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PIRITA LATJA

**RECOVERY OF BIRD COMMUNITIES IN AFROTROPICAL
RAINFORESTS AFTER ANTHROPOGENIC DISTURBANCES**

Responses to natural regeneration and active restoration

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Recovery of bird communities in Afrotropical rainforests after anthropogenic disturbances. Responses to natural regeneration and active restoration

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ABSTRACT

Anthropogenic pressure on tropical rainforests presents one of the most alarming threats to the Earth's biodiversity of our time. Because of extensive tropical forest loss, an increasing proportion of biodiversity depends on regenerating forests for survival. However, rates of tropical forest recovery after disturbances are highly variable, and while some areas recover naturally, some areas need assistance in the form of restoration. With the ever-growing proportion of degraded and secondary forests across tropical landscapes, it is important to understand how forests regenerate after disturbances, and how they are able to maintain viable populations and support emerging communities.

The aim of this dissertation was to study the recovery of bird communities in differently regenerating rainforests in Kibale National Park (KNP), Uganda, after human-induced disturbances. The objectives were to explore how bird community compositions and functional groups (classified by forest dependence or feeding guild of birds) recover in naturally regenerating and actively restored forests, and to examine how they are related to the vegetation structure of the differently regenerating forests.

Birds were sampled by point counting in naturally regenerating clear-cuts of former timber plantations and selectively logged forests, in actively restored abandoned agricultural and grasslands, and in adjacent primary forests. To assess how the community compositions and the functional groups of birds are related to the vegetation structure, datasets of vegetation structure and tree species diversity collected from the same sampling areas were used.

The findings of my dissertation indicate that the recovery of bird communities in naturally regenerating forests takes long after human-induced disturbances. In naturally regenerating forests, the bird community compositions of clear-cuts of former timber plantations and selectively logged forests differed from those in adjacent primary forests after 19 and 43 years of natural regeneration, respectively. Furthermore, the communities of clear-cuts differed from those in selectively

logged forests. The forest regeneration in the naturally regenerating forests of KNP has been slow or arrested due to the persistence of a shrub *Acanthus pubescens* in logging gaps. This arrested succession and the slow recovery of some characteristics of the forest (e.g., tree species composition and/or the number of large trees) most likely contribute to the slow recovery of bird communities.

The results of my dissertation show, for the first time in the Afrotropics, that bird communities can start recovering rapidly after human perturbations with the help of active restoration of rainforests. Although only the first 16 years of active restoration were covered in this dissertation, the gradual change in bird community compositions along the restoration gradient offers hope that bird community recovery, and therefore possibly also the recovery of other taxa, can be helped by restoration. The results indicate that if the rate of recovery would continue equally rapidly also after the studied time period, the time needed for full recovery would be approximately 20 years. However, this estimation is most likely a best-case scenario, as natural succession processes in tropical forests are not necessarily linear. It remains to be seen how bird community recovery continues to proceed during the coming decades. As for now, it seems that active restoration of rainforests promotes rapid initial bird community recovery.

The formation of emerging bird communities in both naturally regenerating and actively restored forests was strongly related to the increasing complexity of vegetation structure towards older forests. My dissertation identified tree basal area and tree species diversity as the best predictors of bird communities in these forests. Additionally, gap cover in the naturally regenerating forests, and the cover of the elephant grass *Pennisetum purpureum* in the actively restored forests, predicted the bird community compositions. In actively restored areas, *P. purpureum* initially necessitated restoration actions by suppressing the natural forest regeneration. Fortunately, the restoration actions seem to be sufficient to allow decreasing cover of *P. purpureum* through time, start of forest regeneration and the recovery of bird communities.

The bird functional groups showed consistent responses to natural regeneration and active restoration of rainforests. In naturally regenerating forests, even four decades of natural regeneration has not allowed full recovery of forest specialist birds as their communities in the selectively logged forests differed from those in primary forests. In actively restored forests, the abundance of the most vulnerable bird functional groups, that is, forest specialists, frugivores and understory insectivores, responded positively to the decreasing landscape openness associated with the reducing cover of *P. purpureum*, and to the increasing tree basal area and canopy closure towards older restoration forests. In particular, it was promising that the abundance of frugivores increased towards older restoration forests, since the recovery of regenerating forests could be accelerated by seed dispersal provided by frugivores.

While the responses of birds to vegetation structure were clear in naturally regenerating and actively restored forests, they were variable in primary forests; for

example, forest specialists were more abundant in gaps. This could be related to the small gap dynamics of the primary forests, where the tree community generates best in small gaps, and naturally occurring treefall gaps provide suitable microhabitats for feeding for forest birds.

In conclusion, the timescale might be long for rainforest bird community recovery after human-induced disturbances. It seems that the recovery might be slow in naturally regenerating forests if the forest regeneration is arrested, and this highlights the need to preserve primary forests as habitats for birds. However, the active restoration of rainforests can promote rapid initial bird community recovery. This is of high significance, because an increasing proportion of tropical biodiversity depends on the regrowth of forests for survival.

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CAB Thesaurus: birds, tropical rain forests, community ecology, species composition, recovery, biodiversity, vegetation, ecological disturbance, disturbed forests, logging effects, natural regeneration, ecological restoration, afforestation, national parks, Uganda, Africa

Yleinen suomalainen asiasanasto: linnut, lintukannat, sademetsät, trooppinen vyöhyke, toipuminen, palautuminen, biodiversiteetti, kasvillisuus, metsäkato, metsätuhot, metsänuudistus, metsittyminen, metsitys, kansallispuistot, Uganda, Afrikka

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Joensuu, 15th August 2017

Pirita Latja

LIST OF ABBREVIATIONS

ANOSIM	analysis of similarity
ANOVA	analysis of variance
CCA	canonical correspondence analysis
KNP	Kibale National Park
NMDS	non-metric multidimensional scaling
PERMANOVA	permutational multivariate analysis of variance

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman Numerals I-III.

- I Latja P., Malinga G.M., Valtonen A., Roininen H. 2015. Recovery of bird communities after selective logging and clear-cutting in Kibale National Park, Uganda. *Ostrich*, 87: 57-65.
- II Latja P., Valtonen A., Roininen H. 2016. Active restoration facilitates bird community recovery in an Afrotropical rainforest. *Biological Conservation*, 200: 70-79.
- III Latja P., Valtonen A., Roininen H. Recovering vegetation structure and tree diversity modify the bird community compositions in regenerating Afrotropical rainforests. Manuscript.

The above publications have been included at the end of this thesis with their copyright holders' permission.

AUTHOR'S CONTRIBUTION

- I) Author modified the original research idea formulated in the research group of Heikki Roininen.
- II) Author planned the studies together with the other authors.
- III) Author was responsible for the organising and carrying out fieldwork to collect data in all original articles.
- IV) Author conducted all data analyses with the assistance of Anu Valtonen.
- V) Interpreting the results was done by the author with the support of co-authors.
- VI) Author was the main author and wrote first drafts of all articles.
- VII) The articles were produced together with the co-authors.

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1 INTRODUCTION

1.1 LOSS OF TROPICAL RAINFORESTS

Tropical rainforests are among the most important biomes on Earth, harbouring at least half of the Earth's terrestrial biodiversity (Dirzo & Raven, 2003), and providing a variety of essential ecosystem services, including carbon and energy cycle regulation (Townsend et al., 2011) and soil erosion prevention (Labrière et al., 2015). Yet, despite their importance, tropical rainforests are threatened by an increasing amount of land use change and various other human perturbations. The dominant causes of deforestation in the tropics are agricultural expansion and commercial logging (Geist & Lambin, 2002, Brandt et al., 2017). Forest loss is highest in South America where it is driven by agricultural expansion for soybean and cattle ranching (4.0 million hectares were lost per year between 2000 and 2010; Rudel et al., 2009; FAO, 2010). Africa suffered the second largest net loss of primary forests between 2000 and 2010 (3.4 million hectares annually; FAO, 2010). For example, in Uganda, the forests once part of the second largest area of continuous moist tropical forest of the world, the Congo basin forest in Central Africa, have been now fragmented to a handful of remaining forest tracts (Duveiller et al., 2008, Brandt et al., 2017). The Congo basin forests are still believed to experience relatively low pressure due to their inaccessibility and lack of local markets (Duveiller et al., 2008). The forests of Uganda, on the other hand, have mostly been converted into small-scale agriculture land, and the remaining forests, even in protected areas, are further threatened by population growth and agricultural encroachment (Sassen et al., 2013; Brandt et al., 2017).

Accompanying the land clearance, an expanding network of roads is fragmenting the tropical forest landscape. Road networks expose the remaining forest tracts to edge effects, and allows for easier colonisation of people and alien species in previously inaccessible areas (Dirzo & Raven, 2003). Further, this enables illegal hunting, the exploitation of non-timber forest products, and fires to spread from nearby farms or to be set by poachers (Laurance & Balmford, 2013).

Anthropogenic pressure on tropical rainforests continues to present one of the greatest threats to biodiversity of our time. The human population is estimated to grow to 9.7 billion by 2050 (UN, 2015), and the pressure to increase food production and agricultural land will increase in the coming decades (Tilman et al., 2001). More than half of the area once covered by closed canopy tropical forests has already been cleared (Wright, 2005), and forest loss continues at a rapid rate, with annual net decrease estimates ranging from 6.8 million hectares (1990–2005; FAO & JRC, 2012) to 8.6 million hectares (1990–2000; Mayaux et al., 2005). At the same time, the proportion of secondary forests in the tropics is increasing (FAO, 2010). However, there is still much debate about their ability to maintain viable populations (Wright & Muller-Landau, 2006; Gardner et al., 2007; Arroyo-Rodriguez et al., 2015).

1.2 NATURAL REGENERATION OF TROPICAL RAINFORESTS

Natural disturbance is fundamental to the development, structure and composition of forest ecosystems (Brokaw, 1985; Attiwill, 1994). Disturbance varies from frequent low intensity gap-creating events (e.g., treefalls) to infrequent high intensity landscape level events (e.g., fire) that can markedly alter entire stands (Attiwill, 1994). Following disturbance, natural succession (hereafter natural regeneration) takes place. During natural regeneration, the canopy gaps created by disturbance become dominated by herbaceous plants and early-successional pioneer tree species that can take advantage of increased light (e.g., Uhl et al., 1981; Uhl & Jordan, 1984). Rapid growth of the pioneer species can form a closed canopy within only a decade after the disturbance (Kanowski et al., 2003). Following the formation of a closed canopy, the availability of understory light decreases dramatically, favoring the establishment of shade-tolerant later-successional tree species and reducing the herbaceous vegetation cover. Gradual turnover of species composition in canopy and subcanopy layers takes place, and, eventually, the death of canopy trees creates gaps and thus increases resource availability for new recruits (Olivier & Larson, 1996). The old-growth stage is highly dynamic and characterized by a complex vertical and horizontal structure. Understory light conditions become more heterogeneous during later stages of succession and create more diverse opportunities for seedling and sapling recruitment. In addition to natural disturbances, regeneration can take place after human-induced disturbances such as after agricultural land is abandoned or following forest clearance (Brown & Lugo, 1990; Finegan, 1996; Chazdon, 2003).

In the tropics, natural regeneration is determined by a complex set of factors and can take multiple different successional pathways (Arroyo-Rodriguez et al., 2015). At local level, regeneration, that is, the recolonisation of species, is directed by abiotic drivers, such as soil and microclimatic conditions, and by biotic interactions such as herbivory, competition and seed dispersal (Arroyo-Rodriguez et al., 2015). At regional level, land use history determines the amount of old-growth forests in the landscape, and therefore their connectivity to regenerating forests (Chazdon, 2008). The local and regional drivers are further affected by the relative severity and frequency of the disturbance events (Chazdon, 2008; Holl & Aide, 2011; Arroyo-Rodriguez et al., 2015). From a plant's perspective, for example, these drivers may act as regenerative barriers by limiting dispersal and growth (Arroyo-Rodriguez et al., 2015).

Rates of tropical forest recovery are highly variable (Chazdon, 2008; Meli et al., 2017). While natural forest regeneration appears to proceed rapidly and species accumulate at high rates in some recovering tropical forests (e.g., Letcher & Chazdon, 2009; Omeja et al., 2016), in others the forest regeneration can become arrested due to the persistent cover of grasses, herbs or shrubs (Chapman & Chapman, 1997; Paul et al., 2004). The arrested succession involves a shift of community structure to "alternative stable state", where a few species (e.g., grasses,

herbs or shrubs) change ecosystem processes and make system resilient to successional changes (Suding et al., 2004). For example, invasive grasses could alter nitrogen cycles and promote fire, which further benefits invasive grasses at the expense of native shrubs and prevent the natural establishment of tree seedlings in forest gaps (Chapman & Chapman, 1997; Suding et al., 2004). Consequently, areas of arrested succession might hold impoverished communities and a lower potential to deliver ecosystem functions (Zahawi & Augspurger, 1999; Arroyo-Rodriguez et al., 2015). For instance, failure to attract seed dispersers could have severe consequences for forest recovery because most moist tropical rainforest tree species are globally dependent on animal-assisted seed dispersal (Howe, 1984; Wunderle, 1997; Shoo et al., 2015).

1.3 HUMAN-ASSISTED RESTORATION OF TROPICAL RAINFORESTS

In areas where natural regeneration of the forest is slow or arrested, active restoration actions may be needed to enhance their recovery and re-establishment of carbon sinks (e.g., Lamb et al., 2005; Rodrigues et al., 2011). With practices such as assisted natural recovery, planting of indigenous tree species or spreading tree seedlings in restored areas, active restoration aims to re-instate ecological processes that accelerate the recovery of the forest structure, ecological functioning and biodiversity levels towards those seen in typical old-growth forests (Lamb et al., 2005; Shono et al., 2007; Chazdon, 2008; Holl & Aide, 2011). When successful, active restoration can speed the recovery in ecosystems where natural recovery could take decades (Dobson et al., 1997). In addition to the factors that determine the natural regeneration of forests, the recovery of restored forests is steered by the diversity and density of the planted trees, further maintenance of the restored forests, and the surrounding land use matrix (Kanowski et al., 2003; Chazdon, 2008).

Recent international initiatives to increase restoration of degraded forests and to halt deforestation worldwide emphasise the need to study and understand restoration processes in the tropics. Most remarkable of these initiatives is the Aichi target with the goal of restoring at least 15% of degraded ecosystems globally by 2020 (CBD, 2010), and the 2014 New York Declaration on Forests, which aims to restore 350 million hectares by 2030 (UN, 2014). On the other hand, a recent global review by Meli et al. (2017) did not find consistently positive effects of active restoration on the recovery of former agricultural lands or logged sites when compared with passive restoration, that is, actions that enable natural regeneration; the recovery was not faster or more complete in actively restored sites than in passively restored sites. This suggests that in many degraded forest areas natural regeneration could offer a feasible way to restore disturbed areas (Holl & Aide, 2011).

1.4 RECOVERY PATTERNS OF BIRDS IN REGENERATING TROPICAL RAINFORESTS

In the tropics, the extinction and endangerment of birds is primarily driven by the ongoing habitat loss caused by extensive crop expansion (BirdLife International, 2013). Approximately 40% of the world's ice-free land cover has been converted to agricultural purposes (Foley et al., 2005) and, for example, croplands comprise up to 10.7% of the land area of tropical countries (Phalan et al., 2008). Of the 1,313 globally threatened bird species, 79% occur within the remaining tropical forests (Sodhi et al., 2011; BirdLife International, 2013). Birds are suitable indicators of habitat change because they are taxonomically well known, easily identified in the field, and their responses to anthropogenic disturbances often mirror those of other species (Raman & Sukumar, 2002; Zakaria et al., 2005; Barlow et al., 2007a). More importantly, birds provide key ecosystem services in the tropical forests and, therefore, they are an essential part of the functioning and the recovery of these forests (Sekercioglu, 2006; Morrison & Lindell, 2012; Karp & Daily, 2014). Birds may facilitate the recovery of degraded forests via pollination, pest control and seed dispersal (Sekercioglu, 2006). Especially, lack of seed arrival is often a major barrier to tropical forest recovery (Neilan et al., 2006; Reid et al., 2012; Caves et al., 2013; Moran & Catterall, 2014). Thus, the presence of seed-dispersing bird species could represent the return of vital functions to recovering forests; while the failure of their return could mean a reduced rate of recovery of avian-dispersed rainforest plants and other biota (Sekercioglu, 2011; Caves et al., 2013; Moran & Catterall, 2014).

Bird communities of recovering tropical rainforests often differ from those in primary forests in terms of species richness, community composition and trophic structure. Typically, changes in the forest dynamics caused by human-induced disturbances alter the community and functional composition of birds, so that forest specialist species become largely replaced by generalist and non-forest species (e.g., Owionji, 2000; Sekercioglu, 2002; Edwards et al., 2009; Burivalova et al., 2014). Secondary tropical forests can contribute substantially as habitats for birds, but their habitat quality differs depending on their vegetation structure (Munro et al., 2011). In particular, structural complexity, closed canopy and a relatively open understory have been identified as key components determining the bird community composition in tropical forests (MacArthur & MacArthur, 1961; Raman et al., 1998; Sekercioglu, 2002; Felton et al., 2008). Structurally complex and diverse vegetation increases the number of niches and consequently forest (specialist) species richness (Roth, 1967; Farwig et al., 2008). Closed canopy and open understory create conditions similar to primary forests and increase the habitat suitability for shade-dependent understory insectivores, which is among the guilds most vulnerable to fragmentation and other human perturbations (Ansell et al., 2011; Stratford & Stouffer, 2013; Powell et al., 2015). Frugivorous species generally decrease in abundance as a result of disturbances, but granivorous

species benefit from them, as they are capable of using food resources in disturbed, more open areas (Gray et al., 2007).

An important factor improving the recovery of bird communities in fragmented tropical forest landscapes is the connectivity of the forests (Reid et al., 2014). For many forest-dependent birds, colonisation from undisturbed primary forests through a high-contrast matrix (e.g., pastures, roads) to regrowth forests is slowed, or possibly prevented, by their limited dispersal abilities (Sekercioglu et al., 2002; Catterall et al., 2012; Deikumah et al., 2014). In tropical Australia, for example, the use of restoration plantings by birds was improved with closer and larger primary forests (Freeman et al., 2015), and in Costa Rica, the compositional similarity of birds to primary forests was greatest in plantations embedded in landscapes with high tree cover (Reid et al., 2014).

1.5 AIMS OF THE THESIS

Preserving old-growth primary forests is essential to conserving tropical biodiversity (Gibson et al., 2011), especially in the Afrotropics where the continued, rapid loss of primary forests continues to be a concern (FAO, 2010). Up to 65% of the Earth's tropical rainforests are degraded or secondary forests (FAO, 2010), and they therefore represent the dominant type of natural vegetation in many human-modified tropical landscapes (Chazdon et al., 2009; Gardner et al., 2009). Consequently, an increasing proportion of tropical biodiversity relies heavily on the capacity of the secondary forests to regenerate and act as refugia (DeWalt et al., 2003; Chazdon, 2014). Although the potential of tropical regrowth forests to provide habitats for rainforest fauna, including birds, is widely recognised and debated (Wright & Muller-Landau, 2006; Gardner et al., 2007; Chazdon, 2014), their role in maintaining viable populations, or in determining the emerging bird communities, remains poorly understood, particularly in the Afrotropics (but see Sekercioglu, 2002; Farwig et al., 2008).

The aim of my thesis was to study the recovery of bird communities in differently regenerating tropical rainforests after human-induced disturbances; to examine whether naturally regenerating or actively restored rainforests could reinstate the community compositions of birds typical of those in primary forests; to examine how bird functional groups recover in differently regenerating rainforests; and to uncover which vegetation structure characteristics are associated with the emerging bird communities in the recovering forests.

The specific study objectives were:

1. To explore the recovery patterns of bird community compositions in naturally recovering and actively restored rainforests (I, II).
2. To examine how different bird functional groups, that is, feeding guilds and habitat categories classified by the forest dependence of birds, are recovering in naturally regenerating and actively restored rainforests (I, II).
3. To identify the vegetation structure and tree diversity characteristics that are most strongly associated with changes in the bird community compositions emerging in naturally regenerating or in actively restored rainforests, and how these characteristics structure the bird community compositions in primary forests (III).
4. To identify the vegetation structure and tree diversity characteristics that are most strongly associated with the abundances of the most vulnerable bird functional groups, that is, understory insectivores, frugivores, and forest specialists (III).

2 MATERIALS AND METHODS

A general outline of the materials and methods is presented here. A more detailed description of the methodology is provided in the original papers I-III.

2.1 STUDY AREA

The study was conducted in Kibale National Park (KNP; 795 km²) in western Uganda (0°13' to 0°41' N and 30°19' to 30°32' E; Fig. 1). Kibale represents a mid-altitude moist tropical rainforest and has old-growth primary forests (60%), as well as naturally regenerating logged forests, grasslands and wetlands (Struhsaker, 1997). The elevation in Kibale ranges from circa 1,000 m a.s.l. in the southern parts to circa 1,600 m a.s.l. in the northern parts. The mean annual rainfall in the region is 1,547 mm (1903–2001) with a bimodal rainfall pattern, the rainy seasons being in March–May and September–November (Chapman et al., 2005). The mean daily minimum and maximum temperatures are 14.9 and 20.2 °C, respectively (1990–2001; Chapman et al., 2005).

Kibale forest has a long history of human impacts, including commercial logging and clearing for agriculture (Chapman & Lambert, 2000). Following the past large-scale anthropogenic disturbances in KNP, the natural regeneration in some areas has been slow or arrested, as the forest gaps or deforested areas have become largely dominated by either herbaceous growth, primarily the shrub *Acanthus pubescens*, or grasses, primarily elephant grass *Pennisetum purpureum*, resulting in limited tree regeneration (Chapman & Chapman, 1997; Chapman et al., 1999; UWA-FACE, 2006). In addition, the lands surrounding KNP are in extensive agricultural use (Fig. 1).

Study I was conducted in the northern parts of KNP in study sites that represent seven naturally regenerating and two primary forest sites (Table 1, Fig. 1, in study I). The naturally regenerating study sites were logged in different times and intensities, and left to regenerate naturally without human assistance. These include 9–19 years old regenerating clear-cuts of former timber plantations, and 42–43 years old selectively logged forests.

Study II was conducted in the active restoration areas in the southern parts of KNP (Table 1, Fig. 1, in II), where the study sites were located within an area of 10,000 ha of the Uganda Wildlife Authority – Forests Absorbing Carbon Dioxide Emissions (UWA-FACE) project area (UWA-FACE, 2006). The restoration areas were deforested and degraded in the past as a result of illegal encroachment that lasted more than 20 years (Chapman & Lambert, 2000; UWA-FACE, 2006). Following the eviction of the encroachers in 1992, the formerly occupied areas became largely dominated by elephant grass (*P. purpureum*) due to recurring fires spread from neighboring subsistence farms or set by poachers (UWA-FACE, 2015).

Elephant grass suppressed naturally regenerating tree seedlings, and halted or slowed the natural succession in these areas (UWA-FACE, 2006). In 1993, Kibale became a National Park and, in 1994, the Ugandan government and the Face the Future Foundation (previously The Face Foundation) started a restoration programme with indigenous tree plantings to re-establish carbon sinks and to enhance the recovery of the deforested areas and their biodiversity (UWA-FACE, 2006). Restoration activities consisted of fire prevention (by establishing 10m fire breaks, and by use of fire monitoring towers) and replanting with indigenous tree seedlings starting in 1995 (400 seedlings/ha). Seedlings were collected or raised from seeds collected from surrounding forest not affected by agricultural encroachment. Seedlings were raised using local forest soil without fertilizers (Omeja et al., 2011). Plantings included indigenous tree species such as *Albizia grandibracteata*, *Bridelia micrantha*, *Cordia africana*, *Cordia mellenii*, *Croton macrostachyus*, *Croton megaloscarpus*, *Erythrina abyssinica*, *Ficus natalensis*, *Mimusops bagshawei*, *Prunus africana*, *Spathodea campanulata*, *Sapium ellipticum*, *Warburgia ugandensis*. These species are fast-growing and resistant to grass root competition and therefore able to outgrow the grasses (UWA-FACE, 2011). Planting sites were created by clearing elephant grass from 2m wide paths, and seedlings were planted every 5m unless an existing naturally regenerating seedling occurred. Following planting, any grasses regrowing along planting paths were weeded two to three times a year to protect the seedlings from fire and to limit competition. After five years the planted areas were left unmanaged, excluding fire protection (Omeja et al., 2011; UWA-FACE, 2011, 2015).

The six study sites in active restoration areas represent a restoration gradient, consisting of 3–16 years old restoration plantings of indigenous trees. In addition, three primary forest study sites near the active restoration areas, and two primary forest study sites near the naturally regenerating forests were used as reference areas (Table 1, Fig. 1, in II). The primary forests in both the northern and the southern parts of KNP have never experienced commercial harvesting or large-scale or mechanised logging (Struhsaker, 1997; Chapman et al., 2005; Kasenene, 2007).

Study III used the field measurements of studies I and II.

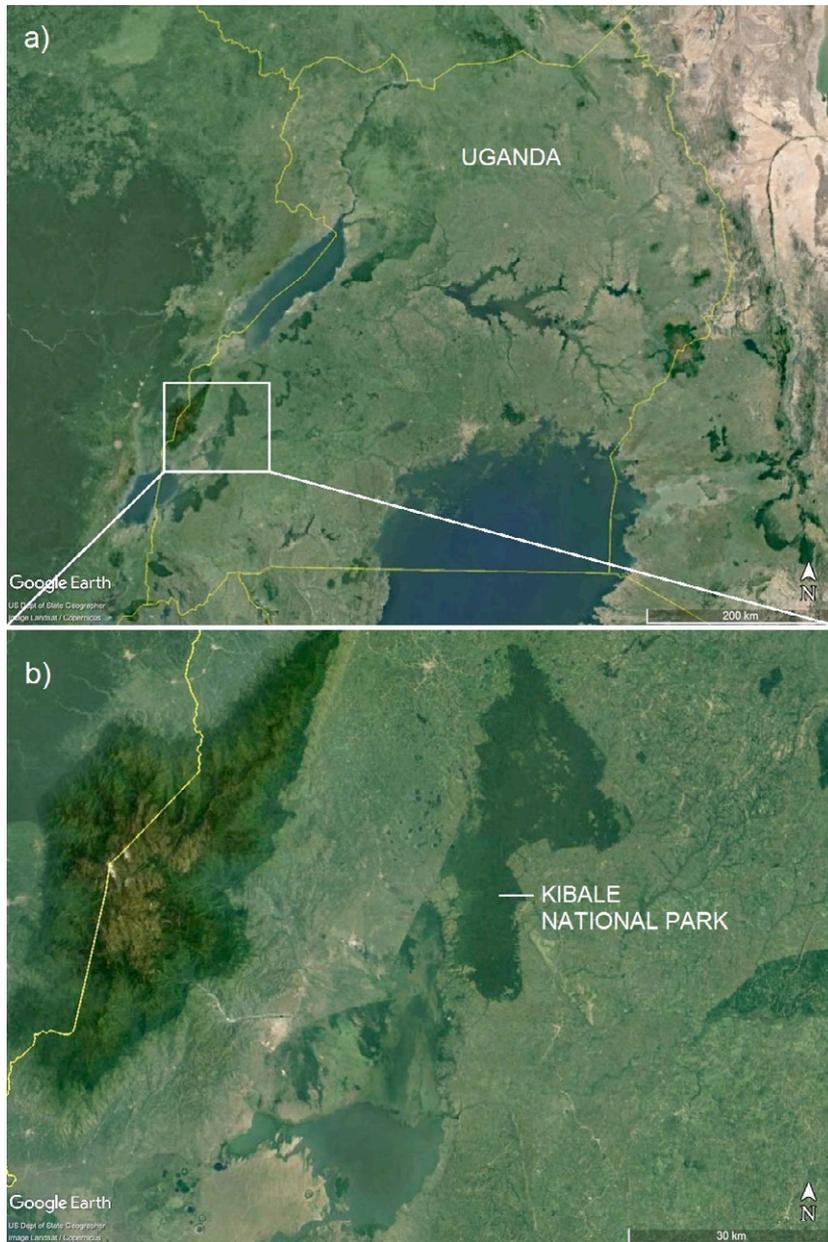


Figure 1. A Landsat map showing a) remaining forest tracts in Uganda (dark green), and b) the extent of agricultural lands (light green) surrounding the forests in Kibale National Park in western Uganda. State borders are marked with yellow line. Map data: Google / US Dept of State Geographer.

2.2 METHODS

2.2.1 Bird sampling

The bird data were collected by point counts (11–31 points per study site) at a total of 340 points whose locations were randomised with a grid system in each study site: 174 points in the naturally regenerating and the nearby primary forests were sampled in September–October 2011 (including a total of 2,688 individuals from 115 species; I), and 166 points in the actively restored and the nearby primary forests were sampled in September–October 2013 (including a total of 2,170 individuals from 119 species; II). Points were surveyed once. Upon arriving at the sampling point, the observer (PL) waited for two minutes to allow birds to recover from any disturbance. All the bird individuals heard or seen were then recorded within a 10-minute interval within a 100-m radius. All point counts were conducted between 07:00 and 11:30 hours during periods of peak bird activity. Counts were made only in the mornings with no rain or heavy wind that could decrease the bird activity or the number of birds detected. The visit order of the study sites (and the points in them) was randomised on a daily basis in each sampling morning.

Bird nomenclature follows Clements et al. (2015). Birds were assigned to three habitat categories according to their forest dependence: forest specialists, forest generalists, and forest visitors (Bennun et al., 1996; I, II, III). Forest specialists occur primarily in the forest interior and are the species most likely to disappear when the forest is modified to any great extent. Forest generalists may occur both in undisturbed and disturbed habitats such as forest edges or modified or fragmented forests, and are also frequently found in secondary forests. They do, however, depend on forests for some of their resources, such as nesting sites. Forest visitors mainly occupy non-forest habitats and are not dependent on forests. Their presence in a forest may be an indication of forest disturbance (Bennun et al., 1996).

In study II, the birds were also assigned to 11 feeding guilds according to their feeding and foraging behaviour (following Dranzoa, 1995; and Waltert et al., 2005). In study III, a broader classification of two feeding guilds was used: understory insectivores and frugivores (hereafter, the most vulnerable bird functional groups, including forest specialists).

2.2.2 Vegetation datasets

In order to assess how the bird community compositions are related to the vegetation structure of the forest, study III used datasets of vegetation structure and tree community composition that were collected at the same points at which the bird data were collected. The dataset of the naturally regenerating and the nearby primary forests was collected in April–October 2011 (including 135 tree taxa; Owiny et al., 2016), and the corresponding dataset from the actively restored and the nearby primary forests was collected in February–April 2013 (including 111 tree

taxa). Seven variables describing the vegetation structure and tree diversity were calculated for each sampling plot: 1) total estimated stem density/ha, 2) total estimated basal area (dbh \geq 5 cm) (m²/ha), 3) canopy closure (cover), 4) gap cover, 5) cover of *A. pubescens*, 6) cover of *P. purpureum*, and 7) tree species diversity (Shannon's diversity index).

2.3 DATA ANALYSIS

Differences in the rarefied total species richness of birds in the naturally regenerating and the nearby primary forest study sites, and in the actively restored and the nearby primary forest study sites, were compared using 95% confidence intervals (I, II), and differences in bird species density (number of species/point), Shannon's diversity index, and Berger-Parker dominance index of birds were tested with one-way ANOVA or the Kruskal-Wallis test in naturally regenerating and the nearby primary forest study sites (I).

In the active restoration sites, a possible directional change in the abundance and in the mean proportion of birds in each feeding guild and habitat category along the restoration gradient was tested using Pearson correlations between these and the age of restoration planting (II). Pearson correlations were also used to test for a possible directional change in the species density, Shannon's diversity index and Berger-Parker dominance index of birds, as well as in the total abundance of birds, along the restoration gradient (II).

Indicator species analysis was used to explore the species characterising three age groups in the naturally regenerating and nearby primary forest study sites: 1) 9-19-year-old clear-cuts, 2) 42-43-year-old selectively logged forests, and 3) primary forests (I).

Permutational multivariate analysis (PERMANOVA) and analysis of similarity (ANOSIM) were used to test for differences in the community compositions of birds among the naturally regenerating and nearby primary forest study sites (PERMANOVA; I), and among the actively restored study sites (ANOSIM; II). Non-metric multidimensional scaling (NMDS) was used to visualise the patterns in bird community compositions (I, II).

To estimate the time needed for bird community recovery in the actively restored study sites, the change in similarity of bird communities of each restoration study sites to the five primary forest study sites was modelled as a response to the number of years since restoration started (II). The fit of two models were compared: 1) linear change, and 2) non-linear change following negative exponent function (an ecologically more realistic scenario; Matthews et al., 2009; Freeman et al., 2015). All multivariate analyses were based on the Bray-Curtis similarity measure (I, II). In the naturally regenerating and the nearby primary forest study sites, the aforementioned analyses (excluding indicator species analysis) were conducted separately for all birds, and for forest specialist species (I).

Canonical correspondence analysis (CCA) was used to quantify the degree to which vegetation structure and tree diversity variables predict the bird community compositions in the naturally regenerating, actively restored and the two primary forests (III). CCA was also used to illustrate the relationship between the bird community composition and the age of the sampling points in the actively restored study sites, and to show how bird species optima (the peak abundance of a species) are located along the age gradient (II).

Linear mixed effect models were fitted to determine how well the vegetation structure and tree diversity predict the abundances of the most vulnerable bird functional groups in the naturally regenerating, actively restored, and the two primary forests (III).

3 RESULTS AND DISCUSSION

3.1 BIRD COMMUNITY RECOVERY IN NATURALLY REGENERATING RAINFORESTS

The results of my dissertation show that the recovery of bird communities after human-induced disturbances might take long in naturally regenerating tropical rainforests (I). In forests recovering from clear-cut and selective logging, the bird community compositions differed distinctively from those in nearby primary forests, even after 19 and 43 years of natural regeneration, respectively. Previously, it has been estimated that bird species richness and diversity increase rapidly during the first decades of natural regeneration in tropical forests, with recovery estimates of 20-40 years (Raman et al., 1998; Dunn, 2004; Bowen et al., 2007). As shown by the results of my dissertation (I), however, the compositional similarity to primary forests recovers more slowly (Bowen et al., 2007; Chazdon et al., 2009), and the slow, gradual recovery of forest specialist species could even take over a century (Raman et al., 1998).

The slow recovery rate of bird communities could result from the slow recovery of tree communities in the naturally regenerating forests of KNP. Forest regeneration after logging in KNP has been slow or arrested, and many of the logging gaps are dominated by *Acanthus pubescens*, which is a shrub commonly found in disturbed sites and forest edges throughout East Africa (Paul et al., 2004; Bonnell et al., 2011). The herbaceous undergrowth attracts elephants to the sites, and by feeding on *A. pubescens* and favouring the disturbed sites, elephants increase seedling mortality by trampling the undergrowth, thus keeping the disturbed sites disturbed (Lawes & Chapman, 2006). Comparable effects of large mammals on vegetation, and consequently on birds, have been described in other tropical regions: for example, in Costa Rica, collared peccary alteration of understory and canopy vegetation structure likely contributes to declines of understory birds through the loss of foraging microhabitats and microclimatic change (Visco et al., 2015). Accompanied by a lack of any aggressive colonising tree species, the recovery time for the naturally regenerating forests of KNP has been estimated to be from 74 to 158 years (Bonnell et al., 2011).

Bird community recovery tracks the vegetation succession so that, as the vegetation matures, species specialised to more open, disturbed habitats disappear, and old-growth specialists colonise from remnant primary forests (Raman et al., 1998; Chazdon, 2003). The tree species composition of tropical forests recovers more slowly than their structural aspects, such as basal area, canopy height, or density of large living trees (DeWalt et al., 2003). As a result, the arrested succession of KNP's naturally regenerating forests and the slow recovery of some characteristics of the

forest (e.g., tree species composition and/or the number of large trees) most likely slow the bird community recovery (DeWalt et al., 2003; Smith et al., 2015).

3.2 ACTIVE RESTORATION OF RAINFORESTS ASSISTS THE RECOVERY OF BIRD COMMUNITIES

The findings of my dissertation demonstrate for the first time in the Afrotropics that bird communities can start recovering rapidly after human-induced disturbances with the help of active restoration of the rainforests (II). The gradual recovery of bird community compositions, along an age gradient that covers the early restoration phase up to 16 years, offers hope that bird community recovery and, therefore, possibly the recovery of other taxa, can be helped by active restoration. Active restoration of rainforests has not always resulted in rapid recovery of bird assemblages. In Australia, the initial avifaunal recovery was rapid during the first decade of restoration but slowed during the second decade (Catterall et al., 2012; Freeman et al., 2015). In Costa Rica, no differences were found between bird communities of actively restored and abandoned naturally regenerating pastures (Reid et al., 2012).

The recovery of birds appeared to be linear during the first phases of active restoration and my results imply that if recovery continues as rapid also in the future, bird communities could reach a predisturbance-state after approximately 20 years of active restoration (II). However, in the long-term, natural succession processes are not necessarily linear between a starting point and an end point, which is typically similar to reference states (Bullock et al., 2011; Meli et al., 2017). In KNP, the recovery of birds could be slow because some aspects of forest structure recover more slowly than others (e.g., the number of large trees; DeWalt et al., 2003), or because of the low connectivity of KNP's forests in the landscape (Fig. 1); this could limit the dispersal of the most specialised forest birds (Sekercioglu et al., 2002). For example, in India, the recovery of bird communities in naturally regenerating secondary forest fragments slowed after approximately 25 years (Raman et al., 1998). Previous estimates of bird community recovery during tropical forest regeneration range from 30 to 150 years (Raman et al., 1998; Dunn, 2004; Catterall et al., 2012; Thinh et al., 2012). Therefore, estimation of a recovery time of 20 years seems to be overly optimistic. It remains to be seen how bird community recovery in the actively restored forests of KNP continues to proceed during the next decades. At present, it seems that active restoration promotes rapid initial bird community recovery.

3.3 STRUCTURAL COMPLEXITY OF VEGETATION AND TREE DIVERSITY STEER BIRD COMMUNITY FORMATION IN REGENERATING RAINFORESTS

The formation of emerging bird communities in naturally regenerating and in actively restored rainforests of KNP was strongly steered by the increasing complexity of vegetation structure towards older forests (III; see also Raman et al., 1998; Aerts et al., 2007). My dissertation identified tree basal area and tree species diversity as the best predictors of bird communities both in naturally regenerating and in actively restored forests. In addition, gap cover in the naturally regenerating and the cover of the elephant grass *Pennisetum purpureum* in the actively restored forests were found to have a strong predictive power of bird community compositions. These findings are in line with previous research that has highlighted the importance and the positive influence of the structural complexity of vegetation for recovering faunal assemblages in tropical rainforests (Sekercioglu, 2002; Tews et al., 2004). In particular, the development of a closed canopy (here, described as a larger tree basal area in the older forests) is a key factor for forest bird species richness, diversity and community composition (MacArthur & MacArthur, 1961), as a closed canopy creates microclimatic conditions suitable for shade-dependent forest interior birds with limited gap-crossing abilities (Lees & Peres, 2009; Stratford & Stouffer, 2013).

In the actively restored forests, the bird community recovery, and presumably the succession of the vegetation, was strongly related to the occurrence of *P. purpureum*, which decreased towards older restoration forests (III). This is a grass that initially necessitated active restoration efforts after it suppressed the natural forest regeneration and caused arrested succession in the study region (Zahawi & Augspurger, 1999; UWA-FACE, 2006). In the worst case, such areas under arrested succession could fail to attract avian seed dispersers, which have a vital part in forest recovery in the tropics (Wunderle, 1997). Fortunately, the active restoration efforts in the study area seem to be sufficient to allow forest regeneration and the recovery of natural bird communities.

While the complexity of the vegetation structure steers the emerging bird communities in the naturally regenerating and actively restored forests of KNP, there were no associations between any of the studied vegetation structure or tree diversity characteristics and the bird communities in the primary forests of KNP (III). This could be related to the variation of bird communities among the five reference primary forests used in this dissertation. The bird communities of the two primary forests in the northern parts of KNP near the naturally regenerating forests differed significantly from each other (I), and the similarity values of bird communities for all five primary forests used in this dissertation ranged from 51% to 70% (II). This variation makes it more difficult to estimate when the communities of disturbed areas have recovered. The high variation among primary forests could result from differences in local ecological conditions or in the species colonisation

history, leading to "alternative states" (Sutherland, 1974; Fukami & Nakajima, 2011; Temperton et al., 2016), that is, there is not only one possible endpoint of succession in primary forests but the different primary forests represent alternative states.

3.4 BIRD FUNCTIONAL GROUPS AS INDICATORS OF TROPICAL RAINFOREST RECOVERY

The forest specialist species density and diversity were lower in naturally recovering clear-cut forests than in primary forest (I). The communities of forest specialists differed between the recovering 9-19-year-old clear-cut forests, the 42-43-year-old selectively logged forests, and the primary forests (I). This indicates that even four decades of natural regeneration has not allowed full recovery of the specialist birds. Although study I of this dissertation did not investigate the responses of different feeding guilds to the natural regeneration of rainforests, the results of the indicator species analysis suggest that no feeding guild turnover is taking place between the differently aged recovering forests and primary forests (I). Instead, the differences seem to be associated with the forest dependence of birds. The species characterising the forests recovering from clear-cuts were either non-forest visitor species or generalists (visitor: Grey-backed Camaroptera *Camaroptera brachyura*; generalists: Little Greenbul *Eurillas virens* and Yellow-rumped Tinkerbird *Pogoniulus bilineatus*). The openness of the forest created by disturbance attracts birds that do not require the characteristics of interior primary forests for surviving. Instead, they can take advantage of the feeding and breeding resources provided in the disturbed areas. In selectively logged and primary forests, the indicators were either forest generalist or forest specialist species (generalist: Yellow-whiskered Greenbul *Eurillas latirostris*; specialists: Black-faced Rufous Warbler *Bathmocercus rufus*, Buff-throated Apalis *Apalis rufogularis* and Yellow-throated Tinkerbird *Pogoniulus subsulphureus*) (I). The majority of the bird species composition in recovering forests is often naturally formed by generalist species and their predominance in some feeding guilds could influence the association between the guilds and the habitat. However, the presence of forest specialists in recovering forests could indicate that these forests have gained some of the biodiversity values that were lost during logging.

In the actively restored forests, the abundances of the most vulnerable functional groups, that is, forest specialists, frugivores and understory insectivores were associated with the age and the structural complexity of the restored forests (II, III). These groups responded positively to the decreasing landscape openness associated with the reducing cover of the elephant grass *P. purpureum*, and to the increasing tree basal area and canopy closure towards increasingly older restoration forests (III). This is logical as the structural complexity of vegetation increases with the site age (Kanowski et al., 2003; Munro et al., 2011). Particularly, it was promising that the abundances of frugivores increased towards older restoration

forests. Restoration processes could be accelerated by frugivores (Aerts et al., 2007; MacGregor-Fors et al., 2010) because they play such an important role in seed dispersal and, therefore, in the actual recovery of moist tropical forests (Shoo et al., 2015). In naturally regenerating forests, the foliage-gleaning insectivores that were more abundant in the younger restoration sites were non-forest visitor or generalist species, such as the Black-necked Weaver (*Ploceus nigricollis*) or White-chinned Prinia (*Schistolais leucopogon*) (II). In some cases, foliage-gleaning insectivores could help regulate herbivore populations of planted trees (Reid et al., 2012).

In primary forests, understory insectivores decreased with increasing tree species diversity, and forest specialists decreased with increasing canopy closure but increased with increasing gap cover and the cover of the shrub *A. pubescens* that is usually associated with gap openings, especially in KNP (III; Paul et al., 2004). These mixed responses could be related to the small gap dynamics in mature Afrotropical rainforests. Afrotropical rainforests have experienced fewer and less intense disturbances than forests in other tropical regions because large-scale disturbances, such as hurricanes or wildfires are rare (Chapman et al., 1999; Cole et al., 2014). This may have prevented the evolution of adaptations that enable rainforests in other tropical regions, particularly in Central America, to recover faster and to respond more dynamically to future disturbances (Cole et al., 2014). Thus, the species in Afrotropical rainforests may be better adapted to small-scale changes in the forest dynamics. Certainly, only a small proportion of KNP's tree community regenerates best in large gaps (larger than those created by the fall of a single tree; Chapman et al., 1999). Contrary to logging gaps, which forest birds are typically unwilling to cross even if they are narrow (Lees & Peres, 2009), the naturally occurring treefall gaps across primary forests provide microhabitats that forest birds use for foraging (Schemske & Brokaw, 1981; Levey, 1989; Edwards et al., 2014). The species in KNP could possibly be less resilient to the increasing amount of human perturbations because of the lack of tree species adapted to large-scale disturbances.

The findings of my dissertation are in line with other studies in emphasising that the classification of birds into different functional groups is essential to understand the processes that take place during tropical forest regeneration (Ghazoul & Hellier, 2000; Gray et al., 2007; Montoya et al., 2012). Feeding guilds may be used to represent the different ecosystem services returning to recovering forests, while bird groups classified based on their forest dependence could show how well the forests are recovering from disturbance (Thiollay, 1997; Gray et al., 2007). The results of my dissertation partially supported the idea that insectivores are more sensitive to structural changes in vegetation, whereas frugivores are more influenced by vegetation community composition (Holmes et al., 1979; Hill et al., 2001; Jankowski et al., 2013; Visco et al., 2015); in KNP, both understory insectivores and frugivores were positively influenced by the increasing complexity of vegetation (III).

3.5 VARIATION IN BIRD SPECIES RICHNESS IN DIFFERENTLY REGENERATING FORESTS HIGHLIGHTS THE NEED FOR MULTIVARIATE APPROACH IN MONITORING THE RECOVERY OF TROPICAL RAINFORESTS

A high variation in bird species richness resulted in a lack of significant differences in this variable among the naturally regenerating, actively restored or primary forests of KNP (I, II). Previously, high bird species richness in regenerating compared to primary tropical forests has been documented in some studies (Blake & Loiselle, 2001), possibly supporting the hypothesis that intermediate levels of disturbance leads to high species richness (Connell, 1978). However, more typically, the species richness of birds has been higher in primary forests than in naturally regenerating forests (reviewed in Barlow et al., 2007b; Edwards et al., 2009; Smith et al., 2015) or plantations (Peh et al., 2006; Barlow et al., 2007b). In some studies, there were no differences in the overall species richness of birds between treatments (Waltert et al., 2005; Reid et al., 2012), although the species richness of several feeding guilds were adversely affected by forest modification; for example, the species richness of insectivores decreased as a result of disturbance (Waltert et al., 2005).

Furthermore, no significant differences or directional changes were found in the species density, diversity or dominance of birds, either among the naturally regenerating and the nearby primary forests, or along the restoration gradient in actively restored sites of KNP (I, II). One possible explanation for the lack of response patterns in these metrics between differently treated and aged forest areas could be bird movement between different habitat types (Neuschulz et al., 2013). It could be that if the recolonisation sources are close (such as in KNP), the old-growth forest species could be present also in younger forest areas, albeit with smaller abundances. In KNP, forest specialists have been found to breed in the naturally regenerating areas in addition to primary forests (Dranzoa, 2000).

Species abundance and community structure metrics reflect different aspects of community recovery, and the degree of recovery varies strongly depending on the land use history and the metric type used (Cole et al., 2014; Meli et al., 2017). Especially, the compositional similarity to reference forests is a slow metric to recover (Dunn, 2004). Although many previous studies have stated the insufficiency of such metrics in predicting the suitability of secondary forests for tropical forest birds (Gardner et al., 2007; Dent & Wright, 2009), species richness in particular is likely to remain a key variable for addressing the changes in bird communities during their recovery after disturbances. However, the variation in species richness and in other univariate metrics presented in this dissertation (I, II) highlights the need to use multiple metrics in evaluating rainforest recovery.

4 CONCLUSIONS

The findings of my dissertation demonstrate that the timescale for rainforest bird community recovery after human-induced disturbances could be long. Even four decades of natural regeneration in selectively logged forests did not allow for full recovery of the most specialised forest birds, and the bird communities of the younger forests recovering from clear-cuts were still far from similar to those of the primary forests. It seems that the local ecological conditions, especially the arrested succession in KNP, slow the bird community recovery.

The results of my dissertation indicate that bird community recovery can be aided by the active restoration of rainforests. The restoration actions in KNP seemed to allow for natural forest regeneration as the cover of elephant grass *P. purpureum* decreased towards older restoration forests, and this resulted in rapid initial bird community recovery during the first 16 years of restoration. It was promising that the abundances of the most vulnerable functional groups, that is, forest specialists, frugivores and understory insectivores, increased towards older and structurally more complex restoration forests. In particular, the return of frugivores is of high significance because as seed dispersers, they have a vital role in forest recovery in the tropics.

In addition, the bird community compositions in naturally regenerating and in actively restored forests were strongly related to the structural complexity of vegetation. Thus, the assistance of the recovery of key vegetation structure characteristics, that is, the tree basal area and canopy closure, likely favours avian recovery.

The large variation found in the bird communities of primary forests makes it more difficult to estimate when the communities of disturbed areas have recovered. In addition, there were no associations between any of the studied vegetation structure characteristics and the bird communities of primary forests. The functional groups showed variable responses to the vegetation structure characteristics; for example, forest specialists were more abundant in gaps. This could be related to the small gap dynamics of the primary forests, where the tree community generates best in small gaps, and naturally occurring treefall gaps provide suitable feeding microhabitats for forest birds.

The results of this thesis show that clear-cut and selective logging of rainforests can have remarkable and far-reaching consequences for communities of birds, and this highlights the need to preserve primary forests as refugia for birds. However, the findings also show, for the first time in the Afrotropics, that active restoration of disturbed rainforests promotes rapid initial bird community recovery. This is of high significance, since there is a strong impetus to restore degraded habitats and to halt the biodiversity loss globally. Due to the short history of restoration actions, it would be beneficial to concentrate future research on how the recovery of restored areas proceeds, by using multiple metrics.

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PIRITA LATJA

Anthropogenic pressure on tropical rainforests presents a major threat to the Earth's biodiversity. This thesis improves our understanding about the recovery of communities and functional groups of birds in naturally regenerating and actively restored Afrotropical rainforests. This understanding is more timely than ever because a number of initiatives aim at increasing restoration of degraded forests, and biodiversity and its conservation will increasingly rely on re-growth forests as refugia.



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