

Institut für Systematische Botanik und Ökologie
Universität Ulm

**Fruit availability and dispersal processes
in a highly fragmented landscape in the
northeastern Brazilian Atlantic Forest
region**

Dissertation

Zur Erlangung des Doktorgrades *Dr. rer. nat.*
Fakultät für Naturwissenschaften der Universität Ulm

vorgelegt von
Ute Christiane Knörr
aus Mönchengladbach

2010

Amtierender Dekan: Prof. Dr. Axel Groß

Erstgutachter: Prof. Dr. Gerhard Gottsberger

Zweitgutachter: Prof. Dr. Steven Jansen

Tag der Promotion: 08.06.2010

*“The most insidious kind of extinction is
the extinction of ecological interactions”*

Daniel H. Janzen, 1974

Table of contents

Acknowledgements.....	V
Summary	VII
Zusammenfassung	X
1 Introduction	1
1.1 Tropical fruits, seeds, and dispersal	1
1.2 The Atlantic Forest – a history of deforestation and fragmentation.....	3
1.3 Aims and hypotheses.....	5
2 Study site and general design	7
2.1 Study site	7
2.2 General study design	10
3 Differences in seed rain composition in large and small Atlantic Forest fragments.....	12
3.1 Abstract	12
3.2 Introduction	12
3.3 Material and Methods.....	14
3.4 Results	19
3.5 Discussion	27
4 Pioneer trees in the seed rain of Atlantic Forest fragments: the case of two <i>Cecropia</i> species.....	32
4.1 Abstract	32
4.2 Introduction	32
4.3 Material and Methods.....	34
4.4 Results	38
4.5 Discussion	42
5 Gut-passage and spitting of seeds by primates and germination success: Implications for regeneration of northeastern Atlantic Rainforest fragments.....	44
5.1 Abstract	44
5.2 Introduction	45
5.3 Material and Methods.....	46
5.4 Results	49
5.5 Discussion	52

6	Post-dispersal seed removal patterns in forest fragments and secondary vegetation patches	55
6.1	Abstract	55
6.2	Introduction	55
6.3	Material and Methods.....	57
6.4	Results	61
6.5	Discussion	66
7	Literature	70
	Appendices	88

Acknowledgements

I am deeply grateful to so many people who, directly or indirectly, helped and supported me during the last three years of my research in Brazil and Germany.

First of all I would like to thank Prof. Dr. Gerhard Gottsberger who gave me the great opportunity to work in his project and enabled me to get to know a fascinating country. I am also grateful to Prof. Dr. Steven Jansen, who accepted to be the second referee for the thesis.

Special thanks go to Dr. Daniel Piechowski for his invaluable assistance in Germany and Recife, for the discussions that always helped me to feel more optimistic about reaching the next step, and for his help with statistical problems.

Without the help of my colleagues many things would not have been possible. In particular I want to thank Thomas Kimmel who did not only introduce me to the Pernambucan culture and history with all its diversity but also helped with innumerable discussions, ideas, contributions, and his input to improve my drafts. I am grateful to Dr. Michael Schessl for his assistance and coordination in Recife, to Dr. Leonhard Krause a.k.a. Mc Gyver for his help with Brazilian “red tape” and his technical support, and to Dr. Holger Teichert for the coordination in Recife. I especially want to thank Evelin Schäfer for her support as project administrator and her ability to make everything possible! To Prof. Dr. Marian Kazda, who provided me with a working space at the Institute of Systematic Botany and Ecology in Ulm.

Thanks to Stella Lorenz and Tobias Weidenlener for providing data for chapter 6.

Many thanks to the counterparts Prof^a Dr^a Maria Jesus Nogueira Rodal and Prof^a M.Sc. Ana Carolina Borges Lins-e-Silva, who provided a working space, for their invitation, collaboration, and the scientific and logistic support – *muito obrigada!* I want to thank Wilkilane Luiz da Silva for her help in the lab, for struggling through tons of leaf litter, and her help with logistic problems.

Agradeço muito a Gênesis Batista Rodrigues, quem me assistiu no campo e sem sua ajuda não teria finalizado o trabalho. Também agradeço a Marcos Antônio das Chagas e Lenilson Barbosa Santos pela companhia e ajuda no campo

Acknowledgements

Dr. Frederico Augusto Cavalcanti de Petribu Vilaça kindly granted the permit to work on the property of the Usina São José S/A and provided accommodation and climate data.

I am grateful to Roberto Siqueira, who let me work at the “Refugio Charles Darwin” for the feeding experiments and to Prof^a Dr^a Maria Adélia Oliveira Monteiro da Cruz who provided the outdoor enclosure for the germination experiments.

Thanks to Luciana Maranhão Pessoa who arranged the tailor for the seed traps. To Nadine and Torsten who build seed traps during their vacation!

I am grateful to Dr^a Ana Luiza du Bocage, Juliana Marques, Jorge Irapuan, Diogo Araújo, and Anderson Alves-Araújo for species determination and help with herbarium specimen organization.

Thanks to Roberta Laurentina Alves Pereira and all the other students the nights at the “casa verde” never got boring.

I want to thank all my friends who made my time in Brazil unforgettable: especially Julio, Renato and Karina! And my friends in Germany, especially Marina, Paulo, Reisl, Holger, and Thomas made my time of thesis writing in Ulm a little more pleasant.

Of course last but not least I am grateful to my parents, my sisters Stefanie and Susanne and my brother Torsten who always supported me.

This study was part of the project "Sustainability of remnants of the Atlantic rainforest in Pernambuco and its implications for conservation and local development", a Brazilian-German scientific cooperation within the program "Science and Technology for the Atlantic Rainforest" funded by CNPq (590039/2006-7) and BMBF (01 LB 0203 A1), permitted and logistically supported by Usina São José S.A./ Grupo Cavalcanti Petribú.

Summary

The Brazilian Atlantic Forest that stretches along 27 lines of latitude along the Atlantic coast has a long history of habitat loss and fragmentation basically starting in the 16th century with the settlement of the Portuguese. Over the past five centuries many threats endangered this unique ecosystem that has one of the world's highest rates of endemism. Wood extraction, intensive agriculture, and urbanization were only the most threatening interventions in the history of the destruction of the Brazilian Atlantic Forest. Nowadays the whole area comprises only around 12% of its original forest cover, including secondary vegetation, and the destruction still goes on. In concert with these direct threats to the Atlantic forest, indirect threats like the disruption of plant-animal interactions may amplify the destruction. The study area, the Pernambuco region, has suffered more than for example the Atlantic Forest in the São Paulo region and none of the forest residuals exceeds 10,000 ha.

This study aimed to elucidate fruit availability and seed dispersal processes in a highly fragmented northeastern Atlantic forest landscape, a sugarcane plantation that has lost almost 50% of its forest cover during the past 35 years. Large frugivores are especially vulnerable to fragmentation and this study should highlight the problems and the prospects for regeneration.

The forest fragments studied are all imbedded in a sugarcane matrix and have varying degrees of isolation, size, preservation, and different successional stages. This variety enabled me to compare differences in seed rain composition with regard to dispersal mode and seed size and the importance of the two frequent pioneer species *Cecropia pachystachya* and *Cecropia palmata* (Cecropiaceae) and the change in abundance of *Cecropia* seed rain with gradients of fragment size and disturbance state.

In the Pernambuco region, a biased seed rain with an impoverishment in large-seeded species has already been shown for edge habitats. The present study aimed to show to which extent this shift may also be true comparing small and large forest fragments and if there is a general lack of large-seeded species in the seed rain. Additionally, experiments on primary and secondary diaspore dispersal should show whether the highly endangered blond capuchin monkey (*Cebus flavius*, Cebidae) can potentially be an effective disperser particularly for large-

seeded local species, by conducting feeding and germination experiments with captive capuchin monkeys and whether secondary dispersal is especially delimited in smaller forest fragments and secondary vegetation patches by carrying out seed removal experiments.

The seed rain study, which was conducted with a total of 105 seed traps within seven different-sized forest fragments, showed a clear difference in seed rain composition as for seed size distribution between small and large forest fragments. Small fragments received considerably more small-sized seeds than large fragments and large fragments more large-seeded seeds and species than small forest fragments. However, since only seven large-seeded species (> 1.5 cm) were collected during a one year period within all sampled fragments it can be assumed that seed rain generally is extremely impoverished towards species with smaller seeds. The expected number of species was much higher for large forest fragments (184) than for small fragments (167). The most frequent species in either habitat, large or small, was *Cecropia palmata* and regression analyses showed that the inflow of *Cecropia* fruits increased with increasing isolation and disturbance of a forest fragment. *Cecropia* fruit rain was also significantly higher in small than in large forest fragments.

Feeding experiments approved capuchin monkeys as very good seed dispersers of native tree species. They swallowed seeds up to 2.3 cm at their longest length of a large proportion of the fruit species offered and germination experiments showed that digested seeds of some species were germinating better than controls but this could not be proved statistically. However, seed ingestion never had a negative effect on germination. On the other hand, seed spitting was not a good way of seed handling because some seeds got damaged and did not germinate at all. There was no difference in time to germination between controls and handled seeds and retention time in the digestive track of the capuchin monkeys was generally very short (mean time: 120 min).

Seed removal experiments, simulated with exotic fruit items in two consecutive years, demonstrated significant differences in the activity of ground-dwelling animals in different-sized forest fragments and different forest types with a higher removal rate in large forest fragments and forests that were more preserved. In open secondary vegetation very few exotic fruit items, i.e. coconut copra or apple pieces, were removed suggesting avoidance by ground-dwelling

animals of those habitats where they are more exposed to threats like hunting and preying. However, closed secondary vegetation patches apparently were equally frequented by secondary dispersers like small forest fragments. No difference in seed removal could be found between edge and interior sites of none of the two size classes. Apple pieces were favored in the first year but not in the second year. Video recordings showed many marsupials feeding on apple pieces and a squirrel removing coconut pieces.

Summing up, the present study showed alarming results from this highly fragmented Brazilian Atlantic Forest region. It showed an impoverishment of seed rain composition and almost an extinction of large-seeded species in the seed rain of the study area and a dominance of small-seeded pioneer species particularly in small, isolated and disturbed fragments. Dispersal services of e.g. the blond capuchin monkey may slow down this trend, but since this species is highly endangered and currently only living in one sole forest fragment in the whole area only connection of the forest fragments with corridors could help to enhance movements between the patches and therefore dispersal activity.

Zusammenfassung

Der Atlantische Regenwald Brasiliens (port.= Mata Atlântica), der sich über 27 Breitengrade entlang der brasilianischen Atlantikküste erstreckt, blickt auf eine lange Geschichte der Zerstörung, die im Wesentlichen mit der Besiedlung der Portugiesen im 16ten Jahrhundert begann. Im Laufe der letzten fünf Jahrhunderte wurde dieses einzigartige Ökosystem mit vielen Bedrohungen konfrontiert. Holzeinschlag und massiver Raubbau, intensive Landwirtschaft, wie zum Beispiel der Anbau von Zuckerrohr für die Gewinnung von Biotreibstoffen, und Urbanisierung sind unter anderem dafür verantwortlich dass heutzutage nur noch 12% (zusammen mit der Sekundärvegetation) der ehemaligen Walddeckung anzufinden sind. Durch ein sehr schnelles Bevölkerungswachstum im letzten Jahrhundert innerhalb der Atlantischen Regenwaldzone entstanden die Millionenstädte São Paulo, Rio de Janeiro, Recife, Salvador da Bahia und Curitiba. Gleichwohl gehört dieses Waldgebiet zu einem der Ökosysteme mit der weltweit höchsten Rate an endemischen Tier- und Pflanzenarten. Das Untersuchungsgebiet liegt innerhalb der so genannten Pernambuco Region, welche noch mehr unter den Folgen der Zerstörung gelitten hat als zum Beispiel der Atlantische Regenwald bei São Paulo. In dieser Region, die die nordostbrasilianischen Staaten Alagoas, Pernambuco und Paraíba mit einschließt, ist keines der Waldfragmente größer als 10.000 ha.

Zusammen mit der direkten Vernichtung des Waldes können indirekte Folgen der Zerstörung wie die Störung von Pflanzen-Tier Interaktionen diesen Trend noch verstärken. Im Rahmen dieser Arbeit sollten Fruchtverfügbarkeit und Ausbreitungsprozesse in einer stark fragmentierten nordostbrasilianischen Atlantischen Regenwaldlandschaft untersucht werden. Diese Landschaft, eine Zuckerrohrplantage, hat während der letzten 35 Jahre fast 50% der Walddeckung verloren. Dieser extreme Verlust an Lebensraum ist größtenteils die Folge der Ölkrise der 70er Jahre des letzten Jahrhunderts als der brasilianische Staat anfang die Produktion von Zuckerrohr zur Herstellung von Biokraftstoff zu subventionieren. Größere Fruchtausbreiter, wie zum Beispiel Affen, sind in Regenwaldfragmenten ganz besonders gefährdet, da ihr Lebensraum stark dezimiert ist und sie eine größere Gefahr eingehen gejagt zu werden.

Die untersuchten Waldfragmente liegen alle inmitten von Zuckerrohrfeldern und sind unterschiedlich stark isoliert, verschieden groß und gehören unterschiedlichen Sukzessionsstufen an. Diese Vielfalt ermöglichte es mir Veränderungen in der Zusammensetzung des Samenregens in Bezug auf die Samengröße und den Ausbreitungstyp herauszuarbeiten und die Bedeutung der beiden sehr häufigen Pionierbaumarten *Cecropia pachystachy* und *C. palmata* (Cecropiaceae) und deren Häufigkeit im Samenregen in verschiedenen großen und unterschiedlich gestörten Fragmenten zu untersuchen. Im nordostbrasilianischen Atlantischen Regenwald konnte schon eine Verarmung an großsamigen Arten in der Waldrandzone eines großen Fragments nachgewiesen werden. Die vorliegende Arbeit hat nun versucht herauszufinden inwieweit diese Verschiebung auch zutrifft, wenn man kleine und große Waldfragmente miteinander vergleicht und ob es eine grundsätzliche Verarmung an großsamigen Arten im Samenregen des Untersuchungsgebiets gibt. Versuche zur primären Samenausbreitung sollten zeigen ob der stark vom Aussterben bedrohte blonde Kapuzineraffe (*Cebus flavius*, Cebidae) ein effektiver Ausbreiter, speziell von großsamigen Arten, sein kann. Dafür wurden Fütterungs- und Keimungsversuche mit eingesperrten Kapuzineraffen durchgeführt. Zudem sollten Versuche zur sekundären Samenausbreitung Aufschluss darüber bringen, ob diese Art der Ausbreitung besonders in kleineren Fragmenten und Sekundärvegetation eingeschränkt ist. Hierfür wurden Auslegeversuche durchgeführt.

Die Untersuchungen zum Samenregen, die innerhalb von sieben verschiedenen großen Waldfragmenten stattfanden, in denen insgesamt 105 Samenfallen aufgestellt wurden, zeigten klare Unterschiede zwischen großen und kleinen Fragmenten in Bezug auf die Samengrößen. Es wurden deutlich mehr kleine Samen in kleinen als in großen Waldfragmenten und mehr großsamige Arten in großen als in kleinen Fragmenten gesammelt. Da aber insgesamt nur sieben großsamige Arten (> 1,5 cm) innerhalb eines ganzen Jahres gesammelt wurden, kann man davon ausgehen, dass der Samenregen in diesen Waldfragmenten generell sehr stark verarmt ist. Die geschätzte Artenzahl war größer für große Waldfragmente (184 Arten) als für kleine (167 Arten). Die insgesamt häufigste Art, in kleinen und großen Fragmenten, war *Cecropia palmata* und Regressionsanalysen konnten zeigen, dass der Eintrag von *Cecropia*-Früchten mit dem Grad der Isolierung und Störung des Fragments anstieg. Zudem

war der *Cecropia*-Früchteeintrag in kleinen signifikant höher als in großen Waldfragmenten.

Die Fütterungsversuche bestätigten, dass Kapuzineraffen sehr gute Samenausbreiter von lokalen Baumarten sein können. Die Affen schluckten Samen mit einer Länge von bis zu 2,3 cm von einem großen Anteil der Früchte, die ihnen angeboten wurden. Die Keimungsversuche zeigten, dass die ausgeschiedenen Samen einiger Arten besser keimten als Kontrollsamens, was aber nicht statistisch nachgewiesen werden konnte. Die Darmpassage hatte auf jeden Fall niemals einen negativen Einfluss auf den Keimungserfolg der Samen. Jedoch hatte das bloße Ausspucken der Samen manchmal einen negativen Einfluss auf die Samen, da sie teilweise angebissen und zerstört wurden und somit keimungsunfähig waren. Es konnte kein Unterschied zwischen den Kontrollen und den ausgeschiedenen bzw. ausgespuckten Samen bezüglich der Zeit bis zur Keimung nachgewiesen werden. Die durchschnittliche Verdauungszeit war mit 120 Minuten sehr kurz.

Die Auslegeversuche, bei denen exotische Fruchtstücke (Kokosnuss und Apfel) große Samen simulieren sollten, zeigten, dass es signifikante Unterschiede bezüglich der Aktivität von am Boden lebenden Tieren in verschiedenen großen Fragmenten und Waldtypen gibt. Die Entfernungsrates war höher in großen und besser geschützten Wäldern. In offenen Sekundärwäldern war die Rate sehr gering, was vermuten lässt, dass nur noch wenige Tiere in diesen Wäldern leben. Dagegen konnte aber kein Unterschied bei der Anzahl der entnommenen Stücke zwischen geschlossenen Sekundärwäldern und kleinen Waldfragmenten festgestellt werden. Es gab gegen die Erwartungen auch keinen Unterschied zwischen dem Waldesinneren und der Waldrandzone keiner der beiden Fragmentgrößenklassen. Apfelstücke wurden im ersten Untersuchungsjahr bevorzugt aber nicht im zweiten. Bei Videoaufnahmen konnten unter anderem einige Beuteltiere beim Verzehren von Apfelstücken und ein Eichhörnchen beim Entfernen von Kokosstücken beobachtet werden.

Die Ergebnisse der vorliegenden Arbeit aus dem nordostbrasilianischen Atlantischen Regenwaldgebiet sind alarmierend. Es zeigte sich eine Verarmung des Samenregens mit sehr wenigen großsamigen Arten und ein Vorherrschen kleinsamiger Pionierarten besonders in kleinen, isolierten und zerstörten Fragmenten. Als guter Ausbreiter könnte zum Beispiel der blonde Kapuzineraffe

(*Cebus flavius*) dabei helfen diese erschreckende Entwicklung aufzuhalten. Da diese bedrohte Primatenart aber nur noch in einem einzigen Waldfragment auf der Zuckerrohrplantage vorkommt, müsste dieses isolierte Fragment durch Waldkorridore mit anderen Fragmenten verbunden werden, damit sich die Affen überhaupt zwischen den Fragmenten bewegen können und somit die Ausbreitung von einigen Pflanzenarten durch den Kapuzineraffen gewährleistet wäre.

1 Introduction

1.1 Tropical fruits, seeds, and dispersal

Dispersal can be defined as the removal or departure of the diaspore¹ from the vicinity of the parent plant. After a successful dispersal the seed establishes by germinating and using parental provisioning (Howe and Smallwood 1982). A fruit is a matured gynoecium that is or is not associated with other floral organs or parts of floral organs. The fruit is bearing one or more seeds, i.e. propagating organs that are products of the sexual reproduction of higher plants. Seeds derive from the ovule and usually consist of a protective seed coat (testa) and enclose the embryo, i.e. the undeveloped young plant. The food reserve for the young plant may be provided by the endosperm, perisperm, or the cotyledons (Jacob et al. 1994).

Besides the dispersal by animals (zoochory), wind (anemochory), water (hydrochory), and ballistic actions (autochory) there are many other ways and modifications of how a diaspore can reach a site (summarized in van der Pijl 1969) like for example endozoochory. This is the consumption and transportation of the diaspore by animals, which will then ingest and defecate the seeds. In general fruits and dispersal mechanisms do not differ between temperate and tropical regions. However, in tropical wet forests fruit characteristics and the dispersal of the diaspore can be distinguished from those of temperate forests by shifts in e.g. the proportions of the different dispersal modes and in seed size. Tropical fruits often have large seeds and a nutritional-rich pulp whereas fruits from temperate regions are mostly small with a lower energy reward. Contrary to dry habitats, in tropical wet habitats diaspores are predominately dispersed by animals (Howe and Smallwood 1982). Since zoochory is the most important mechanism of dispersal in the tropics, I want to concentrate on some characteristics of this syndrome in the following.

Corresponding to the high variety of different-sized vertebrate fruit eaters, which regurgitate, defecate, or drop seeds, seed size varies from very small like

¹ van der Pijl (1969): the unit of the fruit that is dispersed. A diaspore can be seed, fruit, or part of a fruit

those of some *Miconia* species (Melastomataceae) eaten by small birds to very large like *Balanites wilsoniana* fruits (Balanitaceae) that are consumed by African forest elephants (Chapman et al. 1992) or large-seeded fruits consumed by tapirs in the Neotropics (Fragoso and Huffman 2000a). The seed and fruit size and the amount of seeds consumed is correlated with the size of the animal that eats the fruits or seeds respectively (Gautier-Hion et al. 1985, Janson 1983). Often, clumped dispersal occurs when animals defecate several to several thousands of seeds all at once (Howe 1989). This aggregation of seeds or seedlings respectively may be comparable to the situation when fruits or seeds fall directly beneath the parent tree without being dispersed and the seeds as well as the seedlings will be more vulnerable to predation. Only with increasing distance from the parent plant the chance of survival raises (Janzen 1970). Secondary seed dispersal by e.g. ants (Levey and Byrne 1993), dung beetles (Andresen and Feer 2002), and rodents (Forget et al. 1998) may increase the chance of survival by re-arranging seed distribution.

Habitat loss, fragmentation, hunting, and logging may threaten dispersal interactions. The extinction of local food resources can lead to the extinction of frugivores and conversely hunting of animals may threaten plants that depend on those dispersal agents. Hence, the preservation of such plant species requires the conservation of the dispersal agents (Howe 1989). In overexploited regions especially large-seeded tree species suffer from the absence of large frugivores, which are capable of transporting large seeds. However, even if small populations of large animals still existed in fragmented landscapes they would rarely cross certain habitats like agricultural fields to carry large seeds from one fragment to the other (Wunderle 1997). Furthermore, animals that cross non-forest habitats get easily killed by feral dogs and local people (Silva and Pontes 2008). On the other hand, small-seeded species are very resilient and even proliferated in fragmented tropical landscapes (Cramer et al. 2007, Laurance et al. 2006) because animals like small birds and bats that mostly disperse small seeds are not as vulnerable as e.g. large birds and mammals and may cross sugarcane fields with little vertical or horizontal heterogeneity (Galindo-González et al. 2000, Schulze et al. 2000).

1.2 The Atlantic Forest – a history of deforestation and fragmentation

The Atlantic Forest (Port. = Mata Atlântica) extends over a huge area across 27 lines of latitude along the Brazilian Atlantic coast between the state Rio Grande do Norte (3°S) and the southernmost Brazilian state Rio Grande do Sul (30°S), and inland as far as Paraguay and Argentina (Câmara 2003). Since the Atlantic Forest has a broad latitudinal extent and also a wide longitudinal range with decreasing precipitation of up to 4000 mm/year at the coast to 1000 mm in the inland it houses a large variety of different vegetation types (Câmara 2003). The Atlantic Forest encompasses the dense ombrophilous coastal rainforest, the araucaria forests (*Araucaria angustifolia*) in Paraná, the deciduous and semi-deciduous forests in the interior, and the forests dominated by the laurel family (Lauraceae) in the South (Câmara 2003). Additionally, there are some associated ecosystems like mangroves, the coastal restinga forests, which are characterized by sandy, dry, and nutrient-poor soils (Zamith and Scarano 2006), and the *brejos de altitude*. The *brejos* are humid montane forest islands located in the middle of the northeastern semiarid regions and are most likely results of climatic variations that occurred during the Pleistocene and are nowadays remnants within a favorable microclimate (Tabarelli and Santos 2004). The variety of ecosystems that are part of Brazil's Atlantic Forest led to a high diversity and endemism with 8000 species of endemic plants (2.7% of the global total) and 567 species of endemic vertebrates (2.1% of the global total). Due to the combination of its high rate of endemism and habitat loss it was called one of the five 'hottest hotspots' of the world (Myers et al. 2000).

Before the start of the massive destruction of the Brazilian Atlantic Forest over 500 years ago it was one of the largest rainforests of the Americas with around 1.5 million km² of forest cover (Ribeiro et al. 2009). Nowadays only a very small fraction, i.e. 7-8% original primary forests (Galindo-Leal and Câmara 2003) or 11.7% including intermediate secondary forests (Ribeiro et al. 2009), of the original extent of the Brazilian Atlantic Forest remains. The massive destruction started with the settlement of the Portuguese colonists in 1500, although, when they arrived the coastal forest was not totally untouched. Evidences of hunter-gatherers for the region are already about 11000 years old

(Dean 1995). However, with the exploitation of Brazilwood (Port. = Pau-Brasil; *Caesalpinia echinata*) the anthropogenic pressure was pushed to another level. Brazilwood was exploited along the coast from Rio de Janeiro to Ceará (Câmara 2003). Later on, the destruction proceeded with the clearing of forest for settlement, agriculture, and for fuelwood harvesting (Câmara 2003). In the twentieth century the demand for wood was enormous because of rapidly growing cities. Nowadays more than 100 million people live in the cities located within the Brazilian Atlantic Forest region, including the megacities Rio de Janeiro, São Paulo, Salvador, and Recife, and the uncontrolled urban expansion still goes on (Galindo-Leal and Câmara 2003). Since the 1930s ethanol from sugarcane has been used as fuel for cars, but in the 1970s during the oil crisis ethanol became more important and since then sugarcane cultivation was subsidized by the Brazilian government (Marris 2006). Between 1975 and 2004 the ethanol production in Brazil has grown by 3.77% per year (Goldemberg 2008). This rapid growth had destructive effects on the forests in the interior of São Paulo and the already highly depleted northeastern Atlantic Forest (Câmara 2003, Kimmel et al. 2008). In the latter area, also known as the Pernambuco region (including the states Alagoas, Pernambuco, and Paraíba), today only 12.1% of the original forest cover remains and the largest remnant is just around 9,700 ha in size including secondary vegetation (Amarante and Tabarelli 2003, Ribeiro et al. 2009). The Brazilian Atlantic Forest and especially the Pernambuco region lack protected areas and illegal activities like for example logging and poaching lead to further destruction of the forest residuals. The contradictory policies of governmental agencies seem to be counterproductive and do not help to protect the remaining fragments (Galindo-Leal and Câmara 2003). In many cases the only reason for the survival of forest fragments is their location on steep slopes, at inaccessible sites, or in areas with a low productivity (Galindo-Leal 2003).



Figure 1.1 A typical small forest fragment located on the property of the sugar mill São José within the sugarcane matrix

1.3 Aims and hypotheses

The bi-national cooperation program “Disturbance, Fragmentation, and Regeneration of Atlantic Forest in the Pernambuco Region in Northeast Brazil” had as its general objective to evaluate the sustainability and conservation status of rainforest fragments of different sizes. The Brazilian and German working groups emphasized the ecological and structural differences comparing small- (< 30 ha), middle- (30-200 ha), and large-sized (> 200 ha) forest fragments as well as regeneration dynamics of differently developed secondary vegetation patches, which are located on the property of the sugarcane plantation *Usina São José* (see figure 1.1). The present study concentrates on ecological processes but also considers structural elements of different-sized forest fragments. As brought up before, especially obligate mutualisms with seed dispersers may be vulnerable to fragmentation. With this in mind the main goal of this study was to provide an insight into seed rain and dispersal patterns in a highly fragmented landscape and to identify regeneration potentials and threats to this northeastern Atlantic Forest region.

In the first part a seed rain study (chapters 3-4) should help to elucidate whether there are differences in seed rain composition with regard to seed size and dispersal mode (chapter 3) by comparing large and small forest fragments with varying degrees of isolation and disturbance. Furthermore, in chapter 4 a case study focused on one group of trees that might be proliferated in forest fragments (Laurance et al. 2006). By using the two *Cecropia* species occurring in the study area as examples for pioneer tree species, i.e. *Cecropia pachystachya* and *Cecropia palmata* (Cecropiaceae), I wanted to know if, among other reasons, a higher seed rain may be responsible for the high abundance of successional trees particularly in small forest fragments.

The second part of the study (chapters 5-6) focuses on dispersal processes and on forest regeneration potentials and problems. Chapter 5 describes a study about primary seed dispersal and germination success of local species after seed handling. Since capuchin monkeys are known to be very good seed dispersers (Valenta and Fedigan 2009, Wehncke et al. 2003) and a group of the endemic and highly endangered blond capuchin monkey (*Cebus flavius*) lives in one forest fragment in the study area, feeding experiments were performed to check whether local, mostly large-seeded species, could be successfully dispersed. After primary dispersal there is always a possibility for seeds being secondarily dispersed by ground-dwelling animals and the last chapter (chapter 6) deals with a seed removal experiment that was performed in forest fragments of different sizes and successional stages as well as in edge and interior habitats. This study aimed to quantify post dispersal fate of large seeds by using exotic items rather than local species in a fragmented landscape where dispersal interactions are most likely disturbed.

2 Study site and general design

2.1 Study site

The study area is located approximately 40 km north of Recife the capital of the northeastern Brazilian state Pernambuco (Figure 2.1a). The sugarcane plantation *Usina São José* (USJ, Figure 2.1b) encompasses an area of around 250 km² of which 27% are covered with mature forest fragments. These 106 forest patches are mostly irregular-shaped of which 32% are less than 10 ha in size. Additionally there are 96 secondary vegetation patches that range between 0.12 and 130 ha (Trindade et al. 2008). The study area has lost almost 50% of its forest cover since 1975 mostly due to the “pro-alcool” campaign of the Brazilian government in the 1970s that subsidized the cultivation of sugarcane for ethanol production (Trindade et al. 2008). In the whole study area, the USJ, there is only one protected forest fragment, the “Mata da Usina São José” (= Mata de Piedade, Figure 2.1b: #13) (Neto and Silva 2002), which is also the only fragment in the region with a great proportion of its forest located on a plateau, a so-called *tabuleiro*. The remaining *tabuleiros* are all used for sugarcane cultivation and forest patches are only found on the steep slopes with inclinations of mostly over 30% (Trindade et al. 2008).

The whole coastal plain is covered with Cenozoic continental deposits belonging to the Barreiras group of the middle Tertiary to Quaternary age (Mabesoone et al. 1968). The predominant soil is a sandy to loamy podzol (Schessl et al. 2008).

2. Study site and design

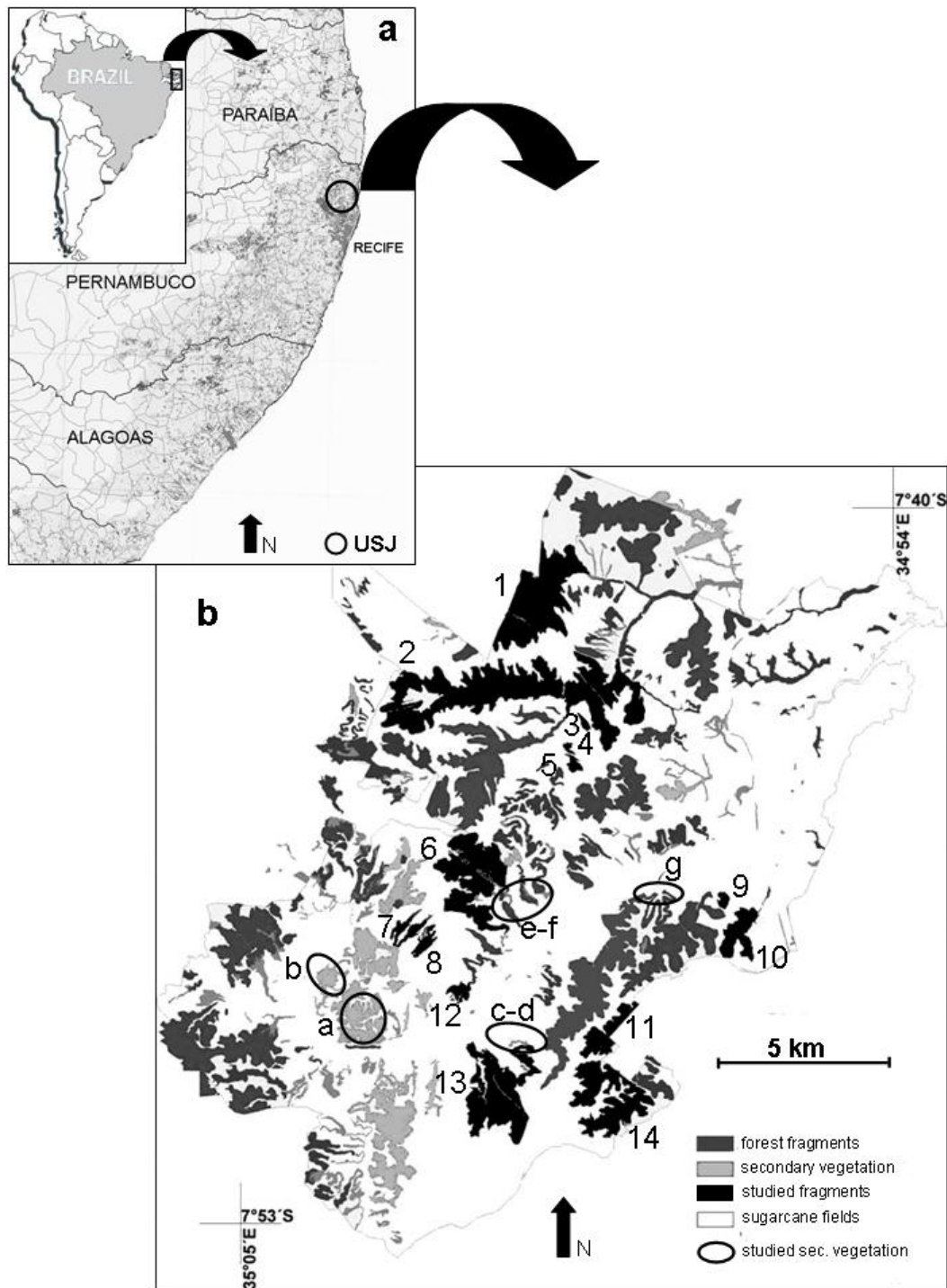


Figure 2.1 (a) Location of the study area in Northeast Brazil (source: SOS Mata Atlântica). (b) Distribution of the forest fragments and secondary vegetation patches within the sugarcane matrix on the sugarcane plantation Usina São José (USJ). Numbers and characters represent studied patches (modified after Schessl, personal communication).

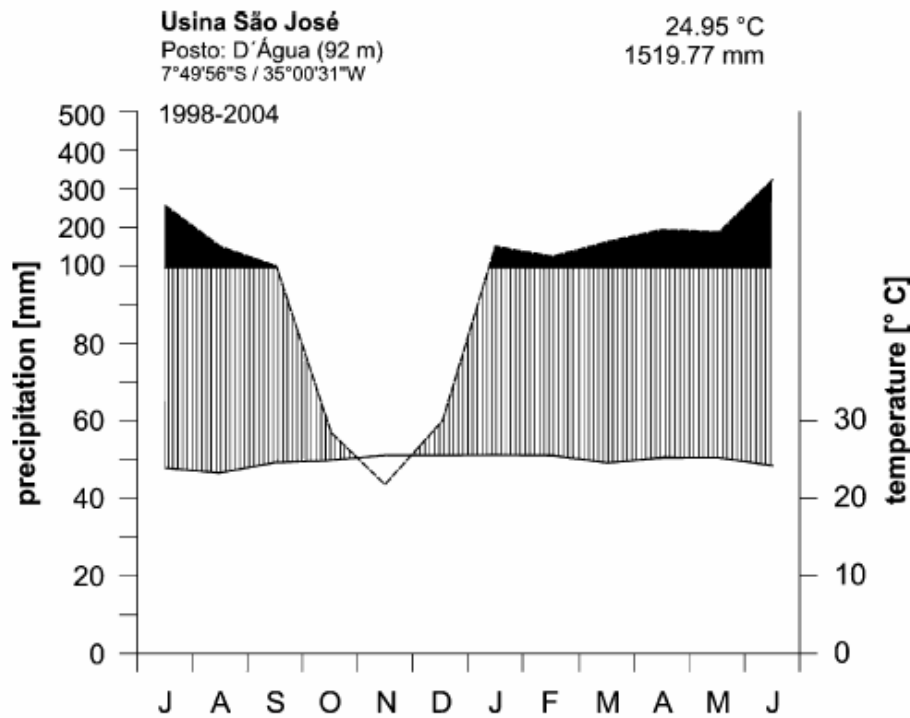


Figure 2.2 Climate chart of the D'Água climate station at the “Usina São José” Pernambuco, Brazil (source: Schessl et al. 2008)

The climate is tropical with strong inter-annual and spatial variation: a pronounced dry season between September and December alternates with a rainy season between January and August (Figure 2.2), and average annual precipitation is much higher near the coastline (2600 mm) than just 11 km inland (1670 mm). Mean annual temperature is 24.95 °C (Schessl et al. 2008).

The vegetation of the study area can be classified as dense ombrophilous forest with transition to semi-deciduous forest (Veloso et al. 1991). Some frequent canopy tree species like *Parkia pendula* (Fabaceae) are completely defoliated during the dry season (Piechowski 2007). 650 plant species, including trees, shrubs, herbs, and lianas, from 379 genera and 105 families were registered on the property of the São José sugar mill (Alves-Araújo et al. 2008). Conspicuous tree species in the region are for example *Eschweilera ovata* (Lecythidaceae), *Brosimum guianense* (Moraceae), *Parkia pendula* (Fabaceae), *Pogonophora schomburgkiana* (Euphorbiaceae), *Protium heptaphyllum* (Burseraceae), and *Tapirira guianensis* (Anacardiaceae) (Guedes 1998, Silva et al. 2008). Typical mammals in the region are for example *Callithrix jacchus* (Callitrichidae), a very

abundant small-bodied primate, the South American coati (*Nasua nasua* Procyonidae), the tayra (*Eira barbara*, Mustelidae), and the rodents *Sciurius aestuans* (Sciuridae), *Dasyprocta prymnolopha* (Dasyproctidae), and *Cuniculus paca* (Cuniculidae) (Cruz and Campello 1998). Many large mammals are threatened with extinction in the northeastern Atlantic Forest zone (Silva and Pontes 2008). Especially threatened is the blond capuchin monkey (*Cebus flavius*, Cebidae) (Oliveira and Langguth 2006).

2.2 General study design

A great part of the study, i.e. the seed rain assessment (chapter 3 and 4), was performed within three large and four small forest fragments (Figure 2.1b). 14 additional fragments and secondary vegetation patches were chosen for seed removal experiments (chapter 6). Seed traps were installed at least 50 m away from the forest edge in groups of five with a distance of 10 m between each trap and at least 20 m between each group (Figure 2.3a). Further explanations of the seed trap design can be read in the material and methods part of chapters 3 and 4.

For a better understanding and interpretation of the seed rain data the forest structure in the seven fragments was analyzed within circular plots with a radius of 5 m that were centered in the middle of each seed trap (Figure 2.3b). Since there were 15 traps in each fragment a total area of 0.82 ha was censused. Following the census methods applied by Condit (1998), all trees and woody lianas with a minimum diameter at breast height (dbh) of 5 cm were considered. The dbh was measured and the tree height was estimated. It was registered if trees were multiple-stemmed, i.e. a sign for vegetative regeneration after tree cutting. Additionally, the percentage of herbs, small lianas, seedlings, and small trees within the circular plots was estimated. Some results are given in the appendices 1 and 2.

Further information on the experimental designs for the different studies is given in the particular chapters.

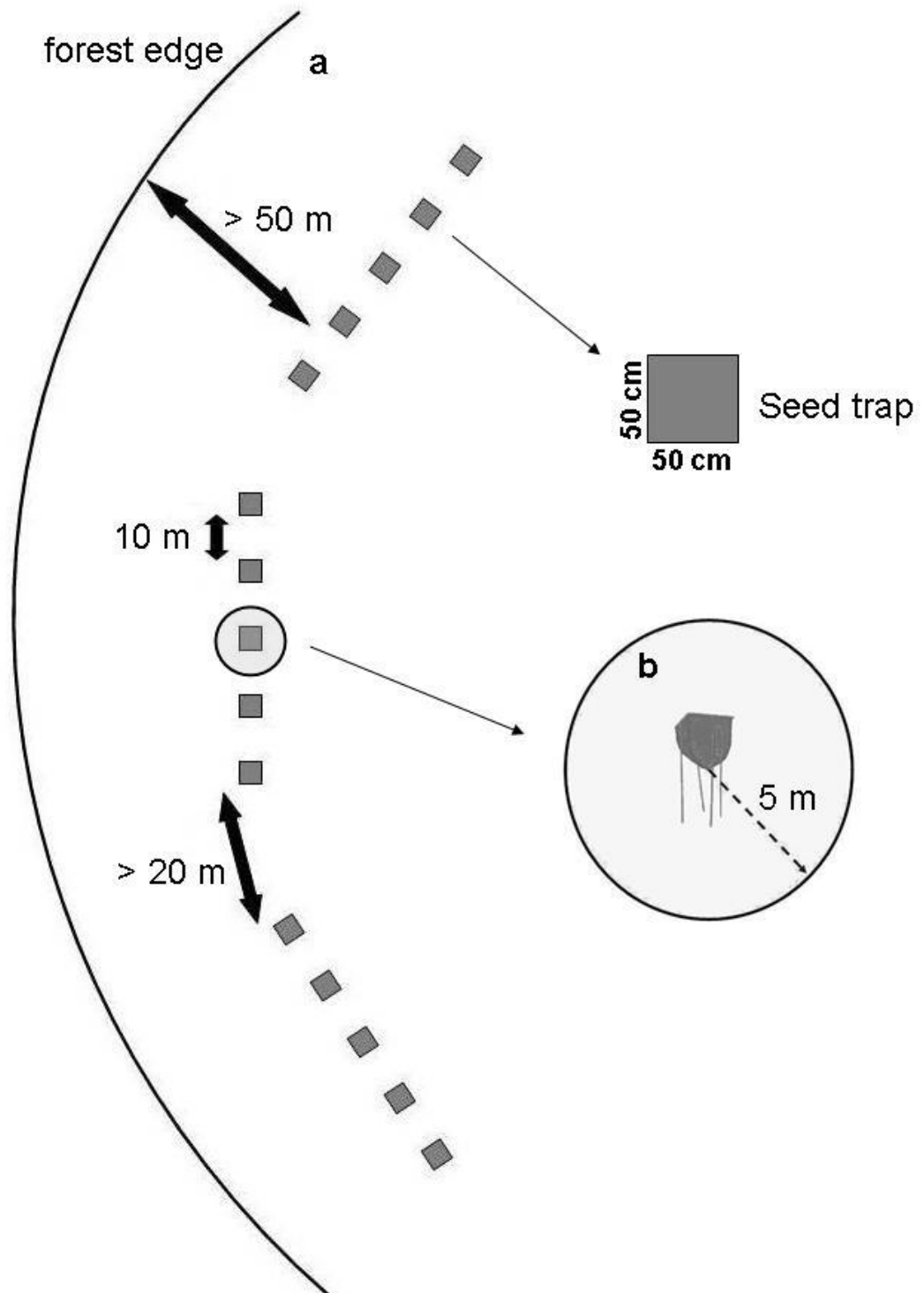


Figure 2.3 Seed trap design with the relative location of each trap within a fragment.

(b) Schematic figure of a circular plot used for the forest structure

3 Differences in seed rain composition in large and small Atlantic Forest fragments

3.1 Abstract

Tropical forests are seriously threatened by fragmentation and habitat loss. However, effects of forest disturbance on biological interactions are insufficiently studied. We assessed seed rain in Brazilian Atlantic Forest fragments in order to identify differences in seed abundance, species richness, seed size, and dispersal modes in small and large forest fragments. In total we installed 105 seed traps and collected seed rain during a one year period in three large and four small forest remnants that were surrounded by a sugarcane matrix. Total seed rain between December 2007 and November 2008 included 20,518 seeds of 149 species. Most species and seeds were animal-dispersed. We registered a significant difference between small and large remnants in the proportion of seeds and species within different categories of seed size. Small fragments received significantly more very small-sized seeds (61%) in comparison to large fragments (35.9%). More large-seeded species were found in the seed rain of large fragments (9.4%) than in small fragments (1.9%). Not only the fragment size was a good predictor for species composition but also the percentage of forest cover a positive predictor for the amount of large-seeded species and a negative predictor for the quantity of small-seeded species. Altogether we just collected seven large-seeded species (> 1.5 cm), of which only one was found in small fragments. In summary, seed rain was biased towards very small and small-sized seeds in small forest fragments and we registered an almost absence of large-seeded species.

3.2 Introduction

Fragmentation and habitat loss are certainly the greatest threats to tropical forests and the effects of fragmentation are innumerable, ranging from abiotic modifications like an unfavorable microclimate in edge habitats with e.g. increased wind disturbance, higher air temperatures, and lower relative humidity (Laurance et al. 2002) to failures in biotic interactions. Especially seed dispersal is limited and mainly large-seeded plant species rely on suitable dispersers like e.g.

tapirs (Fragoso and Huffman 2000b), primates (Chapman 1989), and toucans (Howe et al. 1985). In fragmented landscapes most of these large animals suffer from hunting because hunters have an easy access to forest fragments (Redford 1992). In Amazonian forest for example it has been shown that the body size of animals is negatively correlated with the intensity of hunting (Peres 2000). Large frugivores also suffer indirectly by the lack of habitat and the absence of sufficient food sources because fruit bearing trees may be rare (Phillips 1997, Redford 1992). On the other hand, small-seeded pioneer and wind-dispersed species are more resilient or even favored in fragmented landscapes (Cramer et al. 2007, Dirzo et al. 2007, Tabarelli et al. 1999). The strong disequilibrium in dispersal processes is one reason for impoverished species assemblages in forest fragments that may be reflected in the seed rain. However, most seed rain studies concentrate on forest regeneration on pastures (Holl 1999, Martínez-Garza and Gonzalez-Montagut 1999). There are still very few studies in fragmented landscapes that analyze the composition of species and their ecological role, i.e. dispersal mode or functional trait within forest fragments (Melo et al. 2010, Melo et al. 2006).

Edge habitats receive a lower amount of large seeds, which are dispersed by vertebrates, than the forest interior (Melo et al. 2006), a lower amount of seedlings of large-seeded tree species establishes in smaller forest fragments (Melo et al. 2010) and small-seeded species rapidly increase in small-sized fragments (Michalski et al. 2007).

We analyzed the impact of habitat loss on the assemblage of species with different dispersal modes and seed size classes in the Brazilian northeastern part of the Atlantic Forest. This region is characterized by an extreme degree of fragmentation and habitat loss in the last decades and most of the area is used for sugarcane agriculture (Kimmel et al. 2008, Ranta et al. 1998). We wanted to know if (1) seed rain differs by dispersal mode and seed size in forest fragments with different sizes and varying degree of isolation; and whether (2) species composition in general is biased towards a specific guild of plants. Furthermore, we will discuss the findings with regard to threats to biodiversity and challenges for conservation.

3.3 Material and Methods

Study area

The study was conducted from the beginning of December 2007 to the end of November 2008 in seven Brazilian Atlantic Forest fragments that are distributed on the sugarcane plantation *Usina São José* (USJ) (07°41'04,9" to 07°54'41,6"S and 34°54'17,6" to 35°05'07,2"W). The plantation is located 40 km north of Recife, capital of the federal state of Pernambuco, Northeast Brazil (Fig. 2.1a). The plantation occupies 247 km², of which 27% are covered with irregular shaped forest remnants that are imbedded in a sugarcane matrix (Trindade et al. 2008).

According to interviews with local inhabitants (Kimmel, personal comm.) and a review by Kimmel et al. (2008) the whole area was mostly forest until the 1950s. On aerial photographs from 1969, 1974, and 1981 it can be recognized that two of the three large fragments we used for our seed rain study (# 6 & 13, Fig. 2.1b) did not considerably change in shape and size at least since 1969. Four fragments were isolated between 1974 and 1981 (# 1, 3, 4, and 9; Fig. 2.1b) during the “pro-alcool” program of the Brazilian government that subsidized the cultivation of sugarcane for the production of bio fuels (Kimmel et al. 2008, Ranta et al. 1998). The small fragment *Pézinho* (# 8) is the only forest that was already isolated before 1969 and moreover grew in size since this period.

The climate is tropical with a rainy season between January and August and a marked dry season between September and December. Mean annual rainfall is 1,500 mm with strong inter-annual and spatial variations and mean annual temperature is 25°C (Schessl et al. 2008). The bedrock is a Tertiary conglomerate on beach-ridged terraces of the Barreiras group (Dominguez et al. 1990a) and the predominant soil is a sandy to loamy red-yellowed podsol (Schessl et al. 2008). The vegetation can be classified as lowland rainforest with transition to semideciduous forest (Veloso et al. 1991). Recently, 650 plant species from 379 genera and 102 families, of trees, shrubs, lianas, and herbs were documented in the study area (Alves-Araújo et al. 2008).

Sampling design

Seed traps were installed in seven different-sized forest fragments: four small (9-30 ha) and three large (306-389 ha) (Fig. 2.1b).

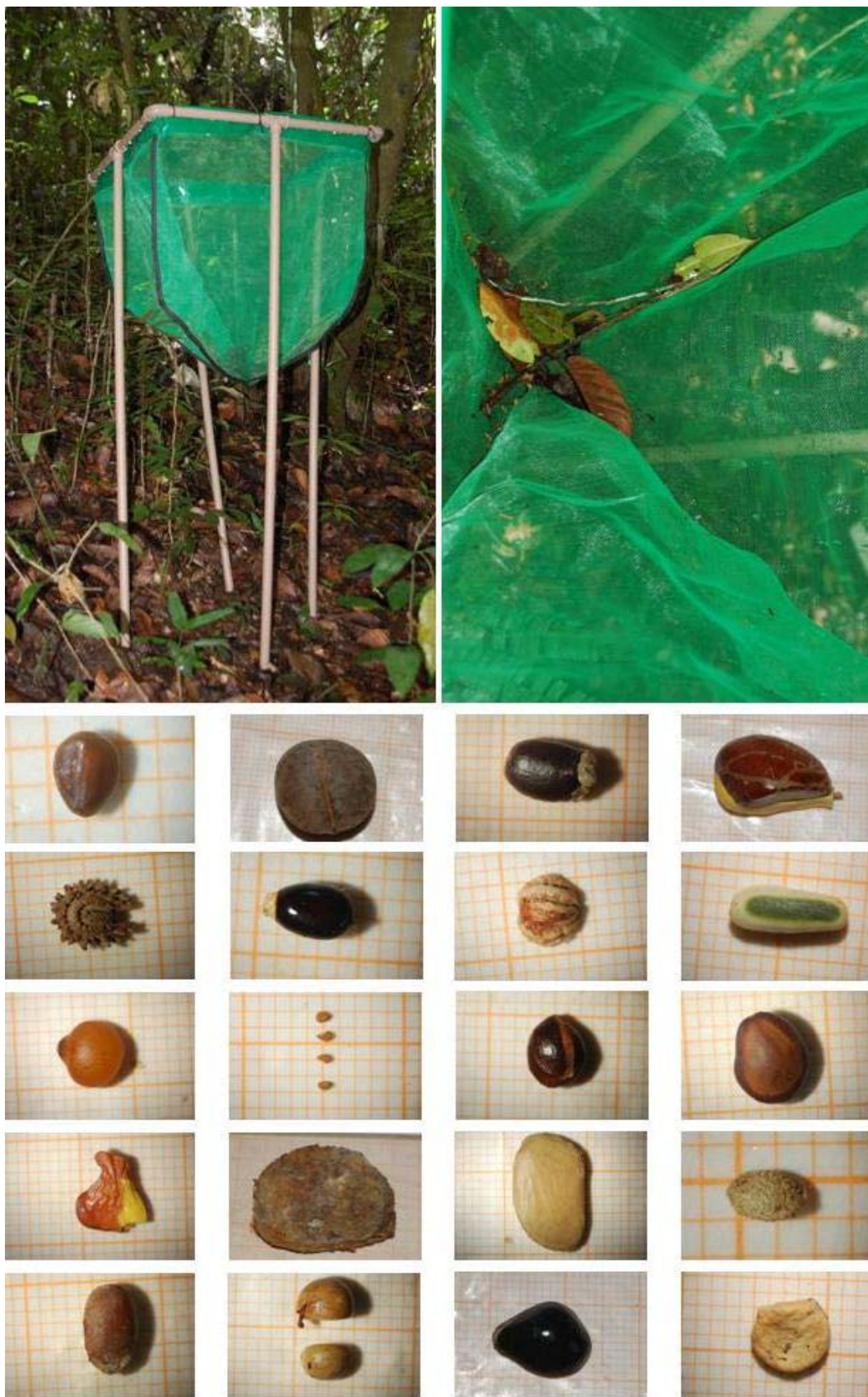


Figure 3.1 Top: seed trap and sample before collection with leaf litter; bottom: selection of seeds found in the traps (see appendix 3 for species names)

A frame of PVC tubes with a collecting area of 0.25 m² (0.5 x 0.5 m) with a mesh bag made out of mosquito net and a mesh-size of ≤ 1 mm was used as collecting device. The frame-construction was supported by four PVC tubes at approximately 1 m above the ground (Figure 3.1). This trap design is recommended for effective seed collecting because it prevents bouncing of the seeds (Stevenson and Vargas 2008). Within every fragment we put three lines of five traps. The distance between each trap in one line was always 10 m and the lines were at least 25 m away from each other. All traps were installed on slopes. Even though edge effects can alter forest structure up to 400 m (Laurance et al. 2002), we put all traps in all fragments at a distance of 60 m - 80 m from the nearest forest border in order to keep the design similar for all sites regardless of the size of the forest remnants, because the width of some small remnants did not even exceed 200 m at the widest point. The valleys of the fragments have been avoided because of their different species assemblages and forest structure. We also evaded early secondary vegetation patches within the fragments that show a different species composition as well. Independence of each individual trap was tested by applying a Mantel test based on distance matrices and 10,000 permutations to analyze if there is any spatial autocorrelation (Fortin and Gurevitch 2001). A positively spatially autocorrelation affects the estimation of degrees of freedom and the differences within groups will appear small, which can result in a type I error (Quinn and Keough 2002). The Mantel statistic was performed with XLSTAT 2009.5.01 trial version. Only within one fragment we detected a significant correlation but the r value, which is comparable to Pearson's r (Reynolds and Houle 2002), was below 0.3 and could consequently be neglected.

The samples were collected monthly and after drying, litter was separated from the seed/fruit fraction. The latter fraction was examined with a dissecting microscope and only apparently ripe seeds were considered, i.e. aborted seeds were sorted out. All fruits were opened to count the seeds². Seeds were weighed, counted, and measured. The seeds were assigned to family, genus, species, or morphospecies with the help of literature (Alves-Araújo et al. 2008, Barroso et al.

² In this study I emphasized the role of the seeds, i.e. the part of the diaspores that may have been epizoochourisly or synzoochorously dispersed and then establish at new sites

1999, Lorenzi 2002a, Lorenzi 2002b, Roosmalen 1985), herbarium collections (IPA), local taxonomists, and internet sources like live plant photos and herbarium vouchers (<http://fm2.fmnh.org/plantguides/>; <http://sciweb.nybg.org/science2/VirtualHerbarium.asp>). All species and morphospecies were classified as animal- or abiotically-dispersed (autochorous or anemochorous) based on fruit/seed structure, i.e. fleshy parts or wings, observations, and literature (Pijl 1969, Roosmalen 1985). Additionally, species were classified into four categories of seed size according to their longest length following Melo et al. (2006) except for their fifth category of very large seeds, because we collected only one species whose seeds were over 3 cm. The categories were (1) very small: < 0.3 cm; (2) small: 0.3-0.6 cm; (3) medium: 0.6-1.5 cm; and (4) large: > 1.5 cm. A sample of each (morpho-) species was photographed and stored as a reference collection.

Data Analysis

During the one year study some of the samples were lost due to trap destruction and even robbery of the traps. Since these were individual cases and there were sufficient replications we did not remove the data of the according months from the analysis. Besides, it was not possible because these events were randomly spread throughout the whole year. The numbers of seeds per trap was extrapolated (0.25 m²) to one m² for some of the results shown. To compare the number of seeds per trap in large and small fragments we calculated a GLM (Generalized linear models sensu McCullagh and Nelder 1999) simulated one way ANOVA. We applied GLM because our count data was not normally distributed. The habitat with two levels (large/small fragments) was the predictor for the number of seeds with traps as replicates (dependent variable). Since we had count data, the model was constructed for a Poisson distribution with a log-link function. When modeling count data the variance is often greater than the mean, i.e. the data is overdispersed. We corrected for overdispersion by multiplying the standard errors by $\sqrt{(\chi^2/df)}$ (Agresti 2007).

Furthermore, we determined the forest cover (sensu Fahrig 1997; see Table 3.1), i.e. the amount of forest habitat within a defined area, by calculating the percentage of forest, not including young secondary vegetation (*capoeira*), within a circle centered in the middle of each fragment with a radius of 1250 m.

3. Seed rain

The importance of FC on species abundance was tested applying linear regression. It is assumed that the amount of habitat cover is a determinant for species survival (Develey and Metzger 2006, Fahrig 1997).

The statistical analyses were performed with STATISTICA 6.1 (StatSoft. Inc. 2002).

Table 3.1 Some information on the forest fragments considered in the study

Name	Number on map (Fig. 2.1b, chapter 2)	Size [ha]	Forest cover [%]
Pézinho	8	30.6	14.7
Vespas	5	13.81	26.3
Gota	3	8.1	43.1
St. Helena	9	11.85	27.6
Macacos	6	331.12	60.2
Piedade	13	297.51	51.1
Zambana	1	387.85	60.9

A G-test (Sokal and Rohlf 1995) was applied to test differences among the two habitats (small/large fragments) in proportions of seeds and species within categories of seed size and the two dispersal modes (animal-dispersed and abiotically-dispersed).

For the comparison of the accumulation of species in small and large fragments during the one year of seed collection we calculated sample-based rarefaction. Since the observed number of species is usually a biased estimator of the accurate species richness (Chazdon et al. 1998), the rarefaction method estimates the number of species expected in a random number of individuals taken from a collection (Krebs 1989). Besides, this enabled us to compare the number of species of the two habitats with unequal sampling effort, as we included four small-sized fragments with 60 trap samples each month and only three large fragments with 45 trap samples each month in the study. Additionally, we calculated Chao 2 (Chao 1987) as a nonparametric estimator because it provides the best estimates for a small number of samples and it works with incidence data (presence/absence) (Chazdon et al. 1998). This way the large difference in the number of seeds between traps was not a problem for the calculation. We

calculated all diversity statistics using EstimateS (Version 8.20, R. K. Colwell, <http://purl.oclc.org/estimates>).

3.4 Results

General observations

Total seed rain included 20,518 seeds of 149 species, of which 102 were found in small and 105 in large forest remnants. The species with the highest number of seeds, i.e. 33% of all seeds collected, was the animal-dispersed pioneer tree *Cecropia palmata* (Cecropiaceae), followed by the wind-dispersed liana *Gouania virgata* (Rhamnaceae) in small fragments (20.4%) and the animal-dispersed pioneer tree *Schefflera morototoni* (Araliaceae) in large fragments (19.4%) (Table 3.2).

The average seed rain, including all trees, lianas, and herbs collected, was 65.1 seeds $\text{m}^{-2} \text{mo}^{-1}$ in all fragments (as measured with 0.25 m^2 traps), 80.5 seeds $\text{m}^{-2} \text{mo}^{-1}$ in small and 44.67 seeds $\text{m}^{-2} \text{mo}^{-1}$ in large fragments. The difference in the average number of seeds per trap between large and small fragments was significant (Table 3.3). This result must be due to the differences of seed fall between April and June, where small fragments received a considerable higher amount of seeds, because the difference was not as pronounced in the rest of the months (Fig. 3.1). However, in two months (March and October 2008), average seed rain was higher in large fragments. We registered a seasonality in the quantity of seeds with an elevated seed rain between December 2007 and June 2008 and a peak in March (large fragments) and April (small fragments). Apparently, the amount of seeds fallen into the traps increased with beginning of the rainy season, and decreased by the end of the rainy/beginning of the dry season (Fig. 3.2).

Table 3.2 All species with the highest number of seeds (=at least 10 seeds collected in the course of one year) in order of the most frequent named first. Life form subdivided into tree, treelet (includes shrubs), liana (includes woody lianas and vines), and herb. Extrapolated number of seeds m⁻² as measured with 0.25 m² seed traps. Seed size class: (1) very small: < 0.3 cm; (2) small: 0.3-0.6 cm; (3) medium: 0.6-1.5 cm; and (4) large: > 1.5 cm. Finally, dispersal mode: a (animal-dispersed), w (abiotically-dispersed). MS=morpho species.

FAMILY	Species	Life form	total number of seeds m ⁻²	number of seeds m ⁻² in small fragments	number of seeds m ⁻² in large fragments	seed size class	dispersal mode
CECROPIACEAE	<i>Cecropia palmata</i> Willd.	Tree	257.79	360.07	121.42	very small	a
RHAMNACEAE	<i>Gouania virgata</i> Reissek	Liana	112.42	148.53	64.27	very small	w
ARALIACEAE	<i>Schefflera morototoni</i> (Aubl.) Maguire, Steyerl. & Frodin	Tree	80.23	62.33	104.09	small	a
MYRTACEAE	<i>Calyptanthes</i> cf. <i>brasiliensis</i> Spreng	Treelet	42.90	75.07	0	small	a
DILLENIACEAE	<i>Dolichocarpus dentatus</i> (Aubl.) Standl.	Liana	40.19	43.93	35.20	small	a
MELASTOMATACEAE	<i>Miconia</i> cf. <i>francavillana</i> Cogn.	Tree	35.66	0.33	82.76	small	a
EUPHORBIACEAE	<i>Pogonophora schomburgkiana</i> Miers ex Benth.	Tree	32.91	41.33	21.69	small	a
MS 72			22.86	31.80	10.93	medium	a
MELASTOMATACEAE	<i>Mikonia prasina</i> (SW.) DC.	Treelet	20.72	36.20	0.09	very small	a
CECROPIACEAE	<i>Cecropia pachystachya</i> Trécul	Tree	18.21	30.80	1.42	very small	a
MALPIGHIACEAE	sp. 1	Liana	12.57	16.20	7.73	small	w
ANNONACEAE	<i>Xylopia frutescens</i> Sieb. ex Presl	Tree	11.01	19.27	0	medium	a
MS 112			11.01	5.07	18.93	small	a
MALPIGHIACEAE	<i>Byrsonima sericea</i> DC.	Tree	8.30	13.67	1.16	small	a
FABACEAE	<i>Apuleia leiocarpa</i> (Vogel) J.F. Macbr.	Tree	6.63	6.80	6.40	medium	w
SIMAROUBACEAE	<i>Simarouba amara</i> Aubl.	Tree	4.46	2.20	7.47	medium	A

Table 3.2 *continued*

FAMILY	Species	Life form	total number of seeds m ⁻²	number of seeds m ⁻² in small fragments	number of seeds m ⁻² in large fragments	seed size class	dispersal mode
MELASTOMATACEAE	<i>Henriettea succosa</i> (Aubl.) DC.	Tree	4.27	6.07	1.87	very small	a
MS 5			3.62	6.07	0.36	small	a
ASTERACEAE	<i>Mikania obovata</i> DC.	Liana	3.35	5.27	0.80	small	w
RANUNCULACEAE	<i>Clematis dioica</i> L.	Liana	2.82	0.47	5.96	small	w
MS 194			2.74	3.73	1.42	small	a
POLYGONACEAE	<i>Coccoloba</i> sp.1		2.29	2.00	2.67	small	a
MS 225			2.21	1.27	3.47	medium	a
SOLANACEAE	<i>Solanum</i> sp.	Shrub	2.17	3.27	0.71	very small	a
ANACARDIACEAE	<i>Tapirira guianensis</i> Aubl.	Tree	2.17	3.13	0.89	medium	a
FABACEAE	<i>Pterocarpus violaceus</i> Vogel	Tree	2.17	3.8	0	medium	w
FABACEAE	<i>Bowdichia virgilioides</i> Kunth	Tree	1.83	3.2	0	medium	w
MELIACEAE	<i>Trichilia lepidota</i> Mart.	Tree	1.68	0.07	3.82	small	a
MYRTACEAE	<i>Psidium guianense</i> Sw.	Treelet	1.56	2.27	0.62	very small	a
MS 36			1.56	2.73	0	medium	a
ANNONACEAE	<i>Anaxagorea dolichocarpa</i> Sprague & Sandwith	Treelet	1.41	2.33	0.18	medium	w
FABACEAE	<i>Macrosamanea pedicellaris</i> (D.C.) Kleinhoonte	Tree	1.41	1.4	1.42	small	W

Table 3.2 *continued*

FAMILY	Species	Life form	total number of seeds m ⁻²	number of seeds m ⁻² in small fragments	number of seeds m ⁻² in large fragments	seed size class	dispersal mode
MS 86			1.26	0.53	2.22	medium	A
MORACEAE	<i>Brosimum guianense</i> (Aublet) Huber	Tree	1.22	0.2	2.58	medium	A
MALPIGHIACEAE	sp. 2	Liana	1.22	2.13	0	small	w
FABACEAE	<i>Senna macranthera</i> (DC. ex Collad.) H.S. Irwin & Barneby	Treelet	1.14	2	0	small	a
PASSIFLORACEAE	<i>Passiflora</i> sp. 1	Liana	1.03	1.73	0.09	small	w
SAPOTACEAE	<i>Pouteria</i> sp. 1	Tree	0.91	0	2.13	large	a
POACEAE	sp.1	Herb	0.88	1.53	0	very small	a
APOCYNACEAE	<i>Himatanthus phagedaenicus</i> (Mart.) Woodson	Tree	0.84	1.07	0.53	medium	W
RUBIACEAE	<i>Psychotria carthagenensis</i> Jacq.	Treelet	0.8	0.67	0.98	small	a
MS 226			0.8	0	1.87	medium	a
FABACEAE	<i>Diplotropis</i> cf. <i>incexis</i> Rizzini & A. Mattos	Tree	0.72	0	1.69	medium	w
DILLENIACEAE	<i>Davilla</i> cf. <i>kunthii</i> A. St.-Hil.	Liana	0.72	0.8	0.62	very small	a
MALPIGHIACEAE	<i>Niedenzuella</i> cf. <i>acutifolia</i> (Cav.) W.R. Anderson	Liana	0.72	1.27	0	small	w
SAPINDACEAE	<i>Serjania salzmänniana</i> Schltr.	Liana	0.72	1	0.36	medium	W
MS 207			0.65	0.07	1.42	medium	A
MS 185			0.61	0.6	0.62	small	a

Table 3.2 *continued*

FAMILY	Species	Life form	total number of seeds m ⁻²	number of seeds m ⁻² in small fragments	number of seeds m ⁻² in large fragments	seed size class	dispersal mode
MS 29			0.50	0.53	0.44	very small	a
MS 7			0.42	0.73	0	small	a
CHRYSOBALANACEAE	<i>Hirtella racemosa</i> Lam.	Treelet	0.42	0.67	0.09	medium	a
RUBIACEAE	<i>Palicourea marcgravii</i> A. St.-Hil.	Treelet	0.42	0.13	0.8	small	a
CURCUBITACEAE	<i>Psiguria triphylla</i> (Miq.) C. Jeffrey	Liana	0.38	0.53	0.18	medium	a
LECYTHIDACEAE	<i>Eschweilera ovata</i> (Cambess.) Miers	Tree	0.38	0.53	0.18	large	a

Table 3.3 *GLM results for the number of seeds per trap within two habitats (small and large fragments)*

Effect	df	Wald (χ^2)	p
Intercept	1	1111.825	>0.001
Fragment size	1	14.645	>0.001

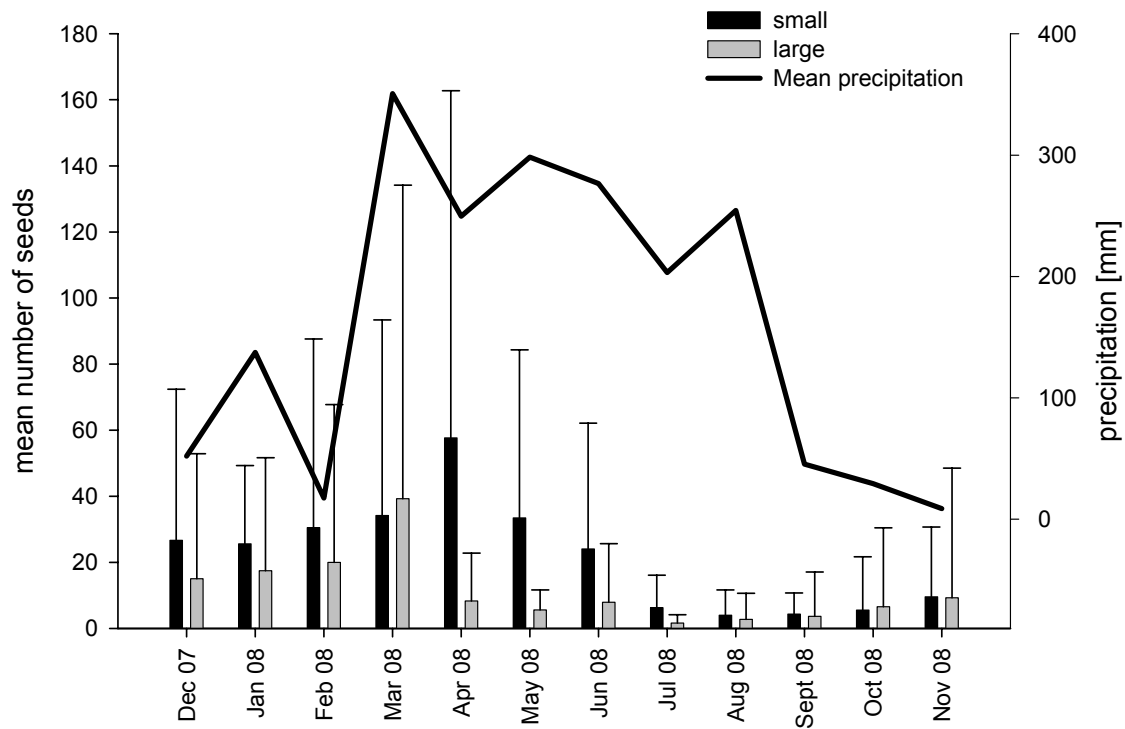


Figure 3.2 Mean and standard deviation of the number of seeds per month in small and large forest fragments and mean monthly precipitation

Species richness

The species number differed little between small and large fragments, but considering the unequal sample size, the difference was bigger. This is shown by the rarefaction curves and Chao 2 estimators for the cumulative number of species (Fig. 3.3). The Chao 2 estimator indicates that the expected species richness in large fragments was 183.15 ± 30.79 spp. and hence considerably higher than in small fragments (166.8 ± 30.84 spp.).

Size and dispersal pattern

Small and large forest fragments differed significantly in the proportion of seeds ($G = 14.658$, $df = 3$, $p = 0.002$) and species ($G = 9.608$, $df = 3$, $p = 0.022$) within different categories of seed size.

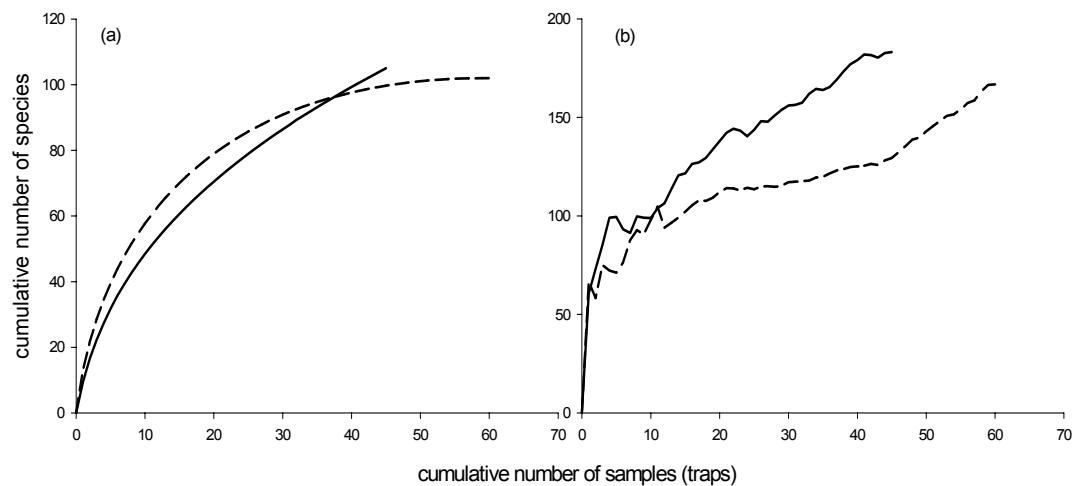


Figure 3.3 (a) Sample-based rarefaction curve (=expected species accumulation curve) and (b) Chao 2 richness estimator for the cumulative number of species. Solid lines: large forest fragments; dashed lines: small forest fragments.

We registered more large-seeded and less small-seeded species in the seed rain of large fragments than in small fragments (Fig. 3.4b) and 61.17% of the seeds collected in small fragments were very small, by contrast in large fragments, this group of seeds only contributed 35.9% to all collected seeds (Fig. 3.4a).

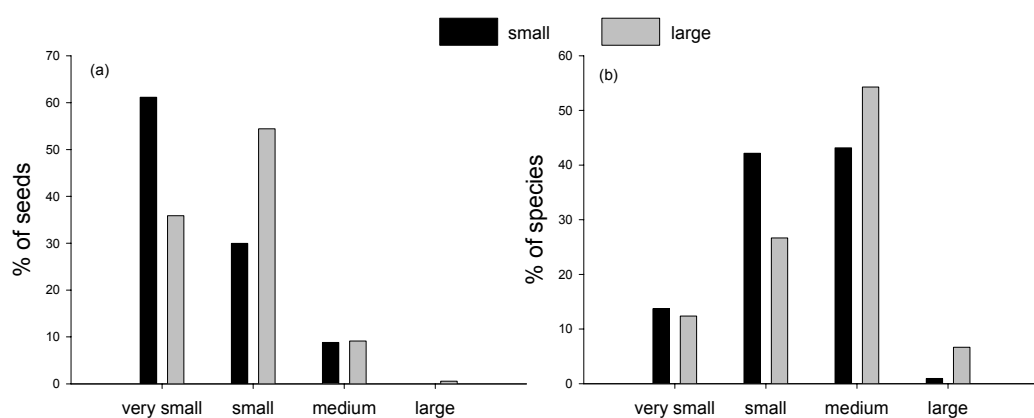


Figure 3.4 Percentage of seeds (a) & species (b) in small (black columns) and large (grey columns) forest fragments within different seed size classes

3. Seed rain

There were only seven large-seeded species in the seed rain of all habitats and all seven species were collected in large fragments but only one of these in small fragments, which was the common tree *Eschweilera ovata* (Lecythidaceae). The other large-seeded species were a *Pouteria* species (Sapotaceae), *Symphonia globulifera* (Clusiaceae), *Andira nitida* (Fabaceae), *Thyrsodium spruceanum* (Anacardiaceae), and one unidentified species, which are all animal-dispersed. However, there was also one wind-dispersed large-seeded species, the sub-canopy tree *Aspidosperma spruceanum* (Apocynaceae).

In general, most species and seeds were dispersed by animals (81.88% and 80.66% respectively) and we did not detect a significant difference between the two categories of fragment size (Table 3.4).

Table 3.4 Proportion of animal- and abiotically-dispersed seeds and species in all habitats (total) and small and large fragments

	total	small	large	G	df	p
% of species						
animal-dispersed	81.88	78.43	81.90	0.38	1	0.54
abiotically-dispersed	18.12	21.57	18.10			
% of seeds						
animal-dispersed	80.65	79.64	83.08	0.39	1	0.53
abiotically-dispersed	19.35	20.36	16.92			

The distribution of animal- and abiotically-dispersed species within the four seed size classes was significantly different comparing the two categories of fragment size. Small fragments received more very small- and small-sized species than large fragments and large fragments more medium- and large-sized species than small fragments that were zoochorous (Fig. 3.5a). Most animal-dispersed species were medium-sized. The same pattern but less pronounced was found for abiotically-dispersed species (Fig. 3.5b). Nevertheless, there was no difference in the distribution within the seed-size categories of the relative number of seeds between the two habitat types.

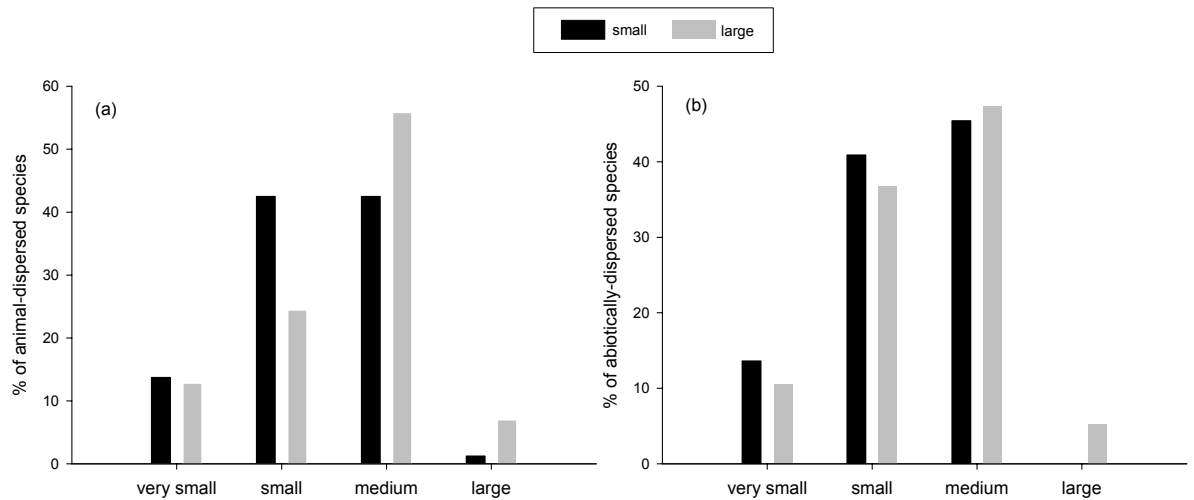


Figure 3.5 *Percentage of animal- (a; $G = 11.185$, $df = 3$, $p = 0.01$) and abiotically- (b; $G = 7.95$, $df = 3$, $p = 0.047$) dispersed seeds in small (black columns) and large (grey columns) forest fragments within different size classes*

The relationship between the percentage of forest cover (FC) and the percentage of very small-seeded and large-seeded species at the particular sites shows the importance of the forest cover as a good determinant for species occurrence (Fig. 3.6). The lower FC was the higher was the percentage of small-seeded species and the higher FC was the higher was the amount of large-seeded species. These relationships were both significant and explained 57% and 71%, respectively, of the variation in the data.

3.5 Discussion

Our findings underline that fragmentation leads to a biased, impoverished seed rain, especially in small fragments. We registered a dominance of very small-sized seeds and almost a lack of large-seeded species in the seed rain of small fragments. But both fragment size classes received a relatively high number of very small and small seeds. In small fragments we found a considerably higher number of seeds per month. Seed fall was highest at the beginning of the raining season when conditions for seed germination are most favorable (Foster 1982).

3. Seed rain

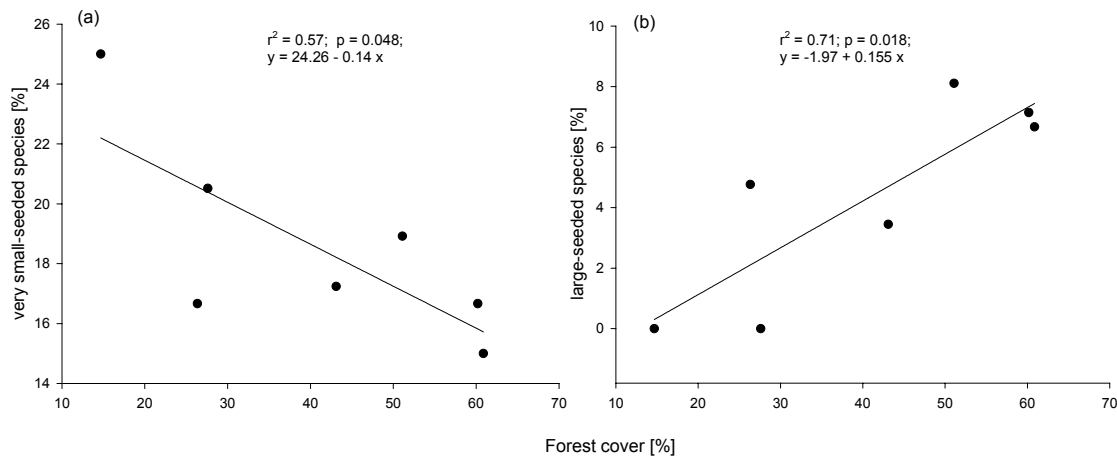


Figure 3.6 Relationship between the percentage of very small- (a) and large-seeded (b) species and the forest cover

The degree of isolation of a fragment played a major role in the proportion of species of different size-classes, i.e. the more isolated (=little FC) the smaller the chance a large seed reached a trap either by wind or by animal. We looked at the forest cover at a relatively small scale, only for the surrounding area of 1250 m radius centered in each fragment. However, the 20% habitat cover Fahrig (1997) suggested as a species survival threshold seems also to play a role for the subsistence of large-seeded species. This may be explained by the fact that many medium- to large-bodied mammals but also birds, which may play an important role as dispersers, depend on a minimum of habitat to survive (Develey and Metzger 2006).

The general pattern of the proportion of animal- to abiotically-dispersed species was similar to the numbers Howe & Smallwood (1982) suggested for fruits that are adapted to animal consumption in tropical forests. But the proportions within seed size categories were strongly biased to animal-dispersed small-sized seeds. Small and very small seeds, respectively, are often of pioneer trees that are dispersed by birds or bats and are usually not threatened by dispersal limitations. Instead they apparently proliferate in fragmented landscapes (Michalski et al. 2007). And indeed, the most common species in the seed rain of both small and large fragments was the pioneer tree *Cecropia palmata*. Still,

Cecropia seed rain was comparatively more abundant in small fragments (Knörr et al., unpubl.). The second most frequent species in small patches was *Gouania virgata*, a wind-dispersed liana that was also very common in seed bank studies of a semi-deciduous forest in southeastern Brazil (Grombone-Guaratini and Rodrigues 2002). This can be explained by the typically high abundance of lianas at disturbed sites and forest edges (Laurance et al. 2001). In large fragments *Schefflera morototoni* was the second most frequent species, which is also considered a fast growing pioneer typically found in large light gaps or disturbed areas and mostly dispersed by birds (Crow and Grigal 1979). The number of species and seeds that are large-seeded is appallingly low; in small fragments we even only found one species. This species is *Eschweilera ovata*, a very common species in the region (Mori 1995) that shows vegetative regeneration after tree cutting (personal observation). It can be classified as a climax species as well as a pioneer, because it is abundant in well and badly preserved forest fragments (Ferraz and Rodal 2006, Kimmel et al. 2010) and can be used for the recuperation of degraded areas (Lorenzi 2002b). It is dispersed by scatterhoarding rodents and also by frugivorous bats (Lorenzi 2002b).

In a study of a large northeastern Atlantic Forest fragment (Melo et al. 2006) the seed rain of interior and edge habitat was compared. It revealed similar but less pronounced results for the edge habitat as we found for small fragments. Small forest fragments seem to be more threatened as edge habitat per se. Studies about species composition in Amazonian forest fragments revealed comparable trends, i.e. large fragments maintained a higher abundance of hardwood trees and small-seeded pioneers proliferated in small fragments (Laurance et al. 2006, Michalski et al. 2007).

Considering the number of species we found in the course of one year, it seems very low comparing it with the number of species Melo et al. (2006) found in only one large Atlantic Forest fragment. They collected 146 species during one year. This is only three species less than we collected within seven fragments in the same amount of time. Maybe this is due to their higher sampling effort but also because the fragment they worked in is one of the largest fragments of the Atlantic forest of Northeast Brazil and it comprises some rare large-seeded trees (Oliveira et al. 2004). The expected number of species, determined by the Chao 2 estimator, was higher in large fragments than in small fragments. This can be a

result of a species-area relationship (Plotkin et al. 2000) and also acts in concert with the other results shown. This impoverishment of species assemblages found in our seed rain study could be caused by (1) a lack of dispersal, (2) wood extraction, and (3) a high tree mortality. A decrease of dispersal of large-seeded species and a proliferation of small-seeded species in disturbed areas and small fragments in particular due to a higher hunting pressure has already been shown by various authors (Cramer et al. 2007, Galetti et al. 2006, Melo et al. 2010). In the study area we tested the activity of ground dwelling animals and seed removal in differently disturbed and sized forest fragments and showed that in preserved and larger patches the probability of dispersal was much higher (see chapter 6). By contrast, Kimmel et al. (2010) found relatively many large-seeded species in secondary vegetation (*capoeira*) in the region. However, they argue that more than the half of those are consumed by humans (e.g. *Talisia esculenta*, Sapindaceae) and may have been introduced this way. The only larger primate in the study area that may be a good seed disperser, a capuchin monkey (*Cebus flavius*), is restricted to only one forest patch (*Macacos*). Unfortunately, further studies about mammal diversity are missing for the study area. Wood extraction is also a serious problem in the study area and we found a higher amount of multiple-stemmed trees that can be a result of tree cutting in small fragments than in large fragments (Knörr et al. in prep.). Logging is not only a direct reason for the lack of slow-growing hardwood trees but also positively correlates with the abundance of small-seeded pioneers (Michalski et al. 2007). A higher tree mortality of fruit bearing emergent trees in forest fragments has been proved in the Amazonian Forest (Laurance et al. 2000) and may also be a problem in the region.

Ultimately, our results are alarming and reflect the situation of the northeastern Atlantic Rainforest with an impoverishment of species assemblages and a threatened fauna (Melo et al. 2006, Silva and Pontes 2008, Tabarelli et al. 1999). Despite two of the large fragments on the sugarcane plantation USJ are much longer isolated than most of the small fragments they preserved more large-seeded species. This can be misleading insofar that these trees are still present but do not have a high potential to be dispersed far from the mother tree and even less between forest patches. Only by connecting patches with forest corridors to increase movement of large frugivores like the endemic highly endangered *Cebus*

flavius would help to preserve tree and animal diversity. We suggest that studies on dispersal in this region are necessary to learn more about the reasons for the patterns found.

4 Pioneer trees in the seed rain of Atlantic Forest fragments: the case of two *Cecropia* species

4.1 Abstract

The effects of forest fragmentation are numerous and the impoverishment of forest fragments through the proliferation of successional trees is perhaps one of the most threatening of these. Using the seed rain of *Cecropia pachystachya* and *Cecropia palmata*, we investigated whether there were differences with gradients in fragment size and disturbance. We collected fruits with seed traps over a one-year period in different-sized forest fragments, which were surrounded by a sugarcane matrix. We modeled the annual number of seeds against vegetation and landscape structure predictors that could possibly explain the variations in *Cecropia* seed rain in forest fragments. Average annual number of seeds per m² ranged from 42 to 998 among the seven sites and was significantly higher in smaller fragments than in the larger fragments ($F=42.3$; $p < 0.001$). A multiple regression model was significant and explained 57% ($r^2=0.57$) of the variation in the response variable. Forest fragments that were more disturbed and isolated had a higher inflow of *Cecropia* seeds. Our study demonstrates the importance of forest fragment size on the proliferation of secondary tree species in agricultural tropical landscapes.

4.2 Introduction

Tropical forests across the whole world suffer from human disturbance and habitat fragmentation. This is especially the case with the Brazilian Atlantic Forest, which has experienced great habitat loss since the 16th century, mostly due to agricultural exploitation, especially for monoculture sugarcane plantation (Dean 1995, Young 2003). In particular, the north-eastern part of the Atlantic Forest is highly fragmented and still experiencing loss of forest area. Nowadays only 12.1% of the original, pre-settlement Atlantic Forest cover remains in the north-eastern Pernambuco area, including restinga, mangrove forest, and forests in early successional stages (Kimmel et al. 2008, Ribeiro et al. 2009). Thus, the

Brazilian Atlantic Forest is one of the most threatened ecosystems in the world (Myers 1988). It is known for its high plant biodiversity and high rate of endemism (Mori et al. 1981, Myers et al. 2000) but fragmentation processes lead to an alteration of species composition and ecological processes (Girão et al. 2007, Laurance et al. 2002, Santos et al. 2008, Tabarelli et al. 1999). One especially alarming phenomenon is the impoverishment of forest fragments by the proliferation of early successional trees (Laurance et al. 2006, Tabarelli and Lopes 2008). The increase in importance of this group of trees could result from various processes. Firstly, a serious problem is the extinction of mammals and birds that function as important seed dispersers, especially for large-seeded climax trees (Silva and Tabarelli 2000, Wright et al. 2007). The north-eastern Brazilian Atlantic Forest is probably one of the most threatened areas with at least eight critically endangered terrestrial vertebrates (Brooks and Rylands 2003). The remaining small-bodied birds and mammals, like fruit-eating bats, disperse mainly small-seeded pioneer trees like *Cecropia* and *Miconia* species (Garcia et al. 2000). Secondly, there is always a higher risk of illegal selective logging and the harvesting of old-growth trees for firewood (Tabarelli et al. 2005), thus raising the proportion of early successional species. Thirdly, the reason for the proliferation of successional trees and thus a decline in climax trees could also be the consequence of an increased seed rain from successional trees and elevated mortality of climax trees in forest fragments caused principally by edge effects (Laurance et al. 2006, Laurance et al. 2000). Moreover, these effects of fragmentation, which lead to an impoverished assemblage of species interact synergistically (Laurance and Cochrane 2001). Finally, the structure of the fragmented landscape, e.g. the size of forest fragments, their shape, and their degree of isolation may also play an important role in this context (Hill and Curran 2003, Metzger et al. 2009).

We selected *Cecropia palmata* and *Cecropia pachystachya* as exemplars of pioneer species and surveyed the seed rain of the two species in small and large Brazilian Atlantic Forest fragments. The forest fragments that we sampled had different degrees of disturbance and isolation. This allowed us to explore the reasons for the increased density of successional trees in forest fragments. We chose the genus *Cecropia* because it is the most important Neotropical genus of fast-growing pioneer trees (Swaine and Whitmore 1988, Zalamea et al. 2008).

These trees settle rapidly on degraded areas and forest edges, and produce a large amount of small fruits (Alvarez-Buylla and Martínez-Ramos 1990, Fleming and Williams 1990, Lobova and Mori 2004, Válio and Scarpa 2001). Furthermore, *Cecropia* trees benefit the most after fragmentation has occurred. *Cecropia sciadophylla* for example increased over 1000% in density in Amazonian forest fragments 15 years after fragmentation (Laurance et al. 2006).

4.3 Material and Methods

Study area

The study was carried out at the Usina São José (USJ) (07°41'04,9" to 07°54'41,6"S and 34°54'17,6" to 35°05'07,2"W), a sugarcane plantation located 50 km north of Recife, capital of the federal state of Pernambuco, Northeast Brazil (Fig. 2.1). The bedrock is a Tertiary conglomerate on beach-ridged terraces of the Barreiras group (Dominguez et al. 1990b) and the predominant soil is a sandy to loamy red-yellowed podsol (Schessl et al. 2008). The climate is tropical with a rainy season between January and August and a marked dry season ($<100 \text{ mm mo}^{-1}$) between September and December (Schessl et al. 2008). The annual rainfall is around 1500 mm but there are strong variations ranging from 770 mm in 1998 to 2960 mm in 2004. Rainfall also varies greatly across the region: the coastland receives 2600 mm, whereas just 11 km inland, there is a rainfall of 1520 mm. The mean annual temperature is 25°C (Schessl et al. 2008). The total forest cover of the Usina São José is around 6600 ha (27% of the total area) and is comprised of 110 forest remnants, which are mostly irregularly shaped (Trindade et al. 2008). The surrounding matrix consists exclusively of sugarcane fields and thus there is a sharp boundary line between these two ecosystems that hardly share any plant or animal species (Ranta et al. 1998). After Veloso et al. (1991), the vegetation can be classified as lowland rain forest with transition to semideciduous forest. There are over 200 species of trees and treelets and more than 250 species of herbs and shrubs documented in this area (Alves-Araújo et al. 2008).

Seed rain sampling design

The seed rain assessment was carried out over a period of one year between December 2007 and November 2008. We chose seven forest fragments of varying sizes in order to show possible differences in seed dispersal of the two pioneer species *Cecropia palmata* Willd. and *Cecropia pachystachya* Trécul (Cecropiaceae), among the studied fragments. In a study on species composition and forest structure that took place in six of the seven studied fragments was not found a single *Cecropia* individual in the forest interior, between 50 and 100 m away from the forest edge, and in the edge zone (0-50 m from the forest border) were documented an average of 3.5% *Cecropia* trees (Lins-e-Silva, unpublished data). No *Cecropia* trees were located in the direct neighborhood of any of the traps. Large fragments ranged between 298 ha and 388 ha, and the four small fragments between 8 ha and 31 ha. Figure 2.1b in chapter 2 shows the distribution of all patches on the sugarcane plantation. A total number of 105 seed traps were installed in these fragments, 15 within each fragment. There are few studies which address the effectiveness of different trap designs, but Stevenson & Vargas (2008) recommend mesh traps on a PVC frame in order to avoid bouncing effects. We also applied this method by constructing a frame of PVC tubing with a collecting area of 0.25 m² (0.5 x 0.5 m) and with a mesh bag made out of mosquito net with a mesh-size of ≤ 1 mm. The frame-construction was supported by four PVC tubes 1 m above the ground. Within every fragment, there were three lines of five traps (groups) and these lines were at least 25 m away from each other. The distance between each trap in one line was always 10 m (Fig. 2.3, chapter 2). All traps were installed on slopes. Even though edge effects can alter forest structure up to 400 m (Laurance et al. 2002), we installed all traps in all fragments at a distance of 60 m - 80 m from the nearest forest border, because the width of some small remnants did not even exceed 200 m at the widest point and we wanted to keep the design similar for all sites regardless of forest fragment size. We avoided putting the traps in the valley of the fragments because of their different tree species assemblages and forest structure. Besides this, we also avoided any early secondary vegetation patches within the fragments that showed a different species composition. Independence of each individual trap was tested by applying a Mantel test based on distance matrices and 10,000 permutations to analyze if there was any spatial autocorrelation (Fortin and Gurevitch 2001). A positive spatial

autocorrelation affects the estimation of degrees of freedom and the differences within groups will appear small, which can result in a type I error (Quinn and Keough 2002). The Mantel statistic was performed with XLSTAT 8.6.01 trial version. Within three of the seven studied fragments we detected significant autocorrelation, but the values for r , which is similar to a Pearson's r (Reynolds and Houle 2002), were equal or below 0.3. This indicates only a weak correlation (Fowler et al. 1998). Fortin & Gurevitch (2001) had comparable p - and r -values for their data set and claimed that there was no spatial autocorrelation. Furthermore, direct seed rain cannot occur because of the absence of *Cecropia* trees within a radius of at least 50 m around the seed traps. Besides, the possibility of dispersal underneath or close to the mother tree is unlikely, since e.g. Alvarez-Buylla & Martinez-Ramos (1990) found that the spatial distribution of dispersed fruits of *Cecropia obtusifolia* in Mexico is highly heterogeneous and Fleming & Williams (1990) argue that most vertebrates spend little time at *Cecropia* trees before moving away.

The content from the traps was collected monthly over the one-year period. After drying the samples in an oven at 60°C for at least 24 h, the samples were initially sorted to remove large litter. Finally, the small litter and the remaining fruit/seed items were separated from the *Cecropia* fruits using a dissecting microscope. The fruits were then counted, measured, and weighed. The dispersal unit of the genus *Cecropia* is not the seed but the fruit; dispersers consume the infructescence, digest the pulp derived from the fleshy perianth, and defecate the fruit (Lobova et al. 2003). However, even if the item that is dispersed is technically a fruit we will talk about *Cecropia* seeds. *Cecropia* species are mostly dispersed by bats, birds, and monkeys (Roosmalen 1985).

Landscape and disturbance metrics

We calculated landscape metrics, which can possibly explain the pattern of the distribution of *Cecropia* seeds. We determined the forest cover (FC) (Develey and Metzger 2006) for every fragment i.e. calculating the percentage of forest, not including young secondary vegetation (*capoeira*) within a circle centered in the middle of each fragment with a radius of 1250 m. We also calculated the interior-to-edge ratio (IERATIO) (Forman and Godron 1981), and the clusters that indicate the area of fragments separated by gaps less than 20 m wide (CLU20)

(Metzger et al. 2009). For all GIS-based computations, we used satellite images with high spatial resolution (4m) (Trindade et al. 2008) that were geo-referenced. The calculations were performed with GPSU 4.2. Besides, vegetation structure was documented for every sampling site by measuring the diameter at breast height (dbh) and height of trees with a dbh ≥ 5 cm within a circle with a radius of 5 m centered in the middle of every seed trap (Barbosa and Pizo 2006). We then calculated the mean of both parameters (MDIAM, MHEIGHT) and added up the number of tree individuals for each group of five traps (NOIND). Within these circular plots, we additionally documented if the trees were multiple-stemmed (MSTEM) as a consequence of stem-borne shoots after tree cutting (Dunphy et al. 2000) and assigned the percentage of multiple-stemmed individuals of an entire fragment as a disturbance index.

Data analysis

Differences in the number of *Cecropia* seeds between small and large fragments were tested using analysis of variance (single factor ANOVA). We decided to add up the number of seeds for 12 months rather than considering every month as one replicate and summed up *Cecropia* seeds of an entire group of five traps to avoid autocorrelation in time and space and to minimize zero counts. Accordingly, our response variable was the annual number of *Cecropia* seeds per group of five traps. To match parametric assumptions, data of our dependent variable was \log_{10} -transformed. Furthermore, we applied multiple linear regression models to analyze the relationship between *Cecropia* seed rain distribution and structural, landscape, and disturbance metrics. Aside from the complete additive model, we applied the best subset method to find the smallest subset of predictors that best explain the variation in the response variable. We used Mallows' C_p , which compares a specific reduced model to the full model (Quinn and Keough 2002), to determine the fit of the model. As predictors, which potentially explain the variation in the response variable, we used the variables FC, IERATIO, CLU20, MDIAM, MHEIGHT, NOIND, and MSTEM. We chose the IERATIO (interior-to-edge ratio) metric rather than the absolute area of the fragments because firstly, we already have a size comparison by comparing large and small fragments with the analysis of variance and secondly IERATIO possibly better expresses the

importance of successional trees in forest edge species assemblages. All statistical analyses were performed with STATISTICA 6.1 (StatSoft. Inc. 2002).

4.4 Results

In total, we collected 7245 *Cecropia* seeds during the 12 months of surveying, the major part were *C. palmata* seeds and only 6.6% (478) were *C. pachystachya* seeds. 102 out of 105 traps had at least one *Cecropia* seed in the course of the year. The three traps without seeds were all within large forest fragments. In 2008, the fruiting peak was during March. March marks the onset of the rainy season and has the highest precipitation of 345 mm (USJ/unpubl. data). Seeds were not continuously available. In October, during the dry season, we did not find any *Cecropia* seed. Average annual seed rain per m² (as measured by 0.5 x 0.5 m seed traps) varied from 42 ± 58 to 998 ± 1250 (mean \pm SD) among the seven sites. Figure 4.1 shows the variation of *Cecropia* seed rain within the forests across the fragments.

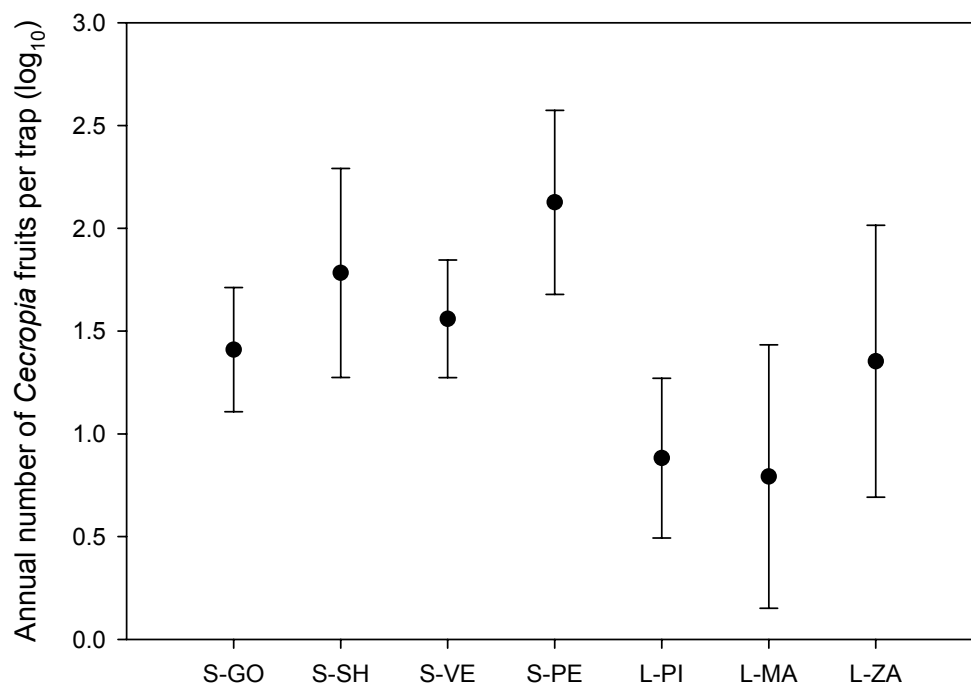


Figure 4.1 Number *Cecropia* fruits (Mean \pm SD) in the four small (S) and three large (L) forest fragments

Small and large fragments differed significantly in the mean number of *Cecropia* seeds per trap and year (one-way ANOVA: $F=42.3$; $p<0.001$). We collected 31 ± 61 in large fragments and 98 ± 188 seeds (mean \pm SD) in small fragments per trap and year.

Table 4.1 ANOVA table of the full additive and the best model

	df	MS	F	p
<i>Full additive model</i>				
Regression	6	0.63	3.09	0.04
Residual	14	0.21		
<i>Best model (FC×MSTEM×IERATIO)</i>				
Regression	3	1.21	6.78	0.003
Residual	17	3.04		

The fragmentation index forest cluster (CLU20) was highly correlated with the other variables and the tolerance value was unacceptably low (< 0.1). Therefore we excluded this predictor variable to avoid collinearity. The full additive model i.e. the combination of the six remaining predictor variables was highly significant (Table 4.1) and explained 57% ($r^2=0.57$) of variation in the dependent variable, the annual number of seeds per group. Only the regression coefficient of the predictor variable forest cover (FC) was significant in the full model. The relatively high value indicates its high relative importance in the explanation of the model. It implies that the lower the percentage of forest cover was, the higher the chance that a *Cecropia* seed reached this specific site; FC ranged from 15 to 61%. The simple linear regressions of the variables (Fig. 4.2) also show the explanatory value of the forest cover (FC), which explains 41% ($r^2=0.41$) of the variation in the data. The number of multiple-stemmed trees explains 29% and the interior-to-edge ratio 16% of the variation of *Cecropia* seed rain between groups of traps.

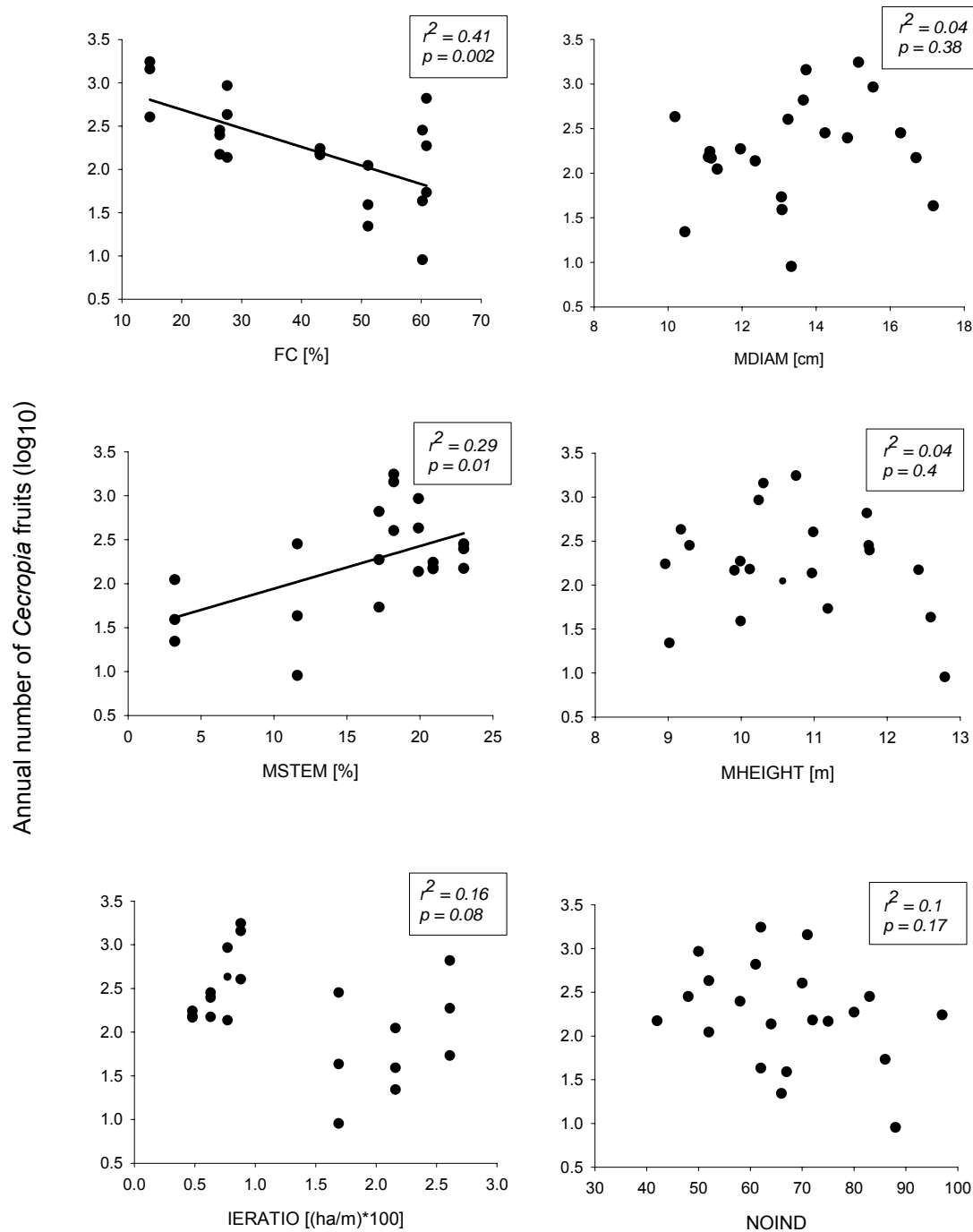


Figure 4.2 Relationship between the six predictor variables and the annual number of *Cecropia* fruits per group of five traps (log₁₀)

We found a negative relationship, which was not significant, between the relative amount of interior habitat and the number of *Cecropia* seeds, i.e. the more border habitat the higher the *Cecropia* seed rain (Fig. 4.2). Nevertheless, it was

inconsistent between the groups of fragment size, which was also reflected by the change in sign of the β coefficients of the IERATIO in the multiple regression models compared to the single regression (Table 4.2). The best subset selection reveals the same trend; the predictor variables FC, MSTEM, and IERATIO were included in the best model. The r^2 (0.54) of the best model is just a little below the r^2 -value of the full additive model i.e. it explained 54% of the variation in *Cecropia* seed rain. The tree diameter, tree height, and the number of trees at the sampling site did not influence the dispersal of the seeds.

Table 4.2 Parameter estimates of the full additive and the best model

	β	t	p
<i>Full additive model</i>			
Intercept		2.31	<0.05
FC	-0.686	-2.22	<0.05
MSTEM	0.483	1.96	0.067
IERATIO	0.509	1.63	0.126
MDIAM	0.125	0.49	0.635
MHEIGHT	-0.213	-0.89	0.39
NOIND	-0.018	-0.08	0.935
<i>Best model (FC×MSTEM×IERATIO)</i>			
Intercept		4.0	<0.001
FC	-0.769	-3.06	0.007
MSTEM	0.469	2.12	<0.05
IERATIO	0.503	1.75	0.098

4.5 Discussion

Cecropia palmata and *C. pachystachya* seeds were not continuously available; both had a pronounced fruiting peak and their presence varied over the 11 months between December 2007 and November 2008, in contrast to *C. obtusifolia* in Veracruz, México, where the fruits were available throughout the whole year (Alvarez-Buylla and Martínez-Ramos 1990).

Previous studies about forest structure in disturbed and fragmented landscapes revealed that there is an obvious rise in the relative importance of successional trees and *Cecropia* in particular (Laurance et al. 2006, Tabarelli and Lopes 2008). We showed that *Cecropia* seed fall in a fragmented landscape of the north-eastern Brazilian Atlantic Forest region was not only significantly higher in small forest patches (<50 ha) in comparison to large patches (>300 ha) but also significantly increased in inverse proportion to the amount of forest cover (FC). Additionally, *Cecropia* seed fall was greater in fragments that were more disturbed or, to be more precise, have been more exploited in the past because of their higher percentage of multiple stemmed trees.

With these differences of gradients in *Cecropia* seed rain we could demonstrate that the proliferation of successional trees in forest fragments may in fact be caused by an increased seed rain of these pioneer species. The forest cover, i.e. the proportion of forest within a certain area centered in the middle of each fragment, can be viewed as an index for the combination of size and the degree of isolation of a forest fragment. It is thought to be a predictor for the persistence of mammal and bird species (Develey and Metzger 2006, Fahrig 2003). Laurance et al. (1998) found an increase of successional trees in smaller fragments and hypothesized that a heavy seed rain from pioneer species growing in the surrounding matrix must have occurred. Less forest cover could also imply more border habitat and possibly more open *capoeira* habitats (young secondary vegetation, which was not assigned as forest and hence not included in our calculation for the index FC) as the surrounding matrix. But surprisingly, the quantity of border habitat was not a very strong predictor for the amount of *Cecropia* seed rain. The *Cecropia* species studied typically occur in open habitats and riparian forests (*C. pachystachya*; personal observation), and open habitats and forest borders (Sposito and Santos 2001). Hence the possibility of dispersal into the forest by

bats, birds, as well as primates (e.g. *Callithrix jacchus*) could have been much higher in these areas with a lower percentage of forest cover. It is not likely that the vegetation structure, e.g. the tree density at the sites, influenced the inflow of *Cecropia* seeds because firstly, our results did not show any significant relationship between the amount of seeds at a site and the structure of the vegetation surrounding the traps and secondly, our study design was as similar as possible for all fragments, we avoided heavy disturbed and young secondary vegetation patches and treefall gaps, and the traps were placed more or less at the same distance from the edge in every fragment. Hence all traps were within an area that was somehow influenced by edge effects (Laurance et al. 2002). However, a large part of the variation in our data could not be explained by our regression models. This is most probably due to the different histories of the individual fragments as well as other structural components beyond the scope of our collected metrics, which could have affected the dispersal of *Cecropia* and the presence of *Cecropia* trees respectively.

In summary, we showed that there is a higher *Cecropia* seed rain in smaller fragments, at sites with a high disturbance rate, and in fragments that have a low percentage of forest cover. This also implies that a heavy seed rain of these pioneer species will most likely alter and impoverish species composition, especially at those sites that are already suffering more heavily from fragmentation processes than others. This involves a replacement of climax species, especially in border habitat and small forest fragments (Santos et al. 2008). Furthermore, these results emphasize the importance of connecting forest fragments by corridors and conserving larger fragments so that the chances of a proliferation of pioneer species, as is often found in small isolated fragments and border habitats, is minimized. As recommended and reviewed by various authors (Beier and Noss 1998, Debinski and Holt 2000, Pardini et al. 2005, Ranta et al. 1998), clusters of fragments could be connected by corridors. These could be established by reforestation and natural regeneration. This could work against the problems caused by these unfavorable habitats, by enhancing movements between fragments and increase species richness.

5 Gut-passage and spitting of seeds by primates and germination success: Implications for regeneration of northeastern Atlantic Rainforest fragments

5.1 Abstract

In the northeastern Brazilian Atlantic Forest most medium- to large-bodied mammals are highly endangered or already extinct. As the only medium-sized primate in the study area, forest fragments within a sugarcane plantation about 40 km north of Recife, the endemic and highly endangered *Cebus flavius* (Cebidae) may play an important role as seed disperser especially of medium- to large-seeded species. Recently, only few small groups of this capuchin monkey could be observed and observations on feeding ecology are very scarce. Since feeding ecology of *C. flavius* is probably similar to the same-sized *C. libidinosus*, we conducted feeding experiments with individuals of this species, which were kept in a small zoological station. For the experiments we offered fruits of native tree species. Spit and digested seeds were planted and germination success compared with controls. For most species we could detect a slight but not significant positive effect on germination after digestion (e.g. *Inga thibaudiana*, *Tapirira guianense*), other species did not germinate at all (*Byrsonima sericea*), neither digested seeds nor controls. Seeds up to 2.3 cm at their longest length were swallowed by *Cebus* and digestion time was very short (55-240 min; mean time: 120 ± 51.4 min). We could not detect a difference in germination latency between defecated or spit seeds, respectively, and control seeds. Our observations suggest that capuchins are important dispersers of native tree species. However, in the study area the single population of *C. flavius* is restricted to only one relatively large fragment (*Mata dos Macacos*, 357 ha) and a re-connection via corridors with the surrounding fragments is necessary to enable the monkeys to re-colonize the surrounding habitat and to eventually positively influence the regeneration of the forest.

5.2 Introduction

One of the most crucial aspects for the successful recruitment of a plant is the quality or effectiveness of seed dispersal. Dispersal enables the seed to escape the vicinity of the mother tree where it has a significantly better chance of survival (Janzen 1970, Connell 1971). The post-dispersal fate of a seed also has to be considered. Rodents play an important role for both secondary seed dispersal but also seed predation and dung beetles may positively influence the recruitment by reducing seed clumping and also raise the possibility of seed survival by burying seeds (Andresen 1999, Andresen and Feer 2002). Another important aspect for success or failure of seed germination is the handling of the seeds by the disperser. The passage through a frugivore's gut for example can affect germination positively or negatively (Traveset and Verdú 2001) depending on both the plant and the animal species. An additional crucial factor for successful dispersal is the sufficient abundance of seed dispersers which depends on the integrity of the habitat. In fragmented landscapes animal-plant interactions are directly disturbed by the reduction of habitat, fragmentation of populations and edge effects as well as by the facilitated access of hunters and wood cutters (Laurance et al. 2002, Peres 2001a). In the highly fragmented northeastern Atlantic Forest most medium- to large-bodied mammals and large-billed birds are endangered or already extinct (Silva and Pontes 2008, Silva and Tabarelli 2000). As the only remaining medium-sized primate in the study area (Silva and Pontes 2008), a sugarcane plantation north of Recife (capital of Pernambuco), the endemic and highly endangered *Cebus flavius* Schreber 1774 (Cebidae) may play an important role as seed disperser especially of medium- to large-seeded species. But until now only few small groups of this capuchin monkey could be observed and especially observations on feeding ecology are very scarce (Pereira et al. unpubl.). The only other primate in the area, the very common small-sized monkey *Callithrix jacchus* Linnaeus 1758 (Callitrichidae), feeds on various fruit species (Alonso and Langguth 1989) but swallows only small seeds like e.g. those of *Miconia* or *Cecropia* species (Knörr unpubl.). On the other hand monkeys of the genus *Cebus* can swallow much larger seeds and were observed to disperse

seeds in average 216 and up to almost 850 m away from the parent tree (Wehncke et al. 2003).

Cebus flavius, the blond capuchin monkey, is a medium-sized (1.8 – 3 kg) and endemic to the northeastern Atlantic Forest region between the South of the State of Rio Grande do Norte in the north and the State of Alagoas in the south (Oliveira and Langguth 2006). Since the only groups of blond capuchin monkeys in the study area could not be followed because of very steep slopes and because capuchin monkeys in general are very difficult to follow for prolonged periods (Wehncke et al. 2003), we decided to do feeding experiments with captive *Cebus* monkeys. The feeding ecology and behavior of species of the genus *Cebus* are generally similar (Reis et al. 2006) and as we could not work with captive *C. flavius* we conducted feeding experiments with *Cebus libidinosus* Spix 1823 individuals, who were kept in a small zoological station. The effect of gut passage can differ substantially between plant species. Hence, we tested the handling and effect of gut passage of several native plant species to find out if capuchin monkeys have the potential to be good dispersers and whether they can hence actively help to retain biodiversity in the endangered northeastern Atlantic Forest of Brazil.

5.3 Material and Methods

Feeding experiments

Fruits of different tree species were collected in forest fragments of the *Usina São José* (USJ), a sugarcane plantation located in the federal state Pernambuco in Northeast Brazil. Fruits chosen were usually medium-to large-seeded (0.5 – 2.5 cm). They showed features of a bird-monkey syndrome, i.e. these fruits, mostly fleshy berries, capsules, drupes, and occasionally pods, are often brightly colored, have succulent pulp or arillate seeds, and usually no protective seed cover (Gautier-Hion et al. 1985, Simmen and Sabatier 1996). The fruits were either picked from the forest floor or gathered directly from the trees sometimes using a pole tree pruner. Only fresh and ripe fruits that did not show a sign of rot or predation were used. The fruits were always harvested shortly before they were fed to the monkeys and kept in paper bags so that they did not start to ferment as

fast as in plastic bags (personal observation). Dry weight of seeds was taken and seeds were measured.

The experiments were conducted with captive bearded capuchin monkeys (*Cebus libidinosus*, Cebidae) at a small zoological station (Refugio Charles Darwin) close to the sugarcane plantation Usina São José (USJ). The body weight of *Cebus libidinosus* ranges between 2.5 – 3.7 kg (Fragaszy et al. 2004b). We worked with a total of five individuals (four male and one female), who were kept in three separate cages.

The fruits were presented to the primates and time of feeding was recorded. No more than five fruits were offered simultaneously to avoid that the monkeys loose interest in the fruits because usually they are fed with convenient food like bananas and are not dependent on fruits that require a higher degree of handling. The handling of the fruits was recorded as (1) fruit was dropped without interest; (2) the pulp was removed and seed spit out; (3) fruit/pulp with seed was swallowed. Additionally, notes were taken when seeds were masticated and destroyed or when fruits like those of some Sapotaceae species had to be opened before eating. When seeds were spit out they were collected and kept for the germination experiments. If seeds were swallowed we waited until they were defecated. Time of defecation was recorded and the scats were collected. In both situations, spit or defecated, samples were collected with a long spoon because we were not allowed to enter the cages. Unfortunately for this reason not all samples could be collected because they were out of reach.

Germination experiments

To examine whether seeds survived or germinated better after spitting or passage through the gut of *Cebus* than control seeds, germination experiments were performed. In the evening of each feeding day, fecal samples were analyzed for seeds and planted in plastic bags that were filled with soil (Figure 5.1). We used potting soil that was always mixed in the same way from a local nursery. Seeds were not totally cleaned of feces before planting. Control seeds, i.e. conspecific seeds that were removed from the fresh fruit before planting. The bags were placed on tables inside an outdoor enclosure with natural light on the campus of the UFRPE (Universidade Federal Rural de Pernambuco) and were watered

5. Primary seed dispersal

regularly. The samples were protected from strong sun light by a shade cloth. Seeds were checked weekly to bi-weekly for germination.



Figure 5.1 (A) Fruit of Posoqueria latifolia; (B) Captive bearded capuchin monkey eating Pouteria gardneri fruits; (C) P. gardneri seeds sorted out of scats; (D) Germination experiments: Pradosia lactescens seedlings (left side) and a germinated Posoqueria latifolia seed (right side)

Data analysis

Differences in the proportion of germinated seeds were tested via χ^2 contingency tables with Yates' correction. It reduces the error of approximation by subtracting 0.5 from the difference of each observed value and therefore prevents overestimation of statistical significance for small data (Sokal and Rohlf 1995). Differences in latency times between groups of seed handling (gut passed/spit) and control seeds were analyzed with the Mann-Whitney U-Test because the data did not match parametric assumptions and we had a very small number of seed samples for some species (Fowler et al. 1998).

5.4 Results

Table 5.1 shows all species that were fed to the *Cebus* monkeys and the characters of their fruits and seeds. In total we offered 17 different species of which 11 were swallowed together with the seeds. Except for the fruits of *Virola gardneri*, which the monkeys did not seem to like, all other fruit species were eaten mostly enthusiastically. Some fruits, like the hard coated berries of the Sapotaceae species, were opened with the help of tools like wood sticks or stones, or by beating the fruits against the perches. After opening the seeds of *Dialium guianense* the *Cebus* monkeys threw away the whitish aril without eating it, but masticated and ate the seeds. The only planted seeds that did not germinate after spitting and gut passage but their respective controls were the seeds of *Inga laurina* and *Pouteria bangii*, respectively. However, *P. bangii* seeds did germinate after spitting and we could only plant one defecated seed. Both *Byrsonima* species did not germinate at all after six month of observation, neither defecated nor control seeds.

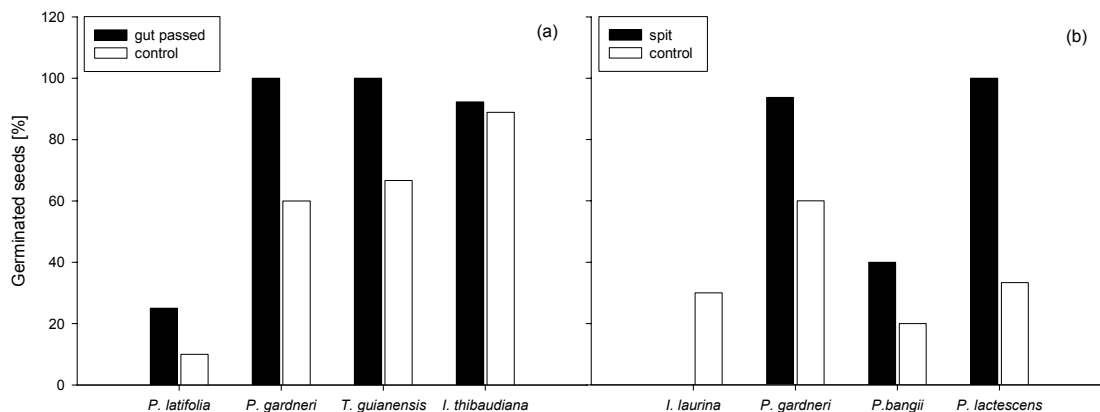


Figure 5.2 *Germination experiments for some selected tree species after passage through Cebus guts and spitting. Germination success in per cent of seeds planted after (a) gut passage and (b) spitting*

In the majority of cases spit and gut-passed seeds germinated better than controls (Figure 5.2), but for none of the species this relationship was significant mostly due to a very small sample size. We did not detect a difference in the number of days until seeds germinated between gut-passed or spit seeds and controls for none of the species shown in Figure 5.3.

Mean retention time of the seeds in the digestive tract of the *Cebus* monkeys was 120 ± 51.4 min (ranging from 55-240 min). Since we did not stay overnight there is a high possibility that some seeds remained longer than 240 min in the digestive tract, which were then defecated the next morning. There was a negative significant relationship between the seed weight and the time it took to be defecated ($r = -0.52$; $p = 0.04$). The lighter the seed was, the longer was the retention time. The relationship between retention time and seed size was also negative but not significant ($r = -0.34$; $p = 0.2$).

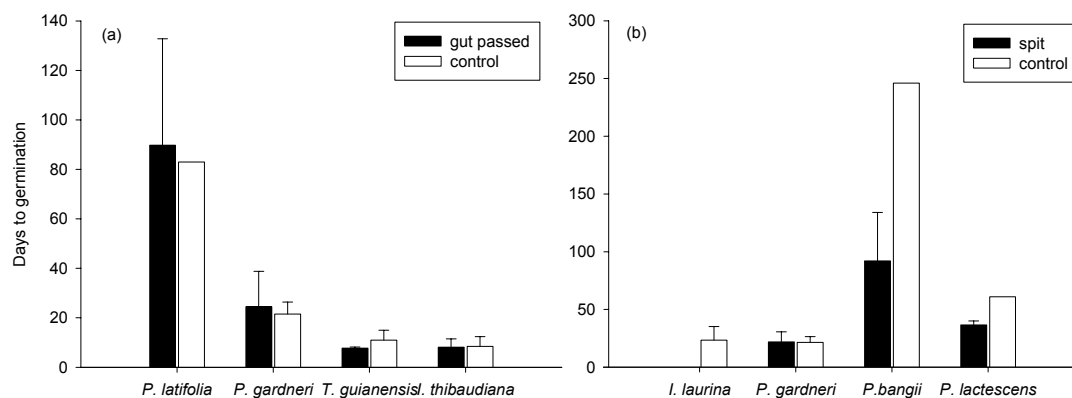


Figure 5.3 Number of days (mean±SD) of latency for (a) defecated seeds and (b) spit seeds

Table 5.1 List of plant species fed to captive Cebus libidinosus monkeys with information on their characteristics and handling by Cebus

Species, Family	Type of fruit	Seed handling	Seed weight [g]	Seed length [mm]
<i>Brosimum guianense</i> (Aubl.) Huber, Moraceae	infructescence	spit	0.29	12
<i>Byrsonima crista</i> A. Juss., Malpighiaceae	drupe	swallowed ***	0.2	10
<i>Byrsonima sericea</i> DC., Malpighiaceae	drupe	swallowed ***	0.09	6
<i>Cecropia palmata</i> Willd., Cecropiaceae	achene	swallowed	<0.001	1
<i>Clarisia racemosa</i> Ruiz & Pav., Moraceae	infructescence	pulp eaten and seeds dropped	3	25
<i>Dialium guianense</i> (Aubl.) Sandwith, Fabaceae,	pod	masticated and destroyed	0.28	11
<i>Diploon cuspidatum</i> Hoehne, Sapotaceae	berry	swallowed **	0.5	23
<i>Inga blanchetiana</i> Benth., Fabaceae	pod	swallowed **	0.2	15
<i>Inga laurina</i> (Sw.) Willd., Fabaceae	pod	spit *	0.2	14
<i>Inga thibaudiana</i> DC., Fabaceae	pod	spit ** and swallowed **	0.2	14
<i>Parkia pendula</i> (Willd.) Benth. ex Walp., Fabaceae	pod	masticated, swallowed	0.1	8
<i>Posoqueria latifolia</i> (Rudge) Roem. & Schult., Rubiaceae	berry	swallowed **	0.35	15
<i>Pouteria bangii</i> (Rusby) T.D. Penn, Sapotaceae	berry	spit **, swallowed ***	0.8	12
<i>Pouteria gardneri</i> (Mart. & Miq.) Baehni, Sapotaceae	berry	spit **, swallowed **	0.44	15
<i>Pradosia lactescens</i> (Vell.) Radlk., Sapotaceae	berry	spit **	1.15	29
<i>Tapirira guianensis</i> Aubl., Anacardiaceae	drupe	swallowed **	0.2	10
<i>Virola gardneri</i> (A. DC.) Warb., Myristicaceae	capsule	dropped without eating	3.9	25
* only control germinated; ** germinated; *** no germination; without asterisk: no germination experiments				

5.5 Discussion

The results represent only a small insight to the seed dispersal capacity of northeastern Brazilian Atlantic Forest tree species by *Cebus* monkeys. The data confirmed the high potential of capuchin monkeys to be very effective seed dispersers for native tree species, including endangered large-seeded species (Silva and Tabarelli 2000). The seed dispersal potential of different *Cebus* species was shown by various authors (Moura and McConkey 2007, Simmen and Sabatier 1996, Valenta and Fedigan 2009, Wehncke et al. 2003).

The use of tools to open fruits has already been observed for wild *Cebus libidinosus* individuals (Fragaszy et al. 2004a) and we noticed this behavior also for captive *C. libidinosus*. They often used their perches as anvils and stones as tools skillfully without destroying the seeds.

Although our results show that germination success was almost always better for defecated or spit seeds, the difference was not very pronounced and it could not be proved statistically. This may be due to our very low sample size but the slight positive effect can also be considered as a neutral effect on germination. Other studies on seed germination potential after passage through capuchin monkey's gut showed both a positive (Valenta and Fedigan 2009, Wehncke and Dalling 2005) and a neutral effect (Zhang and Wang 1995). The latter study only concentrated on one species (*Ziziphus cinnamomum*), whereas the other two studies looked at several species. The contribution of seed spitting to seed dispersal is controversially discussed in literature but most authors say that seed spitting is a poor mechanism of seed dispersal. Some authors claim that seeds that were not swallowed are not dispersed at all (Andresen 1999) and Valenta & Fedigan (2009) even found a negative effect of seed spitting on the germination success. Lambert (1999) argued that there was at least a little chance of dispersal of up to 10 m away from the parent's tree when redbellied monkeys spitted seeds in Uganda. In our study only one species was negatively affected by seed spitting. *Inga laurina* has very delicate seeds and while eating the mesocarp off the seeds they were often injured by *Cebus*. Ultimately, we also think that seed spitting is a poor way of dispersal. In the study area there are almost only rodents and bats left that are able to disperse large diaspores. These animals disperse the seeds only synzoochorously, i.e. without swallowing and hence, *Cebus flavius* maybe the

only frugivore who eats e.g. some of the large-seeded Sapotaceae species. In our study *C. libidinosus* swallowed seeds that had a length of up to 2.3 cm (*Diploon cuspidatum*). But size alone was not the only restriction for the captive capuchin monkeys to swallow the seeds. For example a lot of *Brosimum guianense* fruits were fed whose seeds are only about 1.2 cm long but none was swallowed, the pulp was eaten and seeds were then spit. *Cebus capucinus* in Panamá (Wehncke et al. 2003) also consumed *Brosimum* fruits with seeds of the same size but no seeds were found in the feces. However, in the same study seeds up to 3 cm long were swallowed and defecated. This behavior could be explained by the ease with which seeds of *Brosimum* separate from the pulp, whereas the studied Sapotaceae seeds bear a slippery skin around their seeds which facilitates swallowing.

The time of seed retention in the digestive tract was very short but comparable with other *Cebus* studies (Wehncke et al. 2003). Other primate species have much longer retention times like e.g. spider monkeys about 4.5 h (Link and Di Fiore 2006) and howler monkeys even about 20 h (Julliot 1996). The rapid turn over of *Cebus*' gut content may be explained by the low protein content of the fruits consumed, i.e. the capuchin monkeys have to gain the required energy by turning over a large quantity of fruits each day (Milton 1984). The negative relationship between seed weight and seed size, respectively, and the amount of time to defecation is surprising. Actually one would expect that it should be the other way around as already shown by Julliot (1996). On the other hand Wehncke et al. (2003) did not find an effect of seed size on gut passage time for *Cebus* monkeys. Unlike the study of Valenta & Fedigan (2009) where ingested seeds germinated faster than controls we did not detect an influence of gut passage and seed spitting on germination potential. Again, this can be explained by our small sample size.

Apparently, the seeds of native tree species are attractive to capuchin monkeys. These animals can be considered very important dispersers and may survive in many more forest fragments than they currently do. However, the blond capuchin monkey is highly endangered because they are held as pets and persecuted as crop raider (e.g. sugarcane) (Oliveira and Langguth 2006). A reintroduction or facilitation of re-colonization by the reforestation of forest corridors could not only increase the size of existing populations and habitats of

5. Primary seed dispersal

this extremely endangered species, but may also prevent the local extinction of many tree species in the study region.

6 Post-dispersal seed removal patterns in forest fragments and secondary vegetation patches

6.1 Abstract

This study investigated whether post-dispersal seed removal differed in 21 northeastern Brazilian Atlantic Forest fragments with varying sizes, different forest structure, successional stage, and between edge and interior sites. By presenting a total of 14,420 big chunks of exotic fruit items (coconut copra and apple) we simulated post-dispersal removal of large seeds at the beginning of the dry season of two consecutive years. The items were displayed, 10 of each fruit species, within mini-plots that were arranged in transects of 15 plots and removal checked after 24 hours. The experiments were accompanied by video monitoring and thread-marking experiments. Removal was significantly higher in large fragments than in small fragments but did not differ between edge and interior sites. Apple pieces were favored in the first but not in the second year. Considerable differences in item removal were registered between categories of forest types with lowest removal in open secondary vegetation and highest in preserved large forest fragments. We filmed *Didelphis* and *Marmosa* species (Didelphidae) eating apple pieces and Guianan squirrels (Sciuridae) and dung beetles removing coconut pieces. However, most of the species consuming or removing items could not be identified and no larger rodents like pacas or agoutis were observed. The patterns found provided a first insight into post-dispersal seed removal processes in a highly endangered fragmented landscape.

6.2 Introduction

A multitude of threats to tropical forests especially the disruption of animal-plant interactions are reinforced in fragmented landscapes. The modification and reduction of habitat has varying effects on mutualistic interactions like secondary seed dispersal by ground dwelling small- and large-bodied rodents and therefore on post-dispersal seed fate (Cole 2009, Galetti et al. 2006, Jorge and Howe 2009).

Hunting pressure on vertebrates is higher in forest fragments than in continuous forest because of the easy access (Peres 2001b). The alteration of tree species assemblages from mostly large-seeded climax species to small-seeded pioneer species particularly in edge habitats and small forest fragments (Laurance et al. 2006) make large-seeded species a priority in tropical forest conservation. Especially the highly fragmented northeastern Brazilian Atlantic Forest region is suffering from a gradual loss of large-seeded tree species (see chapter 1; Melo et al. 2006) mostly due to a lack of dispersal interactions (Silva and Tabarelli 2000). Until now only few studies on secondary seed dispersal and seed predation exist for this highly fragmented region (Pimentel and Tabarelli 2004, Pinto et al. 2009, Silva and Tabarelli 2001) and these studies concentrated on single fragments and did not consider possible modifications for patches with varying size, disturbance state, and successional state. We wanted to get a first insight into secondary seed dispersal processes in a fragmented landscape of the northeastern Atlantic Forest by conducting seed removal experiments in edge and interior habitat of large and small forest fragments and within fragments of different successional stages, sizes, and structures. For the experiments we used exotic fruit items weighing around 5 g (Chauvet and Forget 2005) like coconut copra and apple pieces, which should represent large seeds or diaspores respectively. We chose exotic items rather than seeds of local species to eliminate the error of conspecific seed density that might increase the chance of predation (Janzen 1970). Another reason for the use of coconut copra and apple was the great amount of material we needed for the experiments that was impossible to gather outside the main fruiting season. Large diaspores (>1 g) attract larger rodents like agoutis or pacas, and also small rodents like rice rats, spiny pocket mice or squirrels (Brewer and Rejmánek 1999, Pimentel and Tabarelli 2004).

We assume that edge and interior habitats will differ in respect to their removal rates with more items removed in interior habitats (Chauvet and Forget 2005) and that there will be a varying activity of item removal within the five categories of forest types. The question is to which extent the effects of forest fragmentation will be reflected by simulating post-dispersal seed fate with coconut and apple pieces.

6.3 Material and Methods

Study site and study design

The study was conducted at the Usina São José (USJ), a sugarcane plantation in northeastern Brazil approximately 40 km north of Recife the capital of Pernambuco state.

The climate is tropical with a pronounced dry season between September and December. Mean annual rainfall is 1,500 mm and average annual temperature 25°C (Schessl et al. 2008). The study site is composed of plateaus and deep valleys with steep slopes. The latter areas are mostly forested because of their limitations for land use (Trindade et al. 2008). The vegetation can be classified as lowland rainforest with transition to semideciduous forest (Veloso et al. 1991).

The sugarcane plantation occupies 247 km², of which 27% are covered with irregular-shaped forest remnants that are imbedded in a sugarcane matrix (Trindade et al. 2008). Additionally there are some regenerating secondary vegetation patches of different ages that were formerly used for sugarcane cultivation (Kimmel et al. 2010). The whole area was mostly forest until the 1950s. On aerial photographs from 1969, 1974, and 1981 it can be recognized that some of the large fragments (*Macacos & Piedade*, Table 6.1 and figure 2.1, chapter 2) did not change considerably in size at least since 1969. However, most fragments were isolated between 1974 and 1981 during the “pro-alcool” program of the Brazilian government that subsidized the cultivation of sugarcane for the production of bio fuels (Kimmel et al. 2008).

The experiments were carried out in two consecutive years each time at the beginning of the dry season between mid-September and end of November 2007, and between mid-August and end of October 2008 respectively. In order to achieve comparable data for the two surveys we deliberately chose to work at the same time of the year in both cases to avoid bias due to differences in fruit supply and hence differences in hoarding behavior (Jorge and Howe 2009). During the first year we concentrated on forest edge and forest size effects on seed removal of exotic food items working in five small (6.3 - 39.7 ha) and three large (298 - 388 ha) forest fragments. In the second year we emphasized the impact of the successional and preservation state of forest fragments and fallow vegetation by

working in the same fragments as in the first year and 13 additional forest and secondary vegetation patches.

Table 6.1 Characteristics of forest and secondary vegetation patches used in the study. Forest categories: C1=capoeirinha, C2=capoeira, C3=small- and middle-sized forest fragments, C4=very irregular-shaped large forest fragments, C5= preserved regular-shaped large forest fragments; Survey: 1=2007, 2=2008; total area of patch; Interior-to-edge-ratio: (circumference/area)*1000

Labeling on map (chapter 2)	Name	Forest category	Survey	Area [ha]	Interior-to-edge ratio
f	Gato	C1	2	14.81	5.3
g	Entrada	C1	2	22.11	4
b	Capoeira 2	C1	2	20.59	5.3
e	Rato	C2	2	3.21	3.7
d	Capoeira T1	C2	2	1.32	1
c	Capoeira T2	C2	2	0.66	1.7
a	Capoeira 1	C2	2	127.6	5.8
12	Urubú	C3	2	20.56	5.6
7	Ambar	C3	1/2	39.7	5.4
10	BR	C3	2	91.37	13.2
11	Chave	C3	2	89.29	12.2
3	Gota	C3	1/2	8.1	4.8
8	Pézinho	C3	1/2	30.6	8.8
9	Sta Helena	C3	2	11.85	7.8
4	Suábio	C3	1/2	6.31	4.7
5	Vespas	C3	1/2	13.81	6.3
12	Córrego do Gí	C4	2	303.12	12
2	Palmeira	C4	2	500.42	16
6	Macacos	C5	1/2	331.12	16.9
13	Piedade	C5	1/2	297.51	12.1
1	Zambana	C5	1/2	387.85	21.8

These 21 forests were grouped following their size, successional, and disturbance state to five categories: (C1) early secondary vegetation (*capoeirinha*) with an open canopy (canopy closure is ca. 10%; T. Kimmel, pers. comm.), few trees, and a dense shrub layer; (C2) better developed secondary vegetation

(*capoeira*) with a closed canopy (ca. 70% canopy closure; T. Kimmel, pers. comm.) characterized by small trees; (C3) small- and middle-sized forest fragments (8 – 90 ha); (C4) very irregular-shaped large forest fragments (303-500 ha); (C5) preserved, regular-shaped large forest fragments (298 – 389 ha). Attributes of all fragments are listed in table 6.1.



Figure 6.1 Mini-plot with apple (a) and coconut (b) items after 24 h of exposure.
Three coconut and none of the apple pieces were removed

Secondary dispersal experiments

Transects were installed in edge and interior habitat in the first year and only within forest and secondary vegetation patches in the second year. In the case of the edge-interior comparisons in 2007 we installed three pairs of transects within each large fragment and only one pair within small fragments. One pair represents one interior and one edge transect, which were installed parallel to each other. Every transect had a total length of 350 m and consisted of 15 mini-plots that were placed 25 m apart to avoid autocorrelation (Forget et al. 1998). Each mini-plot was cleared of leaf litter and received 10 coconut and 10 apple items.

Coconut and apples were cut up to pieces of equal size that always weighed 5 g (\pm 0.5 g). The items were prepared a day before they were placed in the forest and stored in the fridge overnight. Before starting the experiments we tested the best time for surveillance and found out that within 24 hours a great part of the items were removed and hence we limited the duration of observation to one day to avoid the consumption of entire items by ants (personal observation). The items were placed during daytime and left items were counted the following day (Figure 6.1). Starting time varied but duration of observation was always exactly 24 h. Some mini-plots within large forest fragments during the first survey could not be considered for the data analysis due to rotten coconut pieces that might have biased the results.

Seed fate experiments

We video-monitored seed fate for a total of 78 h to distinguish seed dispersers and predators (Jansen and den Ouden 2002) and to receive information on possible scatter-hoarders. For the video monitoring we used a camera with infra-red light (Sony[®] DCR –SR 90) that allowed recordings overnight. The camera was protected against rain with a weather-proof cover and was put on a tripod. The camera battery limited recordings to two consecutive hours (during dawn) in the first year. In the second year we used a car battery as energy supply and recordings could be performed for up to 21 hours limited by the camera's memory card.

In order to relocate the removed items and to clarify if they were scatter-hoarded or eaten, we thread-marked the exotic items for one observation, i.e. 10 coconut and 10 apple pieces, by piercing the items with white 15 cm long threads and tying little white plastic flags to the ends of the threads. Additionally, the experiment was video-monitored. The thread mark method proved to be helpful for elucidating seed fate in dense tropical forests (Forget and Wenny 2002). We searched for removed thread-marked items within a circle with a radius of ca. 15 m.

Data analysis

Percentages and means for the number of items removed or left were calculated as well as for the number of mini-plots without removal.

We applied a fixed effect factorial ANOVA design to analyze the data of both years. The response variable was the percentage of removed items and since even after transformation the data set with mini-plots as replicates did not match parametric assumptions each transect was considered a replicate for all statistical analyses. We tested whether the proportion of removed exotic fruit pieces varied with respect to the habitat within each fragment (edge or interior), the type of item (coconut copra/apple) and the size of the fragment (small or large). In the second year the categorical predictors for the percentage of removed items were the type of item with two levels (coconut copra/apple) and the forest category with five levels as introduced before. A repeated measure ANOVA tested whether the removal of both exotic items differed between the two surveys for the interior habitats of the eight fragments observed in both years. The year was treated as within block treatment (repeated measures), and the patch size category (small/large) and the type of item as a between block treatment. To meet assumptions of normality removal percentages were arcsine-squareroot transformed when necessary.

Additionally, linear regression models were applied in order to analyze the relationship between three predictor variables and the mean number of items removed in 2008. As predictors, which may explain the variation in the response variable, we chose the patch area, the interior-to-edge ratio of each patch, and the forest category (state of fragment). The response variable and the predictor variables patch size and interior-to-edge ratio were log-transformed to match parametric assumptions.

All statistical analyses were performed with STATISTICA 6.1 (©Stat. Soft. Inc.).

6.4 Results

Secondary dispersal experiments

In the first year the percentage of mini-plots without removal was considerably higher in small fragments ($40.74\% \pm 14.74$) than in large fragments ($8.18\% \pm 10.44$). Accordingly the percentage of removed items was significantly higher in large than in small fragments but the habitat, i.e. edge and interior sites, did not affect animal activity significantly (Table 6.2).

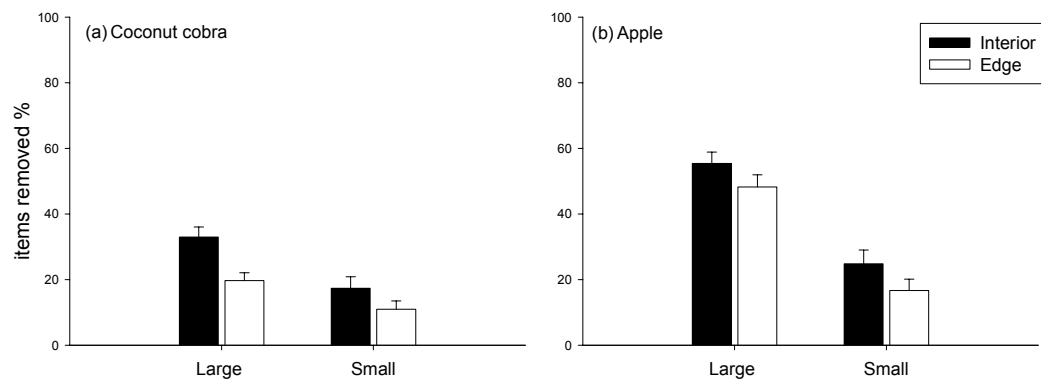


Figure 6.2 Percentages (mean±SE) of exotic items (a: coconut cobra; b: apple) removed 2007 along edge and interior transects within large and small forest fragments

Only a few more items of both apple and cobra were removed in interior habitats (Figure 6.2). In 2007 apple pieces were significantly more removed or eaten than coconut pieces.

Table 6.2 Results of a factorial ANOVA for the percentage of total removal in 2007 with size class (large/small), habitat (interior/edge), and item (coconut/apple) as fixed effects

Factor	df	F	p
Intercept	1	292.693	0.000
Size class	1	14.703	0.000
habitat	1	3.656	0.062
item	1	8.230	0.006
Size class x habitat	1	0.023	0.880
Size class x item	1	2.218	0.143
Size class x habitat x item	1	0.027	0.870
Significant results are in bold			

However, the removal of coconut pieces did not significantly differ from apple removal in 2008 (Table 6.3). This was persistent within all five forest categories. We could not detect any significant differences between classes of fragment size and the habitat or the type of exotic item in 2007.

Table 6.3 Results of factorial ANOVA for the percentage of items removed in 2008 with forest category (C1-C5) and item (coconut cobra/apple) as fixed effects

Factor	<i>df</i>	<i>F</i>	<i>p</i>
Intercept	1	338.539	0.000
class	4	28.309	0.000
item	1	0.337	0.566
Category x item	4	0.402	0.806

Significant results are in **bold**

Item removal was considerably varying between the five forest categories. Figure 6.3 clearly shows that in large forest fragments with little disturbance (category 5) the removal of diaspores was much higher than in the other four categories.

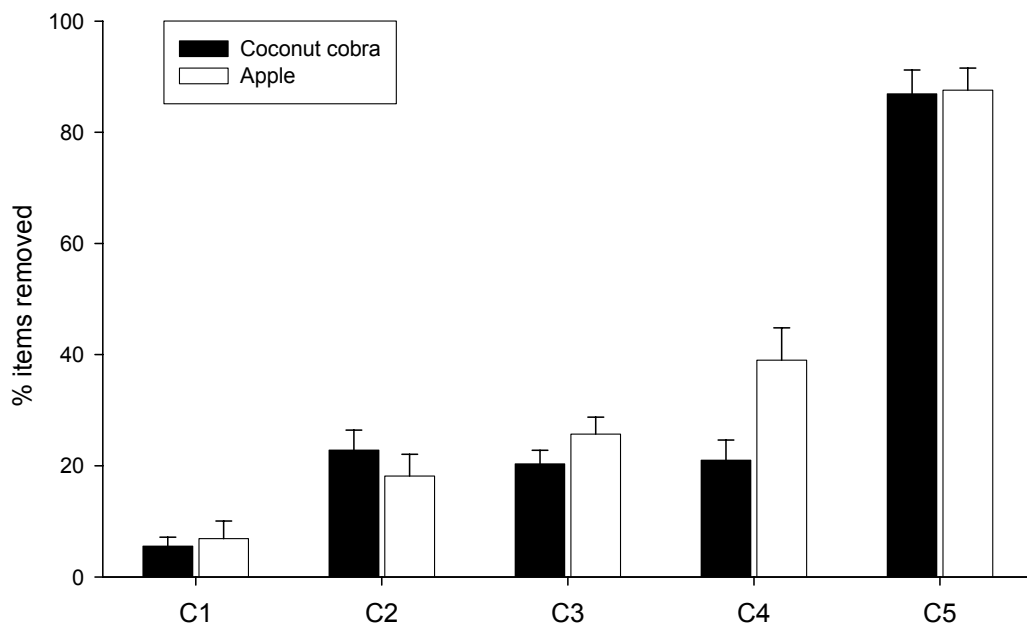


Figure 6.3 Percentages (mean±SE) of exotic items removed in 2008 along interior transects within patches of five categories of forest types: C1=capoeirinha, C2=capoeira, C3=small forest fragments, C4=disturbed large forest fragments, C5= preserved large forest fragments

Within fragments of this category mean removal rate was always over 80% whereas in open capoeira habitats it was less than 20%. More developed secondary vegetation (C2) did not differ in regard to item removal from small forest fragments.

Table 6.4 Percentage and standard deviation of the number of mini-plots without removal within the five forest categories

Forest category	Mini-plots without removal (% \pm SD)
C1	60 \pm 24.04
C2	33.33 \pm 27.22
C3	24.44 \pm 24.72
C4	10 \pm 14.14
C5	0

Furthermore, the percentage of mini-plots without removal was very high in open secondary vegetation (60% \pm 24.04) and decreased gradually from one category to the other and in little disturbed large forest fragments none of the mini-plots was without removal (Table 6.4). This trend was also reflected by the results of the linear regression models (Figure 6.4). Mean number of items removed increased significantly from worse to better preserved forests. The forest category predictor explained over 60% of variation in the data ($r^2=0.61$, $p<0.0001$). The area of the patches was not a good predictor for animal activity, but the relationship between area and the perimeter was a significant predictor for the number of items removed. The more edge habitat the less removal by animals was found. However, the interior-to-edge ratio only explained 21% of variation in the data ($r^2=0.21$, $p<0.05$). The additive multiple regression model of the three combined predictor variables was highly significant, however, it did not explain much more variation as the simple regression with forest type as predictor ($r^2=0.62$, $p<0.001$). This is due to the little explanatory value of the other two predictor variables in the additive model. Only the standardized regression coefficient (β) of the forest category is significant in the multiple regression model.

Comparing removal in interior habitat of large and small forest fragments between the two consecutive years, we registered a highly significant difference (Table 6.5). However, the actual pattern remained the same, i.e. removal was much higher in large forest fragments in both years, but the difference appeared much more pronounced in the second year. There was no difference between apple and coconut cobra removal between the two surveys.

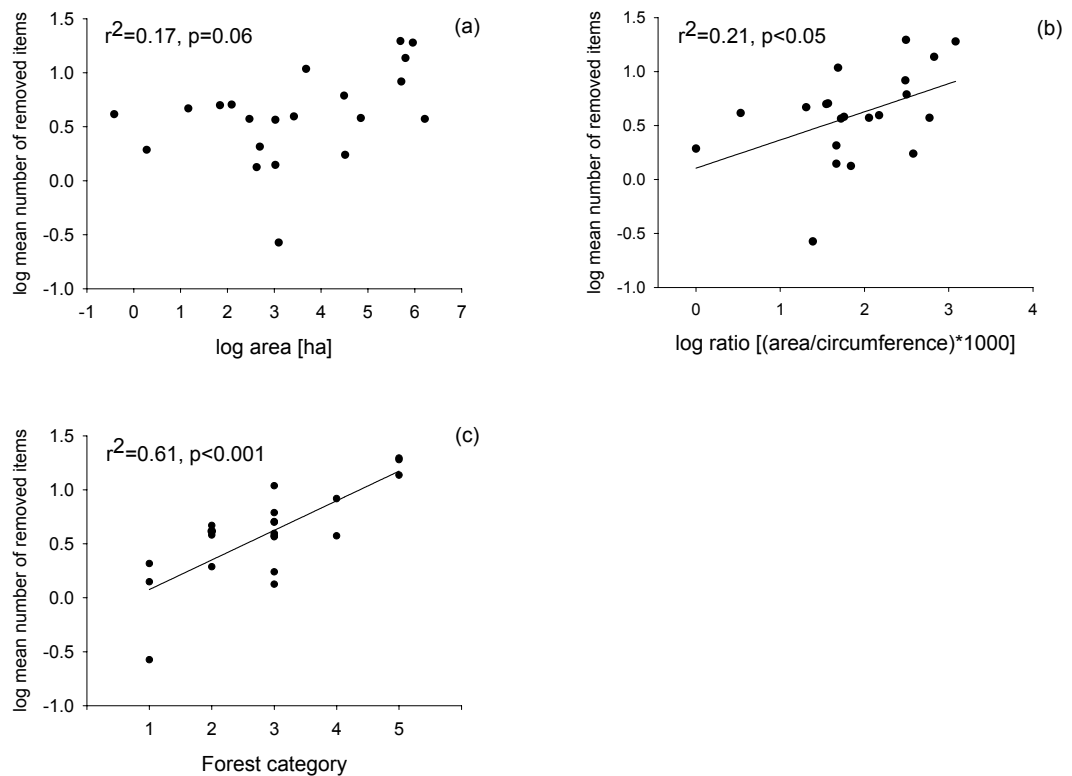


Figure 6.4 Relationship between the mean number of items removed (log-transformed) and the three predictor variables (a) area of fragment, (b) area-to-edge ratio, and (c) forest category

Seed fate experiments

During the 78 hours of video monitoring no large rodents like diurnal agoutis (*Dasyprocta* sp.) or nocturnal pacas (*Cuniculus paca*) were registered. The only identified rodent species feeding and removing items was the diurnal Guianan

squirrel (*Sciurus aestuans*, Sciuridae). At least two species of marsupials were recorded feeding on the items: most likely a big-eared opossum (*Didelphis aurita*, Didelphidae) and a mouse opossum species (*Marmosa* sp., Didelphidae). We could also observe dung beetles lifting up coconut pieces and rolling them away. Some of the filmed animal species feeding on and removing the faked diaspores could not be identified due to bad illumination.

17 of the 20 thread-marked coconut cobra and apple items were removed. However, only two pieces, both coconut cobra items, could be found buried intact in the soil. Six threads with flags were found without the item. The items and threads were found at distances from 94 cm to 394 cm away from the mini-plot. The remaining nine thread-marked pieces could not be relocated.

Table 6.5 Results of the repeated measures ANOVA. Year of survey as repeated measures (2007/2008); size class (large/small) and item (coconut cobra/apple) as between effects

Factor	df	F	p
Intercept	1	279.740	0.000
Year	1	37.592	0.000
Year x size class	1	22.559	0.000
Year x item	1	3.476	0.087
Year x size class x item	1	1.716	0.215
Significant results are in bold			

6.5 Discussion

Our results showed differences in diaspore removal activity between categories of forest size and forest types. We registered a considerably reduced removal of items in small forest fragments and open *capoeira* habitats in comparison to large fragments and less disturbed large forest patches, respectively. Differences between the two fragment size classes were even more pronounced in the second year. The distinct removal of exotic items in the study area, which may represent secondary dispersal of large seeds, perfectly reflects the problems of fragmentation already shown elsewhere: seeds were also more frequently secondarily dispersed in large forest fragments than in small fragments in southern Costa Rica (Cole 2009). Small rodent species that scatter-hoard seeds are

much more affected by fragmentation in the northeastern Brazilian Atlantic Forest than for example marsupials and mammal diversity is lower in small fragments (Asfora and Pontes 2009). Small mammal abundance also decreased with decreasing fragment size in a fragmented landscape in Southeast Brazil (Pardini et al. 2005). The altered mammal abundance in fragmented landscapes and especially in small forest fragments may explain the patterns found in our study. However, Jorge & Howe (2009) found opposite results in the Central Amazon region where the number of seeds removed was larger in small fragments than in large fragments but on the other hand in small fragments seeds were more eaten than buried.

Contrary to our expectations interior and edge sites did not affect animal activity as much as we expected. This result differs from the observations Chauvet & Forget (2005) made in edge and interior habitats of forest islands in French Guiana where coconut cobra removal by terrestrial mammals was significantly reduced in edge habitats. We would have expected that a higher fruit availability at edge sites as observed in the study area (Schessl et al. 2008) and edge avoidance of small mammals (Stevens and Husband 1998) and e.g. agoutis (Dubost 1988) reduce the demand for seeds of consumers at those sites that are characterized by a dense understorey. On the other hand, a study in Costa Rican montane wet forest also did not find effects of distance from the forest edge on the percentage of seeds removed for most of the species studied (Holl and Lolow 1997). Some animals are favored at disturbed sites and prefer edge habitats (Pardini 2004) and this is possibly one reason for the little pronounced differences between edge and interior sites in our study. Interestingly, Fonseca (1989) found out that the habitat structure of Brazilian Atlantic primary and secondary forest fragments was a good predictor for small mammal diversity with the highest diversity of small mammals in 20 year old secondary vegetation. His results are not necessarily contradictory to our findings. Firstly, item removal did not differ between old secondary vegetation (C2) and small forest fragments (C3) in our study and secondly, he also found out that mammal diversity decreased with the herbaceous volume, i.e. the density of the shrub layer, within the secondary forests. This again would explain that item removal was very low in open secondary vegetation with a thick shrub layer that is avoided by small mammals.

The fact that at least during the first survey apple pieces were more eaten or removed than coconut pieces can be due to the higher abundance of animals like opossums that prefer softer fruits and are usually eating and swallowing fruits with small seeds (Cáceres and Monteiro-Filho 2007) rather than secondarily disperse and bury cleaned seeds or dry fibrous fruits with few large seeds like small and large rodent species do (Gautier-Hion et al. 1985). The video monitoring experiments support our findings and hypotheses insofar that we generally saw more marsupials feeding on items than rodents. Furthermore, marsupials only ate apple pieces mostly directly at the place where they found them without carrying them away. In the Neotropics only rodents are known to cache seeds whereas in Australia at least one species of marsupials behaves similarly and was observed to scatter-hoard seeds (Forget and Vander Wall 2001). Another reason for the preference of apple items in 2007 may be due to the higher water content of the apple pieces. Since the study was conducted in the dry season the mammals may have had a higher requirement of water and therefore preferred apple pieces (P.-M. Forget, pers. comm.). Usually the diet of e.g. large rodents conforms to the season insofar that fleshy fruit pulp is chiefly eaten in the main fruiting season and buried seeds serve as food source when fresh fruits are rare (Dubost and Henry 2006).

We did not film any larger rodents like nocturnal pacas (*Cuniculus paca*) or diurnal black-rumped agoutis (*Dasyprocta prymnolopha*). Agoutis are not very abundant in the area. At least in a study about *D. prymnolopha* density in a fragment approximately 40 km away from the study site were registered only 8.5 ind/km² (Silva and Tabarelli 2001). In a non-hunted site agouti density can reach 31 ind/km² (Jorge and Peres 2005). In the study area hunting pressure is very strong on agoutis and pacas (personal observation). The only rodent identified, the Guianan squirrel (*Sciurius aetuanus*), has also been observed to be one of only two animal species that dispersed *Bactris acanthocarpa* in a forest fragment close to our study area (Silva and Tabarelli 2001). We could also observe dung beetles moving the items out of the view of the camera. Dung beetles usually roll and bury seeds that are covered with primary disperser's (e.g. monkeys) feces and hence protecting them against seed predators (Andresen and Feer 2002). But seed burying of diaspores that fell directly from the tree without being digested has

already been observed e.g. in Brazilian Cerrado vegetation (Gottsberger and Silberbauer-Gottsberger 2006).

The video monitoring observations have to be discussed with caution. First of all the recordings represent only a first view on caching and dispersal behavior in the study area because the total duration of the filming was too short. Secondly, not all animal species could be identified due to bad light conditions.

The number of thread-marked items was insufficient to discuss the results. However, our observations at least showed that exotic food items, especially coconut cobra because this was the only item type buried during the video recordings, can simulate secondary dispersal or predation of large seeds because they were buried like real seeds and we could observe if items were eaten entirely or destroyed.

Nevertheless, to show post-dispersal seed fate in this highly fragmented landscape experiments with seeds of native species are necessary. Our study gives a first view on ground-dwelling animal activity in different-sized forest fragments and patches of varying successional and disturbance state in the northeastern Atlantic Forest region.

7 Literature

- Agresti A. 2007. An Introduction to Categorical Data Analysis. - Wiley-Interscience, New Jersey.
- Alonso C, Langguth A. 1989. Ecologia e comportamento de *Callithrix jacchus* (Primates, Callitrichidae) numa ilha de floresta Atlântica. - Rev Nordestina Biol 6: 105-137.
- Alvarez-Buylla ER, Martínez-Ramos M. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. - Oecologia 84: 314-325.
- Alves-Araújo A, Araújo D, Marques J, Melo A, Maciel JR, Irapuan J, Pontes T, Lucena MFA, Bocage ALD, Alves M. 2008. Diversity of angiosperms in fragments of Atlantic Forest in the state of Pernambuco, northeastern Brazil. - Bioremed Biodiv Bioavail 2: 14-26.
- Amarante A, Tabarelli M. 2003. Identificação de Remanescentes da Mata Atlântica Trecho Paraíba/Alagoas. - CEPAN, Recife.
- Andresen E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. - Biotropica 31: 145-158.
- Andresen E, Feer F. 2002. The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. - In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (eds), Seed Fate: Predation, Dispersal and Seedling Establishment, pp. 331-349. CABI Publishing, Oxfordshire, Cambridge.
- Asfora PH, Pontes ARM. 2009. The small mammals of the highly impacted northeastern Atlantic Forest of Brazil, Pernambuco Endemism Center. - Biota Neotropica 9: 31-35.

- Barbosa KC, Pizo MA. 2006. Seed rain and seed limitation in planted gallery forest in Brazil. - *Restoration Ecol* 14: 504-515.
- Barroso GM, Morim MP, Peixoto AL, Ichaso CLF. 1999. Frutos e Sementes: Morfologia Aplicada à Sistemática de Dicotiledôneas. - Universidade Federal de Viçosa, Viçosa.
- Beier P, Noss RF. 1998. Do habitat corridors provide connectivity? - *Conserv Biol* 12: 1241-1252.
- Brewer SW, Rejmánek M. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. - *J Veget Sci* 10: 165-174.
- Brooks T, Rylands AB. 2003. Species on the brink: critically endangered terrestrial vertebrates. - In: Leal CG, Câmara IDG (eds), *The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook*, pp. 360-371. Island Press, Washington, Covelo, London.
- Cáceres NC, Monteiro-Filho ELA. 2007. Germination in seed species ingested by opossums: implications for seed dispersal and forest conservation. - *Braz Arch Biol Tech* 50: 921-928.
- Câmara IG. 2003. Brief history of conservation in the Atlantic Forest. - In: Galindo Leal C, Câmara IG (eds), *The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook*, pp. 31-42. Island Press, Washington, Covelo, London.
- Chao A. 1987. Estimating the population size for capture-recapture data with unequal catchability. - *Biometrics* 43: 783-791.
- Chapman CA. 1989. Primate seed dispersal: the fate of dispersed seeds. - *Biotropica* 21: 148-154.
- Chapman LJ, Chapman CA, Wrangham RW. 1992. *Balanites wilsoniana*: elephant dependent dispersal? - *J Trop Ecol* 8: 275-283.

- Chauvet S, Forget PM. 2005. Edge effects on post-dispersal seed removal in a fragmented rain forest in French Guiana. - *J Trop Ecol* 21: 113-116.
- Chazdon RL, Colwell RK, Denslow JS, Guariguata MR. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northeastern Costa Rica. - In: Dallmeier F, Comiskey JA (eds), *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies*, pp. 285-309. United Nations Educational, Scientific and Cultural Organization, Paris.
- Cole RJ. 2009. Postdispersal seed fate of tropical montane trees in an agricultural landscape, southern Costa Rica. - *Biotropica* 41: 319-127.
- Condit R. 1998. *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. - Springer, Berlin, Heidelberg.
- Connell JH. 1971. On the role of natural enemies in preventing exclusion in some marine animals and rain forest trees. - In: Den Boer PFD, Gradwell GR (eds), *Dynamics of Populations: Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations*, pp. 298-312. Pudoc, Wageningen.
- Cramer JM, Mesquita RCG, Williamson GB. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. - *Biol Cons* 137: 415-423.
- Crow TR, Grigal DF. 1979. A numerical analysis of aborescent communities in the rain forest of Luquillo mountains, Puerto Rico. - *Plant Ecol* 40: 135-146.
- Cruz MAOM, Campello MLCB. 1998. Mastofauna: primera lista e um estudo sobre o *Callithrix jacchus* Erxleben, 1777 (Callitrichidae: Primates) na Reserva Ecológica de Dois Irmãos. - In: Machado IC, Lopes AV, Pôrto KC

- (eds), Reserva Ecológica de Dois Irmãos: Estudo em um Remanescente de Mata Atlântica em Área Urbana, pp. 253-269. SECTMA, Recife.
- Dean W. 1995. With Broadax and Firebrand: Destruction of the Brazilian Atlantic Forest. - University of California Press, Los Angeles.
- Debinski DM, Holt RD. 2000. A survey and overview of habitat fragmentation experiments. - *Conserv Biol* 14: 342-355.
- Develey PF, Metzger JP. 2006. Birds in Atlantic forest landscapes: effects of forest cover and configuration in a severely fragmented ecosystem. - In: Laurance WF, Peres CA (eds), *Emerging Threats to Tropical Forests*, pp. 269-290. The University of Chicago Press, Chicago.
- Dirzo R, Mendoza E, Ortiz P. 2007. Size-related differential seed predation in a heavily defaunated neotropical rain forest. - *Biotropica* 39: 355-362.
- Dominguez JML, Bittencourt ACSP, Leão ZMAN, Azevedo AEG. 1990b. Geologia quaternária costeiro do estado de Pernambuco. - *Rev Bras Geociencias* 20: 208-215.
- Dominguez JML, Bittencourt ACSP, Leão ZMAN, Azevedo AEG. 1990a. Geologia Quaternária Costeiro do Estado de Pernambuco. - *Rev Bras Geociencias* 20: 208-215.
- Dubost G. 1988. Ecology and social life of the red acouchy, *Myoprocta exilis*; comparison with the orange-rumped agouti, *Dasyprocta leporina*. - *Zoology* 214: 107-123.
- Dubost G, Henry O. 2006. Comparison of diets of the acouchy, agouti and paca, the three largest terrestrial rodents of French Guianan forests. - *J Trop Ecol* 22.

- Dunphy BK, Murphy PG, Lugo AE. 2000. Tendency for trees to be multiple-stemmed in tropical and subtropical dry forests: studies of Guanica forest, Puerto Rico. - *Tropical Ecology* 41: 161-167.
- Fahrig L. 1997. Relative effects of habitat loss and fragmentation on population extinction. - *J Wildl Manage* 61: 603-610.
- Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. - *Annu Rev Ecol Syst* 34: 487-515.
- Ferraz EMN, Rodal MJN. 2006. Caracterização fisionômica - estrutural de um remanescente de floresta ombrófila montana de Pernambuco, Brasil. - *Acta Bot Bras* 20: 911-926.
- Fleming TH, Williams CF. 1990. Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. - *J Trop Ecol* 6: 163-178.
- Fonseca GAB. 1989. Small mammal species diversity in Brazilian tropical primary and secondary forests of different sizes. - *Rev Bras Zool* 6: 381-422.
- Forget PM, Milleron T, Feer F. 1998. Patterns in post-dispersal seed removal by neotropical rodents and seed fate in relation to seed size. - In: Newbery DM, Prins HHT, Brown N (eds), *Dynamics of Tropical Communities*, Blackwell Science, Oxford.
- Forget PM, Vander Wall SB. 2001. Scatter-hoarding rodents and marsupials: convergent evolution on diverging continents. - *Tree* 16: 65-67.
- Forget PM, Wenny D. 2002. How to elucidate seed fate? A review of methods used to study seed removal and secondary seed removal. - In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (eds), *Seed Fate: Predation, Dispersal and Seedling Establishment*, pp. 379-393. CABI Publishing, Oxfordshire, Cambridge.

- Forman RTT, Godron M. 1981. Patches and structural components for a landscape ecology. - *Bioscience* 31: 733-740.
- Fortin M-J, Gurevitch J. 2001. Mantel tests - spatial structure in field experiments. - In: Schreiner SM, Gurevitch J (eds), *Design and Analysis of Ecological Experiments*, pp. 308-326. Oxford University Press, Oxford, New York.
- Foster RB. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. - In: Leigh JR, EG, Rand AS, Windsor DM (eds), *The Ecology of a Tropical Forest*, pp. 151-171. Smithsonian Institution Press, Washington, D.C.
- Fowler J, Cohen L, Jarvis P. 1998. *Practical Statistics for Field Biology*. - John Wiley & Sons, Chichester, New York, Weinheim, Brisbane, Singapore, Toronto.
- Fragaszy D, Izar P, Visalberghi E, Ottoni EB, Oliveira MGD. 2004a. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. - *Am J Primatol* 64: 359-366.
- Fragaszy D, Visalberghi E, Fedigan LM. 2004b. *The Complete Capuchin: The Biology of the Genus Cebus*. - Cambridge University Press, New York.
- Fragoso JMV, Huffman JM. 2000a. Seed-dispersal and seedling recruitment patterns by the last neotropical megafaunal element, the tapir. - *J Trop Ecol* 16: 369-385.
- Fragoso JMV, Huffman JM. 2000b. Seed-dispersal and seedling recruitment patterns by the last Neotropical megafaunal element, the tapir. - *J Trop Ecol* 16: 369-385.
- Galetti M, Donatti CI, Pires AS, Guimarães Jr, P.R., Jordano P. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. - *Bot J Linnean Soc* 151: 141-149.

- Galindo-González J, Guevara S, Sosa VJ. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. - *Conserv Biol* 14: 1693-1703.
- Galindo-Leal C. 2003. Putting the pieces back together: fragmentation and landscape conservation. - In: Galindo-Leal C, Câmara IG (eds), *The Atlantic Rain Forest of South America - Biodiversity Status, Threats, and Outlook*, pp. 372-380. Island Press, Washington, Covelo, London.
- Galindo-Leal C, Câmara IG. 2003. Atlantic Forest hotspot status: an overview. - In: Galindo-Leal C, Câmara IG (eds), *The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook*, pp. 3-11. Island Press, Washington, Covelo, London.
- Garcia QS, Rezende JLP, Aguiar LMS. 2000. Seed dispersal by bats in a disturbed area of southeastern Brazil. - *Rev Biol Trop* 48: 125-128.
- Gautier-Hion A, Duplantier JM, Quris R, Feer F, Sourd C, Decoux JP, Dubost G, Emmons L, Erard C, Hecketsweiler P. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. - *Oecologia* 65: 324-337.
- Girão LC, Lopes AV, Tabarelli M, Bruna EM. 2007. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic Forest landscape. - *PLoS ONE* 2: e908.
- Goldemberg J. 2008. The Brazilian biofuels industry. - *Biotechnology for Biofuels* 1: 1-7.
- Gottsberger G, Silberbauer-Gottsberger I. 2006. Life in the Cerrado: a South American Tropical Seasonal Ecosystem. Vol. 2. Pollination and Seed Dispersal. - Reta, Ulm.

- Grombone-Guaratini MT, Rodrigues RR. 2002. Seed bank and seed rain in a seasonal semi-deciduous forest in south-eastern Brazil. - J Trop Ecol 18: 759-774.
- Guedes MLS. 1998. Vegetação fanerogâmica da reserva ecológica de Dois Irmãos. - In: Machado IC, Lopes AV, Pôrto KC (eds), Reserva Ecológica de Dois Irmãos: Estudo em um Remanescente de Mata Atlântica em Área Urbana, pp. 157-172. SECTMA, Recife.
- Hill JL, Curran PJ. 2003. Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. - J Biogeography 30: 1391-1403.
- Holl KD. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. - Biotropica 31: 229-242.
- Holl KD, Lolow ME. 1997. Effects of species, habitat, and distance from edge on post-dispersal seed predation in a tropical rainforest. - Biotropica 29: 459-468.
- Howe HF. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. - Oecologia 79: 417-426.
- Howe HF, Schupp EW, Westley LC. 1985. Early consequences of seed dispersal for a Neotropical tree (*Virola surinamensis*). - Ecology 66: 781-791.
- Howe HF, Smallwood J. 1982. Ecology of seed dispersal. - Annu Rev Ecol Syst 13: 201-228.
- Jacob F, Jäger EJ, Ohmann E. 1994. Botanik. - Fischer, Jena.
- Jansen PA, den Ouden J. 2002. Observing seed removal: remote video monitoring of seed selection, predation and dispersal. - In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (eds), Seed Fate: Predation, Dispersal and

- Seedling Establishment, pp. 363-378. CABI Publishing, Oxfordshire, Cambridge.
- Janson CH. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. - *Science* 219: 187-189.
- Janzen DH. 1970. Herbivores and the number of tree species in tropical forests. - *Amer Nat* 104: 501-528.
- Jorge MLSP, Howe HF. 2009. Can forest fragmentation disrupt a conditional mutualism? A case from Central Amazon. - *Oecologia* 161: 709-718.
- Jorge MLSP, Peres CA. 2005. Population density and home range size of red-rumped agoutis (*Dasyprocta leporina*) within and outside a Natural Brazil nut stand in southeastern Amazonia. - *Biotropica* 37: 317-327.
- Julliot C. 1996. Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. - *Int J Primatol* 17: 239-258.
- Kimmel T, Nascimento LMD, Piechowski D, Sampaio EVSB, Rodal MJN, Gottsberger G. 2010. Pollination and seed dispersal modes of woody species of 12-year-old secondary forest in the Atlantic Forest region of Pernambuco, NE Brazil. - *Flora*: 10.1016/j.flora.2009.12.022.
- Kimmel T, Piechowski D, Gottsberger G. 2008. The history of fragmentation of the lowland Atlantic Forest of Pernambuco, Brazil. - *Bioremed Biodiv Bioavail* 2: 1-4.
- Krebs CJ. 1989. *Ecological Methodology*. - Harper Collins Publisher, New York.
- Lambert JE. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redbellied monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. - *Am J Phys Anthropol* 109: 365-386.

- Laurance WF, Cochrane MA. 2001. Synergistic effects in fragmented landscapes. - *Conserv Biol* 15: 1488-1489.
- Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE. 2000. Rainforest fragmentation kills big trees. - *Nature* 404: 836.
- Laurance WF, Ferreira LV, Merona JMRD, Laurance SG, Hutchings RW, Lovejoy TE. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. - *Conserv Biol* 12: 460-464.
- Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. - *Conserv Biol* 16: 605-618.
- Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, Capretz RL. 2006. Rain forest fragmentation and the proliferation of successional trees. - *Ecology* 87: 469-482.
- Laurance WF, Pérez-Salicrup D, Delamônica P, Fearnside PM, D'Angelo S, Jerzolinski A, Pohl L, Lovejoy TE. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. - *Ecology* 82: 105-116.
- Levey DJ, Byrne MM. 1993. Complex ant-plant interactions: rain forests ants as secondary seed dispersers and post-dispersal seed predators. - *Ecology* 74: 1802-1812.
- Link A, Di Fiore A. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. - *J Trop Ecol* 22: 235-246.
- Lobova TA, Mori SA. 2004. Epizoochorous dispersal by bats in French Guiana. - *J Trop Ecol* 20: 581-582.

- Lobova TA, Mori SA, Blanchard F, Peckham H, Charles-Dominique P. 2003. *Cecropia* as a food resource for bats in French Guiana and the significance of fruit structure in seed dispersal and longevity. - *Am J Bot* 90: 388-403.
- Lorenzi H. 2002b. Árvores Brasileiras: Manual de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil (Vol. 2). - Instituto Plantarum, Nova Odessa, SP.
- Lorenzi H. 2002a. Árvores Brasileiras: Manual de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil (Vol. 1). - Instituto Plantarum, Nova Odessa, SP.
- Mabesoone JN, Tinoco TM, Coutinho PM. 1968. The Mesozoic-Tertiary boundary in northeastern Brazil. - *Paleogeol Paleoclim Paleoecol* 4: 161-185.
- Marris E. 2006. Sugarcane and ethanol: drink the best and drive the rest. - *Nature* 444: 670-672.
- Martínez-Garza C, Gonzalez-Montagut R. 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. - *Plant Ecol* 145: 255-265.
- McCullagh P, Nelder JA. 1999. Generalized Linear Models. - Chapman & Hall, Boca Raton, London, New York, Washington D.C.
- Melo FPL, Dirzo R, Tabarelli M. 2006. Biased seed rain in forest edges: evidence from a Brazilian Atlantic Forest. - *Biol Cons* 132: 50-60.
- Melo FPL, Martínez-Salas E, Benitez-Malvido J, Ceballos G. 2010. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. - *J Trop Ecol* 26: 35-43.
- Metzger JP, Martensen AC, Dixo M, Bernacci LC, Ribeiro MC, Teixeira AMG, Pardini R. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. - *Restoration Ecol* 142: 1166-1177.

- Michalski F, Nishi I, Peres CA. 2007. Disturbance-mediated drift in tree functional groups in Amazonian Forest fragments. - *Biotropica* 39: 691-701.
- Milton K. 1984. The role of food-processing factors in primate food choice. - In: Rodman P, Cant J (eds), *Adaptations for Foraging in Nonhuman Primates*, pp. 249-279. Columbia University Press, New York.
- Mori SA. 1995. Observações sobre as espécies de Lecythidaceae do leste do Brasil. - *Bol Bot* 14: 1-31.
- Mori SA, Boom BM, Prance GT. 1981. Distribution patterns and conservation of eastern Brazilian coastal forest tree species. - *Brittonia* 33: 233-245.
- Moura ACDA, McConkey KR. 2007. The Capuchin, the Howler, and the Caatinga: seed dispersal by monkeys in a threatened Brazilian forest. - *Am J Primatol* 69: 220-226.
- Myers N. 1988. Threatened biotas: "Hot spots" in tropical forests. - *The Environmentalist* 8: 187-208.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. - *Nature* 403: 853-858.
- Neto CAMU, Silva JMC. 2002. Análise de representatividade das unidades de conservação no estado de Pernambuco. - In: Tabarelli M, Silva JMC (eds), *Diagnóstico da Biodiversidade de Pernambuco*, pp. 707-715. Secretaria de Ciência, Tecnologia e Meio Ambiente, Recife.
- Oliveira MA, Grillo AS, Tabarelli M. 2004. Forest edge in the Brazilian Atlantic Forest: drastic changes in tree species assemblages. - *Oryx* 38: 389-394.
- Oliveira MMd, Langguth A. 2006. Rediscovery of Marcgrave's Capuchin Monkey and designation of a Neotype for *Simia flavia* Schreber, 1774 (Primates, Cebidae). - *Bol Mus Nac nov sér Zool* 523: 1-16.

- Pardini R. 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. - Biodiv Cons 13: 2567-2586.
- Pardini R, Souza SM, Braga-Neto-R., Metzger JP. 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. - Biol Cons 124: 253-266.
- Peres CA. 2001b. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. - Conserv Biol 15: 1490-1505.
- Peres CA. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. - Conserv Biol 14: 240-253.
- Peres CA. 2001a. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian Forest vertebrates. - Conserv Biol 15: 1490-1505.
- Phillips OL. 1997. The changing ecology of tropical forests. - Biodiv Cons 6: 291-311.
- Piechowski D. 2007. Reproductive ecology, seedling performance, and population structure of *Parkia pendula* in an Atlantic Forest fragment in northeastern Brazil. - Doctoral Thesis, Universität Ulm.
- Pijl L van der. 1969. Principles of Dispersal in Higher Plants. - Springer, Berlin, Heidelberg, New York.
- Pimentel DS, Tabarelli M. 2004. Seed dispersal of the palm *Atfalea oleifera* in a remnant of the Brazilian Atlantic Forest. - Biotropica 36: 74-84.
- Pinto SRR, Santos AM, Tabarelli M. 2009. Seed predation by rodents and safe sites for large-seeded trees in a fragment of the Brazilian Atlantic Forest. - Braz J Biol 69: 763-771.

- Plotkin JB, Potts MD, Yu DW, Bunyavejchewin S, Condit R, Foster R, Hubbell S, LaFrankie J, Manokaran N, Lee H-S, Sukumar R, Nowak MA, Ashton PS. 2000. Predicting species diversity in tropical forests. - PNAS 97: 10850-10854.
- Quinn GP, Keough MJ. 2002. Experimental Design and Data Analysis for Biologists. - Cambridge University Press, New York.
- Ranta P, Blom TOM, Niemala J, Joensuu E, Siitonen M. 1998. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. - Biodiv Cons 7: 385-403.
- Redford KH. 1992. The empty forest. - Bioscience 42: 412-422.
- Reis NR, Peracchi AL, Pedro WA, Lima IP. 2006. Mamíferos do Brasil. - Biblioteca Central da Universidade Estadual de Londrina, Londrina.
- Reynolds CE, Houle G. 2002. Mantel and partial Mantel tests suggest some factors that may control the local distribution of *Aster laurentianus* at Îles de la Madeleine, Québec. - Plant Ecol 164: 19-27.
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. - Biol Cons 142: 1141-1153.
- Roosmalen MGMV. 1985. Fruits of the Guianan Flora. - Institute of Systematic Botany, Utrecht University, and Silvicultural Department of Wageningen, Agricultural University, Utrecht, Wageningen.
- Santos BA, Peres CA, Oliveira MA, Grillo A, Alves-Costa CP, Tabarelli M. 2008. Drastic erosion in functional attributes of tree assemblages in Atlantic Forest fragments of northeastern Brazil. - Biol Cons 141: 249-260.

- Schessl M, Luiz da Silva W, Gottsberger G. 2008. Effects of fragmentation on forest structure and litter dynamics in Atlantic rainforest in Pernambuco, Brazil. - *Flora* 203: 215-228.
- Schulze MD, Seavy ND, Whitacre DF. 2000. A comparison of the phyllostomid bat assemblages in undisturbed neotropical forest and in forest fragments of a slash-and-burn farming mosaic in Petén, Guatemala. - *Biotropica* 32: 174-184.
- Silva AG, Sá-e-Silva IMM, Rodal MJN, Lins-e-Silva ACB. 2008. Influence of edge and topography on canopy and sub-canopy structure of an Atlantic Forest fragment in Igarassu, Pernambuco state, Brazil. - *Bioarmed Biodiv Bioavail* 2: 41-46.
- Silva APDJ, Pontes ARM. 2008. The effect of a mega-fragmentation process on large mammal assemblages in the highly-threatened Pernambuco Endemism Centre, north-eastern Brazil. - *Biodiv Cons* 17: 1455-1464.
- Silva JMC, Tabarelli M. 2000. Tree species impoverishment and the future flora of the Atlantic Forest of Northeast Brazil. - *Nature* 404: 72-74.
- Silva MG, Tabarelli M. 2001. Seed dispersal, plant recruitment and spatial distribution of *Bactris acanthocarpa* Martius (Arecaceae) in a remnant of Atlantic Forest in Northeast Brazil. - *Acta Oecol* 22: 259-268.
- Simmen B, Sabatier D. 1996. Diets of some French Guianan primates: composition and food choices. - *Int J Primatol* 17: 661-693.
- Sokal RR, Rohlf FJ. 1995. *Biometry*. - W.H. Freeman & Company, New York.
- Sposito TCS, Santos FAM. 2001. Scaling of stem and crown in eight *Cecropia* (Cecropiaceae) species of Brazil. - *Am J Bot* 88: 939-949.
- Stevens SM, Husband TP. 1998. The influence of edge on small mammals: evidence from Brazilian Atlantic Forest fragments. - *Biol Cons* 85: 1-8.

- Stevenson PR, Vargas IN. 2008. Sample size and appropriate design of fruit and seed traps in tropical forests. - J Trop Ecol 24: 95-105.
- Swaine MD, Whitmore TC. 1988. On the definition of ecological species groups in tropical rain forests. - Plant Ecol 75: 81-86.
- Tabarelli M, Lopes AV. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. - Biotropica 40: 657-661.
- Tabarelli M, Mantovani W, Peres CA. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. - Biol Cons 91: 119-127.
- Tabarelli M, Pinto LP, Silva JMC, Hirota M, Bedê L. 2005. Challenges and opportunities for biodiversity conservation in the Brazilian Atlantic Forest. - Conserv Biol 19: 695-700.
- Tabarelli M, Santos AMM. 2004. Uma breve descrição sobre a história natural dos brejos nordestinos. - In: Porto KC, Cabral JJP, Tabarelli M (eds), Brejos de Altitude em Pernambuco e Paraíba: História Natural, Ecologia e Conservação, pp. 17-24. Ministério do Meio Ambiente, Brasília.
- Traveset A, Verdú M. 2001. A meta-analysis of the effect of gut treatment on seed germination. - In: Levey DJ, Silva WR, Galetti M (eds), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation, pp. 339-350. CABI International, Wallingford.
- Trindade MB, Lins-e-Silva ACB, Silva HP, Figueira SB, Schessl M. 2008. Fragmentation of the Atlantic Rainforest in the northern coastal region of Pernambuco, Brazil: recent changes and implications for conservation. - Bioremed Biodiv Bioavail 2: 5-13.
- Valenta K, Fedigan FM. 2009. Effects of gut passage, feces, and seed handling on latency and rate of germination in seeds consumed by capuchins (*Cebus capucinus*). - Am J Phys Anthropol 138: 486-492.

- Válio IFM, Scarpa FM. 2001. Germination of seeds of tropical pioneer species under controlled and natural conditions. - *Rev Bras Botânica* 24: 79-84.
- Veloso HP, Rangel-Filho ALR, Lima JCA. 1991. Classificação da Vegetação Brasileira, Adaptada a um Sistema Universal. - IBGE, Rio de Janeiro.
- Wehncke EV, Dalling JW. 2005. Post-dispersal seed removal and germination selected tree species dispersed by *Cebus capucinus* on Barro Colorado Island, Panama. - *Biotropica* 37: 73-80.
- Wehncke EV, Hubbell SP, Foster RB, Dalling JW. 2003. Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species. - *J Ecol* 91: 677-685.
- Wright SJ, Stoner KE, Beckman NG, Corlett RT, Dirzo R, Muller-Landau H, Nuñez-Iturri G, Peres CA, Wang BC. 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. - *Biotropica* 39: 289-291.
- Wunderle JM. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. - *Forest Ecol Manag* 99: 223-235.
- Young CEF. 2003. Socioeconomic causes of deforestation in the Atlantic Forest of Brazil. - In: Galindo-Leal C, Câmara IG (eds), *The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook*, pp. 103-117. Island, Washington, Covelo, London.
- Zalamea P-C, Stevenson PR, Madriñán S, Aubert PM, Heuret P. 2008. Growth pattern and age determination for *Cecropia sciadophylla*. - *Am J Bot* 95: 263-271.
- Zamith LR, Scarano FR. 2006. Restoration of a restinga sandy coastal plain in Brazil: survival and growth of planted woody species. - *Restoration Ecol* 14: 87-94.

Zhang SY, Wang LX. 1995. Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. - *Biotropica* 27: 397-401.

Appendices

Appendix 1 dbh-class distribution [%] within the seven fragments studied

dbh classes [cm]	Pézinho	Vespas	Gota	Santa Helena	Macacos	Piedade	Zambana
5-10	51.24	39.19	58.61	61.25	45.92	61.62	48.90
10,1-15	19.40	23.65	22.95	14.38	20.17	18.92	23.79
15,1-20	12.44	15.54	10.25	6.88	14.16	9.19	14.54
20,1-25	4.98	5.41	4.10	6.25	8.15	4.86	4.41
25,1-30	4.48	6.76	1.23	4.38	3.00	1.62	3.96
30,1-35	2.99	2.70	0.41	1.88	0.86	1.08	1.32
35,1-40	1.49	0.68	1.64	1.25	1.29	1.08	0.00
> 40	2.99	6.08	0.82	3.75	6.44	1.62	3.08

Appendix 2 Total number of trees (dbh ≥5 cm) and number and % of multiple-stemmed trees within 15 circular plots for all seven studied fragments

fragment	total number of trees	number of trees with multiple- stemmed trees	% multiple- stemmed trees
Piedade	185	6	3.24
Macacos	233	27	11.59
Zambana	227	39	17.18
Pézinho	203	37	18.23
Sta Helena	166	33	19.88
Gota	244	51	20.90
Vespas	148	34	22.97

Appendix 3 Species names in order of appearance in figure 3.1, chapter 3

<i>Gouania virgata</i> , Rhamnaceae	<i>Thyrsodium spruceanum</i> , Anacardiaceae	<i>Xylopia frutescens</i> , Annonaceae	<i>Eschweilera ovata</i> , Lecythidaceae
<i>Cissampelos andromorpha</i> , Menispermaceae	<i>Pogonophora schomburgkiana</i> , Euphorbiaceae	<i>Psychotria carthagenensis</i> , Rubiaceae	<i>Macrosamanea pedicellaris</i> , Fabaceae
undet.	<i>Miconia</i> sp., Melastomataceae	<i>Trichilia lepidota</i> , Meliaceae	<i>Stryphnodendron pulcherrimum</i> , Fabaceae
<i>Pterocarpus violaceus</i> , Fabaceae	<i>Andira nitida</i> , Fabaceae	<i>Sclerolobium densiflorum</i> , Fabaceae	<i>Cecropia palmata</i> , Cecropiaceae
<i>Psiguria triphylla</i> , Curcubitiaceae	<i>Calyptanthus</i> cf. <i>brasiliensis</i> , Myrtaceae	<i>Anaxagorea dolichocarpa</i> , Annonaceae	<i>Schefflera morotoni</i> , Araliaceae

Erklärung

Ich versichere hiermit, dass ich die Arbeit selbstständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt sowie die wörtlich oder inhaltlich übernommenen Stellen als solche kenntlich gemacht habe.

Ferner erkläre ich, dass die von mir vorgelegte Dissertation bisher nicht im In- oder Ausland in dieser oder ähnlicher Form in einem anderen Promotionsverfahren vorgelegt wurde.

Ute Christiane Knörr

Curriculum Vitae

Personal Details

Name	Ute Christiane Knörr
Date of birth	25 September 1977
Place of birth	Mönchengladbach, Germany

Education

Since 2006	Doctoral candidate, Institute for Systematic Botany and Ecology, Ulm University, Germany. Title: Fruiting, fruit characteristics, seed dispersal patterns, seed rain and its importance for regeneration processes in fragments of the Atlantic Rainforest. Supervised by Prof Dr. Gerhard Gottsberger
2003	M.Sc. in Environmental Sciences (German Diplom), University of Duisburg-Essen, Germany. Title: Populationsökologie von <i>Graffenrieda emarginata</i> (Melastomataceae) und <i>Purdiaea nutans</i> (Cyrillaceae) im Höhengradienten eines südecuadorianischen Bergregenwaldes Supervised by Prof Dr. G.-B. Feige and Prof. Dr. S. W. Breckle
1997	A-level (German Abitur): Gymnasium an der Gartenstrasse, Mönchengladbach, Germany.

Work Experience

Since 2006	Research assistant, Institute for Systematic Botany and Ecology, Ulm University. Project: Sustainability of remnants of the Atlantic rainforest in Pernambuco and its implications for conservation and local development
-------------------	------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------

-
- 2004-2005** Research assistant, Department for Environmental and Conservation Programs, Dr. Robin Foster. Field Museum of Natural History in Chicago, USA
- 2004** Field research assistant, Department of Plant Systematics, University of Bayreuth.
Project: "Influence of tree logging on vines and lianas in a montane rain forest of Southern Ecuador", "Estación Científica San Francisco", Ecuador
- 2003** Research assistant, Lippe-Verband / EGLV (Association for waste water and waterbodies), Essen, Germany
- 2002 – 2003** Student research assistant, Department of Hydrobiology, University of Duisburg-Essen. EU Project: "Identification and Designation of Heavily Modified Water Bodies under the Water Framework Directive" (=MAKEF)
- 2000** Volunteer at the Biological Reserve "Maquipucuna", Ecuador field assistant; maintenance of ecological trails etc.
- 1998 – 2002** Member of the student council of the biology department, University of Duisburg-Essen

Scientific Presentations

- KNÖRR, UC (2009): Seed rain in northeastern Brazilian Atlantic Forest fragments. Latin America Symposium, Bonn. (poster)
- KNÖRR, UC, PIECHOWSKI, D, GOTTSBERGER, G (2009): Fragment size effects on *Cecropia* species in the seed rain of northeastern Atlantic Forest fragments. Joint Annual Meeting ATBC/GTÖ, Marburg. (talk)
- KNÖRR, U, GOTTSBERGER, G (2008): Does forest fragment size influence seed rain in the fragmented Atlantic forest of NE Brazil? – 21st Annual Meeting of the Society of Tropical Ecology (gtö), Hohenheim. (poster)

Curriculum Vitae

KNÖRR, U, GOTTSBERGER, G (2007): Tamanho de fragmento da floresta Atlântica em Pernambuco influencia a produção de frutos e sementes.- In: Barbosa LM, Santos Junior Dos, NA (Org.), A Botânica no Brasil, pesquisa, ensino e políticas públicas ambientais. 58° Congresso Nacional de Botânica, São Paulo. (poster)

KNÖRR, U., HOMEIER, J., BRECKLE, S.-W. (2004): Population structure of two tree species in the altitudinal gradient of a montane rain forest in Southern Ecuador. 17th Annual Meeting of the Society for Tropical Ecology, Bayreuth. (poster)

Memberships

Since 2009 Association of Tropical Biology and Conservation (ATBC)