Degradation of Atlantic Forest in NE Brazil and Dynamics of its Regeneration

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A Mata dos Macacos

Seu Floro me mostrou as árvores da mata dos macacos. Nós paramos num morro e vimos o corrego de mata em baixo. Aqui ele me falou os nomes. Eu só consigo me lembrar do começo, das primeiras palavras. Toda enumeração de árvores é fantasia minha.

“Só daqui eu vejo:” sambaquim, pau d’óleo, cabotã, cupiúba, visgueiro, jaguarana, angelim, sucupira mirim, sucupira preta, cocão, embauba branca e roxa, amescla de cheiro, louro maiado, louro seda, dendê, ingá de macaco, ingá peluda, ingá-i, pau d’aico, bucho de veado, oiti coró, guapeba, pau ferro, jitaí, murici branco, murici boi, olho de boi, angola, brassa apagada, sabiá, jaca, manga, pau de jangada, genipapo, mutamba, bordão de velho, praíba, quirí preto e branco, urucuba, pitanga, urucum, bananeira, coco de fuso, macaiba, oiticica, massaranduba, cabotã de rego, bamboo, fávinha, amarelo, .
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Summary

The Atlantic Forest originally covered 15% of the Brazilian territory. Today about 11 to 16% of its original extension is still covered with forest. To a large extent (32–40%) this forest cover is intermediate secondary forest. Only about 1% of the original forest is legally protected. In the northernmost part of this biome, the Pernambuco Endemism Center, the situation is particularly extreme. The forest cover is among the lowest and the percentage of secondary forest is the highest of all Atlantic Forest subregions.

It was generally assumed that in this region the reduction of forest cover and formation of forest fragments took place at least 300 years ago and that the existing remnants already reached relaxation, i.e. the current situation would represent the final stage of degradation. However, a review on the processes of fragmentation since colonial times shows how these developments continued during the agricultural revolution up to the present. The amount of produced sugar in Pernambuco state has increased in the last century from 140,000 t per year in 1900 to 1,200,000 t in the year 1990. Considering that local scientists univocally agree that this was achieved by an expansion of cultivated land, it can be concluded that forest cover was about 80% in 1900. Since the availability of industrially produced fertilizers in the 1950’s and the initiation of the governmental Proalcool campaign in 1975 the forest cover was reduced by at least 50% only in the last 35 years. The existing forest fragments are hence mostly less than 35 years old and will further deteriorate.

There are many speculations about the vulnerability of dispersal modes of plant species in the context of environmental degradation. In an analysis of 26 recent and 21 40 year old tree surveys conducted in the Pernambuco Endemism Center the dispersal modes of top quality timber species and of disturbance-favored tree species were related to their abundances in well- and badly-preserved forest fragments. Large-seeded, bird-dispersed species have average abundances of 5.1 ± 4.6% in well-preserved forest fragments and lack almost completely in badly-preserved fragments (0.4 ± 0.8%). The situation is very similar for large-seeded, endozoochorous timber tree species, which have abundances of about 4.5 ± 3.1% in well-preserved and 0.6 ± 1.2% in badly-preserved forest fragments. Anemochorous timber species are similarly abundant in better- (4.4 ± 5.0%) and
badly-preserved forest fragments (5.3 ± 11.0%). However, large-seeded, synzoochorous timber species are relatively equally abundant in forest fragments of better (1.1 ± 1%) and worse (0.6 ± 0.7%) conservation status. Large-seeded synzoochorous species are also among disturbance-favored species. The difference between well-preserved (7.5 ± 3.0) and badly-preserved sites (9.7 ± 5.9) is not very pronounced. Also ant-dispersed species are of more or less similar abundance at better (1.6 ± 4.1%) and less-well preserved sites (3.7 ± 5.6%). However, disturbance-favored species, which are small-seeded and endozoochorous, reach very high abundances at badly-preserved sites (14.4 ± 11.3%) as compared to well-preserved sites (5.2 ± 3.8%).

The capacity of abandoned areas to recover secondary vegetation, plant species diversity and diverse seed dispersal and pollination mutualisms is receiving increasing attention by scientists studying biodiversity conservation at the landscape level. We studied the seed dispersal and pollination modes of woody species of two 12 year old secondary forest patches on sites formerly used for sugarcane cultivation. Sixty plots were installed covering a total area of 0.6 ha. A total of 61 woody species were registered. Although the study sites were isolated from old-growth forests by a matrix of sugarcane monocultures, the array of dispersal modes were similar to old-growth forest analyzed by other working groups, as were the percentage of vertebrate-dispersed species (83.6%). The percentage of large-seeded species was larger than expected (18%) given the local extinction of large-bodied mammals and birds. These large-seeded plants may have arrived at the sites through dispersal by rodents and bats, and since more than half of the large-seeded species are consumed by humans, they may have reached the study areas this way also. Most pollination modes found in forest fragments in the region were also present in the secondary forest; the exception was that no pollination mediated by vertebrates was found among the studied species, neither by birds nor by bats. A high percentage of species showed an unspecialized pollination mode (55.7%). Pollination by hawkmoths was most common among canopy individuals (42.7%) and many sub-canopy individuals were pollinated by large bees (39.8%). This was due to the high abundance of a few species like the hawkmoth-pollinated Inga ingoides, and Albizia saman in the canopy, the large bee-pollinated Gustavia augusta, and Senna georgica in the sub-canopy.
Summary

In human-dominated landscapes environmental degradation as e.g. dispersal limitation, severely affects the ability of forests to regenerate and to re-colonize abandoned sites. The direct seeding method was experimentally tested as a tool to overcome dispersal limitation and accelerate natural regeneration. Seeds of 22 native tree species were sown in twelve year old secondary vegetation. Two physiognomies of secondary vegetation were differentiated: open sites with no or underdeveloped canopy and closed sites with a canopy. The seeds of most species were collected in the rainy season. Most seeds germinated shortly after planting in the midst of the rainy season. The germination rates were similar at open and closed sites. No differences in seedling performance between early and late successional species and light- and heavy-seeded species could be recognized. The highest mortality was registered at the end of the first dry season obviously due to low precipitation. Most other environmental factors, as leaf litter cover or type of undergrowth had little effect on seedling performance. The main differences in mortality rate were clearly linked to the presence or absence of a canopy. At sites with a canopy the survival rate was significantly higher than at open sites. The formation of a canopy can be recognized as a successional facilitation process which is necessary for the establishment of most tested species. Direct seeding proved to be a good alternative for the enrichment of secondary vegetation that already had developed a canopy.

Summarizing the findings it can be stated that the environmental situation in Pernambuco is more severe than imagined before. The majority of forest fragments that were surveyed in the last years are badly-preserved. Even characteristic species were often lacking. The dominant species are typical secondary species. Although abandoned sites may still develop secondary forest, species that e.g. depend on large birds for dispersal were not registered. A large proportion of tree species will only reach these sites if actively planted. All species which were directly sown into secondary forest could establish within the time of observation. An effective landscape management, including re-connecting forests remnants via corridors, is necessary to preserve the still existing unique biodiversity in this endemism center.
Zusammenfassung


Es existieren viele Spekulationen darüber wie anfällig verschiedene Ausbreitungsmodi von Pflanzen für Umweltdegrdierung sind. In einer Analyse von 26 rezenten und 21 40 Jahre alte Vegetationsaufnahmen aus dem Pernambuco Endemismus-Zentrum wurden die Ausbreitungsmodi von hochwertigen Edelholzarten und von störungsresistenten Baumarten in Relation zur ihren Abundanzen in gut und schlecht erhaltenen Waldfragmenten gesetzt. Großsamige an Ausbreitung durch Vögel angepasste Arten haben eine durchschnittliche Abundanz von 5,1 ± 4,6% in gut erhaltenen Wäldern und fehlen fast vollständig in schlecht erhaltenen Wäldern (0.4 ± 0.8%). Die Situation ist sehr ähnlich für
Zusammenfassung

Endozoocore Edelholzarten, die eine Abundanz von 4,5 ± 3,1% in gut erhaltenen und 0,6 ± 1,2% in schlecht erhaltenen Wäldern haben. Windausgebreitete Edelhölzer sind in schlecht (5,3 ± 11,0%) und gut erhaltenen Wäldern (4,4 ± 5,0%) ähnlich abundant. Großsamige synzoochore Edelhölzer sind ähnlich abundant in stark gestörten (0,6 ± 0,7%) wie in gut erhaltenen Wäldern (1,1 ± 1%). Großsamige synzoochore Arten gibt es auch unter störungsresistenen Arten. Der Unterschied zwischen gut (7,5 ± 3,0) und schlecht erhaltenen Wäldern (9,7 ± 5,9) ist nicht sehr ausgeprägt. Auch Ameisen ausgebreitete Arten sind in ebenfalls in gut (1,6 ± 4,1%) und schlecht erhaltenen Wäldern (3,7 ± 5,6%) ähnlich abundant. Kleinsamige endozoocore Arten erreichen sehr hohe Abundanzen in schlecht erhaltenen Wäldern (14,4 ± 11,3%) verglichen mit gut erhaltenen Wäldern (5,2 ± 3,8%).

Wie vielfältig sind Pflanzen-Tier-Interaktionen in Sekundärwald der auf aus der Nutzung genommenen Flächen aufwächst? Wir haben die Ausbreitungs- und Bestäubungsmodi von holzigen Arten eines zwölf Jahre alten Sekundärwaldes studiert, der auf einer Fläche aufgewachsen ist auf der zuvor intensiv Zuckerrohr angebaut wurde. Sechzig Parzellen mit einer Gesamtflache von 0,6 Hektar wurden angelegt. Insgesamt wurden 61 holzige Arten registriert. Obwohl die studierte Fläche durch Zuckerrohrfelder von älteren Wäldern isoliert ist, ist die Komposition von Ausbreitungs- und Bestäubungsmodi der von altestehenden Wäldern sehr ähnlich, die von anderen Arbeitsgruppen untersucht wurden, so zum Beispiel der Anteil von Arten die durch Wirbeltiere ausgebretet werden (83,6%). Der Prozentanteil von großsamigen Arten war größer als erwartet (18%), wenn man berücksichtigt, dass alle größeren Säugetiere und Vögel lokal ausgerottet sind. Diese großsamigen Pflanzen könnten teilweise durch Nager und Fledermäuse ausgebretet worden sein; da mehr als die Hälfte dieser Arten auch von Menschen gegessen werden, könnten sie auch auf diese Weise ausgebretet werden. Die meisten Bestäubungsmodi die in den Waldfragmenten der Region vorkommen wurden auch in dem Sekundärwald verzeichnet, mit der Ausnahme, dass keine Bestäubung durch Wirbeltiere, weder durch Vögel noch durch Fledermäuse, unter den untersuchten Arten anzutreffen war. Ein großer Anteil der Arten zeigte einen unspezialisierten Bestäubungsmodus (55,7%). Bestäubung durch Nachtfalter war unter Baumindividuen am häufigsten (42,7%) und viele Individuen des Unterwuchses wurden durch große Bienen bestäubt (39,8%). Dies
ist durch die hohe Abundanz weniger Arten wie die nachtfalterbestäubten Bäume *Inga ingoides*, und *Albizia saman* und die bienenbestäubten Unterwuchsarten *Gustavia augusta* und *Senna georgica* begründet.


1. Introduction

In the northernmost part of the Atlantic Forest, the Pernambuco Endemism Center (PEC), deforestation (Galindo-Leal and Camara 2003), defaunation (Silva and Pontes 2008, Farias et al. 2007) and the exploitation of forest resources (Galetti 2001, Freyre 2004) have reached a limit which does not only peril this unique ecosystem (Silva and Tabarelli 2000a, Silveira et al. 2004), but also negatively affects the inhabitants of the region (CONDEPE 2001, CPRH 2001). The Brazilian law requires the reforestation of especially sensitive sites as riversides, steep slopes and along the edges of tablelands, and as well of a minimum area per property (Código Florestal 2001). Ideally these measures will also lead to a higher degree of connectivity between forest fragments and therefore assure the integrity of the genetic diversity of populations, the re-colonization of suitable habitat by numerous species and the formation of meta-populations (Código Florestal 2001).

Although the juridical basis is theoretically clear, the biological background is not. Will the existing forest fragments remain and under which conditions? How much of the present biological diversity may endure and maintain proper functions, including vital ecosystem services, under this heavy human impact? These questions were the focus of the project “Sustainability of remnants of Atlantic rainforest in Pernambuco and its implications for conservation and regional development” within the framework of the German-Brazilian cooperation “Science and Technology for the Atlantic rainforest in Brazil”.

The aim of the present sub-project was to analyze the regenerative dynamics of secondary vegetation (capoeira), comparing younger and older patches, with special attention to flowers and fruits, and the possibility to accelerate succession by planting. “Capoeiras and capoeirões are anthropogenic phases of secondary vegetation and do not constitute forest types” (Veloso et al. 1991). The augmentative of capoeira is capoeirão (plural: capoeirões) and is used for later stages of succession. Capoeirinha is the diminutive of capoeira, and is used for early stages of succession and also extremely degraded sites that are incapable to develop forest structure but remain dominated by scrubs or weeds (Miller 2000). Whether or not capoeira may eventually develop the structure of a mature forest depends on the integrity of its surrounding landscape. However, the large majority of forest fragments in the study region are small, i.e. below 100 ha.
Figure 1: Sites to be reforested. a: water reservoir Barragem Botafogo, drinking water supply. On the left some forest, in the back the runoff from the sugarcane field may enter directly the water body, the required forest belt width is 100 m. b: river Botafogo, some trees (mostly *Inga ingoides*) grow along its course, the required forest belt width is 30 m. c: river Botafogo in the rainy season, a bridge was washed away. d: edge of a tableland (*tabuleiro*) forest belt width: 100 m. The given numbers of forest width according to Código Florestal (2001).
(Trindade et al. 2008, Ranta et al. 1998) and such small fragments are heavily influenced by edge effects (Laurance et al. 2002), so that with regard to many functional attributes they become similar to secondary vegetation (Santos et al. 2008). One consequence of this development is that it becomes almost impossible to classify a given forest fragment as fallow vegetation, vegetation that regenerated after clear-cut, selectively logged forest or the result of permanent exploitation. In fact the fragments classified as forest by Santos et al (2008) were classified as *capoeira* and forest by Fernandes (2003) and Roda and Santos (2005) classified them as initially to intermediate secondary forest, with some very old sites within. In the Pernambuco endemism center 58.3% of the total forest cover is intermediate secondary forest (Silva and Casteleti 2003, Ribeiro et al. 2009). The largest forest fragment in the whole PEC is the Marshall Newton Cavalcanti military training ground, it is mainly secondary forest (Andrade et al. 2005). Altogether it has a size of almost 10,000 hectares (Amarante and Tabarelli 2003). It was part of a sugar plantation and the forest regenerates since 1944 (Andrade et al. 2005, Pereira et al. 2005). However, the particular history of forest remnants is mostly unknown (Andrade and Rodal 2004). Even when the structure of a forest appears well-preserved, e.g. in terms of large trees and tree species richness, it does not imply that the ecosystem fully functions (Redford 1992). The absence of certain animal species has profound implications (Redford 1992). Even the large forest fragment Coimbra was found impoverished in mammal species richness and abundance compared to other smaller remnants in the PEC (Pontes et al. 2006a). In the study area, the sugarcane plantation São José, no well-preserved forest remnants, not to mention continuous forest, are left (Foury 1968, Trindade et al. 2008). All forest remnants have been subdued to intense exploitation of timber since the XVI century (Foury 1968, Galetti 2001). Regeneration took mostly place in the absence of many important dispersers, as tapirs, capuchin monkeys, and toucans (Farias et al. 2007, Silva and Pontes 2008). An extreme loss of forest cover in the last four decades and resulting edge effects further complicates regeneration (Laurance et al. 2002, Trindade et al. 2008, Piechowski and Gottsberger 2008, Silva et al. 2008b) while the exploitation of forest resources continues (Cunha and Albuquerque 2006, Albuquerque et al. 2008).
1. Introduction

The main questions of the present study were:

- Which influence do the dispersal modes of top quality timber species and of disturbance-favored tree species have on their abundance in forest fragments in the PEC?

- Which kind of fruits and seeds are still being dispersed in this anthropogenic landscape? Which pollination modes are present in the secondary vegetation? Does the regeneration of forest, in its broader sense, still take place? May such secondary vegetation serve as functioning corridor to re-connect forest remnants?

- Are seeds that are artificially dispersed into secondary vegetation physiognomies able to germinate and is the establishment of seedlings possible?
2. The history of degradation and fragmentation of the Atlantic Forest of Pernambuco

Summary
This review summarizes and links classical works with recent publications to give an overview of the main processes of fragmentation of the Atlantic Forest of Pernambuco since colonial times and to show how these processes continued during the agricultural revolution up to the present. The Atlantic Forest of Pernambuco is an extremely endangered endemism center and an unknown number of its biota is already extinct while others are at the rim of extinction. Sugarcane has always been the main economic factor in the forest zone and so until now sugarcane fields dominate this region. The broad river valleys were the first to be used for sugarcane cultivation. Gradually also the slopes of hills were converted into sugarcane fields. With the improvement of roads and the construction of railroads since the XIX century more remote and mountainous regions were colonized. Since the availability of industrially produced fertilizers in the nineteen fifties and the initiation of the Proalcool campaign the large but nutrient-poor tablelands or tabuleiros and other beforehand less suitable areas were used as well. The forest cover was reduced by at least 50% in the last 35 years. The presently still forested sites are simply not suitable for the cultivation of sugarcane due to their strong inclination or necessary to preserve the water resources. They are protected by law, nevertheless their maintenance is not guaranteed. For the growing demand of biofuels the production of sugarcane turned a focus of international attention.

Introduction
The Brazilian Atlantic Forest is one of the five most important global hotspots (Myers et al. 2000). It contains five areas of endemism. Two of them are located in the very North of the biome: the Brejos de Altitude (hereafter brejos) forests on higher elevations surrounded by a thorn scrub caatinga and the Atlantic Forest north of the Rio São Francisco. The lowland Atlantic Forest also named Pernambuco endemism area (PEC), encompasses the eastern parts of the states
2. The history of degradation and fragmentation of the Atlantic Forest of Pernambuco

Rio Grande do Norte, Paraiba, Pernambuco and Alagoas (Silva and Casteleti 2003). Besides endemic mammal and bird species (Pontes et al. 2006b, Silveira et al. 2004) they are unique for sharing many faunistic and floristic elements with the Amazonian Forest from which they are isolated since the Oligocene to Miocene and which differentiates them from the other bio-geographic regions of the Atlantic Forest (Andrade-Lima 1960, Andrade-Lima 1982, Gottsberger and Silberbauer-Gottsberger 2006a). The total forest cover of the Pernambuco endemism area is only 4.5% of its original extension range (Figure 3) (SECTMA 2002). This chapter mainly treats the forests located in the state of Pernambuco and Alagoas, but the described processes took and still take place in the neighboring states as well (Andrade 1957, Andrade 1959a, Freyre 2004, Andrade 2005).

The early time of colonization

The indigenous Tupí who lived in the lowland practiced coivara i.e. slash-and-burn agriculture and planted yucca, corn, beans, and peanuts and many other plant species besides being hunters and gatherers (Dean 1997, Dantas et al. 2006). According to Soares (1987) (among other chronists) the inhabitants of Pernambuco were the Caeté and north of the Rio Paraiba lived the Potiguara, both speaking the same language Tupinambá (Soares 1987). Further inland and also inhabiting the mountain forest (brejos) were living and still live more heterogeneous tribes of various language groups (Dantas et al. 2006). After Cabral had discovered the route from Europe to Brazil in 1500, Portuguese and French merchants traded with the various Tupí groups. European products were exchanged mainly for Brazilwood (Caesalpinia echinata) (Freyre 2004, Andrade 2005). The population density in the coastal region at this time can hardly be reconstructed, the guesses range from 0.6 to 9.5 persons per km² (Fausto 1992).

In 1535, Duarte Coelho arrived in Brazil. He was sent by the Portuguese crown and was in charge of the capitânia Pernambuco. With him and his followers began the implementation of sugarcane plantations on a large scale, the enslavement of firstly indigenous people and later of Africans, and the fragmentation of the Atlantic Forest of Pernambuco (Andrade 2001, Freyre 2004). The Caeté did not peacefully accept the invasion and attacked major settlements, e.g. Igarassú (Staden 1993) and killed the Bishop Sardinha who shipwrecked at
the shore of Alagoas (Soares 1987). This was taken by the Portuguese as a reason to declare guerra justa, i.e. justified war. This war resulted in the massacre, enslavement and flight of many Tupi to the Amazon region (Fausto 1992). However, several villages remained in Pernambuco, Alagoas and Paraíba at least up to the XVIII century, with inhabitants speaking lingua geral which is basically Tupi (Dantas et al. 2006, Sampaio 1901). There are still several Potiguara villages in Paraíba (Palitot and Souza Júnior 2005). Forced labor and cultural oppression by the European colonizers united indigenous, Africans and their descendents in several revolts (Pereira et al. 2005, Andrade 2004). The contacts between these ethnic and cultural groups led to the emergence of a popular culture, which incorporates indigenous knowledge about wildlife and also cultivated plants (Freyre 2004). However, the rich landowners were ignorant of this traditional knowledge and did not value it (Freyre 2004). Comparing the current local names of plants with those registered by Piso and Marcgraf (1648), who were informed by the local indigenous population, it is very obvious that with a few exceptions of species, which received Portuguese or pidgin names, the names have changed very little (Pickel 2008).

The sugarcane plantations were established along the main rivers, the rios do açúcar – the “sugar rivers”, where the most fertile soil, the massapé was encountered (Freyre 2004, Andrade 2005). Less suitable areas were used for other crops, necessary for food supply (Freyre 2004; Andrade 2005). The surrounding forests served as source of firewood, especially for the sugar mills. The Pernambucan anthropologist, sociologist, and historian Gilberto Freyre (1900-1987) experienced the time when the small sugar mills (engenhos) still existed. According to him, even the best woods were burned to ashes that were used as fertilizer, served as firewood, or for fence construction (Freyre 2004).

The development of the sugarcane agriculture in Pernambuco was quicker than in the neighboring states of Bahia, Paraíba and Espírito Santo and continued even in years of crisis (Galvão and Gonçalvez 1986). The number of sugar mills was five in 1550 and increased up to 66 in 1584, 144 in 1630 – 1637 (during the time of the Dutch conquest), and about 3,500 in the second half of the nineteenth century (Andrade 2001). Although the first sugarcane mills were installed on the island of Itamaracá, the more southern part of Pernambuco was more quickly colonized due to more fertile soils and a more favorable climate (Andrade 1979).
Large parts of Alagoas remained mainly out of control of the Portuguese colonizers. However, it was considered a forest reserve of the Portuguese merchant navy (Moreira and Freitas 1907b). The rivers were used to transport the wood to the ports (Moreira and Freitas 1907b). The wood of these forests was preferably used even in other regions of Brazil because it was not straight but bent, which made it especially useful for marine construction (Moreira and Freitas 1907b). In northern Alagoas the quilombo dos Palmares, which was inhabited by more than eleven thousand people living in several villages, resisted until 1694 (Nieuhof 1993). *Quilombolas* were mainly Africans and Afro-Brazilians that escaped slavery and lived in communities (*quilombos*) (Carvalhos 1996).

The rivers played a major role in the colonization of the forest zone of Pernambuco, because they were the best mean of transport (Andrade 2001). There were little ports at the river estuaries from where the sugar was sent by boat to the capital Recife (Andrade 2001). The first lost forest habitats were consequently the broad river valleys. The rivers cross the forest zone from west to east, and the plantations along them fragmented the beforehand continuous forest.

**The nineteenth century**

There is evidence that in the nineteenth century large wooded areas still existed in the west of the forest zone. Koster (1993) described the region north of Recife as partially swampy, and mostly densely covered with forest, and only some open areas where sugarcane was planted (the village of Paulista). The dense forest caused a humid climate and blocked the winds coming from the Atlantic Ocean (Koster 1993). The map “Florestas da Capitânia de Pernambuco” from 1799 shows a strip of cultivated land along the coastline but only forests in the west (Webb 1979). They provided refuge to two rebellious movements: in the north the *quilombolas* inhabiting the forests of Catucá, and in the South the Cabanos, called after their housings, mere straw huts (in Portuguese *cabana*) (Andrade 2004).

The forests of Catucá were located at the western frontier of the sugarcane fields, between Apipucos (Recife) in the South, Vitória de Santo Antão in the West, and Goiana in the North, close to the border of Paraíba (Carvalhos 1996). They were not one continuous forest but were intersected by sugarcane fields and mills and trails along which cattle and cotton were transported from the interior to Recife (Carvalhos 1996). Military repression of the *quilombolas* was not always
successful but expensive (Carvalhos 1996). It was thus decided to destroy the forests, so that the rebels would lose their shelter (Carvalhos 1996). One major step into this direction was the donation of forested lands to German settlers; thus the colony Amélia was founded in 1829 (Carvalhos 1996). These settlers made their living in producing charcoal (Carvalhos 1996). A large part of the forest disappeared this way and the quilombo became effectively fought, yet the settlers encountered such difficulties that they finally left the state, whereas the quilombo returned strongly attacking even main sugarcane mills (Carvalhos 1996).

The center of combat in the war against the cabanos was the dense forests around Água Preta, close to Alagoas (Andrade 2004). The main part of the movement surrendered in 1835 (Andrade 2004). The last cabano leader was imprisoned as late as 1849 (Andrade 2004). After fighting the cabanos, the governmental forces moved northwards to put an end to the quilombo Catucá in 1837 (Carvalhos 1996; Andrade 2004).

The development of the western part of the forest zone was much slower than the coastal region (Andrade 2001). The means of transport were ox wagons and donkeys. Only in the nineteenth century the government constructed roads to support the sugar mills in these areas, connecting them with Recife.

The emergence of the usinas and the industrialization of sugarcane cultivation
Considering that about 90% of the cultivated land in the forest zone of Pernambuco are used for the cultivation of sugarcane (CONDEPE 2001), and that production of sugar and the area used for its cultivation are highly correlated for the time between 1949 and 1992 (Spearman rank order correlation: 0.98; p < 0.05) then we may assume that forest cover in the year 1900 was about 80% in the state of Pernambuco (assuming that productivity per hectare in the first half of the XX century was half that of the second). This becomes obvious when we look at the sugar production between 1800 and 1990 (Figure 1). This development of forest cover reduction was similar to those of the states Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo (Instituto Socioambiental 2001).
At the end of the nineteenth century the first *usinas* emerged, factories that quickly outran the smaller sugarcane mills and took over their land (Andrade 2001; Freyre 2004). The direct effect of this development was that the forests encountered between the smaller estates and fields were often cleared (Andrade 2001; Freyre 2004). Each *usina* consumed about 100 ha of forest per year as firewood (Neto and Tabarelli 2002). Only the domestic need of firewood was larger (Foury 1968). Since the *usinas* are permanently trying to expand their productive land they forced rural workers and their families to abandon their homes and the sites they used for subsistence agriculture (Andrade 2001, CONDEPE 2001). The resulting rural exodus continues up to the present (CONDEPE 2001). Most people are driven to small towns or cities (Montes and Cosulich 1998, Andrade 2001, CONDEPE 2001). In the second half of the nineteenth century railroads of the Great Western Railroad Company were built to connect Recife to Timbaúba, Vitória de Santo Antão and Palmares (Andrade 2001). This made the installation of *usinas* in the regions of the upper Capibaribe-mirim, Tracunhaém, Siriji and Capivaribe rivers possible (Andrade 2001).
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Figure 2: Images of the landscape in Pernambuco and Alagoas in the 1950s. a: dry forest of Engenho Ventura, municipality Nazaré da Mata, Pernambuco (Andrade-Lima 1961). b: tableland forest converted into sugarcane field (Andrade 1959b). c: Cerradão growing on tableland in Alagoas (Andrade 1959b). d: Tributary stream of the São Miguel river and tablelands covered with forest,
location where the *Mitu mitu* was lastly observed (Silveira et al. 2004), today completely covered with sugarcane fields, picture by Andrade (1959b).

The production of firewood for the trains, which exclusively ran on firewood (Foury 1968), led to deforestation and severe declines in humidity. This was the case in the regions which are located at the western slopes of the Borborema and hence receive less rain, which comes from the South-East. This resulted in an advance of the caatinga, e.g. around the Serra das Russas (Andrade 2005).

In the first half of the twentieth century the yields of sugar per hectare in Pernambuco were very low in comparison to other centers of this agriculture (Andrade 2001). Since the thirties new sugarcane varieties were introduced, and irrigation, herbicides, insecticides and fertilizers were implemented to increase productivity (Andrade 2001). These measures led to a stronger isolation of the forest fragments firstly because poisoned fields cleared of any unwanted herbs represent a strong barrier for animal migration and, secondly, the abandonment of a matrix of subsistence farming that meant a much higher connectivity between the forest fragments due to a larger variety of cultivated plants, including many fructiferous trees that offered various resources as nectar, pollen, fruits and shelter, resulted in a monoculture of a grass that does not produce any mutual resources (Westerkamp and Gottsberger 2000). The process of intensification of agriculture continues up to the present (Montes and Cosulich 1998, Andrade 2001, CPRH 2001).

Also other industries consumed large amounts of firewood among others: soap works, cement plants, and backeries (Foury 1968). The largest textile company in South America was the *Companhia de Tecidos Rio Tinto* in Paraíba and the *Companhia de Tecidos Paulista* in Pernambuco, both owned by the Lundgren family. In Rio Tinto the indigenous Potiguara were forced to sell 60,000 hectare of mostly forested land to the company, shortly before it would have been recognized as indigenous reserve (Palitot and Souza Júnior 2005).

**The Proalcool campaign**

In 1975 the Brazilian government initiated the Proalcool campaign that had as its goal an increase in the alcohol production. Since then the forest cover in
Pernambuco and Alagoas was reduced by more than 50%, as shown in the following.

Figure 3: The area used for sugarcane cultivation in the two federal states of Alagoas (AL) and Pernambuco (PE) (Lima 2003).

The industrialization of the agricultural production had severe effects on forests located on sandy tablelands, the *tabuleiros* (Figure 2b, c, d), the mountainous region in the North of Alagoas and southern Pernambuco, and also other regions that were beforehand less affected. The *tabuleiros*, are typical for the northern part of the forest zone (Andrade-Lima 1954) and most of lowland of Alagoas (Tavares et al. 1975a). The soil of the *tabuleiros* is poor in nutrients and organic matter (Andrade-Lima 1970). Hence, initially they were not used for the cultivation of sugarcane, but their forests were partially cut to extract the wood and afterwards secondary forests established (Andrade-Lima 1970), while other parts were used to raise cattle (Andrade 2005). The conversion into sugarcane fields began only in the fifties, since when the *vinasse*, a by-product of sugar production, is being used as fertilizer (Andrade 2001). Due to mechanization, the plain *tabuleiros* became the best suited areas to plant sugarcane (CPRH 2001, Andrade 2005). In Northern Pernambuco (Usina São José), characterized by large *tabuleiros* the loss between 1975 and today was 52.6% (Trindade et al. 2008) (Figure 4b-c). In the state of Alagoas the loss between 1968 and today was 56.2%
2. The history of degradation and fragmentation of the Atlantic Forest of Pernambuco

(Tavares et al. 1975a, Instituto Socioambiental 2001). The situation was probably similar in Rio Grande do Norte and Paraíba (Barbosa 1996). Large parts of the state of Alagoas resembled recently colonized, with sugarcane fields full of burnt tree trunks (Andrade 1959b). In the seventies this process was still going on and conversely sites of strong inclination were taken out of usage and developed into secondary forests (Andrade-Lima 1970, Carvalho 1971).

Some natural small *Cerrado* forest patches grew on the *tabuleiros* (Figure 2c). Often these forests are referred to as *tabuleiro*-forest itself. In Pernambuco this vegetation is probably completely extinct (Sampaio and Gamarra-Rojas 2002). However some degraded patches still exist in Paraíba (Krause pers. comm.).

The Mutum de Alagoas (*Mitu mitu*), probably once distributed in the whole lowland forest of the PEC, was last encountered in the forest of São Miguel dos Campos (Alagoas) in 1951 (Figure 2d), is now extinct in the wild (Silveira et al. 2004). The same happened to populations of howler monkeys (*Alouatta belzebul*) in São Miguel dos Campos (Coimbra-Filho et al. 2006). Also other sites, which had been conserved, degraded considerably in the last decades: for example the reserve Gurjaú was considered virgin forest in 1954 (Andrade-Lima 1954a). Up to the seventies the reserve was almost completely surrounded with forest, whereas in the eighties the forests outside the reserve had mainly disappeared and even the remnants inside the reserve suffer increasingly from illegal occupation (Marangon et al. 2004). Ranta et al. (1998) calculated a forest cover of 23.3% in a region of 2674 km² (ten municipalities) in South Pernambuco. They used maps provided by the SUDENE of 1974, i.e. one year before the Proalcool campaign. The actual forest cover in the same municipalities is 9.1% (SOS Mata Atlântica 2008). The forest loss in the region between 1974 and today was hence 60.8% (Figure 4d-e).
Figure 4a-e: a: The Pernambuco Endemism Center and its division into semideciduous and evergreen forest. Dark spots are forest remnants; the stripped region in the north is an area of contact between the two types. b: The forest cover in 1968 according to aerial photographs. c: The current forest cover. d: The forest cover in south Pernambuco 1974, modified after Ranta et al. (1998). e: The forest cover in the same region in 2008 (outlines as in 3d) (SOS Mata Atlântica).
According to Andrade-Lima and Lira (1974), the largest forest reserves of northeastern Brazil were located in the mountainous south of Pernambuco and the north of Alagoas. They were even recommended for sustainable logging (Andrade-Lima 1974). Most of these forests have given room for sugarcane fields. The opening and improvement of roads led to the installation of usinas even in the most distant valleys, e.g. the Usina Serra Grande (Andrade 2005).

The national institute for colonization and land reform (INCRA) distributed about 35,000 ha of land among settlers in Pernambuco (CONDEPE 2001). How much of the land was covered by forest is not published, it can only be deduced, as in reports forested land was referred to as “unproductive” (Dean 1997). On the photographs mentioned above can be recognized that, e.g. the Engenho Caiana, and the settlements Pitanga I and II were completely forested (Figure 5d). These measures did not considerably improve the extremely unequal distribution of land (Andrade 2005).

The Brejos

Brejos which were the main deforestation events initiated in the fifties for the cultivation of coffee (Gomes 2004, Andrade-Lima 1977). Deforestation led to severe declines in precipitation, in some areas resulting in a change of the vegetation from forest to scrub-forest (Gomes 2004). However, most of the coffee plantations were abandoned and the sites are now covered with secondary forest (Silva et al. 2008b, Andrade-Lima 1977).

Current situation

The economic development and disorganized occupation of land in the last years led to many losses of natural habitats (CPRH 2001, SECTMA 2002). The largest current threats to the forest remnants are the uncoordinated growth of cities, due to growing population, allotment of farms and rural residences, and the extraction of wood and fuel wood consumed in rural areas or urban centers (CPRH 2001). The only two forest fragments (Mata da Usina São José = Mata de Piedade), and the Mata da Compania Agroindustrial Gioana, north of Recife are reported to be well-preserved (CPRH 2001) and covering parts of a tabuleiro (SECTMA 2002). However, the latter is used as a waste disposal (CPRH 2001), and the highway (BR-101) cutting through the remnant was recently broadened (Jamel et al. 2006).
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Figure 5a-f: A large part of the actual forest cover in the PEC is early to intermediary secondary forest. a: early open stage of secondary vegetation (*Capoeirinha*), the trees are *Cecropia palmata*. b: recently cleared intermediary forest and remnant in the background. c: the largest forest fragment in the PEC is mainly intermediary forest (municipality Abreu e Lima, military training ground M. N. Cavalcanti). d: a single tree remained of a forest cleared by the INCRA
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(Pitanga I). e: one of the most dominant secondary forest species is *Samanea saman*, it sheds its leaves in the dry season. f: very strong erosion is a common sight in sugarcane fields.

Of 40 ecological reserves in Pernambuco only two are sufficiently protected, the others suffer heavy environmental pressure from their environment (SECTMA 2002). The forest of the ecological reserve São Bento in the municipality of Abreu e Lima north of Recife almost disappeared. During ten years it became to 90% devastated by an invasion of members of a movement of landless people (CPRH 2001). The percentage of forest cover on private properties declined about 35% from 1980 to 1995 (Sampaio and Gamarra-Rojas 2002). Analyzing several landscapes in Pernambuco and Alagoas, Amarante and Tabarelli (2003) come to similar conclusions: forest cover was reduced by 10% between 1989 and 2001. However, at least Guaríbas (Paraíba), Goiana, Serra das Mascarenhas (Pernambuco), Gurjaú, the mountainous region between the north of Alagoas and Pernambuco including Murici, Serra Grande and Frei Caneca, are regions where a considerable forest cover still remains, partially inhabited also by a range of animals, like howler monkeys, capuchin monkeys and rare birds.

**Conclusions**

There were some decisive events that caused a gradual fragmentation of the Pernambucan lowland Atlantic Forest. Many of these took place in recent time and the forest fragments are still endangered by ongoing deforestation. One of the most elaborate and influential works on this topic is by Ranta and co-workers (1998). Despite its obvious values in analyzing the fragmentation pattern from 1974, they drew some conclusions that are probably based on insufficient investigations: firstly, they regard the fragments mainly as results of deforestation that took place 300 to 500 years ago and hence assume that extinction processes of vulnerable species must already have taken place. Secondly, they believe the situation was stable. Conversely, a lot of fragmentation occurred in recent time and the precarious situation of the existing forest fragments should not be underestimated. In fact, measures must be taken to preserve the existing remnants from further degradation, ranging from protection against over-exploitation to the implementation of biological corridors between neighboring fragments (Ranta et
al. 1998, SECTMA 2002). This is especially important in cases where populations of rare or endemic animals could be joined or where they could re-colonize neighboring forest fragments (Oliveira and Langguth 2006, Farias et al. 2007). The movements of animals are a main vehicle for pollen and seeds which is essential for ecosystem functioning (Gottsberger and Siliberbauer-Gottsberger 2006b). A monitoring of the sugarcane industry by consumers of bio-fuel, as e.g. the European Union might be an incentive for conservation efforts, but certification schemes are lacking (Friends of the Earth Europe 2008). The growing demand is much more likely to have a devastating effect on the environment and local people (Friends of the Earth Europe 2008). The juridical framework is theoretically clear: the decree 750/93 does not allow any cutting, exploitation or repression of natural vegetation in the Atlantic Forest domain, if not exceptionally authorized by the Brazilian institute for the environment and natural resources IBAMA (Decreto 750 1993). The legislation further demands that along rivers and on inclined sites natural vegetation should be allowed to grow, which, if implemented, increased connectivity between forest remnants (Código Florestal 2001).
3. The influence of dispersal modes on the abundance of top quality timber species and of disturbance-favored tree species in a human-dominated landscape

Summary:
There are many speculations about the vulnerability of dispersal modes of plant species in the context of environmental degradation. In this study 26 recent and 21 40 year-old tree surveys conducted in the Pernambuco Endemism Center were analyzed with regard to the dispersal modes of top quality timber species and of disturbance-favored tree species and their abundances in well- and badly-preserved forest fragments. Large-seeded, bird-dispersed species have average abundances of 5.1 ± 4.6% in well-preserved forest fragments and lack almost completely in badly-preserved fragments (0.4 ± 0.8%). The situation is very similar for large-seeded, endozoochorous timber tree species, which have abundances of about 4.5 ± 3.1% in well-preserved and 0.6 ± 1.2% in badly-preserved forest fragments. Anemochorous timber species are similarly abundant in better- (4.4 ± 5.0%) and badly-preserved forest fragments (5.3 ± 11.0%). However, large-seeded, synzoochorous timber species are relatively equally abundant in forest fragments of better (1.1 ± 1%) and worse (0.6 ± 0.7%) conservation status. Large-seeded synzoochorous species are also among disturbance-favored species. The difference between well-preserved (7.5 ± 3.0) and badly-preserved sites (9.7 ± 5.9) is not very pronounced. Also ant-dispersed species are of more or less similar abundance at better (1.6 ± 4.1%) and less-well preserved sites (3.7 ± 5.6%). However, disturbance-favored species, which are small-seeded and endozoochorous, reach very high abundances at badly-preserved sites (14.4 ± 11.3%) as compared to well-preserved sites (5.2 ± 3.8%).

Introduction:
In human-dominated landscapes including biodiversity hotspots mutual interactions especially between plants and animals are endangered. Intense hunting and habitat loss lead to defaunation including the loss of seed-dispersers
The influence of dispersal modes on the abundance of selected tree species

The absence of dispersers such as large-billed birds (e.g. toucans) can lead to dispersal limitation in species with highly specialized dispersal mode, e.g. in *Virola flexuosa* (Holbrook and Loiselle 2009). Non-dispersed seeds have drastically reduced survival rates (Janzen 1970, Connel 1971). Galetti (2000) has shown that the large toucan, *Ramphastos vitellinus*, forages preferably on fruits with high lipid content and the species *Virola gardneri* with the highest lipid content is also the species with the largest seeds and could only be dispersed by large toucans such as *R. vitellinus*. Under heavy disturbance pressure we can assume that in the long run a self-energizing effect establishes: environmental degradation and hunting reduces disperser populations, whereas selective logging and recruitment failure due to non-dispersal reduce the availability of food for the remaining animals and the result is the extinction of both mutual partners.

In human-dominated landscapes a large proportion of habitat is not only suffering from fragmentation, selective logging, and defaunation, but is actually secondary. It originates either from clear-cuts or abandoned fields (Whitmore 1990, Terborgh 1992). Re-sprouting is a very important way of regeneration of trees when stumps or roots are still present (Sampaio et al. 1993, Skatulla 2002). However, in areas without means of vegetative regeneration and no remaining seed bank, establishment can only take place via dispersal. When important dispersers are absent or do not cross the surrounding matrix many plant species will never reach such sites. The resulting vegetation is of relatively low diversity and may even show a tendency towards stagnation of succession (Mesquita et al. 2001).

Of the Brazilian Atlantic Forest, the Pernambuco Endemism Center (PEC) suffered the most from habitat loss and fragmentation and only 5% (when including young secondary growth 11.5% respectively), of the original forest cover is left (Silva and Casteleti 2003, Ribeiro et al. 2009). The phenomenon of seed dispersal was addressed by Silva and Tabarelli (2000b), who stated that about 33.9% of tree species, including all large-seeded, animal-dispersed species are locally threatened due to the local extinction of their avian dispersers in the PEC. Without considering the particular dispersal mode, Santos et al. (2008) found that the percentage of species with large seeds is significantly smaller in small forest fragments, forest edge, and secondary forest, compared to the interior.
of a very large forest fragment. In secondary vegetation the number of large-seeded species was highest in the oldest stands (Santos et al. 2008).

The objective of this study was to analyze and interpret the abundances of top quality timber and disturbance-favored tree taxa with regard to their dispersal modes in surveys conducted in well- and badly-preserved forest fragments. It is hypothesized that:

- Large-seeded, species are more abundant in better-preserved forest fragments compared to fragments that suffered from degradation.

- Disturbance favored species are supposed to have small seeds.

**Material and Methods:**

**Study Region:** The PEC extends along the Brazilian coast from Rio Grande do Norte in the north to the river São Francisco in the south (Silva and Casteleti 2003). It covers four main relief types: a coastal plain with a maximum altitude of about 100 m a.s.l., a region of low hills (up to 200 m altitude), coastal tablelands (tabuleiros) with altitudes up to 200 m, and a relatively low but still mountainous region (Planalto da Borborema) in the West, with altitudes up to 1000 m (SECTMA 2006, Tavares et al. 2000). The climate ranges from humid at the coast to sub-humid and dry-humid, in the interior (SECTMA 2006). The “brejos de altitude” are natural forest islands located on higher altitudes where the eastern weather sides of the mountains receive higher precipitation compared to the surroundings. Combined with lower temperatures, this leads to a sub-humid climate (Andrade-Lima 1972, SECTMA 2006, Andrade 2005). The flora of the brejos de altitude located on the eastern side of the Planalto da Borborema is more closely related to lowland forests than to the flora of those located further west; hence, they are regarded as part of the PEC (Andrade-Lima 1961, Ferraz and Rodal 2006, Tavares 2000). According to the climate, forest types in the PEC range from evergreen to deciduous (Andrade-Lima 1961). These two types might be further distinguished into evergreen forests, and semi-deciduous and deciduous forest. The latter is more similar to the caatinga dry scrub vegetation (Rodal et al. 2008, Cestaro and Soares 2004, IBGE 1992, Veloso et al. 1991). Further types are restinga forests, close to the beach dunes, and mangrove forests (Andrade-Lima...
3. The influence of dispersal modes on the abundance of selected tree species

1961). These forest types, deciduous and semi-deciduous forest, are not further considered here.

Figure 1: The Atlantic Forest domain and forest types in the Pernambuco Endemism Center (after IBGE (2004) and Andrade-Lima (1961)) and the localities of surveys. The numbers indicate the surveys as in Table 1. 1 = Campus UFPB, Buraquinho; 2 = Primavera, Sta. Tereza; 3 = Triunfo, Mata do Estado; 4 = Campinas, Avião; 5 = São João, Eng. Amparo; 6 = Dois Irmãos, Tejipió; Curado 1, Curado 2; 8 = Gurjaú (Periquito, Mané do Doce, Prejuí, Cuxió; 9 = Zumbi; 10 = Vasconcelos Sobrinho; 11 = Rio Formoso; 12 = Caldeiras; 13 = Serra Grande fragments; 14 = Coimbra; A = surveys by Andrade Lima and Lira (1974); A1/A2 = Santa Rita, Veneza; A3 = Porto Calvo; T = surveys by Tavares et al. (1975); T1 = Jundiá; T2 = Novo Lino; T3 = Porto Calvo = T4 = Joaquim Gomes; T5 =
Matriz de Camaragibe; T6 = Porto de Pedras; T7 = Flexeiras; T8 = São Luís de Quitunde; T9 = Passo de Camaragibe; T10 = Rio Largo; T11 = Chã do Pilar; T12 = Boca da Mata; T13 = Marechal Deodoro; T14 = São Miguel dos Campos; T15 = Barra de São Miguel.

The rate of habitat loss is extremely high in the PEC and most of the land is used for sugarcane cultivation (Freyre 2004). In the last 50 years cultivated areas increased firstly, due to the implication of modern technologies, which turned beforehand unsuitable and mainly forested tablelands (tabuleiros) into fields and secondly, the sugar and alcohol industry profited from governmental subsidy (Andrade 2001). In northern Pernambuco and Alagoas, which are both characterized by large tabuleiros, the loss between 1968 respectively 1975 and today was about 50% (Trindade et al. 2008, Tavares et al. 1975b).

Defaunation is very intense in the PEC. The large-billed toucan *Ramphastos vitellinus*, was originally distributed in the whole PEC, but it was already rare and had limited distributions in the nineteen forties (Lamm 1948, Berla 1946). Today there are no more registers in the region north of Recife (Farias et al. 2002, Farias et al. 2007). Larger mammals important for endozoochorous dispersal as larger monkeys are hardly encountered: Howler monkeys (*Alouatta belzebul*) today are known from only one single forest fragment in the state Pernambuco (Cruz et al. 2002). The endemic capuchin *Cebus flavius* is so rare that it was re-discovered by science only four years ago (Pontes et al. 2006b). On the other hand rodents as agoutis (*Dasyprocta* spp.) and large fruit-eating bats, e.g. *Artibeus jamaicensis* and *A. lituratus* are found in most mammal surveys (Silva and Pontes 2008, Cruz et al. 2002).

Timber exploitation has a long history in the region: already in the XVI century Brandão apud Abreu (1956) and Piso and Marggraff (1648) mentioned several precious wood species. Since this time they were used for construction by the Portuguese marine (Moreira and Freitas 1907a). Wood from Pernambuco was preferred to that from Bahia or other regions (Moreira and Freitas 1907a). Harvesting continued up to the of twentieth century (Andrade-Lima and Lira 1974, Tavares et al. 1975b, Foury 1968, Andrade-Lima 1977).

A large part of the forest fragments are very young secondary forests (Kimmel et al. 2008). In the sixties and seventies some sites were taken out of
cultivation because they were difficult to cultivate and less compatible compared to the newly cultivated tabuleiros (Carvalho 1971) and in the nineties because governmental subsidy stopped (Kimmel et al. 2009). The presently existing forest fragments show a structure, which is altered to an unknown degree and the specific history of usage remains mostly unknown (Andrade and Rodal 2004).

**The surveys:** All plant surveys conducted in the PEC, in which the relative abundance or number of individuals per species is given, are considered. All tree individuals with a minimum diameter at breast height (dbh) of 5, 10, 20 or 30 cm are included. In recent surveys the minimum dbh was 5 to 10 cm. Of 26 recently conducted surveys 24 took place in forest fragments that are characterized by the authors as badly-preserved or secondary. Sometimes it was mentioned or it could be recognized on aerial photographs of 1969 and later, that the sites regenerated after abandonment of fields, or after clear-cut. Five surveyed fragments are located in an urban matrix, the other are surrounded by sugarcane fields and other rural matrices. Some regenerating patches are located within a large fragment (coimbra).

Of the 21 surveys published in the 1970s, 16 were conducted in well-preserved forest fragments. The minimum dbh was 20 and 30 cm. In the surveys by Tavares et al. (1975) the trees were identified by professional rangers who applied the local common names. A few species are combined by the authors, e.g. *Diplotropis purpurea* and *Bowdichia virgilioides* are both listed as sucupira. In which case the species treated separately in recent surveys had to be combined as well, in order to allow comparisons (Table 3).

Information about the surveys and forest fragments is summarized in Table 1. The location of surveys is displayed in Figure 1.

**Tree species chosen:** All species considered occur in the whole area studied (PEC) (Guedes 1998, Grillo et al. 2005, Alves-Araújo et al. 2008).

1. **Top quality timber:** All species listed by Andrade-Lima (1970) as top quality timber were considered (Table 2). Only the genus *Ocotea* was not included, because no epithetons were given and some *Ocotea* species are considered only second-class timber. Altogether 29 species were taken into account (see Table 2).
2. Disturbance-favored species: Hyper-abundance is an indication for species which are disturbance-favored (Laurance et al. 2002). Species which occurred in at least two surveys, with abundances of ten percent or more were considered hyper-abundant. Further, these surveys must not be located very close to each other. Hyper-abundant tree species are: *Byrsonima sericea*, *Cecropia palmata*, *Eschweilera ovata*, *Mabea occidentalis*, *Pogonophora schomburgkiana*, *Tapirira guianensis*, *Thrysodium spruceanum*.

All tree species and their synonyms and attributes are listed in Table 2.

**Dispersal modes:** The classification of dispersal modes is based on morphology of dispersal units and literature review (Table 2).

1. **Anemochory:** Dispersal units with wing- or plume-like structures are anemochorous.

2. **Synzoochory:** This dispersal mode is assumed when the seed is above 1.5 cm, and bare of fruit parts and hence the scatter-hoarding animals usually consume the seeds themselves, or the dispersal unit bears such tissues but the seed or pyrene (in the following simply seed) is too large to be swallowed (Smythe 1978). Large seeds are also dispersed by bats (Janzen et al. 1976, van der Pijl 1982). The dispersal by rodents and bats might overlap, e.g. in Lecythidaceae (Prance and Mori 1979).

3. **Endozoochory:** The dispersal units bear fleshy or other nutrient-rich tissues, others than the seeds themselves. When the seeds are below 1.5 cm in length they are considered small-seeded, above this threshold as large-seeded. Large birds as toucans swallow seeds, but do not defecate but regurgitate them (van der Pijl 1982). They are hence considered as a proper dispersal mode (see below).

4. **Large-seeded bird-dispersed species:** Species which have seeds of at least 1.5 cm in length and fit the concept of the bird-dispersed syndrome as listed by van der Pijl (1982):

   1. Relatively hard, dull-colored fruits opening and exposing the conspicuous seeds with sarcotesta or aril;
   2. The typical color is red or orange;
   3. Bright-shining colors in combination with shiny black;
   4. No or little smell;
5. Poisonous or bitter seeds;
6. Seeds remaining a considerable time at the tree;

5. Ant-dispersed species: Van der Pijl (1982) described two types of dispersal by ants: a more diffuse “Puschkinia-type”, and a more specific type which involves the presence of an oil-containing small organ, the elaiosome. The seeds of Euphorbiaceae have a specific outgrowth, the caruncle, which serves as an elaiosome, and hence aids for the dispersal by ants (Webster 1994).

Results:
1. Top quality timber: 12 of the 29 tree species were anemochorous (Table 2). Of these, most individuals were Bowdichia virgilioides (Table 3). Five species had dispersal units which show adaptations to synzoochorous dispersal. Most individuals in this group were Andira spp. and Lecythis pisonis (Table 3). Ten were endozoochorous, of which eight had large seeds, and only two small seeds (Table 2). The two small-seeded species were combined as one group in Figure 2, because they were not very abundant (Table 3). Finally, two species, Virola gardneri and Copaifera langsdorffii, had large seeds and showed clear adaptations to bird dispersal (Table 2).

The abundances of top quality timber species were relatively higher when higher dbh values are applied. However, characteristic patterns of abundances of the dispersal modes could be recognized in well-preserved as well as in badly-preserved fragments, independently of the dbh applied (Figure 2). Anemochorous and synzoochorous species were comparably abundant at well- and badly-preserved sites. Obvious exceptions are the anemochorous Tabebuia spp. which were five times more abundant in well- compared to badly preserved sites (Table 3). By contrast, the large-seeded endozoochorous and the large-seeded bird-dispersed species were both of high abundance in well-preserved forest fragments, and of much lower abundance at badly-preserved sites (Figure 2).
One very obvious difference between the surveys published in the nineteen seventies compared to more recent studies, is that some species were not named anymore. Especially in the case of *Peltogyne recifensis*, endemic to Northeast Brazil, this is very conspicuous, as it was named in five of 21 old surveys. Although it is anemochorous, its heartwood named purpleheart made it a target for selective logging (Silva 1976). In part this disappearance might be due to misidentification, because *Hymenaea* and *Peltogyne* are very similar to each other when sterile. Some species named by Andrade Lima (1970) were not listed in any survey: apparently, *Peltogyne floribunda* was very rare (Andrade-Lima 1954b) and the natural areas of distribution of *Myrocarpus fastigiatus* and *Tabebuia serratifolia* were perhaps located in the drier semi-deciduous forest (Sartori and Tozzi 2004, Andrade and Rodal 2004, Lopes 2007, Andrade et al. 2006).
3. The influence of dispersal modes on the abundance of selected tree species

Figure 3: a: Aerial photograph of the Piedade forest in 1969 showing widely spaced tree crones due to selective logging. b: satellite image from 2004. The gaps are closed mainly with crowns of the secondary species *Sclerolobium densiflorum* (Krause pers. comm.).

**Disturbance-favored species:** The spectrum of dispersal modes was not the same as in the top quality timber trees (Table 2). None of the identified disturbance-favored species was wind-dispersed. The three endozoochorous species were all small-seeded. There were also two ant-dispersed species, a dispersal mode not found among top quality timber. However, the synzoochorous dispersal units of two species were functionally similar to those of the top quality timber species.

In well-preserved forest fragments the abundances of the three dispersal modes were relatively similar. Whereas in badly-preserved fragments the small-seeded endozoochorous species were of much higher abundance than in well-preserved fragments. Synzoochorous and ant-dispersed species are also more abundant at badly-preserved sites, but not so much higher as the latter group (Figure 4). Apparently, not all species followed this trend: *Mabea occidentalis* and *Eschweilera ovata* were both slightly higher abundant in better preserved forest fragments (Table 3).
3. The influence of dispersal modes on the abundance of selected tree species

Figure 4: Abundances of disturbance-favored tree species per dispersal mode in well- and badly-preserved forest fragments in the PEC. In well-preserved forest fragments, disturbance favored species are of considerably less total abundance than in badly-preserved fragments. Also in well-preserved forest fragments, the different dispersal modes are of relatively similar abundance, whereas in badly-preserved fragments especially small-seeded endozoochorous species are very abundant. small endo. = small-seeded endozoochorous; synzoo. = synzoochorous; ant-disp. = ant-dispersed (myrmecochorous).

Discussion:
In many aspects our findings are coherent with what Silva and Tabarelli (2000b) and Peres and Roosmalen (2001) predicted, because species with large bird-dispersed seeds and such which are primarily dispersed by primates are indeed virtually absent in badly-preserved forest fragments. However, species with large seeds adapted to synzoochorous dispersal such as *Eschweilera ovata* and *Thyrsodium spruceanum* are apparently not suffering similar consequences, but on the contrary may even be successful in forming large populations under disturbed conditions. Also anemochorous top quality timber species are of similar abundances in well- and badly-preserved forest fragments. This, however is not true for all species, e.g. *Tabebuia* spp. which are apparently less abundant at badly-preserved sites. The pattern of abundances of species belonging to the various dispersal modes parallels the presence of the dispersing animals. As mentioned above, the large toucan *Ramphastos vitellinus* has become very rare in the PEC, the only three sites where recently relatively high abundances of large-seeded bird-dispersed *Virola gardneri* were registered were also the only places where this bird has been observed recently (of the sites where both, bird and tree
censuses have been conducted: the Serra do Mascarenhas (survey no. 25, 26; Table 1) and Serra Grande (survey no. 19; Table 1) (Roda 2004, Farias et al. 2002). Also as mentioned before, large frugivorous bats (*Artibeus jamaicensis, A. lituratus*) and rodents (*Dasyprocta* spp.), who are important for synzoochorous dispersal (Janzen et al. 1976, Smythe 1978, van der Pijl 1982), were commonly found in most censuses, which explains that e.g. the genera *Andira* and Lecythis with large seeds did not lack in badly-preserved fragments.

Usually it is assumed that in tropical rainforests pioneer species proliferate under disturbed conditions, especially fragmentation and edge-formation (Santos et al. 2008, Michalski et al. 2007). However, the successional status of taxa is not always well determined. In Table 2 it can be seen that of those five species with were classified by more than one author there are three designated as both: as pioneer as well as early secondary and at the same time as late secondary or shade-tolerant, but only two species which are univocally regarded as either early or late secondary. Typical pioneers and disturbance-favored species are: *Cecropia palmata, Tapiria guianensis* and *Byrsonima sericea*. However, some of the most abundant tree species in obviously very disturbed fragments are not typical pioneers. *Pogonophora schomburgkiana* for instance is ant-dispersed (Skatulla 2002) and hence relatively hindered in colonizing distant, newly available sites as abandoned fields. Indeed ant-dispersed species are absent in several badly-preserved forest fragments. The ability of *P. schomburgkiana* to proliferate under disturbed conditions is probably linked to its ability to re-sprout after cutting (Skatulla 2002). In *Mabea occidentalis* the abundances were in average even higher in well-preserved forest fragments. Several points have to be considered to explain this contradiction: first, also well-preserved forest fragments are not primary forest (Figure 3) and some disturbance might have caused abundances of e.g. 18% in the coimbra fragment (Lopes et al. 2009), or surveys were conducted in a specific habitat, e.g. along river valleys (Oliveira 2003), where extreme abiotic factors favor the proliferation of particular species.

In this study only two groups of species were considered top quality timber and disturbance-favored species, nevertheless both add up to a considerable number of all tree individuals in the PEC. *Virola gardneri* for example is one of the most characteristic trees of the original forest. Sensitive species should receive special care in reforestation projects or should be grown in an arboretum to
3. The influence of dispersal modes on the abundance of selected tree species

prevent their local extinction. Of course it would make much more sense to protect a complete ecosystem, but the actual situation in Northeast Brazil is that even officially protected areas are unsustainably overexploited (Marangon et al. 2004, CPRH 2001).
Table 1: Characterization of Analyzed forest fragments in the PEC. ha = hectare; - = data not available.

<table>
<thead>
<tr>
<th>number in map</th>
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<th>source</th>
<th>conservation status</th>
<th>matrix</th>
<th>size (ha)</th>
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<th>altitude (m. a.s.l.)</th>
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<td>Feitosa (2004)</td>
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<td>851</td>
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1 The forest of dois irmãos is partially well-preserved. However, it is closely located to Recife and therefore was exploited for high quality timber and intensively used for hunting for centuries (Ducke 1953). Also only parts of it are being protected, wood extraction, the opening of trails, and construction of private houses are common (Bezerra 2006).
Table 2: List of species mentioned and their attributes. Timber quality according to Andrade-Lima (1970). Seed size is without wings. Synonyms are given in square parentheses (after W3Tropicos). Anemo = anemochorous; end = endozoochorous; myr = myrmecochorous; syn = synzoochorous; es = early secondary, ls = late secondary; p = pioneer; s-t = shade-tolerant. Timber quality: 1 = top quality; 2 = second class; 3 = third class. References: 1 = Roosmalen (1985); 2 = Lobova and Mori (2005); 3 = Woodson (1960); 4 = Mori and Brown (1994); 5 = Silva (1976); 6 = Peternelli et al. (2004); 7 = van der Pijl (1982); 8 = Silva and Tabarelli (2000b); 9 = Alves Júnior et al. (2006); 10 = Lins-e-Silva and Rodal (2008); 11 = Santos et al. (2008) 12 = Mansano et al. (2004); 13 = Skatulla (2002) 14 = Sartori and Tozzi (2004); 15 = Lorenzi (1992); 16 = Pennington (1990).

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<td>es (9, 10), p (11)</td>
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<td>large (8)</td>
<td>ls (9, 10), p (11)</td>
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<td>small (1)</td>
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Elaeocarpaceae  **Sloanea obtusifolia** (Moric.) Schum.  
Euphorbiaceae  **Mabea occidentalis** Benth.  
Euphorbiaceae  **Pogonophora schomburgkiana** Miers ex. Benth.  
Fabaceae  **Andira fraxinifolia** Benth.;  **A. nitida** Mart. ex Benth.  
Fabaceae  **Bowdichia virgilioides** Kunth  
Fabaceae  **Diptotropis purpurea** (L.C. Rich.) Amsh.  
Fabaceae  **Dipteryx odorata** (Aubl.) Willd. =  **Coumarouna odorata** Aubl.  
Fabaceae  **Myrocarpus fastigiatus** Allemão  
Fabaceae  **Zollernia paraensis** Huber  
Lecythidaceae  **Eschweilera ovata** (Cambess.) Miers [= **E. luschnathii** (Berg) Miers]  
Lecythidaceae  **Cariniana brasiliensis** Casar. [= **C. legalis** (Mart.) Kuntze]  
Lecythidaceae  **Lecythis pisonis** Cambess.  
Malpighiaceae  **Byrsonima sericea** DC.  
Meliaceae  **Cabralea canjerana** (Vell.) Mart.  
Meliaceae  **Cedrela odorata** L.  
Mimosaceae  **Platymenia foliolosa** Benth.  
Moraceae  **Clarisia racemosa** Ruiz Pav.  
Myristicaceae  **Virola gardneri** Warb.  
Sapotaceae  **Manilkara salzmanii** (A.DC.) Lam.  
Sapotaceae  cf.  **Micropholis compta** Pierre  

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<th>Species Name</th>
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<td>Lecythidaceae</td>
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<td>anem (15) small (15) 1</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Lecythidaceae</td>
<td><strong>Lecythis pisonis</strong> Cambess.</td>
<td>syn (11) large (8) ls (9) 1</td>
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</tr>
<tr>
<td>Malpighiaceae</td>
<td><strong>Byrsonima sericea</strong> DC.</td>
<td>end (1) small (8) p (10, 11) 2</td>
<td></td>
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</tr>
<tr>
<td>Meliaceae</td>
<td><strong>Cabralea canjerana</strong> (Vell.) Mart.</td>
<td>end (15) small (15) 1</td>
<td></td>
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<td></td>
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<tr>
<td>Meliaceae</td>
<td><strong>Cedrela odorata</strong> L.</td>
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<td>Mimosaceae</td>
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<tr>
<td>Moraceae</td>
<td><strong>Clarisia racemosa</strong> Ruiz Pav.</td>
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<tr>
<td>Myristicaceae</td>
<td><strong>Virola gardneri</strong> Warb.</td>
<td>end (1) large (8) s-t (11) 1</td>
<td></td>
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<tr>
<td>Sapotaceae</td>
<td><strong>Manilkara salzmanii</strong> (A.DC.) Lam.</td>
<td>end (1) large (8) 1</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Sapotaceae</td>
<td>cf.  <strong>Micropholis compta</strong> Pierre</td>
<td>end (16) large (16) es (9) 1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1The species is named by Ducke (1953) for the interior of Pernambuco.

2Although the species is named several times for the PEC by various authors no specimens are registered on species link. According to the species description in the Flora Neotropica the species occurs only in the Atlantic Forest from Rio de Janeiro up to Bahia (Pennington 1990).
3. The influence of dispersal modes on the abundance of selected tree species

Table 3: Average abundances and standard deviations of species or genera of top quality timber species in well- and badly-preserved forest fragments. SD = standard deviation; synzoo. = synzoochorous; small endo. = small-seeded endozoochorous; large endo. = large-seeded endozoochorous; ant-disp. = ant-dispersed; bird-disp. = large-seeded bird-dispersed.

<table>
<thead>
<tr>
<th>dispersal mode</th>
<th>taxa</th>
<th>well-preserved average abundance ± SD</th>
<th>badly-preserved average abundance ± SD</th>
</tr>
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<tbody>
<tr>
<td>anemochorous</td>
<td>Aspidosperma limae, Bowdichia virgilioides, Diplotropis purpurea „sucupira“</td>
<td>0.07 ± 0.16 1.31 ± 0.99</td>
<td>0.06 ± 0.19 2.43 ± 2.36</td>
</tr>
<tr>
<td></td>
<td>Astronium fraxinifolium</td>
<td>0.10 ± 0.25</td>
<td>0.00 ± 0.00</td>
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<tr>
<td></td>
<td>Caraipa densifolia</td>
<td>1.96 ± 3.52</td>
<td>2.15 ± 9.60</td>
</tr>
<tr>
<td></td>
<td>Cariniana brasiliensis</td>
<td>0.06 ± 0.15</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>Cedrela odorata</td>
<td>0.05 ± 0.07</td>
<td>0.07 ± 0.31</td>
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<tr>
<td></td>
<td>Plathymenia foliolosa</td>
<td>0.46 ± 1.73</td>
<td>0.46 ± 1.7</td>
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<td></td>
<td>Tabebuia spp.</td>
<td>0.48 ± 1.46</td>
<td>0.09 ± 0.22</td>
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<tr>
<td>synzoo.</td>
<td>Andira spp.</td>
<td>0.43 ± 0.68</td>
<td>0.26 ± 0.40</td>
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<td></td>
<td>Dipteryx odorata</td>
<td>0.01 ± 0.06</td>
<td>0.01 ± 0.03</td>
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<td></td>
<td>Eschweileria ovata</td>
<td>6.57 ± 3.09</td>
<td>4.43 ± 4.37</td>
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<td></td>
<td>Hymenaea spp.</td>
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<td>0.17 ± 0.41</td>
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<td>Lecythis pisonis</td>
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<td></td>
<td>Thyrsodium spruceanum</td>
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<td>5.26 ± 5.14</td>
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<td>Zollernia paraensis</td>
<td>0.17 ± 0.42</td>
<td>0.00 ± 0.01</td>
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<tr>
<td>ant-disp.</td>
<td>Mabea occidentalis</td>
<td>1.64 ± 0.94</td>
<td>0.92 ± 2.17</td>
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<tr>
<td></td>
<td>Pogonophora schomburgkiana</td>
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<td>2.76 ± 5.0</td>
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<tr>
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<td>4.52 ± 6.65</td>
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<td>Cecropia palmata (C. spp.)</td>
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<td>Tapirira guianensis</td>
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<td>large endo.</td>
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<td>0.81 ± 1.28</td>
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<td>Micropholis sp.</td>
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<td>bird-disp.</td>
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<td>Virola gardneri</td>
<td>4.29 ± 4.24</td>
<td>0.27 ± 0.62</td>
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</table>
4. Seed dispersal and pollination modes of woody species of 12-year-old secondary forest

Abstract
The capacity of degraded areas of secondary vegetation to recover plant species diversity and pollination and seed dispersal mutualisms is receiving increasing attention by scientists studying biodiversity conservation at the landscape level. We studied the seed dispersal and pollination modes of woody species of two 12 year old secondary forest patches on sites formerly used for sugarcane cultivation. Sixty plots were installed covering a total area of 0.6 ha. A total of 61 woody species were registered. Although the study sites were isolated from old-growth forests by a matrix of sugarcane monocultures, the array of dispersal modes were similar to old-growth forest analyzed by other working groups, as were the percentage of vertebrate-dispersed species (83.6%). The percentage of large-seeded species was larger than expected (18%) given the local extinction of large-bodied mammals and birds. These large-seeded plants may have arrived at the sites through dispersal by rodents and bats, and since more than half of the large-seeded species are consumed by humans, they may have reached the study areas this way. Most pollination modes found in forest fragments in the region were also present in the secondary forests. The exception was that no pollination mediated by vertebrates was found among the studied species, neither by birds nor by bats. A high percentage of species showed an unspecialized pollination mode (55.7%), and pollination by hawkmoths was most common among canopy individuals (42.7%) and many sub-canopy individuals were pollinated by large bees (39.8%). This was due to the high abundance of a few species as the hawkmoth pollinated Inga ingoides, Albizia saman in the canopy and the large bee pollinated Gustavia augusta Senna georgica in the sub-canopy.

Introduction
The Atlantic Forest stretches over 27 degrees of latitude along the Brazilian coastline and covered 1,363,000 km² in pre-Columbian times (Hirota 2003). It is one of the global biodiversity hotspots (Myers et al. 2000). However, over 92% of its original area has been cleared for agriculture, cattle rearing, mining and other
uses and the remaining forest patches are highly fragmented (CPRH 2001, Frickmann Young 2003, Hirota 2003). The Brazilian populations is concentrated in this coastal area with approximately 106 million people living in the biome (Hirota, 2003).

The forests north of the Rio São Francisco are known as the Pernambuco Endemism Center (PEC) due to the high number of species unique to the area, but this region has suffered the highest levels of deforestation and forest fragmentation in the biome and only about 5% of the original forest cover remains (Silva and Casteleti 2003). Here, the rates of habitat fragmentation are the highest and only about 5% of the original forest cover is left (Silva and Casteleti, 2003). The remaining forest forms an “archipelago” of small fragments in a matrix of sugarcane monocultures (Ranta et al. 1998). Even though the sugarcane fields can be used by an array of animal species to fulfill their energetic demands they are likely to function as a sink, because here they are even more threatened to be hunted or slaughtered by people and feral dogs (Fernandes 2003, Silva and Pontes 2008). At least half of these forest fragments consist of secondary vegetation in early or suppressed stages of succession (Ribeiro et al. 2009).

Forest fragments on the large sugarcane plantations are protected against fire and logging to ensure the water supply needed for sugar production (Girão et al. 2007). In addition, marginal lands that were profitable to cultivate during the time of governmental subsidies (between 1980 and 1990) were abandoned after this support ended (Ranta et al., 1998). Also the migration of rural people from settlement on the plantations to coastal settlements resulted in land abandonment (Andrade 2001). Secondary forests developed on these sites following various trajectories depending on time since abandonment, disturbance intensity, history of use, edaphic, and other biotic and abiotic conditions, and the vegetation physiognomies range from open grass and shrub to close secondary forest sites (Kimmel 2006). It is often suggested that this secondary vegetation can aid conservation efforts by acting as buffer zones around old-growth forest, stepping stones and corridors for forest species moving between forest patches, or even as refuges for forest species(Ranta et al. 1998, Sanderson et al. 2003, Laurance 2007, Bihn et al. 2008, Santos et al. 2008, Lopes et al. 2009).

The possibility of natural succession to take place via vegetative means or dispersal of diaspores is of vital importance for forest conservation at the
4. Seed dispersal and pollination modes of woody species of secondary forest

landscape level. (Rodrigues et al. 2009). In a recently published guidebook to promote reforestation in the region it is assumed that natural regeneration cannot occur where the seed bank was eliminated and where many dispersers, especially birds, have been extirpated, and will only occur if sites are situated directly besides existing forests (Alves-Costa et al. 2008). Seeds larger than 15 mm are thought to be hardly dispersed at all (Silva and Tabarelli 2000a). Another important point is the functional diversity of the resulting vegetation, especially in terms of plant-seed-disperser and plant-pollinator interactions. It could be shown for plant-pollinator systems that an increase in diversity of one partner leads to an increase of diversity of the other (Fontaine et al. 2006). Santos et al. (2008) found that the flora of forest fragments and secondary forest patches contain fewer large-seeded species dispersed by vertebrates and more pioneer plant species than continuous forest, and Lopes et al. (2009) comparing small fragments and secondary forest with continuous forest confirmed that the former contain fewer vertebrate-pollinated species and individuals, and have a higher abundance and diversity of species that are pollinated by diverse small insects. A loss of functional diversity of these interactions in secondary forest compared to old-growth forest was also reported for Costa Rica (Chazdon et al. 2003).

In this study, we analyzed the dispersal and pollination modes of woody plant species in 12-year-old secondary forests, including the undergrowth, to investigate the resilience and degree of integrity of plant-animal interactions of an area formerly used for sugarcane cultivation and to evaluate the role secondary forests have in conserving this endangered biome.

Material and Methods

Study Site

The study was conducted at the São José sugarcane plantation in the municipalities of Igarassu and Araçoiaba, Pernambuco. Mean annual precipitation is 1,520 mm and mean average temperature is 25°C (Schessl et al. 2008). The rainy season lasts from January to August with a pronounced dry season, with monthly precipitation below 100 mm, from September to December (Schessl et al., 2008). The red-yellow podzolic soil is sandy to loamy (Schessl et al., 2008), with clay content varying from 8% to 32% and that of sand from 91% to 55%
(Freitas et al. pers. comm.). The original vegetation is dense lowland rainforest with transition to semideciduous forest (Veloso et al. 1991).

The plantation retains 206 forest fragments, with both mature and secondary forest represented, covering 28% of the property (Trindade et al. 2008). The fragments have a mean size of 61 ha, varying from 0.12 to 498 ha, and differ in age and history (Trindade et al., 2008). Most of the fragments are irregularly shaped and are found along steep hillsides and rivers, at 30 to 110 m a.s.l. (Schessl et al., 2008; Trindade et al., 2008). The four most important forest tree species in these fragments are *Thrysodium schomburgkianum* Benth. (Anacardiaceae), *Eschweilera ovata* (Camb.) Miers. (Lecythidaceae), *Tapirira guianensis* Aubl. (Anacardiaceae), and *Pogonophora schomburgkiana* Miers. ex Benth. (Euphorbiaceae) (Rocha et al. 2008, Silva et al. 2008a, Silva et al. 2008b).

Two secondary forest sites (hereafter referred to as *capoeira*) of sufficient size for the installation of plots and of known age of about 12 years of regeneration were chosen: Capoeira 1: lat 7°48′55″ S; long 35°02′15″ W, 130 ha, at Engenho Campinas; and Capoeira 2: lat 7°48′05″ S; long 35°02′15″ W, 20 ha, at Engenho Cumbe de Baixo (Fig. 1). The soil is relatively rich in clay (20%) and silt (17%), but the sand content clearly dominates (63%) (Freitas et al. pers. comm.). The study forests cover steep slopes, and in Capoeira 1 there is an area of partially flooded forest along the river valley. The minimum distance to the next older forest fragment is 50 m. The sites were used as pastures at least since 1969 and aerial photographs from 1969, 1975, and 1981 and interviews with local inhabitants show that the sites were completely cleared between 1975 and 1981 for sugarcane cultivation. Sugarcane cultivation was abandoned a few years later and the sites reverted to pasture. Following a change of ownership in 1995, these sites were abandoned altogether. Only the river valley in Capoeira 1 is sometimes used as temporary pasture, which, combined with the flooding following the construction of a small dam led to the establishment of grassland dominated by exotic *Urochloa mutica* (Forsk.) Nguyen (Poaceae). The forest has a canopy height of 12 m interspersed with open sites probably resulting from escaped fires from the surrounding sugarcane fields.
4. Seed dispersal and pollination modes of woody species of secondary forest

Figure 1a-e: a: Sphingophilous flower of *Inga ingoides*. b: Beetle on cantharophilous *Desmoncus* sp.. c: Melittophilous *Gustavia augusta* flower. d: Fruit of *Samanea saman* (picture by U. Knörr). e: Fruit and seeds of synzoochorous *Swartzia pachystachia*. 
Data collection and analysis

Fieldwork lasted for 24 months from January 2007 to December 2008. Thirty plots of 10 x 10–m were established in each of the two sites, covering a total area of 0.6 ha, with subplots of 5 x 5–m in each. The distance between the plots was 10 m. All trees with a diameter (dbh) of a minimum of 5 cm at breast height (1.3 m) (hereafter called canopy trees) were marked and measured in the plots; individuals of 1 to 5 cm dbh (hereafter called sub-canopy) were marked and measured in the subplots. Plant species were identified by comparison of collected fertile and sterile material with specimens of the herbarium IPA (Instituto Agronómico de Pernambuco) and the herbarium PEUF (Universidade Federal Rural de Pernambuco). The collected specimens are deposited at the same herbaria. We calculated the number of individuals per hectare by extrapolating the number of individuals found in the 0.6 ha. The flowers and fruits of all studied species were collected and classified. Only fertile individuals were considered for the classification of pollination and seed dispersal modes.

The classification of dispersal modes were based on the fruit morphology. Anemochory was characterized by wing- or plume-like structures of the dispersal unit and exozoochory by hooks to cling to fur or feathers of animals. In the case of endozoochory the dispersal units often bear fleshy or other nutrient-rich tissues, others than the seeds themselves. Synzoochory was assumed when the dispersal unit lacked , the seed being the reward for scatter-hoarding animals, or the seed has a pulp covering but is too large to be swallowed by any extant animals (large animals capable of swallowing these seeds, like tapirs, are extinct in the study area (van der Pijl 1982, Lobova and Mori 2007, Silva and Pontes 2008). A special case of synzoochory is stomatochory: the dispersal of seeds by birds or bats, which do not ingest, but carry them in their mouth (van der Pijl 1982, Lobova and Mori 2007), but because rodents and bats might disperse the same seeds, e.g. in Lecythidaceae (Prance and Mori 1979) stomatochorous fruits were not treated separately. Fruits were classified as myrmecochorous when the diaspores were very small, shiny and had elaiosomes (van der Pijl 1982). Autochorous fruits are those with an explosive opening capsules, or the absence of any of the above-mentioned attributes, and small-sized seeds, which makes scatter-hoarding unlikely, at least by larger rodents like agoutis.
Species with seeds up to 15 mm long were considered small-seeded, while those larger than this classified as large seeded following Santos et al. (2008).

The classification of pollination modes was based upon floral structure, time of floral activity (diurnal/nocturnal), and in most cases on flower visitor observations and literature references (Table 1). Flower visitors were recorded and their behavior was observed. Probable effective pollinators, i.e., animals that contacted pollen and stigma, were distinguished from flower visitors that could not act as pollinators. The expected pollination modes were the same as in Girão et al. (2007). With two exceptions: firstly we included wasp pollination in melittophily and the inclusion of pollination by thrips (Thysanoptera). The pollination modes were: pollination by bats (chiropterophily), non-flying mammals, bees (small and large; melittophily), beetles (cantharophily), birds (ornithophily), diverse small insects (DSI), flies (myiophily), moths (settling while flower visiting; phalenophily), hawkmoths (sphingids; hovering while visiting flowers; sphingophily), butterflies (psychophily) and wind (anemophily).

Results

Altogether, 61 species were identified, 21 of them being canopy-only species (considering only fertile adults) and 22 sub-canopy-only species. Sixteen species were found fertile in both groups and two species, Ocotea glomerata and Xylopia frutescens were found only infertile. The three most abundant canopy species were Inga ingoides, Albizia saman, and Casearia sylvestris. The most abundant sub-canopy species were Gustavia augusta, Senna georgica, and Casearia sylvestris.

The density of the canopy trees was 1,828 individuals/ha, that of the fertile sub-canopy was 2,433 individuals/ha and 2,140 individuals/ha were infertile juveniles. Only fertile individuals were included in the analysis.

The majority of canopy and sub-canopy species (94.6% and 86.8%, respectively) were primarily vertebrate-dispersed: only 5.4% and 10.5% were wind-dispersed or autochorous, and only one sub-canopy species (2.6%), represented by seven individuals, was dispersed by ants (Table 1).
Table 2: Dispersal modes and seed-size classes in percent, of fertile woody species and fertile individuals of the canopy and sub-canopy, collected in two capoeiras, Usina São José, Zona da Mata, state of Pernambuco. Small seeded = seeds up to 15 mm, large seeded = seeds greater than 15 mm.

<table>
<thead>
<tr>
<th>Dispersal mode</th>
<th>Canopy species</th>
<th>Canopy individuals</th>
<th>Sub-canopy species</th>
<th>Sub-canopy individuals</th>
</tr>
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<tbody>
<tr>
<td>endozoochory</td>
<td>70.3</td>
<td>84.3</td>
<td>71.1</td>
<td>57.2</td>
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<tr>
<td>synzoochory</td>
<td>19.4</td>
<td>6.2</td>
<td>10.5</td>
<td>26.6</td>
</tr>
<tr>
<td>exozoochory</td>
<td>0.0</td>
<td>0.0</td>
<td>2.6</td>
<td>0.8</td>
</tr>
<tr>
<td>myrmecochory</td>
<td>0.0</td>
<td>0.0</td>
<td>2.6</td>
<td>0.3</td>
</tr>
<tr>
<td>anemochory</td>
<td>5.6</td>
<td>2.2</td>
<td>10.5</td>
<td>6.0</td>
</tr>
<tr>
<td>autochory</td>
<td>5.4</td>
<td>4.8</td>
<td>5.3</td>
<td>9.0</td>
</tr>
<tr>
<td>small seeded</td>
<td>73.0</td>
<td>74.4</td>
<td>86.8</td>
<td>71.8</td>
</tr>
<tr>
<td>large seeded</td>
<td>27.0</td>
<td>25.6</td>
<td>13.2</td>
<td>28.2</td>
</tr>
</tbody>
</table>

Of the 51 vertebrate-dispersed species, 45 were endozoochorous. More than half of these (30 species) had shiny, red, orange, yellow, black or red and black-combination diaspores that typically attract birds although some such as *Elaeis guianensis* that have shiny orange-red fruits with large seeds that are scatter-hoarded. Additional seven species had small seeds with pulp attached that are likely dispersed by birds as well bats and other small mammals, and reptiles. The fruits of a further six species were likely to attract mainly mammals and reptiles: *Annona glabra*, *Inga ingoides*, *Talisia esculenta*, and five species are known to be dispersed by cattle or are used as fodder: *Albizia saman*, *Apeiba tibourbou*, *Guazuma ulmifolia*, *Senna georgica* and *Albizia polycephala* (Janzen and Martin 1982; Lorenzi, 2002; Sampaio and Gamarra-Rojas, 2002). Fruits of *A. tibourbou* were all parasitized by larvae and killed before ripening. Seven species were probably scatter-hoarded or carried by bats and *Triumfetta althaeoides* fruits have hooks to cling to fur or feathers of bypassing animals.

The majority of canopy and sub-canopy species had small seeds (73.0% and 86.8%). Approximately similar percentages of all individuals, namely 74.4% of the canopy and 71.8% of the sub-canopy, had small seeds (Table 1). Of the 11 large-seeded species, six had fruits that are also consumed by humans: *Annona glabra* (common name: Araticum), *Acrocomia intumescent* (Macaíba), *Elaeis guineensis* (Dendê), *Inga ingoides* (Ingá beira do rio), *Pouteria grandiflora* (Oiti triturá) and *Talisia esculenta* (Pitomba). The infructescences of *E. guineensis* were
also frequently found to be used as baits for hunting. *Eschweilera ovata*, *Gustavia augusta*, *Swartzia pickelii*, *Strychnos parvifolia* and *Rauvolfia grandiflora* were the other five large-seeded species.

**Table 1**: Total number of fertile and infertile individuals, diameter groups, pollination and dispersal modes of woody species occurring in two capoeiras, Usina São José, Zona da Mata, state of Pernambuco. Ind = Number of individuals; Diam = Diameter group: 1 = sub-canopy, 1* = juvenile (infertile), 2 = canopy, 3 = sub-canopy and canopy, 3* = fertile only in the canopy; Poll - pollination modes: ane = anemophily, can = cantharophily, gen = generalist pollination, mela = melittophily (large bees), mesma = melittophily (small bees), myio = myiophily, phal = phalenophily; psych = psychophily; sphi = sphingophily; thrips = pollination by thrips; Disp = dispersal modes: anem = anemochory, aut = autochory, endo = endozoochory, exo = exozoochory, myr = myrmecochory, syn = synzoochory; Seed = Seed and/or pyrene size class: s = small (1–15 mm), l = large (>15 mm); Ref = References: 1 = Janzen and Martin (1982), 2 = Buchmann (1983), 3 = Henderson (1995), 4 = Proctor et al. (1996), 5 = Arista et al. (1997), 6 = Lorenzi (2002), 7 = Sampaio and Gamarra-Rojas (2002), 8 = Gottsberger and Silberbauer-Gottsberger (2006), 9 = Westerkamp et al. (2006), 10 = Moore (2001), 11 = Krause (2008), 12 = M. Braun (pers. comm.), 13 = M. Ulbricht (unpublished) (2006).

<table>
<thead>
<tr>
<th>Family/Species</th>
<th>Ind</th>
<th>Diam</th>
<th>Poll</th>
<th>Disp</th>
<th>Seed</th>
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<td><em>Tapirira guianensis</em> Aubl.</td>
<td>97</td>
<td>3*</td>
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<td>endo (8)</td>
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<td>thrips (8)</td>
<td>endo</td>
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<td>anem</td>
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<td><em>Himatanthus phagedaenicus</em> (Mart.) Woodson</td>
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<td>2</td>
<td>sphi</td>
<td>anem</td>
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<td><em>Rauvolfia grandiflora</em> Mart. ex A. DC.</td>
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<td>3</td>
<td>mela</td>
<td>endo</td>
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<tr>
<td><em>Schefflera morototoni</em> (Aubl.)</td>
<td>52</td>
<td>3*</td>
<td>gen</td>
<td>endo</td>
<td>s</td>
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<tr>
<td>Maguire, Steyerm. &amp; Frodin</td>
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</table>
4. Seed dispersal and pollination modes of woody species of secondary forest

**ARECACEAE**

- *Acrocomia intumescens* Drude 35 3* can (3,10) syn l 3,10
- *Desmoncus* sp. 20 1 can endo s
- *Elaeis guineensis* Jacq. 2 2 can (4) syn l 4

**ASTERACEAE**

- *Tilesia baccata* (L.) Pruski 7 1 gen endo s
- *Erechtites hieraciifolius* (L.) Raf. ex DC.
  - 7 1 gen anem s

**CAESALPINIACEAE**

- *Apuleia leiocarpa* (Vogel) J.F.Macbr. 13 1 gen anem s
- *Senna georgica* Irwin & Barneby 202 3 mela (2) endo (6,7) s 2,6,7

**CECROPIACEAE**

- *Cecropia palmata* Willd. 107 2 gen endo s

**CHRYSOBALANACEAE**

- *Hirtella racemosa* Lam. 27 1 psych (5) endo s 5

**CLUSIACEAE**

- *Visnia guianensis* (Aubl.) Pers. 97 3 gen endo s

**CORDIACEAE**

- *Cordia nodosa* Lam. 73 1 gen endo s
- *Cordia polyecephala* (Lam.) I.M. Johnst.
- *Cordia sellowiana* Cham. 8 3* gen endo s

**EUPHORBIACEAE**

- *Pera ferruginea* (Schott) M. 7 1 gen myr s

**FABACEAE**

- *Machaerium hirtum* (Vell.) Stellfeld
- *Swartzia pickellii* Killip ex Ducke
  - 167 3 mela (2) syn l 2

**FLACOURTIACEAE**

- *Casearia sylvestris* Sw. 390 3 gen (8) endo s 8
- *Casearia hirsuta* Sw. 127 3 gen endo s
- *Casearia cf. javitensis* (Kunth) 150 3 gen endo s

**HERNANDIACEAE**

- *Sparattanthelium botocudorum* Mart. 27 1 gen (13) endo s 13

**LAURACEAE**

- *Ocotea glomerata* Benth. & Hook.f.
  - 7 1* myio (11) endo s 11

**LEYCHIDIDACEAE**

- *Eschweilera ovata* (Cambess.) Miers 62 3* mela (11) syn (11) l 11
4. Seed dispersal and pollination modes of woody species of secondary forest

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Coded Species</th>
<th>Seed Dispersal Mode</th>
<th>Pollination Mode</th>
<th>Notes</th>
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<tr>
<td>LOGANIACEAE</td>
<td>Gustavia augusta L.</td>
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<td></td>
<td>D. Don</td>
<td>Miconia hipoleuca (Bonpl.)</td>
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<td>Miconia minutiflora (Bonpl.)</td>
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<td>Albizia saman (Jack.) F. Müll.</td>
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<td>1,6,7</td>
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<td>Inga ingoides (Rich.) Willd.</td>
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<td>MORACEAE</td>
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<td>MYRTACEAE</td>
<td>Campomanesia dichotoma (O.Berg) Mattos</td>
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<td>92 3 gen endo s</td>
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<td>Psidium guianense Pers.</td>
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<td>Eugenia sp.</td>
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<td>Myrtaceae sp. 4</td>
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<td>Myrtaceae sp. 5</td>
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<td>NYCTAGINACEAE</td>
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<td>30 3 gen endo s</td>
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<td>Lundell</td>
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<td>PIPERACEAE</td>
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<td>Piper marginatum Jacq.</td>
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<td>13</td>
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<td>POLYGONACEAE</td>
<td>Coccoloba mollis Casar</td>
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<td>RUBIACEAE</td>
<td>Alsieis pickelii Pilger &amp; Schmale</td>
<td>27 1 gen anem s</td>
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<tr>
<td></td>
<td>Genipa americana L.</td>
<td>2 2 mela endo s</td>
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<td>Psychotria capitata Ruiz &amp; Pav.</td>
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<td>Psychotria bracteata DC.</td>
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<td>SAPOTACEAE</td>
<td>Pouteria grandiflora (A.DC.)</td>
<td>15 3 phal syn I</td>
<td></td>
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<td></td>
<td>Baehni</td>
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<td>SAPINDACEAE</td>
<td>Cupania cf. oblongifolia Mart.</td>
<td>808 3* gen endo s</td>
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<td>Cupania paniculata Cambess.</td>
<td>62 3* gen endo s</td>
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<tr>
<td></td>
<td>Cupania revoluta Rolfe</td>
<td>50 3* gen endo s</td>
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Melittophilous (large and small bees), cantharophilous, phalenophilous, and pollination by various small insects (DSI) pollination modes were encountered among canopy and sub-canopy species. The only psychophilous species, *Hirtella racemosa*, was part of the sub-canopy, while the sphingophilous species *Inga ingoides*, *Albizia saman*, *Albizia polycephala*, and *Himatanthus phagaedanicus* and the only myiophilous species *Guazuma ulmifolia* were only encountered fertile in the canopy stratum. Only infertile individuals were found of the single thrips-pollinated species, *Xylopia frutescens*. Ornithophily and chiropterophily, were not encountered (Fig. 2). The species *Cecropia palmata* was categorized as generalist, as it was frequently visited by e.g. bees of the genus *Trigona* and is also wind pollinated. The largest number of species, both, in the canopy and sub-canopy stratum, as well as most individuals in the sub-canopy had generalist flowers. Among canopy individuals, sphingophily was the most common syndrome (40.2%). This was mainly due to the abundance of *Inga ingoides* and *Albizia saman*. Altogether, four canopy species (10.8%) were pollinated by sphingids (Fig. 2). A large number of sub-canopy individuals were pollinated by large-bees (39.8%), compared to only 15.4% of the species. This asymmetry was due to the abundance of *Gustavia augusta* and *Senna georgica*.
4. Seed dispersal and pollination modes of woody species of secondary forest

Figure 2: Pollination modes in percent, of woody species and fertile individuals of the canopy and sub-canopy, in two capoeiras, Usina São José, Zona da Mata, state of Pernambuco. gen = generalist pollination, sphi = sphingophily (sphingids), mela = melittophily (large bees), mesma = melittophily (small bees), phal = phalenophily (moths), can = cantharophily (beetles), myio = myiophily (flies), psych = psychophily (butterflies).

Discussion
The studied secondary forest is a good example of how the mutual interactions between plants and animals look like after recuperation of sites that were intensively used for agriculture. As the sites were completely cleared and used for sugarcane cultivation during the 1980s, all of the existing tree species must have reached these sites, crossing at least the 50 m that separate Capoeira 1 from the nearest old growth forest fragment. In spite of that, canopy and sub-canopy vertebrate-dispersed species accounted for more than 80%, just as in an old-growth forest in the region (Santos et al., 2008). These values are only slightly below those Chazdon (2003) found for Costa Rican secondary and old-growth forests. Furthermore, relatively more canopy species had large seeds than in forest edge tree communities or other secondary forests inside the largest fragment of the region (Santos et al., 2008). This is surprising considering the unprecedented local mass extinction of large-bodied mammals and large frugivorous birds in the region and that many surviving species have ranges limited to particular forest fragments (Silva and Pontes 2008, Farias et al. 2007) and exemplifies the
resilience of the highly degraded area. The main dispersers at the study site were supposedly agouti (*Daysprocta agouti*), fox (*Cerdocyon thous*), raccoon (*Procyon cancrivorus*), and lizard (*Tupinambis teguixim*), besides bats, various small to medium-sized bird species, small rodents and marsupial species. These animals or their footprints were frequently observed and they are well-known fruit dispersers (Nelio 2006, Castro and Galetti 2004, van der Pijl 1982, Lobova et al. 2003, Lobova and Mori 2007). Relatively large animals are of importance with regard to the dispersal of the large seeds embedded in fruit pulp of *Annona glabra*, *Inga ingoides*, *Rauvolfia grandiflora*, and *Strychnos parvifolia*. The diaspores of *Swartzia pickelii*, *Gustavia augusta* and *Eschweilera ovata* are almost bare of any fleshy pulp, therefore we assume that they must have been scatter-hoarded by *D. agouti*, however the latter might well be dispersed by bats (Prance and Mori, 1979). Some fruit trees with large seeds, such as *Acrocomia intumescens*, *Elaeis guineensis*, *Pouteria grandiflora*, and *Talisia esculenta* were probably not only dispersed by wildlife but also by humans and domestic animals that foraged at the sites when they were used as pastures. The second most important tree species, *Albizia saman*, the second most important sub-canopy species *Senna georgica*, *Albizia polycephala*, *Apeiba tibbourbou* and *Guazuma ulmifolia* are likely to have reached the sites with cattle, such as cows, and horses as its fruits serve as fodder (Janzen and Martin 1982, Lorenzi 2002, Sampaio and Gamarra-Rojas 2002). However, diaspores adapted to particular animals might not reach the sites due to dispersal limitation. For example, the seeds of the chiropterophilous tree *Parkia pendula*, a common species of the Atlantic Forest fragments nearby (Piechowski and Gottsberger 2008), were observed to be consumed and hence probably also dispersed by *Cebus flavius* monkeys, which are restricted to one single forest fragment at the São José plantation. Due to this disperser limitation, these seeds did not reach the capoeiras (Vlasaková and Piechowski, unpublished). Seeds of this species, directly sown into the studied secondary forest, germinated and the saplings developed normally so the sites were suitable for recruitment (Kimmel, unpublished).

Myrmecochorous small seeds with elaiosomes were only found in the tree *Pera ferruginea*. Species dispersed by ants are likely to have problems in colonizing sites cleared from stumps from which vegetative regeneration can take place, without any remaining seed bank, and that are not connected to existing
forests, because ants do not carry seeds across long distances, and those that do as leaf-cutting ants, cut emerging seedlings (Horvitz and Schemske 1986, Costa et al. 2007, Silva et al. 2007).

We found almost all expected pollination modes: cantharophily, phalenophily, psychophily, myiophily and sphingophily; pollination by thrips was not encountered among fertile individuals, but juveniles of the thrips-pollinated *Xylopia frutescens* were found. However, we did not find any flowers adapted to vertebrates, neither birds, non-flying mammals, nor bats. This reflects the degradation of the analyzed vegetation, since in more intact vegetation of analyzed South American vegetation types pollination by bats and birds occurs (Dulmen 2001, Machado and Lopes 2004, Ramírez 2004, Yamamoto et al. 2007, Gottsberger and Silberbauer-Gottsberger 2006b, Girão et al. 2007, Lopes et al. 2009). There is a parallel to the results of Lopes et al. (2009) who found much less bat-, non-flying mammal- and bird-pollinated species and individuals in secondary forest plots, and altogether less species and individuals pollinated by vertebrates. Chazdon et al. (2003) found less bat-pollinated species but more hummingbird-pollinated species in secondary forests, compared to old-growth forests. The ornithophilous herb *Heliconia psittacorum* L.f. (Heliconiaceae), the ornithophilous liana *Lundia cordata* (Bignoniaceae) and the two chiropterophilous lianas, *Mucuna pruriens* (L.) DC. and *M. urens* (L.) Medik. (Fabaceae), occurred in young secondary vegetation (T. Kimmel, unpublished), but were not part of our analysis due to their growth form.

Both canopy and sub-canopy of the analyzed capoeiras had more species with generalist than with bee flowers. This is exceptional since melittophily was the main pollination mode in all other studies conducted elsewhere in Neotropical biomes (Dulmen, 2001; Machado and Lopes, 2004; Ramírez, 2004; Yamamoto et al., 2007; Gottsberger and Silberbauer-Gottsberger, 2006; Girão et al., 2007; Lopes et al., 2009). Comparing secondary forest with old-growth forest, Chazdon et al. (2003) and Lopes et al. (2009) observed relatively more tree species pollinated by diverse small insects in secondary forest and small forest fragments than in continuous old-growth forest. These comparisons lead to the assumption that the earlier the successional stage is, or the smaller the forest fragments are, the more species are pollinated by various small insects and show a generalist pollination mode.
In opposition to the results of Girão et al. (2007), who assumed that hawkmoth pollination decreases with increasing disturbance, and Lopes et al. (2009), who found no typical pioneer species to be hawkmoth-, or beetle-pollinated, a relatively large number of sphingophilous species and individuals were found in the canopy of the studied capeiras. Among canopy individuals, sphingophily was even the most common pollination mode. This can be explained by the high abundance of the tree species *Inga ingoides* and *Albizia saman*. In addition, beetle-pollinated *Annona glabra*, *Elaeis guineensis*, *Acrocomia intumescens* and *Desmoncus* sp. were found and considering their habitat are definitely pioneers. A shift from a moderate percentage of species pollinated by large bees to much higher percentage of individuals, in the sub-canopy, can also be explained by the uneven abundance of species, which is a typical feature of young secondary vegetation (Harper et al. 1996). Wind-pollination is not totally absent in the studied vegetation: however, the only wind-pollinated species, *Cecropia palmata*, was categorized as generalist because it was also pollinated by diverse small insects.

Classification is one major source for bias in analyzing a plant community’s pollination modes. First, flowers are not always specialized to specific pollinators (Johnson and Steiner 2000). Second, different observers may come to different results, e.g., *Inga edulis* and *I. thibaudiana* were classified to be bird-pollinated by Chazdon et al. (2003), and to be bat-pollinated by Lopes et al. (2009). According to Vogel (1968) *I. sessilis* is probably the only member of the genus clearly adapted to bats and none is adapted to bird pollination. Third, in some cases the way of calculating the scores of pollination modes differ from each other. In some studies single species account for more than one pollination mode (e.g., Dulmen, 2001; Ramírez, 2004; Yamamoto et al., 2007), while in others one species can only have one mode of pollination (Chazdon, 2003; Machado and Lopes, 2004; Gottsberger and Silberbauer-Gottsberger, 2006; this study). Forth, careful literature analysis and correct data extraction from literature are crucial. The occurrence of pollination by non-flying mammals in *Mabea occidentalis* in continuous old-growth forests and its lack in forest fragments, or low occurrence in secondary forest, is regarded as one of the most conspicuous symptoms of degradation in the Pernambucan rainforest (Girão et al., 2007; Lopes et al., 2009). However, the classification of the species to be non-flying mammal-pollinated is
4. Seed dispersal and pollination modes of woody species of secondary forest

based on Steiner (1983), who described this species to be clearly bat-pollinated. Fifth, the case of *Ocotea glomerata*, which occurred in the capoeiras, is an example for the need of detailed ecological studies of single species. It has open unisexual flowers, visited by a wide range of insects, and it could only be shown through a laborious study that only fly species effectively pollinate them (Krause 2008). Sixth, flower-visitors may profit from floral resources independent from pollination mode or success. This is often of importance for animal populations, including endangered or rare mammals, especially in times of scarcity of other resources (Janson et al. 1981, Garber 1988, Marín-Gómez 2010). The two most common canopy species *Inga ingoides* and *Samanea saman* bear easily accessible flowers with relatively large amounts of nectar (Kimmel, unpublished). Hummingbirds were observed to feed also on melittophilous flowers of *Genipa americana* and *Rauvolfia grandiflora* and many others.

The study took place in one of the world’s most endangered hotspots of biodiversity (Myers et al., 2000) and indeed there are several implications for nature conservation and restoration that can be drawn from our findings. The fact that regeneration of secondary forest took place after complete clearing, including the elimination of the seed bank by sugarcane cultivation, and spatial isolation from diaspores sources, gives hope that the much-discussed reforestation is feasible without high costs. According to Brazilian legislation (Código Florestal 2001), river banks, slopes with an inclination above 45°, and 100 m broad strips along the borders of tablelands must be reforested, which will prevent erosion and contribute to the re-connection of fragments via corridors and stepping stones, necessary to preserve the biodiversity of existing fragments (SECTMA 2002). We think that most sites would only have to be taken out of cultivation and protected against fire that can spread from neighboring sugarcane fields and regeneration would occur by itself. Most animal groups that mutually interact with plants and are therefore of high importance for ecosystem functioning, will find suitable partners in the secondary vegetation and are hence supposed to be able to use it as habitat or for migration. The encountered gaps in the composition of pollination modes, especially the absence of bat pollination and the lack of seeds typically dispersed by large birds or monkeys, and species dispersed by ants, should be bridged by active reforestation.
5. Germination and performance of seedlings after direct seeding in secondary vegetation

Summary:
In human-dominated landscapes environmental degradation as e.g. dispersal limitation, severely affects the ability of forests to regenerate and to re-colonize abandoned sites. The direct seeding method was experimentally tested as a tool to overcome dispersal limitation and accelerate natural regeneration. Seeds of 22 native tree species were sown in twelve year old secondary vegetation of degraded Atlantic forest of NE Brazil. Two physiognomies of secondary vegetation were differentiated: open sites with no or underdeveloped canopy and closed sites with a canopy. The seeds of most species were collected in the rainy season. Most seeds germinated shortly after planting in the midst of the rainy season. The germination rates were similar at open and closed sites. No differences in seedling performance between early and late successional species and light- and heavy-seeded species could be recognized. Most seedlings died at the end of the first dry season obviously due to low precipitation. Most other environmental factors, as leaf litter cover or type of undergrowth had little effect on seedling performance. The main differences in mortality rate were clearly linked to the presence or absence of a canopy. At sites with a canopy the survival rate was significantly higher than at open sites. The formation of a canopy can be recognized as a successional facilitation process which is necessary for the establishment of most tested species. Direct seeding proved to be a good alternative for the enrichment of secondary vegetation that already had developed a canopy.
5. Germination and performance of seedlings after direct seeding in secondary vegetation

Introduction

We face an unprecedented degree of destruction of natural forests and at the same time societies become increasingly aware of the vital ecosystem services forests provide (Miyawaki 2004). The Brazilian law demands the preservation of forest or reforestation along riversides, on steep slopes, along the edges of tablelands, and as well a minimum forest area per property (Código Florestal 2001). This way soil erosion should be reduced, the genetic integrity of wildlife populations preserved, and the well-being of human populations assured (Código Florestal 2001). The implementation of these laws depends on the knowledge of forest regeneration, and monetary and other resources necessary. Under natural conditions deforested sites, e.g. after a landslide, are re-colonized and the resulting vegetation will eventually reach maturity, a process known as succession (Harper et al. 1996). The ability of secondary vegetation to establish in a landscape without (or despite) human interference is its resilience (Rodrigues et al. 2009). Environmental degradation reduces the resilience of a landscape, for example by dispersal failure. The mobile phase of plants, the diaspore, containing the seed(s), become virtually immobile, due to the absence or extremely reduced abundance of many animal species, important as dispersal agents (Kimmel et al. 2009, Alves-Costa et al. 2008, Silva and Pontes 2008). A negative development may occur: dispersal failure leads to a decrease of tree populations providing key resources (Terborgh 1986), which further negatively affects the populations of frugivorous dispersing animals (Redford 1992).

In the study region, the Pernambuco Endemism Center (PEC), of the Brazilian NE Atlantic forest, about 95% of the original forest cover are converted into agricultural land and cities, which is the highest rate of deforestation of the Brazilian Atlantic forest (Silva and Casteleti 2003). As mentioned above, according to the law, large areas are supposed to be reforested (Alves-Costa et al. 2008). Most existing forest fragments are small and dominated by edge-habitats (Trindade et al. 2008, Ranta et al. 1998). The vegetation of small forest fragments and forest edges resemble the vegetation of regenerating sites in many functional attributes and is formed by only a sub-set of the original species composition (Santos et al. 2008). When it is intended that the vegetation includes ecologically or economically important species, human interference is necessary (Wunderle 1997). Another aspect that has to be considered is the protection of the still
existing biodiversity, especially in centers of endemism. The degradation of small forest remnants happens gradually through time (Laurance et al. 2002). In large parts of the PEC a reduction of forest cover of about 50% took place only about 50 years ago (Tavares et al. 1975a, Kimmel et al. 2008, Trindade et al. 2008). Therefore we can assume that relaxation, i.e. the final state of degradation, is not yet reached and that forest remnants will degrade further and species will go extinct if these fragments are not protected by buffer zones or re-connected via corridors.

Compared to other types of reforestation the advantage of direct seeding is that no greenhouse is necessary or that no saplings have to be bought. Instead the seeds only have to be collected, which of course depends on accessible native forest remnants. When seeds are collected in the vicinity it is guaranteed that the resulting grown up plants bear the genetic adaptations of the local population to local conditions (Alves-Costa et al. 2008). The planting of young trees that originate from tissue culture is also not favorable because they are clones (George et al. 2007). The resulting low genetic variability may lead to the spread of pests (Roberts et al. 2009) and even reproduction failure, due to self-incompatibility, because individuals with the same genotype may not fertilize each other. Self-incompatibility is very common among rainforest trees (Girão et al. 2007). Direct seeding has proved to be a suitable way of enriching fallow vegetation resulting from slash-and-burn agriculture in Mexico, in the Amazon region (Bonilla-Moheno and Holl 2009, Camargo et al. 2002), and even on bare soil left over after bauxite mining in Amazonia (Parrotta and Knowles 1999). Especially large-seeded species have a high potential to regenerate in secondary forest (Cole 2009). In the study area the unassisted succession of abandoned sugarcane fields led to the development of open or closed physiognomies, i.e. with or without a canopy (Kimmel 2006). Using the direct seeding method we experimentally tested if there are differences in seedling performance in open and more closed vegetation. We also wanted to find out whether or not late successional species are better suited for establishment in fallow vegetation than early successional species (Camargo et al. 2002, Parrotta and Knowles 1999) and if there is a positive relationship between seed weight and performance (Camargo et al. 2002). Furthermore we tested which other environmental factors, such as undergrowth type, undergrowth density, or soil coverage with litter, are influential for establishment.
Material and Methods

Study site: The study was conducted at the sugarcane plantation São José, in the municipality of Araçoiaba, in the state of Pernambuco. The climate is tropical with a harsh dry season between September and December with monthly precipitation below 100 mm and a rainy season from January to August. Mean annual precipitation is 1,520 mm, and mean average temperature is 25°C (Schessl et al. 2008). At the studied two secondary forest patches the mean annual precipitation for 2008 and 2009 was 2140 mm. The red-yellow podzolic soil is sandy to loamy (Schessl et al. 2008). The original vegetation is dense lowland Atlantic rainforest with transition to semideciduous forest (Veloso et al. 1991).

On the plantation, 206 forest fragments and secondary forest patches remain, covering 28% of the area (Trindade et al. 2008). Most of them are very irregularly shaped and extend along steep hills and rivers, at 30 to 110 m a.s.l. (Trindade et al. 2008, Schessl et al. 2008). The four most important forest tree species in these fragments of old-growth forests are Thyrsodium spruceanum Benth. (Anacardiaceae), Eschweilera ovata (Camb.) Miers. (Lecythidaceae), Tapirira guianensis Aubl. (Anacardiaceae), and Pogonophora schomburgkiana Miers. ex Benth. (Euphorbiaceae) (Rocha et al. 2008, Silva et al. 2008a, Silva et al. 2008b).

Two patches of secondary vegetation (hereafter capoeira) of known age of about 12 years were chosen for sowing: (lat 7°48’42” S; long 35°02’71” W, 130 ha and 20 ha). The plantings were conducted on slopes of 38°±16°. The content of sand varies from 55% to 63%, that of clay 18% to 32%, and that of silt from 13% to 19% (Freitas pers. comm.). The area was used as pasture at least since 1969 and was completely cleared between 1975 and 1981 for sugarcane cultivation. A few years later the area was used as pasture again. In 1995, the sites were finally abandoned. The slopes are mainly covered with secondary forest, with 1,828 individuals/ha and a canopy height of 12 m. Interspersed more open sites have a tree density of 500 individuals/ha. The three most abundant canopy species were Inga ingoides (Rich.) Willd. (Fabaceae), Albizzia saman (Jacq.) F. Muell. (Fabaceae), and Casearia sylvestris Sw. (Flacourtiaecae) (Kimmel et al. 2009) (Kimmel et al. 2009). The undergrowth in the forest consisted mainly of Piper marginatum Jacq. (Piperaceae) and a few Cyperaceae (Scleria sp.), whereas the
open sites were dominated by *Lasiacis ligulata* Hitchc. & Chase (Poaceae) (among others).

**Seed collection and planting:** Altogether 4179 seeds of 22 native species and one variety were collected mostly at the borders of local forest fragments (Table 1). The variety is *Brosimum guianense* “var. petit”, in the sense of a not clearly defined taxon below species level (Wagenitz 1996). Varieties are common in *B. guianense* (Berg 1972). Most seeds were sown the same or next day after collection. Only in the first year some seeds were stored in paper bags in a non-air-conditioned room from 2 up to 39 days. Tree species were identified by comparison with specimens at the herbaria IPA (Instituto Agronômico de Pernambuco), and the PEUFR (Universidade Federal Rural de Pernambuco).

**Table 1:** Species planted; their seed weight and successional status. Species marked with an asterisk* were stored before planting; disp. = dispersal; es = early secondary; ls = late secondary; endo = endozoochorous; sb = adapted to dispersal by birds mainly small birds; lb = dispersal by large birds; syn = synzoochorous; anemo = anemochorous.

<table>
<thead>
<tr>
<th>family</th>
<th>species</th>
<th>seed weight [g] (n= 5)</th>
<th>successional status</th>
<th>disp. mode</th>
<th>number of seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td><em>Tapirira guianensis</em> Aubl.</td>
<td>0.2 es endo</td>
<td></td>
<td></td>
<td>450</td>
</tr>
<tr>
<td></td>
<td><em>Thrysodium spruceanum</em> Benth.</td>
<td>1.3 es syn</td>
<td></td>
<td></td>
<td>552</td>
</tr>
<tr>
<td>Anacardiaceae</td>
<td><em>Xylopia frutescens</em> Aubl.</td>
<td>0.1 es endo sb</td>
<td></td>
<td></td>
<td>216</td>
</tr>
<tr>
<td>Annonaceae</td>
<td><em>Aspidosperma discolor</em> A.DC.</td>
<td>0.07 ls anemo</td>
<td></td>
<td></td>
<td>108</td>
</tr>
<tr>
<td>Apocynaceae</td>
<td><em>Aspidosperma spruceanum</em> Benth. ex Müll.</td>
<td>0.35 ls anemo</td>
<td></td>
<td></td>
<td>252</td>
</tr>
<tr>
<td>Bombaceae</td>
<td><em>Eriotheca crenulicalyx</em> A. Robyns</td>
<td>0.2 ls anemo</td>
<td></td>
<td></td>
<td>72</td>
</tr>
<tr>
<td>Burseraceae</td>
<td><em>Protium giganteum</em> Engl.</td>
<td>0.3 es endo sb</td>
<td></td>
<td></td>
<td>300</td>
</tr>
<tr>
<td>Burseraceae</td>
<td><em>Protium heptaphylum</em> (Aubl.) Marchand</td>
<td>0.3 es endo sb</td>
<td></td>
<td></td>
<td>228</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td><em>Sapium sp.</em></td>
<td>0.1 es endo sb</td>
<td></td>
<td></td>
<td>180</td>
</tr>
<tr>
<td>Fabaceae</td>
<td><em>Inga blanchetiana</em> Benth.</td>
<td>0.2 es endo</td>
<td></td>
<td></td>
<td>42</td>
</tr>
<tr>
<td>Fabaceae</td>
<td><em>Inga thibaudiana</em> DC.</td>
<td>0.2 es endo</td>
<td></td>
<td></td>
<td>60</td>
</tr>
</tbody>
</table>
5. Germination and performance of seedlings after direct seeding in secondary vegetation

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Seed number</th>
<th>Germination period</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fabaceae</td>
<td><em>Parkia pendula</em></td>
<td>0.1</td>
<td>Is</td>
<td>endo</td>
</tr>
<tr>
<td>(Willd.) Benth. ex Walp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabaceae</td>
<td><em>Copaifera langsdorffii</em></td>
<td>1.14</td>
<td>ls</td>
<td>endo lb</td>
</tr>
<tr>
<td>Moraceae</td>
<td><em>Brosimum guianense</em></td>
<td>0.11</td>
<td>es</td>
<td>endo</td>
</tr>
<tr>
<td>(Aubl.) Huber</td>
<td>&quot;var. petit&quot;</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moraceae</td>
<td><em>Brosimum guianense</em></td>
<td>0.19</td>
<td>ls</td>
<td>endo</td>
</tr>
<tr>
<td>(Aubl.) Huber</td>
<td><em>Brosimum rubescens</em></td>
<td>0.40</td>
<td>ls</td>
<td>endo</td>
</tr>
<tr>
<td>Moraceae</td>
<td><em>Clarisia racemosa</em></td>
<td>3.01</td>
<td>ls</td>
<td>endo</td>
</tr>
<tr>
<td>(Ruiz Pav.)</td>
<td><em>Helicostylis tomentosa</em></td>
<td>0.6</td>
<td>ls</td>
<td>endo</td>
</tr>
<tr>
<td>(Poepp. &amp; Endl.) Rusby</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Myristicaceae</td>
<td><em>Virola gardneri</em></td>
<td>3.9</td>
<td>Is</td>
<td>endo lb</td>
</tr>
<tr>
<td>Warb.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sapindaceae</td>
<td><em>Cupania sp.</em></td>
<td>0.14</td>
<td>es</td>
<td>endo sb</td>
</tr>
<tr>
<td>Sapotaceae</td>
<td><em>Diploon cuspidatum</em></td>
<td>0.5</td>
<td>ls</td>
<td>endo</td>
</tr>
<tr>
<td>(Hoehne) Cronquist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sapotaceae</td>
<td><em>Pouteria bangii</em></td>
<td>0.7</td>
<td>ls</td>
<td>endo</td>
</tr>
<tr>
<td>(Rusby) T.D. Penn.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sapotaceae</td>
<td><em>Pouteria torta</em></td>
<td>3.8</td>
<td>ls</td>
<td>syn</td>
</tr>
<tr>
<td>(Mart.) Radlk.</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

Seeds were sown at three sites in the forest and at three neighboring open sites. The distance between the six sites ranged from one to three kilometers. Three to twelve seeds were planted in each of 435 miniplots of 60 x 40 cm. These miniplots were cleaned of herbs with a machete. It was avoided to destroy regenerating tree saplings. The soil was hoed up so that the seeds could be placed in the soil and covered with a thin layer of about 1 cm of substrate. The distance between the miniplots was about 4 m, depending on the surrounding vegetation and inclination. The emergence and disappearance of seedlings was observed monthly until January 2009.

**Statistical analysis:**
Closely located miniplots containing seeds of the same species were combined and treated as a single repetition, because it was not guaranteed that treatments were independent. The number of seeds per plot did not significantly effect the
germination rate (Pearson product moment analysis: $r = -0.02$), nor the survival rate (Spearman rank correlation: $r = 0.12$). Establishment performance was defined by the germination and survival rate. The germination rate was defined as the highest number of seedlings observed divided by the number of seeds sown (Bonilla-Moheno and Holl 2009). The germination rate was square root transformed to meet parametric assumptions (Quinn and Keough 2002). The influence of storage time on germination was calculated using Pearson product moment distribution. Since storage time obviously influenced the germination rate, except for *Parkia pendula*, only seeds stored up to three days were considered in the analysis of germination rates, except for *P. pendula*. A one-way analysis of variance (ANOVA) was used to check for differences in germination rates between species. A post-hoc Tuckey HSD test was applied to find out which species' germination rates differed from each other. A factorial ANOVA was used to test the influence of abiotic and biotic predictor variables: seed weight; successional status: from literature and complemented by personal observations on the habitat of the parent tree (old-growth forest or early secondary vegetation) (Lins-e-Silva and Rodal 2008, Santos et al. 2008); number of seeds per plot or combined plots respectively; physiognomy type: open or closed; slope inclination: very steep, steep, almost horizontal; position at the slope: top, middle or bottom; species of closest neighboring tree; type of undergrowth: dicots (mainly *Piper marginatum*), monocots (mainly Cyperaceae and/or Poaceae) or mixed; density of undergrowth: four degrees of density from very little to dense; density of leaf litter: soil mostly exposed, partially covered, or completely covered.

The survival rate was defined as the number of seedlings counted in January in the year after sowing, in per cent of seeds sown. The data of the response variable was not normally distributed and a transformation was not possible. In many miniplots no seedlings survived, only in a few low numbers of survivors were registered and in many miniplots more than half of the seedlings survived. To analyze these data they were converted into a binary set. Generalized linear models (GLM) allow the analysis of binary data using logistic regression (Quinn and Keough 2002). Logit link was applied as link factor, as it is appropriate for binary data (Quinn and Keough 2002). Storage time did not influence the survival rate of seedlings, hence all seedlings were considered for analyses.
Results
The seeds of most species were available between March and May which in 2007 and 2008 corresponded to the early to middle rainy season. In most species the highest number of seedlings was registered in May and June, which in these years was in the middle of the rainy season. Hence, most seeds germinated within one month. An example of a species with this behavior is *Tapirira guianensis* (Figure 1a, b; 2a, b). Where seedlings were observed shortly after seeding the species are considered recalcitrant (Table 2). Most seedlings of seeds collected outside the rainy season were also registered in May and June, i.e. these seeds took longer to germinate than average (Figure 2). This was the case in *Pouteria bangii* (Figure 2c) (collected October 2008), *Xylopia frutescens* (December 2007), *Cupania* sp. (December) and partially in *Virola gardneri* (December 2007). The latter species was also collected in the wet season. However, some species behaved different: the highest number of seedlings that germinated from *Parkia pendula* seeds sown in 2007 was registered in September 2008, i.e. in the dry season one year after seeding. *P. pendula* is also the only species where storage did not affect the germination rate. In *Helicostylis tomentosa* and *Pouteria cf. torta*, both collected in May 2008 the highest number of seedlings was registered in January 2009. The main cause of mortality of seedlings was drought: besides the obvious drying of seedlings, the number of living seedlings dropped following the decline in monthly precipitation (Figure 2a-d). However, drought affected seedlings of less than one year of age much more than seedlings older than one year (Figure 2a). The second drought period led to much lower mortality than the first. In *Tapirira guianensis* 64% of the seedlings survived the first drought (January 2008), 70% of these survivors were alive after the second drought (January 2009). In *Thyrsodium spruceanum* 75% of the seedlings survived the first drought and of these 94% also survived the second drought. In *Brosimum guianense* only 35% of seedlings survived the first dry period but 76% of these were alive at the end of the observations. Another main cause is the trampling down by people, who entered the secondary vegetation for working or hunting (Figure 2a). It was also often observed that seedlings were cut but the above ground plant body was left lying beside its base, perhaps this was done by leafcutter ants. In *Thyrsodium spruceanum* many seedlings recovered from this and resprouted. Sometimes, but
Figure 1 a-e: a: *Tapirira guianensis* seedling. b: *T. guianensis* sapling, about one year old. c: *Copaifera langsdorffii* seedlings. d: *Aspidosperma spruceanum* seedlings. e: *Clarisia racemosa* sapling.
less frequently, all recognizable parts of the plant were removed. Some seeds and seedlings were washed away during heavy rain. This was proved by the emergence of seedlings some meters further down the slope. Diseases or pests like fungi were rarely recognized.

Figure 2: Curve of percentage of seedlings counted as percentage of sown seeds and the monthly precipitation (fine line). Black columns represent seedlings at closed sites, grey at open sites. The asterisks mark the time of seeding. The performance of all species is directly linked to the amount of rainfall. a: *Tapirira guianensis* sown in 2007: most seedlings appeared shortly after seeding and their number decreased with the lower precipitation after July. With the onset of the second rainy season the number became stable again. The arrow marks an event of trampling when plantation workers entered the secondary vegetation and killed...
Germination and performance of seedlings after direct seeding in secondary vegetation

a forth of the total population. b: *T. guianensis* sown in 2008 at open and at closed sites. The population at open sites declined significantly more than the population at closed sites. c: *Pouteria bangii* seeds sown in October, germinated with the onset of the next rainy season. d: *Parkia pendula* seeds sown in March 2007 germinated partially shortly after seeding, at the end of the first rainy season and partially in the second rainy season. The total number of seedlings declined in both dry seasons. Note that this is one cohort; the seedlings resulting from the seeding in 2008 are not displayed.

The germination rates were significantly different between several species (Table 2). Early and late successional species performed equally well (Table 2). In most cases the mortality rates were quite similar between species. The germination rates were not significantly correlated with seed weight (Figure 3).

### Table 2: Species planted, their germination and survival rate and standard deviation, at open and at closed sites. Species marked with an asterisk* were stored before planting. Results of both years are combined. rec = recalcitrant; dor = dormant.

<table>
<thead>
<tr>
<th>species</th>
<th>germination rates [%]</th>
<th>survival rates [%]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>closed sites</td>
<td>open sites</td>
</tr>
<tr>
<td><em>Tapirira guianensis</em></td>
<td>rec 50.9 ± 23.0</td>
<td>67.0 ± 22.0</td>
</tr>
<tr>
<td><em>Thysodium spruceanum</em></td>
<td>rec 34.4 ± 25.0</td>
<td>38.0 ± 33.4</td>
</tr>
<tr>
<td><em>Xylopia frutescens</em> (a)</td>
<td>dor 6.5 ± 4.2</td>
<td>5.6 ± 7.3</td>
</tr>
<tr>
<td><em>Aspidosperma discolor</em></td>
<td>rec 11.5 ± 6.3</td>
<td>-</td>
</tr>
<tr>
<td><em>Aspidosperma spruceanum</em></td>
<td>rec 74.5 ± 16.7</td>
<td>-</td>
</tr>
<tr>
<td><em>Eriothecaa crenulaticalyx</em></td>
<td>rec 54.6 ± 24.9</td>
<td>-</td>
</tr>
<tr>
<td><em>Protium giganteum</em></td>
<td>rec 43.3 ± 20.0</td>
<td>-</td>
</tr>
<tr>
<td><em>Protium heptaphyllum</em></td>
<td>rec 6.6 ± 6.0</td>
<td>-</td>
</tr>
<tr>
<td><em>Sapium sp.</em></td>
<td>rec 0.0</td>
<td>-</td>
</tr>
<tr>
<td><em>Inga blanchetiana (a)</em></td>
<td>rec 22.2 ± 38.5</td>
<td>-</td>
</tr>
<tr>
<td><em>Inga thibaudiana (a)</em></td>
<td>rec 19.0 ± 23.9</td>
<td>-</td>
</tr>
<tr>
<td><em>Parkia pendula</em> (a)</td>
<td>dor 12.4 ± 8.3</td>
<td>13.0 ± 1.6</td>
</tr>
<tr>
<td><em>Copaifera langsdorfii</em></td>
<td>rec 45.8 ± 7.2</td>
<td>50.0 ± 22.0</td>
</tr>
<tr>
<td><em>Brosimum guianense &quot;var. petit&quot;</em> (a)</td>
<td>rec 16.7 ± 14.4</td>
<td>38.9 ± 21.0</td>
</tr>
<tr>
<td><em>Brosimum guianense</em></td>
<td>rec 31.3 ± 13.9</td>
<td>37.5 ± 39.7</td>
</tr>
<tr>
<td><em>Brosimum rubescens</em></td>
<td>rec 45.1 ± 28.4</td>
<td>-</td>
</tr>
<tr>
<td><em>Clarisia racemosa</em></td>
<td>rec 46.9 ± 24.0</td>
<td>-</td>
</tr>
<tr>
<td><em>Helicostylis tomentosa</em></td>
<td>dor 9.7 ± 9.1</td>
<td>-</td>
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</table>
5. Germination and performance of seedlings after direct seeding in secondary vegetation

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>Germination Rate</th>
<th>Duration</th>
<th>Germination Rate</th>
<th>Duration</th>
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</thead>
<tbody>
<tr>
<td>Virola gardneri (a)</td>
<td>dor</td>
<td>26.7 ± 22.3</td>
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<td>34.7 ± 43.1</td>
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<tr>
<td>Cupania sp. (a)</td>
<td>dor</td>
<td>12.5 ± 7.2</td>
<td></td>
<td>33.3 ± 28.9</td>
<td></td>
</tr>
<tr>
<td>Diplooon cuspidatum</td>
<td>rec</td>
<td>24.3 ± 11.5</td>
<td></td>
<td>9.8 ± 2.8</td>
<td></td>
</tr>
<tr>
<td>Pouteria bangii</td>
<td>rec</td>
<td>80.1 ± 8.5</td>
<td></td>
<td>66.1 ± 38.5</td>
<td></td>
</tr>
<tr>
<td>Pouteria torta (a)</td>
<td>dor</td>
<td>4.4 ± 7.7</td>
<td></td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>

a = species with significantly lower germination rates than the other species (one-way ANOVA: df: 19; F: 6.9; p = 0.000; Post-hoc Tuckey HSD test; df = 105; MS = 3.7).

Figure 3: Average germination rate and standard deviations plotted according to average seed weight (common logarithm). Seed weight ranged from 0.09 to 3.9 g. Filled dots = early successional species; open dots late successional species. No difference between early and late successional species could be recognized. Species with the light seeds had also low germination rates, whereas those with heavier seeds tended to have higher germination rates.

The survival rate was also not related to seed weight (Spearman rank: -0.06). The germination rate significantly decreased with storage time (Pearson: r = -0.34; p < 0.05). The survival rate of the emerged seedlings was not affected by storage time.

The registered environmental factors did only partially influence the performance. The germination rates under Cecropia palmata were significantly higher than under other tree species and in middle dense undergrowth significantly more seeds germinated than at sites with very little or very dense
5. Germination and performance of seedlings after direct seeding in secondary vegetation

undergrowth (Table 3). The most severe effect on performance was the physiognomy type, survival rates were significantly lower at open sites compared to closed sites (Table 3). Slope inclination, position at the slope, undergrowth type and leaf litter density had no significant effect on seedling performance.

**Table 3:** Effects of environmental factors on seedling performance: The physiognomy type was partially auto-correlated to other predictor variables; therefore all results below the third row are calculated only from seedlings in the closed physiognomy.

<table>
<thead>
<tr>
<th></th>
<th>germination rates (one-way ANOVA)</th>
<th>survival rates (GLM simple regression)</th>
</tr>
</thead>
<tbody>
<tr>
<td>physiognomy type</td>
<td>F: 0.0; p = 0.920</td>
<td>Wald Stat.: 16.79; p = 0.000*</td>
</tr>
<tr>
<td>successional status</td>
<td>F: 0.1; p = 0.748</td>
<td>Wald Stat.: 0.72; p = 0.396</td>
</tr>
<tr>
<td>slope inclination</td>
<td>F: 2.6; p = 0.057</td>
<td>Wald Stat.: 0.80; p = 0.370</td>
</tr>
<tr>
<td>position at the slope</td>
<td>F: 0.3; p = 0.719</td>
<td>Wald Stat.: 1.13; p = 0.287</td>
</tr>
<tr>
<td>neighboring tree</td>
<td>F: 2.1; p = 0.047*</td>
<td>Wald Stat.: 1.73; p = 0.189</td>
</tr>
<tr>
<td>undergrowth type</td>
<td>F: 1.1; p = 0.331</td>
<td>Wald Stat.: 0.07; p = 0.740</td>
</tr>
<tr>
<td>undergrowth density</td>
<td>F: 3.5; p = 0.019*</td>
<td>Wald Stat.: 0.27; p = 0.606</td>
</tr>
<tr>
<td>leaf litter density</td>
<td>F: 3.8; p = 0.653</td>
<td>Wald Stat.: 0.40; p = 0.528</td>
</tr>
</tbody>
</table>

**Discussion**

The significantly lower rates of survival at open sites indicate that in the study area a facilitation process, i.e. the formation of a canopy by pioneers is necessary for the successful establishment of most tested tree species during succession. Drought is the main reason for mortality, a canopy provides shade and this way reduces the evaporation rate which enables seedlings to survive. In the study region average annual rainfall is 1520 mm and there are four months with less than 100 mm (Schessl et al. 2008). Also in the Yucatan dry forest in Mexico where rainfall ranges between 1100 and 1260 per year and in dry forest in Ghana, with an annual rainfall of about only 1100 mm, drought was also the main cause of seedling mortality (Bonilla-Moheno and Holl 2009, Lieberman and Li 1992).
In Yucatan the survival of directly sown seedlings was low in young open vegetation (recently abandoned) compared to older secondary forest (8-15 years of regeneration) or primary forest (Bonilla-Moheno and Holl 2009). Opposite results were achieved in the central Amazon region where in most species the survival rates were higher on bare soil compared to pasture, secondary forest and forest (Camargo et al. 2002). There, the annual rainfall was 2500 mm with three months below 100 mm. In French Guianan primary forest (annual rainfall: 2990 mm, two to three months dry season) the seedling community was influenced mainly by seedling recruitment due to seed arrival, nevertheless even here fruiting is seasonal (Norden et al. 2007).

The dominant tree species in the fallow vegetation at the study site were presumably adapted to establish at open sites. These species were not dominant in any other forest fragment in the region which had been surveyed so far. All these other fragments were considerably older, i.e. the species composition may have changed earlier. On the other hand the species which was most characteristic for secondary vegetation (Tapirira guianensis) occurred in high numbers as seedling and sapling but is not yet important among canopy trees (Kimmel et al. 2009).

Also some species which were only found in old-growth forest remnants as Pouteria bangii, Virola gardneri and Parkia pendula showed a behavior which is presumably an adaptation to drought. Their seeds, although available in the dry period, remained dormant until they germinated in the rainy season. Probably then the water availability was sufficient.

The equally good performances of early and late successional species in the secondary forest indicated that most species could establish successfully at the study site, but, however, many species are not dispersed anymore (Silva and Tabarelli 2000a).

In Northeast Brazil many people depend directly on the resources they take from forests, like fuel, construction wood, and medicine. These include dispersal limited Virola gardneri and Copaifera langsdorfi, both sown in this study (Albuquerque et al. 2008, Ferraz et al. 2002). An ecologically important species is Parkia pendula. It is a framework species, i.e. it provides large amounts of floral and fruit resources vital as a supplement in the diet of frugivorous mammals which have to cope with fruit shortages during parts of the year, especially in

One of the most important ecosystem services forests provide is the reduction of erosion. The ability of a forest to prevent erosion is linked to two aspects: (1) the ground is covered with litter, which reduces the direct impulse of rainfall and (2) the presence of deep roots which may prevent landslides (Sidle et al. 2006). In a recently published practical guide book images are shown where a tractor is used for the clearance of weeds (Alves-Costa et al. 2008). This increases the susceptibility towards erosion. In case weed species are blocking succession by suppressing the development of tree seedlings it would be much more reasonable to apply innovative or traditional methods as the planting of pioneers to establish a canopy which will suppress the weeds (Douterlungne et al. 2009).

**Conclusions:** direct seeding can be an effective way of enriching fallow vegetation with species which are of various ecological and economical importances. However, the method did not prove to be successful at open sites. It would be very interesting to test early pioneer species as *Cecropia palmata* for this purpose. However, a previous study (Kimmel et al. 2009) has shown that the resilience of the landscape to regenerate a basic forest structure is still high. This structure, namely the canopy, provides the necessary basis for the enrichment via direct seeding. In environmentally degraded regions seeds of many species are already hard to obtain. This reduced availability of seeds makes it reasonable to use the direct seeding method in addition to the upbringing of saplings in a greenhouse. The ideal method would be to bring rare seeds into the greenhouse where they can be watered and to plant those which are abundant directly into the vegetation.
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6. References


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Ich versichere hiermit, dass ich die vorliegende Arbeit selbständig angefertigt habe und keine anderen als die angegeben 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 anderem Promotionsverfahren vorgelegt wurde.

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