UNIVERSITY OF
EASTERN FINLAND

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RESTORING BIODIVERSITY: RECOVERY OF TROPICAL
RAINFORESTS AFTER ANTHROPOGENIC DISTURBANCES

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Restoring Biodiversity: Recovery of Tropical Rainforests After Anthropogenic Disturbances

Academic Dissertation
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ABSTRACT

Due to tropical rainforest cover loss, conservation of tropical biodiversity will increasingly depend on regenerating forests. It is therefore important to ensure that forests regenerate after anthropogenic disturbance. However, regeneration after disturbance does not always occur naturally due to various reasons which are not clearly understood. In order to design effective strategies to promote forest recovery, understanding the factors that restrict regeneration is important.

The aim of this dissertation was to study the recovery of tropical rainforests after anthropogenic disturbance. The primary objective was to provide scientifically based information of factors that can limit tropical rainforest regeneration and of management methods that can support rainforest recovery in areas where it does not occur naturally.

The experiments were established in an Afrotropical rainforest on clear-cut exotic tree plantations and adjacent old-growth forest and in a selectively logged forest. In the clear-cut plantations and the selectively logged sites, natural forest regeneration has been found to be poor. Factors limiting the emergence, growth and survival of tree seedlings were studied firstly with an early-successional tree species, *Neoboutonia macrocalyx*, in the clear-cut plantation and secondly with tree species representing different successional status in the selectively logged forest, where also the natural recruitment of seedlings was monitored. The factors in the selectively logged forest were studied with an experiment that manipulated vegetation cover (vegetation clearance) and vertebrate herbivory (vertebrate exclusion). Applied nucleation, *i.e.* planting trees as small patches, as a restoration method was studied on the clear-cut plantations. Furthermore, tree community compositions in different aged forests were examined to study the use of exotic tree plantations as nurse crops to promote forest regeneration. Finally, implications for forest restoration are suggested based on the findings from the studies.

This dissertation found that a complex network of factors influences forest regeneration after anthropogenic disturbance. Regeneration in the clear-cut plantations and selectively logged forest was limited by low natural seedling recruitment. On the study sites in the clear-cut plantations, only two naturally established *N. macrocalyx* seedlings were found during the study, and *N. macrocalyx* seedlings emerged under the nuclei, but were absent from the adjacent control sites. On the study sites in the selectively logged forest, natural recruitment was low and limited to only three indigenous, early-successional tree species. Limited seed dispersal to the disturbed sites might have contributed to the low recruitment.

This study also found that in the selectively logged forest, vertebrate exclusion significantly increased overall seedling emergence and performance (height) and significantly reduced the occurrence of seed disturbance events and seedling mortality. In addition, vertebrate herbivory caused more seedling mortality than all other identified mortality factors combined. In the clear-cut plantations, folivory reduced the survival of *N. macrocalyx* seedlings. These findings indicate that vertebrate and insect herbivory could be one of the main factors limiting forest regeneration on disturbed sites.

Furthermore, results also indicate that dense vegetation cover could limit tree seedling emergence, but have a lesser influence on later seedling stages. Creating small patches where vegetation was cleared significantly increased natural seedling recruitment and the emergence of the sown tree species, but did not limit or enhance seedling performance after emergence in the selectively logged forest. Similarly, seedling recruitment was higher under the nuclei trees where vegetation cover was lower, compared to the control sites. However, vegetation clearance reduced mortality of only a few of the species planted in the selectively logged forest and on the clear-cut plantations, high infestation by climbers did not limit the survival of *N. macrocalyx* seedlings.

Several other biotic and abiotic seedling mortality factors were also identified. Regeneration could be limited by mortality

caused by rotting and, to a lesser extent, by elephant trampling, falling debris, drying or heavy rain. However, variation in the occurrence of the different mortality factors among the studied species implies that different tree species can be more susceptible to some mortality factors than others.

The evidence presented in this dissertation indicates that planting nucleus trees can be a useful restoration method to facilitate natural seedling recruitment on anthropogenically disturbed sites where natural regeneration is slow. Planted nucleus trees were able to establish through a dense vegetation cover. Six years after planting, the density of naturally recruited seedlings was significantly higher under the nuclei compared to the control sites, the seedling communities differed between the areas under the nuclei and control sites and the nuclei hosted a higher number of tree species. In addition, this study found that plantations of exotic tree species could be used as nurse crops to facilitate succession where natural regeneration is slow. The tree communities of the clear-cut plantations have become more similar to those of old-growth forests over time, while nearby grasslands where plantations were not established are still void of forest.

In conclusion, forest regeneration after anthropogenic disturbance is limited by biotic and abiotic factors influencing arrival, emergence and survival of seeds and seedlings, which in turn are closely interlinked with the prevailing fauna and flora of the disturbed sites. Based on enhanced understanding of regeneration limitations, restoration efforts can be designed to support forest recovery within a reasonable time.

Preface

I am grateful to everyone who contributed to my thesis and helped me along the way. First and foremost, I am grateful to my main supervisor, Professor Heikki Roininen, who offered me the opportunity to study tropical forests in Africa, to commence my PhD studies and who has been a source of advice and inspiration ever since. I would also like to express my heartfelt gratitude to Dr. Anu Valtonen for her invaluable assistance and encouragement with this dissertation. You always found the way forward, gave great advice and always had the time to help. My sincerest thanks go also to Professor Philip Nyeko who supported and guided me forward, particularly during the early times, and made it possible to conduct the research in Uganda.

I cannot thank enough the great team of research assistants who I was privileged to work with in Kibale National Park. Isaiah Mwesige, Richard Sabiiti, John Koojo and Erimosi Agaba, you made this research possible with your tireless and dedicated work. I am grateful for everything I learned from you about forests and life and I will always remember our days in the forest, come rain or sun, you were always in great spirits. I would like to express my warmest thanks to the Makerere University Biological Field Station in Kibale National Park for being able to stay there during my research and for its staff who made my research possible and always made me feel like home. Thank you all the research colleagues I met at the MUBFS for the great memories, conversations and company during the time spent at the station. Many thanks also to the Tropical Biology Association for their great field course in Kibale. I also wish to express my sincerest thanks to the Academy of Finland and the Finnish Cultural Foundation for providing funding for the research and the Office of the President of Uganda, the Uganda Council of Science and Technology and the Uganda Wildlife

LIST OF ABBREVIATIONS

DistLM	Distance-based linear model
KNP	Kibale National Park
LAE	Leaf area eaten
LSD	Least significant difference
MANOVA	Multivariate analysis of variance
MDS	Multidimensional scaling
PERMANOVA	Permutational multivariate analysis of variance
SIMPER	Similarity percentage analysis

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman numerals I–V.

I   Piiroinen T, Nyeko P and Roininen H. Canopy openness in gaps determines the influence of herbaceous climbers and insect folivory on the survival of a tropical pioneer tree, *Neoboutonia macrocalyx* Pax. *African Journal of Ecology 52: 41-49, 2014.*

II   Piiroinen T, Valtonen A and Roininen H. The seed-to-seedling transition is limited by ground vegetation and vertebrate herbivores in a selectively logged rainforest. *Forest Ecology and Management 384: 137-146, 2017.*

III   Piiroinen T, Valtonen A and Roininen H. Vertebrate herbivores are the main cause of seedling mortality in a logged African rainforest – implications for forest restoration. *Restoration Ecology doi: 10.1111/rec.12460, 2016.*

IV   Piiroinen T, Nyeko P and Roininen H. Natural establishment of indigenous trees under planted nuclei: A study from a clear-felled pine plantation in an Afrotropical rain forest. *Forest Ecology and Management 345: 21-28, 2015.*

V   Piiroinen T, Valtonen A and Roininen H. Exotic plantations can ignite forest succession in the Afrotropics where natural forest regeneration is slow. *African Journal of Ecology 54: 524-528, 2016.*

The above publications have been included at the end of this thesis with the kind permissions from John Wiley & Sons (I, III, V) and Elsevier (II, IV).

AUTHOR'S CONTRIBUTION

The author of this thesis designed the research for studies I-V with Heikki Roininen. For study I, the experiment was established and data was collected by Heikki Roininen and his research group. The author of this thesis was responsible for establishing the experiments and data gathering for studies II-IV. Study V used datasets from studies by Kasenene (2007) and Owiny et al. (2016). The author of this study conducted all data analyses and wrote first drafts of the articles. The articles were produced in collaboration with the co-authors.

Contents

1 Introduction

1.1 LOSS OF TROPICAL RAINFORESTS

Deforestation in the tropics is a major environmental concern of our time, with far-reaching consequences (MEA, 2005). During the past decade, old-growth tropical forests have been converted to agricultural land, pastures and plantations, as well as logged for timber at an unprecedented rate. The far-reaching consequences of these actions include loss of biodiversity (Laurance & Useche, 2009) as well as reduction in the ability of forests to provide a wide range of critical ecosystem services (Lamb et al., 2005) such as regulation of hydrological cycles (Sheil & Murdiyarso, 2009) and control of climate change (van der Werf et al., 2009).

Approximately half of the tropical moist forest cover retains only 50% or less of its tree cover due to deforestation and selective logging (Asner et al., 2009). Globally, the most important factors causing deforestation of tropical rainforests are industrial logging, conversion of forests to agriculture and plantations and forest fires, although the importance of these factors varies between regions (Ghazoul & Sheil, 2010). The largest extent of rainforest clearing has taken place in South America and particularly in the Amazon basin for cattle ranching and cultivation of cash crops such as soybean. In Asia, forest cover loss is mainly driven by expansion of large-scale commercial plantations, for instance for the production of palm oil and rubber, whereas forest cover loss in Africa is mainly due to expansion of subsistence-based agriculture and charcoal production.

1.2 REGENERATION OF TROPICAL RAINFORESTS AFTER DISTURBANCE

Tropical rainforests are constantly influenced by a wide variety of natural disturbance events that alter the forest structure (Brokaw, 1985). These disturbance events, such as treefalls, strong winds and landslides create canopy gaps that are integral to the ecological functioning of tropical rainforests by influencing forest architecture, species composition, diversity and population dynamics (Whitmore, 1989; Ghazoul & Sheil, 2010).

Following the opening of the canopy (Figure 1), gap-phase regeneration occurs either with new recruits or the release of seedlings previously suppressed by the tree cover (Brokaw, 1985). As depicted by the successional theory, herbaceous plants and early-successional tree species dominate the canopy gaps during the early stages of succession due to increased light conditions (Uhl et al., 1981; Brokaw, 1985). However, as the early-successional trees grow and gain canopy dominance, the herbaceous vegetation cover is reduced, allowing for the colonization of later successional tree species. Similarly, gap-phase regeneration can occur following anthropogenic disturbance and the forest's successional pathway can lead from the colonization of early-successional trees towards the establishment of later successional species (Duah-Gyamfi et al., 2014). For instance, forest regeneration after logging can be rapid in some cases (*e.g.*, Cannon et al., 1998; Ding et al., 2012; Duah-Gyamfi et al., 2014). However, in other cases, natural regeneration after logging and other forms of anthropogenic disturbance can be exceedingly slow or arrested, even if reforestation is intended (Chazdon, 2014) (Figure 1). Such variation in the ability of forests to recover after disturbance may be explained by differences in the intensity of disturbance (Chazdon, 2014), the size of the disturbed area and the consequent distance to the forest edge (Denslow et al., 1990; Denslow et al., 1998; Muscolo et al., 2014) as well as factors

related to both biotic and abiotic conditions associated with the disturbance.

The most critical periods in a tree's life are its seed and seedling stages (Fenner, 1987). Consequently, factors that limit the regeneration of tropical rainforests after disturbance can be related to the processes that influence seed arrival, seedling emergence and seedling mortality (Holl, 1999). The arrival of seeds of rainforest tree species largely depends on animals (Howe & Smallwood, 1982; Howe, 1984) and most tropical rainforest seeds remain viable in the soil only for a short period of time (Vázquez-Yanes & Orozco-Segovia, 1993). However, treeless sites might not attract seed dispersers (Schupp et al., 1989). Furthermore, the increased light conditions in canopy openings can benefit herbaceous vegetation (Babaasa et al., 2004; Chazdon, 2014). Consequently disturbed sites can become dominated by dense vegetation cover which can prevent the emergence of tree seedlings (Vàzquez-Yanes et al., 1990; Molofsky & Augspurger, 1992; Dalling & Hubbell, 2002). Disturbance can also result in unfavourable changes in temperature and moisture conditions (Fetcher et al., 1985) or soil properties, such as increased bulk density, decreased soil porosity and loss of soil organic matter, that can influence forest regeneration (Guariguata & Ostertag, 2001).

Due to the changes in biotic and abiotic conditions, seedling mortality factors on sites recovering from anthropogenic disturbance may also differ from those occurring after natural disturbance or in undisturbed forests. Factors that typically cause seedling mortality in tropical forests can include falling debris (Aide, 1987; Clark & Clark, 1989), animal trampling (Clark & Clark, 1989; Alvarez-Clare & Kitajima, 2009), pathogens and herbivory (Schupp et al., 1989; Moles & Westoby, 2004; Spear et al., 2015), competing vegetation cover, unfavourable microclimate or soil properties and lack of mycorrhizae (Holl et al., 2000). However, factors that cause seedling mortality in tropical forests recovering from anthropogenic disturbance have been rarely studied (Jansen &

Zuidema, 2001; Grogan & Galvão, 2006; Palma & Laurance, 2015) and therefore, are relatively poorly understood.

1.3 RESTORATION OF TROPICAL RAINFORESTS

When disturbance has altered forest structure and functioning to the extent that its natural capacity to recover is compromised, forest succession may become arrested and restoration efforts are needed to promote forest regrowth (Parrotta et al., 1997; Chazdon, 2003) (Figure 1). Forest restoration efforts may include approaches known as assisted natural regeneration, where sites are protected from further disturbances, such as grazing or fires, or where the competing vegetation cover, which might hold back regeneration, is controlled (Shono et al., 2007). Restoration can also include introduction of woody species by sowing seeds or planting seedlings that can then further facilitate forest recovery as they grow (Holl, 2012).

When forest restoration in the tropics is conducted by introduction of woody species, it is often carried out by establishing plantations with a limited number of species belonging to a small number of genera, such as *Pinus* and *Eucalyptus* (Lamb et al., 2005). However, although these plantations can be economically profitable, they may fail to provide the same level of goods and services once provided by the indigenous forest. It has been proposed that plantations of exotic trees could also be used as nurse crops (*e.g.*, Parrotta et al., 1997) to facilitate the establishment of slow-growing indigenous tree species in areas where this would not take place naturally. Eventually, the plantations would be logged and the indigenous trees could then take over (*e.g.*, Fimbel & Fimbel, 1996). However, long-term studies that examine exotic woody species as nurse crops are scarce (Ren & Nan Liu, 2008).

Indigenous forest systems could also be re-established by planting indigenous tree species (Lamb et al., 2005), but replanting large areas with indigenous tree seedlings is often limited by high costs and labour inputs (Rodrigues et al., 2009).

An alternative could be to plant indigenous species in small patches (applied nucleation method). Once a sufficient size is reached, these patches of trees could trap wind-dispersed seeds (Franks, 2003; Zahawi et al., 2013), attract animal seed dispersers (Schlawin & Zahawi, 2008), and eventually shade out grasses and other competing vegetation in the favour of tree seedlings (Elliott et al., 2003).

Despite that a range of different restoration methods have been developed, the field of restoration ecology is, however, still relatively young (Aronson & Alexander, 2013). Restoration efforts may fail if the factors that restrict tropical forest regeneration are not clearly understood (Holl, 2012). There is also limited information available of the characteristics of different indigenous species (Wishnie et al., 2007; Pryde et al., 2015), restricting their use in restoration.
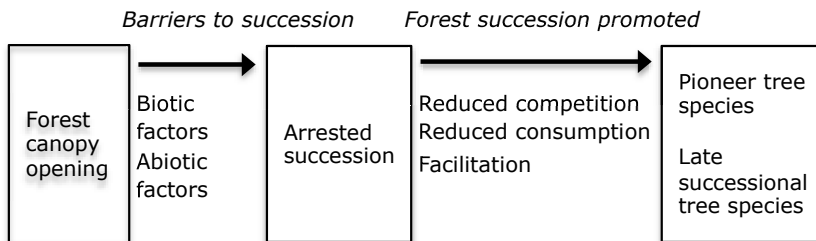
Figure 1. Different biotic and abiotic factors may act as barriers to forest regeneration after canopy opening resulting in arrested succession. Restoration efforts may be needed to reduce competition and consumption of propagules as well as to facilitate forest regeneration.

1.4 AIMS OF THE THESIS

With the rate the area of old-growth forests is reducing, regenerating secondary forests are increasingly becoming the predominant form of tropical forest cover (Wright & Muller-Landau, 2006; Chazdon, 2014). Therefore, conservation of tropical forest biodiversity will increasingly depend on regenerating forests (Chazdon, 2014). For that reason, it is

important to better understand the factors that restrict forest regeneration after anthropogenic disturbance and to use this understanding to assist the development of successful forest management and restoration strategies that can promote forest recovery (Holl, 2012).

The aim of the research described in this dissertation was to study the recovery of tropical rainforest after anthropogenic disturbance. The primary objective was to provide scientifically based information of factors that can limit tropical rainforest regeneration and of methods that can support rainforest recovery in areas where natural recovery is slow or arrested. The specific objectives of the research were:

1. to identify factors limiting the emergence and growth of an early-successional tree species on clear-cut exotic plantations showing slow natural regeneration (I);
2. to identify factors limiting natural seedling recruitment and emergence and performance (height) of sown species, as well as factors causing mortality of sown tree species in selectively logged forests showing slow natural regeneration (II, III);
3. to determine if planting patches (applied nucleation) of an indigenous, early-successional tree species can facilitate natural forest regeneration on clear-cut exotic plantations showing slow natural regeneration (IV);
4. to determine whether the tree community compositions on clear-cut exotic plantations are becoming more similar to those of old-growth forests through time, which would indicate that exotic plantations could be used as a possible restoration method to facilitate natural forest regeneration in areas where it does not take place naturally (V);
5. to provide information that can be used in designing management and restoration programmes for disturbed tropical rainforests (I-V).

2 Materials and Methods

2.1 STUDY LOCATION

The study was conducted in Kibale National Park (KNP), Uganda (Figure 2) (0°13'–0°41'N; 30°19'–30°32'E, 795 km^2). Kibale National Park is a mid-altitude moist evergreen forest (Chapman et al., 1997) comprised of grasslands and papyrus swamps in addition to old-growth forest (Fimbel & Fimbel, 1996). However, past anthropogenic activities, such as selective logging and establishment of plantations of exotic trees and their later clear-cutting, have altered the natural environment of KNP. As a result, KNP also contains secondary and colonizing forests as well as areas dominated by non-tree vegetation where forest regeneration is exceedingly slow (Paul et al., 2004). Selective logging was practiced in KNP in the 1960s and it considerably altered the forest structure (Kasenene, 1987). Tree regeneration on these sites has been slow (Struhsaker et al., 1996). Plantations of exotic tree species were established to convert grasslands, presumably a result of former agricultural activities (Kingston, 1967 after Fimbel & Fimbel, 1996), in KNP into timber production in the 1960s and 1970s (Fimbel & Fimbel, 1996; Struhsaker, 1997). In 1993, the forest became a national park (Struhsaker, 1997) after which the tree plantations have gradually been clear-cut, (Chapman et al., 2002), to allow natural forest recovery (Struhsaker, 1997).
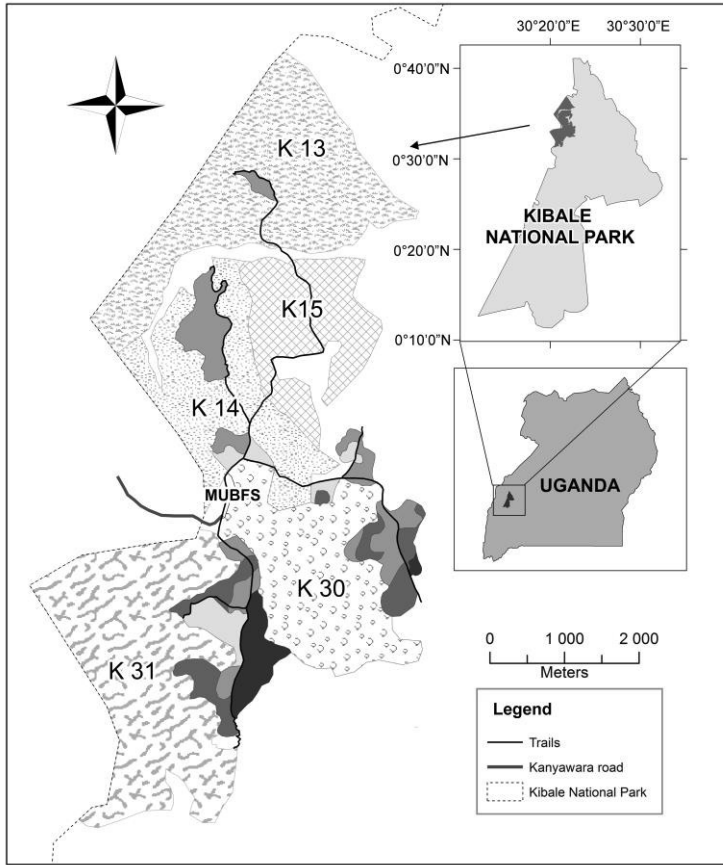
Figure 2. Map of Kibale National Park, Uganda with locations of the forest compartments K13, K14 and K15. MUBFS = Makerere University Biological Field Station. The K30 and K31 are old-growth forest compartments. The different gradients represent the forest compartments and the different colors represent areas where exotic tree plantations were established but later clear-felled.

Studies I and IV were established in the clear-cut exotic tree plantations, on sites where natural regeneration was exceedingly slow. The clear-cutting of the plantations begun in 1993 (Chapman & Chapman, 1996), and some of the sites still showed very limited regeneration when these studies were established in 2006. Studies II and III were established in the

selectively logged forest where natural regeneration was slow or arrested. Selective logging took place from 1968–1969 (Kasenene, 1987), and the sites still showed very limited natural regeneration when this study was established in 2012. Both, the clear-cut plantations and the selectively logged sites were located within a matrix of old-growth or regenerating secondary forests. Study V combined data on tree species densities in the clear-cut exotic plantations reported by Kasenene (2007) (prior and 4–6 years after the clear-cut) and Owiny et al. (2016) (the same plantations 9–19 years after the clear-cut as well as the nearby 42–43-year-old selectively logged forests and old-growth forests).

2.2 STUDY ORGANISMS

In studies I and IV, *Neoboutonia macrocalyx* Pax (Euphorbiaceae) was used to study regeneration barriers in the clear-cut exotic plantations and to test applied nucleation as a restoration method. Here, *N. macrocalyx* was used since it is a relatively common early-successional tree species across East Africa and therefore a species that could be expected to colonize the clear-cut plantations.

Studies II and III, examining seedling emergence and causes of seedling mortality, were conducted with *Albizia grandibracteata, Celtis durandii, Diospyros abyssinica, Funtumia latifolia, Millettia dura, Mimusops bagshawei, Monodora myristica, Neoboutonia macrocalyx, Polyscias fulva, Prunus africana, Uvariopsis congensis* and *Olea welwichii*, which are all indigenous and relatively common tree species in KNP and particularly represent species that are common in forests of different successional status.

2.3 FIELD MEASUREMENTS

2.3.1 Factors limiting regeneration on clear-cut plantations

To study the factors limiting forest regeneration in the clear-cut plantations, 24 canopy gaps (average size 436 m^2) were selected by random stratified sampling; two gaps represented natural tree-fall gaps and 22 represented gaps created by clear-cutting of the plantations where natural regeneration was slow (I). In each gap, eight plots, cleared from ground vegetation, were established.

Seeds of *N. macrocalyx* were collected during April-May 2006 from KNP and randomly divided into two groups; dried and stored or planted in a nursery. The stored seeds and nursery seedlings were then planted into the 192 plots in September 2006 (four plots in each gap with transplanted seedlings (4 seedlings/plot, for each seedling an area of 50 × 50 cm was cleared from vegetation) and four plots with seeds (10 seeds/plot, each plot was 50 × 50 cm)). In each plot, seedling emergence and survival, mortality factors, if definable, and abundance of herbaceous climbers were monitored monthly for 19 months. Emerging leaves were marked monthly, fallen leaves were collected weekly and Leaf Area Eaten (LAE) was measured to examine the intensity of folivory on the seedlings. Canopy openness of the gaps was measured at the end of the study.

2.3.2 Factors limiting regeneration on selectively logged forests

To study the factors limiting forest regeneration in the selectively logged forests, 30 canopy gaps, representing different sizes and areas with different logging histories (*i.e.* compartments), were selected with random stratified sampling (II, III). Gaps of the smallest size class were natural tree-fall gaps while the larger size classes represented selectively logged gaps where forest had not recovered naturally. In each gap, a 10 × 10

m plot was established in a randomly selected location and in each plot, four 1 × 1 m treatment replicates were established. The experimental design had two factors: (1) vegetation cover with two treatments: control and vegetation clearance and (2) vertebrate herbivory with two treatments: control and vertebrate exclusion. The four replicates in each of the gaps were then randomly assigned to the four possible combinations of these treatments.

Seeds of 12 indigenous tree species, representing different successional status, were collected from KNP and sown in the treatment replicates sequentially as species became available (April 2012–June 2013). Emerging seedlings were individually marked and emergence and seedling height were monitored twice a week (April 2012–February 2014). In addition, all tree seedlings that were not representing the sown species (*i.e.*, those recruiting the site naturally after the establishment of the experiment) were marked individually and their height was measured at every monitoring event. Signs of disturbance events of the sown seeds were recorded at each monitoring event as the presence or absence of signs of seed predation or seed removal. Furthermore, soil samples were collected, thermal conditions were measured and plant community composition was recorded at each study gap.

Factors that cause seedling mortality (III) were studied using the same experimental set-up as in Study II. Mortality of the emerged seedlings was monitored twice a week (April 2012–February 2014) and the mortality cause (rodents, other vertebrate herbivores, elephant trampling, rotting, drying, being washed away by heavy rain, falling debris and unknown) of each seedling was determined by using visual cues. Signs of elephant visits and the damage caused by elephants to the treatment replicates and seedlings were recorded.

2.3.3 Applied nucleation as a restoration method to facilitate forest regeneration

The study examining applied nucleation as a forest restoration method (IV) used the same experimental set-up as Study I. The survival and growth of the *N. macrocalyx* seedlings was monitored monthly for the first 19 months (September 2006– April 2008) and again in 2012. In 2012, also the *N. macrocalyx* canopy areas were measured and all naturally established indigenous tree seedlings under the canopies were identified and numbered. Growth and mortality of these seedlings were then monitored every three months for one year. Signs of elephant visits and the consequent seedling mortality they may have caused were also recorded. A control site was established in each gap and all seedlings on the control sites were identified and monitored. Understory vegetation cover was visually estimated and ground vegetation height was measured under the nuclei and at the control sites.

2.3.4 Plantations of exotic trees as nurse crops to facilitate regeneration

To study the potential of exotic tree plantations in facilitating natural regeneration of indigenous tree species (V), published datasets were used on indigenous tree species densities from unlogged exotic plantations, the same plantations 4–6 years after their clear-cut (reported by Kasenene, 2007), the same plantations 9–19 years after clear-cut as well as nearby 42–43-year-old selectively logged forests and old-growth forests (reported by Owiny et al., 2016). The dataset published in Kasenene (2007) included 150 plots (*Pinus*: 60, *Cupressus*: 60, *Eucalyptus*: 30), each 0.06 ha, randomly established in sawmilled (*Pinus*, *Cupressus*) and pitsawn (*Pinus*, *Cupressus*, *Eucalyptus*) plantations. The data included mean stem density/ha estimates for all trees ≥ 1.3 m tall, collected in 2004 (the 4–6-year-old clear-cut plantations). Data from unlogged plantations was obtained

from Fimbel and Fimbel (1994) after Kasenene (2007). The data by Owiny et al. (2016) included 180 plots, each 0.08 ha, distributed between the 9–19-year-old clear-cut plantations, 42–43-year-old selectively logged forests and old-growth forests (14–31 plots in each age class) and included the stem densities of all trees ≥ 1.3 m tall, collected in 2011.

2.4 DATA ANALYSIS

Regression analysis (generalized linear model and curve estimation) was used to study the effects of insect folivory and climber infestation on the survival of *N. macrocalyx* seedlings in the clear-cut plantations (I).

Logistic regression was used to examine if the occurrence of naturally recruited seedlings and seed disturbance events in the selectively logged forest are explained by vegetation cover, vertebrate herbivory, gap size or compartment (II). Linear mixed model was used to analyse whether the overall seedling emergence (of all planted tree species) is explained by vegetation cover, vertebrate herbivory, gap size or compartment. Generalized linear models were then fitted to examine for which of the studied species seedling emergence is explained by vegetation cover, vertebrate herbivory or gap size. Since species were planted sequentially, generalized linear models were also fitted to examine the influence of any previously emerged seedlings (summed seedling heights of the other species at the time of sowing of the focal species) to the emergence of the focal species in order to exclude the possibility that competition was confounding the results.

Non-parametric Kruskal–Wallis test was used to examine whether seedling performance (height) of each of the planted species in the selectively logged forest is explained by vegetation cover, vertebrate herbivory, gap size or compartment (II). Seedling height was measured as the mean height of seedlings in each treatment replicate, measured at the mid-point between emergence and the end of the experiment. Non-

parametric Spearman's correlations were used to examine the association between the quantity of previously established seedlings and seedling performance of the focal species.

Generalized linear models were fitted to examine whether seedling mortality of each of the studied species in the selectively logged forest is explained by vegetation cover, vertebrate herbivory, gap size or compartment (logistic regression models with binomial probability distribution) (III). When seedling mortality differed significantly between the three levels of gap sizes or compartments, the least significant difference (LSD) test was used to examine the pairwise differences.

Logistic regression models were fitted to study whether the occurrence of the observed mortality factors (rodents, other vertebrates, elephant trampling, drying, rotting, rain or unknown) is explained by vegetation cover, vertebrate herbivory, gap size or compartment (III). Logistic regressions were also used to study the possible effects of previously established seedlings on seedling mortality of the focal species.

Paired-samples t-test was used to examine the differences between the two planting strategies, sowing seeds and transplanting seedlings, in terms of *N. macrocalyx* seedling survival and growth in the clear-cut plantations (IV). Paired-samples t-test was also used to compare ground vegetation cover and vegetation height under the nuclei and control sites. Wilcoxon signed rank nonparametric test was used to assess differences in densities of naturally recruited seedlings between areas under the nuclei and control sites. Non-metric multidimensional scaling (MDS) ordination was used to visualize and an unreplicated block design PERMANOVA to test for statistical differences between the seedling communities under the nuclei and control sites.

The differences in the tree communities between the different aged forests (unlogged plantations, 4–6 and 9–19-year-old clear-cut plantations, 42–43-year-old selectively logged forest and old-growth forest) were visualized using non-metric multi-dimensional scaling (MDS) (V). The possible linear successional

pattern between the tree communities in the different aged forests was examined by fitting a distance-based linear model (DistLM) with Bray-Curtis similarity matrix to the tree community data, using age of the study site since logging as the explanatory variable. To examine which tree species contributes most to the differences between the different aged forests, similarity percentages (SIMPER) routine was used (V). Based on the SIMPER results, species that accounted for a total of 50% of the differences between each pair of the age groups were selected and the relative densities of these species were calculated. These relative densities were then visualized and the species were clustered into different successional categories based on the forest age group where their densities were highest. The analyses were conducted with SPSS and Primer-E (Clarke & Corley, 2006). A more detailed description of the methods is provided in the original articles I-V.

3 Results and Discussion

3.1 POOR SEED ARRIVAL AND SEEDLING EMERGENCE LIMIT RECRUITMENT

The key to natural forest regeneration is seedling recruitment, *i.e.* seed dispersal and seedling emergence. The results of this dissertation indicate that recruitment of indigenous trees can be limited on anthropogenically disturbed sites (I, II, IV). Gap-phase regeneration is generally initiated by new recruits, seedlings emerging from the seed bank, seedlings already present in the gap or coppicing stems (Holl, 2012). However, within the study sites on clear-cut plantations, only two naturally established *N. macrocalyx* seedlings were found during the study, regardless that the planted *N. macrocalyx* seedlings survived relatively well and in the vicinity of the study plots, *N. macrocalyx* trees were common. This indicates that recruitment was not limited by lack of seed sources (I). Later on, when the nucleus trees had matured, *N. macrocalyx* seedlings emerged under the nuclei, but were absent from the adjacent control sites (IV). In the selectively logged forest, natural seedling recruitment to the study sites was low and limited to only three indigenous, early-successional tree species with small seeds that can be dispersed by, for example, small birds (II). Considering that the canopy gaps created by selective logging were within a matrix of intact forest containing abundant seed sources, this result was surprising. Findings from these three studies suggest that particularly animal-dispersed and later successional tree species seemed to have difficulties to recruit naturally to the anthropogenically disturbed sites.

A potential factor limiting natural recruitment may therefore be a low level of seed dispersal. Late-successional tree species often have larger seeds and require larger birds and mammals for seed dispersal, but generally, these animals may avoid

treeless sites (Schupp et al., 1989). Since *N. macrocalyx* seeds are animal-dispersed (Chapman et al., 1999), this might explain why the species was common in the intact forest in the vicinity of the plantation gaps but absent inside the canopy gaps. Previous studies have found that seed dispersal limitations can be an important factor contributing to low seedling recruitment in disturbed tropical forests for both early and later successional species (Dalling et al., 2002; Cramer et al., 2007; Cordeiro et al., 2009).

The findings of this dissertation suggest that forest regeneration after anthropogenic disturbance might be limited already by poor arrival of seeds and emergence of seedlings, thus at the very early stages of succession. Since natural recruitment is poor even nearby an old-growth forest, as found in this dissertation, it might be a critical limitation to forest regeneration on sites further away from seed sources. This suggests that active measures, such as introduction of woody species (Holl, 2012) may be required to promote forest recovery on such sites.

3.2 SEED DISTURBANCE AND SEEDLING HERBIVORY LIMIT RAINFOREST REGENERATION

Insect (I) and vertebrate (II, III) herbivory and seed disturbance could limit seedling emergence and survival in tropical rainforests after anthropogenic disturbance and therefore act as barriers to succession. In the selectively logged forest, vertebrate exclusion significantly increased the overall seedling emergence across the studied tree species and significantly reduced the occurrence of seed disturbance events. Seed disturbance pressure in the selectively logged forest could therefore be high. Seed predation in general is relatively common (Janzen, 1971), and there is evidence of it being particularly high in disturbed areas (Holl & Lulow, 1997). These results indicate that seed predation might be one of the factors limiting forest regeneration after anthropogenic disturbance.

Protecting seedlings from vertebrates (vertebrate exclusion) also significantly reduced seedling mortality of most of the studied species in the selectively logged forest, and vertebrate herbivory caused more seedling mortality than all other identified factors combined (33% of the seedlings that died) (III). Vertebrate-caused mortality was the most important mortality cause for most of the studied tree species, although some species were more susceptible to it than others. Vertebrate exclusion had also a significant positive effect on seedling performance. These results support previous studies which have similarly reported that seedling herbivory can restrict regeneration of rainforests by increasing seedling mortality (Sork, 1987; Clark & Clark, 1989; Molofsky & Fisher, 1993).

High levels of folivory reduced the survival of *N. macrocalyx* seedlings in the clear-cut plantations (I). However, seedlings in larger gaps experienced less folivory than seedlings in smaller gaps, which is contradictory to previous findings (Pearson et al., 2003). These results could be explained by the finding that plant tolerance to herbivory might be higher in environments rich in light, such as canopy gaps (Mueggler, 1967; Dalling & Hubbel, 2002), where the higher resource availability might enable particularly pioneer species to compensate leaf area loss by rapid leaf turn-over rates (Chabot & Hicks, 1982; Karban, 2008). Therefore, *N. macrocalyx* might also have shown higher tolerance to herbivory (less observed folivory) in high light environments (large gaps) where it could more quickly replace consumed leaves.

The results of this dissertation indicate that herbivory at the early seedling stage could be another factor limiting forest regeneration after anthropogenic disturbance. Hereby, it is particularly vertebrate herbivory that could limit forest regeneration. Some management implications can be drawn from these findings. Since vertebrate herbivory was high and could limit forest regeneration, supporting the existence of predator communities is important since they could control the high numbers of seed and seedling predators such as rodents (Elliott et al., 2013). Furthermore, since there seemed to be

variation in the susceptibility of the tree species to herbivory, careful selection of tree species to be used, particularly in direct seeding, is important.

3.3 COMPETITION WITH ESTABLISHED VEGETATION LIMITS SEEDLING EMERGENCE BUT HAS A LESSER IMPACT DURING LATER SEEDLING STAGES

Disturbed sites in the tropics often become dominated by a dense vegetation cover which can then limit forest regeneration and act as a barrier to succession (Chazdon, 2014). This dissertation found that creating small patches where the shrub layer was opened, ground vegetation was removed and soil tilled (vegetation clearance treatment) significantly increased natural recruitment and the emergence of the sown species, but did not limit or enhance seedling performance after emergence (II). This might have been caused by several factors. Since germination of early-successional tree species can be triggered by exposure to light (Bazzaz, 1991), a dense vegetation cover could prevent seedling emergence (Uhl et al., 1981; Putz, 1983). However, early-successional species might persist in the soil longer than later successional species, waiting for favourable light conditions to occur (Ellison et al., 1993). Seeds of the three early-successional tree species that naturally recruited to the study sites may have been either newly brought by seed dispersers after the establishment of the experiment or deposited previously and stored in the soil seed bank, but the dense vegetation cover might have prevented their emergence in larger numbers. Similarly, the lower vegetation cover and height under the *N. macrocalyx* nuclei potentially contributed to the higher tree seedling regeneration under the nuclei compared to the control sites (IV).

However, vegetation cover did not notably limit seedling survival, since clearing of the vegetation cover reduced mortality of only a few of the species planted in the selectively logged forest (III). On the other hand, mortality caused by

rodents was significantly higher in treatments where vegetation was not cleared compared to the cleared treatments. This indicates that the dense vegetation cover could increase seedling mortality indirectly by providing shelter for rodents which act as seedling predators (III). In the clear-cut plantations, high infestation by climbers did not limit the survival of *N. macrocalyx* seedlings (I). This species was highly resistant to climbers and seemed to be able to shed lower branches when climber infestation became heavy, thus dislodging climbers and preventing them from reaching apical shoots. Furthermore, in gaps where climbers were abundant, folivory was lower and *N. macrocalyx* survival was higher (I). A potential explanation could be the theory of associational resistance whereby climbers might have caused physical or chemical interference, making it difficult for herbivores to detect the seedlings (Hambäck et al., 2000; Baraza et al., 2006). Alternatively, climbers might have provided resources to the natural enemies of the herbivores, thereby reducing herbivore pressure (Stilling et al., 2003; Barbosa et al., 2009).

The findings from this dissertation indicate that dense vegetation cover might limit forest regeneration, particularly at the early stages of tree life, through restricting germination and seedling emergence. However, vegetation cover would seem to have a lesser influence during later seedling stages, unless fluctuating rodent populations become considerably high. As a management implication, this suggests that patches where vegetation is cleared can support seedling emergence in disturbed forests. However, since this dissertation also found that vegetation clearance increased seedling mortality due to drying, complete clearance of the vegetation, including soil tilling, would not seem to be appropriate. Instead, opening of the shrub layer might be more appropriate for reducing the negative effects of vegetation cover without exposing the seedlings to water stress, an aspect that should be studied in future works.

3.4 REGENERATION MAY BE LIMITED BY DIFFERENT BIOTIC AND ABIOTIC FACTORS THAT CAUSE SEEDLING MORTALITY

In addition to mortality caused by herbivores, the study in selectively logged forest identified several biotic and abiotic factors that cause seedling mortality and may act as barriers to regeneration. Rotting was an important cause of seedling mortality (15% of the dead seedlings) and might have been caused by fungal pathogens (III). Rotting was recorded when leaves or leaflets wilted and eventually fell off and stems softened and eventually started to topple; in many cases, there was a clearly visible, usually white, fungal growth on the stems. However, its importance varied greatly among the planted tree species, suggesting that high variation exists among species in terms of their susceptibility to rotting. The causal agents and susceptibility of different tree species to rotting would thus be an interesting topic for future work. Mortality caused by rotting was higher in the smaller gaps where the microclimate might have been more favourable for fungal pathogens compared to the larger gaps. Microclimate in smaller canopy gaps has indeed been found to be moister than in larger logging gaps (Fetcher et al., 1985).

Previous studies have suggested that elephants could hold back forest succession by trampling seedlings or by knocking over shrubs which then suffocate seedlings (Struhsaker et al., 1996; Paul et al., 2004; Lawes & Chapman, 2006), but this dissertation found no strong support for this theory (III, IV). Despite that elephants killed a considerable number of seedlings by trampling, they were not the main cause of mortality, and elephant visits to certain locations seemed to be relatively infrequent. In the clear-cut plantation, most of the nucleus sites, but only a few of the control sites, were visited by elephants which, on some occasions, caused damage to or mortality of the naturally recruited seedlings (IV). In general, seedling mortality caused by elephants constituted a relatively small proportion (4%) of the overall mortality. Moreover, since elephants are important seed dispersers, their ability to disperse large seeds

could offset their negative impacts on regeneration. In addition to elephant trampling, falling debris destroyed some seedlings but its importance as a mortality factor was minor.

In addition, abiotic factors can limit regeneration through increased mortality. This dissertation found that drought can kill seedlings, but drying was identified as a minor mortality factor (9% of the dead seedlings) and its role as a barrier to forest regeneration could be small (III). Mortality caused by drying was recorded when seedlings dried, leaves and leaflets turned yellow and dry and eventually fell off and stems started to wither and dry, usually beginning from the meristem, but in most cases stems were left standing. In this study, vegetation clearance and soil tilling could have caused water stress to the newly established seedlings, since drying caused more mortality in the vegetation clearance treatments. Heavy rain was identified as a minor mortality cause. Despite seedling mortality was monitored twice a week, the mortality cause remained unknown for a high number of cases (38%). This is often encountered in corresponding studies, indicating the difficulties of studying seedling mortality factors in natural conditions (Fenner, 1987).

The results of this dissertation indicate that forest regeneration after anthropogenic disturbance can be limited due to a wide variety of mortality factors. The variation in the occurrence of the different mortality factors among the studied species, however, implies that different tree species can be more susceptible to some mortality factors than others. Understanding of the characteristics of tree species and the consequent careful selection of suitable species are therefore important considerations for forest restoration.

3.5 PLANTING NUCLEUS TREES PROMOTES NATURAL SEEDLING RECRUITMENT

This dissertation found that nucleus trees could facilitate forest succession by promoting natural seedling recruitment in

anthropogenically disturbed sites where natural regeneration is absent or slow (IV). Planted *N. macrocalyx* seedlings (nucleus trees) performed relatively well and were able to establish through a dense cover of herbaceous plants if light conditions were sufficient. Seedling mortality was highest during the first six months, after which there was no considerable reduction in seedling numbers during the rest of the study (Figure 1, I). Six years after planting, more than half of the transplanted seedlings and seedlings which had emerged from the sown seeds had survived. These results indicate that transplanting seedlings and sowing seeds are equally successful methods (I, IV).

Six years after the sowing of the seeds and transplanting the seedlings of *N. macrocalyx*, the nucleus trees had established continuous canopy areas and the ground vegetation cover and height were lower under *N. macrocalyx* nuclei compared to the adjacent control sites (IV). Seedlings presenting more than 20 indigenous tree species naturally recruited areas under the nuclei (IV, Table 1). The density of recruits was significantly higher under the nuclei compared to the control sites; the seedling communities differed between the areas under the nuclei and the control sites and the nuclei hosted a higher number of tree species. Turnover of recruits was high, but higher in controls in comparison to areas under the nuclei.

The most common species that recruited under the nuclei (*Albizia grandibracteata*) was wind-dispersed, but most of the recruits were animal-dispersed, late-successional species. In particular, the presence of species dispersed by primates and the corresponding absence of these species from the control sites suggest that the nuclei attracted primates. Since primates are key seed dispersers in KNP (Lambert, 2011), continuing seedling recruitment under the nuclei is likely.

The findings from this study indicate that applied nucleation could be used as an effective restoration method after anthropogenic disturbance. The successful nucleation using *N. macrocalyx* might have been a result of some of the characteristics of this species. In particular, *N. macrocalyx* has

large leaves, a wide crown and a rapid growth rate and seems to be highly resistant to dense, competing vegetation cover. The fruits of *N. macrocalyx* might attract frugivores which, in addition to foraging on *N. macrocalyx* fruits, can disperse seeds of other trees under the canopies. Moreover, monopodial growth form, flexible trunks and large leaves of early-successional tree species could act as a protection against climbers (Putz, 1984), which might have also contributed to the success of *N. macrocalyx*. Finally, although elephants visited the nucleus trees, they did not cause damage to them, indicating that the species is not preferred by elephants. In locations where elephants or other large-bodied herbivores are common, selecting nucleus trees which are not preferred by these species would therefore seem important.

3.6 PLANTATIONS OF EXOTIC TREE SPECIES FACILITATE SUCCESSION

This dissertation found that plantations of exotic tree species may facilitate succession after anthropogenic disturbance when natural regeneration is limited. The tree communities of the clear-cut pine plantations became more similar to those of old-growth forests over time (V). Clear-cutting of the plantations seems to have initially dramatically shifted the tree community compositions in a way that the 4–6-year-old clear-cut plantations were clearly distinguished from the tree communities prior to clear-cut and the nearby old-growth forests. Clear-cutting increased the relative densities of some early-successional species. Furthermore, some tree species colonized the plantations only after clear-cutting, suggesting that although the plantations of exotic trees did not help the establishment of these species, they nevertheless enabled their arrival after the removal of exotic trees. However, many tree species which were common in the plantations prior to clear-cut were still common after the clear-cut, indicating that initial

species composition influenced the direction of the early succession.

The change in the tree community composition from 4–6 years to 9–19 years after clear-cutting of the plantations was notable and the tree community compositions 19 years after clear-cut, in particular, were already considerably closer to those of nearby old-growth forests. In the 9–19-year-old forests, the densities of early-successional species were in general lower compared to the situation in the same forests 4–6 years after clear-cutting and some later successional species, which were absent or uncommon in the 4–6-year-old forests, became more common. Although many of the late-successional species common in the nearby old-growth forests were still uncommon 9–19 years after clear-cut, the results indicate that the tree communities in the clear-cut plantations are slowly becoming more similar to those found in the nearby old-growth forests.

The grasslands in KNP, similar to those on which the exotic plantations were established, have shown very little natural regeneration (Zanne & Chapman, 2001; Kasenene, 2007), although the forest has returned to some areas protected from fire (Lwanga, 2003; Omeja et al., 2011). In contrast, based on the findings of this dissertation, forest succession in the former grasslands, where exotic plantations were established and later clear-cut, is proceeding towards old-growth forests, indicating that plantations have facilitated forest succession (Figure 1, IV). It seems that the plantation trees were able to suppress the persistent cover of grasses thus enabling natural colonization of indigenous tree species. After the plantations were clear-cut, the indigenous trees were able to take over and further colonization of indigenous trees took place over time. It should be noted that since various processes might influence forest regeneration over a longer time scale, the results of this dissertation are indicative only of the successional trajectories based on the current situation. Long-term monitoring is required to ascertain the changes in tree community compositions over a longer temporal scale.

These results imply that exotic tree plantations could be used as nurse crops to facilitate forest succession when natural regeneration after anthropogenic disturbance is exceedingly slow. However, although plantations have been traditionally used for restoration (Lamb et al., 2005), the use of exotic trees also involves many risks; the species can spread into an environment in which they can become invasive and replace native species (Langdon et al., 2010; Richardson & Rejmánek, 2011; Calviño-Cancela & Rubido-Bará, 2013) or they can change the soil structure, hydrology and nutrient regimes and cycles (Vitousek, 1990; Fritzsche et al., 2006). These risks should be understood and managed before exotic species are selected. Establishing plantations for restoration could be particularly suitable for regions where income generated by timber species is needed to support restoration efforts (Lamb et al., 2005; Chapman & Chapman, 1996).

3.7 HIGH SPECIES-SPECIFIC VARIATION CALLS FOR ATTENTION TO CAREFUL SPECIES SELECTION IN RESTORATION

This dissertation did not test species-specific differences directly, but found indications of species-specific variation. In the selectively logged forest, seedling emergence of the sown species varied considerably but in general, mid-to late-successional species seemed to have higher and early-successional species lower emergence rates (II). Overall mortality of the emerged seedlings was relatively high but again, there seemed to be considerable variation among the studied species (III). Early-successional species tended to have high and rapid mortality soon after emergence compared to the gradual and lower mortality of later successional species. Although high seedling mortality might have a lesser influence on the overall regeneration potential of a forest, if these species also produce a high number of viable seeds, the high seedling

mortality of pioneers should be considered in direct seeding so that a sufficient number of seeds can be sown.

In general, later successional species seemed to perform better in direct seeding, even though the early-successional species, *N. macrocalyx*, was very successful in the clear-cut plantations. In restoration projects, direct seeding is often conducted using small-seeded early successional species due to their rapid growth (Engel & Parrotta, 2001; Doust et al., 2006), but species with larger seeds tend to perform better due to their larger energy reserves (Tunjai & Elliott, 2012). Using late-successional species for direct seeding on degraded sites that are dominated by dense vegetation might therefore be more successful compared to the use of early-successional species, since the low light availability under the vegetation cover might limit their emergence.

The results indicate there may be high variation among the tree species in their ability to emerge and grow as well as in their susceptibility to different mortality factors, following anthropogenic disturbance. Since this could have implications on the success of forest restoration efforts, testing species-specific differences with a higher number of tree species in the different geographical regions would therefore be an important topic of further research.

Results and Discussion

Table 1. The main results of the five studies of this dissertation

Main conclusions	Specific results from studies I-V				
	I	*II*	*III*	*IV*	*V*
Poor seed arrival and seedling emergence limit recruitment	Natural recruitment low despite nearby seed sources.	Natural recruitment low, limited to 3 pioneer species and determined by vegetation clearance.		Natural recruitment high under nuclei but low on control sites with dense vegetation.	
Seed disturbance and seedling herbivory limit regeneration	Insect folivory reduced survival particularly in low light environments.	Vertebrate exclusion increased seedling emergence. Seed disturbance common.	Vertebrate exclusion reduced seedling mortality. Seedling herbivory was the most important mortality factor.		
Established dense vegetation limits seedling emergence but has a lesser impact during later seedling stages	Climbers did not reduce survival, folivory lower where climbers abundant.	Vegetation clearance increased natural recruitment and emergence of the sown species. Clearance did not limit or enhance performance.	Vegetation cover did not notably limit survival. Mortality caused by rodents higher where vegetation was not cleared.	Natural recruitment higher on cleared sites compared to control sites with dense vegetation.	
Regeneration may be limited by different biotic and abiotic factors that cause seedling mortality			Rotting was an important mortality cause. Trampling by elephants and drying were minor mortality causes.	Elephants caused limited seedling mortality.	

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Main conclusions	Specific results from studies I-V				
	I	II	III	IV	V
Planting nucleus trees promotes seedling recruitment				Nucleus trees established through dense vegetation. Vegetation cover lower under nucleus trees than control sites. Natural regeneration and number of species higher under nucleus than control sites. Also animal dispersed species recruited.	
Plantations of exotic tree species facilitates succession					Tree communities on logged plantations became more similar to those in old-growth forests over time.
High species-specific variation calls for attention to careful species selection in restoration		Emergence varied among different species. Mid-to late successional species seemed to have higher emergence rate than early-successional species.	Mortality varied between species, early-successional species seemed to have high and rapid mortality after emergence compared to late-successional species. Susceptibility to the different mortality factors varied among species.		

4 Conclusions

The findings from this dissertation improve understanding of the recovery of tropical forests after anthropogenic disturbance. By studying how forests regenerate after disturbance, this dissertation identified factors that limit forest regeneration on sites where natural recovery is poor and identified practices with which regeneration could be promoted (Table 1). This thesis found that a complex network of factors influences the ability of a forest to recover and therefore, no single management strategy may apply for a given site. Natural recruitment of tree species to disturbed sites was limited, even when the disturbed sites were located within a matrix of an intact forest with abundant seed sources. This finding implies that restoration efforts are needed on disturbed sites to promote forest regeneration or to avoid very long recovery times.

The poor natural recruitment of tree species might be caused by several factors or their combination. Seed arrival to disturbed sites might be limited since most tropical tree species depend on animals for dispersal, but animals, particularly mammals and larger birds, often avoid treeless open sites. However, even if seeds do arrive, there is a high probability that they will be consumed by seed predators, such as rodents. Furthermore, rodents and other vertebrate herbivores, are also important consumers of seedlings causing high early-stage seedling mortality. Since rodents prefer sites with dense vegetation cover to open sites, their densities tend to be higher in disturbed sites compared to old-growth forests. Therefore, supporting natural predator communities, including predatory birds, could support forest recovery on disturbed sites by controlling rodent populations.

Disturbed sites often become dominated by a dense vegetation cover, whereas the undergrowth in old-growth forests is sparser. If seeds escape predation, their germination,

particularly in the case of early-successional species, might be limited by the vegetation cover, since early-successional species generally need a light trigger to germinate, which might be missing under the dense vegetation on disturbed sites. Thus, germination might not take place unless seeds get deposited where vegetation cover is less dense. However, the seeds that arrive at the disturbed sites tend to be of early successional species since they can be dispersed by, for example, wind and small birds. Whilst dense vegetation cover limits seedling emergence, it has a lesser impact on seedling survival and growth. In some cases, vegetation might even promote seedling survival by protecting seedlings from insect herbivory. Reducing the vegetation cover in disturbed sites could be used as a management practise during the early stages to promote natural recruitment and to support seedling emergence. Reducing the vegetation cover could also reduce seed and seedling predation pressure. However, repeating the vegetation clearing at later seedling stages does not seem to be needed. Also, complete vegetation removal with soil tilling makes seedlings more susceptible to mortality caused by drying and thus would not seem to be an appropriate management approach.

Since natural recruitment to disturbed sites is limited due to various reasons, reforestation efforts may be required to promote forest recovery in a reasonable time. Direct seeding requires little effort, but emergence of the sown species is relatively low and seedling mortality caused by factors such as herbivory, rotting, drying and trampling by large herbivores is high, thus large seed quantities may be needed. Moreover, high variation among species, and potentially even between sites (within the same species), exists in their ability to emerge and survive. Thus, a sound understanding of the characteristics of different indigenous species is required for direct seeding to be successful and therefore, more research is needed to increase knowledge of indigenous tree species. Planted patches of indigenous, early successional species with fast growth rates, animal-dispersed seeds, large leaves and a wide crown were

able to support natural seedling recruitment under their canopies. As the naturally recruited species grow, the canopy coverage of the patches might be extended and further natural recruitment supported. Also, a plantation of exotic tree species was able to facilitate natural forest recovery. Once plantations were clear-cut, the regenerating stand of indigenous trees took over and succession was showing a trajectory towards old-growth forests.

Thus, there are many factors that need to be avoided or that need to be in place in order for seeds to arrive and germinate in disturbed sites and for seedlings to emerge and survive. A better understanding of the complex interactions that are in play in disturbed tropical rainforests helps to understand the reasons why natural regeneration might be limited and how recovery could be promoted. It might also help to design management practices and to use forests in a manner that protects them from becoming degraded. At a time that is witnessing a high pressure on tropical rainforests, understanding how they can grow back is more important than ever.

Ecosystem restoration, including tropical forest restoration, is increasingly being recognized as an important global target. Among these, are the Aichi Biodiversity targets under the Convention on Biological Diversity calling to restore at least 15 per cent of the degraded ecosystems by 2020, the Bonn Challenge endorsed by the UN Climate Summit calling to restore 350 million hectares of deforested and degraded land globally by 2030 and the New York Declaration calling to end natural forest loss by 2030 (Suding et al., 2015). A considerable amount of funding has also been recently allocated to supporting these efforts, such as from the Global Environment Facility (GEF, 2016). There is thus a strong global momentum to transform forest landscapes, including tropical rainforests, from being degraded into being functional ecosystems and to build the science base to inform the restoration efforts (Chazdon et al., 2015; Suding et al., 2015). The findings of this dissertation can be applied to support these restoration efforts.

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Online resource

Supporting information

Exotic plantations can ignite forest succession in the Afrotropics where natural forest regeneration is slow

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Running title: Exotic Plantations Ignite Forest Succession

Table S1. Tree species included in the analysis. Only indigenous tree species from both data sets have been included and where differences in nomenclature exist, the nomenclature was homogenized by using the species (or genus) names accepted by Tropicos (2015).

Tree species	Family
Dasylepis eggelingii J.B. Gillett	Achariaceae
Lindackeria sp. C. Presl	Achariaceae
Rawsonia reticulata Gilg	Achariaceae
Lannea welwitschii (Hiern) Engl.	Anacardiaceae
Pseudospondias microcarpa (A. Rich.) Engl.	Anacardiaceae
Monodora myristica (Gaertn.) Dunal	Annonaceae
Uvariopsis congensis Robyns & Ghesq.	Annonaceae
Conopharyngia sp. G. Don	Apocynaceae
Funtumia sp. Stapf	Apocynaceae
Pleiocarpa pycnantha (K. Schum.) Stapf	Apocynaceae
Rauvolfia vomitoria Afzel.	Apocynaceae
Polyscias fulva (Hiern) Harms	Araliaceae
Phoenix reclinata Jacq.	Arecaceae
Kigelia sp. DC.	Bignoniaceae
Markhamia platycalyx (Baker) Sprague	Bignoniaceae
Spathodea campanulata P. Beauv.	Bignoniaceae
Cordia abyssinica R. Br.	Boraginaceae
Cordia millenii Baker	Boraginaceae
Ehretia cymosa Thonn.	Boraginaceae
Celtis africana Burm. f.	Cannabaceae
Celtis durandii Engl.	Cannabaceae
Celtis zenkeri Engl.	Cannabaceae
Trema orientalis (L.) Blume	Cannabaceae
Euadenia eminens Hook. f.	Capparaceae
Ritchiea albersii Gilg	Capparaceae
Maytenus sp. Molina	Celastraceae
Mystroxylon aethiopicum (Thunb.) Loes.	Celastraceae
Parinari excelsa Sabine	Chrysobalanaceae
Symphonia globulifera L. f.	Clusiaceae
Alangium chinense (Lour.) Harms	Cornaceae
Diospyros abyssinica (Hiern) F. White	Ebenaceae
Croton macrostachyus Hochst. ex Delile	Euphorbiaceae
Croton megalocarpus Hutch.	Euphorbiaceae
Macaranga kilimandscharica Pax	Euphorbiaceae
Neoboutonia sp. Müll. Arg.	Euphorbiaceae
Sapium spp. Jacq.	Euphorbiaceae
Albizia spp. Durazz.	Fabaceae
Dichrostachys sp. (DC.) Wight & Arn.	Fabaceae
Erythrina sp. L.	Fabaceae
Millettia dura Dunn	Fabaceae
Newtonia buchananii (Baker f.) G.C.C. Gilbert & Boutique	Fabaceae
Piptadeniastrum sp. Brenan	Fabaceae

Anthocleista grandiflora Gilg	Gentianaceae
Apodytes dimidiata E. Mey. ex Arn.	Icacinaceae
Premna angolensis Gürke	Lamiaceae
Beilschmiedia ugandensis Rendle	Lauraceae
Strychnos mitis S. Moore	Loganiaceae
Dombeya mukole Sprague	Malvaceae
Leptonychia sp. Turcz.	Malvaceae
Pterygota mildbraedii Engl.	Malvaceae
Carapa grandiflora Sprague	Meliaceae
Entandrophragma sp. C. DC.	Meliaceae
Lovoa swynnertonii Baker f.	Meliaceae
Trichilia splendida A. Chev.	Meliaceae
Bersama abyssinica Fresen.	Melianthaceae
Xymalos monospora (Harv.) Baill. ex Warb.	Monimiaceae
Antiaris toxicaria Lesch.	Moraceae
Bosqueia phoberos Baill.	Moraceae
Ficus brachylepis Welw. ex Hiern	Moraceae
Ficus capensis Thunb.	Moraceae
Ficus exasperata Vahl	Moraceae
Ficus natalensis Hochst.	Moraceae
Ficus stipulifera Hutch.	Moraceae
Ficus vallis-choudae Delile	Moraceae
Morus sp. L.	Moraceae
Strombosia scheffleri Engl.	Olacaceae
Linociera johnsonii Baker	Oleaceae
Olea welwitschii (Knobl.) Gilg & Schellenb.	Oleaceae
Bridelia micrantha (Hochst.) Baill.	Phyllanthaceae
Margaritaria discoidea (Baill.) G.L. Webster	Phyllanthaceae
Pittosporum mannii Hook. f.	Pittosporaceae
Maesa lanceolata Forssk.	Primulaceae
Maesopsis eminii Engl.	Rhamnaceae
Cassipourea sp. Aubl.	Rhizophoraceae
Prunus africana (Hook. f.) Kalkman	Rosaceae
Coffea canephora Pierre ex A. Froehner	Rubiaceae
Craterispermum schweinfurthii Hiern	Rubiaceae
Dictyandra arborescens Welw. ex Hook. f.	Rubiaceae
Hallea rubrostipulata (K. Schum.) J.-F. Leroy	Rubiaceae
Oxyanthus speciosus DC.	Rubiaceae
Pavetta abyssinica Fresen.	Rubiaceae
Psychotria sp. L.	Rubiaceae
Randia malleifera (Hook.) Hook. f.	Rubiaceae
Rothmannia urcelliformis (Schweinf. ex Hiern) Bullock ex Robyns	Rubiaceae
Rytigynia beniensis (De Wild.) Robyns	Rubiaceae
Vangueria apiculata K. Schum.	Rubiaceae
Aeglopsis eggelingii M. Taylor	Rutaceae
Citropsis articulata (Willd. ex Spreng.) Swingle & M. Kellerm.	Rutaceae
Clausena anisata (Willd.) Hook. f. ex Benth.	Rutaceae
Fagara angolensis Engl.	Rutaceae

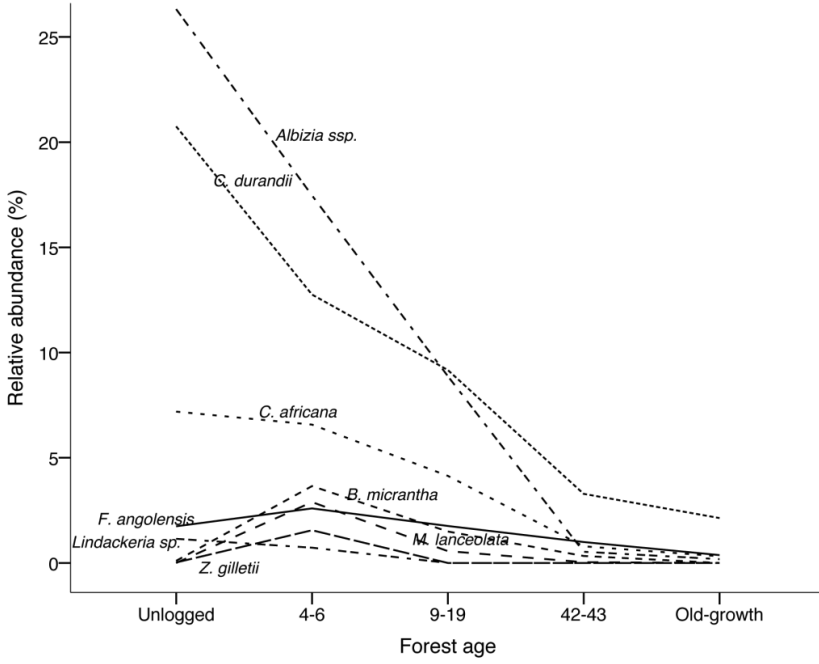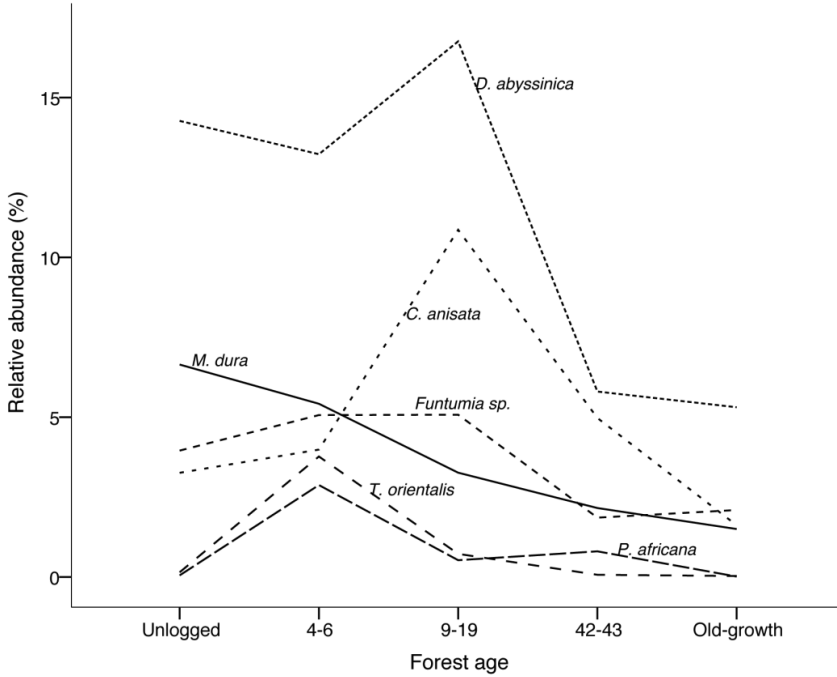|	
Fagaropsis angolensis (Engl.) Dale	Rutaceae
Harrisonia abyssinica Oliv.	Rutaceae
Teclea nobilis Delile	Rutaceae
Zanthoxylum gilletii (De Wild.) P.G. Waterman	Rutaceae
Casearia engleri Gilg	Salicaceae
Dovyalis macrocalyx (Oliv.) Warb.	Salicaceae
Oncoba spinosa Forssk.	Salicaceae
Scolopia rhamniphylla Gilg	Salicaceae
Allophylus dummeri Baker f.	Sapindaceae
Aphania senegalensis (Juss. ex Poir.) Radlk.	Sapindaceae
Blighia unijugata Baker	Sapindaceae
Lychnodiscus cerospermus Radlk.	Sapindaceae
Pancovia turbinata Radlk.	Sapindaceae
Aningeria altissima (A. Chev.) Aubrév. & Pellegr.	Sapotaceae
Chrysophyllum sp. L.	Sapotaceae
Mimusops bagshawei S. Moore	Sapotaceae
Chaetachme aristata E. Mey. ex Planch.	Ulmaceae
Myrianthus arboreus P. Beauv.	Urticaceae
Balanites wilsonianus Dawe & Sprague	Zygophyllacea
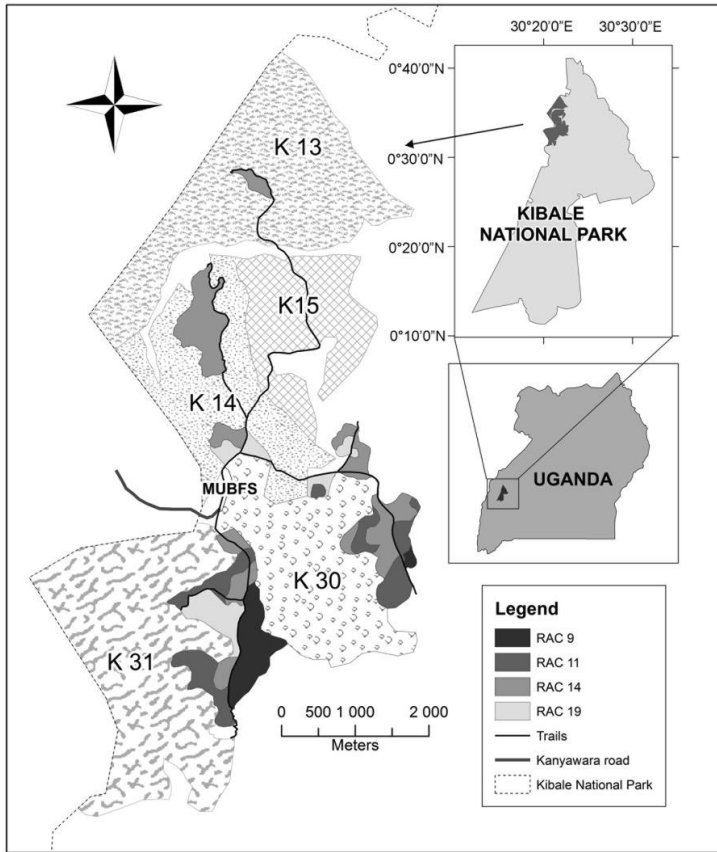
Figure S1. Map of the Kanyawara area of Kibale National Park, Uganda showing the locations of the studied areas. RAC 9–19 represent the 9, 11, 14 and 19 year-old logged exotic plantations (measured in 2011), K13, K14 and K14 represent the 42–43 year-old selectively harvested areas (measured in 2011) and K30 and K31 represent the old-growth forest. MUBFS = Makerere University Biological Field Station.
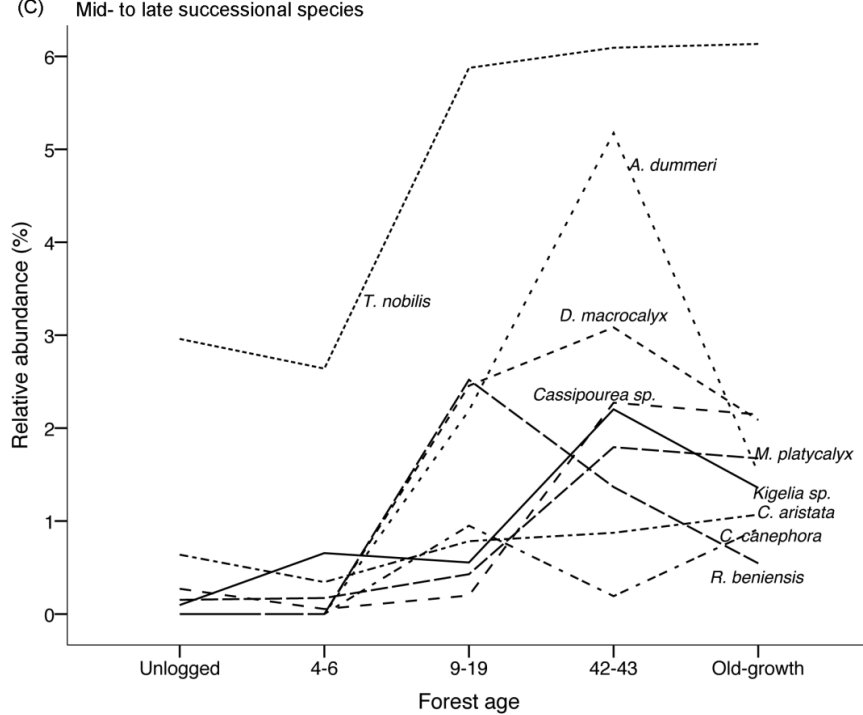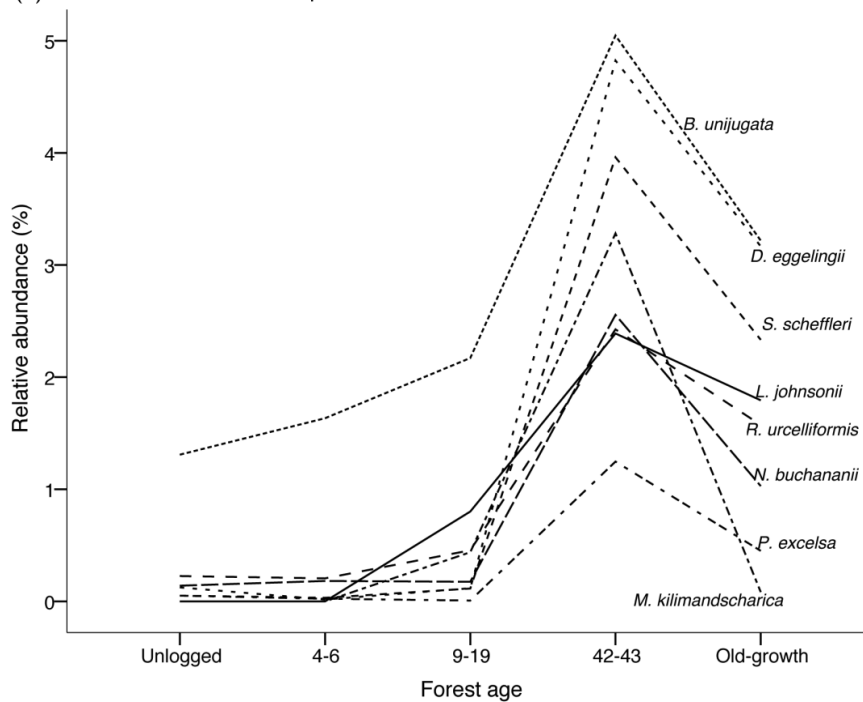
(A) Early successional species

(B) Early to mid-successional species

(C) Mid- to late successional species

A. dummeri
T. nobilis
D. macrocalyx
Cassipourea sp.
M. platycalyx
Kigelia sp.
C. aristata
C. canephora
R. beniensis

(D) Mid- to late successional species

B. unijugata
D. eggelingii
S. scheffleri
L. johnsonii
R. urcelliformis
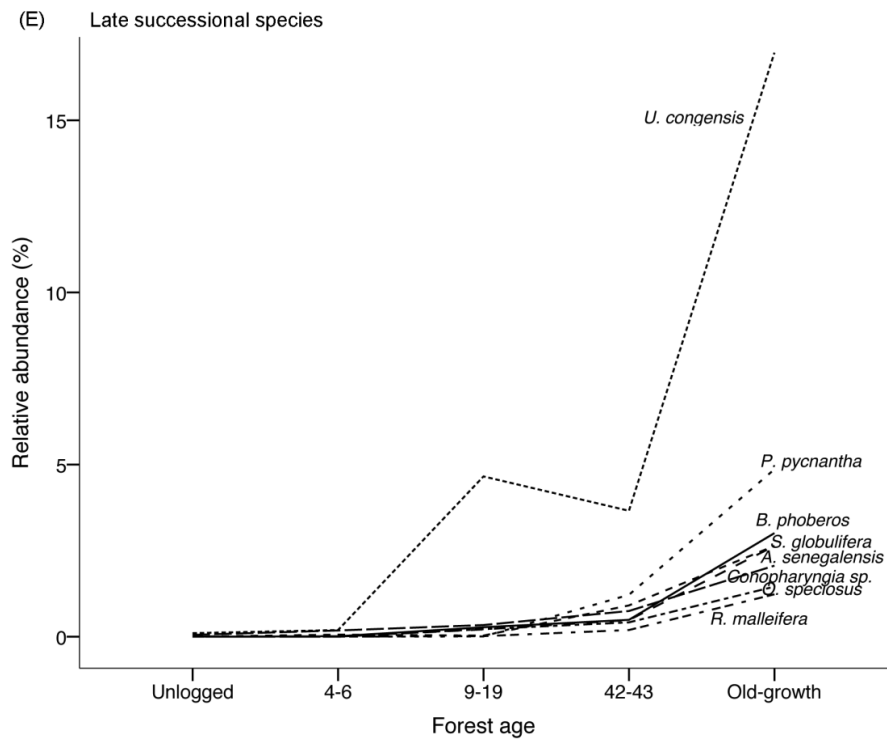*N. buchananii*
P. excelsa
M. kilimandscharica

Figure S2. Relative density of the tree species in different-aged forests; species that distinguish the age groups are shown (i.e., they contribute to 50% of the differences between the different age groups in the SIMPER analysis). Species are presented according to their observed successional status based on their relative densities in the different aged forests; early successional species (A), early to mid-successional species (B), mid- to late successional species (C, D) and late successional species (E).

TIINA PIIROINEN

Tropical rainforests do not always regenerate naturally after anthropogenic disturbances. However, since deforestation has far-reaching consequences it is important to ensure forest regrowth. This thesis provides new information on the recovery of rainforests after anthropogenic disturbances by identifying factors that limit forest regeneration and examining practices that can promote forest regrowth. This information can be used when designing restoration efforts for tropical rainforests.

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