres, M.Jr., Ayres, D.L., Santos, A.S., 2000. BioEstat 2.0: aplicações estatísticas nas áreas das ciências biológicas e médicas. Sociedade Civil Mamirauá, Conselho Nacional de Desenvolvimento Científico e Tecnológico MCT-CNPq, Brasília.
- Barbosa, V.S., 2004. Efeito da fragmentação florestal na taxa de parasitismo de fungos associados ao jardim da formiga cortadeira *Atta laevigata*. MSc thesis. Federal University of Pernambuco, Recife, Brazil.
- Barnola, L.F., Hasegawa, M., Cedeno, A., 1994. Mono- and sesquiterpene variation in *Pinus caribaea* needles and its relationship to *Atta laevigata* herbivory. *Biochemical Systematics and Ecology* 22, 437-445.
- Benitez-Malvido, J., Garcia-Guzman, G., Kossmann-Ferraz, I.D., 1999. Leaf-fungal incidence and herbivory on tree seedlings in tropical rainforest fragments: an experimental study. *Biological Conservation* 91, 143-150.

- Bernays, E.A., Singer, M.S., Rodrigues, D., 2004. Foraging in nature: foraging efficiency and attentiveness in caterpillars with different diet breadths. *Ecological Entomology* 29, 389–397.
- Bierregaard, R.O.Jr., Gascon, C., 2001. The biological dynamics of forest fragments project. In: Bierregaard, R.O.Jr., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*. Yale University Press, London, pp. 5-12.
- Bierregaard, R.O.Jr., Gascon, C., Lovejoy, T.E., Mesquita, R. 2001. Fragmentation effects on plant communities. In: Bierregaard, R.O.Jr., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*. Yale University Press, London, pp. 97-106.
- Blanton, C.M., Ewel, J.J., 1985. Leaf-cutting ant herbivory in successional and agricultural tropical ecosystems. *Ecology* 66, 861-869.
- Bréda, N.J.J., 2003. Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. *Journal of Experimental Botany* 54, 2403-2417.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, R.A., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16, 909-923.
- Brown, K.S., Hutchings, R.W., 1997. Disturbance, fragmentation and the dynamics of diversity in Amazonian forest butterflies. In: Laurance, W.F., Bierregaard, R.O.Jr. (Eds), *Tropical Forest Remnants Ecology, Management, and Conservation of Fragmented Communities*. Chicago University Press, Chicago.
- Bruna, E.M., 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. *Oecologia* 132, 235–243.
- Bruna, E.M., 2004. Biological impacts of deforestation and fragmentation. In: Burley, J., Evans, J., Youngquist, J. (Eds.), *The Encyclopedia of Forest Sciences*. Elsevier Press, London, pp. 85-90.
- Carvalho, K.S., Vasconcelos, H.L., 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biological Conservation* 91, 151-157.
- Chapela, I.H., Rehner, S.A., Schultz, T.R., Mueller, U.G., 1994. Evolutionary history of the symbiosis between fungus-growing ants and their fungi. *Science* 266, 1691-1694.
- Chason, J.W., Baldocchi, D.D., Huston, M.A., 1991. A comparison of direct and indirect methods for estimating forest canopy leaf area. *Agricultural and Forest Meteorology* 57, 107-128.

- Chen, J.M., 1996. Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. *Agricultural and Forest Meteorology* 80, 135-163.
- Chen, T.K., Galinis, D.L., Wiemer, D.F., 1992. Cornutin A and B: novel diterpenoid repellents of leaf-cutter ants from *Cornutia grandifolia*. *Journal of Organical Chemistry* 57, 862-866.
- Chen, T.K., Wiemer, D.F., Howard, J.J., 1984. A volatile leafcutter ant repellent from *Astronium graveolens*. *Naturwissenschaften* 71, 97-98.
- Cherrett, J.M., 1968. The foraging behavior of *Atta cephalotes* L. (Hymenoptera, Formicidae) I. Foraging pattern and plant species attacked in tropical rain forest. *Journal of Animal Ecology* 37, 387-403.
- Cherrett, J.M., 1972. Some factors involved in the selection of vegetable substrate by *Atta cephalotes* (L.) (Hymenoptera: Formicidae) in tropical rain forest. *J. Anim. Ecol.* 41, 647-660.
- Cherrett, J.M., 1989. Leaf-cutting ants. In: Lieth, H., Werger, M.J.A. (Eds.), *Ecosystems of the World*. Elsevier, Amsterdam, Oxford, New York, pp. 473-486.
- Cherrett, J.M., Peregrine, D.J., 1976. A review of the status of leaf-cutting ants and their control. *Proceedings of the Association of Applied Biologists* 84, 124-133.
- Clark, D.B., Clark, D.A., Rich, P.M., Weiss, S., Oberbauer, S.F., 1996. Landscape-scale evaluation of understorey light and canopy structure: methods and application in a neotropical lowland rain forest. *Canadian Journal of Forest Research* 26, 747-757.
- Cochrane, M.A., Skole, D.L., Matricardi, E.A.T., Barber, C., Chomentowski, W., 2002. Interaction and synergy between selective logging, forest fragmentation and fire disturbance in tropical forests: case study Mato Grosso, Brazil. *CGCEO Research Advances*. Michigan State University, East Lansing, Michigan.
- Coley, P.D., 1986. Costs and benefits of defense by tannins in a neotropical tree. *Oecologia* 70, 238-241.
- Coley, P.D., 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74, 531-536.
- Coley, P.D., Barone, J.A., 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27, 305-335.

- Cornell, H.V., Hawkins, B.A., 2003. Herbivore responses to plant secondary compounds: a test of phytochemical coevolution theory. *The American Naturalist* 161, 507-522.
- Costa, U.A.S., 2003. Efeito da fragmentação na taxa de crescimento das colônias da formiga cortadeira *Atta laevigata*. MSc thesis. Federal University of Pernambuco, Recife, Brazil.
- Cyr, H., Face, M.L., 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361, 148-150.
- Dalling, J.W., Wirth, R., 1998. Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*. *Journal of Tropical Ecology* 14, 705-710.
- Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14, 342-355.
- DeSouza, O., Schoereder, J.H., Brown, V., Bierregaard, R.O.Jr., 2001. A theoretical overview of the processes determining species richness in forest fragments. In: Bierregaard, R.O.Jr., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*. Yale University Press, London, pp. 13-21.
- Dethier, V., 1954. Evolution of feeding preferences in phytophagous insects. *Evolution* 8, 33-54.
- Devaraj, M.S., 2004. Three tank model. A top down or bottom up dominance analysis. *Journal of Theoretics*, vol. 6-5. (<http://www.journaloftheoretics.com/Links/Papers/TDBU.pdf>).
- Dobois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A., Smith, F., 1956. Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28, 350-356.
- Dyer, L.A., Letourneau, D.K., 1999. Relative strengths of top-down and bottom-up forces in a tropical forest community. *Oecologia* 119, 265-274.
- Emmons, L.H., Dubois, M.A., 2003. Leaf-area index change across river-beach successional transects in south-eastern Peru. *Journal of Tropical Ecology* 19, 473-477.
- Englund, S.R., O'Brien, J.J., Clark, D.B., 2000. Evaluation of digital and film hemispherical photography and spherical densiometry for measuring forest light environments. *Canadian Journal of Forestry Research* 30, 1999-2005.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* 34, 487-515.

- Falcão, P.F., 2004. Efeito da fragmentação florestal na diversidade de plantas cortadas pela formiga cortadeira *Atta laevigata*. MSc thesis. Federal University of Pernambuco, Recife, Brazil.
- Farji-Brener, A.G., 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos* 92, 169-177.
- Farji-Brener, A.G., Ghermanti, L., 2000. Influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia. *Journal of Vegetation Science* 11, 453-460.
- Farji-Brener, A.G., Illes, A.E., 2000. Do leaf-cutting ant nests make "bottom-up" gaps in neotropical rain forests?: a critical review of the evidence. *Ecology Letters* 3, 219-227.
- Farji-Brener, A.G., Sierra, C., 1998. The role of trunk trails in the scouting activity of the leaf-cutting ant *Atta cephalotes*. *Ecoscience* 5, 271-274.
- Ferreira, L.V., Laurance, W.F., 1997. Effects of forest fragmentation on mortality and damage of selected trees in Central Amazonia. *Conservation Biology* 11, 797-801.
- Ferreira, L.V., Prance, G.T., 1999. Ecosystem recovery in terra firme forests after cutting and burning: a comparison on species richness, floristic composition and forest structure in the Jaú National Park, Amazonia. *Botanical Journal of the Linnean Society* 130, 97-110.
- Fonseca, G.A.B., Robinson, J.G., 1990. Forest size and structure: competitive and predatory effects on mammal communities. *Biological Conservation* 53, 265-294.
- Fowler, H.G., Claver, S., 1991. Leaf-cutter ant assemblies: effects of latitude, vegetation, and behavior. In: Huxley, C.R., Cutler, D.F. (Eds.), *Ant-plant Interactions*. Oxford University Press, Oxford, New York, Tokyo, pp. 51-59.
- Fowler, H.G., Pagani, M.I., da Silva, O.A., Forti, L.C., da Silva, V.P., Vasconcelos, H.L., 1989. A pest is a pest is a pest? The dilemma of neotropical leaf-cutting ants: keystone taxa of natural ecosystems. *Environmental Management* 13, 671-675.
- Fowler, H.G., Stiles, E.W., 1980. Conservative resource management by leaf-cutting ants ? The role of foraging territories and trails, and environmental patchiness. *Sociobiology* 5, 25-41.
- Fraenkel, G.S., 1959. Raison d'être of secondary plant substances. *Science* 129, 1466-1470.
- Fraser, L.H., Grime, J.P., 1999. Interacting effects of herbivory and fertility on a synthesized plant community. *Journal of Ecology* 87, 514-525.

Frazer, G.W., Fournier, R.A., Trofymow, J.A., Hall, R.J., 2001. A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission. *Agricultural and Forest Meteorology* 109, 249–263.

Fretwell, S.D., 1977. The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine* 20, 169-185.

Garcia, I.P., Forti, L.C., Engel, V.L., de Andrade, A.P.P., Wilcken, C.F., 2003. Ecological interaction between *Atta sexdens* (Hymenoptera: Formicidae) and the vegetation of a mesophyll semideciduous forest in Botucatu, SP, Brazil. *Sociobiology* 42, 265-283.

Gartlan, J.S., McKey, D.B., Waterman, P.G., Mbi, C.N., Struhsaker, T.T., 1980. A comparative study of the phytochemistry of two African rain forests. *Biochemical Systematics and Ecology* 8, 401-422.

Gascon, C., Bierregaard, R.O., Laurance, W.F., Rankin-de-Mérona, J.M., 2001. Deforestation and forest fragmentation in the Amazon. In: Bierregaard, R.O.Jr., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*. Yale University Press, London, pp. 22-30.

Gentry, A.H., 1996. A field guide to the families and genera of woody plants of Northwest South America (Colombia, Ecuador, Peru). University of Chicago Press. London, Chicago.

Gower, S.T., Norman, J.M., 1991. Rapid estimation of leaf area index in conifer and broad leaf plantations. *Ecology* 72, 1896-1900.

Hagerman, A.E., 1987. Radial diffusion method for determining tannin in plant extracts. *Journal of Chemical Ecology* 13, 437-449.

Hagerman, A.E., 1988. Extractions of tannin from fresh and preserved leaves. *Journal of Chemical Ecology* 14, 453-461.

Hagerman, A.E., 2002. *Tannin Handbook* (pdf version), Oxford.
(<http://www.users.muohio.edu/hagermae/tannin.pdf>)

Haines, B., 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica* in Panama. *Biotropica* 10, 270-277.

Hairton, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. *American Naturalist* 94, 421-424.

- Hale, S.E., Edwards, C., 2002. Comparison of film and digital hemispherical photography across a wide range of canopy densities. *Agricultural and Forest Meteorology* 112, 51–56.
- Hill, J.L., Curran, P.J., 2001. Species composition in fragmented forests: conservation implications of changing forest area. *Applied Geography* 21, 157-174.
- Hölldobler, B., Lumsden., 1980. Territorial strategies of ants. *Science* 210, 723-739.
- Hölldobler, B., Wilson, E.O., 1990. *The ants*. Springer-Verlag, Berlin.
- Howard, J.J., 1987. Leaf-cutting ant diet selection: the role of nutrients, water, and secondary chemistry. *Ecology* 67, 503-515.
- Howard, J.J., 1988. Leaf-cutting ant diet selection: relative influence of leaf-chemistry and physical features. *Ecology* 69, 250-260.
- Howard, J.J., 1990. Infidelity of leaf-cutting ants to host plants: resource heterogeneity or defense induction? *Oecologia* 82, 394-401.
- Howard, J.J., 1991. Resource quality and cost in the foraging of leaf cutter ants. In: Huxley, C.R., Cutler, D.F. (Eds.), *Ant- plant Interactions*. Oxford University Press, Oxford, New York, Tokyo, pp. 42-50.
- Howard, J.J., Cazin, J.Jr., Wiemer, D.F., 1988. Toxicity of terpenoid deterrents to the leaf-cutting ant *Atta cephalotes* and its mutualistic fungus. *Journal of Chemical Ecology* 14, 59-69.
- Howard, J.J., Green, T.P., Wiemer, D.F., 1989. Comparative deterrentcy of two terpenoids to two genera of attine ants. *Journal of Chemical Ecology* 15, 2279-2288.
- Howard, J.J., Wiemer, D.F., 1986. Chemical ecology of host plant selection by the leaf-cutting ant, *Atta cephalotes*. In: Lofgren, C.S., Van der Meer, R.K. (Eds.), *Fire Ants and Leaf-cutting Ants: Biology and Management*. Westview Press, Boulder, pp. 260-273.
- Howe, H.F., Westley, L.C., 1993. *Anpassung und Ausbeutung: Wechselbeziehungen zwischen Pflanzen und Tieren*. Spektrum Akademischer Verlag, Heidelberg, Berlin, Oxford.
- Hubbell, S.P., Howard, J.J., Wiemer, D.F., 1984. Chemical leaf repellency to an attine ant: seasonal distribution among potential host plant species. *Ecology* 65, 1067-1076.
- Hubbell, S.P., Wiemer, D.F., 1983. Host plant selection by an attine ant. In: Jaisson, P. (Ed.), *Social Insects in the Tropics*. University of Paris Press, Paris, pp. 133-154.

Hubbell, S.P., Wiemer, D.F., Adejare, A., 1983. An antifungal terpenoid defends a neotropical tree (Hymenaea) against attack by fungus-growing ants (*Atta*). *Oecologia* 60, 321-327.

Hunter, M.D., 2001. Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology* 3, 77-84.

Hunter, M.D., 2002. Ecological causes of pest outbreaks. In: Pimentel, D. (Ed.), *Encyclopedia of Pest Management*. Marcel Dekker, Inc., pp. 214-217.

Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73, 724-732.

Hunter, M.D., Varley, G.C., Gradwell, G.R., 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences of the United States of America* 94, 9176-9181.

IBGE., 1985. *Atlas Nacional do Brasil: Região Nordeste*. IBGE, Rio de Janeiro.

Jackson, R.B., Hedin, L.O., 2004. Special feature: terrestrial and freshwater biogeochemistry. *Ecology* 85, 2353-2354.

Jaffe, K., Vilela, E., 1989. On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary rainforest. *Biotropica* 21, 234-236.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., Baret, F., 2004. Review of methods for in situ leaf area index determination. Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology* 121, 19-35.

Kalácska, M., Sánchez-Azofeifa, G.A., Rivard, B., Calvo-Alvarado, J.C., Journet, A.R.P., Arroyo-Mora, J.P., Ortiz-Ortiz, D., 2004. Leaf area index measurements in a tropical moist forest: A case study from Costa Rica. *Remote Sensing of Environment* 91, 134-152.

Kempf, W., 1972. *Catálogo Abreviado das Formigas da Região Neotropical (Hymenoptera: Formicidae)*. *Studia Entomologica* 15, 3-344.

Köhler, P., Jérôme, C., Riéra, B., Huth, A., 2003. Simulating the long-term response of tropical wet forests to fragmentation. *Ecosystems* 6, 114-128.

Kraus, T.E.C., Dahlgren, R.A., Zasoski, R.J., 2003. Tannins in nutrient dynamics of forest ecosystems - a review. *Plant and Soil* 256, 41-66.

Krebs, C.J., 1989. Ecological methodology. Harper & Row Publishers, New York.

Krell, F.T., 2004. Parataxonomy vs. taxonomy in biodiversity studies – pitfalls and applicability of `morphospecies` sorting. *Biodiversity and Conservation* 13, 795-812.

Laurance, W.F., 2001. Fragmentation and plant communities: synthesis and implications for landscape management. In: Bierregaard, R.O.Jr., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*. Yale University Press, London, pp. 158-167.

Laurance, W.F., Ferreira, L.V., Rankin-de-Morena, J.M., Laurance, S.G., 1998a. Rain forest fragmentation and the dynamics of amazonian tree communities. *Ecology* 79, 2032-2040.

Laurance, W.F., Ferreira, L.V., Rankin-de-Morena, J.M., Laurance, S.G., Hutchings, R., Lovejoy, T., 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12, 460-464.

Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona, J.M., Gascon, C., Lovejoy, T.E., 1997. Biomass collapse in Amazonian forest fragments. *Science* 278, 1117-1118.

Leblanc, S.G., Chen, J.M., 2001. A practical scheme for correcting multiple scattering effects on optical LAI measurements. *Agricultural and Forest Meteorology* 110, 125-139.

Leigh, E.G., 1999. *Tropical Forest Ecology: a View from Barro Colorado Island*. Oxford University Press. New York.

Littleddyke, M., Cherrett, J.M., 1976. Direct ingestion of plant sap from cut leaves by the leaf-cutting ants *Atta cephalotes* (L.) and *Acromyrmex octospinosus* (Reich) (Formicidae, Attini). *Bulletin of Entomological Research* 66, 205-217.

Loeuille, N., Loreau, M., 2004. Nutrient enrichment and food chains: can evolution buffer top-down control? *Theoretical Population Biology* 65, 285 –298.

Lowman, M.D., Nadkarni, N.M., 1995. *Forest Canopies*. Academic Press, San Diego, London, Boston, New York, Sydney, Tokyo, Toronto.

Lucas, P.W., Turner, I.M., Dominy, N.J., Yamashita, N., 2000. Mechanical defences to herbivory. *Annals of Botany* 86, 913-920.

Lugo, A.E., Farnworth, E.G., Pool, G., Jerez, P., Kaufmann, G., 1973. The impact of the leaf-cutter ant *Atta colombica* on the energy flow of a tropical wet forest. *Ecology* 54, 1292-1301.

- Mabry, T.J., Gill, J.E., 1979. Sesquiterpene lactones and other terpenoids. In: Rosenthal, G.A., Janzen, D.H. (Eds.), *Herbivores: Their Interactions with Secondary Plant Metabolites*. Academic Press, New York, pp. 501-537.
- MacArthur, R.H., Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press. Princeton.
- Mariconi, F.A.M., 1970. *As saúvas*. Agronômica Ceres, São Paulo.
- Marquis, R.J., Newell, E.A., Villegas, A.C., 1997. Non-structural carbohydrate accumulation and use in an understory rain-forest shrub and relevance for the impact of leaf herbivory. *Functional Ecology* 11, 636-643.
- Matson, P.A., Hunter, M.D., 2004. Special feature: the relative contributions of top-down and bottom-up forces in population and community ecology. *Ecology* 73, 723.
- McNaughton, S.J., Oesterheld, M., Frank, D.A., Williams, K.J., 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341, 142-144.
- Meyer, N., 2003. Einfluß der Waldfragmentierung auf die physikalischen Blatteigenschaften der Wirtspflanzen von Blattschneiderameisen im Atlantischen Regenwald Brasiliens. Diploma thesis. University of Bielefeld, Germany.
- Mintzer, A., 1979. Foraging activity of the mexican leaf cutting ant *Atta mexicana* in a Sonoran desert habitat [Hymenoptera: Formicidae]. *Insectes Sociaux-Social Insects* 26, 364-372.
- Moon, D.C., Stiling, P., 2002. Top-down, bottom-up, or side to side? Within-trophic-level interactions modify trophic dynamics of a salt marsh herbivore. *Oikos* 98, 480-490.
- Moutinho, P., Nepstad, D.C., Davidson, E.A., 2003. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. *Ecology* 84, 1265-1276.
- Mueller, U.G., Rehner, S.A., Schultz, T.R., 1998. The evolution of agriculture in ants. *Science* 281, 2034-2038.
- Müller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. John Wiley & Sons, Inc., USA.
- Murcia, C., 1995. Edge effects in fragmented forests: application for conservation. *Trends in Ecology and Evolution* 10, 58-62.

- Murdoch, W.W., 1966. Community structure, population control, and competition – a critique. *American Naturalist* 100, 219-226.
- Nichols-Orians, C.M., 1991. Environmentally induced differences in plant traits: consequences for susceptibility to a leaf-cutter ant. *Ecology* 72, 1609-1623.
- North, R.D., Howse, P.E., Jackson, C.W., 2000. Agonistic behavior of the leaf-cutting ant *Atta sexdens rubropilosa* elicited by caryophyllene. *Journal of Insect Behavior* 13, 1-13.
- Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118, 240-261.
- Oliveira, M.A., 2003. Efeito da fragmentação de habitat sobre as árvores em trecho de floresta Atlântica nordestino. MSc thesis. Federal University of Pernambuco, Recife, Brazil.
- Orr, M.R., 1992. Parasitic flies (Diptera: Phoridae) influence foraging rhythms and caste division of labor in leaf-cutter ant, *Atta cephalotes* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 30, 395-402.
- Patricio, E.F.L.R.A., Cruz-López, L., Maile, R., Tentschert, J., Jones, G.R., Morgan, E.D., 2002. The propolis of stingless bees: terpenes from the tibia of three *Frieseomelitta* species. *Journal of Insect Physiology* 48, 249-254.
- Peñaloza, C., Farji-Brener, A.G., 2003. The importance of treefall gaps as foraging sites for leaf-cutting ants depends on forest age. *Journal of Tropical Ecology* 19, 603–605.
- Picard, N., Karembe, M., Birnbaum, P., 2004. Species-area curve and spatial pattern. *Ecoscience* 11, 45-54.
- Pimentel, D.S., Tabarelli, M., 2004. Seed dispersal of the palm *Attalea oleifera* in a remnant of the Brazilian Atlantic Forest. *Biotropica* 36, 74-84.
- Planchais, I., Pontailleur, J.Y., 1999. Validity of leaf areas and angles estimated in a beech forest from analysis of gap frequencies, using hemispherical photographs and a plant canopy analyzer. *Annals of Forest Science* 56, 1-10.
- Pokorny, R., Marek, M.V., 2000. Test of accuracy of LAI estimation by LAI-2000 under artificially changed leaf to wood area proportions. *Biologia Plantarum* 43, 537-544.
- Pyke, G.H., 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15, 523-575.

Pyke, G.H., Pulliam, H.R., Charnov, E.L., 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 52, 137-154.

Quinlan, R.J., Cherrett, J.M., 1979. The role of fungus in the diet of the leaf-cutting ant *Atta cephalotes* (L.). *Ecological Entomology* 4, 151-160.

Rankin-de-Mérona, J.M., Hutchings, R.W., 2001. Deforestation effects at the edge of an Amazonian forest fragment. In: Bierregaard, R.O.Jr., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: the Ecology and Conservation of a Fragmented Forest*. Yale University Press, London, pp. 107-120.

Ranta, P., Blom, T., Niemela, J., Joensuu, E., Siitonen, M., 1998. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. *Biodiversity and Conservation* 7, 385-403.

Rao, M., 2000. Variation in leaf-cutter ant (*Atta* sp.) densities in forest isolates: the potential role of predation. *Journal of Tropical Ecology* 16, 209-225.

Rao, M., Terborgh, J., Nunez, P., 2001. Increased herbivory in forest isolates: implications for plant community structure and composition. *Conservation Biology* 15, 624-633.

Rinker, H.B., Lowman, M.D., Hunter, M.D., Schowalter, T.D., Fonte, S.J., 2001. Canopy herbivory and soil ecology: the top-down impact of forest processes. *Selbyana* 22, 225-231.

Roces, F., 2002. Individual complexity and self-organization in foraging by leaf-cuttings ants. *Biological Bulletin* 202, 306-313.

Rockwood, L.L., 1973. Distribution, density, and dispersion of two species of *Atta* (Hymenoptera: Formicidae) in Guanacaste province, Costa Rica. *Journal of Animal Ecology* 42, 803-817.

Rockwood, L.L., 1976. Plant selection and foraging patterns in two species of leaf-cutting ants (*Atta*). *Ecology* 57, 48-61.

Rockwood, L.L., Hubbell, S.P., 1987. Host plant selection, diet, diversity, and optimal foraging in a tropical leaf-cutting ant. *Oecologia* 74, 55-61.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5, 18-32.

Scheiner, S.M., 2003. Six types of species-area curves. *Global ecology and biogeography* 12, 441-447.

- Schlaepfer, M.A., Gavin, T.A., 2001. Edge effects on lizards and frogs in tropical forest fragments. *Conservation Biology* 15, 1079-1090.
- Shepherd, J.D., 1982. Trunk trails and the searching strategy of a leaf-cutter ant, *Atta colombica*. *Behavioural Ecology and Sociobiology* 11, 77-84.
- Shepherd, J.D., 1985. Adjusting foraging effort to resources in adjacent colonies of the leaf-cutting ant, *Atta colombica*. *Biotropica* 17, 245-252.
- Silva, A., Bacci, M.Jr., de Siqueira, C.G., Bueno, O.C., Pagnocca, F.C., Hebling, M.J.A., 2003. Survival of *Atta sexdens* workers on different food sources. *Journal of Insect Physiology* 49, 307-313.
- Silva, J.M.C., Tabarelli, M., 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404, 72-74.
- Soudani, K., Trautmann, J., Walter, J.M., 2001. Comparaison de méthodes optiques pour estimer l'ouverture de la canopée et l'indice foliaire en forêt feuillue. *Sciences de la vie* 324, 381-392.
- Tabarelli, M., Mantovani, W., Peres, C.A., 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* 91, 119-127.
- Terborgh, J., Lopez, L., Nuñez, P.V., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L., 2001. Ecological meltdown in predator-free forest fragments. *Science* 294, 1923-1926.
- Theis, N., Lerda, M., 2003. The evolution of function in plant secondary metabolites. *International Journal of Plant Science* 164, 93-102.
- Thies, C., Steffan-Dewenter, I., Tschamtkke, T., 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101, 18-25.
- Thies, C., Tschamtkke, T., 1999. Landscape structure and biological control in agroecosystems. *Science* 285, 893-895.
- Thompson, J.N., 1999. The evolution of species interactions. *Science* 284, 2116-2118.
- Trumble, J.T., Kolodny-Hirsch, D.M., Ting, I.P., 1993. Plant compensatory for arthropod herbivory. *Annual Review of Entomology* 38, 93-119.
- Tschamtkke, T., Steffan-Dewenter, I., Kruess, A., Thies, C., 2002. Characteristics of insect populations on habitat fragments: a mini review. *Ecological Research* 17, 229-239.

- Turner, I.M., 2001. *The Ecology of Trees in the Tropical Rain Forest*. Cambridge University Press. Cambridge.
- Vasconcelos, H.L., 1990a. Foraging activity of two species of leaf-cutting ants (*Atta*) in a primary forest of the central Amazon. *Insectes Sociaux - Social Insects* 37, 131-146.
- Vasconcelos, H.L., 1990b. Habitat selection by the queens of the leaf-cutting ant *Atta sexdens* L. in Brazil. *Journal of Tropical Ecology* 6, 249-252.
- Vasconcelos, H.F., Cherrett, J.M., 1995. Changes in leaf-cutting ant populations (Formicidae: Attini) after the clearing of mature forest in Brazilian Amazonia. *Studies on Neotropical Fauna and Environment* 30, 107-113.
- Vasconcelos, H.L., Fowler, H.G., 1990. Foraging and fungal substrate selection by leaf-cutting ants. In: Van der Meer, R., Jaffe, K., Cedeno, A. (Eds.), *Applied Myrmecology - A World Perspective*. Westview Press. Boulder, San Francisco, Oxford, pp. 411-419.
- Veblen, T.T., Stewart, G.H., 1980. Comparison of forest structure and regeneration of Bench and Stewart islands, New Zealand. *New Zealand Journal of Ecology* 3, 50-68.
- Veloso, H.P., Rangel-Filho, A.L.R., Lima, J.C.A., 1991. *Classificação da Vegetação Brasileira Adaptada a um Sistema Universal*. IBGE, Rio de Janeiro.
- Vilela, E.F., 1986. Status of leaf-cutting ant control in forest plantations in Brazil. In: Lofgren, C.S., Van der Meer, R.K. (Eds.), *Fire Ants and Leaf-cutting Ants. Biology and Management*. Westview Press. Boulder, London, pp. 399-408.
- Watson, D.J., 1947. Comparative physiological studies in the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Annals of Botany* 11, 41-76.
- Whitmore, T.C., 1997. Tropical forest disturbance, disappearance, and species loss. In: Laurance, W.F., Bierregaard, R.O.Jr. (Eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 3-12.
- Whitmore, T.C., Brown, N.D., Swaine, M.D., Kennedy, D., Goodwin-Bailey, C.I., Gong, W.-K., 1993. Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical rain forest. *Journal of Tropical Ecology* 9, 131-151.
- Wilson, E.O., 1986. The defining traits of fire ants and leaf-cutting ants. In: Lofgren, C.S., Van der Meer, R.K. (Eds.), *Fire Ants and Leaf-cutting Ants*. Westview Press, Boulder, London, pp. 1-9.

Wink, M., 2003. Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective. *Phytochemistry* 64, 3-19.

Wirth, R., Almeida, W.R., Barbosa, V., Falcão, P.F., Knoechelmann, C.M., Silveira, Ú.A., Urbas, P., Vieira-Jr., M.A., Leal, I.R., 2003a. Forest fragmentation process increases density of leaf-cutting ants in the Brazilian Atlantic rain forest (Poster). 16th annual meeting of Tropical Ecology Society (GTÖ). Rostock, Germany.

Wirth, R., Beyschlag, W., Ryel, R., Herz, H., Hölldobler, B., 2003b. Herbivory of Leaf-cutting Ants: a Case Study on *Atta colombica* in the Tropical Rainforest of Panama. Springer-Verlag. Berlin, Heidelberg, New York.

Wirth, R., Weber, B., Ryel, R.J., 2001. Spatial and temporal variability of canopy structure in a tropical moist forest. *Acta Oecologica* 22, 235-244.

Wratten, S., 1992. Population regulation in insect herbivores – top-down or bottom-up? *New Zealand Journal of Ecology* 16, 145-147.

Zucker, W.V., 1983. Tannins: does structure determine function? An ecological perspective. *The American Naturalist* 121, 335-365.

APPENDIX

Appendix I. Identified species in the diet of *Atta cephalotes* colonies in the interior of the continuous forest (IN), at the edge of the continuous forest (ED), and in the interior of the forest fragment (FR). t = tree, s = shrub, h = herb, l = liana, P = pioneer, S = shade tolerant. The identification was carried out in co-operation with Falcão (2004).

FAMILY / SPECIES	Regeneration strategy	Growth form	Habitat		
			IN	ED	FR
ANACARDIACEAE					
<i>Tapirira guianensis</i> Aubl.	P	t	x	x	x
<i>Thyrsodium spruceanum</i> Benth.	P	t	x	x	x
ANNONACEAE					
<i>Guatteria pogonopsis</i> Mart.	S	t		x	
<i>Xylopia cf. benthani</i>	S	t			x
ARACEAE					
<i>Philodendron</i> sp.	P	h	x		
ARALIACEAE					
<i>Schefflera morototoni</i> (Aubl.) Maguire, Steyerm. & Frodin,	P	t	x	x	x
ASTERACEAE					
<i>Conocliniopsis prasiifolia</i> (DC.) R. King. & H. Rob.	P	h		x	x
BIGNONIACEAE					
sp.1			x		
BOMBACACEAE					
sp.1	P		x	x	x
BORAGINACEAE					
<i>Cordia corymbosa</i> (L) G. Don	P	s		x	
<i>Cordia selloviana</i> Cham.	P	t			x
BURCERACEAE					
<i>Protium giganteum</i> Engl.	S	t			x
CAESALPINACEAE					
<i>Bauhinia forficata</i> Link	P	t			x
<i>Dialum guianensis</i> (Aubl.) Sandwith	P	t	x	x	x
CLUSIACEAE					
<i>Rheedia brasiliensis</i> (Mart.) Planch. Ex Triana	S	t	x		
<i>Symphonia globulifera</i> L. f.	P	t	x	x	x
<i>Tovomita mangle</i> G. Mariz	S	s	x	x	x

FAMILY / SPECIES	Regeneration strategy	Growth form	Habitat		
			IN	ED	FR
<i>Tovomita brevistaminea</i> Engl.	S	t	x	x	x
<i>Vismia guianensis</i> (Aubl.) Pers.	P	s	x	x	
CRUCIFERAE					
sp.1	P	h		x	
DILENIACEAE					
<i>Davilla</i> sp.	P	l	x		
ELAEOCARPACEAE					
<i>Sloanea</i> sp.	S	t			x
ERYTHROXILACEAE					
<i>Erythroxylum mucronatum</i> Benth.	P	t	x	x	
<i>Erythroxylum squamatum</i> Sw.	P	t			x
EUPHORBIACEAE					
<i>Croton floribundus</i> Spreng.	P	t	x	x	x
<i>Chamaesyce hyssopifolia</i> (L.) Small	P	h			x
<i>Hyeronima alchornoioides</i>	P	t	x	x	x
<i>Mabea occidentales</i> Benth.	S	t	x	x	x
<i>Philanthus</i> sp.	P	s	x		
<i>Senefeldera verticilata</i>	P	t	x	x	x
<i>Stilingia brevifolia</i>	P		x		
FLACOURTIACEAE					
<i>Banara guianensis</i> Aubl.	P	t		x	
GESNERIACEAE					
sp.1	P			x	
LAURACEAE					
<i>Ocotea glomerata</i> (Nees) Mez	P	t	x	x	x
LECYTHIDACEAE					
<i>Escheweilera</i> sp.	S	t	x	x	x
<i>Lecythis lurida</i> (Miers.) S. A. Mori	S	t			x
<i>Lecythis pisonis</i> Cambess.	S	t	x	x	x
<i>Lecythis</i> sp.	S	t	x	x	x
MALPIGHIACEAE					
<i>Byrsonima crispa</i> A. Juss.	P	t	x		
<i>Byrsonima sericea</i> A. DC.	P	t		x	x
<i>Byrsonima</i> sp.	P	t		x	
<i>Mascagnia</i> sp.	P	l	x		x
MARANTACEAE					
<i>Stromanthe tonckat</i> (Aubl.) Eichl	S	h	x		

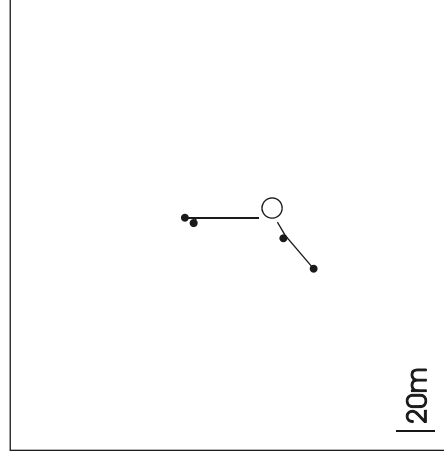
FAMILY / SPECIES	Regeneration strategy	Growth form	Habitat		
			IN	ED	FR
<i>Calathea</i> sp.	S	h			x
MELASTOMATACEAE					
<i>Clidemia hirta</i> (L.) D. Don	P	s		x	
<i>Clidemia</i> sp.	P	s		x	
<i>Henriettea succosa</i> (Aubl.) A. DC.	P	t		x	
<i>Miconia hypoleuca</i> (Benth.) Triana	P	t	x	x	x
<i>Miconia prasina</i> (Sw.) DC.	P	t		x	x
<i>Miconia nervosa</i> (Sm.) Triana	P	t		x	x
<i>Pterolepsis</i> sp.	P	h		x	x
sp.1	P		x		
MENISPERMACEAE					
<i>Cissampelos</i> sp.	P	l			x
MIMOSACEAE					
<i>Inga edulis</i> Mart.	S	t		x	
<i>Inga striata</i> Benth.	P	t	x	x	x
<i>Inga thibaudiana</i> A. DC.	P	t	x	x	x
<i>Inga</i> sp.	P	t		x	x
MONIMIACEAE					
<i>Siparuma guianensis</i> Aubl.	S	t	x	x	x
MORACEAE					
<i>Brosimum guianensis</i> (Aubl.) Huber	P	t			x
<i>Ficus</i> sp.	P	t		x	
<i>Helicostylis tomentosa</i> (Poepp. & Endl.) Rusby	S	t	x		x
<i>Sorocea hilarii</i> Gaudichand.	S	t	x	x	x
MYRSINACEAE					
<i>Myrsine</i> sp.	P	t	x	x	x
MYRTACEAE					
sp. 1	S		x		x
NYCTAGINACEAE					
<i>Pisonia</i> sp.	S	s		x	x
sp.1			x	x	x
sp.2			x		x
PASSIFLORACEAE					
<i>Passiflora</i> sp.		l		x	
PIPERACEAE					
<i>Piper</i> sp.	P	s	x		x

FAMILY / SPECIES	Regeneration strategy	Growth form	Habitat		
			IN	ED	FR
PONTEDERIACEAE					
<i>Eichornia</i> sp.		h		x	
QUINACEAE					
<i>Quina</i> aff <i>paraensis</i> Pires et Fróes	S	t		x	
RHAMACEAE					
<i>Gouanea blanchetiana</i> Miq.	P	l		x	
RUBIACEAE					
<i>Chiococca alba</i> (L.) Hitch	P		x		
<i>Coutarea hexandra</i> (Jacq.) K. Schum	P	t	x	x	
<i>Palicourea blanchetiana</i> Schltldl.	P	s		x	
<i>Psychotria</i> sp.1	P	s		x	
<i>Psychotria</i> sp.2	P	s			x
<i>Rhandia armata</i> (SW.) DC.	P	s	x		
sp.1	P			x	x
sp.2	P			x	
SAPINDACEAE					
<i>Cupania racemosa</i> (Vell.) Radlk.	P	t			x
<i>Dilodendrom bipinatum</i> Radlk.	S	t			x
<i>Paullinia rubiginosa</i> Cambess.	P	l	x		
SAPOTACEAE					
<i>Chrysophyllum</i> sp.	S	t	x		
SIMAROUBACEAE					
<i>Picrammia</i> sp.	S	t			x
SOLANACEAE					
<i>Physalys neesiana</i> Sendtn.	P	s		x	
<i>Solanum asperum</i> Rich.	P	s	x		
<i>Solanum</i> sp.	P	s		x	
VERBENACEAE					
sp.1	P	h	x	x	
VIOLACEAE					
<i>Payparola blanchetiana</i>	S	t	x	x	x
VOCHYSIACEAE					
<i>Vochysia oblongifolia</i> Warm.	S	t	x	x	x
Unidentified specimen in herbarium					
sp.1			x	x	x

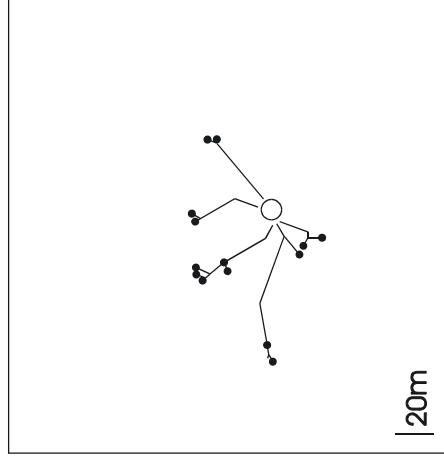
FAMILY / SPECIES	Regeneration strategy	Growth form	Habitat		
			IN	ED	FR
Pteridophyta					
BLECHNACEAE					
Blechnum sp.				x	

Appendix II-I. Foraging trails of *A. cephalotes* colony I in the interior of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

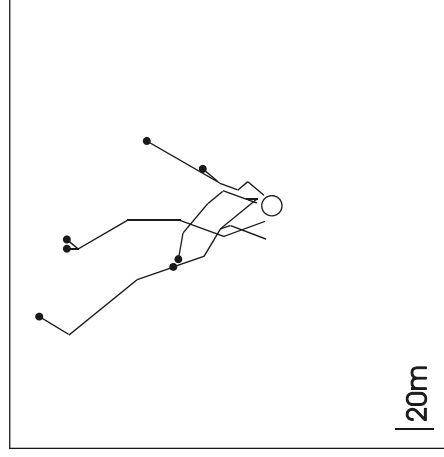
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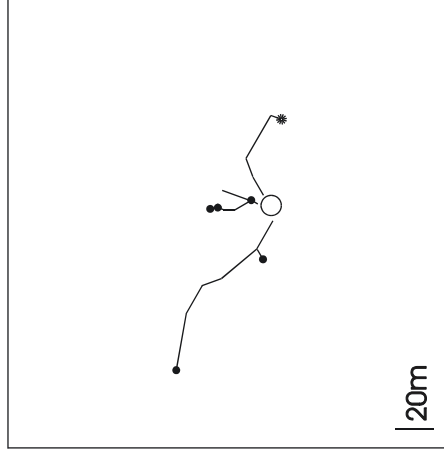
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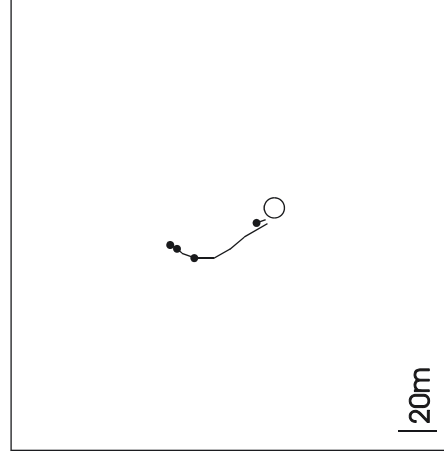
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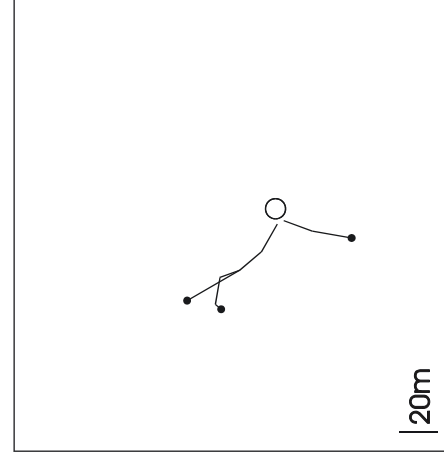
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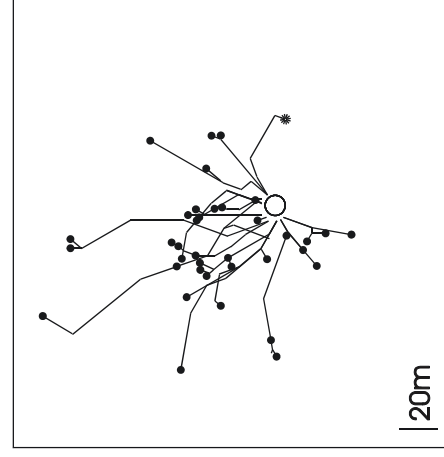
May 2003



July 2003

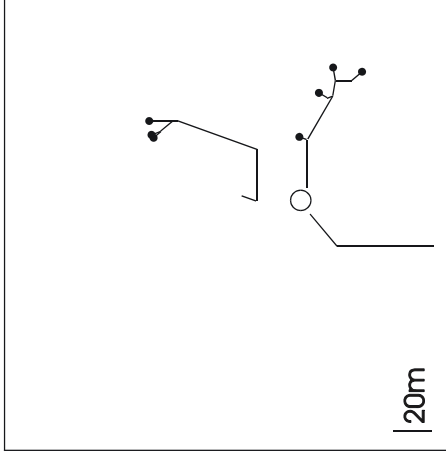


Annual

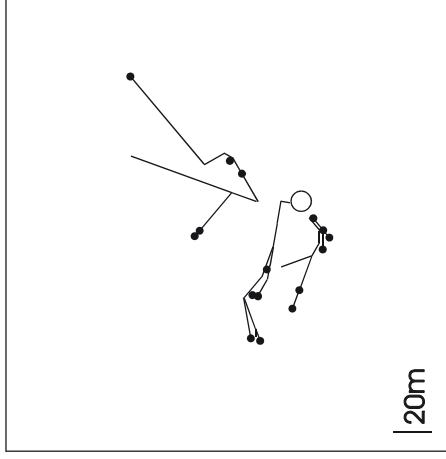


Appendix II-II. Foraging trails of *A. cephalotes* colony II in the interior of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

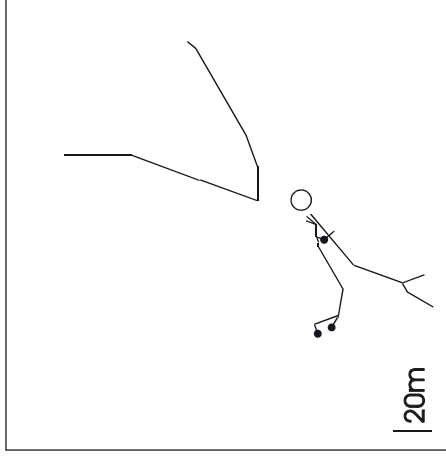
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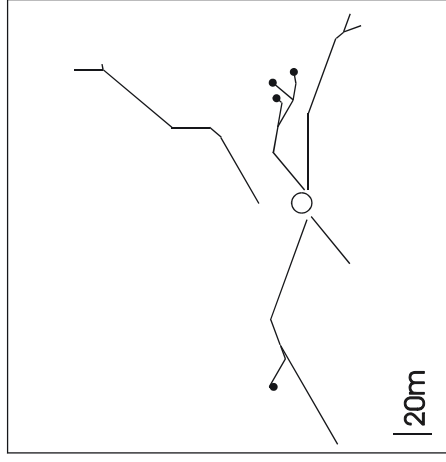
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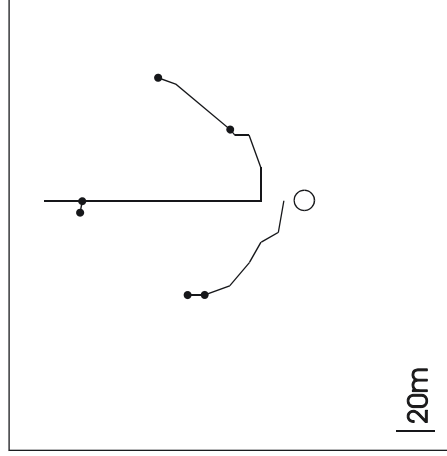
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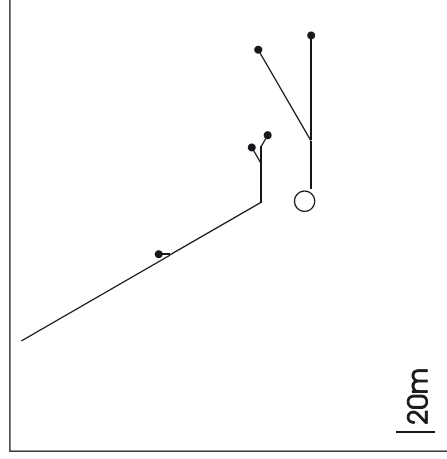
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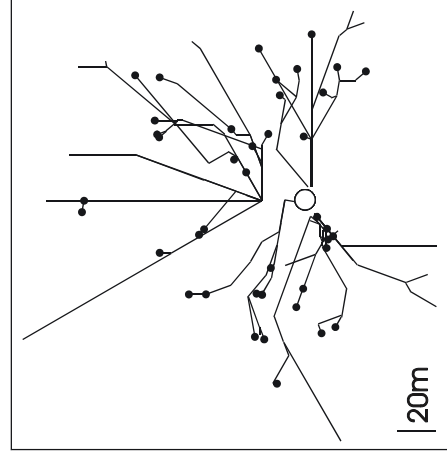
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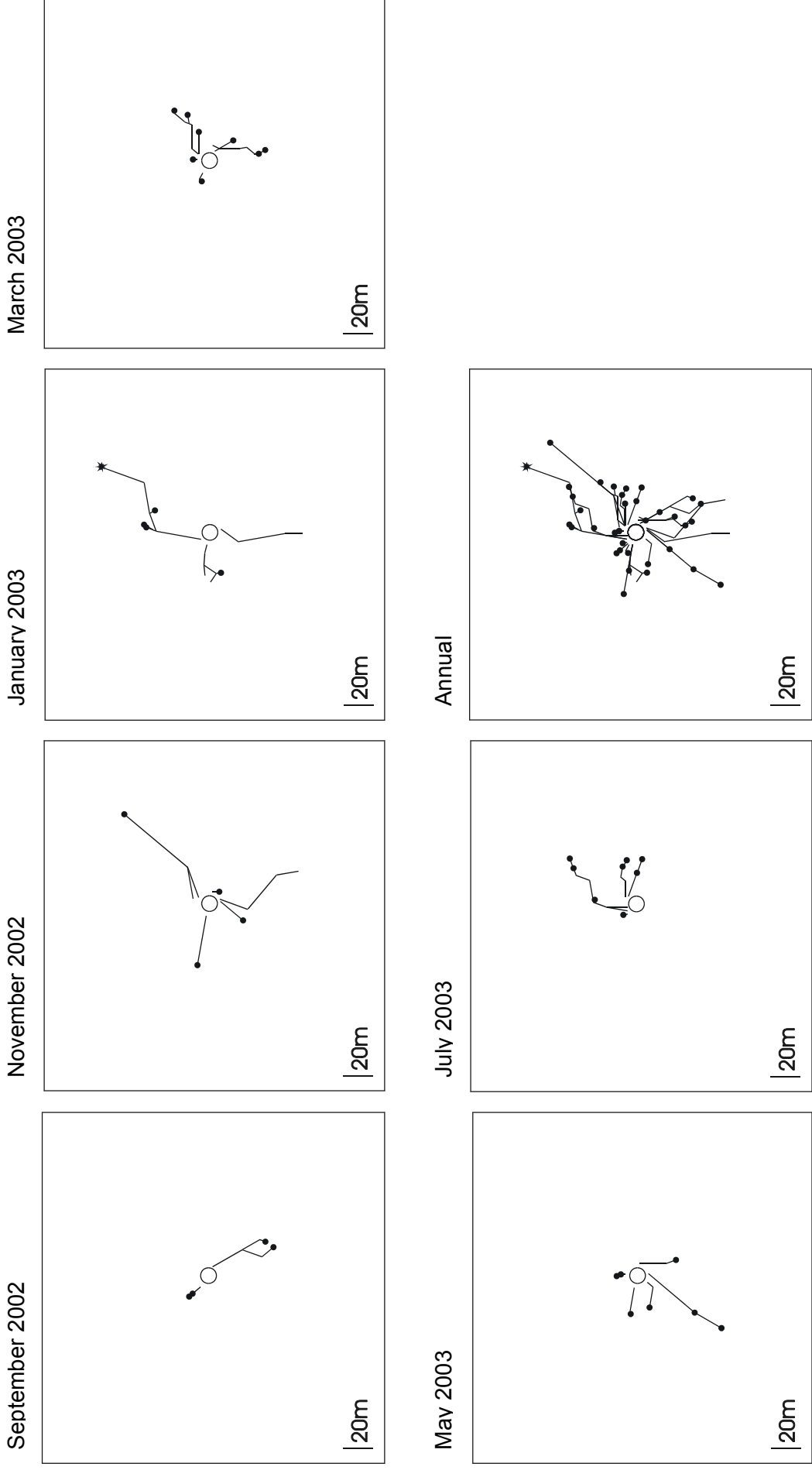
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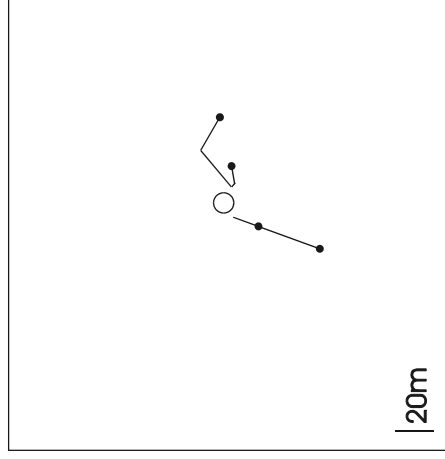


Appendix II-III. Foraging trails of *A. cephalotes* colony III in the interior of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees, stars indicate harvested blossoms fallen on the forest floor.

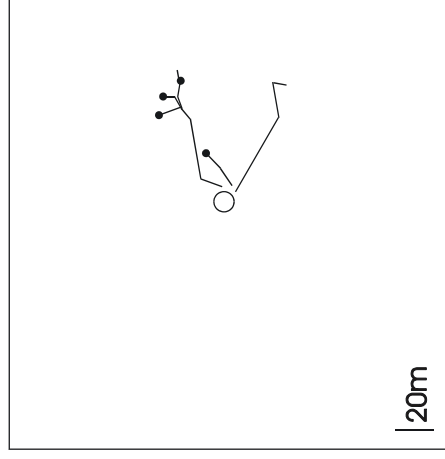


Appendix II-IV. Foraging trails of *A. cephalotes* colony IV in the interior of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

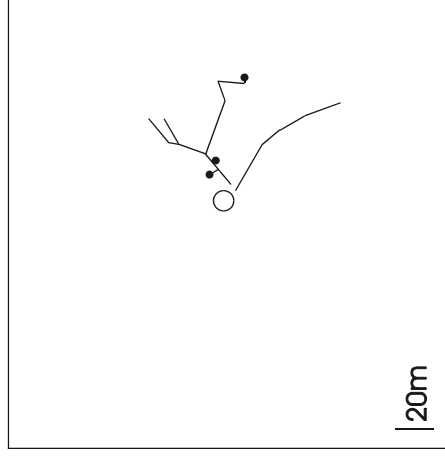
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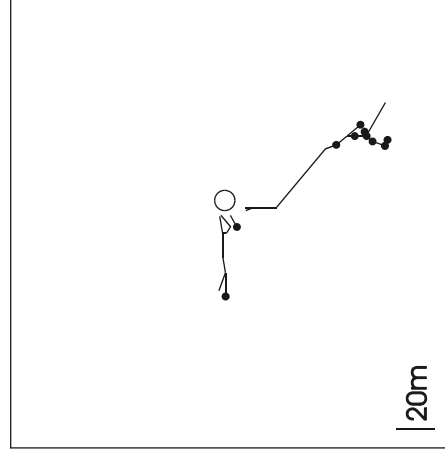
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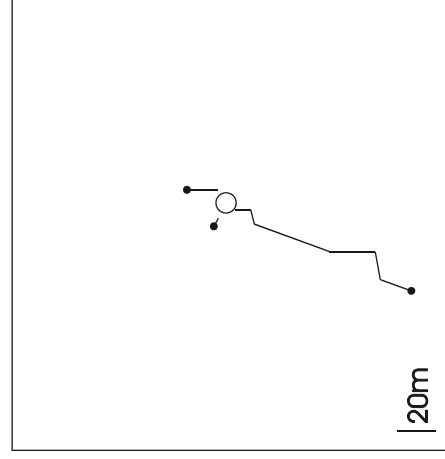
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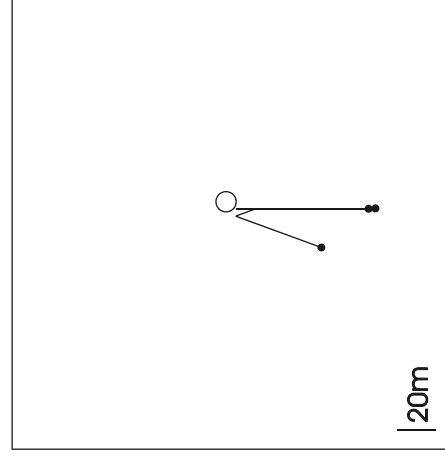
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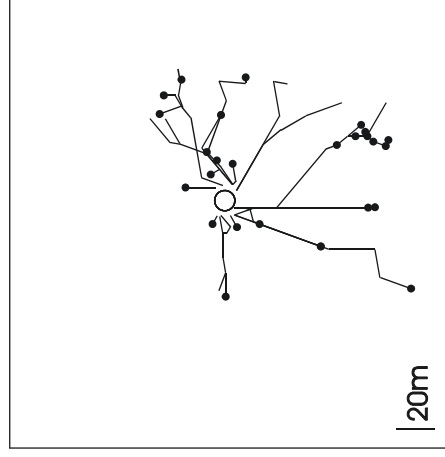
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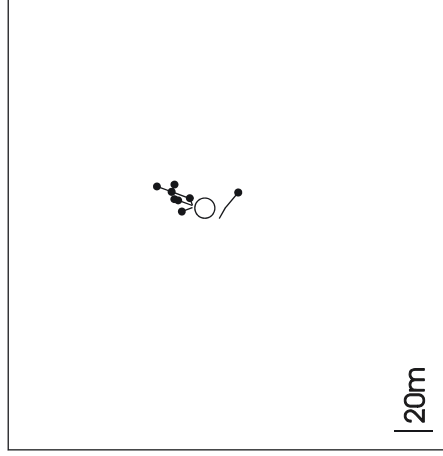


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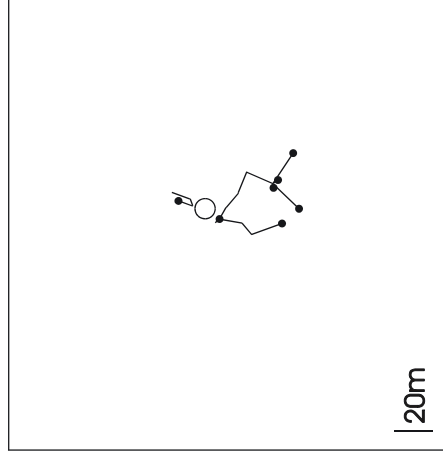


Appendix II-V. Foraging trails of *A. cephalotes* colony V at the edge of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

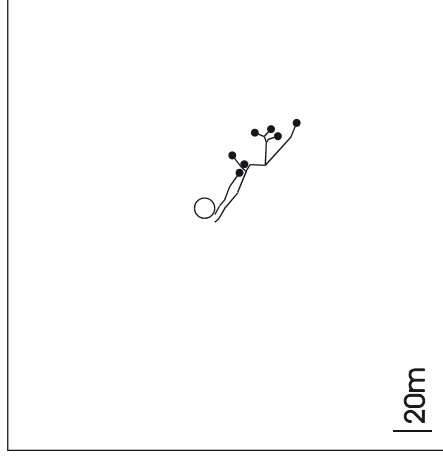
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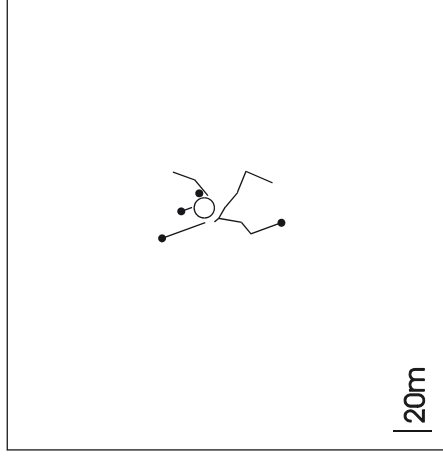
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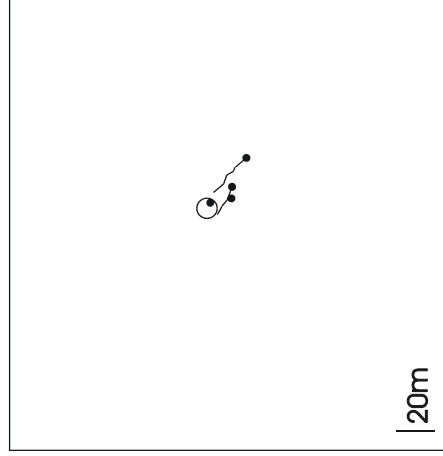
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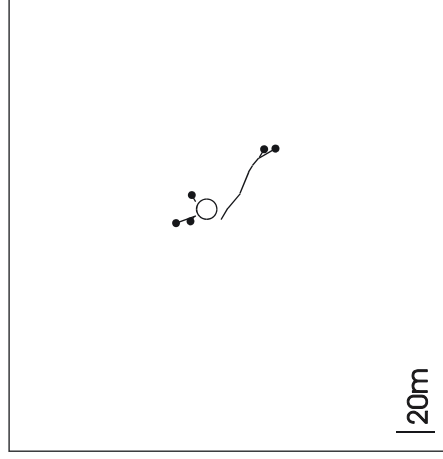
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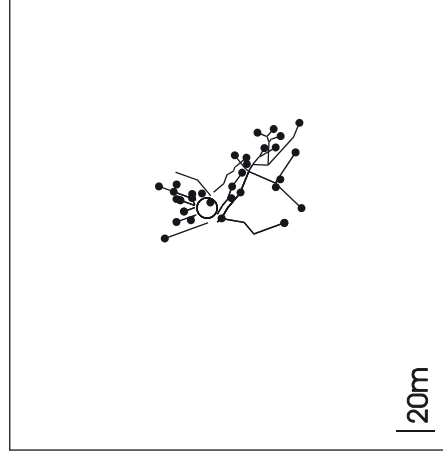
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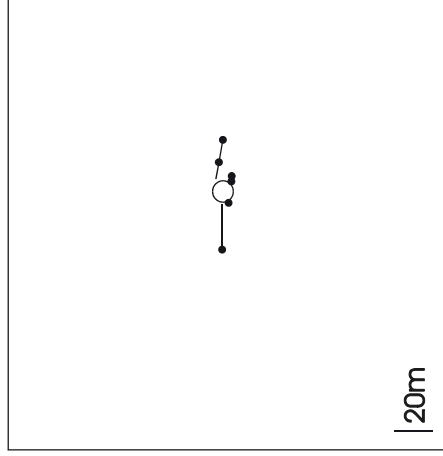


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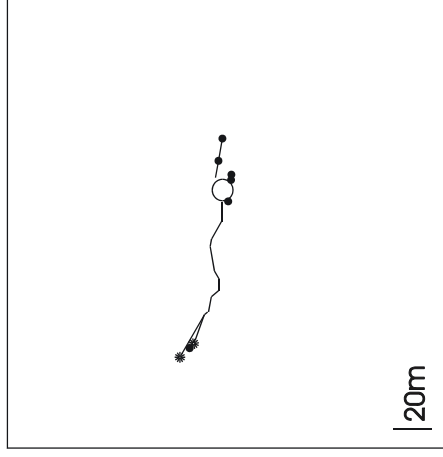


Appendix II-VI. Foraging trails of *A. cephalotes* colony VI at the edge of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

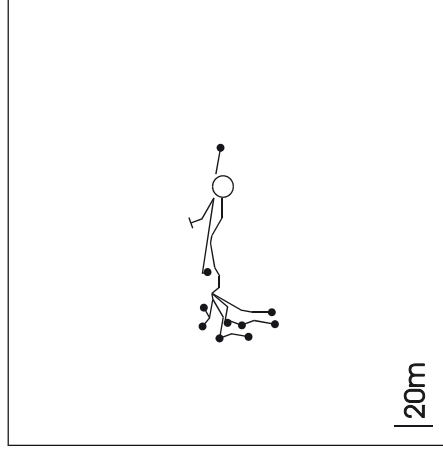
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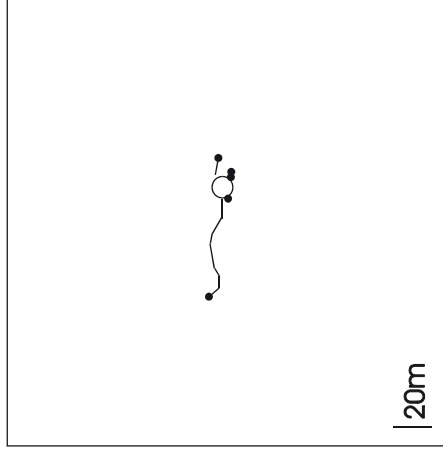
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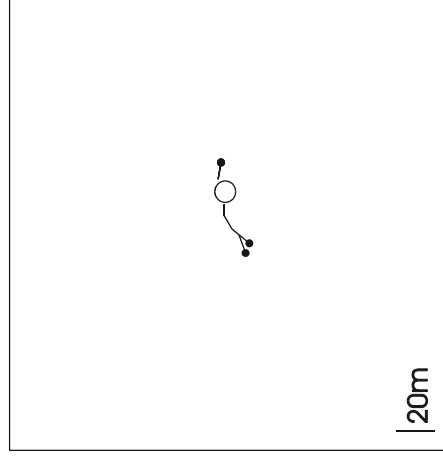
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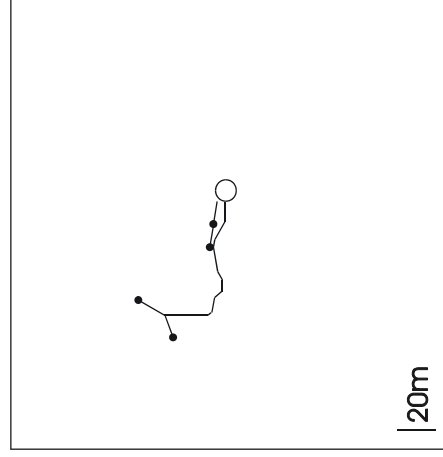
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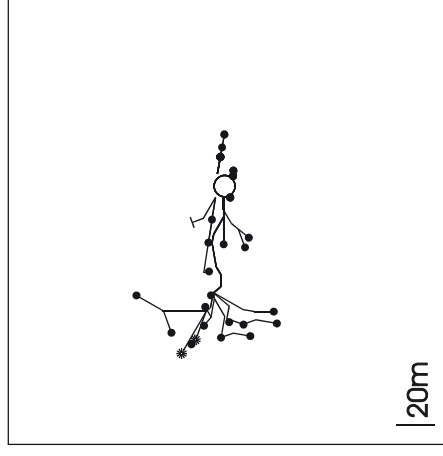
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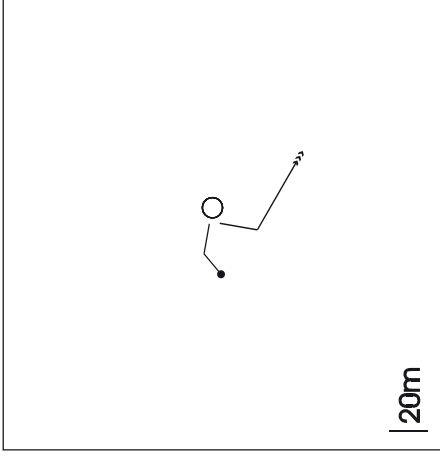


Annual

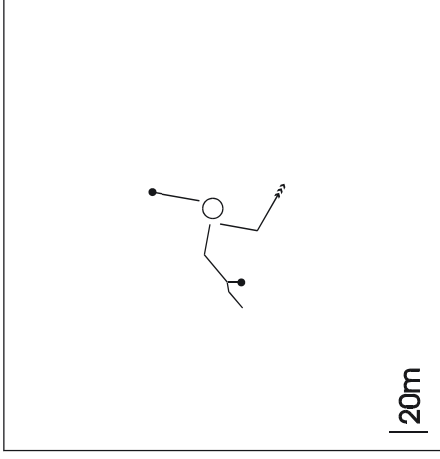


Appendix II-VII. Foraging trails of *A. cephalotes* colony VII at the edge of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees, arrows indicate harvested herbs in the open field.

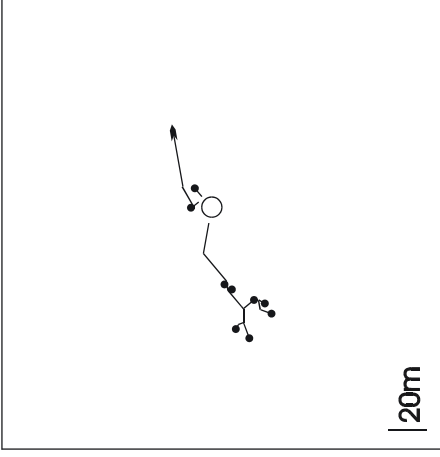
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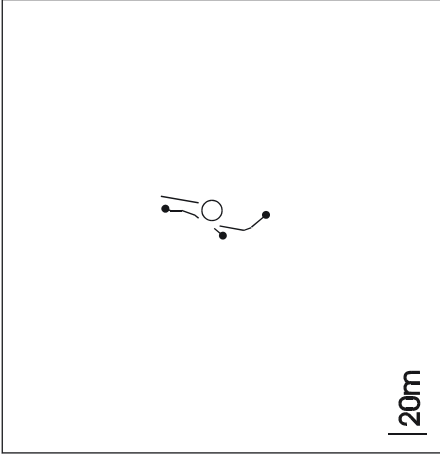
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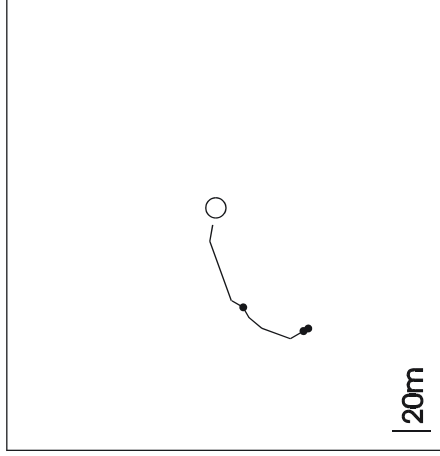
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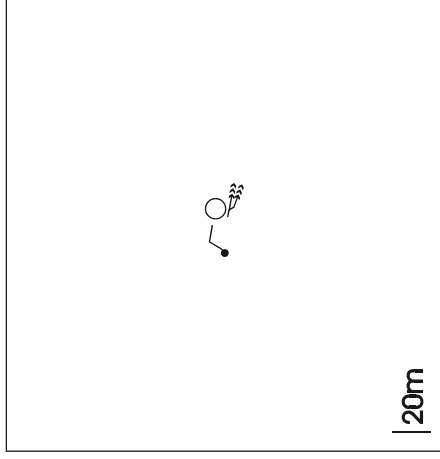
March 2003



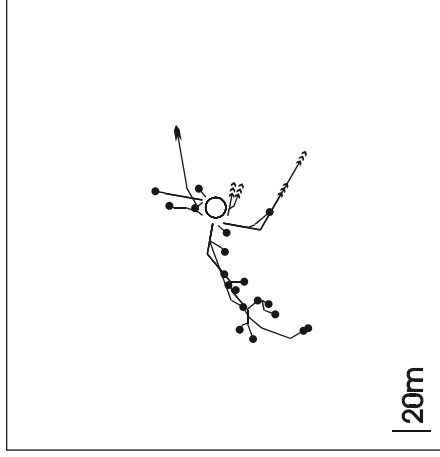
May 2003



July 2003

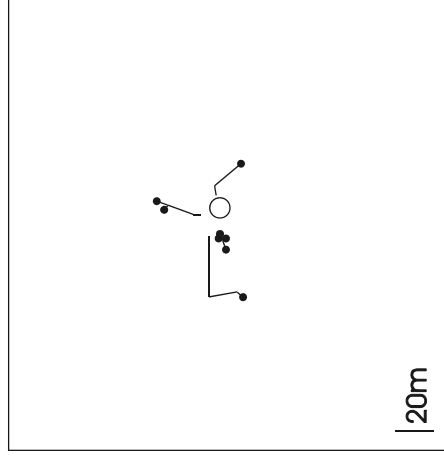


Annual

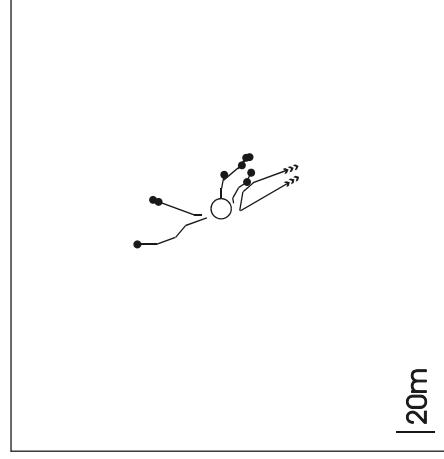


Appendix II-VIII. Foraging trails of *A. cephalotes* colony VIII at the edge of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees, arrows indicate harvested herbs in the open field.

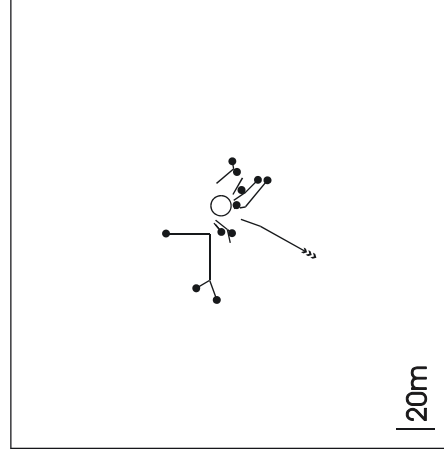
September 2002



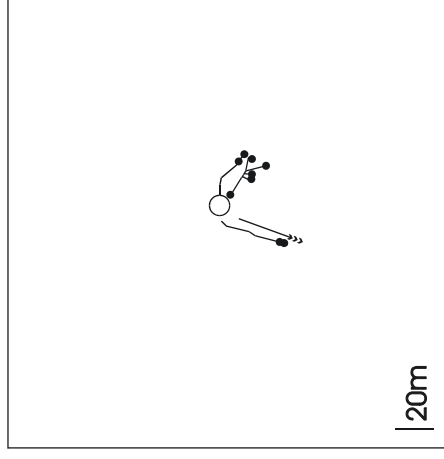
November 2002



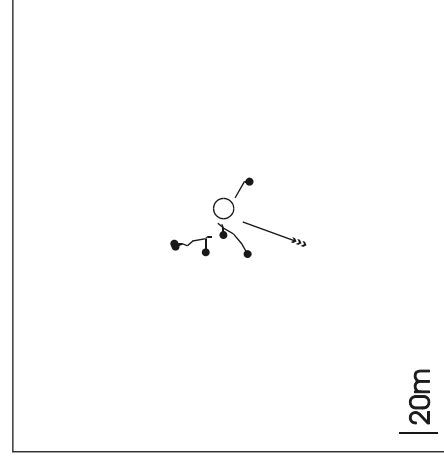
January 2003



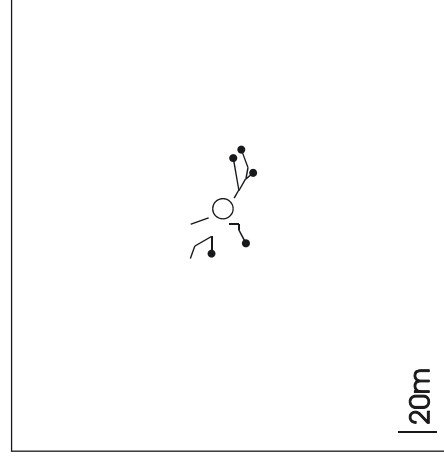
March 2003



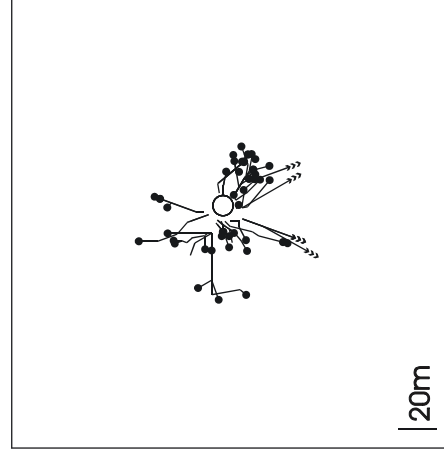
May 2003



July 2003

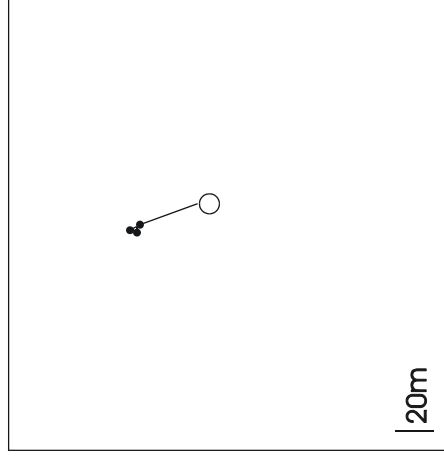


Annual

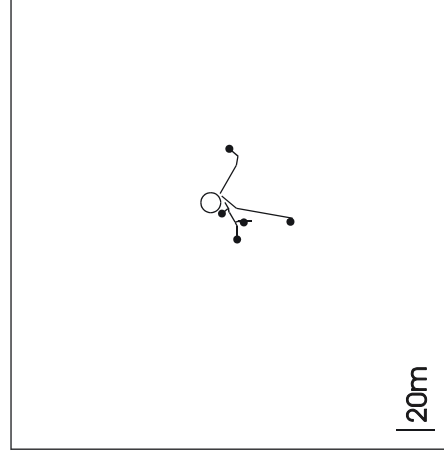


Appendix II-IX. Foraging trails of *A. cephalotes* colony IX at the edge of the continuous forest mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

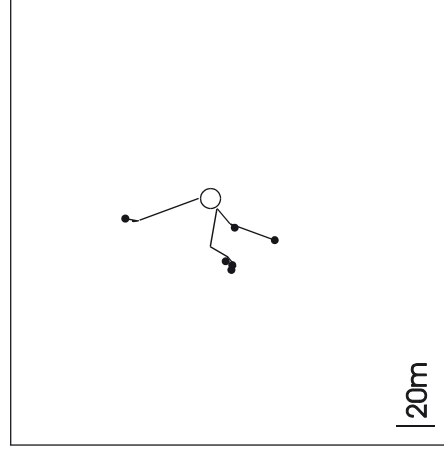
September 2002



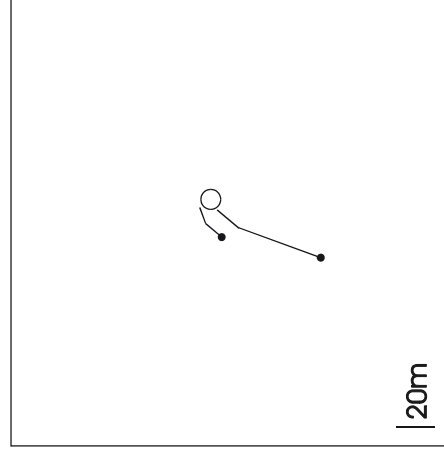
November 2002



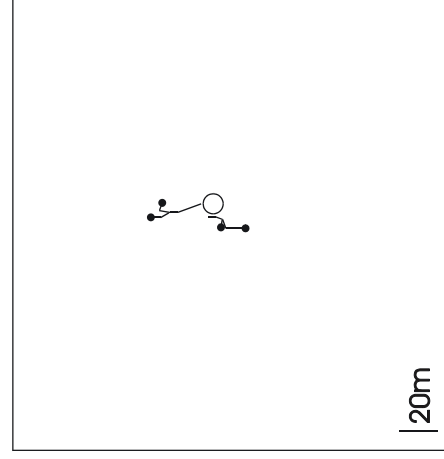
January 2003



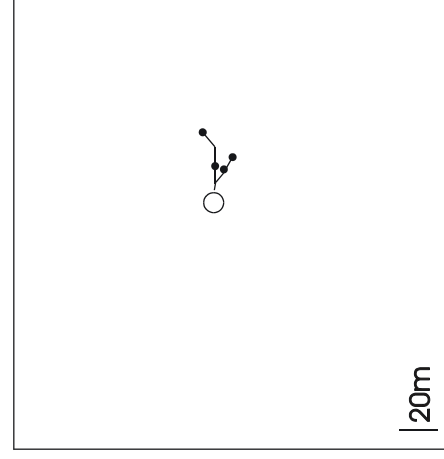
March 2003



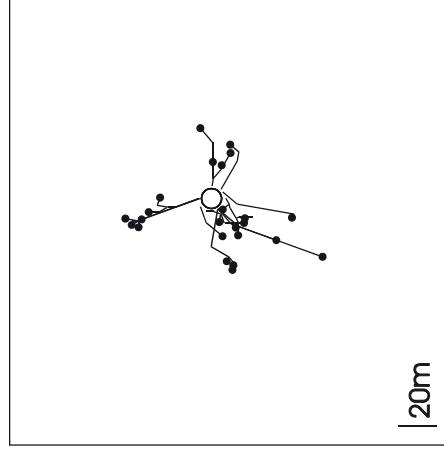
May 2003



July 2003

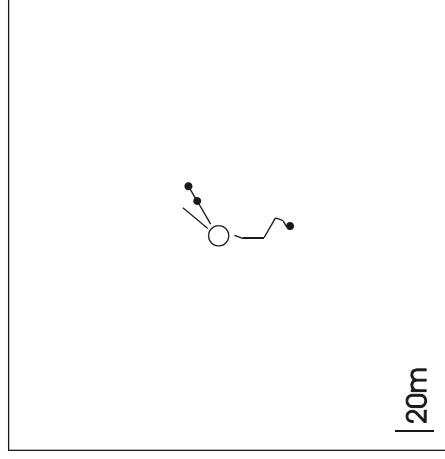


Annual



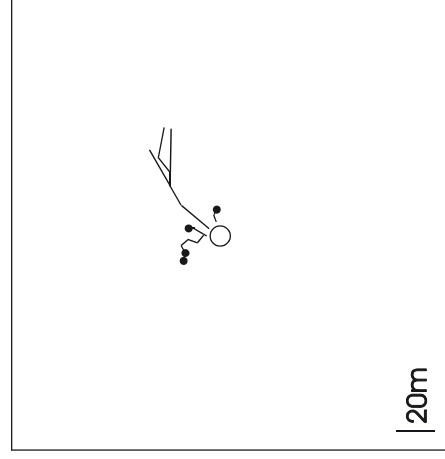
Appendix II-X. Foraging trails of *A. cephalotes* colony X in the interior of the forest fragment mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. *Lines* indicate foraging trails, *dots* indicate harvested trees, *stars* indicate harvested blossoms fallen on the forest floor.

September 2002



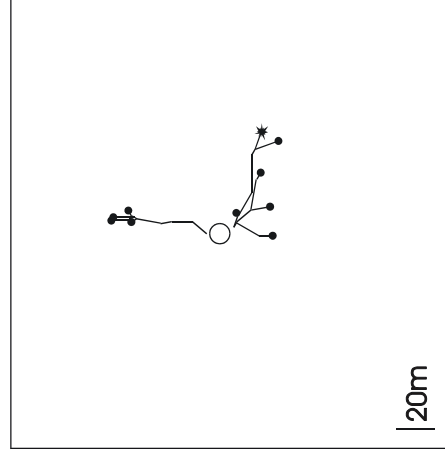
| 20m

November 2002



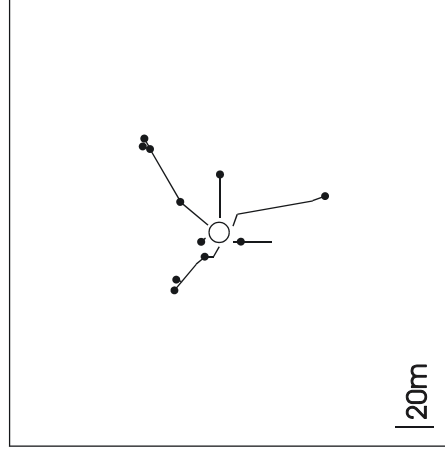
| 20m

January 2003



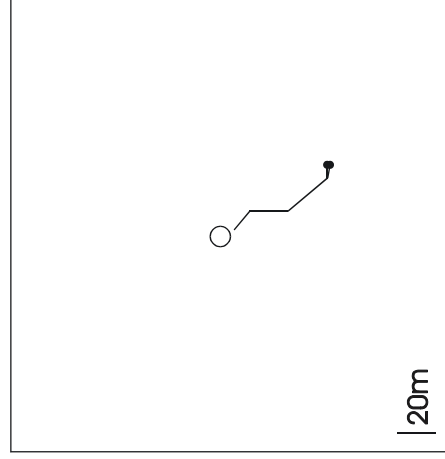
| 20m

March 2003



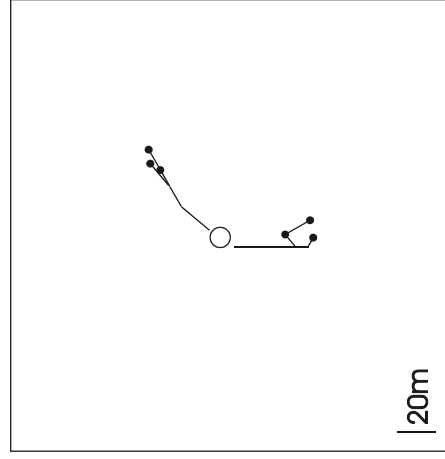
| 20m

May 2003



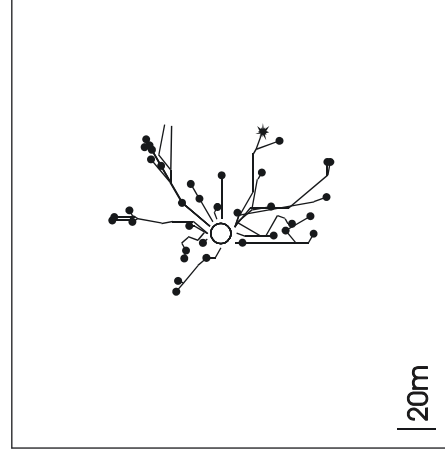
| 20m

July 2003



| 20m

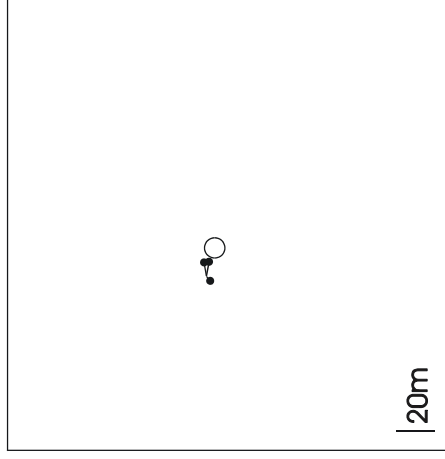
Annual



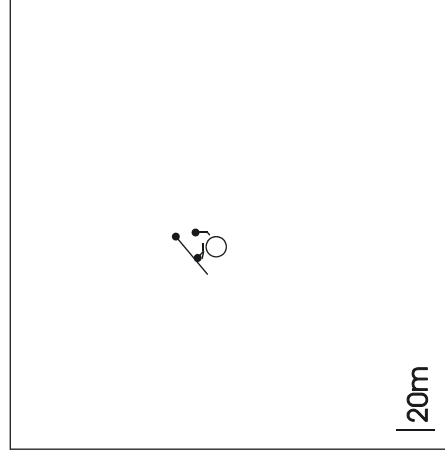
| 20m

Appendix II-XI. Foraging trails of *A. cephalotes* colony XI in the interior of the forest fragment mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

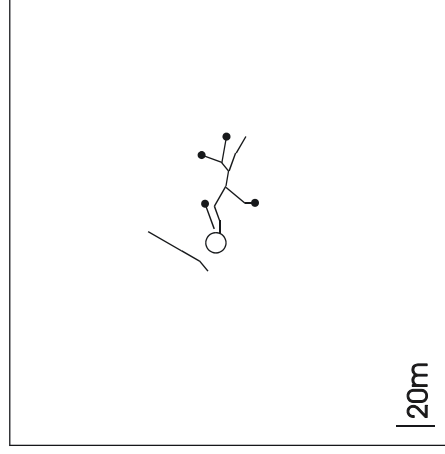
September 2002



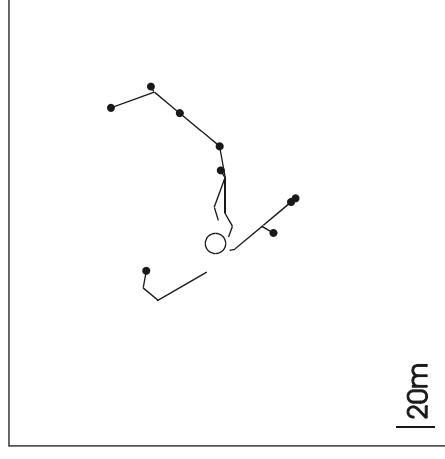
November 2002



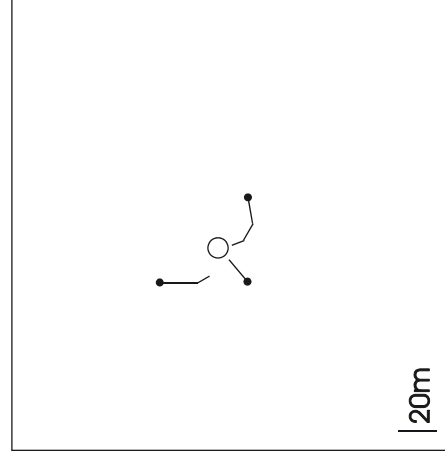
January 2003



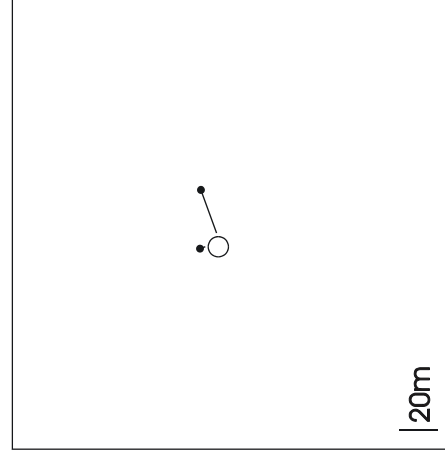
March 2003



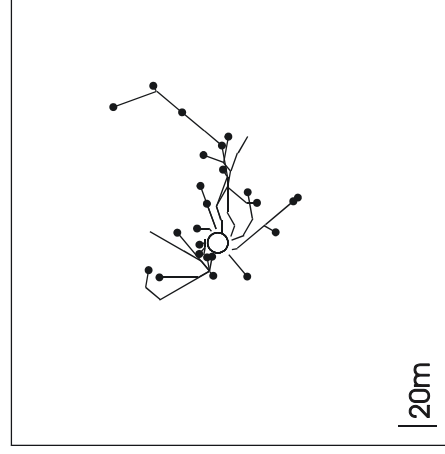
May 2003



July 2003

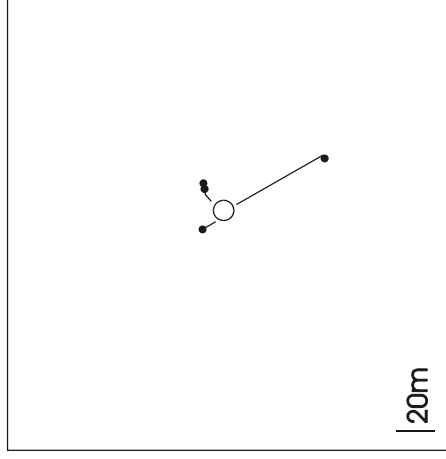


Annual

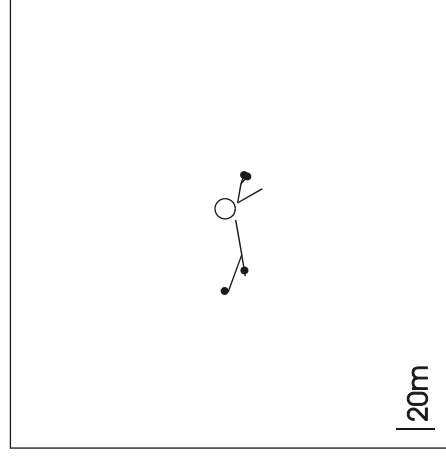


Appendix II-XII. Foraging trails of *A. cephalotes* colony XII in the interior of the forest fragment mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

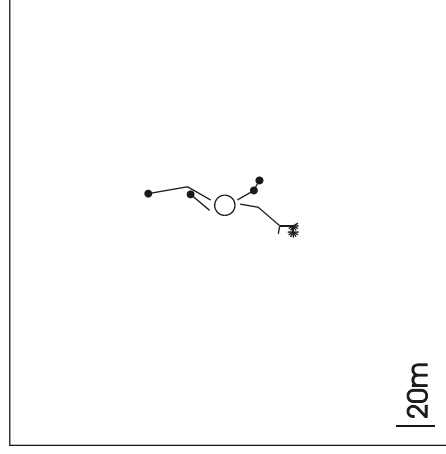
September 2002



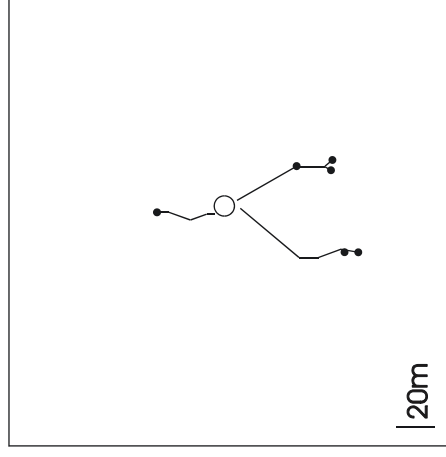
November 2002



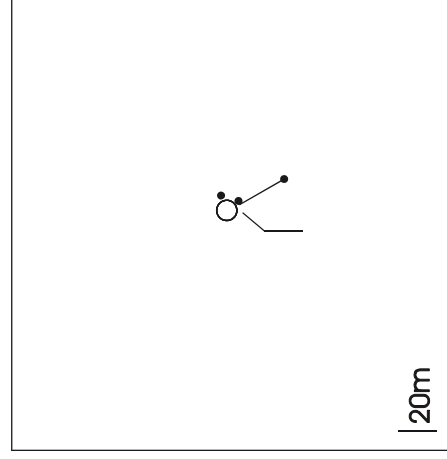
January 2003



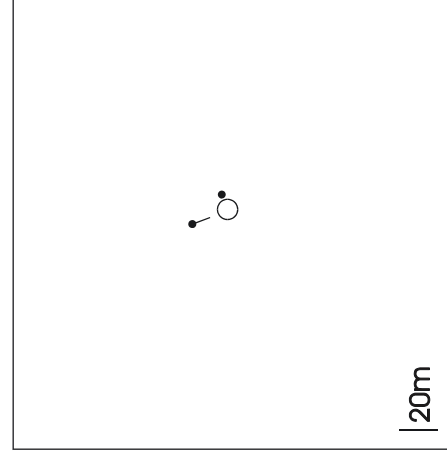
March 2003



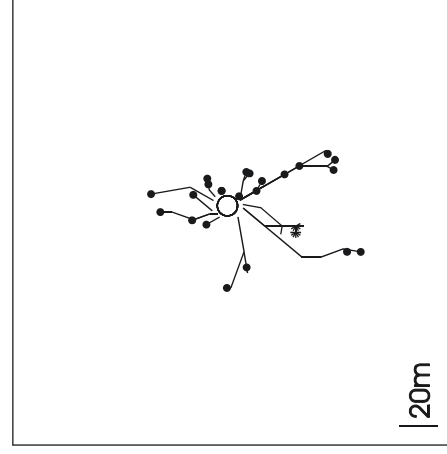
May 2003



July 2003

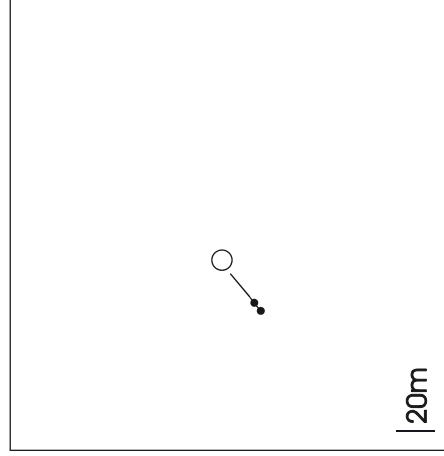


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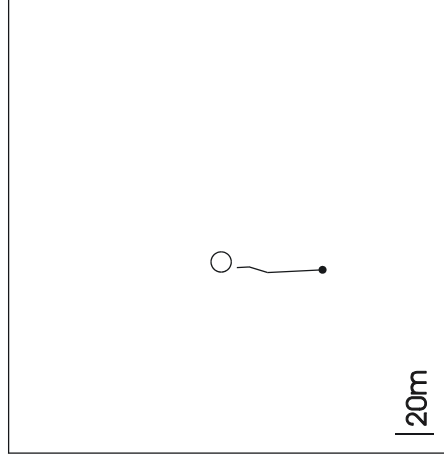


Appendix II-XIII. Foraging trails of *A. cephalotes* colony XIII in the interior of the forest fragment mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. Nest is indicated by the central circle. Lines indicate foraging trails, dots indicate harvested trees.

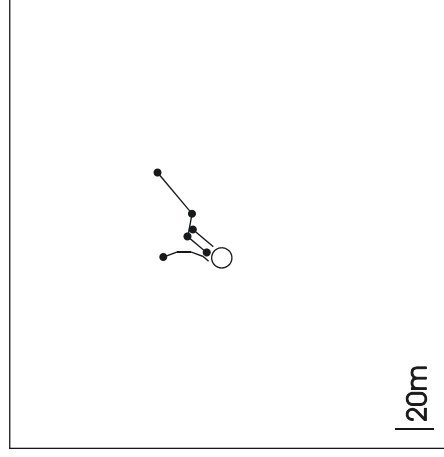
September 2002



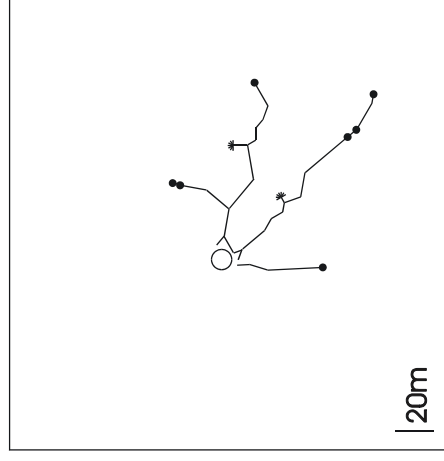
November 2002



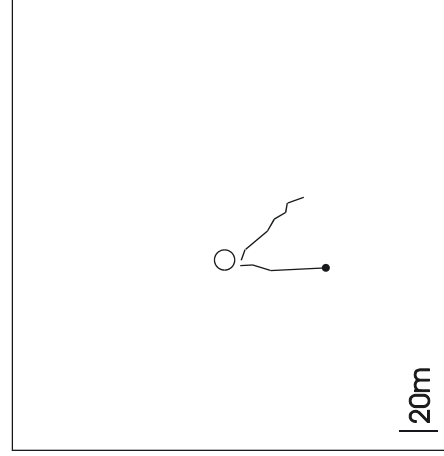
January 2003



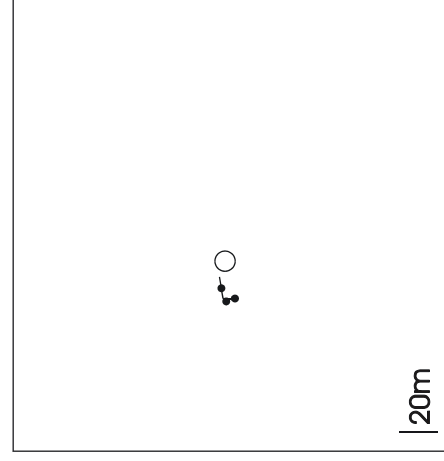
March 2003



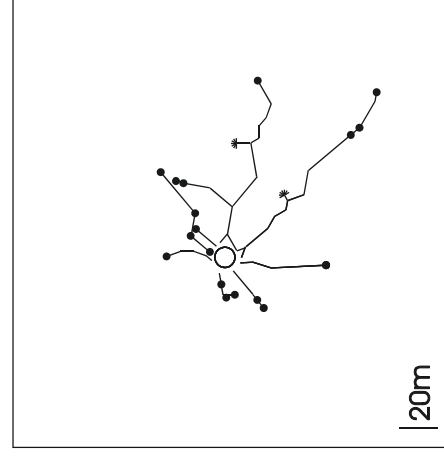
May 2003



July 2003

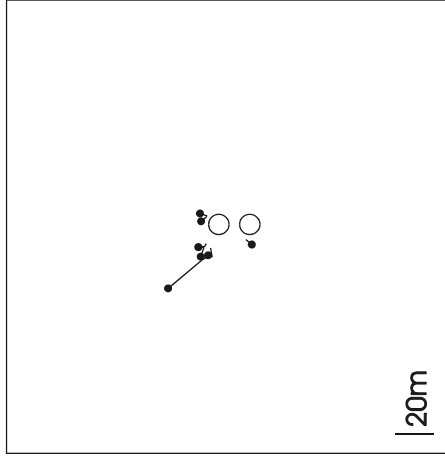


Annual

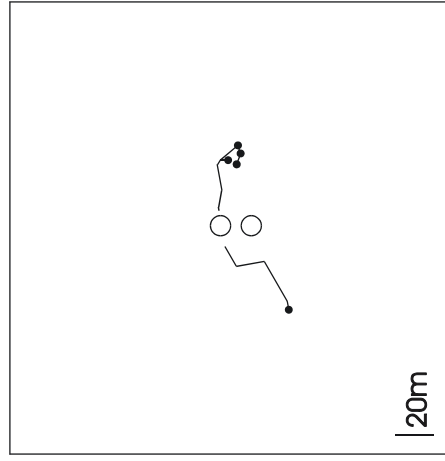


Appendix II-XIV. Foraging trails of *A. cephalotes* colony XIV in the interior of the forest fragment mapped at bimonthly intervals during one year (September 2002 – July 2003). Annual foraging area is achieved by cumulative plotting all observed months on the top of each other. The nest consisted of two distinct mounds indicated by the two central circles. Lines indicate foraging trails, dots indicate harvested trees.

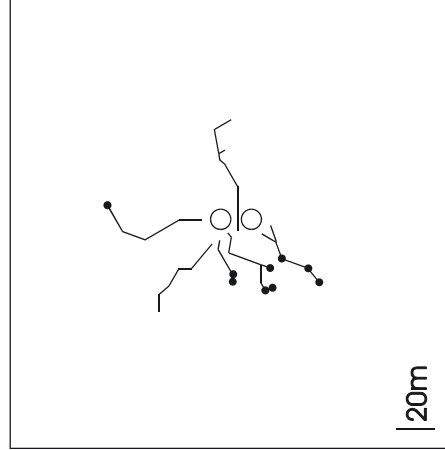
September 2002



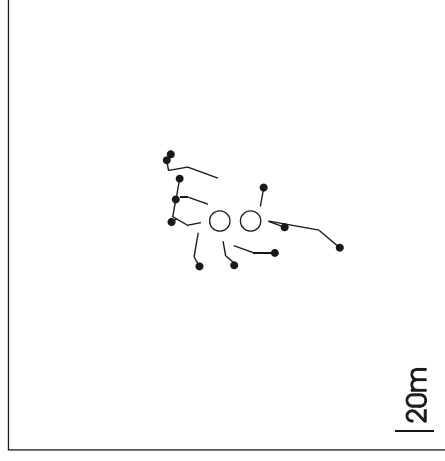
November 2002



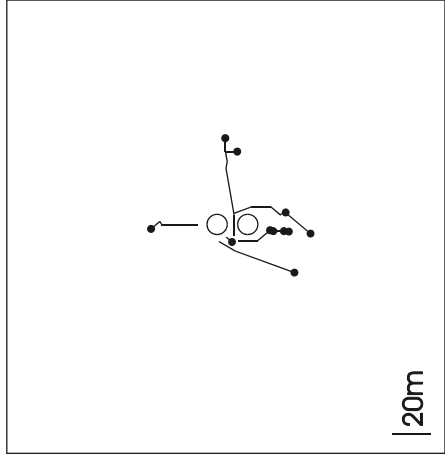
January 2003



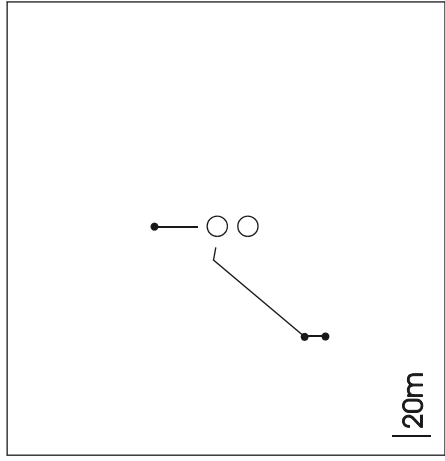
March 2003



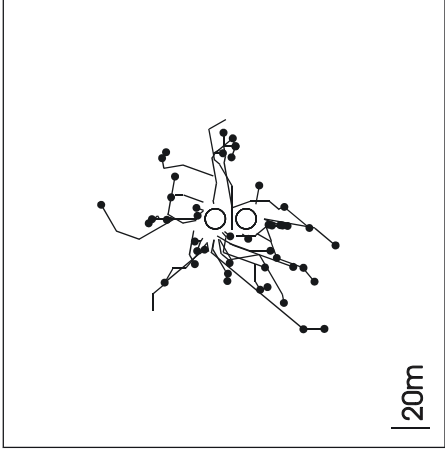
May 2003



July 2003



Annual



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Place of birth	Sonda, Estonia
Nationality	Estonian

Education and employment

2001 – 2005	Ph.D. studies at the Department of General Botany, Technical University of Kaiserslautern, Germany
2002 – 2004	Field work at the Federal University of Pernambuco (UFPE), Recife, Brasil
June, 2001	M.Sc. at the Department of Botany and Ecology, University of Tartu, Estonia
2000 – 2001	Scholarship holder at the Swiss Federal University of Technology (ETH Zürich), Switzerland
June, 1999	B.Sc. at the Department of Botany and Ecology, University of Tartu, Estonia
1984 – 1985	Miina Härma Gymnasium, Tartu, Estonia

Publications

Urbas, P., Araújo M.V.Jr., Leal, I.R. and Wirth, R. Cutting more from cut forests – effects of habitat fragmentation on leaf-cutting ant herbivory in the Brazilian Atlantic forest. *Biological Conservation* (submitted).

Urbas, P., Zobel, K., 2000. Adaptive and inevitable morphological plasticity of three herbaceous species in a multi-species community: Field experiment with manipulated nutrients and light. *Acta Oecologica* 21, 139-147.

Ryser, P., Urbas, P., 2000. Ecological significance of leaf life-span among central-European grass species. *Oikos* 91, 41-50.

Contributions to scientific symposia

Urbas, P., Bieber, L., Leal, I.R., Nascimento, M.S., Wirth, R., 2004. What leaf-cutting ants want? Interplay between plant defensive compounds and sugar in the diet of a dominant herbivore (Poster). 17th annual meeting of Society for Tropical Ecology (GTÖ). Bayreuth, Germany.

Araújo, M.V.Jr., Jutras, M., Urbas, P., Wirth, R., Leal, I.R., 2003. Do leaf-cutting ants (*Atta laevigata*) reveal bigger herbivory rate in fragmented forests? (Poster). 6th Congress of Ecology of Brazil. Fortaleza, Brazil.

Costa, U.A.S., Urbas, P., Wirth, R., Leal, I.R., 2003. Effect of forest fragmentation on leaf-cutting ant (*Atta laevigata*) colony growth rate (Poster). 6th Congress of Ecology of Brazil. Fortaleza, Brazil.

Urbas, P., Meyer, N., Wirth, R., Leal, I.R., 2003. Forest fragmentation affects the quality of the harvest of a dominant herbivore – evidence from leaf traits. 54rd National Botanical Congress of Brazil. Belem, Brazil.

Urbas, P., Almeida, W.R., Barbosa, V., Falcão, P.F., Knoechelmann, C.M., Silveira, Ú.A., Vieira-Jr., M.A., Leal, I.R., Wirth, R., 2003. Increase of leaf-cutting ant colony density through forest fragmentation: a result of altered trophic structure? (Oral presentation). 16th annual meeting of Society for Tropical Ecology (GTÖ). Rostock, Germany.

Wirth, R., Almeida, W.R., Barbosa, V., Falcão, P.F., Knoechelmann, C.M., Silveira, Ú.A., Urbas, P., Vieira-Jr., M.A., Leal, I.R., 2003. Forest fragmentation process increases density of leaf-cutting ants in the Brazilian Atlantic rain forest (Poster). 16th annual meeting of Society for Tropical Ecology (GTÖ). Rostock, Germany.

Urbas, P., Falcão, P.F., Almeida, W.R., Vieira-Jr., M.A., Barbosa, V., Silveira, Ú.A., Knoechelmann, C.M., Leal, I.R., Wirth, R., 2002. Forest fragmentation affects leaf-cutting ant distribution density (Poster). 53rd National Botanical Congress of Brazil. Recife, Brazil.

ERKLÄRUNG

Hiermit versichere ich, dass ich die vorliegende Dissertation in allen Teilen selbständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Darüber hinaus erkläre ich, dass die vorliegende Dissertationsschrift weder vollständig noch teilweise einer anderen Fakultät mit dem Ziel vorgelegt worden ist, einen akademischen Grad zu erwerben.

Kaiserslautern, den 01. Dezember 2004

Pille Urbas