

Ecosystem engineering in fragmented forests

Edge-mediated hyper-abundance of leaf-cutting ants and resulting impacts on forest structure, micro-climate and regeneration

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Edge-mediated hyper-abundance of leaf-cutting ants
and resulting impacts on forest structure,
microclimate and regeneration

vom Fachbereich Biologie der Universität Kaiserslautern
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... answers to the key questions would come hard.
Everything is complicated. Species respond to fragmentation in idiosyncratic and unexpected ways, some of the latter representing novel physical and biological phenomena. Every species, it turns out, really is connected to everything else, ...

Edward O. Wilson

In his forward to “Lessons from Amazonia”, which synthesizes 20 years of experimental fragmentation research in the Brazilian Amazon.

Preface

The book at hand is a cumulative doctoral thesis written at the University of Kaiserslautern, Germany in the department of Plant Ecology and Systematics (Prof. Dr. Burkhard Büdel). The results presented are based mainly on research conducted in the Brazilian Atlantic Forest between 2005 and 2008 as part of an ongoing research cooperation of Dr. Rainer Wirth (Department of Plant Ecology and Systematics, University of Kaiserslautern) with Prof. Dr. Inara R. Leal and Prof. Dr. Marcelo Tabarelli (Department of Botany, Universidade Federal de Pernambuco, Recife, Brazil). Included are also results of some additional experiments conducted in the laboratories at the University of Kaiserslautern. This thesis is integrated into the “InTroFF-Project” which comprises a central part of the research conducted within the framework of the “Projeto Serra Grande”.

PROJETO SERRA GRANDE: Conservando o melhor do Centro de Endemismo Pernambuco. The Projeto Serra Grande was initiated in 2001 by the Center of Environmental Research in Northeast Brazil (Centro de Pesquisas Ambientais do Nordeste, CEPAN). The ongoing project is a joint venture of CEPAN, the Usina Serra Grande (a privately owned sugar cane plantation) and the University of Pernambuco in Recife, Brazil (Universidade Federal de Pernambuco,

UFPE) and is coordinated by Marcelo Tabarelli. The objective of the project is to develop and implement management regimes for natural resources that guarantee the protection of biodiversity and the integrity of the Atlantic Forest within the holding of the Usina Serra Grande. Thereby, the project aims to develop a regional model for sustainable development and use of natural resources in the area. Within the framework of the Projeto Serra Grande a range of often interconnected research projects are integrated, which describe the local diversity of various species groups and investigate ecosystem functioning in the heavily fragmented Atlantic Forest. Central results have been published in a book describing the species composition of the Atlantic Forest of Northeast Brazil (Pôrto et al. 2005. Diversidade Biológica e Conservação da Floresta Atlântica ao Norte do Rio São Francisco. Ministério do Meio Ambiente Brasília, Brasil) and can be accessed on the website of CEPAN (<http://www.cepan.org.br/>) Among the specific research projects integrated into Project Serra Grande is “InTroFF”.

INTROFF (Interações troficas em florestas fragmentadas) - This project (coordinated by Inara Leal and Rainer Wirth) examines the consequences of habitat fragmentation on food webs using the trophic cascade plant - fungus/leaf-

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cutting ant - predator/parasite as a model system. The consequences of habitat fragmentation on food webs had been completely neglected in fragmentation related research in the past, although the importance of trophical interactions for local species coexistence and biodiversity is increasingly acknowledged. The underlying causes for an increase of leaf-cutting ant densities with increasing habitat disturbance were assessed in a doctoral thesis by Pille Urbas (2001-2004), which identified control by both resource availability (bottom-up forces) and predation and parasitism (top-down forces) to be less effective in fragmented compared to continuous forests.

The project has focused in the beginning on fragmentation induced changes in the behavior and ecology of leaf cutting ants and has been extended in 2005 to incorporate the complementary view with a focus on effects of leaf-cutting ants in a fragmented forest. Specifically, we study the consequences of high leaf-cutting ant

nest densities in fragmented forest habitats on microclimate and forest regeneration, which is part of the present thesis.

THE PRESENT THESIS is organized into five major sections: “Setting the scene”, “*Atta* in a fragmented forest”, “Bottom up control of *Atta*”, “Nest effects of *Atta cephalotes*”, and a concluding “Synthesis”. In the first section the reader is introduced into the theory and basics underlying this thesis followed by a review of the response of herbivores to fragmentation and forest edge creation. Chapters on *Atta* in a fragmented forest will present spatial and temporal patterns of leaf-cutting ant densities in a fragmented forest followed by a chapter on a possible bottom-up mechanism controlling *Atta* densities. The forth section will cover the effects leaf-cutting ant nests have on forests. The thesis concludes with a synthesis of the findings of this thesis about interaction effects of forest fragmentation and leaf-cutting ants.



Acknowledgements

This thesis would not have been possible without numerous people to whom I am deeply grateful for their help, support and encouragement throughout the last years.

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Financial and logistic support for this study was received by several agencies.

The central workshop of the University of Kaiserslautern helped to plan and constructed radiation shields for measuring equipment and the electronics workshop of the university designed and built amplifiers that were essential for the successful microclimatic measurements presented in this study.

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A.F.W. SCHIMPER-STIFTUNG

für ökologische Forschungen außerhalb Europas
– von Heinrich und Erna Walter –



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PART I

Setting the scene:

1

Introduction

The modern-day world is seeing escalating levels of habitat loss and fragmentation, particularly in the tropical rain forests due to unprecedented rates of deforestation (Laurance and Peres 2006). While most research in the past has concentrated on the documentation of a loss of biodiversity with increasing levels of fragmentation, the recent focus in fragmentation research has shifted towards more mechanistic questions in order to enable predictions about the future of fragmented forests (reviewed e.g. in Laurance 2008). One of the emerging patterns is that much of the ecological alteration faced by fragmented forests can be assigned to edge-effects (Tabarelli and Gascon 2005). There is an increasing sense of urgency and awareness that understanding the edge-induced disruption of species interactions are of fundamental importance for a more complete and profound perspective on the impacts of habitat fragmentation and the ecology of fragmented landscapes (Fagan et al. 1999; Hunter 2002).

Leaf-cutting ants of the genus *Atta* are dominant herbivores in the Neotropics (Wilson 1986) and have been identified as keystone-species (Fowler et al. 1989). Based on the observation of the disturbances these ants can cause in tropical forests they have been named ecosystem engineers (Rico-Gray and Oliveira 2007; Wirth et al. 2003), which is an organism controlling the availability of resources for other organisms by altering their physical environment (Jones et al. 1994). In contrast to other prominent ecosystem engineers that have been substantially decimated by human activities (e.g. beavers and elephants: Dunham 2008; Hood and Bayley 2008; Syphard and Garcia 2001) some species of leaf-cutting ants profit from anthropogenic landscape alterations and increase in abundance with increasing agricultural land-use, deforestation and/or disturbance (Fowler et al. 1986; Jaffe and Vilela 1989; Jonkman 1979). Thus, leaf-cutting ants are very suitable as a model to investigate the potentially cascading effects caused by herbivores and ecosystem engineers in modern anthropogenic landscapes following fragmentation and to study their coexistence with humans, the most pervasive and dominating ecosystem engineers on earth.

This thesis aims to describe the interplay between consequences of forest fragmentation for leaf-cutting ants and resulting impacts of leaf-cutting ants in fragmented forests. In doing so, I hope to (1) advance the understanding of the biology and functioning of fragmented ecosystems, (2) quantify the impact of leaf-cutting ant activities in this type of landscapes, (3) prove the importance of leaf-cutting ants as ecosystem engineers and, thereby, to (4) provide an example of an ecosystem engineer that in many ways differs from classic examples and thus might be of interest for the advancement of the theoretical concept of ecosystem engineering and the knowledge how particular organisms can shape ecosystems and communities.

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ECOSYSTEM ENGINEERING: THEORY AND CONCEPTS

The concept of ecosystem engineering was formally introduced by Jones et al. (1994; 1997b) who defined ecosystem engineers as “organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats”. Jones and colleagues stated that while species interactions in general had been identified as a principal force structuring ecosystems and despite a wealth of examples of organisms modifying or creating habitats, there was a conspicuous lack of systematic description and definition of such processes. They called the process “ecosystem engineering” and the organism responsible “ecosystem engineer”. In addition, they differentiated between autogenic engineers that change the environment via their own physical structures (i.e. their living or dead tissues) and allogegenic engineers that change the environment by transforming living or non-living materials from one physical state to another, by mechanical or other means. While there was some debate over the term “ecosystem engineer” (e.g. Jones et al. 1997a; Power 1997) it is now frequently used and there is an extensive list of examples for organisms that impact their environment in the defined way (see e.g. Hastings et al. 2007; Jones et al. 1994 and references therein). Even though it seems hard to come up with an example of important autogenic engineers spontaneously, there can be no doubt that trees forming a forest do much more than to provide food and directly compete for resources (e.g. cast shade, moderate temperature, increase humidity, stabilize soils, provide shelter, etc. Jones et al. 1997b). Prominent and well known examples for drastic habitat modifications by allogegenic engineers are easier to find: For example, the dam constructions by beavers (*Castor canadensis*) in Europe and North America and the destruction of trees and shrubs by elephants (*Loxodonta africana*) in African woodlands and savannahs (Naiman 1988). Similarly, animals much smaller in size can act as ecosystem engineers, above all the frequently mentioned ants (Elms 1991; Lobry de Bruyn and Conacher 1994; Rico-Gray and Oliveira 2007; Wirth et al. 2003) and termites (Dangerfield et al. 1998). In respect to ants, the concept of ecosys-

tem engineering is especially useful to highlight their more hidden and indirect effects on ecosystems in view of the multitude of interactions that closely tie ants to virtually all terrestrial ecosystems (Rico-Gray and Oliveira 2007).

Only some engineers cause dramatic effects, while ecosystem engineering with small or cryptic effects is virtually ubiquitous (Jones et al. 1997b). In fact, it is difficult to imagine a life strategy that does not in some way lead to a degree of modification of the abiotic environment. Therefore, it was proposed to restrict the use of the term ecosystem engineer to organisms that generate “significant influences on ecological processes” (Reichmann and Seabloom 2002). Yet, the term ecosystem engineer is not synonymous with “keystone species” (Wilby 2002). The concept was created to formalize interactions among organisms that are mediated by the physical environment, without reference to effect size (Wilby 2002). In some respect the concept of ecosystem engineering is analogous to trophic interactions, in which every organism participates but not every organism is a keystone herbivore or predator. Therefore, it might be of limited value just to name an organism ecosystem engineer without quantifying the size of the influence and possible impacts. Given that physical alterations of the environment by organisms are widespread, the most productive research in this field is to quantify the strength of the impacts of these interactions on ecological systems (Jones et al. 1997b) but because studies of this type are extremely laborious they have rarely been conducted, leaving an open field for investigations. Also the integrated description of trophic interactions and ecosystem engineering in “interaction webs” is a very promising and needed approach to better understand the functioning of ecosystems (Wilby et al. 2001). Especially in anthropogenically modified landscapes, where a multitude of disturbances can alter trophic and non-trophic interactions in different synergistic or antagonistic ways, the formal application of the idea of ecosystem engineering can yield new insights into the role of species played for ecosystem functioning.

The concept of ecosystem engineering provides a clear framework by distinguishing between interactions between organisms and the

abiotic environment (the engineering *per se*) and the consequences of these processes for other organisms. In its complete form, studies on ecosystem engineering thus involve two distinct but linked hypotheses (1) an organism influences a set of abiotic conditions and (2) these altered conditions in turn influence a set of biological traits (Hastings et al. 2007). When, as a consequence, the species composition in the ecosystem is altered, ecosystem engineering functions as an ecological filter.

ECOLOGICAL FILTERS – Environmental filters are a metaphor useful to describe the order of invasion and establishment of species in regenerating sites as was explicitly formulated by Mueller-Dombois and Ellenberg (1974). Research in the following decades demonstrated that beside abiotic (environmental) filters also biotic filters are important determinants of the species composition of an area. This gave rise to the term of ecological filters or assembly rules (Keddy 1992; Weiher et al. 1998; Weiher and Keddy 1999).

Generally speaking, ecological filters represent processes that are of importance in selecting species from the potential species pool to contribute to the biota (framework of pools and filters sensu Geho et al. 2007; Keddy 1992). In this framework one assumes that the actual species composition is a subset of the total diversity of species existing, which is selected in a three step process by environmental and dispersal constraints and interactions among the species within a pool (Fig. 1). In a stable ecosystem the functioning of these filters causes the species composition to be reasonable constant, but all filter effects can be drastically altered during and in the aftermath of disturbances. Historically, ecologists viewed the natural world as inherently stable assuming that any disturbance would result in an ordered successional progression leading back to the original climax state (the equilibrium paradigm). Yet, ecosystems are marked by frequent disturbances (some natural and many man-made) that continually push them in alternate directions. This was acknowledged in the nonequilibrium paradigm, which implies (1) that ecological equilibria do exist but are scale-dependent and embedded in non-equilibrium conditions, (2) that predictable endpoints to the successional process are rare, (3)

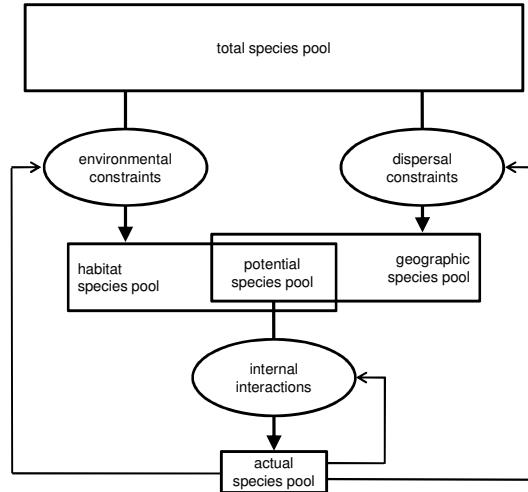


Figure 1: Schematic representation of changes to species pools during three stages of ecological filtering (reproduced with modifications from Belyea 2004). Boxes represent species pools; solid-headed arrows represent the determinants (dispersal and environmental constraints and internal interactions) for the inclusion into each pool; open headed arrows represent feedbacks of the biota onto the filters. Of the total species pool only a subset (geographic species pool) will arrive at the site, either by dispersal or by emergence from a propagule bank. Species in another subset (habitat species pool) are capable of establishing under the environmental conditions at the site. The intersection of these two subsets (potential species pool) includes species that arrive at the site and could establish viable populations. Finally, a whole suite of biotic interactions among the species like competition, facilitation, trophic interactions, and others determines which species form the actual species pool. Note how the established species feed back to the filters and modify for example the dispersal or environmental constraints.

that multiple stable states may exist, and (4) that some quasi-stable states can persist for long periods (Hobbs and Norton 2004). In light of this uncertainty about the nature of ecosystems it is of fundamental importance to understand the functioning of ecological filters and how these filters are distorted in human disturbed ecosystems in order to forecast future developments and derive managing guidelines for conservation and restoration (Temperton et al. 2004). One focus area for such attempts are tropical rain forests that are very suitable to study ecological filters because of the high biodiversity and the wealth of species interactions. At the same time these forests are among the world's most threatened ecosystems because of various human activities coupled with a high population pressure in tropical countries causing alarming levels of forest destruction.

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FRAGMENTATION OF TROPICAL FORESTS

Habitat fragmentation, and the consequent creation of artificial forest edges, is one of the most pervasive and disturbing results of present-day human land use dynamics (Aguilar et al. 2006; Whitmore 1997) and the topic of habitat fragmentation has acquired an increasing importance in the context of tropical forests over the last three decades (e.g. Bierregaard Jr. et al. 2001; Laurance and Bierregaard Jr. 1997; Laurance et al. 2002; Schelhas and Greenberg 1996). Fragmentation is commonly defined as a process wherein continuous habitats are divided into smaller remnants isolated from each other by a matrix that is different from the original habitat (Fahrig 2003). Initial research on fragmentation was inspired by the equilibrium theory of island biogeography (MacArthur and Wilson 1967) and research interest was fueled by the SLOSS debate (Are a single large or several small (SLOSS) reserves a superior mean for conserving biodiversity?; see Simberloff and Abele 1982). In conclusion, a number of studies examined the general question of a “minimum critical size” of protected areas and tried to extract conservation guidelines (Tabarelli et al. in press). Recently, the focus in fragmentation research has shifted towards more mechanistic questions in order to enable predictions about the future of fragmented forests (reviewed e.g. in Laurance 2008). While most research has focused on the documentation of a loss of biodiversity in fragmented landscapes minor attention has been devoted to species interactions in fragmentation-related research (reviewed by Debinski and Holt 2000; Hobbs and Yates 2003). Yet there is an increasing sense of urgency and awareness that edge-induced disruptions of species interactions are of fundamental importance for a more complete and profound perspective on the impacts of habitat fragmentation and the ecology of fragmented landscapes (Fagan et al. 1999; Hunter 2002).

RATES OF DEFORESTATION AND THE FUTURE WORLDWIDE SCENARIO – The last two decades have seen escalating levels of habitat loss and fragmentation, particularly in the tropical rain forests due to unprecedented rates of tropical deforestation (Laurance and Peres 2006). In the Brazilian Amazon and likewise in tropical Asia

deforestation has reached rates of more than 2 million ha/yr (Wright 2005). In the future, the relentless growth of human populations and economy will continue to alter tropical landscapes, likely causing the conversion of most tracts of old-growth forest into assemblages of small fragments and regenerating forest patches (Aide and Grau 2004; Wright 2005) embedded in a human-managed, harsh matrix (Tabarelli et al. 2004; Tabarelli et al. in press). This type of anthropogenic and highly fragmented landscape is already predominating across many previously forested tropical countries (Corlett 2000; Harvey et al. 2008; Sodhi et al. 2004). Consequently, the remaining forest has been in the largest parts drastically altered by fragmentation causing alarming levels of species extinction.

LOSS OF BIODIVERSITY – The most frequently invoked effect of habitat fragmentation is a drastic loss of biodiversity (e.g. Benitez-Malvido and Martinez-Ramos 2003; DeSouza et al. 2001; Fahrig 2003; Krisko 2000; Santos et al. 2008; Tabarelli et al. 2004; Turner 1996). Generally area effects cause a loss of biodiversity in small fragments since species have minimum patch size requirements (DeSouza et al. 2001). In addition some species specific risks to disappear in fragmented landscapes have been elucidated. Species at higher trophic levels (Holt et al. 1999), with lower mobility (Wright 1981), with greater ecological specialization (Krauss et al. 2003) and with greater taxonomic age (Ricklefs and Bermingham 2001) tend to respond stronger negatively to fragmentation than those with opposite characteristics (Laurance 2008). On a whole fragmented tropical forests tend to turn into impoverished and often early successional systems (Oliveira et al. in press; Tabarelli et al. in press). The processes driving these changes can be assigned into two groups of mechanisms, namely (1) the fragmentation effects *per se* and (2) edge effects.

FRAGMENTATION EFFECTS – The conversion of previously continuous habitat into smaller remnants embedded into a newly created matrix causes an inevitable loss of habitat (Fahrig 2003). In addition, the remaining habitat is divided into various smaller areas with different

degrees of isolation (i.e. habitat fragmentation *per se sensu* Fahrig 2003; Gascon et al. 2001). Fragmentation promotes rapid and predictable shifts in patterns of biological organization on population to ecosystem level due to a suite of fragmentation-related processes including habitat loss (area effects), sample effects (due to non-random clearing of forests), creation of forest edges, rupture of biological connectivity, subdivision/isolation of populations, and post-isolation proliferation of invasive species (Fahrig 2003; Laurance 2008; Laurance et al. 2002; Laurance et al. 2006). Moreover, tropical forest fragmentation facilitates and usually operates simultaneously with other human-induced disturbances such as logging, fire, and hunting (Laurance and Cochrane 2001; Peres 2001). In combination most of these alterations lead to pronounced detrimental consequences for ecosystem functioning (*i.e.* energy flux, nutrient cycling, hydrological budgets) and the long-term persistence of biodiversity in anthropogenic landscapes (Bierregaard Jr. et al. 2001; Laurance and Bierregaard Jr. 1997). Finally, intensity and magnitude of fragmentation-induced changes are greatly modulated by the spatial arrangement of forest fragments (landscape configuration) and the matrix harshness (Ferraz et al. 2007; Laurance et al. 2002; Tabarelli and Gascon 2005). Although the total effect caused by habitat fragmentation results from a myriad of processes (as listed above), much of the ecological alteration faced by fragmented forests (e.g. disruption of species interactions, species loss, biomass collapse, exotic species invasion) can be assigned to edge-driven changes or edge-effects (D'Angelo et al. 2004; Saunders et al. 1991; Tabarelli and Gascon 2005).

EDGE EFFECTS INCLUDING SECOND ORDER EFFECTS & CASCADES – The diverse physical and biotic changes resulting from the occurrence of abrupt and artificial margins are referred to as edge effects (Bierregaard et al. 2001), which greatly result from differences in structural complexity and biomass between the juxtaposed ecosystems, the ‘patch contrast’ *sensu* Harper et al. (2005). Recently published reviews (e.g. Foggo et al. 2001; Harper et al. 2005; Hobbs and Yates 2003; Laurance et al. 2002; López-Barrera et al. 2007; Murcia 1995; Saunders et al. 1991; Yahner 1988) have revealed an extensive suite of

edge-effects on forest remnants (for a compilation see also Fig 2).

Compared to the forest interior, the forest edge is a more illuminated, desiccated and wind-exposed habitat (Laurance 2001). These conditions promote the elimination of emergent trees, an increased number of treefalls and the collapse of aboveground biomass (Laurance et al. 2000; Laurance et al. 1998a), thereby leading to lower canopy cover and a reduced vertical stratification close to forest edges (Chen et al. 1992; Harper et al. 2005; see also Fig. 2). It is likely that such characteristics make forest edges much more susceptible to desiccation and environmental extremes through greater variability in microclimatic parameters (Kapos 1989; Saunders et al. 1991). Increased light availability fuels the proliferation of pioneer or successional plants (trees, lianas, and shrubs), while populations of some shade-tolerant trees are expected to face strong declines on forest edges (Martinez-Garza et al. 2005; Tabarelli et al. 2004). Over time, pioneers can account for over 80% of species and individuals of tree assemblages in this habitat (Laurance et al. 2006; Oliveira et al. 2004b). In addition to this biased ratio of pioneers to shade-tolerant plants, the nutritional value of foliage may be enhanced at forest edges (e.g. Fortin and Mauffette 2001). Together increased quantity and/or quality of foliage can be an important factor controlling the abundance of herbivores (bottom-up control: which is the regulation of populations on higher trophic levels by the availability of food resources), yet this possible consequence of edge creation for populations of herbivores has not been explicitly addressed previously.

Like plants, many groups of animals have been reported to show increased or decreased abundances in forest edges and fragmented landscapes, including some herbivores, predators and parasites. In both tropical and temperate forests, large-area demanding species and forest habitat specialists (particularly vertebrates) are expected to be extirpated from severely-fragmented landscapes, including forest edges (Terborgh 1992). Decreased densities in forest edges have been documented, e.g., for some insectivorous birds (edge-avoiders), ants (Carvalho and Vasconcelos 1999), and parasitic insects (Laurance et al. 2002; Tscharntke et al. 2002). In contrast, canopy-foraging insectivorous

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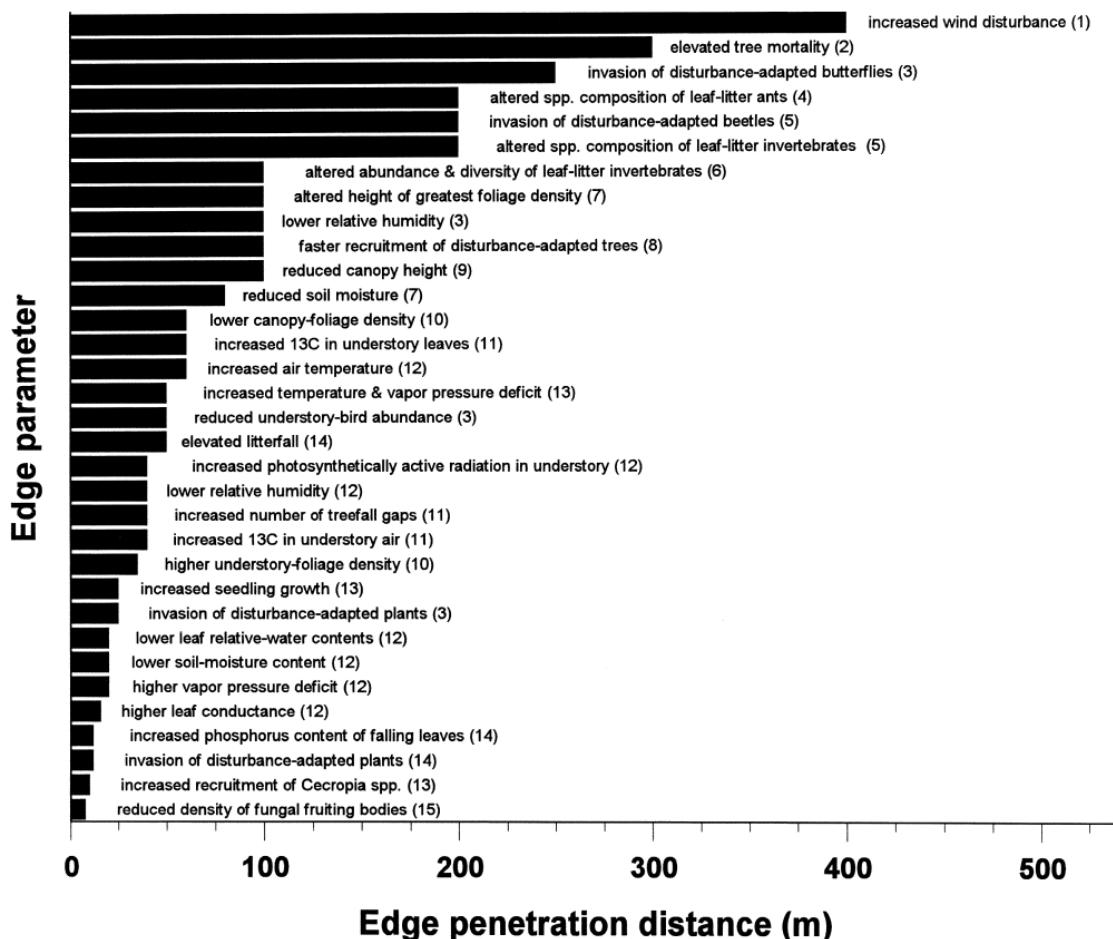


Figure 2: Penetration distances of different edge effects into the forest remnants of the Biological Dynamics of Forest Fragments Project (reproduced from Laurance et al. 2002 with datasources as cited therin). Sources: (1) Lewis 1998; (2) Laurance et al. 1998, 2000; (3) Lovejoy et al. 1986; (4) Carvalho and Vasconcelos 1999; (5) Didham 1997b; (6) Didham 1997a; (7) Camargo and Kapos 1995; (8) Laurance et al. 1998b; (9) Camargo 1993; (10) Malcom 1994; (11) Kapos et al. 1993; (12) Kapos 1989; (13) Sizer and Tanner 1999; (14) Bierregaard et al. 1992; (15) R. K. Didham, unpublished data.

birds (Lovejoy et al. 1986; Strelke and Dickson 1980), small folivorous/omnivorous mammals, and other generalist vertebrate predators (especially matrix users) appear to be favoured and reach increased abundances at forest edges or concentrate their foraging activities in this habitat (Laurance 1994; Laurance et al. 2002; Malcolm 1997).

Direct alterations of the physical environment at forest edges and the associated shifts in the biota can secondarily cause changes in the populations of other species, sometimes called “cascading effects”. Such effects of one species population on another can be caused through trophic webs (e.g. herbivory; Arnold and Asquith 2002) and predator-prey relationships (e.g. Fonseca and Robinson 1990) either as bottom-up

or top-down regulation (control of population size on lower trophic levels by loss of individuals to higher trophic levels). Also, a multitude of other species interactions can link one species to another (e.g. pollination: Aizen and Feinsinger 1994; seed dispersal: Silva and Tabarelli 2000).

Finally, the magnitude and intensity of edge-effects (sensu Harper et al. 2005) are greatly modulated by edge evolution, orientation and structure, as well as by the patch contrast (Chen et al. 1995; Didham and Lawton 1999; Murcia 1995). Most edge-effects described in the literature have been reported to penetrate less than 100 m and few as far as 400 m (Harper et al. 2005; Laurance et al. 2002; Matlack 1993; Fig. 2). In extreme cases, edge effects have been demonstrated to penetrate as far as (several)

kilometers into the forest (Alverson et al. 1988; Ewers and Didham 2008). Such extension of impacts appears to be enough to turn large parts of fragmented forests into a simplified and impoverished habitat in comparison to continuous forest in terms of (1) plant species richness (particularly trees), (2) taxonomic and ecological composition of flora and fauna (i.e. ecological groups based on life-history traits), (3) micro-habitat heterogeneity, and (4) trophic structure and complexity (loss of trophic levels and trophic interactions). Consequently, patterns of biological organization from organism to ecosystem level may be completely altered or disrupted in those portions of the remnants under the influence of edge effects (see Foggo et al. 2001). Collectively, cascades of abiotic, direct biotic and indirect biotic edge effects (*sensu* Murcia 1995) are expected to dramatically alter the nature of biological organization along forest edges. In a conservation context there is therefore a strong interest not only in the magnitude,

but also in the “extent” (i.e. depth of influence) of these edge effects, because the protection of unaltered core habitats is of principal importance when designing protected areas.

In summary, a wealth of studies has documented alterations of the physical environment and species composition along forest edges. In contrast, comprehensive studies about alterations of biotic interactions and ecosystem functioning along edges are scarce, yet they are of vital importance for an understanding of edge impacted forests and for predictions about the future of modern-day landscapes that are dominated by edge affected habitats. In the present study we are investigating in detail the impacts of forest edges on populations of leaf-cutting ants in the Brazilian Atlantic forest and address the impacts resulting from the various interactions of these ants with their environment. Thereby, we demonstrate, exemplarily, how plant-herbivore interactions can be altered at forest edges after human activities.

THE BRAZILIAN ATLANTIC FOREST

The Atlantic forest comprises the second largest block of forest in the new world tropics after the Amazon region and shows a high degree of biodiversity and endemism (8567 endemic species in a total of 21361 species of vascular plants, amphibians, reptiles, birds, and mammals: Myers et al. 2000). Regardless of this characteristics, the Atlantic forest has only quite recently attracted major research attention (documented in the special issue "The Brazilian Atlantic Forest" of *Biotropica* 32 (4b); Morellato and Haddad 2000). The Atlantic forest runs in a band along the Atlantic coast of Brazil and includes some parts of Paraguay and Argentina (Galindo-Leal and Camara 2003; Tabarelli et al. 2005). The main area of Atlantic forest lies along the Serra do Mar and Serra da Matiqueira, in Southeast Brazil, within the states of São Paulo, Rio de Janeiro, Minas Gerais and Espírito Santo (Leme and Siqueira Filho 2007). A smaller part occurs north of the Rio São Francisco on the lowlands of the Barreiras Formation and the foothills of the Borborema Plateau along the coastline of Alagoas, Pernambuco, Paraíba and Rio Grande Do Norte (Fig. 3A, B; Tabarelli et al. 2005).

THE ATLANTIC FOREST OF NORTHEAST BRAZIL: PERNAMBUCO CENTER OF ENDEMISM

– Despite covering only 4% of the total area within the Atlantic Forest, the Atlantic forest of Northeast Brazil accommodates more than two thirds of the total bird fauna (Roda 2003), and other species groups show also a very high biodiversity (Tabarelli et al. 2005). There is a high degree of endemism (averaging nearly 50% overall and as high as 95% in some groups; Brown and Brown 1992) in the region, which has been defined as the Pernambuco center of endemism (Silva and Casteletti 2003).

The highest proportion of plant biodiversity is represented by trees (Tabarelli et al. 2005) of which the families Leguminosae, Euphorbiaceae, Sapotaceae, Apocynaceae, Moraceae and Chrysobalanaceae are the most diverse (Oliveira et al. 2004a). These families have their center of diversity in the Amazon region (Gentry 1982; Pennington 1990; Prance 1979), which today is divided from the Atlantic forest by extensive tracts of open dry vegetation (Caatinga). During the late Pleistocene / early Holocene, however, these forests have been connected (Siqueira Filho

and Leme 2007; Tabarelli et al. 2005). The disjunct distribution of many “Amazonian-northeastern” tree species is a remaining consequence and proof of this ancient connection (Tabarelli et al. 2005). In addition to species shared with the Amazon, there is a minimum of 106 tree species that the Atlantic Forest of the Northeast shares with Atlantic Forest of the Southeast of Brazil (i.e. Rio de Janeiro and São Paulo; Tabarelli et al. 2005). The overlap of species from different regions together with a high number of endemic species contributes to the high diversity found in the Atlantic Forest of Northeast Brazil (Tabarelli et al. 2005). Because this forest is strongly endangered and has lost already more than 90% of what previously existed due to destruction by clearing and fragmentation it is considered one of the highest-priority hotspots for biodiversity conservation on earth (Fonseca et al. 2004; Myers et al. 2000). Sadly, still little is known about this biome and new species are discovered every year (Tabarelli et al. 2005) but without substantial conservation efforts these are “discoveries on the brink of extinction” (Silva et al. 2002).

FRAGMENTATION HISTORY – The Atlantic Forest of Northeast Brazil has a long disturbance history (reviewed in Tabarelli et al. 2007). Its degradation began with the arrival of the Portuguese in the early 16th century with the extraction of brazilwood (*Caesalpinia echinata*) from the

areas that today are the states of Pernambuco and Bahia. Because of large scale sugarcane plantations in the area degradation became much more aggressive and most of the coastal forest on fertile clay floodplains in the Brazilian Northeast had already been cleared in the early 18th century (Dean 1995). Early in the 20th century, practically all the forest of floodplains and valley headlands had already disappeared, leaving forest remnants only on the steepest and most inaccessible slopes. Forest fragmentation accelerated during the oil crisis of the 1970 when alcohol production was increased by the conversion of additional forest area into sugarcane plantation (Pró-Álcool Program; Coimbra-Filho and Camara 1996). Thus, much of the remaining forest was replaced by sugar cane plantations leaving only about 2% of the original area covered in forest and creating still smaller and more isolated forest fragments causing the impression of “hundreds of small forest fragments, most of which are less than 50 ha in size, restricted to hilltops embedded in an immense sea of sugar cane” (Ranta et al. 1998; Tabarelli et al. 2007).

SERRA GRANDE – The Usina Serra Grande is a privately owned sugarcane plantation located within the Endemism Center of Pernambuco in which's property the present study was conducted. The total area of the usina amounts to 26,000 ha, of which 8,000 ha are covered by



Figure 3: Study landscape within the Atlantic Forest of northeast Brazil (modified from Girao et al. 2007). (A) Map of South America showing Brazil in grey and the region “Northeast Brazil” in dark grey; the rectangle is amplified in B. (B) Coastal area of Northeast Brazil showing the distribution of the Atlantic Forest of Northeast Brazil (i.e. Pernambuco Center of Endemism), note original (grey) and current (black) distribution of this forest in the region; rectangle represents the study landscape (amplified in C). (C) Configuration of remaining forest fragments (grey polygons) in the landscape of “Serra Grande”. The dark grey polygon shows the fragment mainly used in this thesis, the 3,500 ha Coimbra forest. White areas represent the matrix of sugar-cane cultivation.

forest (distributed over hundreds of remnants ranging in size from less than 2 up to 3500 ha) and 12,350 ha are planted with sugarcane monoculture (Santos et al 2008). The area is located at the border between the states of Alagoas and Pernambuco, situated on a low-elevation plateau (300-400 m above sea level) about 50 km inwards from the coastline (9° S, 36° W; Fig. 3B). The region has a tropical climate characterized by a 5-mo dry season (<110 mm/mo) lasting from September to January (annual precipitation about 2000 mm). The prevailing soils are latosols and podzols (IBGE 1985). Among the multitude of small and very small forest remnants, which are embedded into this old agricultural landscape, lies the single largest and best preserved remnant of Atlantic Forest of NE-Brazil, locally called Coimbra (Santos et al. 2008; Fig. 3C). Coimbra forest covers approximately 3500 ha of largely well-conserved lower montane rain forest (Veloso et al. 1991) and still retains a full complement of plant species and many of the vertebrate groups typical of vast undisturbed tracts of Atlantic forest, such as large-seeded trees and large frugivorous birds (Chiarello 1999; Galetti et al. 2006; Silva and Tabarelli 2000; Tabarelli et al. in press).

THE IMPORTANCE OF HERBIVORES

Interactions between herbivores and plants are an auspicious area of research because they constitute an important component of almost any ecosystem (Cyr and Pace 1993) positioned at the very base of food webs between the primary production by plants and higher trophic levels. As ecosystems are structured by the flow of energy from plants through consumers, predators and decomposers, herbivores can drastically affect ecosystem level properties such as primary productivity, resilience, species richness, diversity of food webs, and patterns of nutrient cycling (Crawley 1983; Huntly 1991). Therefore, herbivory is among the processes and driving forces that organize ecosystems (Hobbs 1996; Huntly 1991; Thompson 1999).

The last decades have witnessed a growing body of evidence that herbivores profoundly influence vegetation structure and communities (Hulme 1996). In a comprehensive meta-analysis Bigger and Marvier (1998) concluded that

and Peres 2002). However, large mammals such as tapirs and white-lipped peccaries have been extirpated throughout the region due to overhunting (Silva and Tabarelli 2000).

To ensure watershed protection and water supply for sugar-cane irrigation, Coimbra forest and most other forest fragments in Serra Grande have been strictly protected against disturbances such as wildfires and logging (Santos et al. 2008). Special care is taken that during the yearly burning of the sugar cane prior to harvesting in the dry season forest edges do not catch fire. This is ensured by clearing strips of several meters width between forest edges and the remaining sugarcane before the latter is torched (personal observation). This has guaranteed the spatial stability of the borders of forest fragments and consequently the occurrence of both reproductive pioneer and shade-tolerant trees along post-closure forest edges (Melo et al. 2006). The edge zone (first 100 m of forest) has been, in fact, shown to be largely dominated by pioneer tree species (Oliveira et al. 2004b) that apparently are able to form multi- rather than single-generation pioneer assemblages (Tabarelli et al. in press).

herbivores have a strong negative impact on the biomass of the plants they feed on with a impact as high as or higher than competition within the plant community. On the other hand, herbivores might have positive effects on plant populations by increasing resource availability. Whether, in sum, these effects produce an “optimum response” of ecosystems to herbivory remains a topic of ongoing scientific debate (see for example Belsky et al. 1993; Dyer et al. 1993). By consuming plant-tissues, herbivores are able to reduce plant survival and fitness (Crawley 1983; Marquis 1984), and limit plant population size (i.e. top-down regulation). On the level of individual plants, herbivory is generally considered deleterious for the plants that suffer it and potentially beneficial for its neighbours (Crawley 1993) in terms of survival, growth and reproduction (Zamora et al. 1999). As a consequence, herbivores greatly affect the organization and species richness of plant communities (Hulme

1996) and differential herbivory is known to influence pace and trajectory of plant succession, via suppression of early or late successional species (Brown 1990; Zamora et al. 1999).

At the time of initiation of this work no studies had specifically evaluated the impact herbivores have on forest edges and remnants at an ecosystem level and studies on a population or community level were scarce (see e.g. Benitez-Malvido and Lemus-Albor 2005; Fagan and Bishop 2000; Jules and Rathcke 1999; Meiners et al. 2000; Meiners et al. 2002; Sork 1983). Strong evidence of the effects of an intense herbivory pressure on a tropical forest was compiled recently on land bridge islands with extremely high densities of

howler monkeys and/or leaf-cutting ants where the plant community was drastically reduced and only unpalatable plants remained (Rao et al. 2001; Terborgh et al. 2006; Terborgh et al. 2001). Given the indications that herbivores might profit from forest fragmentation and the high potential of herbivores to in turn impact fragmented forests (as described above) it is surprising that plant-herbivore interactions have received only minor attention in fragmentation related research (reviewed by Debinski and Holt 2000; Hobbs and Yates 2003). This study is going to address such interacting effects of forest fragmentation and the activities of herbivores using leaf-cutting ants as a model system.

LEAF-CUTTING ANTS IN PRISTINE AND ANTHROPOGENIC LANDSCAPES

Eusocial insects are at the ecological center of terrestrial ecosystems (Wilson 1990). Among eusocial insect the ants (Formicidae, Hymenoptera) comprise the most diverse group with close to 10000 known (probably 20000 existing) species grouped into 16 subfamilies (Hölldobler and Wilson 1990). A relatively small yet exceptionally successful group of ants are the fungus-growers from the tribe Attini. The conspicuous colonies of leaf-cutting ants have already intrigued some of the first European naturalists arriving in the New World tropics (e.g. Belt 1874; Brent 1886; Müller 1874) and the fascinating biology of leaf-cutting ants has been extensively studied ever since (reviewed in Cherrett 1989; Cherrett and Cherrett 1975; Cherrett et al. 1989; Hölldobler and Wilson 1990; Rico-Gray and Oliveira 2007; Stradling 1991; Wheeler 1907; Wirth et al. 2003). Leaf-cutting ants are prime pests in the Neotropics (e.g. Cherrett 1986) and therefore exists a wealth of studies on leaf-cutting ants in the context of agriculture and agroforestry, yet studies on leaf-cutting ants in anthropogenically disturbed natural habitats are virtually lacking (but see pioneering works of Vasconcelos 1988; Vasconcelos and Cherrett 1997; Vasconcelos et al. 2006).

THE ATTINI: PHYLOGENY AND GEOGRAPHIC RANGE OF FUNGUS-GROWING ANTS – Members of the myrmicine tribe Attini share with macrotermite termites and certain wood-boring

beetles the sophisticated habit of culturing and eating fungi. The Attini are a morphologically distinctive group comprised of 12 genera and more than 200 species (Wirth et al. 2003) which is monophyletic (Schultz and Meier 1995; Wetterer et al. 1998) supporting the hypothesis that fungus growing in attine ants has evolved only once.

The two genera of the so-called leaf-cutting ants, *Acromyrmex* and *Atta* form the group of the “higher attini” with three additional genera (Weber 1972) while the remaining seven genera are assembled in the “lower attines” (Schultz and Meier 1995; Wetterer et al. 1998). The lower attines do not cut and use leaves as the main cultivating substrate for their symbiotic fungus, but rather collect a large variety of dead vegetable matter, insect frass or other kinds of organic material (Leal and Oliveira 2000). They are generally assumed to be of lower ecological importance. Of the two true leaf-cutting ant genera, *Acromyrmex* has the greater species diversity (24 species, 35 subspecies), whereas *Atta* comprises only 15 species (Bolton 1995).

The tribe Attini is restricted to the New World, where members are found between approximately 40°N and 44°S (Cherrett 1989). The leaf-cutting ants are found somewhat more tropical (33°N and 44°S) including Mexico and Central and South America, though a few species live in the southern portions of the United States of America, and some have even adapted to the

more arid habitats in the southwestern states (Hölldobler and Wilson 1990; Kempf 1972). The most widespread *Atta* species are *A. sexdens* and *A. cephalotes* (Cherrett 1989, Fig. 4). These are also the *Atta* species occurring in Northeast Brazil (Correa et al. 2005) where the recent description of *A. cephalotes* from Alagoas added to the verified distribution of this species (Correa et al 2005; compare also Fig 4).

Atta species show some degree of habitat specialization often connected to the type of plant material they use mainly as substrate for their fungus. *Atta vollenweideri* for example, which occurs in pastures and savannas, specializes on the exploitation of grasses (Cherrett 1986). *Atta cephalotes*, on the other hand is a woodland species *sensu* Jaffe and Vilela (1989) and Rockwood (1973) that concentrates foraging on pioneer trees (Farji-Brener 2001), while *A. sexdens* forages more opportunistically on a variety of resources (Vasconcelos 1990) and occurs in a wide range of habitats (Fowler et al. 1989; Vasconcelos 1990). Such different degrees of habitat and harvest specialisation turn some species of leaf-cutting ants more vulnerable to (or more able to profit from) human disturbances and can account for their fate in man-made landscapes. An extreme example of which occurs in the coastal plains of Brazil where the endemic species *Atta robusta* is severely endangered because of its replacement by *Atta sexdens* following human disturbance (Fowler 1995).

Despite some species-specific peculiarities in the behavior and habitat preference of some *Atta* species, many life history traits of the species are very similar. Thus, I am going to present some basics of their living and ecology accordingly, irrespectively of the *Atta* species used in the investigations.

ANT FUNGUS SYMBIOSIS – Members of the myrmicine tribe Attini exhibit the complex habit of culturing and eating fungi (Weber 1966; Weber 1972). The ants harvest plant material, but rather than digesting it directly, they cultivate a fungus on it, which in turn feeds the colony (Belt 1874). In this mutualistic association, the ants benefit because the fungus provides enzymes that break down plant tissue (Martin and Weber 1969; Siqueira et al. 1998; but see Abril and Bucher 2002) and detoxify certain plant secondary compounds (Martin 1979; Powel and



Figure 4: Approximate distribution of six species of *Atta* indicated by the areas encircled (reproduced from Weber 1969). Brazilian distribution after Gonçalves (1960). Six additional species are found in Brazil. The western boundaries of *Atta* in South America have not clearly been established. Within a geographical area the ranges of *sexdens* and *cephalotes* are ecological. 1. *Atta texana* Buckley. 2. *Atta mexicana* F. Smith. 3. *Atta insularis* Guerin. 4. *Atta cephalotes* L. 5. *Atta sexdens* L. 6. *Atta vollenweideri* Forel.

Stradling 1991), thus enabling the ants to make use of plant material that would otherwise not be available to them. In exchange, the fungus is cultured in an advantageous environment (Roces and Kleineidam 2000; Stahel and Geijskes 1940; Weber 1972) and kept virtually free of competition from other microorganisms by constant tending and application of antibiotic compounds that the ants produce (North et al. 1997; Wilkinson 1999). Last but not least the ants provide huge quantities of high quality substrate. Fresh leaves and other plant cuttings are brought into the nest, degraded by the ants and inserted into the garden substratum where they are rapidly overgrown by the fungus (for details see Hölldobler and Wilson 1990).

Most fungi cultivated by the Attini belong to the Basidiomycete family Lepiotaceae (Agaricales: Basidiomycota), and the great majority belong to two genera, *Leucoagaricus* and *Leucocoprinus* (Leucocoprineae) (Chapela et al. 1994; Johnson 1999; Mueller et al. 1998; Mueller et al. 2001). Over the last 50 million years, the close

ant/fungus mutualism has resulted in the evolution of unique behavioral (e.g. elaborate manuring regimes that maximize fungal harvest, and mechanically “weeding” competing fungi), physiological, and anatomical modifications (e.g. secretion of antibiotic “herbicides” to control weed molds and the loss of digestive enzymes substituted by fungal enzymes) in the ants, which distinguish the Attini from other Formicidae. Corresponding morphological and biochemical modifications are seen in at least some of the fungal associates (Chapela et al. 1994; Hinkle et al. 1994; Hölldobler and Wilson 1990; Mueller et al. 1998).

The fungus cultivated by *Acromyrmex* and *Atta* produces swellings at the tips of hyphae, called “gongylidia”, and densely packed clusters of these are called “staphylae”. Ants and larvae feed on this food bodies. *Atta* workers prefer staphylae over hyphae (Quinlan and Cherrett 1978; Quinlan and Cherrett 1979) and live longer when feeding on staphylae (Bass and Cherrett 1995). Thus the gongylidia bodies appear to contain the best balanced blend of nutritional components, which is not yet entirely understood (Mueller et al. 2001). While the larvae are able to subsist and grow entirely on the staphylae, the fungus appears not to be the only source of nutrition for leaf-cutting ant workers. In addition, they drink plant sap while cutting leaves (1976) and carbohydrates ingested with the sap provide the main energy source for adult workers (up to 95%, Quinlan and Cherrett 1979). As a result workers select the plant material they harvest based on a combination of the fungus and their own requirements.

FOOD PLANT SELECTION – Interactions between leaf-cutting ants and their environment can only be understood mechanistically based on a profound perspective of their food plant selection. Leaf-cutting ants are highly polyphagous but at the same time highly selective (Howard and Wiemer 1986; Rockwood 1976). They use up to 50% of the species of a given forest flora in their colony’s foraging territory each year (Vasconcelos and Fowler 1990; Wirth et al. 2003). The collected material consists mainly of fresh leaves but can contain substantial amounts of fruits, flowers or other non green plant material (Wirth et al. 1997). For fresh leaves, leaf properties such as secondary compounds (Howard 1987; Hubbell

and Wiemer 1983; Hubbell et al. 1983; Littledyke and Cherrett 1976), toughness (Cherrett 1972; Nichols-Orians and Schultz 1989) and nutrient content (Barrer and Cherrett 1972; Berish 1986) have been identified to influence the choice of plant species. While some cutting of small understory vegetation and seedlings has been reported (Vasconcelos and Cherrett 1997) most harvesting by leaf-cutting ants occurs in the canopies of trees. The ants can discriminate on a very fine scale, making it likely that they strongly react to changes in plant species composition or foliage quality following forest fragmentation. They often cut from a particular tree of a species or even out of particular leaves within that tree, while other plants nearby (or other leaves within the plant) remain untouched. Significant intraspecific variation in leaf quality, together with the ants’ capability of fine discrimination among leaf material could account for such spatio-temporal patterns of resource exploitation (Fowler and Stiles 1980; Rockwood and Hubbell 1987), though empiric evidence for this argumentation is scarce (Howard 1990) and leaf-properties differentiating the attractiveness to the ants even within an individual plant remain obscure. Yet, I hypothesize that alterations in the plant quality along forest edges contribute to the attractiveness of this parts of the forest to leaf-cutting ants.

While generally species of leaf-cutting ants are assumed to be rather equivalent ecologically there is evidence for species-specific differences in the degree of foraging specialisation. This in turn can explain at least in some parts the different disposition of *Atta* species to profit from habitat alterations (as described above). For example, *Atta sexdens* forages opportunistically, simultaneously using trees and a wide variety of (ephemeral) resources for fungus-culturing including seedlings, juveniles, flowers, and dead leaves from ground litter (Vasconcelos 1990, pers. obs.). In contrast *A. cephalotes* concentrates its foraging on fresh leaves of large forest trees (Vasconcelos 1990) with a clear preference for pioneer species (Farji-Brener 2001), which are more frequent in forest edges and gaps (Laurance et al. 1998a; Laurance et al. 2006; Oliveira et al. 2004b).

IMPORTANCE AS HERBIVORES – Leaf-cutting ants are considered the dominating herbivores of the New World tropics (Wilson 1986) based on

estimates that between 12 and 17% of leaf production is consumed by leaf-cutting ants (Cherrett 1989). For example in some Panamanian rain forests as much as 80% of the apparent leaf damage may be caused by *Atta* species (Cherrett 1989; Wint 1983) and a single colony can remove up to 15% of the standing leaf crop from the colony's foraging area (Urbas et al. 2007; Wirth et al. 2003). Reports for biomass consumption rates of free living *Atta* colonies range from 22 to 940 kg/col/yr (Herz et al. 2007 and references therein). For the portion of Barro Colorado Island (Panama) where *A. colombica* occurs (100 ha), the population (49 colonies) harvested 13.2 tons of biomass/yr, which is equivalent to 2.1% of the available foliage in the forest (Herz et al. 2007). These results indicate that the defoliation by leaf-cutters is more modest than previously thought. On the other hand, there is indication that herbivory by leaf-cutting ants at the margins of the Brazilian

Atlantic Forest increased compared to the interior of the forest after anthropogenic fragmentation, concentrating the ants impact at the forest edge (Chin and Yeston 2007; Urbas et al. 2007).

The importance of leaf-cutting ants as herbivores and the effects on the ecosystem resulting from their foliage removal have been investigated in a comprehensive study about *Atta colombica* in the Panamanian rain forest (Wirth et al. 2003). This study demonstrated an increase in resource heterogeneity in the forest because of a patchily distributed increase in light availability and nutrient concentrations. Nutrients were concentrated from large quantities of harvested plant material in the refuse dumps of colonies. Finally, the authors conclude that leaf-cutting ants are an integral part of the ecosystems of the New World tropics. In fact, they supplant to some extent populations of large herbivorous mammals, which are relatively sparse through most of the New World tropics. The effects of

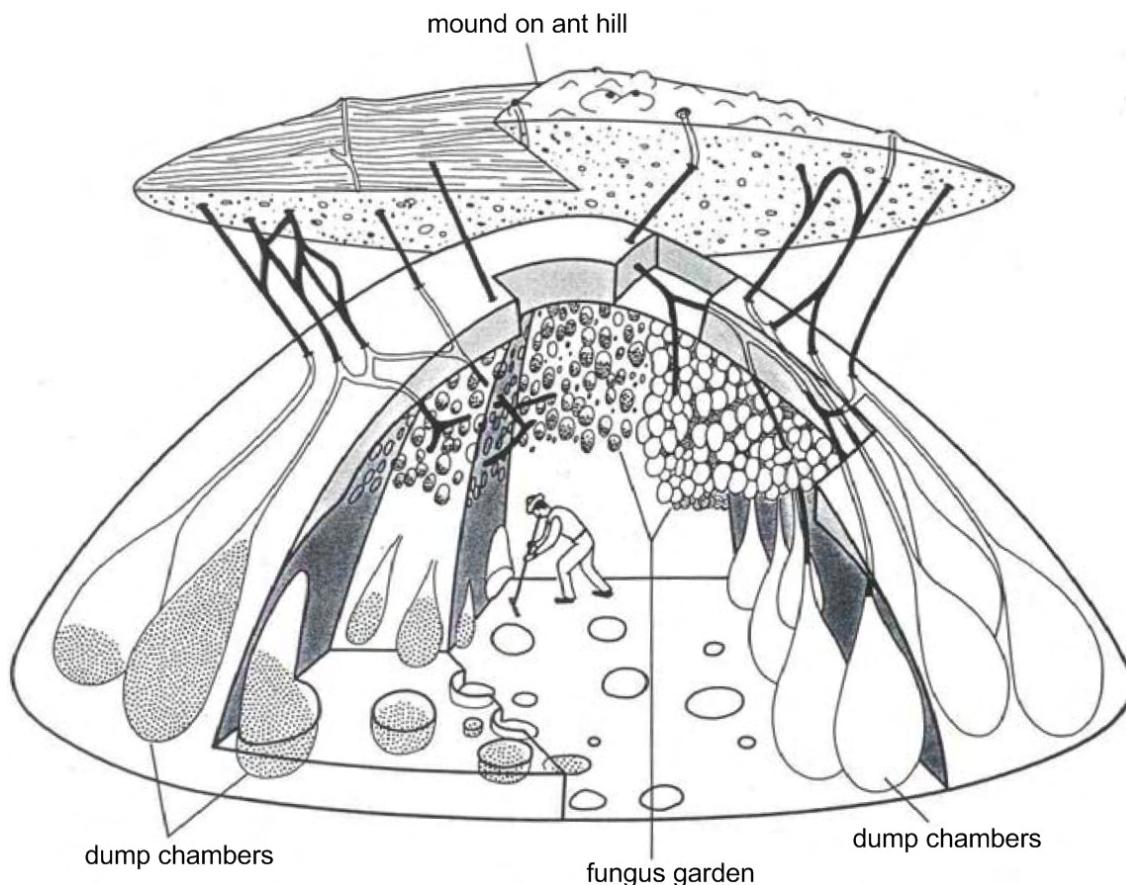


Figure 5: The plan of a mature nest of the leaf-cutting ant *Atta vollenweideri*, based on actual excavations. The upper mound of soil was brought to the surface by the ants during the digging of the nest. The dump chambers contain exhausted substrate. The fungus is cultured in the fungus garden chambers. (Hölldobler and Wilson 1990, modified from J.C.M. Jonkman, in Weber 1979)

leaf-cutting ants on their environment are not caused alone by the removal of foliage. In addition to pruning the vegetation, they stimulate new plant growth, break down plant material, and enrich the soil (Wirth et al. 2003). Yet, their impacts exceed herbivory related effects caused for example by construction of large long-lived nests which are considered disturbances in the forest with the potential to influence plant regeneration in tropical systems (Garrettson et al. 1998).

NEST CONSTRUCTION - The ultimate size reached by colonies of *Atta* is enormous. For example, one *A. sexdens* nest, more than 6 years old, contained 1920 chambers, of which 248 were occupied by fungus garden and ants. The loose soil that had been brought out and piled on the ground by the ants during the excavation of their nest weighed approximately 40 tons (Fowler et al. 1986) (Fig. 2). Leaf-cutting ant nests frequently reach more than 100 m² in surface area and 6 m or more in depth of subterranean chambers (Hölldobler and Wilson 1990). Effects of these conspicuous structures include (1) soil disturbances (Alvarado et al. 1981; Perfecto and Vander Meer 1993), (2) the improvement of soil penetrability (Moutinho et al. 2003), (3) removal of litter resulting in bare ground (Weber 1972), (4) enrichment of soil nutrients by the year-long harvesting activity (Haines 1978; Moutinho et al. 2003; Sternberg et al. 2007; Verchot et al. 2003), (5) the establishment of “bottom-up” gaps above nests (Farji-Brener and Illes 2000; Hull-Sanders and Howard 2003), and (6) the alteration of the plant community at nest sites (Corrêa et al. submitted; Garrettson et al. 1998). At nest sites the understory vegetation growing on or overhanging the immediate nest surface is constantly cleared leading to an increased light availability (Farji-Brener and Illes 2000; Hull-Sanders and Howard 2003) above nests. Recently, additional openings in the canopy above nests have been observed (pers. obs., Corrêa et al. submitted), but have not been investigated systematically despite the importance of canopy gaps for microclimatic conditions at nest sites. Generally, an altered, more open forest structure at nest sites compared to undisturbed forest should permit a higher interception of light that should secondarily change other climatic parameters such as temperature and humidity of air and soil. Yet, before

this study, an investigation of climatic parameters other than light has been completely lacking for leaf-cutting ant nests.

ATTA IN ANTHROPOGENIC LANDSCAPES – Leaf-cutting ants are prime pests in the Neotropics (e.g. Cherrett 1986; Cherrett and Peregrine 1976; Fowler et al. 1989), which attack a wide range of agricultural crops, notably citrus (*Citrus* spp.), cacao (*Theobroma cacao*), cassava (*Manihot esculenta*), coffee (*Coffea arabica*), maize (*Zea mays*), cotton (*Gossypium hirsutum*), and forest plantations like eucalyptus and pine (Cherrett 1986), thus creating various prejudices complicating the coexistence of leaf-cutting ants and humans (Fowler et al. 1989). Current estimates of economical losses are hard to come by but Amante (1972) estimated annual sugar cane losses in São Paulo State to reach 6.3 million US\$ and Robinson (1979) estimated annual losses over all of Paraguay to range between 6.3 and 7.9 million US\$. Trying to estimate the global potential losses that could result from leaf-cutting ants in the absence of control Cherrett (1986) gives “an often-quoted figure” of 1000 million US\$ cited after Townsend (1923). Little has changed since these earlier reports and irrespectively of the exact amounts of the economic losses, leaf-cutting ants remain a significant pest of important agricultural products (Barreto et al. 1998; Zanetti et al. 2003; Zanuncio et al. 1996). Consequentially exists a wealth of studies on leaf-cutting ants in the context of agriculture and agro-forestry (e.g. Blanton and Ewel 1985; Hernandez et al. 1999; Varon et al. 2007; Zanetti et al. 2000; Zanuncio et al. 2004) and leaf-cutting ant management and population control activities (e.g. Cherrett and Peregrine 1976; Varón Devia 2006; Zanuncio et al. 2000; Zanuncio et al. 1999).

There is clear evidence that some species of leaf-cutting ants strongly benefit from human-driven habitat alterations (Cherrett 1986). Numerous studies have documented populations of leaf-cutting ants to increase with increasing agricultural land use, deforestation and/or disturbance (Fowler et al. 1986; Jaffe and Vilela 1989; Jonkman 1979). Specifically, elevated colony densities have been recorded in transformed vegetation such as pastures (Fowler 1983) and plantations (Jaffe 1986; Oliveira et al. 1998) and early successional forests (Vasconcelos and

Cherrett 1995). In addition to changes in colony abundance there can be shifts in the species composition of leaf-cutting ant communities. For example, mature forest in central Amazonia showed very low nest density of the leaf-cutting ants *Atta cephalotes*, *Atta sexdens*, and *Acromyrmex hystriculus*. In contrast, in regrowth forests no nests of *A. cephalotes* and *A. hystriculus* were found, even though these forests supported a density of *Atta* and *Acromyrmex* nests up to twenty times greater than that found in mature forest. The species typical of the more disturbed regrowth areas were *Atta laevigata* and *Acromyrmex laticeps*, which do not occur in mature forest (Vasconcelos et al. 2001; Vasconcelos and Cherrett 1995).

Studies on leaf-cutting ants in anthropogenically disturbed natural habitats or remnants of natural habitats in anthropogenic landscapes are relatively scarce and elevated densities of leaf-cutting ants were reported only recently for isolated forested islands (Rao 2000; Terborgh et al. 2001). Data about the population densities of leaf-cutting ants within forest remnants following fragmentation had been virtually lacking (but

see Vasconcelos 1988). Nevertheless, such estimates are of great importance for the understanding of the functioning of forest fragments given the ecological significance of leaf-cutting ants. For example, rates of herbivory by *Atta* at forest edges and within forest fragments have been observed to be drastically elevated compared to the interior of continuous forest (Rao et al. 2001; Urbas 2004; Urbas et al. 2007). These results underline the importance of leaf-cutting ants in fragmented forests where the moderate impacts on the plant community as demonstrated in pristine ecosystems (Wirth et al. 2003) might be drastically enlarged resulting potentially in pronounced negative consequences for the plant community and the ecosystem as a whole. Therefore exists a need for accurate estimates of colony densities in forests altered by fragmentation. In addition, the exemplary insights from herbivory rates raise the question whether others of the multifarious impacts and interactions of leaf-cutting ants (as described above) are likewise amplified in forest fragments and forest edges. The present study addresses these questions (as detailed on the following pages).

THIS STUDY

Interacting effects of forest fragmentation and leaf-cutting ants are the general theme of the present study. In a first step, the responses of herbivores to fragmentation and edge creation were evaluated concentrating on leaf-cutting ants as a model organism. The population level responses of leaf-cutting ants to forest fragmentation on a spatial and temporal scale were addressed specifically together with an exploitation of the underlying mechanisms causing the observed patterns (chapters 2 to 5). Subsequently, I analyzed the impacts of hyper-abundant leaf-cutting ants in the heavily fragmented Atlantic Forest of Northeast Brazil (chapters 6, 7 and 9).

OUTLINE – Forest fragmentation and the consequential creation of artificial edges is altering forest structure and ecosystem functioning, generally transforming forests into early successional systems (Tabarelli et al. in press). Edge-induced disruptions of species interactions can be

among the driving mechanisms governing this transformation (Fagan et al. 1999; Hunter 2002). Yet, a systematic review of information available about herbivory at forest edges had not yet been performed. As a basis for the present study we conducted a literature review on plant-herbivore interactions at the forest edge (chapter 2). The review (1) synthesizes published research attempting to detect patterns of herbivore densities and herbivory at forest edges, (2) identifies the underlying mechanisms generating these patterns, and (3) explores their potential impacts for the forest edge as an ecosystem. Field investigations in the heavily fragmented Brazilian Atlantic Forest with leaf-cutting ants as a model system for a dominant herbivore were subsequently carried out to evaluate patterns and hypotheses emerging from this review. Despite numerous documentations of increasing leaf-cutting ant populations with increasing levels of agricultural land use, deforestation, and/or disturbance there had been a conspicuous lack of information on

the response of leaf-cutting ants to forest fragmentation and edge creation (as detailed above). Based on a census of colonies we present quantitative data on the degree of leaf-cutting ant concentration at the forest edge in terms of differences in colony densities between forest edge and interior and estimated how far the edge zone penetrates into the forest (chapter 3). In view of poorly explored vegetation dynamics and little understood ecosystem functioning at aging edges (detailed in chapter 4) the question arises whether high densities of leaf-cutting ants are a transitional or a persisting phenomenon in fragmented landscapes. As a first insight into long-term dynamics of plant-herbivore interactions following fragmentation, we studied the temporal variation of leaf-cutting ant densities at the edge of the Brazilian Atlantic Forest (chapter 4). Regarding the underlying mechanism that is believed to cause leaf-cutting ants to profoundly benefit from edge creation in Neotropical forests there is strong support that a high abundance of palatable and preferentially selected pioneer vegetation controls *Atta* densities (Farji-Brener 2001; Urbas 2004; Urbas et al. 2007). This type of vegetation dominates forest edges (Laurance et al. 2006; Oliveira et al. 2004b). In addition, there is evidence that palatability of plant species at the forest edge can change due to environmentally-induced alterations of leaf characteristics, which also can contribute to a relaxation of bottom-up control (Fortin and Mauffette 2001). Forest edges are characterized by a drier and warmer microclimate with an elevated desiccation risk (Laurance et al. 2001) and the concentrations of variety of compounds in leaves have been demonstrated to change with drought stress (e.g. Arndt et al. 2001; Bradford and Hsiao 1982). Therefore, we asked whether drought stress impacts food plant selection of leaf-cutting ants (chapter 5).

Leaf-cutting ants had been identified as key-stone species in pristine forests (Fowler et al. 1989) where they occur in very low densities (e.g. Wirth et al. 2003 and references therein). In light of the drastic increase of leaf-cutting ant densities along the edge of Coimbra forest (as documented in this thesis), their ecological importance, which is potentially amplified in anthropogenic landscapes immediately comes to

mind. Not only are direct effects from herbivory magnified at the forest edge (Urbas et al. 2007; chapter 4), but also the hypothesized effects from ecosystem engineering. While leaf-cutting ants have been repeatedly described as ecosystem engineers (e.g. Rico-Gray and Oliveira 2007; Wirth et al. 2003) this notion was never strictly tested, yet the conspicuous nests of leaf-cutting ants are considered disturbances with the potential to influence plant regeneration (Garrettson et al. 1998). I quantified alterations in the forest structure with regard to understory and canopy at nest sites and measured the resulting shift in forest microclimate above the nest and along transects in the vicinity of nests (chapter 6). In a follow-up study I tested whether the altered microclimatic conditions at nest sites impact plant regeneration and therefore plant community composition in Coimbra forest by transplanting seedlings of different species into nest centres, at the nest edge, and into the forest understory and comparing their growth and survival (chapter 7). After summarizing the central results of all manuscripts (chapter 8) I will deduce (1) the responses of *Atta* to forest fragmentation and disturbance, (2) the impact of *Atta* in fragmented forests, and (3) the relevance of our findings on *Atta* in fragmented forests for the theory of ecosystem engineering (chapter 9).

AIMS OF THIS THESIS – To summarize, the first part of the present study was designed to (1) uncover general trends in the response of herbivores to edge creation, (2) quantify spatial and temporal patterns in the response of leaf-cutting ants within fragments of Atlantic Forest, and (3) demonstrate a mechanism for intra-specific food plant selection that might contribute to elevated edge densities of *Atta*. Regarding the impact of *Atta* in fragmented forests I aimed to demonstrate that (4) *Atta* acts as an ecosystem engineer with (5) consequential impacts on plant regeneration and thus the composition of the plant community. Finally, I will present together with my coauthors (6) estimates of the total forest area impacted by *Atta* (directly via herbivory and indirectly via ecosystem engineering) comparing forest edge and forest interior and end up with (7) a prognosis about winners and losers in *Atta* dominated forests.

2

Plant-herbivore interactions at the forest edge

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Plant Herbivore Interactions at the Forest Edge

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Abstract An ever-increasing proportion of the global forested landscape is in close proximity to edges and edge effects have been shown to represent key forces affecting both organisms and ecological processes. Despite increasing recognition of edge effects on species interactions, a systematic review devoted to plant-herbivore interactions along forest edges has not yet been performed. Here we synthesize published research attempting to detect patterns of herbivore densities and herbivory at forest edges, identify the underlying mechanisms generating these patterns, and explore their potential impacts for the forest edge as an ecosystem. Key conclusions are that herbivores, especially generalists, profoundly benefit from forest edges, often due to favourable microenvironmental conditions, an edge-induced increase in food quantity/quality, and (less well documented) disrupted top-down regulation of herbivores. Finally, we present evidence and causal explanations that edge-associated herbivores, via a range of direct and indirect impacts, may alter species interactions, delay successional processes at the edge, and amplify the often human-induced changes on forest biota.

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1 Introduction

An edge can be defined as a zone of transition between different types of habitats (Ries et al. 2004). Historically, most research has addressed changes in biotic variables, vegetational transition, and patterns of species diversity in natural edge zones (Fagan et al. 1999). One of the most important patterns documented by this approach is the tendency of increased species diversity in natural edges and ecotones (the “edge effect principle”, sensu Odum 1971). This is now a fundamental concept of ecology and it has been largely applied by wildlife biologists over the past half a century, particularly as a guideline in terms of habitat management in temperate ecosystems (Harris 1988).

During the past two decades, escalating levels of habitat loss and fragmentation, particularly in the tropical rain forests, have greatly revived the interest in the topic of edges (for a review, see Ries et al. 2004). Researchers are now concerned with the fact that the creation of forest edges by human activities (artificial or anthropogenic edges) can act as a huge catalytic source of ecosystem degradation and biodiversity loss in fragmented forests (Fagan et al. 1999; Tabarelli and Gascon 2005). The diverse physical and biotic changes resulting from the occurrence of abrupt and artificial margins are referred to as edge effects (Bierregaard et al. 2001), and they greatly result from differences in the structural complexity and biomass between the juxtaposed ecosystems, the “patch contrast”, sensu Harper et al. (2005).

Habitat fragmentation, and the consequent creation of artificial forest edges, is one of the most pervasive and disturbing results of present-day human land use dynamics (Whitmore 1997; Aguilar et al. 2006). Most forest biota tend to be reduced to archipelagos of small fragments or edge-affected habitats (increased edge-to-interior ratios), which remain immersed within environmentally hostile matrices, such as pastures, croplands, and urban areas (Tabarelli et al. 2004). Although the whole effect produced by habitat fragmentation results from a myriad of processes (see Fahrig 2003), much of the ecological alterations faced by fragmented forests (e.g. disruption of species interactions, species loss, biomass collapse, exotic species invasion) can be assigned to edge-driven changes or edge effects (D’Angelo et al. 2004; Tabarelli and Gascon 2005). Consequently, patterns of biological organization from organism to ecosystem level may be completely altered or disrupted in those portions of the remnants under the influence of edge effects (see Foggo et al. 2001) – hereafter forest edge or edge habitat in contrast to forest interior or core area habitat (i.e. those portions showing no detectable edge influence).

Interactions between plants and herbivores are considered to be one of the key processes shaping life history traits and ecosystem function. By consuming plant tissues, herbivores are able to reduce plant survival and fitness (Crawley 1983; Marquis 1984) and limit plant population size (i.e. consumer regulation). In a comprehensive meta-analysis Bigger and Marvier (1998) concluded that herbivores have a strong negative impact on the biomass of the plants they feed on, and their

impact might be as high as, or higher than, competition within the plant community. As a consequence, herbivores may greatly affect the organization of plant communities and their patterns of species richness (Hulme 1996). Differential herbivory among species is known to influence the pace and trajectory of plant succession, via suppression of early or late successional species (Brown 1990; Zamora et al. 1999). Finally, as ecosystems are structured by the flow of energy from plants through consumers, predators, and decomposers, herbivores can drastically affect ecosystem level properties such as primary productivity, resilience, species richness, diversity of food webs, and patterns of nutrient cycling (Crawley 1983; Hurnly 1991).

Recent reviews (e.g. Yahner 1988; Saunders et al. 1991; Murcia 1995; Foggo et al. 2001; Laurance et al. 2002; Hobbs and Yates 2003; Harper et al. 2005) revealed an extensive suite of edge effects on forest biota with clear detrimental consequences for ecosystem functioning, particularly the long-term retention of biodiversity. Given the increasing recognition of the global importance of edges as a dominating habitat (Yahner 1988; Ries et al. 2004), it is remarkable that minor attention has been devoted to plant-herbivore interactions in fragmentation-related experiments (for reviews, see Debinski and Holt 2000; Hobbs and Yates 2003). To exemplify, one of the most influential reviews on edge effects by Murcia (1995) cited only one article to document herbivory as one of six categories of species interactions disrupted at edges. Since then, there has been an increasing sense of urgency and awareness that edge-induced disruptions of species interactions is a fundamental issue for a more complete and profound perspective on the impacts of habitat fragmentation and the ecology of fragmented landscapes (Fagan et al. 1999; Hunter 2002).

Here we synthesize key findings regarding edge-related changes in patterns of herbivore occurrence and herbivory at the edges of forest ecosystems (excluding seed predation and xylophagia). The present review was conducted to:

1. Detect whether herbivores or herbivory are negatively, positively or neutrally affected by edges;
2. Identify the mechanisms that are proposed to explain these patterns;
3. Explore how plant-herbivore interactions may impact forest edge ecosystems, particularly abiotic conditions, the plant community, and higher trophic levels.

2 What Edges Induce in Forest Remnants

Collectively, cascades of abiotic, direct biotic, and indirect biotic edge effects (*sensu* Murcia 1995) are expected to dramatically alter the nature of biological organization along forest edges and eventually drive the entire remnant to collapse (Gascon et al. 2000). With potential impacts on herbivore populations (see Section 3.2), three groups of edge-related effects must be highlighted: (a) physical and

structural changes of the forest edge, (b) changes in resource availability and quality including the hyper proliferation of pioneer plants and environmentally induced changes of foliage quality, and (c) changes in animal responses to forest edges, including the assemblage of natural enemies.

Compared with the forest interior, forest edges are more illuminated, desiccated, and wind-exposed habitats (Laurance 2001). This promotes elimination of emergent trees, an increased number of treefalls, and a collapse of above-ground biomass (Laurance et al. 1998, 2000), thereby leading to lower canopy cover and a reduced vertical stratification close to forest edges (Chen et al. 1992; Harper et al. 2005). It is likely that such features turn forest edges much more susceptible to desiccation and environmental extremes through greater variability in microclimatic parameters (Kapos 1989; Saunders et al. 1991). Increased light availability fuels the proliferation of pioneer or successional plants (trees, lianas, shrubs), while populations of some shade-tolerant trees are expected to face strong declines on forest edges (Tabarelli et al. 2004; Martinez-Garza et al. 2005). Over time, pioneers can account for over 80% of species and individuals of tree assemblages in this habitat (Oliveira et al. 2004; Laurance et al. 2006). In addition to this biased ratio of pioneers to shade-tolerant plants, foliage nutritional value may be enhanced at forest edges (e.g. Fortin and Mauffette 2001).

Like plants, many groups of animals are reported to present increased or decreased abundance in forest edges and fragmented landscapes, including those that prey on herbivores. In both tropical and temperate forests, large-area-demanding species and forest habitat specialists (particularly vertebrates) are expected to be extirpated from severely fragmented landscapes, including forest edges (Terborgh 1992). Decreased densities in forest edges are documented, e.g. for some insectivorous birds (edge-avoiders), ants (Carvalho and Vasconcelos 1999), and parasitic insects (Laurance et al. 2002; Tscharntke et al. 2002). In contrast, canopy-foraging insectivorous birds (Strelke and Dickson 1980; Lovejoy et al. 1986), small folivorous/omnivorous mammals, and other generalist vertebrate predators (especially matrix users) appear to be favoured and reach increased abundances at forest edges or concentrate their foraging activities in this habitat (Laurance 1994; Malcolm 1997; Laurance et al. 2002).

Finally, the magnitude and intensity of edge effects (*sensu* Harper et al. 2005) are greatly modulated by edge evolution, orientation, and structure, as well as by the patch contrast (Chen et al. 1995; Murcia 1995; Didham and Lawton 1999). Most edge effects described in the literature are reported to penetrate less than 100 m and few as far as 400 m (Matlack 1993; Laurance et al. 2002; Harper et al. 2005). Such extension of impacts appears to be enough to turn forest edges into a simplified and impoverished habitat in comparison to the forest interior in terms of: (a) plant species richness (particularly trees), (b) taxonomic and ecological composition of flora and fauna (i.e. ecological groups based on life history traits), (c) microhabitat heterogeneity, and (d) trophic structure and complexity (loss of trophic levels and trophic interactions).

3 Plant-Herbivore Interactions at the Edge: Patterns and Processes

3.1 Patterns

Most revisions about edge effects emphasize a positive effect of edge creation on herbivores and their damage to vegetation (e.g. Laurance et al. 1997; Foggo et al. 2001; Ries et al. 2004), although few studies in fact present empirical data, and responses are reported to be positive, negative, or neutral. We found a total of 55 articles that investigated whether forest edges affect herbivores and/or herbivory – 28 of them dealing with edge effects on density, abundance, and richness of herbivores (Table 1), and 32 evaluate edge effects on herbivory patterns (Table 2). These articles cover several levels of biological organization and a variety of forest types, ranging from single species interactions (e.g. McGeoch and Gaston 2000) to studies on the community level (e.g. Barbosa et al. 2005), and from tropical (e.g. Urbas et al. 2007) to boreal forests (e.g. Roland 1993), with a predominance of investigations in temperate regions (e.g. Cadenasso and Pickett 2000).

In the case of herbivore responses (e.g. abundance, species richness), the majority of studies (23 articles, 82.1%) presented evidence that edge creation promotes positive effects, but we also registered studies showing negative (four articles, 14.3%) and neutral (five articles, 17.8%) responses (note that the total exceeds 100% because some studies presented several herbivores with differential edge responses; Table 1). There was a clear tendency for studies focusing on insect assemblages (e.g. Barbosa et al. 2005), addressing groups such as the Lepidoptera (Harris and Burns 2000), Coleoptera (Ozanne et al. 2000), and Homoptera (Martinez-Garza et al. 2005), but studies with vertebrates such as deer (Alverson et al. 1988), voles (Ostfeld et al. 1997), or marsupials (Laurance 1990) were also recorded.

Herbivore responses to edge creation were often species-specific (e.g. herbivorous beetle species; Harris and Burns 2000), but a general trend emerged – the increased abundance of generalist herbivores such as deer (Alverson et al. 1988), Homoptera (Ozanne et al. 2000), Orthoptera (Knight and Holt 2005), and leaf-cutting ants (Wirth et al. 2007). Among the more specialized groups, such as Lepidoptera, leaf-miners, and gall-forming insects, responses to edge creation were more variable, including positive, negative, and neutral patterns (e.g. respectively Martinez et al. 2005; Valladares et al. 2006; Julião et al. 2004).

A less clear picture emerged with respect to herbivory rates at forest edges. Of the articles in Table 2, 50% (16 out of 32) reported positive effects of edges (i.e. increased herbivory rates), 11 (34.4%) detected negative, and 10 (31.2%) neutral responses. Paralleling the above response of herbivores, the variation of herbivory rates at forest edges appears to be both species- and site-specific, and studies were biased toward insects and seedling damage (e.g. Meiners et al. 2000; Benítez-Malvido and Lemus-Albor 2005). Studying herbivore damage to seedlings in a deciduous forest in the USA, for example, Cadenasso and Pickett (2000)

Table 1 Edge effects upon abundance, density, richness, or performance of herbivores in forested ecosystems. References are displayed in chronological order. Herbivores are classified as specialists (S) or generalists (G). Three groups of mechanisms causing increased (\uparrow), reduced (\downarrow), or neutral (\leftrightarrow) responses are identified: environmental conditions (C), resources (R), and natural enemies (E). Reports for these mechanisms are distinguished as to whether they are supported by original data (italics), derived from secondary information (normal text), or only hypothetical (in brackets)

Herbivore	Type	Response	Mechanism	Ecosystem	Reference
Positive effects					
Herbivorous insect community	S/G	\uparrow Abundance	C (E)	Temperate forest	Mac Garvin et al. (1986)
White-tailed deer	G	\uparrow Density	R	Temperate forest	Alverson et al. (1988)
Gypsy moth	S	\uparrow Egg mass	C	Temperate forest	Bellinger et al. (1989)
Coppery brushtail and green ringtail possums	G	\uparrow Abundance	R	Tropical rain forest	Laurance (1990)
Herbivorous insect community	S/G	\uparrow Abundance		Amazonian rain forest	Fowler et al. (1993)
Sun-loving butterflies	S	\uparrow Species richness		Amazonian rain forest	Brown and Hutchings (1997)
<i>Hypothenemis euclea</i> (ithomiinae)	S	\uparrow Abundance (1980–1986)	R	Amazonian rain forest	Brown and Hutchings (1997)
Birch tube maker	S	\uparrow Larval density at paper birch	C (R) (E)	Boreal forest	Cappuccino and Martin (1997)
Lepidopteran community	S	\uparrow Abundance	E	Atlantic rain forest	Bragança et al. (1998)
Arthropod herbivorous	S/G	\uparrow Abundance	C	Boreal forests	Jokimäki et al. (1998)
Holly leaf-miner	S/G	\uparrow Prevalence	C	Temperate forest	McGeoch and Gaston (2000)
Forest tent caterpillar	S	\uparrow Larval performance	E	Boreal forest	Rothman and Roland (1998)
Forest tent caterpillar	S	\uparrow Larval performance	R	Boreal forest	Fortin and Mauffette (2001)
Forest tent caterpillar	S	\uparrow Larval performance	C R	Boreal forest	Levesque et al. (2002)
Two species of herbivorous beetles	-	\uparrow Abundance		Podocarp forest	Harris and Burns (2000)
Whilst aphid species	G	\uparrow Density	(C)	Pine plantation	Ozanne et al. (2000)
Beaver	G	\uparrow Herbivory activity	(C) E	Riparian forest	Barnes and Malik (2001)
Female mule deer	G	\downarrow Smaller home-range		Dry forest	Kie et al. (2002)
Herbivorous insect community	S/G	\uparrow Abundance and richness	(C) R (E)	Temperate forest	Major et al. (2003)
Herbivorous insect community	S/G	\uparrow Abundance and richness	R	Atlantic rain forest	Barbosa et al. (2005)

Orthopteran community	G	↑ Abundance of species	R	Sandhill forest	Knight and Holt (2005)
Gall-inducing aphids	S	↑ Species richness	R E	Mediterranean woodland	Martinez et al. (2005)
Leaf-cutting ants	G	↑ Colony density	R	Atlantic rain forest	Urbas et al. (2007)
Leaf-cutting ants	G	↑ Colony density	R	Atlantic rain forest	Wirth et al. (2007)
Negative effects					
Shade-loving butterflies	S	↓ Species richness	C	Amazonian rain forest	Brown and Hutchings (1997)
<i>Hypothenemis euclea</i> (Ithomiinae)	S	↓ Abundance (>1990)	E	Amazonian rain forest	Brown and Hutchings (1997)
Four species of herbiv.	-	↓ Abundance		Podocarp forest	Harris and Burns (2000)
Coleoptera					
Herbivorous Coleoptera	S/G	↓ Abundance and richness	(C)	Pine plantation	Ozanne et al. (2000)
community					
Lepidopteran community	S	↓ Abundance	(C)	Pine plantation	Ozanne et al. (2000)
Neutral					
White pine weevil	S	↔ Performance		Norway spruce plantations	Lavallée et al. (1996)
Red crabs	G	↔ Density		Tropical rain forest	Green et al. (2004)
Gall-forming insects	S	↔ Species richness		Pantanal wetland	Julião et al. (2004)
Herbivorous insect	S/G	↔ Abundance		Boreal forest	Deans et al. (2005)
community					
Herbivorous insect	S/G	↔ Abundance and richness		Bottomland hardwood forest	Ulyshen et al. (2005)
community					

Table 2 Edge effects upon herbivory level or damage rates in forested ecosystems. References are displayed in chronological order. Three groups of mechanisms causing increased (\uparrow), reduced (\downarrow) or neutral (\leftrightarrow) responses are identified: environmental conditions (C), resources (R), and natural enemies (E). Reports for these mechanisms are distinguished as to whether they are supported by original data (italics), derived from secondary information (normal text), or only hypothetical (in brackets)

Herbivore	Response	Mechanism	Ecosystem	Reference
Positive effects				
Herbivorous animals	\uparrow Herbivory		Temperate forest	Sork (1983)
Herbivorous insect community	\uparrow Damage level on bracken	C (E)	Temperate forest	MacGarvin et al. (1986)
White-tailed deer	\uparrow Browning of woody and herbaceous plants	R	Temperate forest	Alverson et al. (1988)
Grey squirrel	\uparrow Damage to beech and sycamore individuals		Temperate forest	Gill (1992)
Forest tent caterpillar	\uparrow Duration of outbreaks	C E	Boreal forest	Roland (1993)
White pine weevil	\uparrow Herbivory of Norway spruce		Norway spruce plantations	Lavallée et al. (1996)
Red-necked pademelon	\uparrow Herbivory and \downarrow growth rate of seedlings	R E	Tropical rain forest	Wahungu et al. (1999)
Red-necked pademelon	\uparrow Herbivory and \downarrow growth rate of seedlings	R E	Tropical rain forest	Wahungu et al. (2002)
Meadow vole	\uparrow Herbivory of seedlings		Mesic deciduous forest	Cadenasso and Pickett (2000)
Herbivorous insect community	\uparrow Herbivory of <i>Acer rubrum</i> seedlings		Temperate forest	Meiners et al. (2000)
Australian brushtail possum	\uparrow Leaf herbivory of mistletoe	(R)	<i>Nothofagus</i> forest	Bach and Kelly (2004)
Invertebrate species	\uparrow Herbivory of holly	C	Holly woodland	Arrieta and Suarez (2005)
Chewing animals	\uparrow Damage of <i>Angophora costata</i> leaf		Sandstone gully and ridge top woodland	Christie and Hochuli (2005)
Orthopteran community	\uparrow Herbivory in eight plant species		Sandhill forest	Knight and Holt (2005)
Gall-inducing aphid	\uparrow Occupancy on <i>Pistacia palaestina</i> plants		Mediterranean woodland	Martinez et al. (2005)
Leaf-cutting ants	\uparrow Herbivory rate	R (E)	Atlantic rain forest	Urbas et al. (2007)
Negative effects				
Herbivorous insect community	\downarrow Herbivory of dogwood	C	Temperate forest	Dudt and Shure (1994)
Herbivorous insect community	\downarrow Herbivory of <i>Eucalyptus camaldulensis</i>	C	River red gum forest	Stone and Bacon (1994)

Herbivorous insect community	↓ Herbivory of <i>Eucalyptus camaldulensis</i>	C	River red gum forest	Stone and Bacon (1995)
White-tailed deer	↓ Herbivory of seedlings		Mesic deciduous forest	Cadenasso and Pickett (2000)
Herbivorous animals	↓ Herbivory on seedlings of <i>Micropholis venulosa</i>	C	Amazonian rain forest	Benitez-Malvido (2001)
Lepidopteran community	↓ Herbivory of saplings	C	Tropical rain forest	Arnold and Asquith (2002)
Herbivorous insects and mammals	↓ Damage and ↑ survival of <i>Quercus rubra</i> seedlings		Temperate forest	Meiners et al. (2002)
Red crabs	↓ Herbivory of <i>Clausena excavata</i> plants		Tropical rain forest	Green et al. (2004)
Herbivorous insects and mammals	↓ Herbivory of <i>Quercus gemmata</i> and <i>Q. xalapensis</i> seedlings		Tropical montane forest	Guzman-Guzman and Williams-Linera (2006)
Herbivorous mammals	↑ Survivorship of tussock grass	E	Chaparral shrubland	Lambrinos (2006)
Leaf-miners species	↓ Herbivory rate	C E	Chaco serrano	Valladares et al. (2006)
Neutral			Temperate forest	Ostfeld et al. (1997)
Meadow voles	↔ Seedling predation		Mesic deciduous forest	Cadenasso and Pickett (2000)
Invertebrate species	↔ Seedling herbivory		Temperate forest	Meiners et al. (2000)
Herbivorous insect community	↔ Herbivory of <i>Fraxinus americana</i> seedlings		Oak-pine forest	Patel and Rapport (2000)
Herbivorous insect community	↔ <i>Adenanthera pavonina</i> survival		Tropical rain forest	Green et al. (2004)
Red crabs	↔ Leaf herbivory of mistletoe		<i>Nothofagus</i> forest	Bach and Kelly (2004)
Herbivorous insect community	↔ Seedling herbivory		Tropical rain forest	Asquith and Mejia-Chang (2005)
Herbivorous mammals	↔ Seedling damage		Tropical rain forest	Benitez-Malvido and Lemus-Albor (2005)
Cattle and large indigenous mammals	↔ Woody seedling abundance and richness		Afromontane forest	Lawes et al. (2005)
Herbivorous insects and rodents	↔ Leaf-damage of five <i>Quercus</i> species		Tropical montane forest	Lopez-Barrera et al. (2006)

recorded higher herbivory by meadow vole (*Microtus pennsylvanicus*), lower herbivory by white-tailed deer (*Odocoileus virginianus*), and no differences in herbivory by invertebrates. At other study sites, however, herbivory damage by the white-tailed deer was observed to increase (Alverson et al. 1988).

Despite the occurrence of species-specific responses, two groups of dominant herbivores are well documented to benefit from forest fragmentation and increased proportion of edge habitats: deer in temperate forests of North America and leaf-cutting ants in the Neotropics. Deer, especially the edge-loving white-tailed deer, have shown increased population densities since the nineteenth century, greatly because of extensive timber harvesting, continued habitat fragmentation, creation of “wildlife openings”, and reduced hunting (Alverson et al. 1988). Recently, we demonstrated that leaf-cutting ant populations (*Atta* spp) strongly benefit from edges in the Brazilian Atlantic forest. The colony density of *Atta cephalotes* was about 8.5 times higher in the first 50-m edge zone than in the >100-m forest interior (Wirth et al. 2007). This edge proliferation of leaf-cutting ants went along with an increased rate of annual herbivory per colony. Equally sized *A. cephalotes* colonies located at the forest edge removed about twice as much leaf area from their foraging grounds as interior colonies (14.3% vs 7.8% colony⁻¹ year⁻¹). This higher herbivory rate within the forest edge zone was a consequence of reduced foraging areas (0.9 ha vs 2.3 ha colony⁻¹ year⁻¹) and a moderately lower leaf area index in this habitat, while harvest rates were the same (Urbas et al. 2007).

3.2 Processes

Regarding causalities for the above patterns, we extracted three main complexes of factors: (a) changes resulting from edge-induced shifts in environmental conditions, (b) resource-based aspects, and (c) responses related to natural enemies (Tables 1, 2). One primary and most noteworthy finding of this review is the scarcity of works that deliberately and directly addressed functional issues or aimed to provide mechanistic explanations for the observed patterns. Only a few studies reporting changes in herbivory along the forest edge included an a priori design to assess the potential causal factors, and most of the explanations given in the literature were based on indirect evidence or deductive reasoning (Tables 1, 2). In the following we try to synthesize the essential mechanisms arising from this review, our own studies on leaf-cutting ants in the Brazilian Atlantic forest, and theoretical considerations.

3.2.1 Microenvironment-Related Processes

Some of the more obvious changes following edge creation are abiotic (see Section 2) and mechanisms derived from organisms’ responses to abiotic factors are best understood (Foggo et al. 2001). While it is reasonable to assume that herbivores, like other groups of organisms, should be directly affected by the considerable microenvironmental alterations in the forest edge zone (Kapos 1989), there is little

concrete evidence for the relevance of this factor. Only in two cases was the improved edge performance of lepidopteran herbivores directly attributed to the increased temperature of boreal forest edges (Cappuccino and Martin 1997; Levesque et al. 2002). Nevertheless, reported changes in herbivore densities and/or herbivore damage were reasonably related to the edge environment. Herbivores that respond negatively include shade-loving (sub)tropical forest interior species (Brown and Hutchings 1997; Arnold and Asquith 2002; Valladares et al. 2006), which may be especially sensitive to deleterious edge conditions (see Section 2).

Increasing herbivory as a result of positive abiotic edge effects is consistently observed in temperate or boreal forests (Tables 1, 2), where edges represent warmer and sunnier habitats than the stand interiors (Matlack 1993; Chen et al. 1995) and may therefore promote a wide range of insect herbivores (for contrasting patterns among species, see MacGarvin et al. 1986). This might be due to two aspects: reduced developmental time for larvae (Cappuccino and Martin 1997) or preferential oviposition on sunlit hosts (Moore et al. 1988). The resulting edge aggregation of adults and early life stages appears to be a more general consequence of edge microclimate and is proposed by several authors (Roland 1993; Jokimäki et al. 1998; McGeoch and Gaston 2000; Tables 1, 2). In addition, microclimate-related edge properties are responsible for higher-order effects on both herbivores and plants via the alteration of trophic interactions, as will be detailed below.

3.2.2 Trophic Processes

Whether the extent of plant-herbivore interactions is enhanced or reduced in a given environmental context depends on the functioning of bottom-up and top-down forces, which act in concert to influence the abundance and distribution of herbivores (Hunter et al. 1997). Bottom-up regulation is hypothesized to affect herbivore populations through food limitation (Mattson and Addy 1975). In contrast, top-down forces are proposed to regulate herbivores through predators and parasites (Hairston et al. 1960). The degree to which plant-herbivore interactions are structured by these two basic processes is a classic debate in ecology (Dyer and Letourneau 1999) which, in the past decade, received new impetus from the study of habitat fragmentation (Tscharntke and Brandl 2004). Research documenting that habitat loss and isolation may lead to the truncation of food chains, especially the release of herbivores from top-down control, is particularly influential (Kareiva 1987; Kruess and Tscharntke 1994; Terborgh et al. 2001; Kondoh 2003), but the role of edges remains largely obscure. In contrast, the trophic regulation of herbivores along forest edges has long been related to resource availability (e.g. Leopold 1933), despite a remarkable paucity of solid empirical data.

Changes in resource availability/quality

Enhanced availability and/or quality of resources are the most commonly invoked processes to causally link the edge habitat with increasing herbivory. The adjustment

of herbivore distribution and feeding behaviour to food value and quantity is reflected in the resource concentration hypothesis (Kareiva 1983) and is based upon general assumptions of optimal foraging theories (see Pyke et al. 1977). Of the 55 papers taken into account, 14 advocated this bottom-up view, but direct evidence is rather limited (five articles, Tables 1, 2). Several resource-related factors accounting for elevated edge herbivory come into question.

One of the most prominent and well documented edge effect in forested ecosystems is a shift in plant community composition towards fast-growing, early-successional species (see also Section 2), which are generally known to be the preferred food of herbivores because of lower levels of quantitative defences and higher nutritive value than shade-tolerant species (Coley 1980). Following this pattern, diversity, abundance, or damage level of herbivores is greater in pioneer-dominated forest stands like, e.g. tree-fall gaps (Richards and Coley 2007). For forest edges, this or variations of this mechanism have been repeatedly proposed (Leopold 1933; Lovejoy et al. 1986; Murcia 1995; Brown and Hutchings 1997; Matlack and Litvaitis 1999), but only rarely addressed explicitly (Barbosa et al. 2005; Urbas et al. 2007; Tables 1, 2).

The drastic (>8.5-fold) increase in colony density and annual herbivory rate of leaf-cutting ants in the Brazilian Atlantic forest (see Section 3.1) gives further support to the relevance of compositional shifts in the plant community as a driving bottom-up mechanism. Increasing edge herbivory due to decreasing foraging areas (see above) can be explained by the greater abundance of highly palatable pioneer species in the edge zone of the studied area in terms of both species and stem number (Oliveira et al. 2004; Grillo 2005). Such an inverse relationship between resource density and foraging area is consistent with predictions of the optimal foraging theory (Ford 1983) and is well documented (e.g. Leal and Oliveira 2000).

Greater herbivore pressure at the forest edge than in the forest interior may result from a range of edge-mediated effects on the palatability of food plants other than those associated with the dominance of early-successional forest plants. There is some evidence that microenvironmental alterations near edges (see Section 2) affect plant performance to the extent that leaves exposed to the edge taste better. For example, Fortin and Maufette (2001) showed that forest tent caterpillars perform better on sugar maple trees at the edge, because their foliage contains higher concentrations of nitrogen and soluble sugars. Likewise, intraspecific and within-plant leaf quality may be improved by edge-induced drought stress (Laurance et al. 2001). Food plant preference of leaf-cutting ants, for example, was linked to drought stress via increased osmolyte concentrations within the leaves (Meyer et al. 2006). Given the fact that folivory was shown to intensify the drought stress of a plant by uncontrolled water loss from wounds (Aldea et al. 2005), it is plausible that edge conditions initiate a positive feedback loop, where stressed plants are attractive to leaf-cutting ants, therefore experiencing higher levels of herbivory damage, which in turn intensifies their drought stress, thus making them even more attractive (Meyer et al. 2006).

Even in the absence of drought stress, edge environments may render individual plants and plant parts more susceptible to herbivory. As a consequence of increased light availability at exposed forest edges (Davies-Colley et al. 2000), more leaves are sunlit, and thus the proportion of sun versus shade leaves is supposed to be higher than in the

forest interior. The preferences for and/or greater survival on sun-leaves is a well known feature in various groups of insect herbivores (for a review, see White 1984) and is often related to their increased nutritive value (Nichols-Orians 1991). We are not aware of studies that attempted to directly correlate herbivory at forest edge versus interior with the availability/quality of sun-leaves (but see MacGarvin et al. 1986). However, a decrease in herbivory has never been associated with edge-induced changes in food availability/quality (Table 2), though there is some circumstantial evidence pointing to the possibility of light-induced plant defence (e.g. Shure and Wilson 1993).

Forest boundaries can have a positive effect on the palatability of resources by modulating fluxes of nutrients. Based on studies in various systems, Pickett et al. (2000) concluded that the enhancement of nitrogen in the forest edge zone (e.g. as fertilizer drift from adjacent agriculture) is a more general process. Since fertilized plants are often more palatable to herbivores than unfertilized plants (Bryant et al. 1987), this impact may well be responsible for increased edge herbivory (see also Major et al. 2003; Christie and Hochuli 2005).

The fact that edges represent high-resource environments for forest plants in terms of light and nutrient availability is likely to lead to a general increase of (leaf) productivity (Laurance et al. 2003) and may thus represent another component of edge-induced herbivore attraction (Major et al. 2003). This is documented for treefall gaps and forest canopies, where highly productive vegetation and increased leaf-turnover generate a persistent source of young, soft leaves, which are frequently preferred by herbivores (Basset 1992; Richards and Coley 2007).

Top-down-related processes

Given the popularity of top-down-related mechanisms in the study of fragmentation effects (Terborgh et al. 2001; Thies et al. 2003), our knowledge about performance, abundance, or predation/infection efficiency of natural enemies in forest edge zones is surprisingly limited. Of 55 articles, only three presented original data to demonstrate that edges influence the top-down control of herbivores, one in which herbivory was lower and two in which it was higher in edge habitats (Tables 1, 2). In a formal respect the latter studies fit the basic pattern uncovered in fragmented landscapes, where the elimination of natural enemies is followed by the subsequent release of lower trophic levels, such as herbivores (Kareiva 1987; Kruess and Tscharntke 2000; Terborgh et al. 2001). Causal explanations are largely related to area loss and isolation, although it is conceivable that island biogeographic studies are inevitably confounded by edge effects (Malcolm 1994). In fact, we suspect that edges may also add to consumer-driven changes in herbivory, as illustrated by the following observations.

The most convincing evidence for a negative edge-influence on top-down processes stems from studies with the tent caterpillar, an important North American herbivore pest, and its natural enemy, a nuclear polyhedrosis virus (Roland 1993; Roland and Kaupp 1995; Rothman and Roland 1998). Pathogen-induced mortality of the herbivore was considerably reduced at the forest edge because virus particles do not remain infectious under high light (particularly

UV-light) and low humidity. Although not properly examined, such adverse environmental edge conditions may also be responsible for reduced parasitism of moisture-loving phorid flies (a specialist parasitoid of leaf-cutting ants) on edge colonies of *A. cephalotes* in the Brazilian Atlantic forest. Almeida (2004) found that both the number of flies attracted to nests and their attack rates were significantly lower in edge habitats.

Edges are called important population sinks, especially for large carnivores (Laurance 2000), some of which may be important control agents of herbivore species. Other than in area-based extinction models, this kind of animal loss is especially due to the tendency of large predators to range outside the boundaries of nature reserves combined with the increased hunting pressure along patch interfaces with human-dominated landscapes (Woodroffe and Ginsberg 1998; Laurance 2000). This can be exemplified by an edge-associated decrease in armadillo predation on leaf-cutting ants along forest fragments in the Brazilian Atlantic forest, where armadillos are subjected to human hunting (Fernandes 2003). During a year-round monitoring of ten *A. cephalotes* colonies, Darrault (2005) found a marginally significant lower number of armadillo burrows in edge colonies (33.0 ± 6.91 colony $^{-1}$) compared with interior colonies (45.6 ± 7.56 colony $^{-1}$).

Generally, there is ample support for negative edge impacts on several groups of predators that have been shown to be vulnerable to edge creation (see also Section 2). However, we still lack studies to evaluate how these changes affect herbivorous edge communities and whether they may be compensated or surpassed by opposing edge effects of increased predator intensities.

In fact, despite a scarcity of published data (Tables 1, 2), there is substantial indirect evidence suggesting that edge herbivory may be decreased by natural enemies. To give some examples, greater predatory impact may arise from:

1. Cross-edge spillover of subsidized predators from the anthropogenic matrix to the natural forest habitat (Rand et al. 2006);
2. Predator avoidance behaviour of herbivores to escape increased mortality risks along the forest edge (Lambrinos 2006);
3. Increased predation/parasitism efficiency – e.g. because of improved visual host location (Valladares et al. 2006).

We recommend future studies to elucidate whether such phenomena are more broadly relevant for the population dynamic of edge herbivores.

4 Impact of Herbivory on the Forest Edge

To date no studies have specifically evaluated the impact that herbivores have on the forest edge at the ecosystem level; and studies on both the population or community level are still scarce (Sork 1983; Jules and Rathcke 1999; Meiners et al. 2000; Benitez-Malvido and Lemus-Albor 2005). Strong evidence on the effects of

a high herbivory pressure on forested ecosystems was compiled in temperate forests on the effects of ungulates – mainly deer (for reviews, see Alverson et al. 1988; Rooney and Waller 2003) and more recently in a tropical forest on land bridge islands with high densities of howler monkeys and leaf-cutting ants (Rao et al. 2001; Terborgh et al. 2001, 2006).

This section aims to explore and propose possible effects based on the general impact of herbivory as demonstrated for different ecosystems and the uncovered patterns of herbivory at the forest edge as described above. It will discuss how the community of herbivores impacts ecosystems on three levels: the abiotic conditions, the plant community, and higher trophic levels.

4.1 Abiotic Conditions

4.1.1 Vegetation Structure and Light Regime

Removing leaves or leaf tissue of plants opens the canopy, allowing a higher proportion of light to penetrate the forest. Thus, herbivory can potentially cause similar effects as the creation of edges per se (see Section 2). In forests, an increased light availability following herbivory has rarely been documented. Wirth et al. (2003) found patches of high light transmittance on the forest floor and increased sunfleck frequency in a tree canopy within the foraging territory of leaf-cutting ants (*Atta colombica*) in a tropical lowland forest in Panama. An even stronger impact was demonstrated for colonies of *Atta cephalotes* whose foraging areas presented 18% less vegetation cover and 40% more diffuse light compared with control sites in the Brazilian Atlantic forest (Correa 2006).

Herbivores influence vegetation structure by more than the removal of foliage, i.e. herbivory per se, for example by trampling and crushing plants, burrowing, forming trails, and nesting (Huntly 1991). Elephants (*Loxodonta africana*) were shown to induce damages in African savannas by breaking and uprooting trees (Augustine and McNaughton 2004) and leaf-cutting ants by creating understory gaps of up to 150 m² (Meyer, unpublished data), predominantly close to the forest edge (Wirth et al. 2007). Preliminary data on the microclimatic effects caused by nest clearings of *A. cephalotes* indicated that about three times as much light reaches the nest compared to the surrounding forest floor accompanied by higher maximum air and soil temperatures, as well as by lower air humidity plus stronger daily fluctuations in all these parameters (Meyer, unpublished data).

Summarizing, increases in light availability induced by herbivores may promote heterogeneity and micro-site diversity in a relatively homogeneous environment, like the interior of a continuous forest (Wirth et al. 2003). In contrast, at the forest edge herbivores enhance the high light availability typical for the edge and ultimately homogenize the microclimate.

4.1.2 Nutrient Cycling

The second important resource for plants are nutrients, the availability of which can be altered by the activity of herbivores. Generally, herbivory increases the cycling rate of macronutrients, because they are often released more rapidly from the faeces of herbivores than from decomposing plants (Zamora et al. 1999). Recent studies in forest systems indicated that herbivores can cause heterogeneity in nutrient concentrations and might influence nutrient availability and plant productivity. Wirth et al. (2003) found leaf-cutting ants to concentrate nutrients derived of leaves gathered in large areas in their refuse dumps and Feeley (2005) showed that clumped defaecation of howler monkeys leads to a local concentration of nitrogen and phosphorus. Higher biomass of fine roots within these resource patches (leaf cutting ant nests: Moutinho et al. 2003; howler monkey latrines: Feeley 2005) indicates nutrient exploitation by the surrounding vegetation.

The concentration of herbivores at forest edges (Table 1) could, in addition to accelerated nutrient cycling, lead to an accumulation of nutrients at edges. In combination with the observed nutrient drift from the surrounding matrix (fertilizer from agricultural systems: Pickett et al. 2000; pollution from urban areas: Christie and Hochuli 2005), forest edges should be generally less nutrient-limited than the forest interior. Possible consequences of such relaxed nutrient limitation were demonstrated on isolated islands under high herbivory pressure for plant productivity (Feeley and Terborgh 2005), with resulting cascading impacts on the whole ecosystem (Terborgh et al. 2006).

4.2 Plant Community

Few herbivores have the potential to alter vegetation communities by killing adult trees. A prominent exception of this occurs during insect outbreaks – a common phenomenon in fragmented forests (see Kondoh 2003, and references therein). Such defoliation calamities were also reported from forest edges (Roland 1993). Which plant species experience the greatest impact depends on the feeding preferences of herbivores and on differences in the plant's ability to tolerate herbivory damage, as discussed below.

4.2.1 Differential Feeding Preference

All herbivores – even highly polyphagous ones – show preferences for certain plant taxa (Bernays and Chapman 1994). Since damage by herbivores is thus not homogeneously distributed across the plant community, herbivores can alter community composition (e.g. Vasconcelos and Cherrett 1997; Terborgh et al. 2001). Especially the preference of dominant herbivores has been demonstrated to strongly impact forests. For example, damage to shrub canopies by elephants cause large reductions in cover of *Acacia mel-*

lifera and *Grewia tenax*, but lesser reductions in cover of *A. etbaica* (Augustine and McNaughton 2004); and deer browsing in temperate forests suppresses tree regeneration of *Abies alba* and *Acer pseudoplatanus* (Ammer 1996).

Generally, pioneer plant species dominating forest edges are believed to be more attractive food sources for herbivores (Coley 1980; see also Section 3.2). Therefore, pioneer and early successional species at the forest edge should be more heavily attacked than later successional species, but the impact of herbivory also depends on the plants' ability to tolerate damage.

4.2.2 Differential Tolerance of Herbivory

Slow-growing plants are believed to be less able to compensate for biomass losses than fast-growing plants and are likely to be more susceptible to herbivory if attacked, especially in habitats with high resource availability (Coley et al. 1985). A community of pioneer plant species at the forest edge should therefore better compensate for losses to herbivory than less abundant later successional species. For example, the two pioneer species investigated by Khan and Tripathi (1991) showed higher growth rates and, consequently, a higher increase in biomass despite higher herbivory rates compared with two shade tolerant species.

4.2.3 Regeneration and Succession at the Forest Edge

While the feeding preference of herbivores seems to discriminate pioneer plant species, their capacity to tolerate damage should favour them. What will be the resulting overall pattern for the species composition at the edge? Forest edges face a dramatic shift in plant species composition subsequent to edge creation. They typically display an impoverished set of species compared with the forest interior and are largely dominated by pioneers (see Section 2). This first change in species composition renders edges more prone to higher-order changes imposed by foliage removal (Harper et al. 2005). Under very high herbivory pressures forest regeneration might be suppressed, resulting in a plant community comprised mostly of resistant, non-palatable species. This was documented, for example, on small land-bridge islands, where leaf-cutting ant (*Atta* spp) populations reached 10–100 times their mainland densities (Rao et al. 2001; but see White 2007). While we have demonstrated that the majority of studies on herbivory at forest edges detect an increase in abundance of and damage by herbivores, documentation of destructive foraging by overabundant herbivores is relatively rare (but see Gilham 1955; Alverson et al. 1988; Roland 1993; Rao et al. 2001). Consequently, it is reasonable to expect some disruption, not a thorough inhibition, of the regeneration process at forest edges.

Succession across the forest edge takes place as: (a) structural development of the edge and (b) forest recovering by recolonization processes in the adjacent matrix. Such recolonization of the matrix occurs when the disturbance, which created the edge, has ceased and can be influenced by herbivory (Meiners et al.

2000). Succession and forest recovering requires edge effect amelioration and the consequent successful establishment of more shade-tolerant or later successional tree species (Gascon et al. 2000). Increased herbivory may depress the recruitment of shade-tolerant trees, while favouring the establishment of pioneer plants in two ways: directly by changing microclimate (particularly light availability) and indirectly by reducing competition with shade-tolerant plants. More pioneers support more herbivores, which in turn promotes the persistence of pioneers: this kind of “positive feedback loop” was proposed to explain replacement of heather by grasses in British uplands exposed to sheep grazing (Palmer et al. 2005). Similarly, elephants prefer to feed on pioneer species, so that open areas offer them more feeding opportunities and the damage they cause, in turn, maintains or increases openness (Sheil and Salim 2004). In the Shimba Hills in Kenya, Höft and Höft (1995) concluded that elephant activity arrests forest succession as their damage promotes regeneration of the most browsed early successional and fast-growing species.

In our study system (see Section 3.1), *Atta cephalotes* concentrates foraging on pioneer species at the forest edge (Falcão 2004; see also Section 3.1). The resulting high herbivory rate is believed to increase light availability and, therefore, enhance regeneration of pioneer plants. In addition, ant nest-related canopy gaps and the resulting changes in microclimate were shown to negatively impact germination and seedling establishment of a typical, shade tolerant forest tree. With increasing distance from nests, *Chrysophyllum viride* showed higher proportions of germination (nest centre = $3.3 \pm 1.6\%$, nest edge = $4.6 \pm 2.3\%$, 5 m = $5.3 \pm 1.9\%$, 25 m = $6.8 \pm 1.6\%$; Correa 2006). In conclusion, leaf-cutting ants profit from the creation of forest edges that they colonize in high densities and help to maintain edge microclimate and pioneer dominance by high herbivory rates and the creation of nest clearings.

4.3 Higher Trophic Levels

Herbivores represent the interface between primary production and higher trophic levels within food webs. An increased abundance of herbivores at the forest edge (see Section 3.1) can attract predators and parasitoids (Matlack and Litvaitis 1999), in a similar way as high densities of palatable pioneer plants offer more resources for herbivores. This is in accordance with current theory predicting that, when primary productivity is high, herbivore populations increase to levels that can support substantial predator populations (Fretwell 1977; Oksanen et al. 1981). Communities of insectivorous birds, for example, concentrate their foraging on forest edges (Strelke and Dickson 1980; Lewke 1982; Lovejoy et al. 1986). Predator concentrations at the forest edge may in turn propagate through the food web affecting other members of the faunal community. Such cascading effects are now widely recognized (Terborgh et al. 2001). Ries and Fagan (2003), for example, reported an edge-induced increase of the (predatory) mantid *Stagmomantis limbata*

leading to higher bird predation rates. Thus, altered plant-herbivore interactions imply not only direct changes in population and community level processes but also indirect effects on edge ecosystem functions.

5 Conclusions and Outlook

This review provides ample evidence that herbivores profoundly benefit from forest edges. This positive edge effect seems more pronounced for herbivore densities rather than herbivore damage, possibly because high plant productivity at the edge masks the true extent of foliage removal. Moreover, generalist herbivores appear to be particularly favoured by edges, while decreased edge abundance of herbivores frequently involves specialists. Increased herbivory pressure at forest edges likely results from a combination of favourable microenvironmental conditions for herbivores and increased food quantity and quality (relaxation of bottom-up control), caused *inter alia* by a shift in plant composition at forest edges. The impact of natural enemies on edge herbivory is less well documented, but there are good examples for an edge-mediated disruption of top-down regulation of herbivores. Although there is strong indirect support for reduced edge herbivory via enhanced top-down control in forest edges, we still lack more conclusive evidence. These general findings emerged despite the relatively low number of available reports (55) which exhibit significant biases toward insects, few plant species, seedling damage and survivorship, and population level impacts. Additional limits of current literature include a noticeable lack of long-term studies and those addressing key herbivores (great foliage consumers), herbivory rates on community level, as well as magnitude and intensity of herbivory-related edge effects.

In addition to amplifying edge-induced microclimatic changes and influencing trophic cascades by the attraction of predators, high densities of herbivores may potentially affect forest edges by speeding up an already accelerated turnover rate of matter and energy. Being directly favoured by the abundance of pioneers and indirectly favouring pioneer plants, herbivores may ultimately delay succession or regeneration at forest edges, thereby amplifying biota modifications triggered by habitat fragmentation. These proposed impacts of increased herbivory on ecosystem structure and function following edge creation are an example of how human activity not only directly disturbs habitats and drives species loss, but also alters species interactions in a way that amplifies disturbance, reduces resilience, and increases the risk of secondary species loss.

Based upon the above findings, future research should: (a) validate and assess the generality of both the patterns and underlying mechanisms proposed here regarding herbivore occurrence and herbivory at forest edges and (b) address more ecosystem-level effects driven by high herbivory loads on forest edges (e.g. changes in primary productivity, nutrient cycling, succession, ecosystem resilience), as such effects are in theory more pervasive in ecological and geographic terms.

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Aerial view onto the heavily fragmented landscape within the Usina Serra Grande, that is typical for the Northeast of Brazil. Shown are remnants of the Atlantic forest embedded into a matrix of sugarcane fields. Note how the irregular form of fragments causes the majority of the forested area to be in proximity to a forest edge. (photo Adriano Gambarini)



View over the matrix of sugarcane monoculture at the end of the rainy season. Forest remnants are restricted to the hill tops while sugarcane is planted in the valleys and on the lower slopes. Many smaller fragments are isolated by vast tracts of sugarcane from other parts of the forest. (photo Adriano Gambarini)



In the dry season the sugarcane is burned to facilitate its harvesting. Special care is taken that forest edges do not catch fire during the process. This is ensured by clearing strips of several meters width between forest edges and the remaining sugarcane before the latter is torched.



View onto a forest edge after the harvesting of the sugarcane at the peak of the dry season. During this time of the year the contrast between forest remnants and surrounding matrix is especially pronounced amplifying a multitude of strong edge effects.



Leaf-cutting ants of the species *Atta cephalotes* construct large nests within the forest, many of which are concentrated close to forest edges. At nest sites the vegetation is drastically reduced by the ants, creating a gap in the understory. The large nest mound is comprised of soil that the ants have excavated during the creation of subterranean chambers.



Within the canopy leaf-cutting ants can defoliate whole tree crowns as seen here. Thereby the ants create gaps of various sizes in the canopy, which allow additional light to reach the shaded forest floor. Especially above the nests of *Atta cephalotes* such openings are frequent and extend the understory gap seen in the previous photo into the canopy.



The microclimatic consequences resulting from the altered forest structure at nest sites were quantified in this thesis. In the center of nests and along transects into the forest incoming light, air temperature and humidity, soil temperature, and water availability in the soil were measured. The white shields visible in the picture enclose the sensors measuring air temperature. Light sensors are mounted on top.



Consequences from microclimatic conditions for plant regeneration were tested directly by transplanting pre-grown seedlings of several species into nest centers (shown here) and into plots along nest-forest transects. Subsequently growth and survival of the seedlings were monitored. The conspicuous seedlings in the picture are of the species *Licania tomentosa*.

PART II

Atta in a fragmented forest

3

Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest

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SHORT COMMUNICATION

Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest

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Leaf-cutting ants (genera *Atta* and *Acromyrmex*) have been denoted key species of American rain-forest ecosystems (Fowler *et al.* 1989) because of their multifarious effects on the vegetation. Being dominant herbivores, cutting up to 13% of the standing leaf crop in a colony's territory per year, they affect directly and significantly individual plants, plant communities and ecosystems (Wirth *et al.* 2003). The considerable ecological impact of these ants is paralleled by the well-known fact that some species strongly benefit from human-driven habitat alterations and represent prime pests throughout Latin America (Cherrett 1986). Numerous studies have documented populations of leaf-cutting ant to increase with increasing agricultural land use, deforestation and/or disturbance (Fowler *et al.* 1986, Jaffe & Vilela 1989, Jonkman 1979). Specifically, elevated colony densities have been recorded in (1) transformed vegetation such as pastures (Fowler 1983) and plantations (Jaffe 1986, Oliveira *et al.* 1998), (2) early successional forests (Vasconcelos & Cherrett 1995), and recently (3) isolated forest remnants (Terborgh *et al.* 2001).

Surprisingly, despite frequent records in disturbed areas, published observations/assessments of increased *Atta* densities along forest edges are completely lacking. This is unexpected considering that an increasing proportion of the global forested landscape is in close proximity to anthropogenic edges (Harper *et al.* 2005) and edge effects are a driving force behind many of the biological alterations induced by forest fragmentation (Fagan *et al.* 1999, Murcia 1995). In fact, generalist

herbivores have been repeatedly observed to be more abundant in edge than interior forests (Barbosa *et al.* 2005, Wirth *et al.*, in press). Here we provide a survey of *Atta* spp. in order to (1) evaluate whether the abundance of colonies changes with distance to the forest edge, (2) estimate the depth of edge influence, and (3) analyse whether *A. sexdens* (L.) and *A. cephalotes* (L.), two co-occurring *Atta* species (cf. Corrêa *et al.* 2005), respond differentially to edges.

The study was carried out in Coimbra, the single largest remnant of the Atlantic forest of north-east Brazil. Located in the state of Alagoas (9°S, 35°52'W), it covers approximately 3500 ha of largely well-conserved lower montane rain forest (Veloso *et al.* 1991), completely surrounded by sugar cane fields along its 40 km of relatively old (at least 60 y) borders (Urbas *et al.* in press). The region has a tropical climate characterized by a 5-mo dry season (< 110 mm mo⁻¹) lasting from September to January (annual precipitation = 2000 mm); the prevailing soils are latosols and podzols (IBGE 1985). The edge zone (0–100 m into the forest) has been shown to be largely dominated by pioneer species (Oliveira *et al.* 2004). We estimated colony densities of leaf-cutting ants (*Atta* spp.) with increasing distance from the forest edge towards the forest interior along 27 haphazardly laid transects. We used pre-existing, narrow (< 1 m) foot trails, which varied considerably in length, ranging from 70 to 3070 m. Trail entrances into the forest were separated on average by 1.67 ± 0.97 km (mean \pm SD). The total distance surveyed was 28 km. Thus, with a fixed belt width of 10 m to each side (as used by Jaffe & Vilela 1989, Wirth *et al.* 2003), the transects amounted to a total area of 56 ha sampled, in which all *Atta* colonies were recorded. Since nest

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mounds were not always visible from transects, we used additional evidence to locate colonies, such as foraging trails (active or physical) or fresh refuse material around nest entrances. Ants were identified as described in Corrêa *et al.* (2005) and voucher specimens were deposited in the collection of the Laboratório de Invertebrados Terrestres da UFPE, Recife, Brazil. The location of each colony was determined using a GPS-receiver equipped with an external antenna (eMap, Garmin Ltd., Romsey, UK) set on averaging mode, resulting in an estimated resolution better than 10 m. Both transects and forest border line were recorded using the tracking function of the GPS. Where GPS data were not available the forest border was estimated based on aerial photographs (scale 1:8000 from 2002, courtesy of M. Tabarelli). All spatial data were compiled in a geographic information system (ArcView GIS 3.2, Environmental Systems Research Institute, Redlands, CA, USA). The forest area was divided into 50-m distance zones parallel to the forest border line, extending up to 1000 m into the forest interior. Transects were intersected with these distance zones, resulting in 180 sample areas (0.36 ± 0.27 ha). The number of colonies occurring per sample area was determined and a colony density calculated. When transects had an area in common (crossings of trails) this was included only once in one of the transects. To account for disproportionate sampling of the forest interior due to a smaller number of long transects, we pooled distance zones > 300 m. This resulted in a total of seven distance zones, i.e. 0–50 m, 50–100 m, 100–150 m, 150–200 m, 200–250 m, 250–300 m and > 300 m. To test whether density of leaf-cutting ant colonies was influenced by ant species or distance, we conducted a repeated-measures ANOVA with species as the main factor and distance as a repeated-measure factor. Differences among distance zones were evaluated with Tukey's post hoc test. As the interaction between variables was of particular interest in this study, we used this design despite deviations from the required ANOVA assumptions. According to Fry (1993) and Zar (1996), this approach was legitimate, because the ANOVA is robust enough if the results are highly significant and can be confirmed by a non-parametric equivalent (e.g. Kruskal–Wallis), as was true in our case. All analyses were carried out using STATISTICA v. 6.0 (StatSoft Inc, Tulsa, USA).

Within the surveyed 56 ha we encountered a total number of 80 *Atta* colonies, 43 belonging to *A. cephalotes* and 37 to *A. sexdens*. The colony densities of these co-occurring leaf-cutting ant species changed drastically with distance to the forest edge (effect of distance: $F_{6,180} = 13.9$, $P < 0.00001$; Figure 1). However, although both species similarly increased along the edge (no main effect of species: $P < 0.78$), the magnitude of the edge effect was species-specific, as indicated by a significant interaction term between species and

distance ($F_{6,180} = 3.07$, $P < 0.007$). Colony density of *A. cephalotes* was low in the forest interior (0.33 ± 1.11 ha $^{-1}$, pooling all zones > 50 m into the forest) and sharply increased by a factor of about 8.5 towards the first 50 m (2.79 ± 3.30 ha $^{-1}$, Figure 1). On the other hand *A. sexdens* was more uniformly distributed. Colony densities in distance zones > 200 m (ranging from 0 ± 0 to 0.19 ± 0.51 ha $^{-1}$) were significantly different from those in the first two zones (2.14 ± 3.32 and 1.79 ± 4.09 ha $^{-1}$, Tukey's post hoc as shown in Figure 1b), indicating that for *A. sexdens* the edge effect might reach up to 200 m into the forest. Combining the two species, colonies occurred about five times more frequently in the 50-m edge zone (4.94 ± 3.67 ha $^{-1}$) than in the forest interior (1.01 ± 2.58 ha $^{-1}$, pooling all zones > 50 m). Variation of colony densities was generally large within distance zones because of colony-free samples due to (1) small sample areas per transect and distance zone and (2) clumped *Atta* distribution throughout the surveyed forest area (pers. obs.).

This study demonstrated for the first time a profound edge effect on the colony density of *A. cephalotes* and *A. sexdens* – two widespread leaf-cutting ant species in Latin America. Our findings suggest that populations of these species strongly benefit from the presence or creation of forest edges, and thus add to the list of disturbed habitats (e.g. secondary forests, plantations, pastures, roads, forest isolates) facilitating the spread of these dominant herbivores. Within the study area *A. cephalotes* was restricted to forested sites, while *A. sexdens* in addition inhabited open areas, such as dirt roads within sugar cane plantations (pers. obs.). This accords with known habitat preferences of the two species: *A. cephalotes* is a fragmentation-sensitive leaf-cutting ant species (Corrêa *et al.* 2005) commonly found in mature or old-growth forests (Jaffe & Vilela 1989, Rockwood 1973), while *A. sexdens* occurs in a wide range of habitats and is known as one of the species benefiting most from human-induced disturbances (Fowler *et al.* 1989, Vasconcelos 1990). We believe that the more uniform within-forest distribution of *A. sexdens* as compared to a pronounced edge concentration of *A. cephalotes* is a consequence of differences in the degree of foraging specialization. *Atta sexdens* forages opportunistically, simultaneously using trees and a wide variety of (ephemeral) resources for fungus culturing including seedlings, juveniles, flowers and dead leaves from ground litter (Vasconcelos 1990, pers. obs.). In contrast *A. cephalotes* concentrates its foraging on fresh leaves of large forest trees (Vasconcelos 1990) with a clear preference for pioneer species (Farji-Brener 2001), which are more frequent in forest edges and gaps (Laurance *et al.* 1998, Oliveira *et al.* 2004). Thus, *A. cephalotes* may respond more pronounced to the frequency of pioneer species, and therefore the edge, than *A. sexdens*.

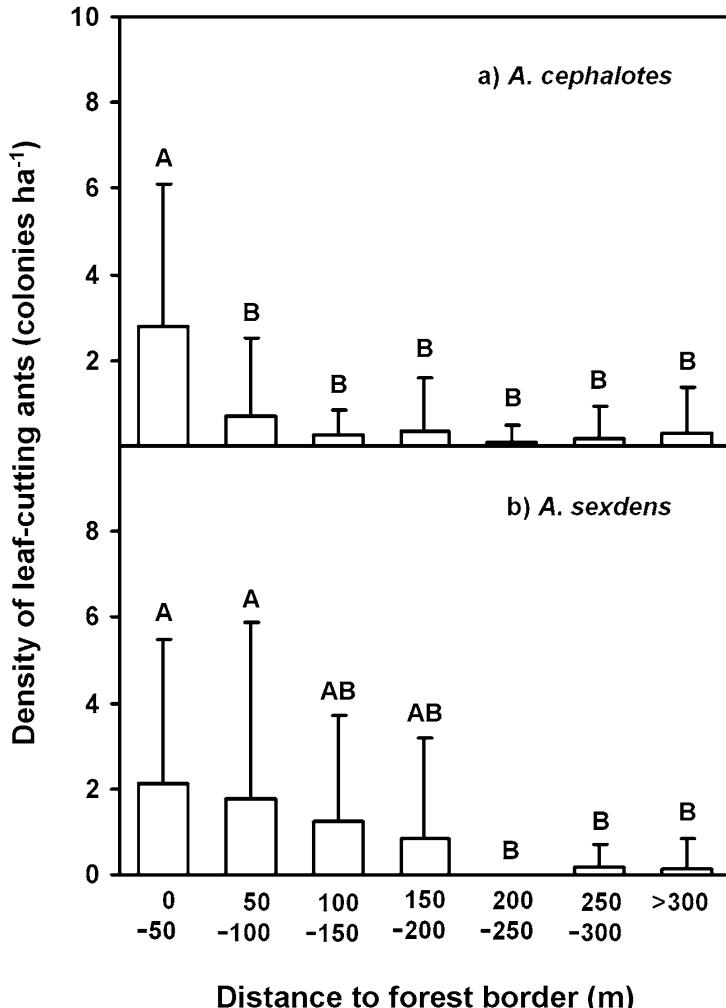


Figure 1. Mean colony density (\pm SD) of *Atta cephalotes* (a), and *Atta sexdens* (b) in seven distance zones paralleling the forest border in the Atlantic forest of north-east Brazil. Different letters indicate significant differences (Tukey's post hoc test, $P < 0.05$). Sample sizes for the different distance zones were as follows: 0–50 m = 23, 50–100 m = 24, 100–150 m = 22, 150–200 m = 22, 200–250 m = 19, 250–300 m = 16, and > 300 m = 54.

Colony densities in the undisturbed forest interior of Coimbra more than 300 m from any edge (0.12 ha^{-1} for *A. sexdens* and 0.31 ha^{-1} for *A. cephalotes*) were within the range reported earlier for *Atta* species in mature continuous rain forests (e.g. Cherrett 1968: 0.6 ha^{-1} , Jaffe & Vilela 1989: 0.045 ha^{-1} , Vasconcelos 1988: 0.03 ha^{-1} , Wirth *et al.* 2003: 0.033 ha^{-1}). We thus are confident that the studied forest remnant was large enough to investigate edge effects without interference from other potential factors, such as fragment size or habitat fragmentation per se. The results indicate that drastic population growth of leaf-cutting ants is not only a feature of secondary forests or small forest fragments, but also takes place along the border of large, relatively

undisturbed forest tracts. In this context our findings may have relevance for forest management and conservation, e.g. to estimate 'Atta-free' core areas of forest fragments.

An increased availability of fast-growing, less effectively defended pioneer species (Coley 1983) has been most frequently invoked to explain high abundances of leaf-cutting ants in secondary forests (Farji-Brener 2001, Jaffe & Vilela 1989, Vasconcelos & Cherrett 1995) because the ants show a clear preference for early successional food plants (Farji-Brener 2001, Wirth *et al.* 2003). We suggest that this bottom-up explanation particularly applies to edge-associated leaf-cutting ant species along pioneer-dominated forest edges (Laurance *et al.* 1998, Oliveira

et al. 2004), although truncated top-down forces and increased availability of nesting sites may also play a role. In fact, as we have demonstrated at the site of this study, *A. cephalotes* colonies harvested considerably more leaf area in edge vs. interior habitats (Urbas *et al.*, in press). As a consequence, edge forests experience a spatial concentration of *Atta* damage caused by both increased colony density and herbivory rate.

In the light of the ever-increasing pervasiveness of edge habitats (Harper *et al.* 2005) and the growing awareness of their significant impact on ecosystem processes (Fagan *et al.* 1999, Laurance *et al.* 2002), edge-driven accumulations of *Atta* colonies may have far-reaching consequences for forest edges in the Neotropics. In synthesis, we suggest that edge creation promotes high *Atta* densities, resulting in drastic changes on forest structure, microclimate, soil disturbance, and any subsequent impact on ecological processes, which may in turn reinforce deleterious edge effects (Fagan *et al.* 1999, Murcia 1995, Wirth *et al.*, in press).

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4

Persisting hyper-abundance of keystone herbivores (*Atta* spp.) at the edge of an old Brazilian Atlantic Forest fragment

as submitted to *Biotropica*

Meyer ST, Leal IR, Wirth R

ABSTRACT

A high abundance of palatable pioneer vegetation at forest edges is believed to cause leaf-cutting ants to profoundly benefit from edge creation in Neotropical forests, where they act as keystone species and disturbance agent. In view of poorly explored vegetation dynamics at aging edges the question arises whether high densities of leaf-cutting ants are a transitional or a persisting phenomenon. As a first insight into long term dynamics of plant-herbivore interactions following fragmentation, we studied the temporal variation of leaf-cutting ant densities, as a proxy for herbivory pressure, at the edge of the Brazilian Atlantic Forest. At physically stable edges of an old forest fragment densities of *Atta cephalotes* and *A. sexdens* (11 and 5 times higher in a 50m-edge zone in comparison to the forest interior) persisted over a four year interval (2001 to 2005) with no significant difference in densities between years. Species-specific relative growth rates ranged from 0.14 to -0.04 /yr, suggesting that populations were approximately at equilibrium. High rates of colony turnover (little less than 50% in 4 years) indicated an average colony life span of about 8 years – a life expectancy considerably lower than previous estimates for *Atta* colonies. Stable hyper abundant populations of leaf-cutting ants accord with the high availability of pioneer plants previously demonstrated at old stabilised forest edges in the region and are expected to persist in time as long as Neotropical forests are characterised by high edge to interior ratios, with potentially long-lasting consequences for the ecosystem.

Key words: colony turnover, edge-effect, forest fragmentation, leaf-cutting ants, life expectancy, population dynamics.

RESUMO

A alta abundância de plantas pioneiras e palatáveis nas bordas de florestas parece ser a razão para a proliferação de formigas cortadeiras nesses habitats, onde atuam como espécies chave e agentes causadores de perturbação. Como poucos estudos investigaram a dinâmica da vegetação de bordas antigas, não se sabe se as altas densidades de formigas cortadeiras é um fenômeno temporário ou persistente. Para entender a dinâmica das interações planta-herbívoro em longo prazo depois da fragmentação, nós estudamos a variação temporal da densidade de formigas cortadeiras como indicativo para a pressão de herbivoria em bordas de Floresta Atlântica Brasileira. Nós observamos que as altas densidades de *Atta cephalotes* e *A. sexdens* na borda da floresta (11 e 5 vezes mais altas nos primeiros 50 m de borda em comparação com o interior da floresta) persistiram ao longo dos quatro anos de intervalo entre os censos (2001-2005), não havendo diferenças significativas entre os anos. As taxas de crescimento relativo variaram de 0,14 a 0,04/ano, sugerindo que as populações encontravam-se próximas ao equilíbrio. As altas taxas de substituição de colônias (ca. 50% em quatro anos) indicaram uma vida média em torno de oito anos – uma expectativa consideravelmente mais baixa que as estimativas anteriores. A hiper-abundância das formigas cortadeiras ao longo do tempo está de acordo com a alta disponibilidade de plantas pioneiras em bordas antigas demonstrada previamente para a região estudada. Como as florestas Neotropicais são atualmente caracterizadas por uma grande proporção borda, é esperada a persistência dessa hiper-abundância ao longo do tempo com consequências para o ecossistema também em longo prazo.

Palavras-chave: dinâmica de populações, efeito de borda, expectativa de vida, formigas cortadeiras, fragmentação florestal, substituição de colônias.

INTRODUCTION

Habitat fragmentation and the resulting creation of artificial forest edges is one of the most pervasive and far-reaching consequences of present-day human land use dynamics (Whitmore 1997). Much of the ecological alterations faced by fragmented forests (e.g. species loss, biomass collapse) can be assigned to edge effects (Tabarelli & Gascon 2005) and understanding edge-induced alterations of species interactions is of fundamental importance for a profound perspective on the impacts of habitat fragmentation and the ecology of fragmented landscapes (Fagan et al. 1999, Hunter 2002). Herbivory is a species interaction considered to be among the key processes shaping life history traits and ecosystem functioning (Huntly 1991) and there is considerable evidence that herbivores profoundly benefit from forest edges (Wirth et al. 2008). A prominent example are leaf-cutting ants (LCA), which have been recognized as keystone species (Fowler et al. 1989) and ecosystem engineers (Wirth et al. 2003) in the Neotropics. It is well documented that populations of some LCA species increase with man-made habitat alterations in pastures (Fowler 1983), plantations

(Jaffe 1986, Oliveira et al. 1998), early successional forests (Vasconcelos & Cherrett 1995), and isolated forest remnants (Rao 2000). In addition LCA (*Atta* spp.) were recently shown to drastically benefit from forest edges in a heavily fragmented landscape of Atlantic Forest in northeast Brazil. Along old forest edges that have been protected throughout the last 60 years (Santos et al. 2008), *A. cephalotes* occurred 8.5 times more frequently in the first 50 m of the forest than further inwards (Wirth et al. 2007).

Edge-driven proliferation of *Atta* populations may have important implications considering the pervasiveness of forest edges and the ecological importance of LCA. Stand-level herbivory rates for *A. cephalotes* in the forest edge, based on colony densities (Wirth et al. 2007) and herbivory rates combined with the size of annual foraging areas (Urbas et al. 2007), amount to 32 percent of the total available foliage. This is about six times the rate in the forest interior (5.7%) and surpasses by far the overall rate of herbivory generally assumed for tropical forests (approx. 11%; Coley & Aide 1991). A high abundance of pioneer vegetation, which is more palatable to the ants, is thought to be the principal (though not sole) mechanism underlying high

LCA densities in secondary forests and forest edges (Farji-Brener 2001, Urbas et al. 2007, respectively; see also Wirth et al. 2008). In other words, fragmented forests, via edge-mediated relaxation of bottom-up forces, suffer increasing herbivory damage by LCA.

In view of poorly explored vegetation dynamics at aging edges and the described interdependence between vegetation composition and *Atta* densities, the future population dynamics of *Atta* in fragmented forests are difficult to predict. While abiotic alterations caused by edge creation are believed to ameliorate within five years due to secondary regrowth sealing the edge (Laurance et al. 2002, but see Gascon et al. 2000), there was still a detectable increase in pioneer densities 13–17 years after experimental fragmentation in the central Amazon (Laurance et al. 2006). In the Atlantic forest 60-year-old edges are largely dominated by pioneer vegetation (Oliveira et al. 2004) and showed altered regeneration patterns compared to the forest interior with a biased and impoverished assemblage of seedlings, particularly in terms of large-seeded trees (Melo et al. 2007). On the other hand, temporal dynamics of LCA populations are poorly studied. Besides evidence that LCA respond to the age of regenerating forests with a drop in colony densities between 30 and 40 years after initiation of the regeneration (Silva 2008) only two studies on LCA dynamics in natural forest systems had been conducted so far but without reference to successional forest dynamics (Perfecto & Vander Meer 1993, Wirth et al. 2003). Even estimates of fundamental parameters like turnover-rates and life expectancies of LCA colonies are lacking for natural forest systems, precluding assessments of the impact these keystone species have on the ecosystem level, since the area impacted over time and the persistence of the impact at any individual location is a direct consequence of the turnover of colonies. In light of these different dynamics the question whether high densities of LCA at the edge of forest fragments are a transitional phenomenon on ecological time scales or a persisting feature of fragmented landscapes remains to be answered. Therefore, analysing temporal variation of LCA densities – as a proxy for herbivory pressure – at the edge of the Brazilian Atlantic Forest with its long fragmentation history presents an excellent opportunity to provide exemplary insights into the long-term dynamics of

plant-herbivore interactions following fragmentation. LCA are adequate model organisms to study these dynamics due to their ecological importance, big, sessile, and long-lived colonies that enable reliable estimates, and the short lifespan compared to trees that allows to collect meaningful data within a few years

The purpose of this study was to assess basic parameters of LCA population dynamics and evaluate whether edge-mediated hyperabundance of LCA persists through time in fragmented landscapes. We present the comparison of two transect-based surveys of *Atta* spp. in a large remnant of the heavily fragmented Atlantic Forest in northeast Brazil, one conducted in 2001 and one in 2005. Mortality, natality, population growth rates, and turnover rates during the interval were calculated for the two species recorded (*A. sexdens* and *A. cephalotes*) based on their measured densities. Three questions were addressed specifically: (1) Does the overall density of LCA change in time? (2) Are there differences in turnover- and population growth rates of the two co-occurring species? (3) Is the pronounced aggregation of LCA colonies at the forest border stable in time? Results are discussed in terms of the persistence of ecological alterations in old fragmented landscapes.

MATERIAL AND METHODS

STUDY SITE. – The study took place in the single largest remnant of the Atlantic Forest in Northeast Brazil locally known as Coimbra (9° S, 35° 52' W), which covers a total of 3,500 ha of lower montane rain forest (Veloso et al. 1991) surrounded by homogeneous matrix of sugarcane monoculture. It is part of the Usina Serra Grande, a 22,000-ha private sugarcane plantation in the state of Alagoas and situated on a low-elevation plateau (300–400 m above sea level). Annual rainfall is approximately 2000 mm, with a 3-mo dry season (< 60 mm/mo) from November to January. Sugarcane cultivation in the area, which dates back to the 18th century, provided the strongest incentive for clearing large tracts of pristine old-growth forests, leaving only 7.25 percent of forest cover (Gusmão Câmara 2003). To ensure watershed protection and water supply for sugarcane irrigation, Coimbra and most other forest fragments remaining in this landscape have been strictly protected against disturbances such as wildfires and logging (Santos et al.

2008). This has guaranteed the spatial stability of forest borders and consequently the occurrence of both reproductive pioneer and shade-tolerant trees along post-closure forest edges (Melo *et al.* 2006). A detailed description of the floral composition of the area can be found in Pôrto *et al.* (2006). Despite the obvious limitations of the landscape configuration available to us (*i.e.*, only a single, unreplicated tract of forest), these features make Coimbra particularly suitable to assess the effects of edge creation as reflected by a number of published studies, *e.g.*, edge effects on the structure of tree assemblages (Oliveira *et al.* 2004, Santos *et al.* 2008) and tree reproductive traits (Girao *et al.* 2007) as well as LCA densities (Wirth *et al.* 2007) and herbivory rates (Urbas *et al.* 2007).

SURVEY OF NEST SITES – To sample populations of *Atta* species, 16 transects were walked along haphazardly chosen, pre-existing, narrow (<1m) foot trails from October 2001 to May 2002. Most trails were roughly perpendicular to the forest edge with trail entrances into the forest being separated on average by 1.6 ± 1.0 km (mean \pm SD). Transects had fixed belt widths of 10m to each side of trails (c.f. Jaffe and Vilela 1989, Wirth *et al.* 2003). Within transects, all *Atta* colonies visible from trails (colonies build nest mounds bare of vegetation that comprise on average 55m²) or located when using additional evidences, such as foraging trails (active or physical) or fresh refuse material around nest entrances, were included in the census. The two species occurring in the area – *A. cephalotes* and

A. sexdens – were identified as described in Correa *et al.* (2005) and voucher specimens were deposited in the collection of the “Laboratório de Invertebrados Terrestres da UFPE” in Recife, Brazil. All colonies and frequent points along transects were marked by GPS (eTrex, Garmin Ltd., Romsey, UK) and with flagging tape in the forest.

Between August and November 2005 transects were relocated within in the forest and rewalked. Transects and the forest border line were recorded using the tracking function of a GPS-receiver equipped with an external antenna (eMap, Garmin Ltd., Romsey, UK). In both census, 17.5 km of transects were walked within the forest representing an area surveyed of 35 ha. The location of colonies was determined by averaging GPS measurements until the estimated error was less than 10m (minimum of 30 positions). All living colonies – either surviving since 2001 or newly founded in the interim – were marked, as well as all dead colonies and positions in the forest where only a flagging remained. Thereby, the position and fate of 36 of the original 40 colonies found in 2001 could be determined; the remaining four lost colonies were excluded from the analysis.

CALCULATION OF POPULATION PARAMETERS – Based on dead, living and new colonies found in 2005, the population of 2001 was computed as the sum of dead and living colonies, while the population of 2005 was comprised from living and newly encountered colonies. Mortality was defined as the number of dead colonies and

Table 1: Number of colonies and densities of *Atta* species found within different zones of Coimbra Forest, Northeast Brazil. Colonies considered dead in 2005 were found alive in 2001, alive colonies were active in both censuses, and new colonies were newly encountered in 2005. Two colonies found in 2001 were determined only to genus and considered for *Atta* spp. only. Four colonies alive in 2001 could not be encountered in 2005 and were therefore excluded from the analysis.

Forest zone	Area surveyed (ha)	Number of colonies and status in 2005			Densities (colonies/ha)	
		dead	alive	new	2001	2005
<i>Atta</i> spp.						
Edge (50m)	2.5	4	8	6	4.77	5.57
Interior	32.6	12	12	13	0.74	0.77
Total	35.1	16	20	19	1.03	1.11
<i>Atta cephalotes</i>						
Edge (50m)	2.5	1	5	4	2.39	3.58
Interior	32.6	2	5	6	0.21	0.34
Total	35.1	3	10	10	0.37	0.57
<i>Atta sexdens</i>						
Edge (50m)	2.5	3	3	2	2.39	1.99
Interior	32.6	8	7	7	0.46	0.43
Total	35.1	11	10	9	0.60	0.54

natality as the number of new colonies, each divided by the population size of 2001. Relative growth rates were determined by subtracting mortality from natality. Turnover rates were calculated as the sum of new and dead colonies in 2005 divided by the sum of total colonies in 2001 and 2005 (e.g. Schoener and Spiller 1987). Life expectancies for colonies (*i.e.* the total time a colony is expected to live) were calculated as the inverse of turnover rates as is commonly done when studying fine roots and leaves (Hikosaka 2005, Withington et al. 2006). All parameters were calculated for each of the two *Atta* species and the genus level based on a 50-m edge zone, the forest interior and the whole forest. The position of the colonies within forest edge or interior was derived from a geographical information system based on GPS-marked forest edges and aerial photographs as detailed in Wirth et al. (2007). Meaningful estimates of population parameters could only be calculated based on the whole area surveyed. Accordingly, densities and parameters describing population dynamics were calculated for the pooled data and bias-corrected accelerated confidence intervals (BCa, 95%) were estimated by bootstrap resampling of the number of colonies found in individual transects. When the confidence interval of a given parameter does not include zero, this parameter is considered statistically significant (Hesterberg et al. 2006). Colony densities within the 50-m edge zone and the forest interior were tested for differences by computing a bootstrap-distribution of the difference between habitats and checking confidence intervals for the inclusion of zero (Hesterberg et al. 2006). Similarly, differences

between years were tested. All bootstrap statistics were computed in R version 2.6.0 (R Development Core Team 2007) using the boot library version 1.2-29 (Ripley 2007) with 5000 randomisations per statistic.

RESULTS

The overall density of *Atta* nests in Coimbra Forest was virtually constant (1.0 vs. 1.1 colonies/ha; Table 1). Of 36 LCA colonies found in 2001, 20 survived until 2005, 16 colonies died in the mean time, and 19 new colonies were founded. Colony densities of *A. cephalotes* increased slightly, while densities of *A. sexdens* tended to decrease. For neither of the two species, however, colony densities were significantly different between years (pair wise comparison via bootstrap of differences; $P > 0.05$). While growth rates for *Atta* spp. and *A. sexdens* were statistically non-significant (Table 2), *A. cephalotes* populations showed a pronounced increase of at least 50 percent ($P < 0.1$) in the edge zone and the whole forest, indicating that, from 2001 to 2005, the LCA community in Coimbra Forest shifted towards a dominance of *A. cephalotes*.

The studied *Atta* populations were highly dynamic. On average, little less than half of all colonies where substituted by new ones within the four-year period of this study, with turnover rates being significant for eight out of nine combinations of taxonomic group and forest zone (Table 2). Based on the 95% confidence intervals estimated for the turnover rate of both *Atta* species pooled over the whole sampled area

Table 2: Parameters describing population dynamics of *Atta* species over a period of four years (2001-2005) within different zones of Coimbra Forest, Northeast Brazil. Negative growth rates indicate a decline in the population. Significant parameters ($P < 0.05$) are shown in bold, marginal significant parameters ($P < 0.1$) in italics. Significances were tested by a bootstrap analysis as indicated in the text.

Forest zone	Mortality	Natality	relative	Growth rate		Turnover rate
					absolute (colonies/ha)	
<i>Atta</i> spp.						
Edge (50m)	0.33	0.50	0.17	0.80	0.38	
Interior	0.50	0.54	0.04	0.03	0.51	
Total	0.44	0.53	0.08	0.09	0.47	
<i>Atta cephalotes</i>						
Edge (50m)	0.17	0.67	0.50	1.19	0.33	
Interior	0.29	0.86	0.57	0.12	0.44	
Total	0.23	0.77	0.54	0.20	0.39	
<i>Atta sexdens</i>						
Edge (50m)	0.50	0.33	-0.17	-0.40	0.45	
Interior	0.53	0.47	-0.07	-0.03	0.52	
Total	0.52	0.43	-0.10	-0.06	0.51	

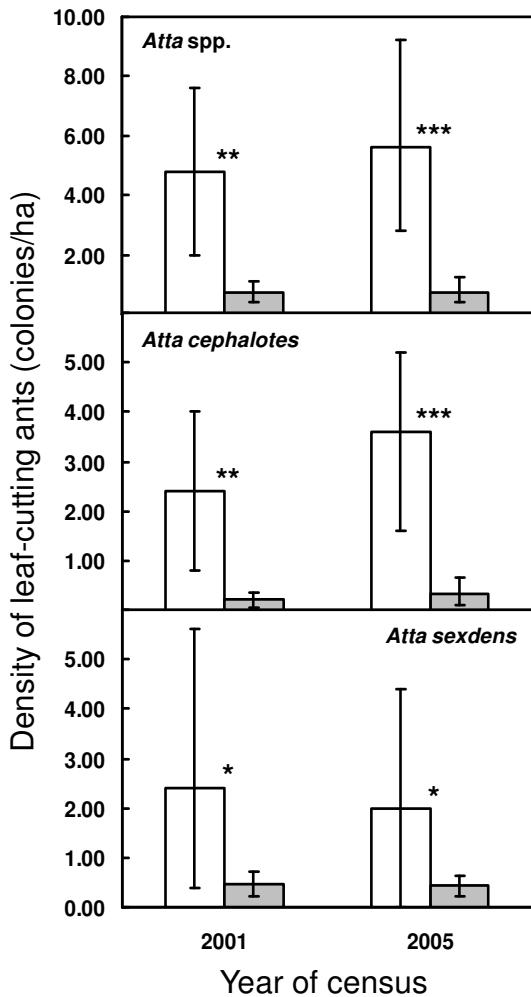


Figure 1: Densities of leaf-cutting ants in a 50m-edge zone (white) and the forest interior (shaded). Shown are medians with 95% confidence intervals derived by bootstrap-resampling. Significant differences between habitats are indicated by asterisks (** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$). Differences were tested by bootstrapping as indicated in the text.

(9.3-15.2 %/yr) the life expectancy for colonies in the study area computes as 8.0 years (6.6-10.8 yr).

The strong concentration of LCA at the edge of the forest persisted during the four years, with densities at the edge being significantly higher for all taxonomic groups in 2001 and 2005 (Fig. 1). *Atta cephalotes* was about 11 times as frequent in the first 50m as in the interior of the forest. For *A. sexdens* this factor was approximately 5. Differences in densities between the years were not significant within distance classes for all taxonomic groups (pair wise comparison via bootstrap of differences; all $P > 0.05$).

DISCUSSION

Colony densities in the interior of Coimbra, more than 50m away from any edge (*A. cephalotes*: 0.21 and 0.34; *A. sexdens*: 0.46 and 0.43 colonies/ha, 2001 and 2005 respectively) were within the range reported earlier for *Atta* species in mature continuous rain forests (e.g. Cherrett 1968: 0.6 col./ha, Jaffe & Vilela 1989: 0.045 col./ha, Wirth *et al.* 2003: 0.033 col/ha). Densities within the first 50m and the forest interior published by Wirth *et al.* (2007) (e.g. *Atta* spp. 4.9 ± 3.7 and 1.0 ± 2.6 , [mean \pm SD] respectively) were based on a sampled area almost twice as big and are in reasonable accordance with the values for 2005 presented here (5.6 [2.8-9.2] and 0.7 [0.4-1.3], median [95%-CI] from bootstrap distributions). In addition, roughly half of all colonies were replaced by new ones during the 4-yr study period. We are thus confident that the area and time span sampled were sufficient to derive meaningful estimates of population parameters.

Colony turnover rates for all combinations of taxonomic groups and forest zones (9-14 %/yr) are in good agreement with estimates for *A. colombica* based on mortality and natality in Panama (11 %/yr; Wirth *et al.* 2003), where an additional 26%/yr of turnover in nest sites (not colonies) was caused by frequent colony movements (Wirth *et al.* 2003). Such relocations of colonies (Fowler 1981), which are characterised by excessive movement for several days and persisting cleared trails connecting old and new nest sites (Herz *et al.* 1998), have never been observed during 8 years of research on LCA (including monthly observations at several colonies) in the study area. Therefore we believe that our estimates have not been biased by migration events. Additionally, the fungal genus *Escovopsis*, which is an important parasite in LCA fungus gardens that potentially can kill whole colonies (Currie *et al.* 1999) and is hypothesised to induce colony relocations in Panama when infection of colonies become excessive (Wirth *et al.* 2003), was never detected during a survey of microfungi in fungus gardens of 20 *A. cephalotes* colonies within our study area (Barbosa 2004). This lack of a principal parasite might account for differences in the frequency of colony movements observed in Panama and Brazil. Based on the documented turnover rates life expectancy for *Atta* colonies

was calculated to be 8 years which lies well below the estimates of 10-20 years (or even more) compiled by Fowler et al. (1986) and indicates that *Atta* colonies might be not as long-lived as commonly believed. This implies that the impact of LCA is distributed more uniformly throughout the habitat since high turnover rates increase the area impacted over time with a shorter persistence of the impact at any individual location. High turnover rates also augment the number of abandoned LCA nest sites, which show altered plant recruitment (Garrettson et al. 1998) and can be distinguish from undisturbed forest sites even 15 years after the death of the colony (Bieber 2006). Clearly, more observations of free living colonies, especially in forest ecosystems, are necessary to obtain more reliable estimates of turnover rates and to, ultimately, estimate the impact of this keystone species on ecosystem level.

There was a strong (though only marginally significant) increase of 50 percent in the abundance of *A. cephalotes* over the study period, accompanied by a slight, non-significant decrease in *A. sexdens*. A shift in the LCA community composition from *A. sexdens* to *A. cephalotes* within Coimbra Forest would be of considerable interest in view of a pattern on landscape level, where *A. cephalotes* appears to be replaced by *A. sexdens* in small forest fragments in the same region (Correa et al. 2005). A strong concentration of *A. cephalotes* along the edge of large forest fragments in contrast to a more homogeneous distribution of *A. sexdens* in the landscape (edge and interior of large and small fragments) could result from dispersal limitation as has been demonstrated for other monogynous ant species where effective queen dispersal is extremely restricted even at small geographical scales (Liautard and Keller 2001, Sundström et al. 2003). There are indications that the two *Atta* species differ in their dispersal abilities. Alates of *A. sexdens* have been frequently observed during nuptial flights throughout the study area including the matrix, while nuptial flights of *A. cephalotes* were never observed and Cherrett (1968) found most queens of *A. cephalotes* in wooded rather than cultivated areas in Trinidad. *Atta cephalotes* might thus be absent from small fragments in the study area because nuptial flights are restricted to large forested areas. Alternatively, differences in the distribution of the two species could be caused by species-

specific habitat preferences (Wirth et al. 2007). *Atta cephalotes*, a woodland species sensu Jaffe and Vilela (1989) and Rockwood (1973), concentrates foraging on pioneer trees (Farji-Brener 2001) frequent at the edge, while *A. sexdens* forages more opportunistically on a variety of resources (Vasconcelos 1990) and occurs in a wide range of habitats (Fowler et al. 1989, Vasconcelos 1990). To elucidate the underlying mechanisms for varying population dynamics within the same landscape, studies on dispersal behaviour and the genetic relatedness among colonies are needed.

The strong aggregation of LCA colonies in the first 50m of the forest found in 2001 was affirmed in 2005. About half of all colonies were replaced by newly founded ones during the four years of the study. Thus, the persistence of spatial distribution patterns was not simply caused by a lack of colony dynamics. Instead, it seems plausible that mechanisms causing the ants' habitat preference in 2001 were still functioning in 2005. As suggested by Urbas et al. (2007), high densities of *A. cephalotes* at the edge of the forest result from relaxed bottom-up control due to a greater availability of pioneer tree species, which are less well defended and the preferred food source of LCA (Farji-Brener 2001). Edge creation is followed by a marked acceleration in tree community dynamics (Laurance et al. 1998) and a hyper proliferation of pioneer species, with an increase in pioneer densities still detectable even 13-17 years after experimental fragmentation in the central Amazon (Laurance et al. 2006). Pioneer-dominated tree assemblages have also been documented in edges of aging fragments of Atlantic Forest after more than 60 years of isolation (Tabarelli et al. 1999, Oliveira et al. 2004), suggesting that such assemblages may be approaching near-equilibrium conditions, rather than represent transient successional stages (Santos et al. 2008). Given the strong evidence for bottom-up control of LCA populations via resource availability (Urbas et al. 2007), it seems reasonable to expect LCA densities to closely follow pioneer tree densities as was observed in regenerating secondary forests (Silva 2008). Consequently, we expect forest fragmentation to be followed by a very dynamic phase characterized by high growth rates, eventually reaching a new steady state with drastically higher LCA densities compared to pre-fragmentation values. A similar

process may have occurred on Barro Colorado Island (Panama) where, presumably, the creation of the laboratory clearing led to a drastic increase in the density of *A. colombica*. Between 1938 and 1966, no more than four colonies of *A. colombica* were present on the island (Weber 1969). However, when studied about 30 years later (1996-1998), an almost constant mean of 52 colonies of *A. colombica* were encountered concentrated within an area of approximately 100 ha adjacent to the laboratory clearing (Wirth et al. 2003). The virtually constant overall density of LCA demonstrated by the present study and the lack of overall population growth accords with the high and constant availability of pioneer plants due to old stabilised forest edges in the region (Santos et al. 2008). As with pioneer trees, high densities of LCA at the forest edges may therefore be a persisting feature of this fragmented landscape. Being dominant herbivores and ecosystem engineers, LCA, in turn, have the potential to maintain species composition and microclimate typical for the forest edge and thereby strengthen pioneer dominance via increased canopy openness due to herbivory and the creation of clearings around their nests (Wirth et al. 2008). Thereby LCA can delay or even change the direction of successional processes at the forest edge and modify forest regeneration (Wirth et al. 2008). As a result, the sustainability of fragments (embedded in harsh matrixes) is at risk because the forest would be unable to regenerate at the edge or to buffer its interior against detrimental edge effects (Gascon et al. 2000). LCA are therefore an example of an organism whose occurrence can enhance the presence and magnitude of edge effects (Fischer and Lindenmayer 2007) and thereby amplify the effects of forest fragmentation, which, like other man-made disturbances, drive natural system towards early successional stages (Bazzaz 1996).

In conclusion, high densities of LCA aggregated along the forest edges are expected to persist in time as long as neotropical forests are characterised by high edge to interior ratios. Proliferation of LCA might be an inherent biological consequence of edge creation with potentially detrimental consequences for regeneration at the edge. Based on the persisting hyper-abundance of LCA at the edge of old fragments we conclude that the ecological importance of LCA in landscapes modified by

man drastically exceeds that in pristine forests where LCA have been named keystone species, despite very low densities.

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PART III

Bottom up control of *Atta*

5

Selecting the drought stressed: effects of plant stress on intraspecific and within-plant herbivory patterns of the leaf- cutting ant *Atta colombica*

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Selecting the drought stressed: effects of plant stress on intraspecific and within-plant herbivory patterns of the leaf-cutting ant *Atta colombica*

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Summary

1. Leaf-cutting ants (LCA) are highly polyphagous but at the same time highly selective dominant herbivores of neotropical rainforests. While a whole range of leaf properties has been identified to influence interspecific host choice, the mechanisms underlying intraspecific and intra-individual herbivory patterns remain obscure. Here, we evaluate the plant-stress hypothesis by analysing whether and how drought stress of food plants positively affects LCA food plant selection.
2. In bioassays with whole plants of *Piper marginatum*, *Atta colombica* workers harvested more than twice the leaf area of stressed than of vigorous control plants. Within individual plants, the attractiveness of a given leaf increased with its stress level.
3. Drought stress induced an accumulation of proline and non-structural carbohydrates in the plant tissue by a factor of 3·5 and 2, respectively, accompanied by a decrease in the leaf water content of about 35%. Moreover, samples taken from preferred leaves within a plant contained more osmolytes than those representing the whole plant.
4. Ants were shown to detect and prefer these osmolytes in bioassays conducted with leaf discs that had been experimentally enriched with proline and/or sucrose. We therefore propose a mechanism that links the preference of LCA to drought stress via the osmolyte concentrations within the leaves.
5. Our results support the plant-stress hypothesis, confirming that stressed plants and plant parts are more attractive to LCA. This may account for intraspecific and intra-individual herbivory patterns of LCA, thus influencing populations of host species through the discrimination of drought-sensitive individuals.

Key-words: Abiotic conditions, food plant selection, non-structural carbohydrates, plant-stress hypothesis, proline

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Introduction

Leaf-cutting ants (LCA) are dominant herbivores of neotropical rainforests (Wilson 1986) and have been named ecosystem engineers owing to their importance for vegetation structure (Wirth *et al.* 2003). They harvest plant material, but rather than digesting it directly, they cultivate a fungus on it, which in turn produces food bodies to feed the colony (Belt 1874). In addition, LCA drink plant sap while cutting leaves (Littledyke & Cherrett 1976) and carbohydrates ingested with the sap provide the main energy source for adult workers (Quinlan & Cherrett 1979). LCA are highly polyphagous but at the

same time highly selective (Rockwood 1976; Howard & Wiemer 1986). Leaf properties such as secondary compounds (Littledyke & Cherrett 1976; Hubbell & Wiemer 1983; Howard 1987), toughness (Cherrett 1972; Nichols-Orians & Schultz 1989) and nutrient content (Barrer & Cherrett 1972; Berish 1986) have been identified to influence the choice of plant species. Published data on the effects of leaf water content on food plant selection by LCA are scarce and inconsistent (positive effects of a high leaf water content on LCA preference: Cherrett 1972; Bowers & Porter 1981; Folgarait *et al.* 1996; no effect: Howard 1987; and negative effects: Blanton & Ewel 1985; Vasconcelos & Cherrett 1996). The relative importance of these leaf traits and in particular the question how both intraspecific and intra-individual variability in leaf features influences herbivory patterns

remains obscure. For example, it has long been puzzling why LCA seldom forage on those individuals of the food plant species currently being exploited that are closest to the nest (Eidmann 1935; Cherrett 1968). This apparent violation of optimal foraging expectations has been interpreted as conservative resource management by LCA (Cherrett 1983), an interpretation that contrasts with observed foraging in homogeneous environments (plantations) where LCA harvest density-dependent (Fowler & Stiles 1980). Significant intraspecific variation in leaf quality, together with the ants' capability of fine discrimination among leaf material could account for the spatio-temporal pattern of resource exploitation (Fowler & Stiles 1980; Rockwood & Hubbell 1987), though empirical evidence for these argumentation is scarce (Howard 1990).

Stress acting on plants can be one factor that alters leaf properties on an intraspecific and/or intra-individual level and thereby might change a leaf's attractiveness to herbivores. The plant-stress hypothesis by White (1984) predicts stressed plant material to be preferentially consumed by herbivores, owing to its higher nutritional quality caused by nitrogen mobilization during the plant's response to the stressing agent. On the other hand, the plant-vigour hypothesis by Price (1991) argues vigorous plant material to be more attractive owing to a higher nutrient availability in growing tissue. Despite considerable effort in testing these hypotheses, available results are conflicting (reviewed in Larsson 1989; Koricheva, Larsson & Haukioja 1998). One prominent stress factor affecting plants is drought (White 1974). Changes in leaf properties induced by drought stress include a lower water content and an increase in osmolyte concentrations (Bradford & Hsiao 1982), with sucrose and proline being predominant (e.g. Sanchez *et al.* 1998; Arndt *et al.* 2001).

Drought stress in the tropics has received growing attention in the last years. There are regular dry seasons in most tropical areas, leading to considerable drought stress for plants (e.g. Engelbrecht & Kursar 2003; Engelbrecht, Kursar & Tyree 2005). Even in unseasonal, equatorial regions, dry periods of up to 35 days occur (Walsh & Newberry 1999). In addition, differences in the water availability of microhabitats, caused for example by the topographic relief, can alter the water status of plants on a small scale (Gibbons & Newberry 2003). With respect to LCA, it is interesting to note that forest edges and fragments, where LCA occur in high densities (Rao 2000; Vasconcelos, Carvalho & Delabie 2001; S. T. Meyer & R. Wirth, unpublished data), are characterized by a drier microclimate (reviewed in Murcia 1995), which makes plants in these habitats more prone to drought stress.

Here, we evaluate whether drought stress of food plants positively affects LCA food plant selection. In particular, the following hypotheses were tested (1) LCA forage preferentially on stressed plants; (2) drought stress increases the osmolyte concentrations in the food plants; and (3) leaves with naturally or experimentally increased osmolyte concentrations are preferred by LCA.

Materials and methods

STUDY SPECIES

Bioassays were conducted with three laboratory colonies of the LCA species *Atta colombica* (Guerin) and plants of the species *Piper marginatum* (Jacquin). The colonies – collected near Gamboa, Panama – were about 3 years old and their fungus garden occupied about 10 l. The plants used were originally collected as seeds or cuttings on Barro Colorado Island in Panama and raised in a greenhouse. LCA are important herbivores on *Piper* species (Dyer *et al.* 1999; Dyer *et al.* 2003). While most *Piper* species are understory plants, *P. marginatum* occurs in tree fall gaps and forest edges (Engelbrecht 1998), which should make it more prone to drought stress in its natural habitat. In the bioassays 50 potted plants (pot diameter 14.5 cm) were used with an average number (\pm SD) of 9.1 ± 3.7 leaves and a mean height of 37.8 ± 8.1 cm.

INDUCTION OF DROUGHT STRESS

To induce drought stress, 25 plants were kept dry while 25 controls were watered daily. Soil water content was determined gravimetrically and declined very uniformly for all plants of the treatment. In a preliminary test it took a maximum of 3 weeks for the plants to show wilting symptoms, accompanied with a decrease of leaf water content and an increase in non-structural carbohydrate and proline concentrations. The content of other amino acids remained unchanged. A significant correlation of osmolyte concentrations per dry weight with the leaf water content showed that these osmolytes were not only passively concentrated because of water loss from the leaves, but also actively accumulated. There was considerable variation in the time it took for a plant to wilt. Therefore wilting stages, which are directly correlated to leaf water potentials (Tyree *et al.* 2002), were used to choose plants for the bioassays rather than employing a fixed time scheme. Plants sufficiently stressed to be used in the bioassays corresponded to Tyree's category 'wilted'. The plants' stress status was quantified as the water content of the leaves as described below.

BIOASSAYS

Two types of bioassays were conducted in this study. One employing whole plants in a dual choice set-up and the other leaf discs presented in a randomized checkerboard design as described by Hubbell & Wiemer (1983). As an enhancement of the latter set-up, we used either leaf discs of stressed and vigorous *P. marginatum* (leaves of four plants each) or leaf discs of *Hedera helix* infiltrated with osmolyte solutions. Infiltration as a method to push water into the air-filled cavities of a leaf was described by Beyschlag & Pfanz (1990) and can be used experimentally to increase solute concentrations in leaf discs for bioassays (H. Herz, personal communication; Berger

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Effects of plant stress on Atta colombica

2004). Treatment discs were enriched in sucrose by 79 mg g⁻¹ fresh weight (FW) or proline by 3·9 mg g⁻¹ FW, or a combination of both osmolytes (same concentrations). Control discs were infiltrated with water. On a 10 × 10 grid, 50 treatment and 50 control discs were randomly distributed and LCA were allowed to collect discs until 50% of one type were harvested. Preference was calculated as a mean acceptability index (MAI) by dividing the number of treatment discs by the total number of discs taken. Index values range from 0 (control preferred) to 1 (treatment preferred). Every treatment was tested five times per colony.

The bioassays with whole plants were conducted in an open Plexiglas arena (60 × 60 cm²) that the ants entered in its centre via a tube at the bottom. Two holes in the floor equally spaced from the centre allowed the potted plants to be placed in the arena from underneath. The holes were covered with two half discs sparing the stem of the plant. Thereby only the plants but not the pots below the arena floor were accessible to the ants. Since they readily explored the entire arena including the two plants, no further care was taken to ensure that both plants were visited in every trial. By outlining the leaf contours before and after the feeding trial, the harvested area of stressed and vigorous plants was determined. Tests were stopped when 30–50% of the leaf area of one of the two plants had been removed. An MAI was calculated by dividing the area cut of the stressed plant by the area cut of both plants. This bioassay was replicated seven times per colony, with in total 21 stressed and 21 control plants. To get a measure of a plants average leaf properties, a leaf punch was taken of every leaf after the experiment, pooled per plant and this 'whole-plant sample' processed as described below. The remains of the leaves were collected to determine their water content gravimetrically. To assess parameters important for harvesting rates, we timed 15 completed cuts from both treatments and measured length of the cut, size of the ant (as width of the head capsula) and area of the fragment.

INTR-INDIVIDUAL PREFERENCE

To describe preference patterns within a plant we quantified how even the ants' harvest was distributed between the leaves of a plant by calculating an evenness index (*E*; Simpson 1949) as:

$$E = \frac{1}{n * \sum_{i=1}^n (A_i/A_{\text{total}})^2}$$

with *n* being the number of leaves on a plant, *A_i* the area cut of the leaf *i* and *A_{total}* the area cut of all leaves of the plant added up. Values approaching 1 indicate a high level of homogeneity.

Corresponding to the MAI an acceptability index was calculated to express the ants' preference for individual leaves within a plant, by dividing the area cut of a leaf by the total leaf area cut of the plant. Like the MAI, this

acceptability index ranges from 1 (only this leaf of the plant was cut) to 0 (this leaf was not cut at all). A standardized leaf water content (water content of a leaf divided by the maximum leaf water content within this plant × 100) was used as an indicator of the stress status of an individual leaf compared with the other leaves of the plant. The relative leaf water content (fresh weight minus dry weight divided by the dry weight of a leaf) served as an independent measure of the stress status of a leaf. The importance of drought stress for the intra-individual selection of the ants was evaluated by correlating the acceptability with the water contents of individual leaves.

In order to compare the osmolyte concentrations of leaves favoured by the ants with the average of the plant, we took away the 11th to 15th fragment that was cut off a plant (hereafter referred to as 'harvest sample'), and processed them as described below.

ANALYSIS OF LEAF PROPERTIES

Plants were sampled by taking leaf punches (whole plant sample) or collecting fragments cut by the ants (harvest sample). After weighing, the material was heated for 1 min in a microwave oven to stop enzyme activity (Popp *et al.* 2003) and dried at least 48 h at 80 °C. The dry material was weighed again to calculate water content, ground to powder in a ball mill and extracted in hot water (1 h 100 °C; Howard 1987). Total non-structural carbohydrates were determined photometrical using the phenol-sulphuric acid method as described by Dubois *et al.* (1956) and modified by Ashwell (1966). Glucose was used as the calibration standard.

Amino acids were measured using a colorimetric detection with ninhydrin (after Moore & Stein 1948, 1954). Although proline forms a red coloured complex with ninhydrin (Chinard 1952; Troll & Cannan 1953), all other proteinogenic amino acids form a blue-violet complex (Breuer & Breuer 1996). By measuring absorbance at 570 nm and 440 nm concentrations of both types were determined simultaneously. Calibration was conducted with proline and leucine. All osmolyte concentrations were expressed as mg substance per g FW since ants are expected to select plants based on the perception of dissolved compounds as they occur in fresh tissue.

Results

LCA showed a marked preference for drought-stressed plant material in every one of 21 dual choice tests employing whole plants. The three colonies used did not differ in their preference and there was no significant interaction (two-way ANOVA, stress: *F*_{1,36} = 26·7, *P* < 0·001; colony: *F*_{2,36} = 0·848, *P* = 0·437; stress × colony: *F*_{2,36} = 0·167, *P* = 0·847). On average, three-quarters of all harvested leaf area were cut from stressed plants (Fig. 1) resulting in an MAI (± SD) of 0·75 ± 0·16. The difference in harvested leaf area was caused by different harvest rates (Table 1). Harvest rates largely depend on

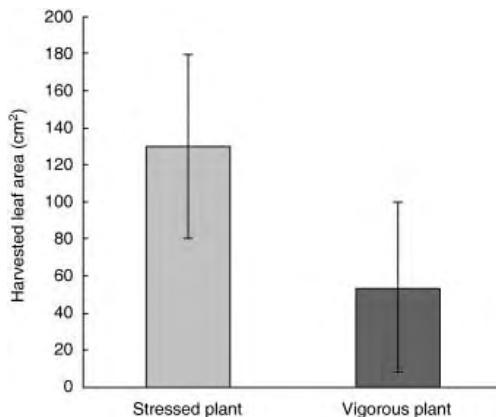


Fig. 1. Comparison of the mean leaf area (\pm SD) harvested of drought-stressed and vigorous control plants of *Piper marginatum* in whole plant bioassays. Shown is the mean of 21 bioassays with three colonies.

four variables: the number of recruited ants, the size of the fragments, the cutting velocity and the size of the foraging ants. Because the latter three parameters were not affected by the stress status of the plants (Table 1), the higher harvest rates are only attributable to an increased number of ants cutting out of the stressed plants. In fact, during the test, the number of ants was visibly higher on stressed as compared with control plants (S. T. Meyer, F. Roces & R. Wirth, personal observation).

Within a plant the ants selected individual leaves, cutting about a third of the leaves of control plants (evenness index of 0.29 ± 0.12). Their harvest was less concentrated within stressed plants (evenness index of 0.54 ± 0.15). The attractiveness of a leaf increased with decreasing standardized water content (i.e. water content relative to maximum leaf water content within the corresponding plant) in stressed plants, while there was no effect of water content on LCA choice within control plants (Fig. 2).

When comparing stressed and unstressed plants (whole-plant sample, Fig. 3), there were highly significant differences in the leaf water content, the concentrations of non-structural carbohydrates (NSC), and proline concentration in leaves (water: $T_{40} = -8.52$, NSC: $T_{40} = 6.94$, proline: $T_{40} = 8.22$, all $P < 0.001$). Drought stress reduced the leaf water content by a third (from 3 to 1.9 g water g⁻¹ dry weight) and at the same time increased osmolyte concentrations in the plants preferred by the

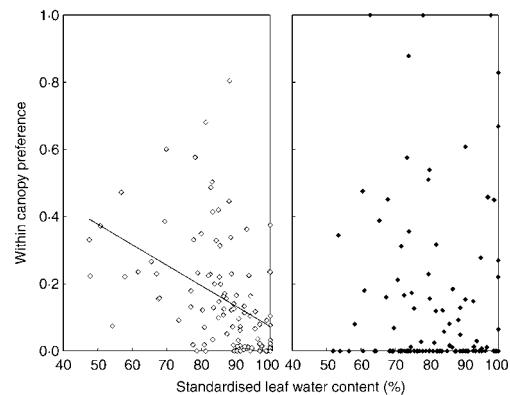


Fig. 2. Relationship between individual leaf attractiveness and standardized leaf water content within stressed (\diamond) and vigorous (\bullet) plants of *Piper marginatum*. Each point represents one leaf. The solid line indicates a highly significant Spearman rank order correlation within stressed plants ($r = -0.576$; $N = 110$; $P < 0.001$), while there was none within vigorous plants ($r = -0.063$; $N = 118$, $P = 0.498$).

ants. On average the stressed plants contained 77 ± 22 mg sugar g⁻¹ FW and 7.6 ± 3.1 mg proline g⁻¹ FW – an increase of 36 mg sugar g⁻¹ FW and 5.5 mg proline g⁻¹ FW compared with unstressed control plants.

Similar patterns emerged when samples of the ants' harvest were compared with the corresponding whole-plant sample. The leaves favoured by the ants within a stressed plant contained significantly less water (paired *t*-test: $T_{19} = -3.80$, $P < 0.001$) and, even though not significant, as a tendency, more sugar and proline (paired *t*-tests: $T_{19} = 2.00$, $P = 0.06$ and $T_{19} = 1.50$, $P = 0.151$, respectively). Within vigorous plants harvested leaves did not differ in water content (paired *t*-test: $T_{14} = -0.62$, $P = 0.542$), but contained significantly more sugar and proline (paired *t*-tests: $T_{14} = 2.78$, $P = 0.015$ and $T_{14} = 4.56$, $P < 0.001$, respectively).

To compare the effect of increased osmolyte concentrations on the ant's selective preference with the effect induced by drought stress, we conducted bioassays employing leaf discs experimentally enriched with sugar and/or proline by infiltration and bioassays with leaf discs of stressed and unstressed *Piper*. LCA showed a strong preference for sucrose, proline and a combination of both – between 54% and 85% of the collected leaf discs were osmolyte enriched (Fig. 4). A two-way ANOVA showed significant differences for different treatments of leaf-

Table 1. Comparison of the harvest rate of LCA on drought-stressed and vigorous plants of *Piper marginatum*, and parameters affecting harvest rates. Values are means \pm SD; differences were tested by *T*- (*T*) or *U*-tests (*U*)

Parameter	Stressed plants	Control plants	df	<i>T/U*</i>	<i>P</i>
Harvest rate (mm ² min ⁻¹)	213 ± 121	109 ± 70	34	78.0*	0.016
Cutting velocity (mm min ⁻¹)	5.2 ± 1.4	5.2 ± 1.8	26	-0.75	0.46
Ant head size (mm)	1.42 ± 0.16	1.45 ± 0.21	29	0.42	0.68
Fragment size (mm ²)	77.4 ± 29.1	86.3 ± 24.0	29	0.94	0.36

* *U*-value.

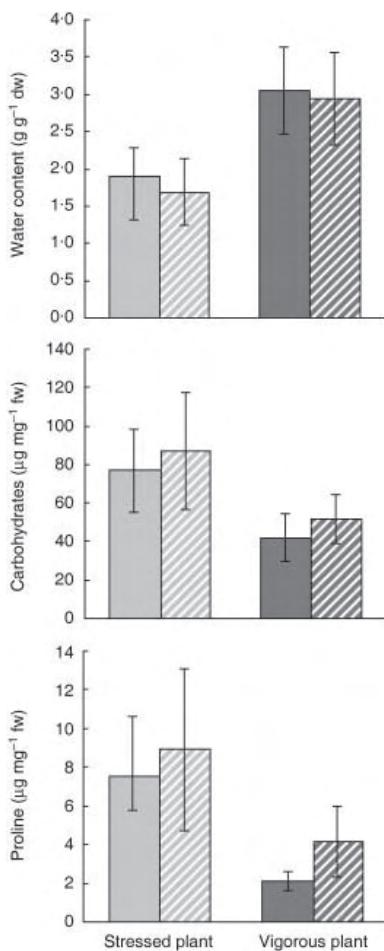


Fig. 3. Comparison of leaf properties relevant to drought stress in *Piper marginatum* leaves measured for whole plants (whole-plant sample, ■) and subsamples harvested by leaf-cutting ants (harvest sample, ▨). Mean water content (\pm SD) is shown in units per dry weight (dw); mean osmolyte concentrations (\pm SD) in units per fresh weight (fw). Note that per plant two samples (one whole-plant and one harvest) were derived and therefore analysed in paired *t*-tests.

discs and colonies studied, but there was no interaction (treatment: $F_{3,45} = 5.408$, $P = 0.003$; colony: $F_{2,45} = 10.4$, $P < 0.001$; treatment \times colony: $F_{6,45} = 0.532$, $P = 0.781$). Colony effects were due to differences in the selectivity of the colonies 1 and 3 (Tukey's *post-hoc* test $P < 0.05$) showing consistently the highest and the lowest preference, respectively, for all types of leaf discs. The ants' preference for stressed *Piper* was not significantly different from that for leaf discs enriched with sugar or sugar and proline; only the infiltration with proline alone was significantly less attractive to LCA.

Discussion

Colonies of *A. colombica* strongly preferred stressed plant material over vigorous. As demonstrated in Table 1 this preference was not caused by differences in the cutting behaviour of individual ants or the ants themselves (i.e.

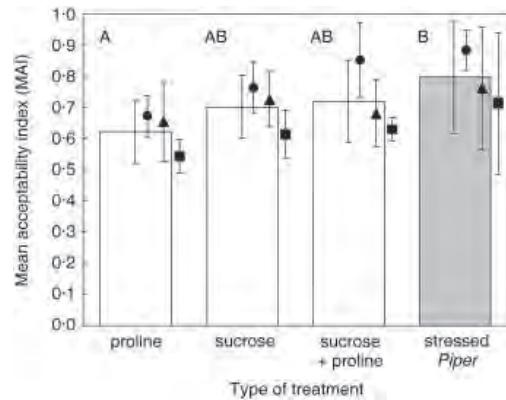


Fig. 4. Preferences (expressed as mean acceptability index, MAI \pm SD) by three leaf-cutting ant colonies for differently treated leaf discs of *Hedera helix* and drought-stressed *Piper marginatum* in pick-up-assays. Symbols show means of individual colonies (● colony 1, ▲ 2, ■ 3; \pm SD) bars in the background represent the mean of the three colonies \pm SD. Different letters indicate significant differences between treatments for the mean of all colonies (Tukey's *post hoc*-test $P < 0.05$). In addition, significant differences existed between colony 1 and 3 (not indicated).

cutting velocity, fragment size determination or worker size), but by differential harvesting rates due to the number of recruited ants foraging on the plants, being therefore a collective response. We thereby confirmed earlier results of Vasconcelos & Cherrett (1996), who found wilted leaves to be more attractive in bioassays than conspecific fresh leaves. On the other hand, our results apparently contrast with those of Howard (1987), who showed the leaf water content to have no effect on food plant choice by LCA. His findings, however, were based on a whole range of plant species, the palatability of which was mainly explained by variation in quality and content of secondary compounds. Naturally, the variability of these properties is much lower among plants of the same species or even within a plant. Therefore other factors such as water content (representing the stress status) gain increasing importance for the intra-specific and within-plant preference pattern of LCA.

We have shown experimentally that concentrations of non-structural carbohydrates and proline increased in *P. marginatum* under drought stress, and that *A. colombica* preferred these osmolytes in leaf discs of unstressed plants, when these were enriched in the same range as measured in the plants subject to drought. We therefore propose a mechanism that links drought stress to the ants' preference for stressed plant material via the osmolyte concentrations within the leaves. This is in agreement with the plant-stress hypothesis by White (1984), which claims that herbivores benefit from the stress-elevated nutritional quality of plant tissue. A similar function of proline as a herbivory cue has been reported for grasshoppers (Haglund 1980).

The accumulation of non-structural carbohydrates and proline, as measured in *P. marginatum*, is a common and well-known physiological response to drought stress

(Delauney & Verma 1993; Arndt *et al.* 2001; for a review see Bewley & Krochko 1982). While osmoregulation is a basic response (Bradford & Hsiao 1982) that should be ubiquitous in angiosperms (Bewley & Krochko 1982), defensive compounds react differently to drought stress (reviewed by Gershenson 1984). We therefore expect the preference for stressed plant material to be a general pattern in intraspecific and intra-individual LCA food plant selection, but owing to the variety of defensive plant compounds, it may be a modulated response varying among different plant species. Since the main group of defensive compounds in the genus *Piper* are phenols (Parmar *et al.* 1997), which are not known to be affected by drought stress (Gershenson 1984), we do not assume such modulation in our experiments, although we cannot completely exclude it.

There was a significant intra-individual selection of leaves, as quantified by the evenness index. Within a stressed plant, the attractiveness of a leaf increased with the stress level. When correlating the preference index with relative rather than standardized leaf water contents (data not shown), there was no significant relationship for the pooled stressed plants. This indicates that the preference of LCA is not an absolute but a relative one, i.e. the ants were comparing and choosing individual leaves within a plant. Within control plants, there was a strong preference for individual leaves, which could not be explained by the leaf's water content, although accompanied by an increase in proline and sugar levels. These compounds can be accumulated due to stress agents other than drought (e.g. temperature, Chu *et al.* 1978; UV radiation, Saradhi, Arora & Prasad 1995) and may increase the acceptability of individual leaves to the ants by the same mechanism as proposed for drought. Since we have no evidence about stress agents acting on our control plants, the cause of the observed variability among leaves in control plants remains elusive.

The attractiveness of carbohydrates to LCA is well documented in the literature (e.g. Cherrett & Seaforth 1968; Barrer & Cherrett 1972; Roces 1993) and Quinlan & Cherrett (1979) stated that carbohydrates ingested by LCA-workers when drinking sap while cutting leaves can satisfy their energetic needs. Here, we report for the first time on the attractiveness of an amino acid, namely proline, to LCA. Previously, there has been only indirect evidence for that as reported by Cherrett & Seaforth (1968), who fractioned extracts from citrus pulp and ended up with a mixture attractive to *Acromyrmex octospinosus* that 'contained mainly amino acids'. Proline is predominant in the haemolymph of many insect species, and it is known to be important as fuel for flight metabolism in flies, beetles and other insects (Sacktor & Childress 1967; Auerswald, Schneider & Gädé 1998). LCA workers of the species *Atta colombica* have high haemolymph proline levels, averaging 20 nmol μl^{-1} haemolymph (F. Roces & S. Krumme, unpublished data), in a similar range as reported for honeybees (Crailsheim & Leonhard 1997). Immediately after cutting a fragment, proline levels in *Atta*-foragers drop to

an average of 16 nmol μl^{-1} haemolymph. This 20% decrease is accompanied by a concomitant increase in alanine levels (F. Roces & S. Krumme, unpublished results). Alanine results from the oxidative pathway of proline (Bursell 1981), thus strongly supporting the idea that proline is indeed used as fuel during cutting by LCA. The preference for drought-stressed leaves, with increased proline concentration, may provide LCA workers with immediate energy for fuelling further foraging activity. Even though the uptake mechanisms for proline in insects are not clear, the ingested proline is expected to show up and be available in the haemolymph after passing through the proventriculus, the valve separating the social crop and the gut, as shown for honeybees (Micheu, Crailsheim & Leonhard 2000).

Our findings are in line with recent work on ecological stoichiometry (the balance of chemical elements in ecological interactions, *sensu* Elser *et al.* 2000), which argues that organisms have evolved to optimize the gain of C- and N-containing macronutrients, such as carbohydrates and amino acids (Raubenheimer & Simpson 2004), and that such adaptations are expected to influence proximate food choices (Kay 2002). Viewed in this light, the selection of stressed plants, with a two-fold decrease of their sucrose : proline ratio (10·1:1) compared with unstressed plants (20·1:1), may reflect optimization of diet selection by N-deprived herbivorous ants (cf. Davidson 2005). However, since the mechanisms underlying the assessment of plant palatability by LCA are unknown, the question whether plant preferences result from the selection of diets with a given macro-nutrient balance remains open.

The foliage collected by LCA is processed as substrate for their symbiotic fungus, therefore it is an open question to what extent the selection of drought-stressed plants is based on the provision of immediate energy sources for the foragers, or the maximization of fungus growth, or a combination of both. The leaf water content *per se* of the collected material seems to be of minor importance for the fungus gardens, since LCA control their humidity by the nest architecture or relocation of gardens within the nest, as evidence in several independent studies indicates (Stahel & Geijskes 1940; Lapointe, Serrano & Jones 1998; Roces & Kleineidam 2000; Kleineidam & Roces 2000). The nutritional quality of drought-stressed plant material for the fungus could not be directly evaluated in this study. However, the preference of the ants was stable over time and no delayed rejection of the stressed plant material was observed, which would be expected if the material had a strong negative effect on the fungus (Knapp *et al.* 1990; North, Jackson & Howse 1999; H. Herz, personal communication). More work is needed to elucidate whether the ants' choice for stressed plants is beneficial for both partners of the symbiosis.

A preference for stressed plant material by LCA has consequences in an ecological context. (1) Within a plant, differentially stressed leaves, analogous to sun *vs* shade and young *vs* old leaves, can represent food

patches of diverse quality. This offers an explanation for the observed within canopy patchiness of LCA herbivory (Fowler & Stiles 1980; Rockwood & Hubbell 1987; Howard 1990). The same holds true for differences and selection of individual plants of the same species. (2) LCA populations have been shown to benefit from disturbed habitats such as forest fragments and edges where they occur in elevated densities (Rao 2000; S. T. Meyer & R. Wirth, unpublished data). Plants in these habitats are known to be more prone to drought stress (Ferreira & Laurance 1997) and might therefore represent a food source of higher quality. (3) There are consequences for the food plant populations. It has been argued that herbivory damage can intensify the drought stress of a plant by uncontrolled water loss through the edges of the wounds (Herz 2001). Aldea *et al.* (2005), for example, demonstrated an additional loss of 45% water within 6 days following insect herbivory and concluded that herbivory damage may exacerbate water stress under field conditions. In combination with the increased palatability of stressed plant tissue, this would lead to a positive feedback loop, where stressed plants are attractive to LCA, therefore experiencing higher levels of herbivory damage, which in turn intensifies their drought stress, thus making them even more attractive. Furthermore it seems legitimate to assume that a similar feedback loop could exist on a habitat level. The high densities of LCA in fragmented and disturbed areas with vegetation prone to drought stress lead to a high herbivory pressure on this habitats. By removing large quantities of foliage especially close to forest edges, LCA may increase microclimatic edge effects, thereby leading to additional drought stress for the plants.

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PART IV

Nest effects of *Atta cephalotes*

6

Ecosystem engineering in a fragmented forest: Altered forest structure and microclimate at nest sites of *Atta cephalotes*

as prepared for Ecology

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ABSTRACT

The modern-day world is seeing escalating levels of habitat loss and fragmentation in tropical rain forests causing a drastic decline in species numbers. Yet, there are some organisms profiting from anthropogenic disturbance. Among these are some species of leaf-cutting ants, which increase in abundance with deforestation and the creation of artificial forest edges. Leaf-cutting ants are considered keystone species in pristine forests where they occur only in very low densities, thus their ecological impacts might be amplified in forest fragments and forest edges. Adding to their importance as dominant herbivores, they have been hypothesized to be ecosystem engineers. This notion was never strictly tested but leaf-cutting ant nests are considered disturbances with the potential to influence plant regeneration. We quantified alterations in forest structure above 36 *Atta cephalotes* nests in the Brazilian Atlantic forest compared to control sites and measured resulting microclimatic changes along transects from nest centers up to 24 m into the forest (11 representative colonies).

Nest sites were virtually free of understory vegetation with a high proportion of dead stems (up to 70%). Canopy openness above colonies increased by ca. 40% compared to controls (5.3 at colony vs. 3.7% at control sites). The less dense forest allowed about 6% of the outside irradiance to penetrate through the canopy at nest centers. Light levels declined exponentially into the forest reaching a third of nest light levels in the forest understory (2%). Likewise maximum and daily amplitudes of soil temperatures declined exponentially along transects from 25 to 23°C and 1.6 to 0.8°C, respectively. Soil moisture content increased significantly from nest centers into the forest, yet effect size was small and no differences were detected for air temperature and humidity. Microclimatic alterations, predominantly light levels, lay within a range that can differentially impact plant regeneration. Therefore we conclusively demonstrate that leaf-cutting ants act as ecosystem engineers with potential impacts especially in fragmented forests. We predict *A. cephalotes* nests to microclimatically modify 6% of the forest area along Coimbra's edges, compared to only 0.6% in the forest interior, because colonies are strongly aggregated at the forest edge.

Key words: leaf-cutting ant, understory gap, canopy opening, light, temperature, soil moisture, edge-effect, nest effect

INTRODUCTION

Organisms modify the abiotic environment in which they live, and this may feed back to the biota. This type of indirect species interaction has been formalized in the concept of ecosystem engineering, which defines an organism controlling the availability of resources for other organisms by altering their physical environment as an ecosystem engineer (Jones et al. 1994). While locally engineers may either increase or decrease patch-level diversity (Crooks 2002), it is generally believed that at large scales a mosaic of engineered and pristine environments will have a positive net effect on species richness and abundance due to the creation of new habitats (Jones et al. 1997, Wright et al. 2002, Wright et al. 2004). Yet, in the modern-day world pristine environments are ever decreasing. Especially in tropical forests human land use dynamics result in catastrophic rates of habitat fragmentation and alteration (Whitmore 1997, Aguilar et al. 2006). The role played by ecosystem engineers in these modern anthropogenic landscapes will be of special interest in the future (Hastings et al. 2007).

Leaf-cutting ants (LCA) of the genus *Atta* have been named ecosystem engineers (Wirth et al. 2003, Rico-Gray and Oliveira 2007), adding to the ants' ecological importance as dominant herbivores in the Neotropics (Wilson 1986). In contrast to other prominent ecosystem engineers that have been substantially decimated by human activities (e.g. beavers and elephants: Syphard and Garcia 2001, Dunham 2008, Hood and Bayley 2008) some species of LCA profit from anthropogenic landscape alterations and increase in abundance with increasing agricultural land-use, deforestation and/or disturbance (Jonkman 1979, Fowler et al. 1986, Jaffe and Vilela 1989, Wirth et al. 2007). In neotropical forests ecosystem engineering by LCA occurs (1) in their foraging area where the removal of up to 15% of the standing leaf crop (Wirth et al. 2003, Urbas et al. 2007) effects the light microenvironment within and below the canopy (Wirth et al. 2003) and (2) at nest sites which are considered disturbances with the potential to influence plant regeneration in tropical systems (Garrettson et al. 1998). LCA nests frequently reach more than 100 m² in surface area and 6 m or more in depth of subterranean chambers (Hölldobler and

Wilson 1990). Effects of these conspicuous structures include (2a) soil disturbances (Alvaredo et al. 1981, Perfecto and Vander Meer 1993), (2b) the improvement of soil penetrability (Moutinho et al. 2003), (2c) removal of litter resulting in bare ground (Weber 1972), (2d) enrichment of soil nutrients by the year-long harvesting activity (Haines 1978, Moutinho et al. 2003, Verchot et al. 2003, Sternberg et al. 2007), and (2e) the establishment of "bottom-up" gaps above nests (Farji-Brener and Illes 2000, Hull-Sanders and Howard 2003). Within this gaps understorey vegetation growing on or overhanging the immediate nest surface is constantly cleared leading to an increased light availability (Farji-Brener and Illes 2000, Hull-Sanders and Howard 2003) above nests. Recently, additional openings in the canopy above nests have been observed (pers. obs., Corrêa et al. submitted) but have not been investigated systematically despite the importance of canopy gaps for microclimatic conditions at nest sites. Generally, an altered, more open forest structure at nest sites compared to undisturbed forest permits a higher interception of light that should secondarily change other climatic parameters such as temperature and humidity of air and soil. Yet, an investigation of climatic parameters other than light is completely lacking for LCA nests. As Popma et al. (1988) have pointed out, in terms of microenvironment there is a continuum across the physical edge of a gap and alterations can penetrate several meters into the forest (Brown 1993). However, LCA nests have been viewed largely as punctual disturbances and their potential impact on the nest vicinity has been ignored.

The microclimatic modifications proposed to occur at LCA nests are of importance for the induction of germination, growth, and survival of plants and might therefore influence recruitment of tree species and forest regeneration (Garrettson et al. 1998, Farji-Brener 2005, Corrêa et al. submitted) in a similar way as in tree fall gaps (Brown 1993, Bazzaz and Wayne 1994, Pearson et al. 2002, Pearson et al. 2003). Such modifications receive special significance in forest islands and edges where LCA occur in persisting high densities (Rao et al. 2001, Wirth et al. 2007, Meyer et al. submitted) and which are already characterized by a more illuminated and dryer microclimate (Murcia 1995, Kapos et al. 1997, Laurance 2004). In this desiccated habitats, LCA

might stabilize the climatic conditions and associated plant community from which they profit (Wirth et al. 2008) and can be among the contributing factors that enable cycles of pioneer self-replacement (Tabarelli et al. in press).

Here we describe colonies of *Atta cephalotes* in a large fragment of the heavily fragmented Atlantic forest of NE-Brazil in terms of forest structure at nest sites and resulting microclimatic alterations. The aim of this study was (1) to give a detailed description of the structure of forest understory and canopy at nest sites of *A. cephalotes* compared to undisturbed control sites in the forest in order to (1a) document the ants' clearing activity in the forest understory and to (1b) check for the presence of canopy gaps, (2) to assess nature, magnitude, and penetration depth of nest-induced microclimatic alterations along gradients penetrating from the nest into the forest, and (3) to estimate the proportion of forest directly altered by *Atta* nests within the interior and the edge of the forest. Emerging patterns will be examined for their potential impact on plant regeneration with special reference to the role of LCA as an ecosystem engineer in fragmented forests.

MATERIAL AND METHODS

STUDY SITE AND SPECIES – The study was conducted in Coimbra, the single largest remnant of Atlantic forest of NE-Brazil (9°S , $35^{\circ}52'\text{W}$). Located in the state of Alagoas, it covers approximately 3,500 ha of largely well-conserved lower montane rain forest (Veloso et al. 1991) situated on a low-elevation plateau (300-400 m above sea level). Coimbra forest is surrounded by a homogenous matrix of sugar cane fields along its 40 km of relatively old (at least 60 y) borders (Santos et al. 2008). The region has a tropical climate characterized by a 5-mo dry season (<110 mm/mo) lasting from September to January (annual precipitation about 2000 mm); the prevailing soils are latosols and podzols (IBGE 1985). The edge zone (0–100 m into the forest) has been shown to be largely dominated by pioneer species (Oliveira et al. 2004) that apparently are able to form multi- rather than single-generation pioneer assemblages (Tabarelli et al. in press). Less well defended pioneer species are the preferred food source of LCA (Farji-Brener 2001).

Two species of the LCA genus *Atta* occur in NE-Brazil, both forming potentially huge colonies (Correa et al. 2005). This study was restricted to the analysis of nests of *A. cephalotes*, a species widespread throughout the Neotropics from Mexico to Bolivia (Kempf 1972). *Atta cephalotes* constructs nests that are characterized by a large central nest mount sometimes accompanied by smaller lateral excavations. In contrast, nests of *Atta sexdens* are rather cryptic with the excavated soil being distributed in small mounds often over large areas, dispersing potential impacts and causing methodological difficulties for size estimates. Nests of *A. cephalotes* are almost an order of magnitude more frequent in the first 50 m of Coimbra forest than in the forest interior (2.8 vs. 0.3 colonies/ha; Wirth et al. 2007). Thus, high colony densities at the edge concentrate the ants' environmental impact in this already disturbed habitat.

FOREST STRUCTURE AT NEST SITES – Parameters describing forest structure at nest sites were estimated for 36 representative colonies of *A. cephalotes*. These were all colonies encountered in a density census along haphazardly chosen pre-existing, narrow (<1 m) foot trails (Wirth et al. 2007) who's center lay within the forest. Colonies occurred from the forest edge up to 800 m into the forest interior and were strongly aggregated at the forest edge (Wirth et al. 2007). As the most fundamental parameter describing colonies colony size was approximated using ellipsoids including all soil excavations done by the colony. Areas bare of understory vegetation showed a marked contrast to the surrounding forest with a clear outline and could also be easily estimated as ellipsoids. To quantify forest structure within these understory gaps and within 20 control plots (5 x 5 m; without any ant influence or disturbance as e.g. tree-fall gaps; randomly located within the first 50 m of Coimbra) all stems with a basal diameter of more than 0.5 cm were counted to calculate stem densities in four different size categories (0.5-2, 2-5, 5-10, >10 cm). In addition, stems were judged to be either living or dead, in order to assess differences in stem mortality between nest and forest.

To test for gaps in the canopy, nests and control plots were compared in canopy openness and measures of light transmission (direct, diffuse, and total transmission) obtained from digital fish

eye photographs (Nikon Coolpix 990 camera with FC-E8 fisheye converter) taken in 50 cm height and analyzed with Gap Light Analyzer 2.0 (Frazer et al. 1999). Since plants respond to microclimatic differences, canopy openness and the proportion of transmitted radiation are better gap size estimates than the physical gap size per se (Whitmore et al. 1993) because physical measures of gap size (e.g. drip line projection sensu Brokaw 1982) cannot allow for small canopy holes, which are important sources of radiation in small gaps and under closed canopy (Mitchell and Whitmore 1993). Calculations of light transmission are based on cloudiness index estimations derived by dividing the mean daily solar radiation measured at four sites close to the study area (Tiba et al. 2004) by the extraterrestrial radiation at that geographic position. All other site factors were estimated based on the cloudiness index as described by Frazer et al. (1999). To approximate the distribution of gap sizes present in the canopy above nests and control sites, fish-eye photographs were intersected into 1000 sky regions so that each sky region represented an equal sized fraction on the hemisphere projected by the fisheye lens (Gap Light Analyzer 2.0; Frazer et al. 1999). Every sky region was assigned into the categories ‘opening’ or ‘foliage’ (more or less than 50% white pixels, respectively). Gaps were defined as connected sky regions identified as opening and the number and size of gaps were determined for every photo as well as the largest gap present. To calculate a rough approximation of the size of the opening represented by a sky region we used the averaged tree height pooled for forest edge and interior of Coimbra (17 m; Oliveira et al. in press) as an average distance of foliage and gaps to the camera. The area of one sky region is thus the surface area of a hemisphere with a radius of 17 m dividing by 1000 (the number of sky regions), which equals about 1.8 m².

MICROCLIMATE – To characterize microclimatic alterations on and around nest sites 11 adult colonies of *A. cephalotes* were chosen. Colonies were selected to be surrounded by homogeneous forest without openings other than the colony (e.g. no tree falls or other gaps). Six of these colonies were found independently from the census mentioned above. Distance of colonies to the forest border ranged from 13 to 295 m and

was determined using a geographic information system based on GPS-recordings as detailed in Wirth et al. (2007). The 11 chosen colonies were representative for the population because they differed neither in nest size ($t = 1.34$, $df = 14.7$, $p = 0.199$) nor in canopy openness ($t = 0.98$, $df = 17.7$, $p = 0.341$) nor transmittance of light (analyzed from fish eye photographs; e.g. total transmittance: $t = 1.33$, $df = 15.9$, $p = 0.201$) from the 36 census colonies as tested in t-tests with logarithmic or square root transformed values. The characterization of microclimatic changes at nest sites was concentrated on three plant-relevant variables: Light (relative light interception and daily sum of photosynthetically active radiation), water content (of soil and air) and temperature (of soil and air). To account for the gradual change in microclimatic conditions between nests and surrounding forest and to determine the penetration depth of microclimatic nest influence into the forest all variables were measured along transects instead of comparing nest sites with undisturbed understory only. All parameters were measured simultaneously every three meters from the edge of the nest up to 24 m into the forest with an additional measuring point at nest centers. To control for confounding effects in case of nearby linear disturbances (forest edge, stream, valley), transects were run parallel to these structures. Photon flux density was measured using gallium arsenide photodiodes (Hamamatsu G118, Hamamatsu, Middlesex, NJ; Pontailler 1990) connected to a Data-logger (LI-1400, LI-COR corp., Lincoln, NE). The signal of sensors connected to the voltage channels of the datalogger was amplified by a factor of about 250 using self-made operational amplifiers. Using all channels of the datalogger a total of 9 photodiodes could be recorded simultaneously. Therefore no light was measured 21 m away from the colony. Ambient photon flux was measured outside the forest with photodiodes connected to two tinytalk dataloggers (Gemini Data Loggers Ltd., Chichester, UK) one measuring the whole daily range of light levels the other measuring low light of up to 300 $\mu\text{E}/\text{m}^2/\text{s}$. All photodiodes were calibrated against a certified quantum sensor (LI-190, LI-COR corp., Lincoln, NE) at the field side. Light climate was expressed as (1) the daily sum of photosynthetically active radiation (daily PPFD) and (2) the fraction of diffuse radiation reaching measuring

points relative to the radiation above the canopy (relative irradiance = RI). The calculation of RI is based on all measurements from the diurnal course when the reference sensor read less than 100 $\mu\text{E}/\text{m}^2/\text{s}$ (to restrict used values to diffuse light) and more than 50 $\mu\text{E}/\text{m}^2/\text{s}$ (to minimize noise when measuring extremely low light levels in the forest understory). Air temperature and humidity was recorded at all 10 transect points using Hobo Pro RH/Temp sensors (Onset Computer Corp., Bourne, MA) equipped with internal dataloggers. Sensors were mounted in actively ventilated radiation shields at a height of 25 cm to represent the milieu at seedling height with photodiodes being installed on top of radiation shields. Soil temperature was measured in 5 cm depth using iButton DS1922L sensors (Maxim Integrated Products, Inc., Sunnyvale, CA). Since soil parameters were expected to show a pronounced spatial heterogeneity (Dam 2001) three sensors with a distance of 40 cm between them were used at every transect point. In the analysis the mean of the three sensors per transect point was used. All sensors recorded the diurnal course of the parameters collecting a data point simultaneously every minute over a period of 24 h from midnight to midnight the following day. From the diurnal measurements of temperatures and air humidity cardinal values (minimum and maximum values as well as daily amplitude and mean) were obtained for further analysis. Soil humidity was measured gravimetrically based on three soil samples per transect point taken around noon of the measuring day. To quantify water availability in the soil the gravimetric water content was converted into matric potentials using the filter paper method described by Deka et al. (1995). Based on calibrations of the used filter paper (Type 589/1, Schleicher & Schuell MicroScience GmbH, Dassel, Germany) against known water potentials by Al-Khafaf and Hanks (1974) the matric potential of soil samples could be determined from the gravimetric water content of filter paper at equilibrium with the sample.

DATA ANALYSIS – Measurements of forest structure and light interceptions derived from fish-eye photographs at colonies and control plots were square root transformed prior to comparison in t-tests. Back-transformed 95% confidence intervals are presented together with

the mean of the factors. Parameters of understory and canopy gaps were analyzed in detail by pairwise comparisons within size classes between colonies and control sites for stem densities, the proportion of dead stems, number of gaps, and gap area in u-tests. The change of microclimatic parameters with distance to *Atta* colonies was analyzed by building non-linear mixed effect models (NLME) as described by (Pinheiro and Bates 2002). Mixed effect models have been frequently used to describe continuous data nested within individual samples that were randomly drawn from a population (e.g. Barrowman et al. 2003, Gillies et al. 2006) Using this approach we can calculate a model representing the average of colonies in the population (fixed effects) and at the same time estimate parameters describing deviations of measurements at individual colonies from the mean microclimatic model (random effects). Models allowed for an exponential (Equ. 1) and/or linear (Equ. 2) relationship between dependent variable and distance to the colony.

$$y = n \cdot e^{s1 \cdot x} + f \quad \text{Equation 1}$$

$$y = s2 \cdot x + n \quad \text{Equation 2}$$

Mathematically functions of exponential curves (Equ. 1) were described by three parameters: the value of the plateau at the end of the curve representing the surrounding forest (f), the value by which the edge of the colony differs from the forest (n), and a parameter "s1" that scales the exponential function and describes how fast the value changes from nest to forest. Linear relationships (Equ. 2) were described by the slope of the curve (s2) and the value at the nest edge (n). During the model building process the inclusion of fixed and random effects were tested for significance comparing nested models in F-statistics and based on the Akaike information criterion (AIC-values). When there was no dependence between the parameter and distance to the colony this is expressed as a model including only a constant (f). Response variables were checked for homoscedasticity and transformed when necessary. For final models residuals and within-group residuals were examined for normality and homoscedasticity. In case of heteroscedasticity a weighting function was included into the model. Random effects were checked for normality (Pinheiro and Bates 2002).

Since obvious limitations in the amount of measuring equipment did not allow us to measure different colonies simultaneously, random effects incorporate the effect of different locations in the forest and different macroclimatic conditions at the measuring day. Measuring days included various weather conditions typical for the dry season in Serra Grande (hot sunny days, different degrees of cloud cover and even some rain showers) and were spread over two month during the peak of the dry season 2005/2006. In addition, analysing RI for differences between colonies at the edge and in the interior of the forest showed no significant effect of habitat. The microclimatic models presented are thus independent from singular colonies, weather conditions, and distances to the forest edge.

Statistics were computed in R (version 2.6.0, R Development Core Team 2007). Mixed effect models were build using the nlme library (version 3.1-85, Pinheiro et al. 2007). U-tests for the comparison of understory and canopy gap characteristics were performed using the exactRankTests library (version 0.8-16, Hothorn and Hornik 2006).

ESTIMATING IMPACTED AREA - In order to estimate and compare the area altered/affected by *A. cephalotes* nests in the interior and at the edge of Coimbra on the level of forest stands, the percentage of both forest zones that was directly modified by the ants was calculated, by multiplying the impacted area per colony with available colony densities at the study site (Wirth et al. 2007). This extrapolation assumes that per colony impact does not differ between habitats. We tested for this assumption by checking the independence of colony size from distance to the forest edge by computing a Pearson correlation. To directly evaluate possible effect of forest zone on microclimate the model for RI was tested for the inclusion of habitat (edge: 6 colonies [13–66 m] and forest: 5 colonies [138–295 m]) as a covariate. Light availability was chosen as the exemplary parameter to analyze the area of microclimatic alterations caused by nests because RI is generally low in the understory of tropical forests and believed to be a limiting factor for plants (Chazdon 1988) and forest structure changes primarily light availability which causes secondary microclimatic changes (Whitmore et al. 1993).

To calculate the area impacted per colony the continuous relationship between microclimatic alterations and distance from nests had to be converted into a radius up to which *Atta* nests alter RI. We based estimates on a conservative threshold value of 0.5% RI. Even smaller difference in light might induce biological effects, since e.g. Montgomery and Chazdon (2002) showed plant growth and survival of different species to increased linearly with light availability in low light environments between 0.2 to 6% RI. The distance from the nest edge up to which alterations beyond the threshold occurred was calculated based on the model for RI (formula in Table 2). Adding this penetration depth to the radii of the average understory gap allowed calculating an ellipsoid representing the area impacted by a colony.

RESULTS

FOREST STRUCTURE AT NEST SITES – Nests of *Atta cephalotes* represented major disturbances in the forest understory of Coimbra. The average size of 36 representative nests was 55 m² (95% CI: 22-136) and showed no correlation with distance to the forest edge (Pearson correlation $r = 0.134$, $df = 34$, $p = 0.438$); therefore no confounding effects of edge distance on our study are to be expected. Nests were associated with zones of strongly reduced understory vegetation concentric with the main mound of the colony, normally exceeding it in size. These understory gaps encompassed on average 48 m² (95% CI: 18-130) and their size correlated to a high degree with the size of the colony (Person correlation $r = 0.637$, $df = 34$, $p < 0.001$). Densities of stems up to diameters of 10 cm were reduced in the nest areas compared to control sites in the forest (Fig. 1A). Stem density in the smallest diameter class (0.5-2 cm) decreased from about 2/m² to less than 1/m². In addition, about 70% of the stems encountered on nests in this size class were dead while less than 10% were dead at control sites. Generally, a much higher proportion of dead stems was encountered at nest sites showing highly significant differences for diameters up to 5 cm (Fig. 1B). Nest sites were de facto free of small living vegetation and contrasted strongly from the surrounding forest, creating an understory gap which was well

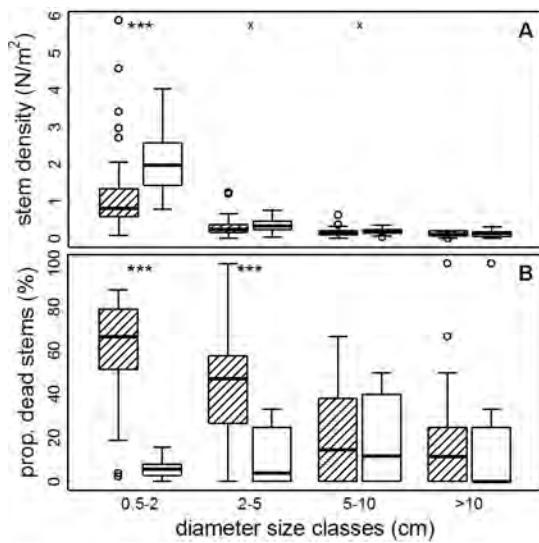


Figure 1: Density of stems (A) and proportion of dead stems (B) in different diameter classes compared between 36 nest sites of *Atta cephalotes* (hatched) and 20 undisturbed control sites (white). Plots show the median with the upper and lower quartile as box and 1.5 times the interquartile range as whiskers. Outliers farther away from the median are shown as open circles. Symbols signify statistical differences in pair-wise comparisons between nests and controls by u-tests (***($p<0.001$), *($p<0.05$)).

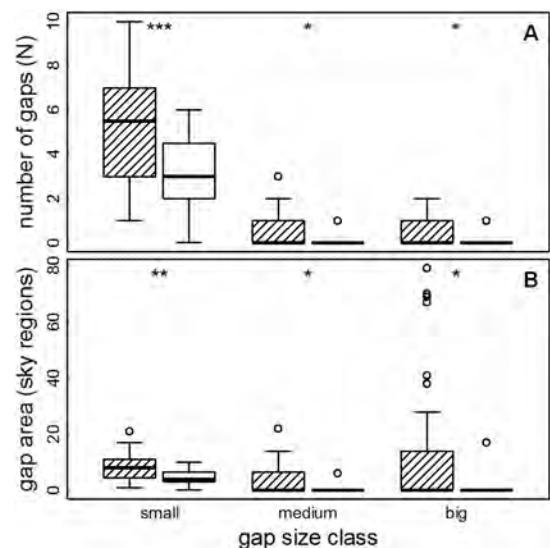


Figure 2: Average number of gaps (A) and area of these gaps (B) in three different gap size classes (small: 1-5, medium: 6-10, big: >10 sky regions) compared between the canopy above 36 nest sites of *Atta cephalotes* (hatched) and 20 undisturbed control sites (white). Plots show the median with the upper and lower quartile as box and 1.5 times the interquartile range as whiskers. Outliers farther away from the median are shown as open circles. Symbols signify statistical differences in pair-wise comparisons between nests and controls by u-tests (***($p<0.001$), **($p<0.01$), *($p<0.05$)).

demarcated from the adjacent understory by a rather distinct edge.

Analysis of fish-eye photographs taken from colony centers demonstrated that alterations of forest structure were not restricted to the understory but exceeded into the canopy (Table 1). Canopy openness measured above colonies increased by ca. 40% compared to control sites (5.3 at colony vs. 3.7% at control sites) allowing for a 46% higher total transmittance of light (7.9 vs. 5.4%). In the canopy above nests the number of small, medium and large gaps was markedly higher compared to control sites (Fig. 2A). While the absolute difference in gap numbers between colonies and controls was highest for the small gaps, this relates only into a relatively low, yet

highly significant, difference in total gap area (Fig. 2B). Big gaps, though not as frequent as smaller ones, cause a much stronger increase in total gap area at nest sites, highlighting their importance for the increased canopy openness above nests. The largest opening within the canopy at nest sites encompassed on average about 7 sky regions (roughly 12 m²) – almost three times the size measured at control sites (2.5 sky regions; table 1). In addition the right side of the 95% confidence interval for gap sizes above colonies extended up to 75 sky regions (roughly 135 m²), while 95% of all control sites had a maximum opening in the canopy equal to or less than 10 sky regions (Table 1).

Table 1: Comparison of parameters derived from fish-eye photographs describing canopy structure above colonies of *Atta cephalotes* and control sites in the Brazilian Atlantic forest. Shown are mean, 95% confidence intervals and significance level from t-tests based on logarithmic transformations. A sky region equals approximately 1.8 m², for details see description in the method section.

parameter	colonies	control	t	df	p
Canopy openness (%)	5.3 (2.4 – 11.7)	3.7 (2.4 – 5.7)	4.3	54	< 0.001
Direct transmittance (%)	8.5 (3.2 – 22.8)	5.9 (3.4 – 10.3)	3.5	54	< 0.001
Diffuse transmittance (%)	7.2 (3.4 – 15.3)	4.9 (3.3 – 7.3)	5.0	54	< 0.001
Total transmittance (%)	7.9 (3.5 – 17.9)	5.4 (3.6 – 8.1)	4.5	54	< 0.001
Largest single opening (sky regions)	6.7 (0.6 – 75.1)	2.5 (0.6 – 10.0)	3.8	54	< 0.001

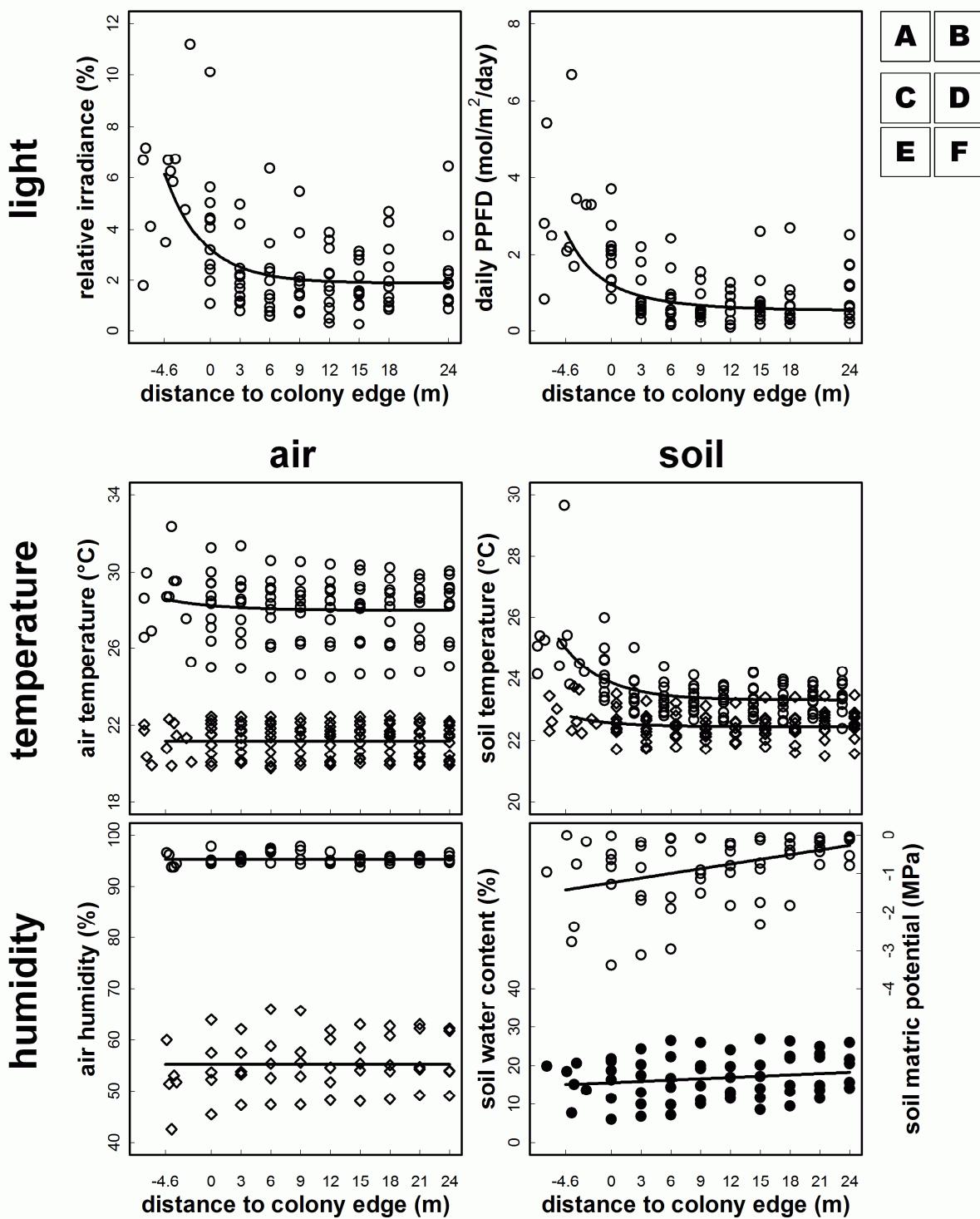


Figure 3: Characterization of microclimatic conditions with increasing distance to nests of *Atta cephalotes* (0 marks the edge of the colonies' understory gap, -4.6 the average distance to the centre of colonies). Lines represent mathematical models describing the data as detailed in the text and presented in table 2. All parameters are based on diurnal measurements with one minute time steps. The available light as the proportion of diffuse light reaching the measuring point and the daily sum of incident photosynthetically active radiation is shown in graphic A and B respectively. The maxima (○) and minima (◇) of air and soil temperature are shown in graphic C and D. The offset on the X-axis in graphic D is only for presentation purposes. Graphic E presents maxima and minima of the air humidity. Availability of water in the soil is presented in graphic F as the gravimetric soil water content in % of the dry weight (●) and the matric potential of the soil (○). Light availability, air temperature and soil temperature are based on measurements at 11 colonies; Air humidity is based on five, soil humidity on six colonies.

Table 2: Mathematical models describing the microclimatic alterations at nest sites of *Atta cephalotes* as continuous functions of distance to the nest edge (x in the model formula measured in meters). Functions are based on and thus valid for $-4.6 \leq x \leq 24$. Lines in the columns for random effect mark that this parameter is represented as a fixed effect only in the final model. The model building process is detailed in the text. Visualizations of the models are shown in figure 3.

parameter	model	Fixed effects (standard error)			Necessary random effects as SD		
		n (nest edge)	s1 (exponential)	s2 (linear)	f (forest)	S1	S2
Relative irradiance (RI)	$y = n \cdot e^{s1 \cdot x} + f$	1.33* (0.297)	-0.253 (0.042)	1.90 (0.312)	0.684	-	0.968
sum of radiation (daily PPFD)	$\ln(y) = n \cdot e^{s1 \cdot x} + f$	0.800* (0.190)	-0.144 (0.036)	-0.596 (0.182)	0.040	-	0.443
Soil temperature maximum	$y = n \cdot e^{s1 \cdot x} + f$	0.668* (0.176)	-0.238 (0.017)	23.3 (0.128)	0.550	-	0.410
Soil temperature minimum	$y = n \cdot e^{s1 \cdot x} + f$	0.106* (0.055)	-0.243 (0.084)	22.5 (0.124)	-	-	0.397
Soil temperature amplitude	$y = n \cdot e^{s1 \cdot x} + f$	0.555* (0.095)	-0.228 (0.032)	0.835 (0.085)	0.252	-	0.265
Soil temperature mean	$y = n \cdot e^{s1 \cdot x} + f$	0.296* (0.069)	-0.252 (0.027)	22.9 (0.118)	0.193	-	0.384
Soil water content	$y = s2 \cdot x + n$	1.56 (2.25)	0.111 (0.048)	5.36	0.102	1.60	0.140
Soil matric potential	$y = s2 \cdot x + n$	-1.23 (0.418)	0.040 (0.016)	0.968	0.036	0.179	
Air temperature maximum	$y = n \cdot e^{s1 \cdot x} + f$	0.247* (0.102)	-0.182 (0.039)	28.0 (0.484)	0.285	-	1.58
Air temperature minimum	$y = f$			21.2 (0.261)			0.861
Air temperature amplitude	$y = n \cdot e^{s1 \cdot x} + f$	0.268* (0.103)	-0.197 (0.036)	6.78 (0.500)	0.290	-	1.632
Air temperature mean	$y = f$			24.0 (0.077)			-
Air humidity maximum	$y = f$			95.4 (0.282)			0.568
Air humidity minimum	$y = f$			55.3 (0.798)			-
Air humidity amplitude	$y = f$			40.0 (0.775)			-
Air humidity mean	$y = f$			81.9 (0.348)			-
				2.46			

*note that for exponential models n represents the value above forest level (f) so that the absolute edge value is n+f.

MICROCLIMATE – Alterations in forest structure at nest sites of *A. cephalotes* caused changes in forest microclimate that were measured in linear transects extending from the edge of the understory gap 24 m into the forest with an additional measurement point at the center of nests. Nest centers received about three times as much light compared to the forest understory with light levels declining exponentially with distance from nests (Fig. 3A and B, Table 2). This pattern was observed for RI (6 vs. 2% RI) as well as for the daily PPFD (2.6 vs. 0.6 mol/m²/d). Neither at nest sites nor in the surrounding forest was RI statistically different between colonies from forest edge or interior since including habitat as a covariate into the model for RI did not increase the explanatory power of the model, yet there was considerable variation between the light levels at individual colonies (random effects; Table 2). Paralleling light levels reaching the forest floor, maximum soil temperatures declined exponentially along transects from 25 to 23°C (Fig. 3E). Minimum soil temperatures were virtually constant at 22.5°C (Fig. 3E). Thus, the course of daily amplitude and mean soil temperatures along transects closely resembled maximum soil temperatures (Table 2). Soil at nest centers was on average 1°C warmer with a daily amplitude twice as large as in the forest understory (1.6 vs. 0.8°C). Gravimetrically measured soil water content showed a statistical trend to increase with distance to the nest (Table 2) but the effect was small (increase from 15% at nest centers to 18% at 24 m from the nest edge; Fig. 3F). Stronger effects became visible when soil water content was converted into soil matric potential to express plant water availability. Matric potential increased linearly from less than -1 MPa at the nest centers to values close to 0 MPa at the end of transects (Fig. 3F) with considerable variation in slope and offset of the curves among colonies (random effects; Table 2). Measurements of air temperature (Fig. 3C) and air humidity (Fig. 3D) changed very little along transects compared to diurnal fluctuations shown as minimum (21°C; 55% RH) and maximum values (28°C; 95% RH) in the graphs. Also, variation between colonies was high (Table 2).

IMPACTED AREA - Microclimatic alterations were not restricted to the nest site itself (Fig. 3)

but penetrated into the surrounding forest. A difference of 0.5 % RI in light availability was present up to about 4 m from the edge of the understory gap around colonies. Therefore, on average, an area of 195 m² (95% CI: 120-318) was influenced by every colony, which is roughly four times the area of an average understory gap 48 m² (95% CI: 18-130). Based on the densities of *A. cephalotes* in the interior and edge of the forest (0.3 and 3 colonies/ha, respectively) the affected area on ecosystem level was 10 times bigger in the forest edge compared to the interior of the forest. The proportion of the total area directly impacted by the presence of *A. cephalotes* nests was thus 6% and 0.6% of forest edge and forest interior, respectively.

DISCUSSION

The present study demonstrates that nest sites of *Atta cephalotes* are associated with a striking reduction of understory vegetation and with canopy openings above nests, allowing for a higher light interception with increased soil temperatures and reduced water availability. Neither canopy gaps above nests nor the resulting microclimatic alterations, which substantially penetrated into the adjacent forest understory, had been previously documented in detail. Extrapolations of the area impacted by the ecosystem engineering of *A. cephalotes* highlight their tremendous potential in forests were LCA are hyper-abundant, as will be discussed at the end of this section together with expected patterns of plant regeneration on and around nests.

Nests of *A. cephalotes* showed marked understory gaps supporting the earlier notion of “bottom up gaps” (Farji-Brener and Illes 2000). These gaps were characterized by a pronounced reduction in stem densities especially in small size classes. These findings corroborate previous data from Garretson et al. (1998) and Hull-Sanders and Howard (2003) that were limited due to small areas sampled per colony or colony numbers, respectively. In addition we demonstrated for the first time a strongly elevated proportion of dead stems up to 5 cm diameter compared to undisturbed forest, thus, indicating that small plants experience elevated mortality at nest sites. We observed different activities of the ants that can induce mortality. Seedlings and saplings can be (1) repeatedly defoliated, (2)

substantially damaged by cutting of their stems, or (3) buried by excavated soil. Thereby, ants cleared areas comparable in size to the disturbance caused by small tree falls (Farji-Brener and Illes 2000). Different from tree fall gaps, however, which are characterized by thriving vegetation at the ground and huge openings in the canopy, nest gaps are practically cleared from understory vegetation but showed only in 6 of 36 colonies a single gap bigger than 50 m². Yet, canopy openness at nest sites was 40% elevated and the canopy showed a higher frequency of holes in all gap size classes. Thus, contrary to prior believes gaps at LCA nests are not restricted to the forest understory (Garrettson et al. 1998, Farji-Brener and Illes 2000, Hull-Sanders and Howard 2003, but see Corrêa et al. submitted) We quantified not only an increase in numbers of small and medium openings in the canopy above LCA nests but also the occurrence of large gaps that are absent in the undisturbed canopy of control plots and propose that different sized gaps above colonies are created by different mechanisms. A high number of small and medium sized openings is typical for the patchy herbivory by leaf-cutting ants (Wirth et al. 2003) and can account for a part of the higher canopy openness above nests. Therefore, it seems there is no specialized behaviour, comparable to the clearing of the nest area on the ground, involved in creating these canopy openings above nests. Rather, small and medium openings seem to be plausible explained by a diffusely elevated cutting probability at nest sites. On the other hand, large and very large gaps in the canopy at nest sites suggest another mechanism. We observed frequent tree falls at nest sites during 8 years of research on LCA in the study area (including year-long observations at several colonies). Elevated mortality for large trees might, likewise to seedlings and saplings, be caused by activities of the ants, since large trees on nests (1) can be repeatedly defoliated by the ants, which ultimately may lead to a depletion of stored reserves, (2) their roots can be cut in the area of the colony which might promote infections in addition to immediate effects of root loss, and (3) trees might lose their support when the soil at nest sites is destabilized by excavation activities of the colony. LCA might thus created gaps themselves or use pre existing gaps for colony foundation (Vasconcelos 1990). The data

on forest structure at nest sites together with the proposed mechanisms indicate that colonies of LCA maintain or even augment gaps at their nest site, irrespectively of the origin of the gap. These LCA gaps do not only drastically differ from tree fall gaps in structure but also regeneration dynamics within these types of gaps differ. Typically, canopy openness in tree fall gaps rapidly decreases by accelerated vegetation growth (Van der Meer and Bongers 1996, Van der Meer 1997). In contrast, colonies will maintain the gap for about eight years, which is the average life expectancy of *A. cephalotes* colonies in our study area (Meyer et al. submitted). While no difference in microclimatic condition could be detected in a tree fall gap after only two years (Fletcher et al. 1985) microclimatic alterations at nest sites will persist at least as long as the colony lives.

Colonies were generally more illuminated and showed higher soil temperatures and lower water availability than the surrounding forest. These parameters responded consistently to the distance from colonies, despite considerable variation among and within colonies possibly attributable to differences in the gap itself, to properties of the surrounding forest, or macroclimatic conditions on the measuring day. Nest centres received about three times as much light as the surrounding forest. In accordance with Whitmore et al. (1993) who found that solar radiation significantly correlated with soil and air temperature and humidity in tropical rain forest gaps, maximum soil temperature closely followed light interception along transects. Since the minimum soil temperatures were almost constant, nest centres experienced on average higher daily amplitudes and moderately higher mean temperatures. Vegetation temperatures, though not measured, are expected to follow the same pattern because, like soil, vegetation absorbs more energy with increasing light irradiance. Higher temperatures of soil and vegetation augment evaporation and transpiration, respectively. In combination these effects promote water loss from the soil and might explain the observed lower water content and water availability at nests. Similarly, lower soil water contents were documented for nests of *A. sexdens* in the Brazilian Amazon by Moutinho et al. (2003) who observed higher root densities in nest soil and propose increased water uptake

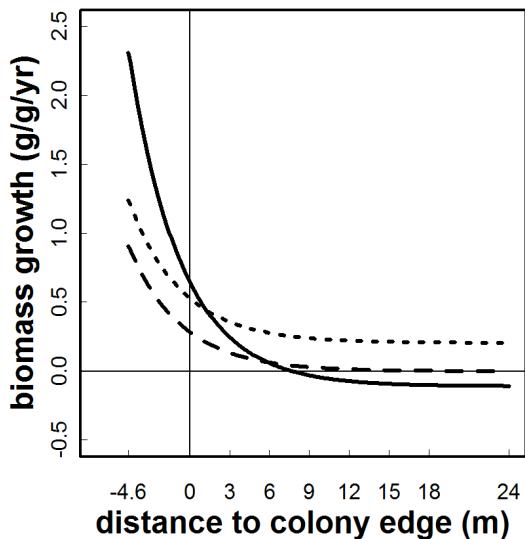


Figure 4: Potential biomass growth per year as function of the distance to nests for seedlings of three shade tolerant species differing in light-dependent growth rates. Models for growth rates were derived from seedlings transplanted into the tropical wet premontane forest at La Selva, Costa Rica by Montgomery and Chazdon (2002; Solid line: *Dipteryx panamensis* $-1.39 + 0.666 \text{ RI}$; dotted line: *Virola koschnyii* $-0.297 + 0.284 \text{ RI}$; dashed line: *Brosimum alicastrum* $-0.471 + 0.249 \text{ RI}$). Original models were divided by 1.17 to derive annual values and used to convert light availability with distance to nests (RI; Fig. 3, Table 2) into potential growth rates.

by trees as a mechanism for reduced water content. Above the soil surface, no or only weak spatial patterns were observed in air temperature or humidity, suggesting sufficient air turbulence to ameliorate differences on these small spatial scales.

The documented microclimatic alterations at nest sites of *A. cephalotes* potentially act as ecological filters at various stages during the life of a tree. Soil temperature and especially the amplitude of temperature fluctuations have been demonstrated to be important for induction of germination and resulting germination rates (Everham et al. 1996, Pearson et al. 2002, Godoi and Takaki 2004). Following germination tree species-specific differences in establishment of seedlings, juvenile growth, and survivorship strongly influence forest dynamics, succession, and species composition and diversity (Kobe 1999). Studies of resource partitioning, using models of tropical tree seedling performance, have traditionally focused on species responses to spatial variation in light availability (Kobe 1999, Montgomery and Chazdon 2002, Gouve-

nain et al. 2007), since light availability is believed to be the principle limiting factor for seedling growth in the light-limited understory of tropical forests (Denslow 1980, Chazdon 1988). Only 1 to 2% of the photosynthetically active radiation available above the canopy reaches the forest floor (Chazdon 1988). We have estimated similar light levels for the forest understory in our study area (1.9%). Under such low light conditions all plant species, irrespectively of their regeneration strategy, tend to increase growth rates with light availability, although the slope and shape of this relationship may be strongly species-specific (Agyeman et al. 1999, Poorter 1999). Along the *Atta* nest forest understory transect we demonstrated a light gradient from 6 to 2% RI. In this range of light availability Montgomery and Chazdon (2002) demonstrated linear increases in growth rates for three shade-tolerant species (*Virola koschnyii*, *Brosimum alicastrum*, and *Dipteryx panamensis*) specifically selected to differ in their light demand. To predict potential impacts of LCA nests on plant regeneration, we used the regression equations of Montgomery and Chazdon (2002) to calculate potential biomass gain per year as a function of distance to the nest based on the measured changes in light availability at nest sites (RI; Fig. 3, Table 2). Resulting models (Fig. 4) demonstrate that all three species have highest potential growth rates on the nest surface. However, during the lifetime of the colony no seedling will achieve this potential due to the zealous nest-clearing behavior of the ants (Haines 1975, Farji-Brener and Silva 1995, Garrettson et al. 1998). Outside the nest area *V. koschnyii* is an example for a species with positive biomass gain in the forest interior yet still profits from increased light availability in the vicinity of nest by increasing biomass gain. The two other species do not gain biomass in the shaded forest understory (*B. alicastrum*) or even loose biomass (*D. panamensis*). Only with the increased light availability in the vicinity of nests do these species reach positive growth rates, indicating that the area surrounding living colonies represent a possible site for the regeneration of plant species which depend on disturbances and cannot survive in the deep shade of an intact forest. Conspicuous is the change of rank between the species comparing forest understory and nest sites (Fig. 4) caused by

species-specific slopes in the light response of growth rates. In the nest area and up to one meter into the forest *D. panamensis* (the lowest ranked species in the forest understory) is expected to outcompete the two other species, markedly demonstrating the functioning of *A. cephalotes* nests as ecological filters and their potential to impact plant community composition. This filter effect offers a possible mechanistic explanation for the altered plant community composition that Corrêa et al. (submitted) have documented at and around nest sites of *A. cephalotes*.

Nest effects penetrated several meters into the forest understory. While dead LCA nests had been previously identified as potential regeneration sites in neotropical forests (Garrettson et al. 1998, Farji-Brener 2005), living nests had not been assumed relevant for forest regeneration since the nest is rigorously cleared by the ants. We demonstrated for the first time the potential of the vicinity of living LCA nests as regeneration sites, thus drastically increasing the proposed filter effect of LCA nests on a temporal scale due to the longevity of colonies (Meyer et al. submitted). On a spatial scale, the area impacted by a single colony is augmented by no less than a factor of four considering the near nest zone with higher light availability. Although the impact per colony did not differ between the forest edge and the forest interior there should be drastic differences in the LCA impact on ecosystem level because of the strong aggregation of colonies at the forest edge. At the edge of Coimbra areas ten times as big as in the interior receive higher light levels due to the ecosystem engineering of *A. cephalotes*. This physical disturbances caused by nests of hyper-abundant (Wirth et al. 2007) and persisting (Meyer et al. submitted) populations of *A. cephalotes* complement their dramatic trophic effects. In the edge zone of Combra *A. cephalotes* exerts an exceptional herbivory pressure removing 32% of the available foliage compared to only one sixth (5.7%) in the forest interior (Urbas et al. 2007, Meyer et al. submitted). This edge herbivory of *A. cephalotes* surpasses by far the overall rate of herbivory generally assumed for tropical forests (approx. 11%; Coley and Aide 1991). Both trophic and physical LCA effects are among the contributing factors that can enable cycles of pioneer self-replacement at forest edges (Tabarelli et al. in press). These cycles and the conco-

mitant domination of closed edges in old fragmented landscapes by pioneer vegetation have been forecast to be the future scenario for tropical forests (Tabarelli et al. in press). Thus, LCA are among the organisms profiting from anthropogenic forest fragmentation that, by their own activities, help to maintain these newly created habitats (Wirth et al. 2008).

In summary, we have documented leaf-cutting ants of the species *Atta cephalotes* to act as ecosystem engineers by maintaining gaps at their nest sites. The ants drastically altered forest structure by opening understory and canopy causing a higher light irradiance on the nest surface and in its vicinity. While higher amplitudes in soil temperatures might impact plant germination, light availability varied in a range that can differentially alter growth rates of seedlings. Thus, *Atta cephalotes* nests act as ecological filters changing the plant community composition, especially at forest edges where colonies of these ants are hyper-abundant. This example of altered ecosystem functioning in a fragmented forest highlights the importance to understand the fate of and role played by keystone species such as ecosystem engineers in man-made landscapes in order to predict future scenarios and effectively protect the threatened biodiversity.

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7

Plant recruitment on and around nests of *Atta cephalotes*: Ecological filters in a fragmented forest

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Meyer ST, Leal IR, Tabarelli M, Wirth R

ABSTRACT

Habitat fragmentation is the most pervasive anthropogenic disturbance in tropical forests and will continue to alter tropical landscapes creating assemblages of small forest fragments embedded in a human-managed, harsh matrix. In this context, the concept of ecological filters (ecological variables and processes shaping the local species composition) is especially promising, yet little used. It facilitates to describe the underlying ecosystem functioning as a network of ecological filters. Here we tested the potential of *A. cephalotes* nests, which occur hyper-abundant along the edges of forest remnants, to function as ecological filters comparing growth and survival of seedlings from six different tree species. At nests, microclimatic conditions are drastically altered since the ants maintain gaps in the canopy and forest understory.

Nests of *A. cephalotes* differentially impacted survival and growth of seedlings. Plants on nests showed higher gross leaf gain compared to understory plants. Yet, the growth of roughly twice as much new leaves at nests as compared to plants in the forest did not translate into a higher net growth rate of whole plants. On the contrary, plants of four of the six species lost leaves during the six months observation period when situated on nests. The other two species showed a net leaf gain (surrogate for overall growth rate) close to zero. Survival differed highly significantly between habitats and species and was generally high in the forest, yet low on nests where it correlated strongly with seed size of the plant species tested.

The disturbance regime created by leaf-cutting ants differed from other disturbances. Two distinct mechanisms governed the effect of nests on plant recruitment: (1) increased light availability and (2) strong cutting pressure on the nest surface. In combination, large-seeded plant species that profit from additional light and have resprouting abilities seem to be best suited to profit from leaf-cutting ant nests because a plant has to tolerate repeated defoliation in order to survive on a nest. Plants able to persist on the nest surface increase their chance to colonize the vacant spot after the death of the colony when they can profit from increased light without suffering cutting by the ants. On an ecosystem scale large populations of *A. cephalotes* at forest edges might amplify edge-driven microclimatic alterations since very high rates of herbivory and the maintenance of canopy gaps above nests allow for an increased light penetration. Thereby, *Atta* promotes light demanding plant species contributing to a disturbance regime that enables self-replacing pioneer communities at forest edges.

INTRODUCTION

Habitat fragmentation has become the most pervasive anthropogenic form of disturbance in tropical forests following unprecedented rates of tropical deforestation (Laurance and Peres 2006). In the next decades, the relentless growth of human populations will continue to alter tropical landscapes causing the likely conversion of most tracts of old-growth forest into assemblages of small fragments and regenerating forest patches (Aide and Grau 2004, Wright 2005) embedded in a human-managed, harsh matrix (Tabarelli et al. 2004). Within forest remnants in these landscapes, an increase in disturbance is favoring early successional trees (Oliveira-Filho et al. 1997, Laurance et al. 1998a, Tabarelli et al. 1999, Laurance et al. 2006) and a correlated decline of old-growth trees (Laurance et al. 1998b, Tabarelli et al. 1999, Metzger 2000). These changes are to a large part driven by edge effects (Laurance et al. 2002, D'Angelo et al. 2004, Tabarelli and Gascon 2005) which usually operate simultaneously with other human-induced disturbances such as logging, fire, and hunting (Laurance and Williamson 2001, Peres 2001). In combination, these different types of disturbances modulate the functioning of ecological filters (those ecological variables and processes that are of importance in shaping the local species pool; Belyea 2004) causing a post-fragmentation retrogressive succession (*sensu* Santos et al. 2008), which represents a major force driving the nature of neotropical forest biotas in anthropogenic landscapes dominated by edge-affected habitats (Tabarelli et al. in press). In this context, the concept of ecological filters is especially promising, yet little studied. It allows for an understanding of underlying ecosystem functioning by assembling a feedback network of ecological filters acting in these human disturbed ecosystems and to ultimately derive managing guidelines for conservation and restoration (Temperton et al. 2004).

Changes in the species composition of edge-affected habitats can cause drastic alterations in species interactions such as dispersal, pollination and trophic cascades. For example, a combination of disrupted bottom-up and top-down control at forest edges has been identified as the underlying cause for an increase in the abundance of generalist herbivores together with

higher levels of herbivory (Wirth et al. 2008). A prominent case of herbivores profoundly benefiting from anthropogenic landscape alterations, agricultural land-use, deforestation and/or disturbance are leaf-cutting ants (Jonkman 1979, Fowler et al. 1986, Jaffe and Vilela 1989) which occur hyper-abundant along the edges of forest remnants (Wirth et al. 2007). Leaf-cutting ants (LCA) of the genus *Atta* are dominant herbivores in the Neotropics (Wilson 1986) and have been identified to be ecosystem engineers (Wirth et al. 2003, Rico-Gray and Oliveira 2007, Meyer et al. in preparation). Multifarious effects of LCA have been documented, including (1) removal of 35% of the available foliage at the forest edge (Urbas et al. 2007, Meyer et al. submitted), (2) reduced vegetation cover (by 18%) and increased light availability (40% more diffuse light) within foraging areas (Correa 2006), (3) seed dispersal of certain forest plants (Dalling and Wirth 1998, Leal and Oliveira 1998, Silva et al. 2007), and (4) the construction and maintenance of huge nests, which frequently reach more than 100 m² in surface area and 6 m or more in depth of subterranean chambers (Hölldobler and Wilson 1990). Effects of these conspicuous structures include (4a) soil disturbances (Alvarado et al. 1981, Perfecto and Vander Meer 1993), (4b) the improvement of soil penetrability (Moutinho et al. 2003), (4c) removal of litter resulting in bare ground (Weber 1972), (4d) enrichment of soil nutrients by the year-long harvesting activity (Haines 1978, Moutinho et al. 2003, Verchot et al. 2003, Sternberg et al. 2007), (4e) the establishment of “bottom-up” gaps above nests (Farji-Brener and Illes 2000, Hull-Sanders and Howard 2003), and (4f) the alteration of the plant community at nest sites (Garrettson et al. 1998, Corrêa et al. submitted).

Recently, we have documented LCA of the species *Atta cephalotes* to drastically alter microclimatic conditions at nest sites acting as ecosystem engineers by maintaining gaps in the canopy and forest understory at nest sites (Meyer et al. in preparation). The ants were shown to open gaps of various sizes in the canopy above nests in addition to drastically reducing understory vegetation and increasing mortality of small plants. Resulting forest structure allowed for a three times higher light level on the nest surface as compared to the forest understory accompanied by an increase in soil temperatures and a

reduction in water availability. Modifications of microclimate and forest structure greatly surpassed previous estimates (Garrettson et al. 1998, Farji-Brener and Illes 2000, Hull-Sanders and Howard 2003, Corrêa et al. submitted) and were demonstrated for the first time to be not restricted to the nest site itself but to penetrate into the surrounding forest. Light levels declined exponentially along nest-forest transects. At about 4 m from the nest edge the relative irradiance was still 25% higher than in the understory (2.5 vs. 2% relative irradiance, respectively). Therefore, an area roughly four times as big as the actual nest (about 200 and 50 m², respectively) was impacted by every colony. Taking into account the high colony densities at the forest edge (3 colonies/ha) the area directly impacted by the presence of *A. cephalotes* nests amounted to 6% of the total area at the forest edge (Meyer et al. in preparation).

In the present study, we examine biological consequences arising from the documented alterations at nest sites and test our prediction that plants on nests have a higher potential growth rates due to microclimatic conditions (Meyer et al. in preparation) while probably suffering more from cutting by the ants (Farji-Brener and Silva 1995, Garrettson et al. 1998) due to nest clearing behavior (the zealous removal of vegetation from the nest surface). Since plant species can differ in their ability to use available light and to tolerate herbivory damage, LCA nests should induce plant species-specific responses (Meyer et al. in preparation). In other words, we tested the potential of *A. cephalotes* nests to function as ecological filters. Nests would act as ecological filters if their presence benefits plant species different from those favored in the undisturbed forest understory following the framework of pools and filters (*sensu* Keddy 1992, Geho et al. 2007). This framework assumes that the actual species composition is a subset of the total diversity of species existing selected by the action of various ecological filters (biotic and abiotic). To test the potential impact of nests on plant recruitment we compared growth and survival of seedlings of six different tree species planted into the center and edge of nests and the undisturbed forest understory. Leaf number, degree and type of damage, as well as survival of seedlings were monitored in detail for 6 months and in an additional census

after 1.5 years in order to test the following hypothesis: (1) Plants on nest show higher growth rates, (2) nest-clearing by *Atta* suppresses vegetation on active colonies, and (3) growth and survival of plants is species-specific due to differential light-use ability and herbivory tolerance. Results will be discussed in terms of the plant functional types most likely to profit from LCA nests. Finally, we try to predict the impact of LCA nests on plant recruitment in modern anthropogenic landscapes considering the effect of nests as an ecological filter in edge-affected and interior parts of forest remnants in which colony densities of these ants and the species composition of the surrounding forest drastically differ.

MATERIAL AND METHODS

STUDY SITE – The study was conducted in Coimbra, the single largest remnant of Atlantic forest of NE-Brazil (9°S, 35°52'W). Located in the state of Alagoas, it covers approximately 3,500 ha of largely well-conserved lower montane rain forest (Veloso et al. 1991) situated on a low-elevation plateau (300–400 m above sea level). Coimbra forest is surrounded by a homogeneous matrix of sugar cane fields along its 40 km of relatively old (at least 60 y) borders (Santos et al. 2008). The region has a tropical climate characterized by a 5-mo dry season (<110 mm/mo) lasting from September to January (annual precipitation about 2000 mm); the prevailing soils are latosols and podzols (IBGE 1985). The edge zone (0–100 m into the forest) has been shown to be largely dominated by pioneer species (Oliveira et al. 2004) that apparently are able to form multi- rather than single-generation pioneer assemblages (Tabarelli et al. in press) and are the preferred food source for LCA (Farji-Brener 2001, Falcão 2004).

STUDY SPECIES – Two species of the LCA genus *Atta* occur in NE-Brazil (Correa et al. 2005), both forming potentially huge colonies. This study was restricted to the analysis of regeneration patterns at nests of *A. cephalotes*, a species widespread throughout the Neotropics from Mexico to Bolivia (Kempf 1972). *Atta cephalotes* constructs nests that are characterized by a large central nest mount sometimes accompanied by smaller lateral excavations. In contrast, nests

of *Atta sexdens* are rather cryptic with the excavated soil being distributed in small mounds often over large areas, dispersing potential impacts. Nests of *A. cephalotes* are almost an order of magnitude more frequent in the first 50 m of Coimbra forest than in the forest interior (2.8 vs. 0.3 colonies/ha; Wirth et al. 2007). Thus, high colony densities at the edge concentrate the ants' environmental impact in this habitat that already is shaped by anthropogenic disturbances, biotic and abiotic edge effects and altered species interactions (Murcia 1995, Wirth et al. 2008 and references therin).

All plant species studied are canopy or emergent trees typical for the Atlantic Forest of NE-Brazil. *Copaifera langsdorffii* Desf., *Pouteria* sp., *Protium heptaphyllum* (Aubl.) Marchand, *Thyrsodium spruceanum* Salzm. ex Benth., and *Virola gardneri* (DC.) Warb. were all encountered in Serra Grande during a census of plant species (Pôrto et al. 2005) and have been classified as shade tolerant tree species (supplementary material in Silva and Tabarelli 2000). The sixth species *Licania tomentosa* (Benth.) Fritsch is a large seeded shade tolerant species typical of the Atlantic forest, which has disappeared from Serra Grande already, probably due to the absence of large dispersing animals (M. Tabarelli, pers. observation). All species have been named light demanding or heliophyte plants (Lorenzi 2002, Oliveira Filho et al. 2004), therefore we expected the species to respond to an increase in light availability despite their ability to tolerate conditions in the shaded understory. Species

comparisons are considered phylogenetically independent, because all species belong to different genera and families. Henceforth, species will be referred to by genus name only.

EXPERIMENTAL SETUP - This study was designed together with measurements for the evaluation of microclimatic effects of *A. cephalotes* nests described in Meyer et al. (in preparation) resulting in a comparable experimental setup. At 8 selected *A. cephalotes* colonies plots of seedlings were established in the center and at the edge of nests and thereafter every 6 m up to 24 m into the forest (4 plots in the forest; 6 plots in total per colony) in order to test for the biological importance of microclimatic alterations at nest sites. Subsequently, the four plots in the forest understory were pooled into one category (forest), since neither of the two principle explanatory variables in the study (light availability and cutting by *Atta*) differed between distance classes across the forest understory (Meyer et al. in preparation and personal observation). Consequently, results in this study will be analyzed comparing three different habitats (1) nest center (2) nest edge and (3) forest understory.

To evaluate potential effects of nest sites on forest regeneration we tested the response of tree seedlings to nest conditions. We used seedlings, because they represent the most vulnerable state during the lifetime of a tree and factors inducing mortality during this stage contribute to a large part to the composition of adult tree communities

Table 1: List of species used in the experiment including family, seed source, seed size, mode of planting, the number of originally planted seeds or transplanted seedlings and the total number of plants that established successfully and were included in the experiment for all species. Values for seed size from Lorenzi (2002).

Species	Family	Seed Source	Seed size (mm)	Mode of planting	Planted seedlings or seeds per plot	Total number of plants
<i>Copaifera langsdorffii</i>	Caesalpiniaceae	One mother tree; Serra Grande	18	seeds	7	30
<i>Licania tomentosa</i>	Chrysobalanaceae	At least 10 mother trees; Campus UFPE	50	seedlings	10	469
<i>Thyrsodium spruceanum</i>	Anacardiaceae	Several mother trees; Coimbra	15	seedlings	7	203
<i>Pouteria</i> sp.	Sapotaceae	One mother tree; Coimbra	12	seeds	8	126
<i>Protium heptaphyllum</i>	Burseraceae	One mother tree; Reserva Dois Irmãos, Recife	13	seedlings	4	130
<i>Virola gardneri</i>	Myristicaceae	Several mother trees; Serra Grande	22	seeds	8	31

(Swaine 1996). We transplanted seedlings and monitored leaf numbers and levels of standing leaf damage, as had been previously done to test for the effects of other ecological factors (e.g. Benitez-Malvido and Kossman-Ferraz 1999, Engelbrecht and Kursar 2003, Benitez-Malvido et al. 2005). Species were collected as seeds from natural populations and either planted directly (as seeds) into the transects in the forest or seedlings were pre-grown in pots and transplanted into the forest (see Table 1). *Copaifera*, *Pouteria* and *Virola* were planted as seeds in September 2005. Due to low germination and establishment rates only small numbers of seedlings were available to study seedling responses, we thus aimed to increase the explanatory power of the experiment. Seeds of *Licania*, *Thrysodium* and *Protium* were sown in April 2006 into individual pots situated in a secondary forest patch at the edge of Coimbra and established seedlings were transplanted in June 2006 into the existing plots at *Atta* colonies. Plot size was about 60 x 200 cm and plants were planted into a 20-cm grid within plots. Existing vegetation was never removed from plots and disturbances were minimized to preserve the structure of the forest understory. In September 2006 we conducted a baseline census during which all plants alive (with leaves or at least a vigorous stem) were recorded (total of 989 plants). During a six-month period of detailed observations (until March 2007), we conducted censuses at four-week intervals. In every census the current number of leaves per plant was recorded together with the number of new leaves since the last census. This enabled us to calculate the total number of leaves that the plant bore since the baseline census including leaves that might have been lost in the interim (cumulative leaf number). In case of species with compound leaves (*Copaifera* and *Protium*) leaflets instead of leaves were counted. When analyzing the number of leaves gained by a plant during the experiment we differentiated between 'net leaf gain', which is the existing difference between the number of leaves at the end and start of the experiment and 'gross leaf gain', which is the number of leaves a plant formed during the experiment irrespective of the fate of the leaves (difference between the cumulative leaf number at the end and the leaf number at the start of the

experiment). In addition to leaf numbers, we visually estimated the percentage of standing leaf damage per plant (percentage of leaf area lost from currently present leaves) attributed to (1) cutting by *Atta*, (2) herbivory by organisms other than *Atta*, and (3) infection by pathogens. In order to gather additional information on the fate of seedlings on a longer time scale, the census was repeated in March 2008, recording the status of plants (dead/alive), the current number of leaves and standing level of damage. It was not possible to determine the cumulative leaf number for the elapsed period of one year.

DATA ANALYSIS AND STATISTICS – Only plants for which at least one leaf was recorded during the censuses were included into the analysis of leaf growth. Pre-grown plants were homogeneous in size and randomly assigned to plots during transplantation, yet at the time of the baseline census most plants at nests showed strong cutting marks from leaf-cutting ants or were already completely defoliated. Therefore, it was not possible to calculate growth rates as recommended in the literature as the difference of the logarithmized leaf numbers (e.g. King 1991, Hoffmann and Poorter 2002) or less frequently used the difference in leaf numbers divided by the leaf number at the start of the observation period (South 1995) because of the undefined logarithm of or division by zero. Instead the absolute difference between the current number of leaves and the number of leaves at the baseline census (net leaf gain) is presented as a surrogate for overall growth rate. Leaf numbers as well as the percentage of standing damage deviated strongly from normal distributions due to a high number of zeros. Therefore, these parameters were analyzed non-parametrically using Kruskal-Wallis-tests with subsequent post-hoc comparisons following the procedure of Dunn described in Zar (1996). The algorithm for this comparisons was programmed in R (version 2.7.1, R Development Core Team 2007). Percentage of survival was compared between habitats and between species in χ^2 -tests and correlations between log transformed seed size (to achieve normality) and seedling survival were tested by Pearson correlations using the functions provided by R.

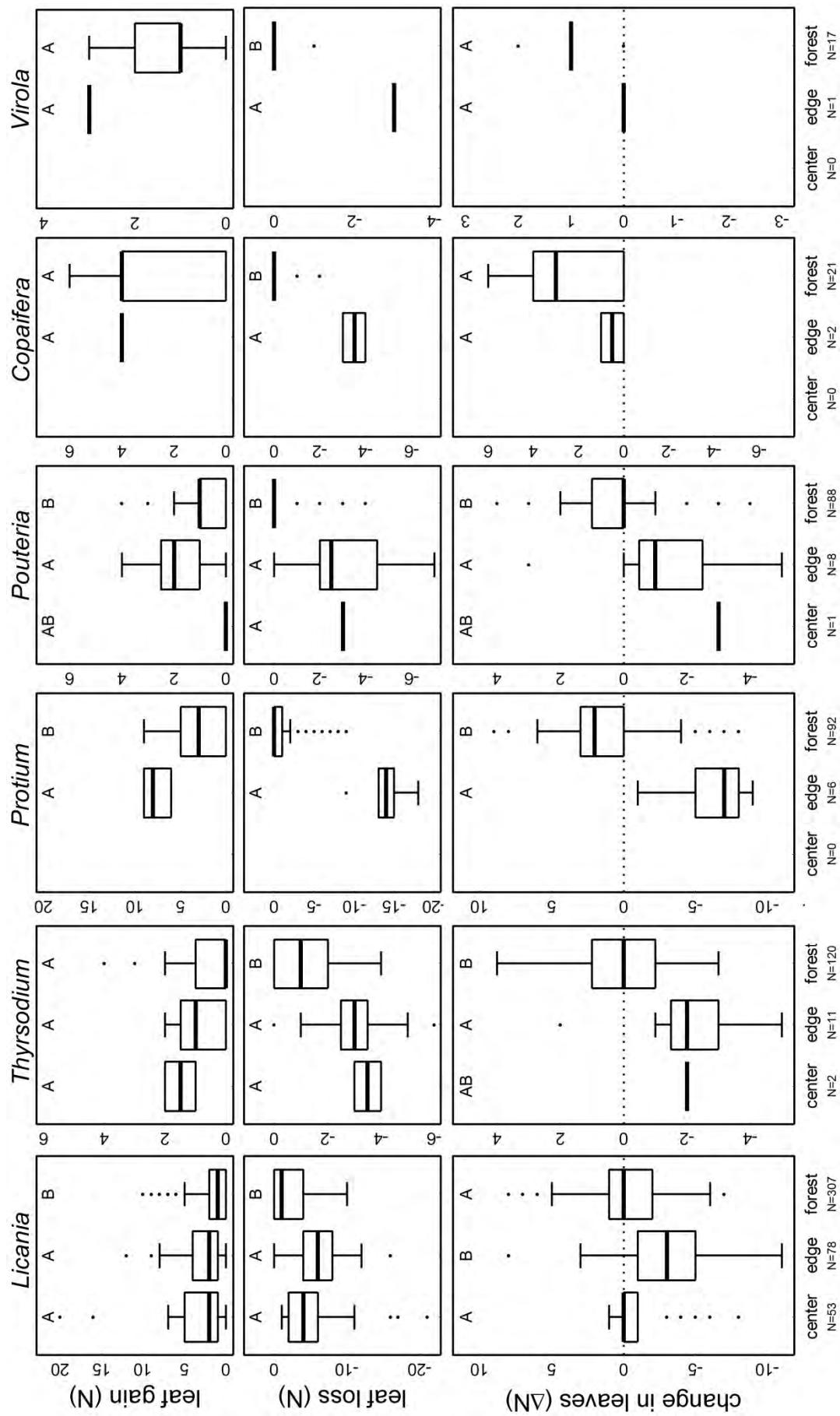


Figure 1: Net changes in leaf numbers (bottom panels) for seedlings of six different tree species over six months in three contrasting habitats: 'center' and 'edge' of *Atta cephalotes* nests and 'forest' understory. The upper panels show cumulative leaf gain, the middle panels show cumulative leaf loss. Bold lines represent the median shown with upper and lower 50% quartiles as box. Whiskers extend 1.5 times the interquartile range and outliers beyond this range are shown as individual dots. Different letters shown within a plot indicate significant differences at $p < 0.05$ in a Dunn's post-hoc comparison, following significant results in a Kruskal-Wallis-test. The number of plants within each category is shown below the graph.

RESULTS

During the six months of detailed observation seedlings of all six species consistently grew more new leaves at nests (centers and edges) than in the forest interior. This increase in gross leaf gain was significant for three of the tested species (Fig. 1, top panels). At the same time seedlings of all six species lost highly significantly more leaves at nests than in the forest (Fig. 1, middle panels). Thus, the growth of roughly twice as much new leaves at nests as compared to the forest did not translate into a higher net growth rate of whole plants. On the contrary, plants of four of the six species lost leaves during the six months observation period when situated on nests. For the other two species (*Copaifera* and *Virola*) net leaf gain (a surrogate for overall growth rate) was close to zero (Fig. 1, bottom panels). Net leaf gain in the shaded forest understory ranged from zero (*Licania* and *Thyrsodium*) to real growth with positive net leaf gain for *Copaifera* and *Virola* and intermediate levels little above zero for *Protium* and *Pouteria*. This pattern was affirmed by the net leaf gain over a period of 1.5 years (not shown). Over this period *Licania* and *Thyrsodium* still retained a net leaf gain of zero while all other species increased their leaf numbers in the forest understory, where survival was generally high ranging from about 40 to 95% depending on species.

Survival differed highly significantly between habitats ($\chi^2 = 124.5$, $df = 2$, $p < 0.001$) and was generally much lower on nests (Fig. 2). Furthermore, species differed in their survival rates ($\chi^2 = 47.2$, $df = 5$, $p < 0.001$) for example survived only 40% of the *Thyrsodium* plants in the forest in contrast to almost 100% of *Copaifera*. In the nest centers the only species surviving for 1.5 years, albeit at low levels, was *Licania*, which, in addition, survived to a similar degree at the nest edge as in the forest understory. For all other species survival at the nest edge was drastically reduced, and *Protium* and *Pouteria* seedlings did not survive at the nest edge at all (Fig. 2). A striking relationship emerged between seedling survival and seed size. While in the forest understory species survived to a similar degree and independently of seed size at the nest edge there was an almost perfect ($r = 0.95$) positive correlation between seed size and the percentage of survival (Fig. 3). In nest centers

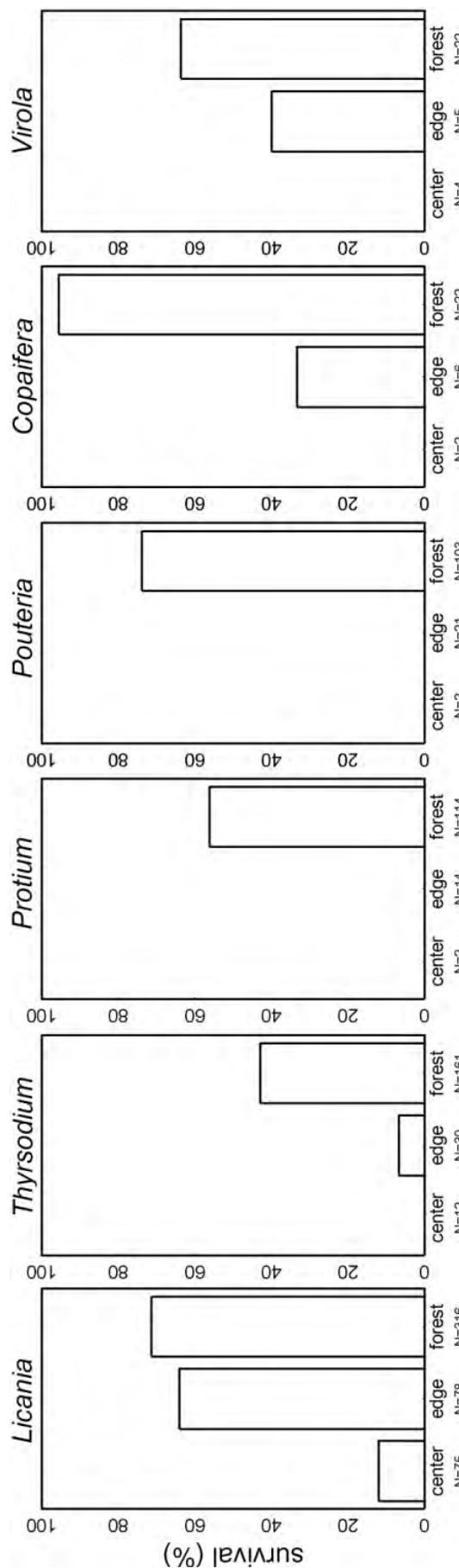


Figure 2: Percentage of surviving seedlings of six different tree species over 18 months in three contrasting habitats: 'center' and 'edge' of *Atta cephalotes* nests and 'forest' understory. The number of plants within each category is shown below the graph. Survival frequency differed highly significantly among habitats ($\chi^2 = 134.7$, $df = 2$, $p < 0.001$) and species ($\chi^2 = 47.8$, $df = 5$, $p < 0.001$).

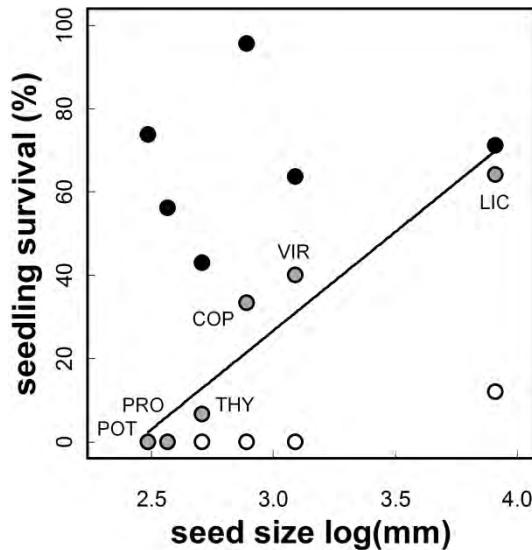


Figure 3: Correlation between the logarithm of seed size and seedling survival in three contrasting habitats. Survival is shown for nest centers (white), nest edges (gray), and the forest understory (black). The line represents a best fit for a highly significant correlation between seed size and seedling survival at the edge of nests ($r = 0.95$, $df = 4$, $p = 0.004$), while there was no significant relationship in the forest ($r = 0.19$, $df = 4$, $p = 0.722$). At nest centers only some seedlings of the largest-seeded species survived. Next to the data points representing the percentage of survival at the nest edge, the species names are given as abbreviations (COP: *Copaifera langsdorffii*, LIC: *Licania tomentosa*, THY: *Thyrsodium spruceanum*, POT: *Pouteria* sp., PRO: *Protium heptaphyllum*, VIR: *Virola gardneri*).

only seedlings of *Licania*, the largest-seeded species, survived.

Three different types of damage to seedlings were recorded during the six months of detailed observation. Seedlings in the center and at the edge of nests were heavily cut by the ants, while those in the forest were hardly cut at all (Fig. 4). Outside of nests, only 7% of plants showed any sign of damage by *Atta* cutting and levels of standing damage on the plants cut were much higher on nests than in the forest. In the forest understory away from nests seedlings were only heavily cut when they happened to be on top of newly established foraging trails (S. Meyer, pers. observation). Levels of herbivory damage from species other than *Atta* were generally very low. Loss of leaf area due to infection increased with distance to nest centers and reached intermediate levels between herbivory and *Atta* cutting (Fig. 4). These patterns emerged irrespectively of the plant species and are thus presented as an average over all six species tested.

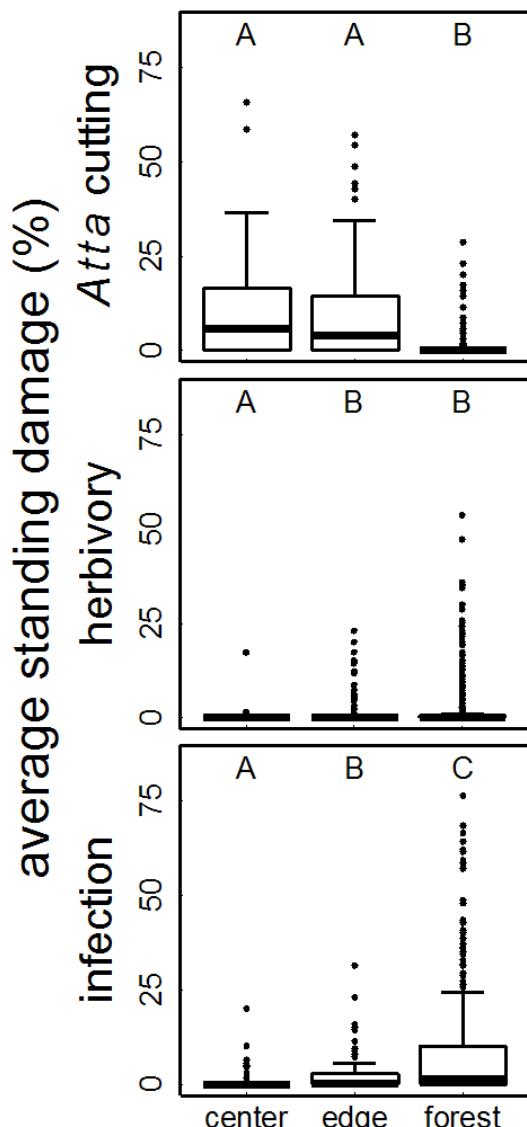


Figure 4: Mean standing leaf damage over six months in three contrasting habitats: ‘center’ and ‘edge’ of *Atta cephalotes* nests and ‘forest’ understory. Six tree species (see text for details) were pooled and leaf damage assigned to (A) cutting by *Atta*, (B) other herbivory, or (C) infection by pathogens. Bold lines represent the median shown with upper and lower 50% quartiles as box. Whiskers extend 1.5 times the interquartile range and outliers beyond this range are shown as individual dots. Different letters shown within a plot indicate significant differences at $p < 0.05$ in a Dunn’s post-hoc comparison, following significant results in a Kruskal-Wallis-test.

DISCUSSION

The present study demonstrates the potential of *Atta cephalotes* nests to differentially impact survival and growth of seedlings from selected shade tolerant tree species. Plants on nests showed higher gross leaf gain compared to

understory plants; yet net leaf gain was lower on nests due to a high leaf loss from *Atta*-cutting. Accordingly, survival was generally low on nests but correlated strongly with seed size of the species. While the two smallest-seeded species did not survive at all on nests, more than 60% of seedlings from the largest-seeded species *Licania* survived at nest edges and some 15% in nest centers. Therefore, survival of seedlings on nests of *A. cephalotes* was strongly species-specific (based on different abilities to tolerate cutting damage) demonstrating the potential of LCA nests to function as ecological filters on the scales of (1) individual nest sites and (2) the ecosystem in LCA-dominated forests as will be discussed below.

Two different mechanisms governed the effect of LCA nests on plant recruitment in our study (1) increased light availability (Meyer et al. in preparation) and (2) strong cutting pressure by the ants as a consequence of nest clearing activities on the nest surface. Since the net change in number of leaves was caused mainly by the number of leaves lost rather than those newly grown during the experiment, nest clearing by *Atta* comprised a stronger filter than light availability did. Levels of standing LCA damage presented are very conservative estimates since only the percentage of leaf area missing of leaves still attached to the plants could be recorded, yet all leaves of plants at nest centers and the vast majority of leaves of plants at the nest edges were cut completely by *Atta* irrespective of plant species (S. Meyer, personal observation). Thus, actual rates of leaf removal on nest sites were much higher (about 100%) and did not differ between species, although absolute numbers of removed leaves might differ due to differences in the number of leaves available. In order for a plant to survive on a LCA nest, the plant has to tolerate complete and in case of successful resprouting repeated defoliation. Survival on nests correlated strongly with the seed size of the six species tested in the experiment. Seed size is a good surrogate for the amount of reserves available to a seedling and its resulting ability to tolerate stress including herbivory (Dalling et al. 1997, Harms and Dalling 1997, Green and Juniper 2004, Moles and Westoby 2004). The strong correlation between the percentage of survival and seed size underlines the predominant importance of the nest clearing behavior of

Atta in determining which plants can establish on a nest.

The disturbance regime created by LCA nests differed from other disturbances and thus likely selects for a separate set of plant species as will be detailed in the following section: (1) Small scale disturbances in continuous forest canopies, like branch and leaf fall or canopy herbivory, are characterized by a very patchy and transient increase in light reaching the forest understory (Chazdon 1988, Wirth et al. 2001, Wirth et al. 2003). Consequently, the forest floor is characterised by a continuum of light levels (Clark et al. 1996, Montgomery and Chazdon 2001) and shade tolerant, slow growing and often large seeded tree species that are adapted to extended periods of deep shade in the understory have been shown to respond to this small or infrequent increase in light availability (Chazdon 1988, Montgomery and Chazdon 2002). (2) Larger disturbances, most frequently caused by tree falls, benefit a set of pioneer species (Van der Meer et al. 1998, Pearson et al. 2003), which have been characterized as light demanding, fast growing and small-seeded (Swaine and Whitmore 1988, Turner 2001). (3) On a yet larger scale, disturbances like forest edges, wind throws, and landslides also favor the establishment of pioneer plants – though a different subset with more desiccation tolerant species because these environments are characterized by a harsher microclimate as compared to tree-fall gaps (Murcia 1995, Lee et al. 2004). (4) LCA gaps comprise an intermediate-sized disturbance showing on average a relative irradiance of 6% with some colonies reaching twice as high values (Meyer et al. in preparation). This relative irradiance lies at the upper end of the range of values reported for small scale disturbances (Nicotra et al. 1999, Montgomery and Chazdon 2002) and at the lower end of reports for tree fall gaps (Chazdon and Fetcher 1984, Pearson et al. 2003). The additional light at nest sites compared to the understory is constantly available due to the nest clearing behavior of the ants, yet plants on nest also suffer from constant LCA cutting. In combination, large-seeded species that can use additional light and have resprouting abilities seem best suited to profit from LCA nests. This combination of functional types differs from those favored by other disturbances highlighting that LCA nests are unique environments.

Effects of LCA colonies are not restricted to the nest but can exceed into the surrounding forest. For example, cutting of seedlings in the foraging areas of LCA colonies and the subsequent induction of mortality had previously been described, yet the experimental exclusion of ants failed to show effects on seedling communities (Vasconcelos and Cherrett 1997). In our study cutting of seedlings outside of nests was extremely scarce and almost entirely restricted to plants situated on newly established foraging trails. This result is in line with the empirical knowledge that *Atta* is a K-strategist which favors to harvest of thick-trunked trees (Cherrett 1968, Wirth et al. 2003). Thus, seedling herbivory seems to be of little importance when ranking the affects of LCA on plant community composition. Defoliation of understory vegetation, especially seedlings and saplings, was restricted to the understory gap at nest sites supporting earlier observations of nest clearing behavior in *Atta* (Garrettson et al. 1998, Meyer et al. in preparation). In contrast, the increase of light availability penetrated up to 4 m from the nest edge into the forest (Meyer et al. in preparation), thus creating a potential regeneration niche in the near nest zone with higher light availability but without high cutting pressure. Unfortunately, our experimental set up did not include plants within a distance up to 4 m from the nest edge. A specifically designed experiment, transplanting seedlings into the near nest zone is necessary to test for the potential of plant regeneration in the vicinity of LCA nests.

A second possibility for plants to profit from increased light at nest sites without suffering cutting by the ants arises after the death of a colony. Dead LCA nest have been demonstrated to be favorable regeneration sites increasing number and diversity of plants (Garrettson et al. 1998). The functional types of plants regenerating on dead *A. cephalotes* nests, on the other hand, have been shown to be very similar to those within the plant community of the surrounding forest (Farji-Brener 2005). Somewhat similar results found Bieber (2006) who demonstrated that species composition of regenerating plants on dead nests in Coimbra forest was more similar to the surrounding forest than other dead nests. She interpreted this result as an indication of recruitment being limited by the arrival of seeds and stressed the point that the composition

of the plant community establishing on a dead nest seem to be strongly influenced by the seeds and plants present at the time of colony death (Bieber 2006). Consequently, this opens a time window for plant regeneration, since plants that already existed as suppressed seedlings on the nest at the time when the colony dies have the highest probability to successfully establish as a subcanopy or canopy tree on the dead nest. This time window is bigger for plants that can withstand *Atta* cutting for longer periods of time (big seeded species with the ability to use the additional light, as detailed above), because these plant species can persist on the nest surface or at its edge waiting for the colony to die and thereby increase their chance to colonize the vacant spot. Therefore, the effects of the function of active LCA nests as ecological filters might still be visible in the plant community on dead nests, thus explaining not only the lack of evidence for small seeded pioneers to benefit from living but also from dead LCA nests (Farji-Brener 2005, Corrêa et al. submitted).

The high cutting pressure on understory and canopy vegetation above LCA nests in concert with increased light availability on and around nests acts as an ecological filter modifying the competitive balance within the plant community. The question arising is: What role play *Atta* nests as ecological filters on an ecosystem scale? (Wirth et al. 2003, Wirth et al. 2008). In the interior of intact forest tracts, where LCA occur in very low densities (Jaffe and Vilela 1989, Wirth et al. 2007) activities of LCA are believed to increase resource heterogeneity and to help maintain or even increase biodiversity (Wirth et al. 2003). In anthropogenic landscapes it is less clear which effects are to be expected, especially in view of drastically increased colony densities at the edge of forest fragments (Wirth et al. 2007, Meyer et al. submitted). In the forest edge zone which is already a disturbed and more illuminated habitat in comparison the forest interior (Murcia 1995, Laurance et al. 2001), very high rates of LCA herbivory (Urbas et al. 2007, Meyer et al. submitted) and the maintenance of canopy gaps above nests allow for an increased light penetration in the foraging areas (Correa 2006) and at nest sites (Meyer et al. in preparation) respectively. The combination of this LCA activities seem to amplify edge-driven microclimatic alterations (Wirth et al. 2008), which

might, in turn, benefit the pioneer vegetation that already dominates the forest edge. Therefore, LCA seem to be among disturbance agents enabling self-replacing pioneer communities at the forest edge ultimately promoting the erosion of plant species from the forest edge furthering the loss of biodiversity (Tabarelli et al. in press). On the other hand this study indicates that LCA create a type of disturbance that differs from tree falls and forest edges in promoting large-seeded species that respond with increased growth to a moderate increase in light availability. Therefore, there is a possibility that ecological filtering by LCA helps to retain some biodiversity (within a reduced set of secondary and intermediate tree species dominating anthropogenically fragmented forests). While there is still considerable debate about the future of tropical landscapes and how much biodiversity will be retained in the long run (Brook et al. 2006, Wright and Muller-Landau 2006a, b, Tabarelli et al. in press) there can be no doubt that (1) understanding the processes shaping plant species composition and how anthropogenic disturbances modify this ecological filters will enable better predictions about the future development in fragmented forests and that (2) the multifarious activities of LCA are among the forces driving ecosystem functioning within this modern landscapes.

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PART V

Synthesis

8

Central results

An ever-increasing proportion of the global forested landscape is in close proximity to edges and edge effects have been shown to represent key forces affecting both organisms and ecological processes in post fragmentation forests and anthropogenic landscapes. Key conclusions from a review of 55 published articles that investigated whether forest edges affect herbivores and/or herbivory are that herbivores, especially generalists, profoundly benefit from forest edges, often due to (1) favourable microenvironmental conditions, (2) an edge-induced increase in food quantity/quality, and (3; less well documented) disrupted top-down regulation of herbivores. There is evidence and some causal explanations that edge-associated herbivores, via a range of direct and indirect impacts, may alter species interactions, delay successional processes at the edge, and amplify the often human-induced changes on forest biota (chapter 2).

A prominent example for important generalist herbivores that profit from forest fragmentation and consequential edge creation are leaf-cutting ants. In a survey of 56 ha of Brazilian Atlantic Forest (Coimbra) divided into 50-m distance zones paralleling the forest edge we encountered a total of 80 *Atta* colonies (43 *A. cephalotes* and 37 *A. sexdens*). *Atta* spp. occurred about 5 times

more frequently in the 50-m edge zone (4.94 ± 3.67 colonies/ha) than in the > 100 -m forest interior (1.01 ± 2.58 /ha). Densities of both species changed similarly with distance to the edge but the magnitude of the effect was species-specific. Colony density of *A. cephalotes* was low in the forest interior (0.33 ± 1.11 /ha, pooling all zones > 50 m into the forest) and sharply increased by a factor of about 8.5 towards the first 50 m (2.79 ± 3.3 /ha), while *A. sexdens* was more uniformly distributed. Colony densities in distance zones > 200 m (ranging from 0 ± 0 to 0.19 ± 0.51 /ha) were significantly different from those in the first 100 m of the forest (2.14 ± 3.32 and 1.79 ± 4.09 /ha), indicating that for *A. sexdens* the edge effect might reach up to 200 m into the forest (chapter 3).

This accumulation of *Atta* colonies at the physically stable edges of Coimbra forest persisted over a four year interval (2001 to 2005). Colony densities of *A. cephalotes* and *A. sexdens* showed no significant difference in densities between years. Species-specific relative growth rates ranged from 0.14 to -0.04 /yr, suggesting that populations were approximately at equilibrium. High rates of colony turnover (little less than 50% in 4 years) indicated an average colony life span of about 8 years – a life expectancy

considerably lower than previous estimates for *Atta* colonies. Stable hyper abundant populations of leaf-cutting ants accord with the constantly high availability of pioneer plants (their preferred food source) previously demonstrated at old stabilised forest edges in the region and are expected to persist in time as long as Neotropical forests are characterised by high edge to interior ratios (chapter 4).

Besides a changed species composition at the forest edge (proliferation of pioneer vegetation) which increases the availability of high quality foliage for leaf-cutting ants at the edge, changes in the quality of leaves of a given plant species have been hypothesised to occur due to physiological responses of the plants to the edge environment. Our results confirmed that drought stressed plants and plant parts are more attractive to leaf-cutting ants which may account for intraspecific and intraindividual herbivory patterns of leaf-cutting ants. Specifically, *Atta colombica* workers harvested more than twice the leaf area of stressed *Piper marginatum* plants than of vigorous control plants in bioassays. Drought stress induced an accumulation of proline and non-structural carbohydrates in the plant tissue by a factor of 3.5 and 2, respectively, accompanied by a decrease in the leaf water content of about 35%. Within individual plants, the attractiveness of a given leaf increased with its stress level and samples taken from preferred leaves within a plant contained more osmolytes than those representing the whole plant. The ants were shown to detect and prefer these osmolytes in bioassays conducted with leaf discs that had been experimentally enriched with proline and/or sucrose. We therefore propose a mechanism that links the preference of leaf-cutting ants to drought stressed plants via the osmolyte concentrations within leaves (chapter 5).

Leaf-cutting ants have been classically viewed as keystone species in pristine forests, where they occur in very low densities. In light of the drastic increase of leaf-cutting ant densities along the edge of Coimbra forest (see chapter 3 and 4 above), their potentially far reaching importance in anthropogenic landscapes immediately comes to mind. Not only effects from herbivory but also the assumed effects from ecosystem engineering could be amplified at

edges. To test this hypothesis, we quantified alterations in the forest structure of understory and canopy at nest sites of *A. cephalotes* in Coimbra forest and measured the resulting change in forest microclimate above the nest and along transects into the vicinity of nests. Nest sites were virtually free of understory vegetation with a high proportion of dead stems (up to 70%). Canopy openness above colonies increased by ca. 40% compared to control sites (5.3 at colony vs. 3.7% at control sites) and ants promoted the number of small, medium, and large gaps in the canopy. The more open forest structure at nest centres allowed about 6% of the outside irradiance to penetrate the canopy. Light levels declined exponentially along the gradient into the forest reaching a third of nest light levels in the forest understory (2%). Likewise, the maximum of soil temperatures and their daily amplitudes declined exponentially along transects from 25 to 23°C and 1.6 to 0.8°C, respectively. Soil moisture content increased significantly from nest centers into the forest, yet effect size was small and no differences were detected for air temperature and humidity along transects. Per colony nest effects did not differ between forest interior and forest edge but due to strongly elevated colony densities at edges we predict 6% of the forest area along edges to be microclimatically influenced by leaf-cutting ants, compared to only 0.6% in the forest interior. Microclimatic alterations lay within a range that can differentially impact plant regeneration (chapter 6). The expected impacts of nest clearing behavior and microclimatic alterations at nest sites on forest regeneration were directly tested by planting seedlings at nest centers, at the edge of the nest clearing, and into the forest understory. Nests of *A. cephalotes* differentially impacted survival and growth of seedlings. Plants on nests showed higher gross leaf gain compared to understory plants. Yet, the growth of roughly twice as much new leaves at nests as compared to plants in the forest did not translate into a higher net growth rate of whole plants. On the contrary, plants of four of the six species lost leaves during the six months observation period when situated on nests. The other two species showed a net leaf gain (surrogate for overall growth rate) close to zero. Survival differed

highly significantly between habitats and species and was generally high in the forest, yet low on nests where it correlated strongly with the seed size of the plant species tested. These results demonstrate conclusively, that the maintenance of nest gaps by leaf-cutting ants is an act of ecosystem engineering and that environmental modifications at nest sites translate into biotic effects. The disturbance regime created by leaf-cutting ants differed from other disturbances. It is shaped by two distinct mechanisms that cause the effect of nests on plant recruitment: (1)

increased light availability and (2) strong cutting pressure on the nest surface (chapter 7).

On an ecosystem scale leaf-cutting ants might have far-reaching impacts because of their large populations at forest edges. They might amplify the edge-driven microclimatic alterations via very high rates of herbivory and the maintenance of gaps above nests allowing for an increased light penetration. Ultimately, *Atta* might contribute to a disturbance regime that enables self-replacing pioneer communities at forest edges as detailed in the following general discussion.

9

General discussion

On the following pages I will discuss the results and conclusions of the preceding manuscripts in order to extract general findings about the interplay between effects of forest fragmentation on leaf-cutting ants and resulting impacts of leaf-cutting ants in fragmented forests. Specifically, I am going to address (1) how *Atta* responds to forest fragmentation and anthropogenic disturbance and (2) what mechanisms cause the increase in *Atta* densities, followed by a closer look at *Atta* as (3) a dominant herbivore and (4) an ecosystem engineer. Finally, I am going to (5) provide some conclusions about “winners and losers” in *Atta* dominated forests and (6) end with an outlook on possible further research on leaf-cutting ants in fragmented forests and the significance of the presented results in the context of biodiversity conservation and environmental management.

RESPONSES OF ATTA TO FOREST FRAGMENTATION AND ANTHROPOGENIC DISTURBANCE

Both *Atta* species occurring in Northeast Brazil (*A. cephalotes* and *A. sexdens*; Correa et al. 2005) increased in population size along the edges of Coimbra forest. Especially for *A. cephalotes* the resulting accumulation of colonies close to the forest edge was very pronounced (colonies were 8.5 times as frequent in the first 50 m of the forest as in the forest interior). This pattern has been documented, until now, only in Coimbra forest. Yet, there is evidence to believe that the accumulation of leaf-cutting ants at forest edges is a general phenomenon in fragmented Neotropical forests based on the following arguments. (1) The hyper-abundance of leaf-cutting ants along forest edges in Coimbra persisted over four years with relative constant populations sizes despite a high degree of colony turn-over. This is in

accordance with the constantly high availability of their preferred food source (pioneer plants) at forest edges (as detailed below). (2) The concentration of a high number of *Atta* colonies at the forest edge and very low colony densities in the forest interior were observed also in the central Amazon at the continuous forest control site of the Biological Dynamics of Forest Fragments Project (called “km 41”) close to Manaus (personal observation). (3) A similar observation stems from Barro Colorado Island (Panama) where, all 52 colonies of *A. colombica* encountered were concentrated within an area of approximately 100 ha adjacent to the laboratory clearing. At the same time the species was absent from the undisturbed forest in other parts of the island (Wirth et al. 2003). (4) Drastically high

densities of leaf-cutting ants were demonstrated for isolated forested islands within lake Guri, Venezuela (Rao 2000; Terborgh et al. 2001) that actually comprise a habitat under strong influence of various edge effects (White 2007). Finally, (5) *Atta* species have long been known to profit from other types of disturbance like e.g. agricultural land use and deforestation (Cherrett 1986; Fowler 1983; Fowler et al. 1986; Jaffe 1986; Jaffe and Vilela 1989; Jonkman 1979; Oliveira et al. 1998; Vasconcelos and Cherrett 1995). In the Neotropical agriculture leaf-cutting ants are prime pests causing an annual economic damage of estimated 1000 million US\$ (Cherrett 1986). Based on this evidence I conclude that high densities of leaf-cutting ants aggregated along forest edges are widespread throughout the Neotropics and are going to persist in time as long as these forests are characterised by high edge to interior ratios. In fact, the proliferation of leaf-cutting ants might be an inherent biological consequence of edge creation with potentially far reaching consequences for these forests (see sections on *Atta* as dominant herbivore and ecosystem engineer; Fig. 1).

Leaf-cutting ants do not only react to large scale disturbances like the ones described above. *Atta cephalotes*, for example, is specialized to live in forest gaps (Cherrett and Peregrine 1976; Jaffe and Vilela 1989). We have observed this affinity also in our study site in Coimbra forest, where colonies of *A. cephalotes* occur frequently close to canopy openings like forest dirt roads, rivers, or very steep slopes, all of which show altered plant species composition (personal observation). Forest gaps represent attractive nesting sites for leaf-cutting ants (Vasconcelos 1990) and the pioneer vegetation that occurs in these gaps forms important resource patches for leaf-cutting ants within the forest interior (Penaloza and Farji-Brener 2003). As a consequence, local, spatially limited anthropogenic disturbances like felling of individual trees for firewood or selective timber extraction might likewise cause *Atta* to become more frequent in forests because this practices also increase the frequency of gaps and pioneer vegetation within the forest (Boudreau and Lawes 2005; Howlett and Davidson 2003; Pereira et al. 2002). Thereby the forest will turn more attractive to leaf-cutting ants likely causing an increase in population size. Given the far-reaching impacts of leaf-cutting

ants (detailed below), such an increase has important implications for conservation. This demonstrates how human interference can profoundly alter the functioning of ecosystems even when management regimes (such as reduced-impact or selective logging) try to minimize human effects.

Timber production is of economical importance only in large tracts of forest, consequently human interests in severely fragmented landscapes is focused on the production of agricultural products in the matrix surrounding forest remnants. Along the edges of these juxtaposed habitats spillover effects can occur in the form that organisms restricted to one habitat frequently range into portions of the other habitat (Rand et al. 2006). Such a behavior has been observed for *A. cephalotes* in coffee plantations where forest edges function as refuges for colonies that forage within the plantations (Varón Devia 2006). Along the edges of Coimbra that separate the forest interior from the surrounding matrix of sugarcane fields we observed a contrasting pattern. Mostly small but very frequent *Atta* colonies (total number of 226 colonies along 16 km of forest edge) situated outside of the forest foraged mainly within the forest (87% of the observed cutting activities and 95% of the recorded foraging trails). Cutting of sugar cane was even less frequent and cutting marks on sugar cane were only observed in the close vicinity of 3% of the colonies (Dohm et al. 2006; appendix p. 151). In view of these results, the labor- and resource-intensive large scale poisoning of *Atta* colonies, which is a common practice within sugar cane plantations (M. Tabarelli pers. comm.) seems not as necessary. Strategies aimed at minimizing or abandoning the practice of *Atta* poisoning along forest edges could reduce the load of toxic chemicals in this landscape with obvious benefits for the environment and the rural human population. Clearly a more detailed investigation is necessary to justify the complete abandonment of *Atta* poisoning in the sugarcane plantations. Yet, the preliminary results are promising that an improvement of the coexistence of leaf-cutting ants and humans in these sugarcane dominated landscapes is possible and demonstrate how basic research about the functioning of fragmented ecosystems can yield applicable insights and help to meliorate the future for humans and environment alike.

MECHANISMS CAUSING THE INCREASE IN ATTA DENSITIES

Generally, there are three distinct complexes of factors that can account for the increase or decrease of animal populations at forest edges (see chapter 2): (1) changes resulting from edge-induced shifts in environmental conditions, (2) resource-based aspects, and (3) responses related to natural enemies. With respect to leaf-cutting ants, there is little evidence for a direct response of the ants to microclimatic conditions. Instead, the attractiveness of forest edges for leaf-cutting ants seems to be a direct consequence of their herbivorous life history. *Atta cephalotes* feeds preferentially on pioneer vegetation (Falcão 2004; Urbas et al. 2007). This type of vegetation is chemically less well defended (Coley 1980; Coley and Kursar 1996; Urbas 2004) and comprises, thus, a food source of higher quality for leaf-cutting ants (Farji-Brener 2001; Urbas 2004). The proliferation of pioneer vegetation at forest edges is among the best documented consequences of forest fragmentation (e.g. Laurance et al. 2006; Oliveira et al. 2004; Tabarelli et al. in press) and turns forest edges into very attractive resource patches for generalist herbivores like leaf-cutting ants (chapter 2) as visualized at the end of this chapter (Fig. 1 process numbered with (1) in the following written as "Fig. 1.1").

The quality of the foliage available to herbivores is not only determined by the species composition of the plant community. The attractiveness of leaves can also vary within a plant species or even within an individual plant. Forest edges represent high-resource environments for forest plants in terms of light and nutrient availability, which is likely to lead to a general increase of (leaf) productivity (Laurance et al. 2003) and may thus represent another component of edge-induced herbivore attraction (Major et al. 2003). Similar effects have been documented for treefall gaps and forest canopies, where highly productive vegetation and an increased leaf-turnover generate a persistent source of young, and soft leaves, which are frequently preferred by herbivores (Basset 1992; Richards and Coley 2007). Leaf-cutting ants are no exception and they prefer sun over shade and young over old leaves (Nichols-Orians 1991a; Nichols-Orians 1992). Generally speaking, the environmental

conditions under which leaves grow can change the acceptability to leaf-cutting ants (Nichols-Orians 1991b). We have demonstrated another previously overlooked environmental impact on the food-plant selection of leaf-cutting ants. They prefer drought stressed over vigorous plants due to the stress-induced increase in leaf nutrient content (chapter 5). These results from experiments in the laboratory have been replicated in the mean time with free living colonies of *A. cephalotes* at the edge of Coimbra forest. In feeding assays ten independent colonies showed a very clear preference for drought stressed plants of the species *Licania tomentosa* (Passlack et al. 2007; appendix p. 153). This preference for drought stressed plants or plant parts is of interest in the context of forest fragmentation because plants at forest edges are more prone to drought stress (Ferreira and Laurance 1997; Laurance and Williamson 2001; Laurance et al. 2001) and might therefore represent a food source of higher quality. Consequently, the preference for drought stressed plant material in combination with the higher susceptibility of plants along forest edges to experience drought stress can be among the contributing mechanisms by which populations of leaf-cutting ants benefit from forest fragmentation and edge creation.

In addition to the relaxed bottom-up regulation demonstrated above, top-down control of leaf-cutting ants at the forest edge seems to be disrupted. The principle predators (armadillos) and specialist parasitoids (phorid flies) of *Atta* in Serra Grande occur less frequently close to forest edges. The number of phorid flies attracted to nests and their attack rates were significantly lower in edge habitats, probably due to adverse environmental edge conditions for this moisture-loving flies (Almeida 2004; Almeida et al. in press). Likewise, Darrault (2005) found a marginally significant lower number of armadillo burrows in edge colonies ($33.0 \pm 6.91 / \text{col.}$) compared to interior colonies ($45.6 \pm 7.56 / \text{col.}$) during a year-round monitoring of ten *A. cephalotes* colonies. This is most likely caused by a higher risk of human hunting for armadillos along the edges of forest remnants (Fernandes 2003; Laurance 2000; Woodroffe and Ginsberg 1998).

ATTA CEPHALOTES AS A DOMINANT HERBIVORE

The quantification of the spatial distribution of colonies within Coimbra forest enabled us to calculate stand-level herbivory rates for *A. cephalotes*. These are based on herbivory estimates for individual colonies by Urbas et al. (2007) and our estimates of colony densities in the forest edge (first 50 m of the forest) and the forest interior. Individual colonies at the edge used a foraging area of 0.9 ha, in which they removed 14.3% of the available foliage. In contrast, in the forest interior colonies harvested 7.8% of the foliage from a foraging area of 2.3 ha (Urbas et al. 2007). Multiplying the herbivory rates with the size of foraging areas in ha and the number of colonies per ha resulted in stand level herbivory rates of ca. 36% at the forest edge – a damage six times as high as in the forest interior (6%). Both estimated stand-level herbivory rates are much higher than estimates of 2% for a population of *Atta colombica* in a late-successional forest (about 100 yr old) on Barro Colorado Island, Panama (Herz et al. 2007). While the colony density in Panama (about 0.5 /ha) was comparable to forest interior values of Coimbra, per colony leaf consumption was lower and the amount of leaves available almost 50% higher (leaf-area index of 6.35 compared to 4.5 in the interior of Coimbra). This may explain the difference in stand level herbivory rates. Along the edges of Coimbra the drastic increase in colony densities entails an exceptional increase in herbivory pressure (Fig. 1.2). The rate of 36% estimated for just one species of leaf-cutting ants (*A. cephalotes*) surpasses by far the overall rate of herbivory generally assumed for tropical forests (approx. 11%; Coley and Aide 1991) supporting the notion that the importance of leaf-cutting ants is elevated at forest edges (Chin and Yeston 2007).

At the edge, stand level herbivory rates exceed the rate of individual colonies because colony density was so high (2.8 col./ha) that annual foraging areas overlapped. Spatio-temporal exclusion strategies seem to enable neighboring colonies to share parts of their foraging areas as follows. (1) Colonies do not use the whole foraging area at a given time but shift the focus of utilization throughout the year (Urbas 2004) and (2) the form of foraging trails

and thus foraging areas is highly dendritic facilitating interlocking foraging patterns (Kost et al. 2005). As a consequence the forest edge as a whole is likely to be exploited by *A. cephalotes* without leaving unaffected areas in between. In addition, the hyper-abundance of leaf-cutting ants at the forest edge is stable in time; in contrast to other insect calamities which occur during outbreak situations (Folgarait et al. 1995; Kondoh 2003; Roland 1993; White 1974). Thus, these ants constitute a drastic and permanent herbivory pressure in these systems turning Neotropical forest edges into *Atta* dominated habitats.

Herbivory is considered to be among the key processes shaping life history traits and ecosystem function. Principally by consuming plant-tissues, herbivores are able to reduce plant survival and fitness (Crawley 1983; Marquis 1984), and limit plant population size (i.e. consumer regulation). The outstanding rates of foliage removal (up to $11 \text{ m}^2/\text{col./day}$; Wirth et al 1997) that often is concentrated on a few plants per day (Wirth et al. 2003) have a high potential to impact the fitness of exploited plants. This was confirmed in an extensive study on the effects of *Atta* herbivory on the reproductive investment of several species from four different plant families (Melastomataceae, Rubiaceae, Lacistemataceae, and Clusiaceae) in the Atlantic Forest by Barbosa (2009), who demonstrated a drastic reduction of flower and fruit set. Since leaf-cutting ants are highly selective (Howard and Wiemer 1986; Rockwood 1976) their impact is not spread evenly over the plant community. Therefore, the populations of some species will suffer a stronger reduction of reproductive success than others. In this way differential herbivory can influence the pace and trajectory of plant succession, via suppression of early or late successional species (Brown 1990; Zamora et al. 1999).

When herbivory is viewed in a broader sense (as the consumption of plant tissue) it also includes the predation of seeds and fruits. About a quarter of the yearly harvest of a leaf-cutting ant colony can be comprised from nongreen material (Wirth et al. 1997) and a substantial portion of this intake are fruits. Seed predation

by leaf-cutting ants involves seed removal and relocation and can contribute thereby to seed dispersal. In fact removal of fruits/seeds by leaf-cutting ants can affect local recruitment patterns of trees (reviewed in Dalling and Wirth 1998). During one year of monthly observations on ant-fruit interactions in Coimbra forest (Costa et al. 2007) leaf-cutting ants of the genus *Atta* were registered to collect a huge variety of fruits (either collecting pulp and leaving large seeds behind or collecting whole fruits when these were small enough to be moved). In fact, the consequent removal of seeds and fruits from foraging areas has been hypothesised to be the underlying mechanism causing the seedling community in foraging areas of *A. cephalotes* to be reduced in terms of abundance and diversity (Silva 2008).

Besides these direct effects of herbivory on the plant community, there are additional indirect effects. The removal of leaves or leaf tissue from plants is an alteration of the physical environment, which opens the canopy allowing a higher

proportion of light to penetrate into the forest. Therefore, herbivory can potentially cause similar effects as the creation of edges per se (Fig. 1.5). In forests, this indirect consequence of herbivory has been tested surprisingly little. Wirth et al. (2003) demonstrated patches of high light transmittance on the forest floor and increased sunfleck frequency in a tree canopy within the foraging territory of leaf-cutting ants (*A. colombica*) in the rainforest of Barro Colorado Island. An even stronger impact was demonstrated for colonies of *A. cephalotes* whose foraging areas showed 18% less vegetation cover and 40% more diffuse light compared to control sites in Coimbra forest (Correa 2006). Again, these effects of *A. cephalotes* are especially far-reaching at the forest edge, where colonies are concentrated. As a consequence, leaf-cutting ants may greatly affect the organization of plant communities and their patterns of species richness (Hulme 1996) by a combination of direct and indirect effects of herbivory (Fig. 1.3 and 1.6).

ATTA CEPHALOTES AS AN ECOSYSTEM ENGINEER

While leaf-cutting ants have previously been called ecosystem engineer based on the increase of light availability due to herbivory in the foraging areas (Wirth et al. 2003) this label was more often used in connection with the conspicuous nests constructed by *Atta* colonies (see for example Rico-Gray and Oliveira 2007). Yet, whether the construction and maintenance of nests comprises an act of ecosystem engineering had never been conclusively tested previous to the present thesis, despite the assumption that the large and long lived nests are disturbances in the forest that have the potential to influence plant regeneration (Farji-Brener and Illes 2000; Garretson et al. 1998; Haines 1975). Here, I demonstrated a whole suite of microclimatic effects resulting from the drastically altered forest structure at nest sites of *A. cephalotes* (chapter 6). While the nest is a local small-scale disturbance in the forest, microclimatic impacts were not restricted to the nest site itself but penetrated several meters into the surrounding forest increasing the impacted area per nest about

four fold. In addition to above ground impacts, many soil properties were strongly altered due to the excavation activities of the colony and the leaf-litter layer was heavily disturbed above nests (Passlack 2007). Similar to the microclimatic impacts, soil modifications were not restricted to nests themselves but continued several meters into the surrounding forest. Specifically, the amount of leaf-litter, of carbon and nitrogen content in the soil, the cation exchange capacity, and the soil conductibility increased with distance from the nest centers. This is very solid evidence that the sampled top soil (upper 10 cm) of leaf-cutting ant nests and to some degree of the surrounding forest is impoverished in nutrients (Passlack 2007). Lower nutrient levels at nest sites compared to forest soils is a result that contrasts with previous studies showing a higher nutrient availability in soil from *Atta* nests (Haines 1978; Moutinho et al. 2003; Sternberg et al. 2007; Verchot et al. 2003). Commonly leaf-cutting ants are assumed to concentrate nutrients in their nest due to the collection and digestion of

huge quantities of plant material (Haines 1978; Wirth et al. 2003). Two peculiarities of our study can explain this discrepancy. Leaf-cutting ant species differ in the habits where they dump their refuse (exhausted fungal substrate, dead fungus and ants), which contains the majority of nutrients leaving a colony (Farji-Brener and Medina 2000). While *A. cephalotes* and *A. sexdens* construct subterranean refuse chambers, *A. colombica* and, to less extent, *A. leavigata* dump refuse onto above ground refuse piles, which are readily available for the exploitation by plants (Farji-Brener and Silva 1996; Haines 1975; Haines 1978; Wirth et al. 2003). Such refuse piles account for the high nutrient concentrations measured in studies of *A. colombica*. Also the soil from nests of *Atta* species with internal refuse chambers shows an increase in nutrient concentrations when samples measured were taken from deep soil portions of the nest (Moutinho et al. 2003; Verchot et al. 2003). Yet, seedling roots in tropical rain forests are most common in the upper soil layers and thus far away from nutrient-rich refuse chambers. Instead they are located in the top soil, which on nests is comprised from mineral soil that the ants have excavated during the nest construction. This top soil layer is impoverished in nutrients compared to the surrounding forest as we have demonstrated by sampling the upper most 10 cm of the soil, which are of relevance for seedling and sapling establishment (Passlack 2007).

In summary, nest sites of *Atta cephalotes* are in many ways different from the surrounding forest above and below the ground. Many of the documented effects can directly influence germination and growth of plant, thus modify forest regeneration. Of particular importance for the establishment of seedlings are light (e.g. Agyeeman et al. 1999; King 1991; Kyereh et al. 1999; and reviewed in Turner 2001), temperature (Vazquez-Yanes and Orozco-Segovia 1982), leaf litter cover (Metcalfe and Turner 1998; Vazquez-Yanes et al. 1990), and soil nutrients (Lewis and Tanner 2000; Turner et al. 1993). Considering that all these factors of importance for the establishment of seedlings are modified at nests by the activities of leaf-cutting ants there can be little doubt that their nests do impact the composition of the plant community. In fact, we have shown differential survival for seedlings of six different tree species on nests of *A. cephalotes* (chapter 7)

and the plant community on *A. cephalotes* nests in Coimbra forest has been demonstrated to be significantly different from the community in the remaining parts of the forest (Corrêa et al. submitted). Based on this evidence, I conclude that the creation and maintenance of large nests by leaf-cutting ants is a true act of ecosystem engineering with far-reaching consequences for the plant community and the ecosystem as a whole.

COMMONALITIES AND CONTRASTS WITH OTHER ECOSYSTEM ENGINEERS – Leaf-cutting ants share with other ecosystem engineers per definition the habit of altering the physical environment. In case of leaf-cutting ant nests, the principle change caused is an increase in light interception. Nests located in the continuous forest interior increase the availability of a resource, which is limiting for plant growth (Wirth et al. 2003). In a similar way limiting resources are increased in African Savannas by termites (soil nutrients; Dangerfield et al. 1998) or in Canadian boreal wetlands by beaver activity (area of open water; Hood and Bayley 2008). Based on such observations of ecosystem engineering aiding other organisms in the ecosystem the idea developed that the influence of ecosystem engineers on abiotic variables and resulting effects on biotic communities may facilitate ecological restoration, help to overcome environmental limitations and counterbalance anthropogenic influences (Hastings et al. 2007). Ecosystem engineering by leaf-cutting ants at the forest edge drastically differs from this idea. While at the forest edge the ants' activities increase the availability of light as they do in the forest interior, forest edges are already more illuminated environments compared to the forest interior. In addition, leaf-cutting ants are much more abundant at the edge and, in consequence, impact larger parts of the forested area (about 6% of the forest at the edge is directly modified by nests of *Atta cephalotes*). The removal of large quantities of foliage further increases light availability. Colony densities at the forest edge were so high that foraging territories overlapped and the forest edge as a whole is impacted by the modifications evoked by the ants. In sum, ecosystem engineering by leaf-cutting ants at the forest edge increases light interception and thereby is synergistic with the effects of anthro-

pogenic edge creation, instead of being antagonistic to them (Fig. 1).

Leaf-cutting ants differ in a second respect from other ecosystem engineers. It is generally assumed, that ecosystem engineers modify their environment in a patch-like manner and that patches of altered habitat become unattractive for the engineer, who in turn moves on. Thereby a mosaic of pristine, altered and regenerating habitat is created enhancing regional habitat diversity (Jones et al. 1997; Wright et al. 2004). In the case of leaf-cutting ants microclimatic impacts generally favor the establishment of light demanding plant species, which, at the same

time, are the preferred food source for the ants. Thus, their activities turn forest edges even more attractive for themselves creating a self-enhancing cycle (Fig. 1). Therefore, this thesis presents an example of an ecosystem engineer that profits from initial human disturbances and contributes to the creation and maintenance of a new disturbance regime and a resulting altered forest that apparently will continue to persist in the future (chapter 4). Within these new forests several other organisms can profit or suffer from the alterations caused by leaf-cutting ants either directly or through cascading effects in form of altered ecosystem functioning.

WINNERS AND LOSERS IN ATTA DOMINATED FORESTS

The principle element of forests is trees. While adult trees are extremely robust and enduring, germinating seeds and establishing seedlings are very vulnerable (Clark and Clark 1991; Lieberman 1996). Yet, factors inducing mortality during this early stage in the lifetime of a tree contribute to a large part to the composition of the adult tree community (Swaine 1996). Nests of the leaf-cutting ant *A. cephalotes* differentially impacted the survival of seedlings from six tree species (chapter 7). Which tree species ultimately benefit from nests depends on a combination of at least three factors. On the one hand, increased light availability favors fast growing, light demanding species. Yet, resulting light levels were far below the amount of light necessary for the establishment of typical short lived pioneer trees. For example *Cecropia obtusifolia*, might need as much as 40% full sun light (Kobe 1999), which is four times as much as the measured maximum of just over 10% measured at a nest of *A. cephalotes* (chapter 6). Therefore, secondary species (often called long-lived or large-seeded pioneers) or even shade tolerant species are more likely to profit from the increased light levels on and around nests. On the other hand, plants on the nest mound suffer from the nest clearing behavior of the ants, running a high risk of being completely defoliated. As a consequence, species that store reserves and have a good resprouting ability are favored. This filter effect of nests has been demonstrated by a very

strong correlation of seed size (a surrogate for stored nutrients and the ability to tolerate stress; Green and Juniper 2004) and survival at the edge of *Atta* nests (chapter 7). No such relationship existed in the forest understory, which demonstrates that nest sites select for other functional attributes in seedlings than the surrounding forest. In nest centers the marked clearing behavior of leaf-cutting ants strongly increased seedling mortality and only the largest-seeded species survived. In fact, all seedlings were completely defoliated within a few months from planting, irrespectively of the plant species. This agrees with observations that leaf-fragments cut during nest clearing are seldom used as fungus substrate and are often left underneath the cut plant or carried onto refuse piles. Thus, nest clearing is not foraging and mechanisms governing food plant selection are not functioning during nest clearing. Consequently, strategies of plant defense against herbivores (secondary chemicals, leaf toughness, and others; Coley and Barone 1996) are not effective on the nest surface. Therefore well-defended plant species do not have an advantage on nests. On the contrary, well-defended plant species are characterized by slow growth, long leaf-lifespan and high costs for leaf construction (Coley 1986; Coley 1988; Stamp 2003). Consequently, the loss of leaves has a stronger negative impact on the energy budget of a well-defended plant compared to faster growing plants. Pioneer plants and

secondary species with high growth rates are better adapted to tolerate loss of leaf tissue because of generally lower investments into leaves and higher leaf-turnover rates (Coley et al. 1985). For example, two pioneer species investigated by Khan and Tripathi (1991) showed higher growth rates and, consequently, a higher increase in biomass despite higher herbivory rates compared with two shade tolerant species. The third effect of leaf-cutting ant nests as a filter that selects plant species is associated with the excavated mineral soil, which forms the nest mound and is impoverished in nutrients. Nutrient poor soil also favors large-seeded species that are able to establish bigger seedlings with well-developed root systems (Kohyama and Grubb 1994). Species with larger seedlings or species with tap roots (see for example Yamada et al. 2005) have a better chance to reach into the deeper nutrient rich parts of the nest. Yet, such seedlings run the risk of their roots being damaged by the ants during nest construction and maintenance. Such a loss might be tolerable for a big tree with roots growing laterally into the deep refuse chambers to acquire nutrients, yet it might be fatal for a seedling.

In combination the increased light availability, high cutting pressure and nutrient-poor soil at nest sites select for species that profit from additional light have high growth rates, low leaf construction costs, and large seeds. The larger amount of reserves stored in such seeds improve the plant's chance to resprout after defoliation by the ants and provide resources for the establishment of a suitable root system. Any seedling on an active nest will be heavily cut and only after the death of the colony plants are able to benefit from the improved growth conditions at nest sites. The functional traits listed above (especially nutrient storage and resprouting ability) enable a seedling to persist longer on an active nest and increase its chance to fill the vacant space after the death of the colony.

CASCADING IMPACTS – Leaf-cutting ants are integrated into a web of trophic interactions in which they not only act as herbivores but also as prey for organisms on higher trophic levels. The hyper-abundance of leaf-cutting ants at the forest edge can potentially attract predators and parasi-

toids (Matlack and Litvaitis 1999), in a similar way, as high densities of palatable pioneer plants offer more resources to these herbivores. Such an effect is in accordance with current ecological theory predicting that, when primary productivity is high, herbivore populations increase to levels that can support substantial predator populations (Fretwell 1977; Oksanen et al. 1981). Such cascading effects are now widely recognized (Terborgh et al. 2001) and have been documented for other herbivores (chapter 2). Yet, the principle predators and parasites for leaf-cutting ants so far studied in Coimbra forest seem not to be able to profit from the additional pray availability at the edge. In case of the parasitic phorid flies, less frequent attacks at the forest edge seems to be caused by adverse environmental conditions for this moisture-loving flies (Almeida 2004; Almeida et al. in press). Likewise, Darrault (2005) found evidence for lower armadillo activity at the forest edge. Armadillos are still hunted within Coimbra forest (Fernandes 2003). Since hunting pressure is generally higher close to forest margins (Laurance 2000; Woodroffe and Ginsberg 1998), increased pray densities at the edge may create an ecological trap (Ries and Fagan 2003). That is amardillos attracted to forest edges by the abundance of leaf-cutting ant colonies have an increased risk of being killed.

Leaf-cutting ants and their multifarious effects form a feedback-loop causing a self-enhancing circle of disturbance (Fig. 1), which contributes to the observed retrogression at the forest edges (Santos et al. 2008; Tabarelli et al. in press). Within this circle, the pioneer vegetation from which the ants themselves have profited in the first place ultimately benefits from the effects of leaf-cutting ants caused by herbivory and ecosystem engineering. Thereby the disturbance regime at the forest edge is strengthened which helps to sustain large populations of pioneer plants and leaf-cutting ants. Apparently, the forest has been disturbed to such a degree by human activities that it has been transformed into a new, alternate state. This state appears to be stable or at least quasi stable indicating that the ecosystem could exist in this form for a long time (Hobbs and Norton 2004). The existence of such a state is on one hand a reason for hope since the ecosystem

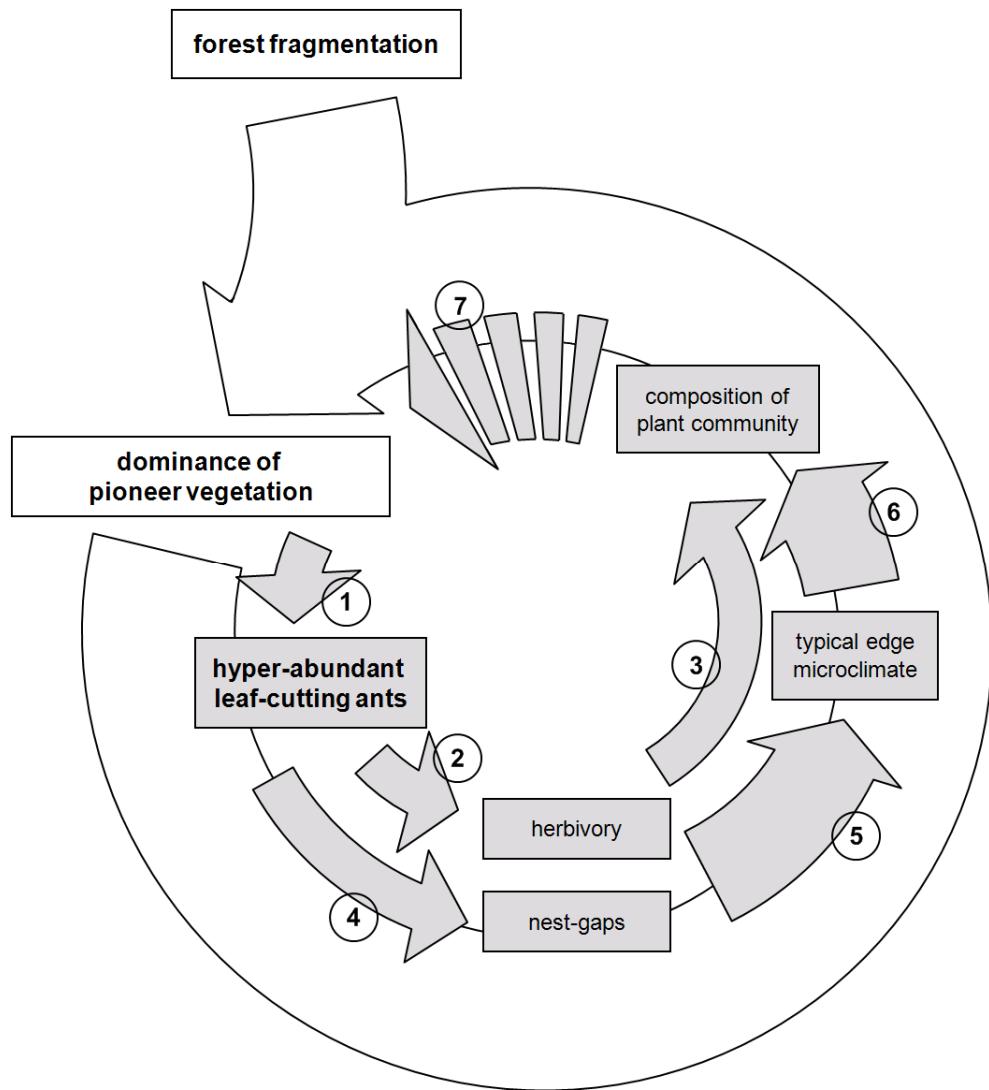


Figure 1: Schematic representation of the self-replacement of pioneer vegetation at the forest edge driven by continuous disturbances following fragmentation (in white). Processes by which hyper abundant leaf-cutting ants at the forest edge contribute to this disturbance regime are presented in a shade of light grey. Ultimately, their activities can benefit the pioneer vegetation from which *Atta* itself has profited in the first place. This positive feedback-loop strengthens the disturbance regime at the forest edge sustaining large populations of pioneer plants and leaf-cutting ants. A tentative approximation of the integration level of processes is indicated by the width of arrows. The broken arrow represents a link that is presently supported only by inconclusive evidence. Numbers identify the individual processes comprising the feedback-loop, which is described in the following.

The pioneer vegetation dominating the forest edge represents a very attractive food source for leaf-cutting ants and the high availability of this resource constitutes the principal factor causing the hyper-abundance of leaf-cutting ants along forest edges (1). These large *Atta* populations generate a tremendous herbivory pressure on forest edges (2) and directly influence the composition of the plant community via selective herbivory (3). In addition, *Atta* colonies build big, long-lived nests and maintain gaps above these nests, opening up the canopy (4). Likewise, the removal of large quantities of foliage from the foraging areas increases canopy openness. Therefore, a higher proportion of light can penetrate the forest canopy due to the environmental modifications induced by the ants (ecosystem engineering by nest gap creation and foliage removal; 5). This additional light, together with the resulting microclimatic alterations, generates conditions typical for forest edges (5). The resulting environmental conditions (a more illuminated and dryer environment than the forest interior) represent an ecological filter acting on the plant community at the forest edge (6). There are some indications that within the plant community more early successional species are favored (7). These species are more likely to profit from the increased light availability and to be able to tolerate loss of leaves due to *Atta* cutting. While additional investigations are necessary to provide conclusive support for the latter link, the potential for a positive feed-back loop (in which leaf cutting ants profit from pioneer vegetation which in turn profits from the ants' activities) is apparent. For more details please refer to the text.

seems to be resilient enough to prevent its complete collapse, which could be caused by retreating forest edges (Gascon et al. 2000). On the other hand, the current forest edges are comprised of a largely impoverished subset of tree species (Oliveira et al. 2004) and functional types (Santos et al. 2008). In addition, there might be an ongoing slow loss of long lived tree species that cannot successfully reproduce in the new forest configuration (post-fragmentation retrogressive succession leading to early successional stages; Tabarelli et al. in press). Together with the trees that have already disappeared or will disappear in the future from forest edges and small fragments also associated animal species are lost (e.g. specialized pollinators, frugivorous birds and mammals; Bierregaard Jr. et al. 2001). As a result the ecosystem as a whole is impoverished and an amelioration of the situation at the forest edges is necessary to improve the chances for a long-term conservation of biodiversity. Yet, there must be considerable doubt that forests as heavily fragmented as the Atlantic forest of Northeast Brazil can naturally return to their original configuration. These fragmented forests have reached a new self-replacing secondary state that is stabilized, among other processes, by hyper-abundant leaf-cutting ants (Fig.1). In order to break this cycle of self-enhancing disturbance additional human activities in form of thoughtful management will be necessary to enable forest regeneration along the edges of the threatened forest remnants. Several possible management options exist to break the circle and meliorate conditions for succession, some of which are

specifically aimed at reducing the impact of leaf-cutting ants on the forest edges. The direct way of reducing leaf-cutting ant pressure is to reduce colony densities. In its most radical form this would signify to poison colonies as it is done within agricultural plantations. In view of the drastic environmental toxicity of commercial leaf-cutting ant baits (Nagamoto et al. 2007), this is, however, a dubious recommendation for biodiversity management. Instead, densities of leaf-cutting ants might be controlled by a bottom-up approach, i.e. reducing the availability of their preferred food plants. The dominance of pioneers along forest edges could be diminished, for example, by enrichment planting with shade tolerant seedlings (many of which are absent from edges because of dispersal limitations and not environmental constraints; Martinez-Garza and Howe 2003). There is convincing evidence that such a strategy can reduce colony densities of leaf-cutting ants. In parts of regenerating forest within Serra Grande colony densities of leaf-cutting ants declined sharply after about 30 to 40 years of regeneration at about the same time when the abundance of pioneer vegetation were dropping (Silva et al. submitted). A second option that should be best used in combination with enrichment planting is to increase the population of predators of leaf-cutting ants by consequently protecting armadillos from human hunting. These efforts will be most successful in combination with a general management and protection plan for the remaining forest fragments in Serra Grande which, naturally, should focus on the ultimate large fragment – Coimbra.

OUTLOOK

Research on leaf-cutting ants in the remnants of the hyper-fragmented Atlantic Forest of Northeast Brazil has come a long way. Starting out with describing the increase of leaf-cutting ant populations along the edges of forest fragments (chapters 3 and 4), the focus moved on to the underlying mechanisms for this increase (doctorate thesis of P. Urbas and chapter 5 of the present thesis), and ended by quantifying the nest-associated impacts on forest structure, microclimate and regeneration (chapter 6 and 7). Together with other pathways by which leaf-

cutting ants can influence the forest, prominently those caused by their exceptional herbivory rates at forest edges, nest impacts cause a whole suite of organisms to be either winners or losers in *Atta* dominated forest. The final step remaining is to put the proposed effects of *Atta* on forest edges to a test. This can be done either (1) theoretically by incorporating both colony densities and per colony effects into models of forest dynamics (e.g. FORMIND; Köhler 2000) or, preferentially, (2) experimentally by excluding leaf-cutting ants from plots at forest edges

(repeatedly poisoning the colonies) and comparing forest structure, regeneration and productivity over several years. We can already conclude, based on the persisting hyper-abundance of leaf-cutting ants at old edges of Coimbra forest and the multifarious impacts documented, that the ecological importance of leaf-cutting ants in anthropogenic landscapes drastically exceeds that in pristine forests where they are commonly believed to be keystone species, despite very low colony densities.

With the different scale of leaf-cutting ant impacts in man-made landscapes comes also an altered net result. Leaf-cutting ants are believed to increase environmental heterogeneity and consequently biodiversity in pristine forests (Wirth et al. 2003). In fragmented forests, on the other hand, their activities contribute to a distur-

bance regime that causes a post-fragmentation retrogressive succession (Fig. 1). Apparently these forests have been disturbed to such an extent by human activities that they have passed over a threshold preventing them from returning to their original configuration. Thereby, fragmented forests have reached a new self-replacing secondary state. In order to break this cycle of self-enhancing disturbance additional human interference in form of thoughtful management will be necessary to facilitate forest regeneration along the edges of threatened forest remnants. Enabling regeneration and restoring ecosystem functioning at forest edges would ameliorate the situation of the forest as a whole and increase the chances for a long-term retention of biodiversity in anthropogenically dominated, fragmented landscapes.

10

Summary

Fragmentation of habitats, especially of tropical rainforests, ranks globally among the most pervasive man-made disturbances of ecosystems. There is growing evidence for long-term effects of forest fragmentation and the accompanying creation of artificial edges on ecosystem functioning and forest structure, which are altered in a way that generally transforms these forests into early successional systems. Edge-induced disruption of species interactions can be among the driving mechanisms governing this transformation. These species interactions can be direct (trophic interactions, competition, etc.) or indirect (modification of the resource availability for other organisms). Such indirect interactions are called ecosystem engineering. Leaf-cutting ants of the genus *Atta* are dominant herbivores and keystone-species in the Neotropics and have been called ecosystem engineers. In contrast to other prominent ecosystem engineers that have been substantially decimated by human activities some species of leaf-cutting ants profit from anthropogenic landscape alterations. Thus, leaf-cutting ants are a highly suitable model to investigate the potentially cascading effects caused by herbivores and ecosystem engineers in modern anthropogenic landscapes following fragmentation. The present thesis aims to describe this interplay between consequences of forest fragmentation for leaf-cutting ants and resulting impacts of leaf-cutting ants in fragmented forests.

The cumulative thesis starts out with a review of 55 published articles demonstrating that herbivores, especially generalists, profoundly benefit from forest edges, often due to (1) favourable microenvironmental conditions, (2) an edge-induced increase in food quantity/quality, and (3; less well documented) disrupted top-down regulation of herbivores (Wirth, Meyer et al. 2008; *Progress in Botany* 69:423-448). Field investigations in the heavily fragmented Atlantic Forest of Northeast Brazil (Coimbra forest) were subsequently carried out to evaluate patterns and hypotheses emerging from this review using leaf-cutting ants of the genus *Atta* as a model system. Colony densities of both *Atta* species occurring in the area changed similarly with distance to the edge but the magnitude of the effect was species-specific. Colony density of *A. cephalotes* was low in the forest interior (0.33 ± 1.11 /ha, pooling all zones >50 m into the forest) and sharply increased by a factor of about 8.5 towards the first 50 m (2.79 ± 3.3 /ha), while *A. sexdens* was more uniformly distributed (Wirth, Meyer et al. 2007; *Journal of Tropical Ecology* 23:501-505). The accumulation of *Atta* colonies persisted at physically stable forest edges over a four-year interval with no significant difference in densities between years despite high rates of colony turn-

over (little less than 50% in 4 years). Stable hyper-abundant populations of leaf-cutting ants accord with the constantly high availability of pioneer plants (their preferred food source) as previously demonstrated at old stabilised forest edges in the region (Meyer et al. submitted; Biotropica). In addition, plants at the forest edge might be more attractive to leaf-cutting ants because of their physiological responses to the edge environment. In bioassays with laboratory colonies I demonstrated that drought-stressed plants are more attractive to leaf-cutting ants because of an increase in leaf nutrient content induced by osmoregulation (Meyer et al. 2006; Functional Ecology 20:973-981). Since plants along forest edges are more prone to experience drought stress, this mechanism might contribute to the high resource availability for leaf-cutting ants at forest edges.

In light of the hyper-abundance of leaf-cutting ants within the forest edge zone (first 50 m), their potentially far-reaching ecological importance in anthropogenic landscapes is apparent. Based on previous colony-level estimates, we extrapolated that herbivory by *A. cephalotes* removes 36% of the available foliage at forest edges (compared to 6% in the forest interior). In addition, *A. cephalotes* acted as ecosystem engineers constructing large nests (on average 55 m²: 95%-CI: 22-136) that drastically altered forest structure. The ants opened gaps in the canopy and forest understory at nest sites, which allowed three times as much light to reach the nest surface as compared to the forest understory. This was accompanied by an increase in soil temperatures and a reduction in water availability. Modifications of microclimate and forest structure greatly surpassed previously published estimates. Since higher light levels were detectable up to about 4 m away from the nest edge, an area roughly four times as big as the actual nest (about 200 and 50 m², respectively) was impacted by every colony, amounting to roughly 6% of the total area at the forest edge (Meyer et al. in preparation; Ecology). The hypothesized impacts of high cutting pressure and microclimatic alterations at nest sites on forest regeneration were directly tested using transplanted seedlings of six species of forest trees. Nests of *A. cephalotes* differentially impacted survival and growth of seedlings. Survival differed highly significantly between habitats and species and was generally high in the forest, yet low on nests where it correlated strongly with seed size of the species. These results indicate that the disturbance regime created by leaf-cutting ants differs from other disturbances, since nest conditions select for plant species that profit from additional light, yet are large-seeded and have resprouting abilities, which are best suited to tolerate repeated defoliation on a nest (Meyer et al. in preparation; Journal of Tropical Ecology).

On an ecosystem scale leaf-cutting ants might amplify edge-driven microclimatic alterations by very high rates of herbivory and the maintenance of canopy gaps above frequent nests. By allowing for an increased light penetration *Atta* may, ultimately, contribute to a dominating, self-replacing pioneer communities at forest edges, possibly creating a positive feed-back loop. Based on the persisting hyper-abundance of leaf-cutting ants at old edges of Coimbra forest and the multifarious impacts documented, we conclude that the ecological importance of leaf-cutting ants in pristine forests, where they are commonly believed to be keystone species despite very low colony densities, is greatly surpassed in anthropogenic landscapes. In fragmented forests, *Atta* has been identified as an essential component of a disturbance regime that causes a post-fragmentation retrogressive succession. Apparently, these forests have reached a new self-replacing secondary state. I suggest additional human interference in form of thoughtful management in order to break this cycle of self-enhancing disturbance and to enable forest regeneration along the edges of threatened forest remnants. Thereby the situation of the forest as a whole can be ameliorated and the chances for a long-term retention of biodiversity in these landscapes increased.

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Appendix

Page 151: Poster “Living outside but cutting within: high colony densities of leaf-cutting ants in front of the forest edge” presented at the 19th annual GTÖ meeting (2006), Kaiserslautern, Germany by Dohm C, Meyer ST, Leal IR, Wirth R.

Page 153: Poster “Cutting the drought stressed: Food plant preference of *Atta cephalotes*” presented at the 20th annual GTÖ meeting (2007), Bonn, Germany by Passlack M, Meyer ST, Leal IR, Wirth R.

Living Outside but Cutting Within

High Colony Densities of Leaf-Cutting Ants in Front of the Forest Edge



Christoph Dohm¹, Sebastian T. Meyer^{1,2}, Inara R. Leal², Rainer Wirth¹

Densities of leaf-cutting ants

Leaf-Cutting Ants (LCA) are dominant herbivores in neotropical rain forests. Since herbivory pressure increases with the number of colonies, estimates of colony-densities can be used to evaluate LCA impact on the forest structure. Until now colonies outside the forest have been widely ignored.



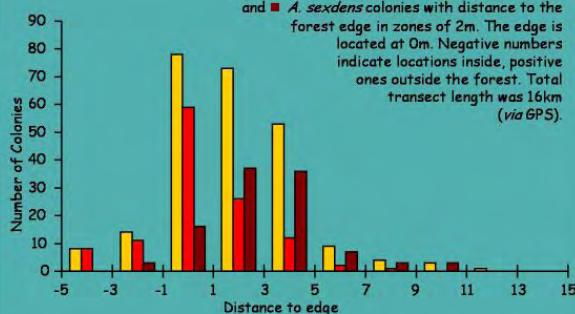
Fig. 1 Soldiers of the LCA-species (A) *Atta cephalotes* and (B) *Atta sexdens*

Study area

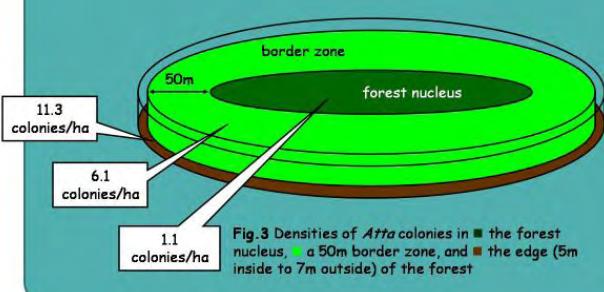
Densities of the two *Atta* species (*A. cephalotes* and *A. sexdens*, Fig.1) occurring in the highly fragmented Atlantic Rainforest of NE Brazil were estimated along the edge of an 3500-ha forest remnant at the Usina Serra Grande, Alagoas. The most common matrix type was sugar cane (84.5%; pasture 8.5%; shrub-land 6.1%). The study was done shortly after the harvesting of the sugar cane, therefore resprouting cane was still young (height 20-50cm).

About their living...

Fig. 2 Distribution of ■ All *Atta*, ■ *A.cephalotes*, and ■ *A. sexdens* colonies with distance to the forest edge in zones of 2m. The edge is located at 0m. Negative numbers indicate locations inside, positive ones outside the forest. Total transect length was 16km (via GPS).

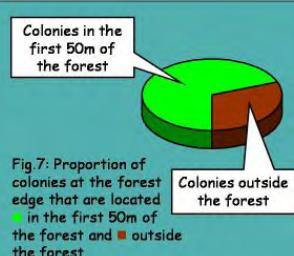


A. cephalotes colonies (N=120) were most common right at the edge between 1m into the forest and 1m outside, while the density of *A. sexdens* colonies (N=106) peaked in the interval of 1m to 5m outside the forest (Fig.2). Of all colonies 95% were found between 5m inside and 7m outside the forest. The density within this edge zone amounted to 11.3 colonies/ha, which was very high compared to previous estimates for the interior and the 50-m border zone of the forest remnant (1.1 and 6.1 colonies/ha, respectively; Fig.3).



Discussion

Given a choice between matrix and forest LCA clearly preferred forest vegetation. Since the edge colonies foraged at the forest border, they should be added to the forest population, when trying to estimate herbivory pressure in this habitat. Colonies in the matrix represented a third of all colonies along the forest edge (Fig.7), which means that based only on colonies inside the forest the herbivory pressure by *Atta* would be underestimated by almost 45%.



LCA preference for border vegetation indicates, that a matrix of sugar cane (even when young) is a less attractive food source.

Nest densities along the edge were high, although colonies lack considerable parts of their food source in their direct vicinity. This might be due to the attractiveness of open areas to founding queens or reflect advantages in constructing and maintaining the nest.

High colony density of LCA outside the forest increases herbivory pressure on the border vegetation



Cutting the drought stressed: Food plant preference of *Atta cephalotes*



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The plant stress hypothesis states that stressed plants are more attractive food sources for herbivores (White 1984). Using laboratory colonies, we could recently demonstrate that leaf-cutting ants prefer drought-stressed over vital plants due to an accumulation of osmolytes in the plant tissue (Meyer et al. 2006). Trees in tropical forest edge habitats are frequently exposed to drought stress. Therefore we hypothesised that edge proliferation of LCA (Wirth et al. *in press*) is due to a drought stress-induced increase in plant palatability. This study aimed to verify preference for stressed plants with colonies at the forest edge of a highly fragmented Atlantic Rainforest in NE-Brazil.



Two whole potted, horizontally lying saplings were offered simultaneously in the vicinity of LCA nests. Harvested leaf area was determined by scanning images and applying a computer program. Preference was calculated as a mean acceptability index (MAI) by dividing the area cut of the stressed plant by the total area cut of both stressed and control plant. Indices ranges from 0 to 1, representing maximum preference for the control or the stressed plants respectively. Remaining leafs and leaf parts were collected to gravimetrically determine their water content.



Fig. 1: Setup for the bioassay with the drought-stressed test plant (right) and vital control (left) lying close to the colony.



In total 10 Bioassays (see right box) were conducted with *Licania tomentosa* (Chrysobalanaceae). We used 10 independent (average distance between colonies 369 m \pm 355) young colonies of *Atta cephalotes* with nest areas between 0.1 and 3 m².



Fig. 2: *Atta cephalotes* cutting fragments out of a leaf



This study took place along the edge of an 3500-ha forest fragment at the Usina Serra Grande, Alagoas in the highly fragmented Atlantic Rainforest of NE-Brazil.



Fig. 3: Forest edge at a harvested sugar-cane field at the Usina Serra Grande, Alagoas, Brazil.



Atta cephalotes workers...

- demonstrated a marked preference for the drought-stressed plant.
- harvested almost three times the leaf area of drought-stressed plants.
- their preference corresponded to a mean acceptability index (MAI) of 0.78 ± 0.14 .

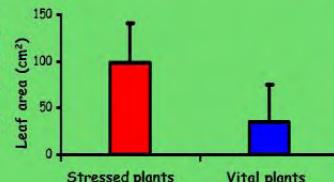


Fig. 4: Mean leaf area (\pm SD) harvested (paired t-test: $T_{10} = 3.96$, $P = 0.003$).

Plants...

- the water content of stressed plants was a third lower than the one of vital controls.

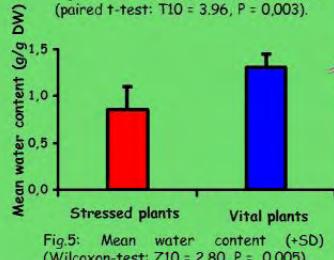


Fig. 5: Mean water content (\pm SD) (Wilcoxon-test: $Z_{10} = 2.80$, $P = 0.005$).



Edge colonies of *Atta cephalotes* strongly preferred stressed over vigorous plants, thus supporting the idea, that the preference for stressed plants -causally linked by increased osmolyte concentrations in leaves (Meyer et al. 2006) - is a general feature of LCA food plant selection. Our findings provide indirect evidence that LCAs may benefit from the increased occurrence of drought-stressed plants in forest edge habitats.

At the forest edge leaf-cutting ants prefer drought-stressed plants

Literature: Meyer, S.T., Roces, F., Wirth, R. (2006) Selecting the drought stressed: effects of plant stress on intraspecific and within-plant herbivory patterns of the leaf-cutting ant *Atta colombica*. *Functional Ecology*, 20:973-981

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Curriculum vitae

October 2008

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Education and Titles

06.1998 **Abitur** (1,1) Graf-Stauffenberg-Gymnasium; Flörsheim am Main
08.2000 **Vordiplom Biology** (1,45) Johannes-Gutenberg-University Mainz
07.2004 **Diploma Biology** (1,1) University of Kaiserslautern
since 09.2004 **Doctoral thesis** University of Kaiserslautern

Research

11.2002- **Experimental study on the radioactive contamination of wild boars**
12.2002 (research assistant) Forschungsanstalt für Waldökologie und Forstwirtschaft
Rheinland-Pfalz, Trippstadt, Germany
01.2003- **Drought resistance of tropical tree seedling** (DAAD Fellowship) fieldwork
04.2003 on tropical ecology; Smithsonian Tropical Research Institute (STRI); Panama

10.2003-	Herbivory and Drought Stress - Interactive effects of plant stress and feeding by leaf-cutting ants (Diploma project) University of Kaiserslautern
06.2004	
07.2005- present	Rain forest fragmentation and high densities of leaf-cutting ants: synergistic effects on microclimate and regeneration of the Brazilian Atlantic Forest. (PhD) Cooperation with Prof. I. Leal und Prof. M. Tabarelli (Universidade Federal de Pernambuco, Recife, Brazil).
10.2006- present	Herbivory and Drought Stress – Food plant selection of leaf-cutting ants in the Brazilian Atlantic Forest. (Coordinator and advisor for graduate students)

Publications

- Meyer ST**, Roces F & Wirth R (2006) Selecting the drought stressed: Effects of plant stress on intraspecific and within-plant herbivory patterns of the leaf-cutting ant *Atta colombica*. *Functional Ecology* **20**, 973-981.
- Wirth R, **Meyer ST**, Almeida WR, Araújo Jr. MV, Barbosa VS & Leal IR (2007) Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a. *Journal of Tropical Ecology* **23**, 501-505.
- Wirth R, **Meyer ST**, Leal IR & Tabarelli M (2008) Plant-herbivore interactions at the forest edge. *Progress in Botany* **69**, 423-448.
- Meyer ST**, Leal IR & Wirth R (submitted) Persisting hyper-abundance of keystone herbivores (*Atta* spp.) at the edge of an old Brazilian Atlantic Forest fragment. *Biotropica*
- Meyer ST**, Leal IR, Tabarelli M & Wirth R (in preparation) Ecosystem engineering in a fragmented forest: Altered forest structure and microclimate at nest sites of *Atta cephalotes*. *Ecology*
- Meyer ST**, Leal IR, Tabarelli M & Wirth R (in preparation) Plant recruitment on and around nests of *Atta cephalotes*: Ecological filters in a fragmented forest. *Journal of Tropical Ecology*

Talks at scientific meetings

- Meyer ST**, Roces F & Wirth R (2005) Selecting the drought stressed: Effects of plant stress on intraspecific and intraindividual herbivory patterns of leaf-cutting ants. *18th annual meeting of Society for Tropical Ecology (GTÖ)*. Berlin, Germany.
- Meyer ST**, Roces F & Wirth R (2005) Selecting the drought stressed: Effects of plant stress on intraspecific and within-plant herbivory patterns of leaf-cutting ants. *Annual meeting of the Association for Tropical Biology (ATBC)*. Uberlandia, MG, Brazil.
- Meyer ST**, Leal IR, Tabarelli M & Wirth R (2007) Leaf-cutting ants as ecosystem engineers: Microclimatic gradients in the vicinity of *Atta cephalotes* nests. *Annual meeting of the Association for Tropical Biology (ATBC)*. Morelia, Mexico.
- Leal IR, Wirth R, **Meyer ST**, Tabarelli M (2007) Proliferação de herbívoros em bordas de florestas. *VIII Congresso de Ecologia do Brasil*, Caxambu, Brazil
- Meyer ST**, Leal IR, Tabarelli M & Wirth R (2008) Hyper-abundant ecosystem engineer (*Atta cephalotes*) impacts microclimate and plant communities at the forest edge. *Annual meeting of the Association for Tropical Biology (ATBC)*. Paramaribo, Suriname.
- Leal IR, Wirth R, **Meyer ST** & Tabarelli M (2008) Edge creation promotes proliferation of herbivores. *Annual meeting of the Association for Tropical Biology (ATBC)*. Paramaribo, Suriname.

Posters at scientific meetings

Meyer ST, Hartard B, Herz H & Berger J (2003) Effect of tannin and total phenols on the feeding preference of a specialized herbivore. *Jahrestagung der Gesellschaft für Tropenökologie*, Rostock, Germany.

Meyer ST & Engelbrecht BMJ (2003) The combined impacts of clipping an drought on seedling mortality for two tropical tree species. *Special Symposium of the BES and Annual Meeting of the ATBC*, Aberdeen, Great Britain

Dohm C, **Meyer ST**, Leal IR, Wirth R (2006) Living outside but cutting within: high colony densities of leaf-cutting ants in front of the forest edge. *19th annual GTÖ meeting*, Kaiserslautern, Germany

Schwarzkopf M, Hartard B, **Meyer ST**, Lakatos M (2006) Tropical lichens as microclimatic indicator? *19th annual GTÖ meeting*, Kaiserslautern, Germany

Meyer ST, Dohm C, Almeida WR , Araújo Jr. MV, Wirth R & Leal IR (2006) Nidificando na matriz, mas forrageando na floresta: Distribuição de colônias de formigas cortadeiras em floresta Atlântica nordestina. *XXI Congresso Brasiliero de Entomologia*, Recife, Brazil

Passlack M, **Meyer ST**, Leal IR, Wirth R (2007) Cutting the drought stressed: Food plant preference of *Atta cephalotes*. *20th annual GTÖ meeting*, Bonn, Germany

Jürgens S, **Meyer ST**, Leal IR, Wirth R (2007) Uncluttered leafcutters: *Atta cephalotes* promotes canopy and understory gaps. *20th annual GTÖ meeting*, Bonn, Germany

Awards

02.2005: **Merian Price**; 3rd Price for the best oral presentation by a young scientist at the 18th annual GTÖ meeting in Berlin

02.2006: **Merian Price**; 1st Price for best poster by a young scientist at the 19th annual GTÖ meeting in Kaiserslautern (together with C. Dohm for “Living outside but cutting within: high colony densities of leaf-cutting ants in front of the forest edge.”)

Grants

- | | |
|---------------------|--|
| 09.2000- | Erasmus Fellowship (Studying Biochemistry, Molecular Biology and Genetics) University of Wales, College Cardiff; Great Britain |
| 07.2001 | |
| 11.2001-
present | e-fellows online scholarship (access to the Internet and over 3000 archives for research purposes, mentor program and online community) |
| 01.2003- | DAAD Kurzstipendium (fieldwork on tropical ecology at the Smithsonian |
| 04.2003 | Tropical Research Institute (STRI); Panama) |
| 07.2003 | Student Support from the British Ecological Society (Participation at the Annual Meeting of the Association for Tropical Biology and Conservation; Aberdeen, Great Britain) |
| 06.2008 | Travel-grant from the University of Kaiserslautern (Participation at the Annual Meeting of the Association for Tropical Biology and Conservation; Paramaribo, Suriname) |

Reviewer for the Journal of Applied Entomology (1) and Journal of Applied Ecology (1)



Myself on top of a nest of the leaf-cutting ant *Atta cephalotes* when measuring light availability using a digital photograph equipped with a fish eye lens.

Declaration

Hiermit versichere ich, dass die vorliegende Dissertation von mir in allen Teilen selbstständig angefertigt wurde und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt wurden.

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

Kaiserslautern, den