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REGENERATION STATUS OF TREE SPECIES WITH DIFFERENT FUNCTIONAL TRAITS IN TROPICAL FOREST REMNANTS

A CASE STUDY OF CRATER FORESTS IN WESTERN UGANDA

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1. <u>Abstract</u>

The current acceleration in tropical forest conversion makes the understanding of the impact of human-induced disturbances on the forest community a core challenge in conservation. Knowledge of how fragmentation affects tree regeneration at community level has received little attention in tropical forest studies up to now, possibly biasing our perception of the current situation in forest fragments. This study was conducted to evaluate the current regeneration status and population structure of the remaining crater forests in the Albertine Rift of western Uganda, as regeneration is suspected to be stagnating in recent years. Based on fieldwork, using fixed-width strip transects in 21 crater forests, we (1) evaluated the current population structure and regeneration potential of four indigenous tree species (*Dombeya torrida*, *Funtumia africana*, *Albizia grandibracteata*, *Ficus sycomorus*) by quantifying the density of different ontogenetic classes, (2) studied the effect of the environmental characteristics of the crater forests and different functional species traits on the species response to fragmentation and the apparent inability of trees to prosper, and (3) analysed the forest monitoring data of the forest around one crater lake (Kyaninga) in order to provide recommendations on the management and conservation of the forests in the crater lake region. First, the overall population structure of the crater forests based on the density of seedlings, saplings, poles and adult trees, showed a greater proportion of adults, followed by poles, saplings and seedlings. Consequently, the current overall regeneration pattern was found to be not optimal, with the population structure being highly dependent on the species identity. In some crater forests, species (especially *F. sycomorus* and *D. torrida*) were represented only by adult trees, which may be due to a poor seed set, seed germination and/or recruitment of seedlings, but was found to be most likely caused by the lack of vertebrate seed dispersers for the animal-dispersed *F. sycomorus*. Conversely, species with a high dispersal capacity seem to overcome a lack of mature trees if a healthy seed source is in close enough proximity. However, this was only the case for the wind-dispersed species (*F. africana*), as we demonstrated that a disruption of the dynamics between trees and animals in the dispersal process of seeds can in fact make a tree more sensitive to the effects of fragmentation (*F. sycomorus*). The strong pioneers (especially *A. grandibracteata*), which were positively correlated with disturbance, were found to still have a fair regeneration cycle and/or relatively high densities in the area. However, also for these species the regeneration cycle was determined to be not optimal. The study revealed that the population structure and the differences between species can be explained by an interaction between species traits and the prevailing environmental factors. We found evidence to suggest that the only way of retaining the diversity in areas outside national parks, is to control human disturbance in the region.

Keywords Tree regeneration ▪ Fragmentation ▪ Anthropogenic disturbance ▪ Forest conservation ▪ Crater lake region ▪ Western Uganda

2. <u>Introduction</u>

A main topic in forest conservation is understanding the long-term persistence of tree populations and how this is affected by anthropogenic environmental pressures (Harrison & Bruna, 1998; Lindenmayer & Fischer, 2006). Habitat fragmentation is a major concern in diverse tropical forests, as it is a driver of extinctions (Haddad et al., 2015). In many cases however, biodiversity loss occurs with a substantial delay after fragmentation has taken place (Diamond, 1972; Halley, Monokrousos, Mazaris, Newmark, & Vokou, 2016). Tropical tree species often depend on a variety of dispersal agents to complete demographic stages such as seed dispersal and seed establishment, which can be disrupted by fragmentation and constrain the population persistence and recolonization ability (Bruna, 2002; Herrera & Garcìa, 2010). Even though current forest patches might appear to be healthy based on the adult tree canopy, it is possible that present species only persist as relict populations without effective recruitment (Vellend et al., 2006). As trees generally have long generation times, extinctions may occur decades after fragmentation has happened (Halley, Monokrousos, Mazaris, Newmark, & Vokou, 2016; Vellend et al., 2006; Kuussaari et al., 2009). This biodiversity loss thus represents a future ecological cost of current disturbance, even in the absence of further perturbations, which is referred to as an extinction debt (Kuussaari et al., 2009; Tilman, May, Lehman, & Nowak, 1994). In order to make an accurate estimate of the capacity of natural areas to maintain diversity, it is essential to identify extinction debts in nature and their potential cause (Vellend et al., 2006). These areas generally still have a conservation potential, and the implementation of effective conservation measures could prevent species from disappearing (Hanski & Ovaskainen, 2002; Kuussaari et al., 2009).

Southwest Uganda, a key part of the Albertine Rift, has a long history of anthropogenic landscape alterations (Plumptre et al., 2007). The majority of forest loss has occurred outside protected areas, mostly related to the mounting human population pressure leading to a growing demand for forest resources and agricultural development (Southworth et al., 2010; Kayanja & Byarugaba, 2011; Santo-Silva, Almeida, Tabarelli, & Peres, 2016). Based on the transformation of bushland and woodland areas from 1990 to 1995, the deforestation rate in Uganda was estimated at 55,000 hectares (0.9%) per year (Obua, Agea, & Ogwal, 2010; Gautam, Manhas, & Tripathi, 2016). Other estimates put the picture at an annual rate of 1.10–3.15%, a particularly high rate of forest loss (Kayanja & Byarugaba, 2011; Obua, Agea, & Ogwal, 2010). Besides national parks such as Kibale National Park and Bwindi Impenetrable National Park, southwest Uganda is home to the crater lake region, including 60 (forest fringed) crater lakes. Recently there has been a growing concern that the number of juveniles established in the remaining crater forests is reduced to below the replacement level necessary to sustain their populations. The causes for this are manifold and could include abiotic as well as biotic factors, such as perturbation intensity, species interactions and species life-history traits (Kuussaari et al., 2009; Cordeiro, Ndangalasi, McEntee, & Howe, 2009).

Fragmentation presents several challenges for tree species in the region, each challenge likely affecting species in a different way and to a different extent. It is therefore essential to consider different tree functional traits in the context of the crater lake region (Ribbens, Silander, & Pacala, 1994). A first key

species characteristic when assessing the impact of fragmentation on the level of regeneration and population persistence of a tree species, is the dispersal syndrome (Cote et al., 2016). Dispersal between patches, and the following recruitment or (re)colonization, may become reduced by fragmentation due to increasing inter-patch distances and isolation (Fahrig, 2007). How different dispersal syndromes influence tree population persistence is dependent on both landscape and dispersal traits, and potentially their interaction (Johst, Brandl, & Eber, 2002). Seed dispersal in the tropics, and especially wind-driven dispersal mechanisms, is a topic that is still not fully understood (Burslem, Pinard, & Hartley, 2005; Bullock, Mooney, & Medina, 1995). The mean and maximum dispersal distance of many plants in the tropics is still unknown, mainly due to difficulties to track some of these mechanisms (Thomson, Moles, Auld, & Kingsford, 2011). However, research on seed shadows in tropical African forests agrees on a general ranking of dispersal syndromes based on the mean distance over which seeds can be dispersed (Thomson, Moles, Auld, & Kingsford, 2011; Clark, Poulsen, Bolker, Connor, & Parker, 2005). Species using biotic vectors are seen with more diffuse spatial distributions and appear to be better dispersers than species using abiotic dispersal vectors (Thomson, Moles, Auld, & Kingsford, 2011; Seidler & Plotkin, 2006). Consequently, animal-dispersed species gain the greatest dispersal distances, with primate-dispersed species reaching further places than bird-dispersed species (Clark, Poulsen, Bolker, Connor, & Parker, 2005). Wind dispersal comes second in row, likely because of the forest canopy altering wind dynamics (Seidler & Plotkin, 2006; Damschen et al., 2014), followed by species depending on ballistic dispersal methods (Clark, Poulsen, Bolker, Connor, & Parker, 2005). Finally, the lowest mean dispersal distance is reached by plants with unassisted drop dispersal (Thomson, Moles, Auld, & Kingsford, 2011).

The emergence of discontinuities in the forest is not the only challenge facing trees in the crater lake region. A second important tree species specific trait is the degree to which the tree products are (economically) valuable to the community. Tree species provide a variety of economic services to local communities, but activities such as selective logging and collecting medicinal products induce a pressure on the harvested tree species (Nowak, 2017). The extent to which this kind of harvesting occurs, is expected to play an essential role in the suspected stagnation of a tree species' regeneration. Because of the high dependency of local people on certain forests products, it is important to consider the value of woody species to the local community.

Finally, the successional niche a species occupies, or the capacity of a species to cope with disturbance, is a third important tree feature to consider in the context of a fragmented area (Dalling, 2008). Forest fragmentation is associated with the creation of "habitat edges", which is generally a challenging physical environment for trees due to the so-called "edge effects" (Benítez-Malvido & Arroyo-Rodríguez, 2008). A profound edge effect is typical for fragmented areas, reducing the number of species in the late-successional stages, and altering the environment in favour of pioneer species (da Silva et al., 2012). Pioneer tree species are known to be only moderately affected or even favoured by fragmentation, due to the ecological role they play (da Silva et al., 2012). These species are the first successional stage of a forest and their presence in disturbed environments and the forest edge area is a reflection of their life-

history traits (da Silva et al., 2012). Trees with typical pioneer characteristics such as an aggregate distribution, adaptation to high light intensity, and in some cases such a rapid growth that they are capable of reaching the canopy within a decade, have an advantage in habitats arisen by disturbance (Dalling, 2008; da Silva et al., 2012). Regeneration of pioneer tree species in tropical forests is typically ongoing along the forest edge or in canopy gaps created by treefalls, as a result of a natural event or caused by human activities (Dalling, 2008; da Silva et al., 2012).

Information about woody species regeneration and the structure of the crater forests is very scarce or derived from protected areas such as national parks (Chapman & Chapman, 2003). As no floristic study has yet been conducted in all of the remaining crater forests, little is known about this ecosystem. A proper understanding of the regeneration dynamics and the factors influencing this process is needed in order to mitigate further reduction and degradation of the crater forests (Parrotta, Knowles, & Wunderle, 1997). Hence, the main objective of this study was to fill the existing knowledge gap in the current status of the forests in the crater lake region. Four indigenous tree species were selected, representing a range of functional and life-history traits, such as dispersal ability, successional niche and local (economic) value or preference. The first objective of this paper was to evaluate the current population structure and regeneration potential of the four tree species in forest remnants surrounding the crater lakes, which is suspected to be stagnating in recent years. If this is the case, responses can be found in the forest structure by quantifying the density of different ontogenetic classes, which is an indicator of regeneration. More specifically, the population density of seedlings, saplings and adults determines the regeneration status of a forest and the population structure of the tree species (Paul, Khan, & Das, 2019). This knowledge helps in the assessment of forest regeneration and the evaluation of the conservation status, while also addressing the deficiency of field data on present species. The second study objective was to determine if the effects of forest fragmentation are different for tree species with different functional traits and economic value. This study focused on four tree species which are all indigenous, representative for the area, occupy a different successional niche, and follow different dispersal strategies. The third study objective was to use the data of a 2.5-year forest monitoring around Lake Kyaninga in an exploratory analysis with extrapolation to the other researched forest fragments. Based on this and the vegetation and population assessment in the forest remnants, some recommendations on the management and conservation of the forest were made. The overall objective was to evaluate the current status of forest regeneration by quantifying the size-class distribution, in association with trees functional traits and the environmental characteristics. Although there is an absence of reference data in a continuous forest and long-term data on the vegetation and history of the craters, the results should give an idea about the key patterns of forest regeneration within this region. The study thereby provides a basis for further research in this part of tropical Africa.

We thereby tested the following hypotheses:

1) Observed tree densities, population structure and current regeneration are hypothesized to differ between species.

2) Environmental (extrinsic) characteristics of the fragmented crater lake region are hypothesized to contribute to the variation between species and their life stages.

3) Species (intrinsic) traits are hypothesised to contribute to the differences in species responses to fragmentation.

    a. The seedling recruitment of species with the capacity to disperse over longer distances is hypothesized to be less associated with the presence of local mother trees, since seeds are expected to be able to arrive from adjacent forest remnants or national parks using either biotic or abiotic dispersal vectors (Parrotta, Knowles, & Wunderle, 1997). We therefore predict that even if none/few mature (fruiting) individuals are found in a forest fragment, seedlings of species with long distance dispersal ability can be present, promoting the regeneration (Cunningham, Campbell, & Belcher, 2005). We therefore expect to find a dependency between seedling density and distance to the nearest seed sources for species with a high dispersal ability. In contrast, we expect species with low dispersal abilities to show no dependence on distance to the nearest seed source, as these species are expected to depend more on the local adult tree density instead.

    b. Species that are economically interesting or valuable to local communities, are hypothesized to be negatively affected by the density of households around the forest fragment. A negative impact is expected especially for seedlings, young saplings and small trees (Popradit et al., 2015). The strength of this effect, however, is expected to be dependent on the species' ability to cope with disturbance, or in other words, the successional niche it occupies.

    c. We hypothesize that pioneer species are less affected or even positively affected by the fragmentation processes than shade-tolerant, late-successional species (Goodale et al., 2012).

4) It is hypothesized there is a direct causal relationship between the nature and prevalence of the ongoing human activities in the crater forests and the observed demographic distributions of the tree species.

3. Methods

3.1 Study area

The study was carried out in the crater lake region, located in the Western region of Uganda (0°23' - 0°42'N and 30°13' - 30°19'E) and part of the East African Rift System (Fig. 1). The crater lakes were formed by rift volcanoes (Fig. 2), with the rift trending in the NE-SW direction (Delcamp et al., 2016). The region is located at an altitude of 925 m to 1520 m and has two distinct wet and dry seasons per year, with a mean annual rainfall of 1749 mm and peaking from March to May and from September to November (Chapman & Chapman, 1999; Melack, 1976). The mean minimum and maximum daily temperatures are respectively 14.87°C and 20.18°C (Chapman & Chapman, 1999).
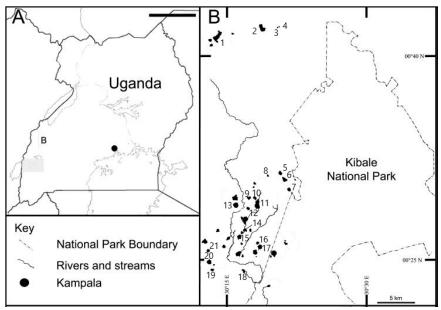
Figure 1 - Map of the studied crater lake region in western Uganda (0°23' - 0°42'N and 30°13' - 30°19'E) where the counts of tree species and measurements of environmental variables were performed, showing the location of (A) the study region in the Edward-George branch of the Rift Valley, (B) Fort Portal (lakes 1-4) and Kasenda district (lakes 5-21). Names of numbered lakes: see Appendix Table S1. Modified from Rumes, 2010.

Figure 2 – Satellite overview of the crater lakes in the Kasenda district. Retrieved from Google earth, 2019.

Figure 3 – Overview of the total area of Lake Kyaninga and its surrounding forest (0°42'5.76"N - 30°17'50.35"E) (left, retrieved from Google earth, 2019) and a part of its crater forest visualized by a drone (right).

The crater lake region, together with the now protected 776 km^2 Kibale National Park, was once part of the historically heavily-forested Tooro District (Chapman, Struhsaker, & Lambert, 2005). Today the area is dominated by smallholder subsistence farming with the remaining forest patches being restricted to the internal slopes of the crater lakes and limited adjacent areas (Chapman & Chapman, 2003). Of the 60 craters that the area is home to, 21 were included in the study since the other craters were subjected to complete logging or agricultural clearance. The included crater forests differed geographically (e.g. distance from the national park, distance to the closest neighbouring crater forest and forest size), in degree of disturbance and presence of possible seed dispersers.

This research was performed in collaboration with Kyaninga Forest Foundation NGO (KFF), a partner of BOS+: a Belgian non-profit organisation funded by the Belgian Cooperation in Forest Conservation and Forest Management. The research is part of a 5-year programme (since October 2017) in western Uganda that focuses on the conservation, restoration and sustainable management and use of forest areas. The head office of KFF is located next to Lake Kyaninga and this forest has been consistently well monitored for disturbances and other events (Fig. 3). We therefore used the monitoring data available (from 11/10/2017 to 6/03/2020) for the crater forest of Kyaninga in the exploratory disturbance analysis.

3.2 Tree species

We focused on four indigenous tree species (*Albizia grandibracteata, Ficus sycomorus, Dombeya torrida, Funtumia africana*), which are representative for the study site (Fig. 4). These species were selected based on differences in functional traits such as dispersal and colonization abilities as well as preferred growth zone, and differences in (economic) value to the local people.

Albizia grandibracteata (Taub.) (Fabaceae) is a typical pioneer species and is regularly found in disturbed areas, secondary forest, forest margins and gaps (Schmitt, 2006). The adult trees bear dense bunches of flat pods (7-15 cm long, 1.5-3 cm wide) that split open (ballistic dispersal), exposing 5–8 flattened seeds (0.88-1.1 cm long, 0.65-0.8 cm wide). The seeds are potentially secondarily carried away for a short distance by the wind or more rarely, eaten as a whole by specialized birds (Schmitt, 2006; Meunier, Lemmens, & Morin, 2010). The tree is widely used by people for many purposes, but especially as firewood and timber because of its light weight which makes it easy to carry or transport. The family to which *A. grandibracteata* belongs is the Fabaceae, of which 12 genera and 13 species are found in protected Albertine Rift forests of western Uganda (Eilu, Hafashimana, & Kasenene, 2004a).

Funtumia africana (Benth.) (Apocynaceae) is an understory to sub-canopy tree species and a non-pioneer light demander with a relatively high shade tolerance (Kiama & Kiyiapi, 2001). Adult trees bear paired follicles (8.4-32 cm long), containing small seeds with a tuft of long, silky hairs (3.2-9 cm long) to aid dispersal by wind (Muhanguzi, Obua, Oreym-Origa, & Vetaas, 2005; Beentje, 2002). Seeds germinate in shade but need more light to become established such as in forest gaps (Hall & Swaine, 1981). This tree is targeted by people for harvest and heavily exploited for its good soft timber for indoor use such as furniture (Hall & Swaine, 1981), and preferred to be cut down because of its remarkably straight bole. Experiences with farmers planting the tree are that the species does not grow well in exposed, open areas such as farms. Because of this, the tree is even felled in forest reserves due to its much sought-after wood. *F. africana* is part of the family of the Apocynaceae, of which 5 genera and 8 species can be found in intact forests of western Uganda (Eilu, Hafashimana, & Kasenene, 2004a).

Dombeya torrida ((J.F.Gmel.) Bamps) (Malvaceae) is a moderate pioneer species and common understory tree in highland woodlands of East Africa, but also on farmland and in secondary forest (Brink, 2008). Adult trees bear globose capsules (max. 1 cm long) which are densely hairy, with 5 compartments each containing 10 small dark brown seeds (0.2-0.3 cm). The seeds are dispersed by being dropped on the ground (drop dispersal), but exceptionally they might also become secondarily dispersed by dove species (the African olive pigeon (*Columba arquatrix*) and the lemon dove (*Aplopelia larvata*)) (Dowsett-Lemaire, 1988). Although the wood is strong and tough, it is not durable and mainly used for construction work (Brink, 2008). In contrary to *F. africana*, the trunk is twisted and seldom straight, which further limits the usefulness of the bole (Beentje, 2002). *D. torrida* belongs to the family of the Malvaceae, of which 5 genera and 7 species grow in intact forests of western Uganda (Eilu, Hafashimana, & Kasenene, 2004a).

Ficus sycomorus (L.) (Moraceae) is a keystone fig species, a canopy tree and secondary forest species with no real characteristics of a pioneer (Medley, 1995). Fig trees have a reproductive mutualism with fig wasps for their pollination (Wang, Yang, Zhao, & Yang, 2005). Adult trees produce round berries (2.8-5 cm in diameter) with a conspicuous opening that may burst at one end (Kassa & Mekasha, 2014). This tree is typically animal-dispersed and the fruit is eaten by large-bodied birds as well as by monkeys (Shanahan, So, Compton, & Corlett, 2001; Berg & Wiebes, 1992). *F. sycomorus* could be useful for the production of charcoal, but it generally takes a long time to dry because of the latex it contains. This tree generally continues to persist in forests as it is not a particular target of the locals for cutting, only in severely disturbed forests its wood is harvested. The family to which *F. sycomorus* belongs is the family of the Moraceae, of which 5 genera and 8 species are present in intact Albertine Rift forests of western Uganda (Eilu, Hafashimana, & Kasenene, 2004a).

Figure 4 – The studied tree species. From left to right: *Dombeya torrida*, *Ficus sycomorus*, *Funtumia africana*, *Albizia grandibracteata.*

3.3 *Determining the variables*

3.3.1 *Dependent variables: seedling, sapling, pole and adult density*

The regeneration of the four tree species was assessed by determining the density of four ontogenetic stages (seedlings, saplings, poles, adults) in each crater forest. In addition to evaluating regeneration, this allowed us to determine the current recruitment, estimated as the number of seedling recruits per unit area (Kiama & Kiyiapi, 2001). The four life stages were distinguished by height and/or the DBH (diameter at breast height). For the purpose of this study, seedlings were defined to be shorter than 0.5 m and having a DBH < 2 cm. Saplings were defined to be larger than 0.5 m and with a DBH < 5 cm. A pole is a young, non-fruiting tree with a DBH ranging from 5 to 15 cm, while an adult tree is above this range (Medley, 1995; Buckland, Borchers, Johnston, Henrys, & Marques, 2007). This density data was gathered through fixed-width strip transect sampling, a form of narrow plot sampling with a variable length but fixed width, for which it is assumed that all targeted plants within the strip are detected (Fig. 5) (Buckland, Borchers, Johnston, Henrys, & Marques, 2007). Each strip transect was set at a width of 5 m, and the length was measured from a distance of 1 m from the waterside because of fluctuating water levels of

the lake. The transect was measured going straight up the ridge of the crater lake until the forest edge, or until a transect length of 100 m was reached (Fig. 5). All transects were placed approximately 30 meters apart and received a coordinate. Within each strip transect, all individuals of the four species were surveyed and categorized into the four ontogenetic or size classes described above. Individuals outside the borders of the strip were not counted, but their presence was noted down. The data gathering was performed during the months July, August and September 2019.
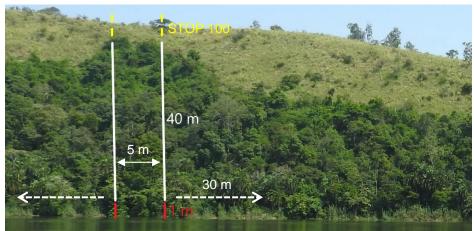
Figure 5 – Design of the fieldwork. Example of a transect with a total length of 40 m, because the chosen maximum transect length of 100 m reaches further than the forest edge (lengths not to scale).

The density of each size class for each species in a crater forest was estimated by dividing the sum of the count data by the transect width (5 m), the total length of all transects, and the number of transects walked within the crater forest (i.e. (total abundance/number of transects)/(0.005*total length of all transects) km^2). Dividing by the total length (and width) and total number of transects was necessary since the number and length of transects per study area varied, depending on the size of the forest and the steepness of the crater slope.

3.3.2   *Explanatory variables*

Two major groups of explanatory variables were measured: environmental (extrinsic) factors and species (intrinsic) traits. The first group included ecological factors (presence of potential seed dispersers), the geographical configuration (forest fragment area, distance from the national park, distance from the nearest neighbouring crater forest) and a proxy of human disturbance. The second group included species dispersal capacity, species successional niche and species preference or economic value to the local community.

3.3.2.1 *Environmental (extrinsic) variables*

Ecological factors

Presence of potential seed dispersers was recorded while walking the transects in the crater forests (which was done over multiple days) and with the help of information provided by local farmers. The most important seed dispersers that are known to be present in the crater lake area are large fruit-eating

birds (great blue turaco (*Corythaeola cristata*), black-and-white-casqued hornbill (*Bycanistes subcylindricus*)) and monkeys (red-tailed monkeys (*Cercopithecus ascanius*), Ugandan red colobus (*Piliocolobus tephrosceles*), black-and-white colobus (*Colobus guereza*), vervet monkey (*Chlorocebus pygerythrus*)). Since feeding activity records have shown that black-and-white colobus monkeys mainly have a diet of leaves and produce faeces which do not contain any whole or viable seeds, they were not taken into the analyses as known seed dispersers (Kisingo & Eustace, 2015; Poulsen, Clark, & Smith, 2001).

Geographical configuration

Satellite imagery from Google Earth was used to quantify variables of the geographical configuration, using the geographic information system QGIS version 3.10 (QGIS Development Team, 2020). Forest fragment area was defined as the surface of remaining forest (tree cover) surrounding the crater lake, measured in km^2. The distance to the nearest monitored crater forest was defined as the minimum Euclidean distance from the center of the focal crater lake to the center of the most nearby one, measured in km. The distance from the national park was defined as the minimum Euclidean distance (km) from the center of the focal crater to the edge of the nearest national park. For all sites the nearest national park was Kibale National Park, except for lake Saaka which is located closer to Semuliki National Park. The forest area and Euclidean distances (measures for fragment connectivity) were both hand-digitized (Fig. 6) (Kramer, van Schaik, & Johnson, 1997; Logsdon, Kapos, & Adams, 2000).

Proxy for disturbance by human activities

As a proxy for anthropogenic pressure on the crater forests, we counted the number of all buildings (houses, schools, farms), with the exception of lodges, in two buffer zones (i.e. 500 m and 1500 m measured from the forest edge) around each focal forest fragment. This was also determined and hand-digitized through satellite imagery (Fig. 6). The proxy for disturbance was quantified as the density of buildings in each buffer zone, measured in unit /km^2.

Figure 6 – Visualisation of the quantification of variables of the geographical configuration and disturbance (here from left to right: lake Kyaninga, lake Ekikoto, lake Kayihara). Red zone around the lake: polygon to quantify the forest size; black and white border: buffer zones placed respectively 500 m and 1500 m from the forest edge; white dots: count of buildings in both buffer zones.

3.3.2.2 *Species (intrinsic) variables*

The four species were ranked following three gradients of species traits in the analyses of this research, each scored on a continuous scale from 1 to 4:

(i)   Species preference and harvest intensity was scored from heavily harvested (score 4), to least preferred (score 1), based on information obtained from contacts from different villages with help from local government officers of Kabarole District, and based on the experience of KFF: *Albizia* (4) – *Funtumia* (3) – *Dombeya* (2) – *Ficus* (1).

(ii)   Dispersal ability was scored from longest (score 4) to shortest (score 1) distance covered: *Ficus* (4) – *Funtumia* (3) – *Albizia* (2) – *Dombeya* (1).

(iii) Successional niche occupancy was scored from typical pioneer (score 4) to shade-tolerant, late-successional species (score 1): *Albizia* (4) – *Dombeya* (3) – *Ficus* (2) – *Funtumia* (1).

3.4 *Data analyses*

3.4.1 *Differences in prevalence of the four species and their ontogenetic stages: regeneration assessment*

As mentioned above, fragmentation is expected to affect species in a different way and to a different extent. Since this research focuses on the regeneration of four different species, we are interested in general differences in tree density between the species and differences in the population structure based on the density of their ontogenetic stages.

To compare the density of each ontogenetic stage between species, we used *general linear mixed models*, adopting site as a random factor. Models were run with the density of each life stage as dependent variable and species as explanatory variable or fixed factor. Site was chosen as a random factor because there is no specific interest in the predicted response of the different crater sites, but only in the variability between these responses. The models were run in R Studio 1.3.959, using the packages lme4 and lmerTest. A type III ANOVA test (with Satterthwaite correction for the degrees of freedom) on the model was performed to determine if density of the considered life stage depended on species identity in general, and with help of the estimated marginal means (function emmeans from library emmeans in R version 3.2.5) we then performed pairwise comparisons between the species. The p-values were adjusted for pairwise comparisons by performing a Tukey-correction.

Secondly, to compare the density of the species over all life stages, a *one-way PERMANOVA* was performed based on life stage-dissimilarity matrices, using PAST software (Hammer, Harper, & Ryan, 2001). Using this test it is possible to determine which species differ from each other in density over all life stages. A PERMANOVA-test is a non-parametric alternative for an ANOVA-test, since not all of the assumptions were fulfilled. Due to multiple pairwise comparisons, a Bonferroni-correction for multiple testing was applied. After determining which species were significantly different from each other, a *linear discriminant analysis* (LDA/CVA) was used to determine in which life stage(s) the species differ

the most. Not all assumptions for an LDA/CVA were met, so we selected a non-parametric alternative, the between-group PCA (Davis, 1986).

Finally, to detect deviations from a 'normal' or 'general' regeneration cycle, we determined for each species if young life stages (seedlings, saplings) were found in crater forests without adults, and the other way around if adults were found but no young cohorts (seedlings, saplings) were present. Again general linear mixed models were used to determine significant differences between the density of the life stages for each species separately, with species density as dependent variable, the life stages as independent variable and site as random factor. Again pairwise comparisons were performed, this time between the life stages per species, with help of the estimated marginal means. The p-values were also adjusted for pairwise comparisons by performing a Tukey-correction.

3.4.2   *Differential effect of environmental factors on species density and population structure*

To explore how environmental gradients drive the variation in the density of the different life stages of the four tree species, a multivariate analysis was performed using the program CANOCO (ter Braak & Šmilauer, 2012). In particular, a *principal components analysis* (PCA), based on a linear response method, was used to explore how the densities of the four ontogenetic stages are correlated with some of the introduced environmental variables (Davis, 1986; Harper, 1999). The choice to use a PCA was based on the gradient length in the data, which measures the beta diversity (the gradient in species turnover) in community composition along the ordination axes (Murtagh & Heck, 1987; Šmilauer & Lepš, 2014). As a response variable, we used a matrix containing the mean site-level densities of the four ontogenetic stages of each species. The included environmental variables were distance to the nearest monitored crater forest, forest area, distance to the national park and the proxy for disturbance. The Pearson correlation test showed that the two disturbance proxies (density of households in a buffer of 500 m, and in a buffer of 1500 m) were strongly positively correlated ($r_{pearson}$ = 0.817, p < 0.001). In addition, forest size was negatively correlated with both disturbance measures, measured in a buffer of 500 m ($r_{pearson}$ = -0.407, p < 0.001) and in a buffer of 1500 m ($r_{pearson}$ = -0.559, p < 0.001). Due to these highly significant intercorrelations, only one disturbance proxy (households in a buffer zone of 1500 m) was used as disturbance measure in the analysis.

In contrary to the dependent variables (the densities of the four ontogenetic stages), the environmental variables differed in their measurement scales. However, after CANOCO reads in the environmental variables, the variables are automatically centred and standardized to zero average and one unit variance ('standardization to unit variance') (Murtagh & Heck, 1987).

In addition to the previously mentioned environmental variables, we related the density patterns and correlations visible in the PCA of *Ficus sycomorus* to the presence or absence of seed dispersers. This was only done for *F. sycomorus* since this is the only species dependent on animals for dispersal. We tested if the presence or absence of each disperser in a crater forest is dependent on the value of

different environmental variables by performing a non-parametric test, a *two-group Mann-Whitney U test*. Using this test, we compared the mean value of each environmental variable between sites where the animal species was found, and sites where the species was absent.

3.4.3   *Differential response of species with different functional traits to fragmentation*

To test for overall effects of species traits on the density of the life stages, we again opted to use *general linear mixed models*, adopting site as a random factor. Models were run with density of each life stage (over all the species) as dependent variable and the three different species traits (value to the local community, successional niche, dispersal ability; on a continuous scale of 1 to 4 (see section 3.3.2.2)) as explanatory variable or fixed factor, to test for a dependency of density of each life stage on the species traits.

For these models the severity of multicollinearity between the independent variables (value to the local community, successional niche, dispersal ability) was quantified by calculating the variance inflation factor (function vif from library car in R version 3.2.5). Since the values of all independent variables were lower than 10 (successional niche = 1.25, dispersal ability = 1.64, value to the local community = 1.64), multicollinearity is not expected to affect our analyses substantially. A type III ANOVA test, with Satterthwaite correction for the degrees of freedom, was used to select the independent variables through a backward selection to come to the most parsimonious model. Subsequently the model summary output was evaluated.

4. Results

4.1 Differences in prevalence of the four species and their ontogenetic stages: regeneration assessment

A total of 1304 adults, 746 poles, 225 saplings and 271 seedlings were recorded across all 21 craters, with signs of regeneration stagnation and differences between the species. Visualizing the mean densities of all life stages per species, it is clear that in general there is a substantially low density of the young cohorts relatively to the adult tree density (Fig. 7). Using a mixed model and pairwise comparisons, differences between life stages for each species were detected (see Appendix Table S2). There were no significant differences between the life stages of *Albizia grandibracteata* and between the life stages of *Funtumia africana* (see Appendix Table S2). There was no significant difference between adult and pole density and between seedling and sapling density of *Dombeya torrida*, but adult density was significantly higher than both seedling density ($p = 0.002$) and sapling density ($p = 0.001$), and also pole density was significantly higher than both seedling density ($p = 0.049$) and sapling density ($p = 0.028$). The adult density of *Ficus sycomorus* was significantly higher than subsequently sapling density ($p < 0.001$), seedling density ($p < 0.001$) and pole density ($p < 0.001$) (see Appendix Table S2).
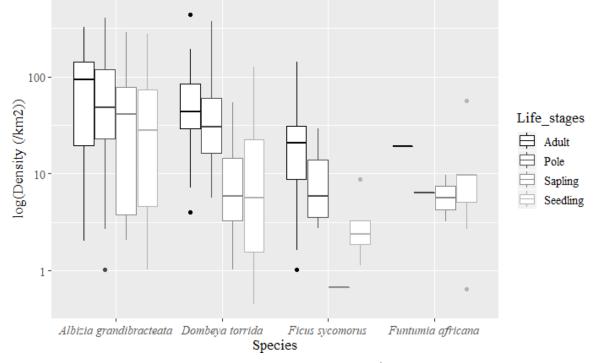

Figure 7 – Boxplot showing all 21 mean density measurements ($/km^2$) in the crater forests on a logarithmic scale for each life stage grouped per species.

In a first step to detect differences between species, it was determined if there were significant differences in density of each of the life stages between the species, using a mixed model and pairwise comparisons.

Seedling density

The ANOVA-test on the model showed there was a highly significant effect of species identity on the seedling density (F = 6.611; p < 0.001). The mean seedling density was highest for *A. grandibracteata* (mean = 45.760 ind/km^2; Table 3), followed by *D. torrida* (mean = 11.987 ind/km^2; Table 3) and *F. africana* (mean = 4.725 ind/km^2; Table 3) and was lowest for *F. sycomorus* (mean = 0.827 ind/km^2; Table 3). Seedling density differed significantly between *A. grandibracteata* and *D. torrida* (p = 0.020; Table 1) and highly significantly between *A. grandibracteata* and *F. sycomorus* (p = 0.001; Table 1), as well as between *A. grandibracteata* and *F. africana* (p = 0.003; Table 1).

Sapling density

We also found a highly significant effect of species identity on the sapling density (F = 7.941; p < 0.001). The mean sapling density was highest for *A. grandibracteata* (mean = 43.886 ind/km^2; Table 3), followed by *D. torrida* (mean = 8.253 ind/km^2; Table 3), *F. africana* (mean = 0.886 ind/km^2; Table 3) and *F. sycomorus* (mean = 0.032 ind/km^2; Table 3). The same species found to differ in seedling density also differed in sapling density. Sapling density differed highly significantly between *A. grandibracteata* and *D. torrida* (p = 0.006; Table 1), between *A. grandibracteata* and *F. sycomorus* (p < 0.001; Table 1), as well as between *A. grandibracteata* and *F. africana* (p < 0.001; Table 1).

Pole density

Also pole density differed highly significantly between the species (F = 7.873; p < 0.001). The mean pole density was highest for *A. grandibracteata* (mean = 86.856 ind/km^2; Table 3), followed by *D. torrida* (mean = 55.033 ind/km^2; Table 3), *F. sycomorus* (mean = 4.042 ind/km^2; Table 3) and *F. africana* (mean = 0.305 ind/km^2; Table 3). Looking at the pairwise comparisons, pole density differed highly significantly between *A. grandibracteata* and *F. sycomorus* (p = 0.001; Table 1), between *A. grandibracteata* and *F. africana* (p < 0.001; Table 1), and differed nearly significantly between *D. torrida* and *F. africana* (p = 0.056; Table 1) and between *D. torrida* and *F. sycomorus* (p = 0.084; Table 1).

Adult density

We also found a highly significant effect of species on the adult density (F = 7.679; p < 0.001). The mean adult density was highest for *A. grandibracteata* (mean = 83.000 ind/km^2; Table 3), followed by *D. torrida* (72.608 ind/km^2; Table 3), *F. sycomorus* (mean = 31.348 ind/km^2; Table 3) and *F. africana* (mean = 0.915 ind/km^2; Table 3). Adult density differed highly significantly between *A. grandibracteata* and *F. africana* (p < 0.001; Table 1) and between *D. torrida* and *F. africana* (p = 0.003; Table 1), and significantly between *A. grandibracteata* and *F. sycomorus* (p = 0.047; Table 1).

Table 1 – Pairwise comparisons between the species per ontogenetic stage, using emmeans. Estimates of density differences were measured in unit /km^2.

Life stage density	Contrast	Estimate	SE	df	t-value	p-value
Seedling	AG-DT	33.77	11.3	60	2.997	**0.0201 ***
	AG-FS	44.93	11.3	60	3.988	**0.0010 ****
	AG-FA	41.03	11.3	60	3.642	**0.0031 ****
	DT-FS	11.16	11.3	60	0.990	0.7554
	DT-FA	7.26	11.3	60	0.644	0.9171
	FS-FA	-3.90	11.3	60	-0.346	0.9856
Sapling	AG-DT	35.633	10.4	60	3.423	**0.0060 ****
	AG-FS	43.854	10.4	60	4.212	**< 0.001 *****
	AG-FA	43.000	10.4	60	4.130	**< 0.001 *****
	DT-FS	8.220	10.4	60	0.790	0.8589
	DT-FA	7.367	10.4	60	0.708	0.8937
	FS-FA	-0.854	10.4	60	-0.082	0.9998
Pole	AG-DT	31.82	21.1	60	1.510	0.4378
	AG-FS	82.81	21.1	60	3.930	**0.0012 ****
	AG-FA	86.55	21.1	60	4.108	**< 0.001 *****
	DT-FS	50.99	21.1	60	2.420	**0.0841 .**
	DT-FA	54.73	21.1	60	2.597	**0.0558 .**
	FS-FA	3.74	21.1	60	0.177	0.9980
Adult	AG-DT	10.4	19.4	60	0.537	0.9498
	AG-FS	51.7	19.4	60	2.667	**0.0471 ***
	AG-FA	82.1	19.4	60	4.238	**< 0.001 *****
	DT-FS	41.3	19.4	60	2.130	0.1553
	DT-FA	71.7	19.4	60	3.702	**0.0026 ****
	FS-FA	30.4	19.4	60	1.571	0.4025

Secondly, a comparison between the species over all life stages showed there was a significant overall difference in total density between the species (p < 0.001), and pairwise comparisons (Bonferroni-corrected) indicated there was a significant difference between all pairs of species, except between *A. grandibracteata* and *D. torrida* (see Appendix Table S3). The eigenanalysis in the between-group PCA showed that 92.49% of the differences between the species could be explained by the first PC-axis, and 99.35% could be explained by the first and the second PC-axis together. So since pole and adult density have the highest loading (coefficient) for PC1, respectively 0.681 and 0.594, they were the best discriminaters between the species (see Appendix Fig. S1; Appendix Table S4). In other words, the species differ the most in pole and adult density.

Finally, we evaluated the co-occurrence of adults and seedlings or saplings, and if there were sites where one of these ontogenetic stages was found alone. In some sites, we found seedlings or saplings for a species, but no adults (Fig. 8). In seven sites (Kasenda, Rukwanzi, Saaka, Nyinambuga, Nkuruba, Murusi, Katanda) where adults were absent, we found seedlings of *Funtumia*, and in two of them we found in addition to seedlings also saplings. A PCA-plot showed that of all surveyed sites, these were the sites that are nearest to the national park (see Appendix Fig. S2). Looking at *Albizia*, there were two

sites (Ntambi, Kanyango) where both seedlings and saplings were found, but adults were absent. Regarding *Dombeya* and *Ficus*, seedlings and saplings were only found in a crater forest if adults were also present.
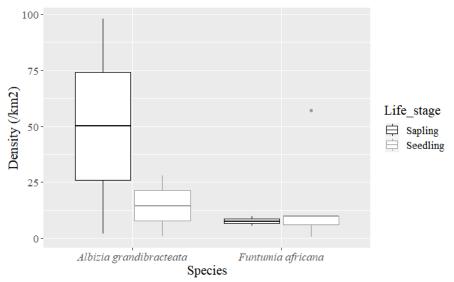

Figure 8 – Boxplot of the density (per km^2) of seedlings and saplings found in sites without adults present.

Vice versa, in other sites, we found adults but no young individuals (Table 2). In 19 of the 21 sites in total, adult individuals of *Dombeya* were found. However, in 10 of these sites no seedlings and/or saplings were found. More specifically, 31.6% of the 19 sites did not contain either seedlings or saplings and an additional 21.1% did contain saplings but no seedlings. 18 sites were home to adults of *Ficus*, however in 17 of these sites no seedlings and/or saplings were present. More specifically, in 72.2% of the sites with adults, neither seedlings nor saplings were found, and in an additional 22% of the sites, seedlings were present but no saplings. Adult individuals of *Albizia* were found in 18 sites, but in 5 of these sites no seedlings and/or saplings were present. More specifically, 5.56% of the 18 sites did not contain either seedlings or saplings, an additional 11.1% did contain saplings but no seedlings and another additional 11.1% did contain seedlings but no saplings. Looking at *Funtumia* there was only one site with adult trees, and this site contained saplings, but lacked seedlings.

Table 2 – Percentage of sites without seedlings, saplings or both, where adults were found.

Species	Sites with adults	Of which without seedlings (%)	Of which without saplings (%)	Of which without seedlings and saplings (%)
Dombeya torrida	19	21.05	0	31.58
Ficus sycomorus	18	0	22.00	72.22
Albizia grandibracteata	18	11.11	11.11	5.56
Funtumia africana	1	100	0	0

To determine if environmental gradients contribute to the variation between species and their life stages, a PCA for each species was performed, including the four ontogenetic stages and environmental variables (distance to the nearest monitored crater forest, distance to the national park, size of the crater forest, proxy for disturbance) (Fig. 9).
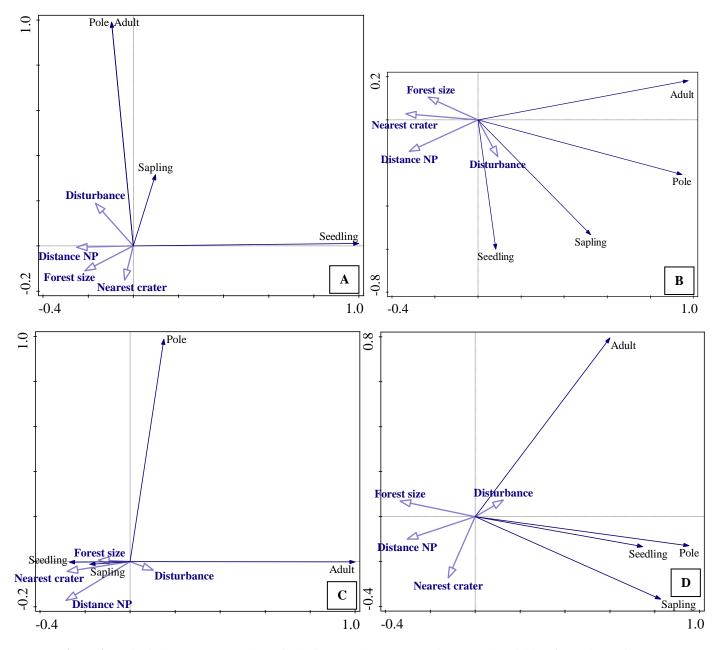

Figure 9 – Principal component analyses including supplementary environmental variables, for each species. A: *Funtumia africana*, B: *Dombeya torrida*, C: *Ficus sycomorus*, D: *Albizia grandibracteata*. Distance NP = distance towards the national park, Nearest crater = distance to the nearest monitored crater lake.

Together, the environmental variables explain 23.6% of the density variation found of *Funtumia africana*, 24.9% of *Dombeya torrida*, 16.0% of *Ficus sycomorus* and 22.1% of *Albizia grandibracteata*.

Funtumia africana

Regarding the PCA of the density found of *Funtumia africana*, the first two PC-axes together accounted for 97.00% of the variance in the dataset ($\lambda1 = 0.8625$ and $\lambda2 = 0.1075$; Fig. 9A; Appendix Table S5). PC-axis 1, which explained the largest part (86.25%) of the total variation, mainly captured gradients in distance to the national park (see Appendix Table S6). This means that mainly this variable created the gradient in the density found of *F. africana* in the crater forests. Looking at the effect of the environment on the density of the different life stages, the variation in seedling density was best explained by the first PC-axis and consequently by distance to the national park (see Appendix Table S7). More specifically, seedling density decreased in craters further away from the national park (Fig. 9A). Seedling density was only poorly correlated with distance to the nearest crater forest, decreased with disturbance and in addition, was only poorly (negatively) correlated with adult tree density (Fig. 9A). Sapling density was not well represented by the ordination (see Appendix Table S7) and adults and poles were only found in one site (Lyantonde), which made an interpretation of a correlation with the environmental variables not reliable.

Dombeya torrida

Considering the PCA of the density found of *Dombeya torrida*, the first two PC-axes together accounted for 93.82% of the variance in the dataset ($\lambda1 = 0.8720$ and $\lambda2 = 0.0662$; Fig. 9B; Appendix Table S5). PC-axis 1, which explained the largest part (87.20%) of the total variation, mainly captured gradients in distance to the national park and the nearest crater forest (see Appendix Table S6). This means that mainly these two environmental variables created the gradient in the density variation found of *D. torrida* in the crater forests. The density of poles, and especially the density of adult trees, was negatively correlated with distance from the national park. The largest part of the variation in seedling density was captured by the second PC-axis (see Appendix Table S7), which mainly captured gradients in disturbance and distance from the national park (see Appendix Table S6). Seedling density was positively correlated with the proxy for disturbance and with distance from the national park, but was only poorly correlated with adult tree density (Fig. 9B). Sapling density was equally well represented by the first and second PC-axis (see Appendix Table S7) and was positively correlated with disturbance and only poorly correlated with distance to the national park (Fig. 9B).

Ficus sycomorus

Looking at the density found of *Ficus sycomorus*, the first two PC-axes together accounted for 99.95% of the variance in the dataset ($\lambda1 = 0.9912$ and $\lambda2 = 0.0083$; Fig. 9C; Appendix Table S5). PC-axis 1, which explained nearly all variation (99.12%), mainly captured gradients in distance from the national park and distance from the nearest crater forest (see Appendix Table S6). This means that mainly these

two environmental variables created the gradient in the density variation found of *F. sycomorus* in the crater forests. The density of the young life stages (seedlings and saplings) was negatively correlated with the adult density, but positively with distance from the national park, distance to the nearest crater lake and increasing forest size. However, the young life stages were not well represented by the ordination (see Appendix Table S7) and additionally saplings were only found in one crater forest (the forest of Kyaninga), which made an interpretation of correlation with the environmental variables not reliable. All the variation in adult trees was captured by the first PC-axis (see Appendix Table S7), and the density of adult trees increased in craters closer to the national park and in craters closer to neighboring sites. All the variation in pole density was captured by the second PC-axis (see Appendix Table S7), which mainly captured gradients in distance from the national park (see Appendix Table S6), with pole density increasing in sites closer to the national park (Fig. 9C).

Additionally, because the seeds of *F. sycomorus* are typically animal-dispersed, it was important to determine if the presence of seed dispersers was influenced by the environment. This was done by comparing the values of the environmental variables between sites where a seed-dispersing species was present or absent (Fig. 10). Distance from the national park and human disturbance intensity influenced the presence of the seed dispersers overall the most, there was a trend where animals were found in craters that were on average located closer to the national park and were less exposed to human disturbance (Fig. 10). Distance to the national park seemed to be the most determining factor for the presence of red-tailed monkeys, turacos and vervet monkeys, while disturbance intensity seemed to be most determining for the presence of hornbills, turacos and vervet monkeys (Fig. 10). The species showed a more varied response to forest size and distance from the nearest neighbouring crater forest. A larger average forest area seemed to be important for the presence of hornbills, and neighbouring crater forests in close proximity seemed to be important for the presence of red colobus monkeys. Testing for significant differences between sites where species were present and where not, we found that the presence of red-tailed monkeys was nearly significantly dependent on the distance from the national park ($p = 0.065$) and that the presence of hornbills was nearly significantly dependent on disturbance ($p = 0.067$) and significantly dependent on forest size ($p = 0.013$). More specifically, red-tailed monkeys were more often found in craters closer to the national park, and hornbills preferred to visit craters with a larger forest size and a lower level of disturbance. Given that seedlings and saplings of *F. sycomorus* were not well represented by the PCA, and thus seemingly not directly related to environmental variables, the lack of early life stages could possibly be attributed to the overall negative response of seed dispersers to the environmental effects of fragmentation, as demonstrated by their absence in crater forests that were more isolated, had a smaller forest size and a higher disturbance intensity.
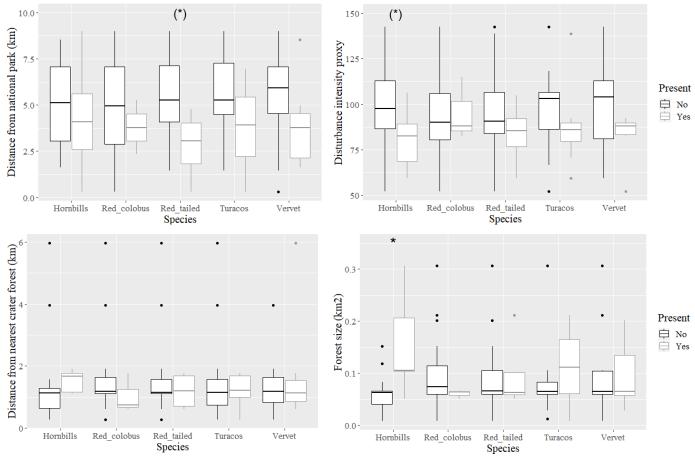
Figure 10 – Boxplots comparing the values of four environmental variables between sites where a seed disperser is found and where it is absent. The considered environmental variables are the distance from the national park (upper left), the disturbance intensity (upper right), the distance from the nearest crater forest (down left) and the forest size (down right). Nearly significant differences (p ≤ 0.07) between groups were marked with **(*)**, significant differences (p ≤ 0.05) were marked with ***** , following a Mann-Whitney U test.

Albizia grandibracteata

Regarding the PCA of the density found of *Albizia grandibracteata*, the first two PC-axes together accounted for 87.04% of the variance in the dataset (λ1 = 0.6871 and λ2 = 0.1833; Fig. 9D; Appendix Table S5). PC-axis 1, which explained the largest part (87.04%) of the total variation, mainly captured gradients in forest size (see Appendix Table S6). This means that mainly the size of the forest created the gradient in the density variation found of *A. grandibracteata* in the crater forests, and all ontogenetic stages (especially the younger ones) were negatively correlated with increasing forest size. Seedling density was positively correlated with adult density (Fig. 9D). The variation in adult density was mainly captured by the second PC-axis (see Appendix Table S7), which mainly captured gradients in distance to the nearest crater lake (see Appendix Table S6), with adult density increasing in sites closer to the national park (Fig. 9D).

4.3 Differential response of species with different functional traits to fragmentation

To determine if intrinsic species traits contributed to the variation between species and their life stages, we ran a mixed model for the density of each ontogenetic stage to determine which species traits significantly influenced the densities.

Seedling density

The successional niche to which a tree species belongs, as well as the economic value of a species to the local people, had a significant effect on seedling density. Increasing pioneer characteristics ($p = 0.013$; Table 3) and higher value of a species to local people ($p = 0.027$; Table 3) both significantly increased the seedling density.

Sapling density

The same species characteristics that had an effect on seedling density, also significantly affected the sapling density. Increasing pioneer characteristics had a highly significantly positive effect on sapling density ($p = 0.005$; Table 3), and value of the species to the local community also had a significantly positive effect on sapling density ($p = 0.024$; Table 3).

Pole density

Pole density was highly significantly dependent on the successional niche to which a species belongs. Increasing pioneer characteristics had a highly significantly positive effect on pole density ($p < 0.001$; Table 3).

Adult density

The same species characteristic that had an effect on pole density, also significantly affected adult density. Increasing pioneer characteristics had a highly significant positive effect on adult density ($p < 0.001$; Table 3).
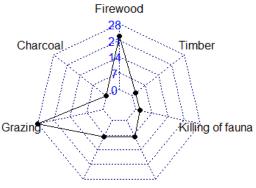
Table 3 – General linear mixed model parameters after backward selection procedure. SP, species; V, usage (economic) value; S, successional score; DT, *Dombeya torrida*; AG, *Albizia grandibracteata*; FA, *Funtumia africana*; FS, *Ficus sycomorus*. Density estimates were measured in unit /km^2.

Life stage density	Significant model parameters	Fixed effects	Estimate	SE	df	t-value	p-value
Seedling	**SP**	Intercept (AG)	45.760	8.383	77.811	5.458	**< 0.001 *****
		DT	-33.773	11.267	60.000	-2.997	**0.003957 ****
		FS	-44.932	11.267	60.000	-3.988	**< 0.001 *****
		FA	-41.034	11.267	60.000	-3.642	**< 0.001 *****
	S + V	Intercept	-30.925	11.625	78.362	-2.660	**0.00947 ****
		S	9.910	3.872	61.000	2.559	**0.01298 ***
		V	8.789	3.872	61.000	2.270	**0.02677 ***
Sapling	**SP**	Intercept (AG)	43.886	7.362	80.000	5.961	**< 0.001 *****
		DT	-35.633	10.411	80.000	-3.423	**< 0.001 *****
		FS	-43.854	10.411	80.000	-4.212	**< 0.001 *****
		FA	-43.000	10.411	80.000	-4.130	**< 0.001 *****
	S + V	Intercept	-33.417	10.515	81.000	-3.178	**0.00210 ****
		S	10.422	3.596	81.000	2.898	**0.00483 ****
		V	8.251	3.596	81.000	2.294	**0.02436 ***
Pole	**SP**	Intercept (AG)	86.86	15.50	78.63	5.603	**< 0.001 *****
		DT	-31.82	21.07	60.00	-1.510	0.136211
		FS	-82.81	21.07	60.00	-3.930	**< 0.001 *****
		FA	-86.55	21.07	60.00	-4.108	**< 0.001 *****
	S	Intercept	-41.102	18.729	81.506	-2.195	**0.031 ***
		S	31.064	6.657	62.000	4.667	**< 0.001 *****
Adult	**SP**	Intercept (AG)	83.00	14.79	75.37	5.610	**< 0.001 *****
		DT	-10.39	19.37	60.00	-0.537	0.59355
		FS	-51.65	19.37	60.00	-2.667	**0.00982 ****
		FA	-82.08	19.37	60.00	-4.238	**< 0.001 *****
	S	Intercept	-24.911	17.574	81.961	-1.417	0.16
		S	28.751	6.075	62.000	4.733	**< 0.001 *****

Based on the monitoring data gathered by KFF in the forest of Kyaninga, it was possible to make an exploratory analysis of the nature and pattern of human disturbances in the forest.

The two most common forms of disturbance during the entire period of monitoring were the gathering of firewood and grazing by cattle, goats and sheep in or along the forest (Fig. 11). Gathering of charcoal did not occur.

Figure 11 – Radar chart showing the number of incidences of each type of disturbance.

Of all disturbance events where trees were destroyed, the small-sized trees (seedlings and saplings) were destroyed in most cases (in 32 cases of all incidences), followed by medium-sized trees (in 23 cases of all incidences) (Fig. 12). Only on few occasions also large trees were felled (in 3 cases of all incidences).
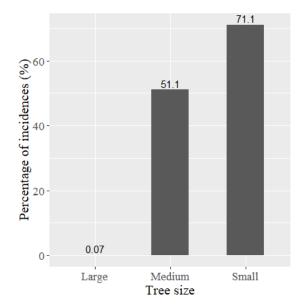

Figure 12 – Barplot showing the percentage of disturbance observations when trees from three size classes (small, medium, large) were found destroyed.

Looking at the time period when trees were found destroyed, loss of trees was higher during the rainy season than during the dry season (Fig. 13).
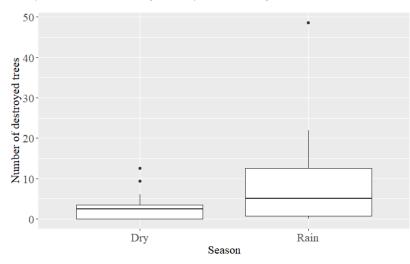
Figure 13 – Boxplot showing the number of trees found destroyed per season.

Looking at the effect of consistent forest monitoring on the number of trees found destroyed, this number clearly follows a downward trend over the time period of monitoring (from 11/10/2017 to 6/03/2020) (Fig. 14).

Figure 14 – Linear regression of number of destroyed trees over all days of monitoring. Three outliers were removed: 159 trees (2018-10-25), 76 trees (2019-03-11), 70 trees (2019-03-22)).

5. Discussion

This study is the first attempt to assess the regeneration cycle in the crater lake region in western Uganda. A fair amount has been learned so far about the effects of fra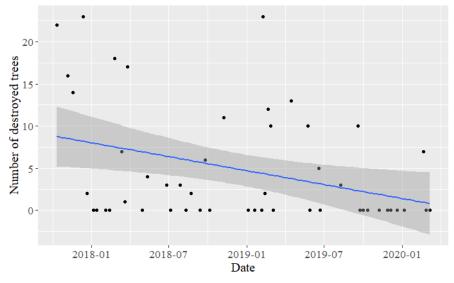gmentation on the integrity of different forest communities (e.g. Ojoyi, Mutanga, Odindi, Betemariam, & Abdel-Rahman, 2015; Laurance, 2000; Lehvävirta, Vilisics, Hamberg, Malmivaara-Lämsä, & Kotze, 2014; Benitez-Malvido, 1998), however, in Uganda, little has been known on tree population persistence in areas outside the national parks. The results suggest that the forest regeneration in a tropical area as fragmented as the crater lake region is not optimal, but the extent of stagnation is profoundly dependent on the species identity. The combination of data on forest fragments with differing environmental characteristics and data on species with different traits, allowed to quantify differences between species' ability to persist in this fragmented tropical area. In doing so, the study has demonstrated that the crater forests are at risk of disappearing, with species on the verge of suffering from an extinction debt. Moreover, this study shows that the extent to which a species' persistence is affected, is dependent on the combination of both environmental factors and species intrinsic traits. Quick conservation and management action is required to prevent this unique ecosystem from disappearing and species to go extinct. The methods used in this study provided accurate information on the demographic structure of different tree species and, along with other studies, showed that tree communities and populations respond to environmental changes after fragmentation. Since predictions about the future trend in forest composition can only be made by knowing the current status of a given forest, research about the current demographic structure and regeneration status is essential for the development of management and conservation plans (Dutta & Devi, 2013; Bogale, Datiko, & Belachew, 2017).

5.1 Differences in prevalence of the four species and their ontogenetic stages: regeneration assessment

5.1.1 Evaluation of the regeneration cycle

The overall pattern of population dynamics of seedlings, saplings and adults of tree species exhibits the regeneration profile, and this was used to determine the regeneration status of the forests in the crater lake region (Malik & Bhatt, 2016). A first finding of this study is that the demographic status and current regeneration potential are to a large extent dependent on the species identity.

The proportion of seedlings and saplings in a population determines the regeneration status of a species and enabled us to predict future trends in the community composition (Khumbongmayum, Khan, & Tripathi, 2006). For both *Albizia grandibracteata* and *Funtumia africana* we did not find significant density differences between the different life stages. For a good reproduction and regeneration potential it is generally considered that the density of seedlings has to be larger than the density of saplings, which in turn has to be larger than the density of adults (Khumbongmayum, Khan, & Tripathi, 2006; Shankar,

2001; Gurmessa, Soromessa, & Kelbessa, 2012). For these two species instead, the density of seedlings did not significantly differ from the density of saplings, which in turn did not differ from the density of either poles or adults. These ratios represent the pattern of a fair regeneration (Khumbongmayum, Khan, & Tripathi, 2006; Shankar, 2001).

On the contrary, we found significant density differences between the life stages of *Ficus sycomorus*. The adult density of *Ficus* was found to be significantly higher than the density of either poles, saplings and seedlings. The density of seedlings and saplings was remarkably low and limited in distribution, with seedlings found in only five of the 18 crater forests containing adults, and saplings in only one. In forests where only adult individuals of a species are present, the regeneration cycle has been altered to such a large extent that the species is no longer considered to be regenerating and expected to disappear if the conditions do not change (Shankar, 2001). Also for *Dombeya torrida* differences in density were found between certain life categories. Both pole and adult density were significantly higher than either the density of seedlings or saplings. Similar to *Ficus*, some crater forests containing adult trees of *Dombeya* did not contain young cohorts. No seedlings were found in 10 of the 19 sites containing adults, and in six of those also saplings were absent.

Thus, both *Dombeya* and *Ficus* were found with a significant shortage of new recruits and are considered to suffer from a poor regeneration cycle (Khumbongmayum, Khan, & Tripathi, 2006, Shankar, 2001). Regarding *Ficus*, this result is in contrast with previous research where animal-dispersed species were found to be less vulnerable to forest loss, with some species even showing positive responses to decreased forest cover (Chapman & Chapman, 2003; Montoya, Zavala, Rodríguez, & Purves, 2008). It is generally considered that the collapse of forest communities suffering from habitat destruction can be prevented by plant-animal interactions, partly due to the large dispersal distances and strong mutualism (Montoya, Zavala, Rodríguez, & Purves, 2008). Given the importance of biotic seed dispersal vectors and the additional dependency of *Ficus* on a specific pollinator (fig wasps), the poor regeneration cycle may reflect a loss of either a seed disperser, a pollinator, or both. Pollinators or vertebrate dispersal vectors may suffer from a population decline in a landscape of fragmented habitats or may move to more suitable areas elsewhere (Henle, Davies, Kleyer, Margules, & Settele, 2004). Previous research indeed has shown that the proportion of mature fig fruits without pollinator wasps increased to a large extent in highly fragmented forests (Wang, Yang, Zhao, & Yang, 2005). Similar results as ours were found in other studies on fragmented tropical forests, where *Ficus* species were also found to have a poor or even no regeneration cycle as a result of reduced dispersal and recruitment success (Henle, Davies, Kleyer, Margules, & Settele, 2004; Maua, MugatsiaTsingalia, Cheboiwo, & Odee, 2019). The results of this and other studies (Tabarelli, Mantovani, & Peres, 1999) indicate that of all dispersal modes, vertebrate-dispersed tree species are most sensitive to fragmentation. The reason why *Dombeya* has a poor regeneration cycle remains unclear, this could possibly be related to the loss of an essential pollinator, or due to fragmentation effects constraining the

establishment of seedlings such as seed predation which increases seed mortality, or intense herbivory, which increases seedling mortality (Herrera & Carcìa, 2010; De Groote et al., 2017). In addition, *Dombeya* has the poorest dispersal capacity of all species, which may be at the root of the increasing difficulty of reaching suitable germination sites in severely disturbed forests.

For *Funtumia* we did not find significant differences in density between the life stages, but the spatial distribution of adult and young life stages showed a reversed pattern in comparison to *Dombeya* and *Ficus*. Adult trees were only found in one crater forest, while seedlings were found in seven sites and in two of them also saplings were found. Several causes may lie at the basis of this pattern. A first explanation for this finding may be that the species is new to the area and seeds have colonized the area with the help of birds and mammals (Maua, MugatsiaTsingalia, Cheboiwo, & Odee, 2019). However, *Funtumia* is a specialized wind-dispersed species and is native to the study area with mature trees known to be present here in the past (Muhanguzi, Obua, Oreym-Origa, & Vetaas, 2005). An alternative explanation could be that the adult trees have been overexploited through the years and that seeds have emerged from seed banks after a period of dormancy (Njunge & Mugo, 2011). However, *Funtumia* is expected to have a very low dormancy capacity because of the morphology of the seed and the generally already very low seed lifespan in the tropics (as there are no hard seasons to overcome) (Vázquez-Yanes & Orozco-Segovia, 1993). The explanation is likely to be somewhere in the middle, and explainable by the species' dispersal ability. Trees of *Funtumia* are highly targeted for harvest by local people, and the species is known to be under a high disturbance pressure. However, because of the morphology of the seeds, they can be expected to be carried over long distances by the wind, likely reaching areas that do not have reproductively mature individuals. Previous research has shown that the most obvious differences in young cohorts in disturbed areas were excesses of the wind-dispersed species and deficiencies of the animal-dispersed species (Terborgh et al., 2008). However, the density of seedlings and saplings present of *Funtumia* is still low, which may be due to the high risk of wind-dispersed seeds to fall in inappropriate places to germinate (Salisbury, 1976). The low number of adult trees and poles is very likely due to the fact that the species is heavily targeted for harvest by local people.

Also for *Albizia*, there were two sites where both seedlings and saplings were found, but adults were absent. Again one of the possible explanations for encountering early recruits without finding parents in the same area could be persistence of seeds in the soil seed bank. The thick seedcoat of *Albizia*, in contrary to *Funtumia*, induces dormancy, hampering quick and uniform germination (Tigabu & Oden, 2001; Willan, 1985). However, in reality seeds of *Albizia* seem to not persist for long in the seedbank. They are very rarely found in the field and if they are, they are always spoiled due to insect predation. This presumption is confirmed by research showing that the viability and vigour of seeds of *Albizia* is rather low, and can in addition be explained by the generally low lifespan of seeds in the tropics (Tigabu & Oden, 2001; Vázquez-Yanes & Orozco-Segovia, 1993). Because of the low dispersal capacity of *Albizia*, seeds are

highly unlikely to arrive from nearby seed sources as can be expected in the case of *Funtumia*. A more likely explanation for encountering seedlings in forests without adults present, is the fact that *Albizia* has the ability of performing vegetative propagation as an adaptive trait against disturbance. *Albizia* is a preferred tree to harvest, which is likely the cause of the absence of adult trees in the two forest fragments, while cut down trees are still able to produce adventive stems from their root system after root cutting or tree felling (Morin, Bellefontaine, Meunier, & Boffa, 2010). This could explain the presence of young life stages in the two forests where adults were absent.

Something to keep in mind while evaluating the regeneration cycle is that the density of seedlings of tropical trees is likely to be dependent on the time of year as the number of seedlings is also related to the time that has passed since the last adult had fruits or seeds available (Muhanguzi, Obua, Oreym-Origa, & Vetaas, 2005). However, the density of seedlings and saplings followed similar patterns and this difference is expected to not have a great influence on our results. Another thing to take into consideration is that patterns of poor reproduction and recruitment can also be related to intense competition from surrounding trees, grazing, lack of safe sites for seedling recruitment or pathogens (Gurmessa, Soromessa, & Kelbessa, 2012).

5.1.2   *Differences between the species*

We found a clear difference between the species, with the density of *Albizia* being highest in all life stages, followed by *Dombeya*. Since both species have pioneer characteristics, this finding is not surprising. This result is supported by other studies which demonstrated that the most rapidly proliferating species, such as pioneers, were even more widespread and abundant in fragments than in a continuous forest (Santo-Silva, Almeida, Tabarelli, & Peres, 2016). However, even while studies found pioneers to be dominant in all age classes in forest fragments, at the same time more than half of the adult pioneer species included in those studies were also lacking seedlings (Santo-Silva, Almeida, Tabarelli, & Peres, 2016). This confirms our finding that the regeneration pattern of *Albizia* is also not ideal despite its strong adaptation to disturbances. The density of *Ficus* was lowest in the seedling and sapling categories, while the density of *Funtumia* instead was lowest in the pole and adult categories when comparing them with the other species, which is in line with the findings of the regeneration assessment.

We did not find a difference in density of seedlings and saplings between *Dombeya*, *Ficus* and *Funtumia*, but these three species all had lower seedling and sapling densities than *Albizia*, which is a typical pioneer species. Looking at adult and pole densities, only the density of *Dombeya* did not differ from the density of *Albizia*, which is not surprising since *Dombeya* is the second strongest pioneer in this study.

Overall density differences were found between all species, except between *Dombeya* and *Albizia*, again likely due to the fact that they are both pioneer species. The four species differed the most in

density of poles and density of adults, which could point towards a substantial difference in economic value of the wood between the species, since poles and adult trees are a preferred construction material.

5.2 _Differential effect of environmental factors on species density and population structure_

In this study, the differences between species and ontogenetic stages were found to be due to an influence of both environmental (extrinsic) factors and functional (intrinsic) traits. First of all, a clear correlation was found between the density of the ontogenetic stages and the environmental variables. The correlations differed to a certain extent between species and in addition between their life stages.

The presence of a clear correlation between ontogenetic stages and environmental variables in this study clearly demonstrates that the persistence of a species is dependent on the environment, which is in agreement with a tree diversity study in the Albertine Rift of western Uganda (Eilu, Hafashimana, & Kasenene, 2004a). On top of that, the environmental effects seem to differ between species. Studies have shown that once a forest has an overall history of fragmentation and degradation, environmental effects of fragmentation on tree species are less clear (De Groote et al., 2017). This is because generalist plant species start dominating the forest community, especially in the understory (Cramer, Mesquita, Bentos, Moser, & Williamson, 2007; De Groote et al., 2017). As there are still clear correlations between the current population structure of a species and the environment in our study, the remaining crater forests are considered to still have a conservation value and potential.

Distance to the national park and to the nearest crater forest created the main gradient in density variation of _Funtumia africana_ in the crater lake region. As previously mentioned, adult trees were only found in one crater forest. This in combination with the fact that seedling density is best explained by distance to the national park and that the density decreases in craters further away from the national park, confirms our hypothesis that species with a high dispersal capacity are still capable of recruiting seedlings in sites where mature trees are absent. Of all surveyed sites, seedlings of _Funtumia_ were only found in the craters located nearest to the national park. On top of that, seedling density is only poorly correlated with adult density in the same crater forest, which only contributes to the previous finding. The fact that the density of seedlings is only poorly correlated with distance to the nearest crater forest, indicates the importance of a healthy and qualitative seed source such as a protected forest like Kibale National Park. This is confirmed by previous studies where seed limitation is not only affected by dispersal capacity, but also by source density (number of possible parent trees) and source strength (potential seed production) (Clark, Macklin, & Wood, 1998). As adults and poles were only found in one site, a correlation with environmental variables is not possible to deduct. However, this low density in combination with limited distribution gives a clear indication of a high harvesting pressure since _Funtumia_ has always been present in the area in the past. Saplings were only found in two sites, which again makes a correlation with the environment difficult. This low density and distribution of saplings

indicates a low density of seedlings in the first place, followed by a low survival from seedling to sapling class. This may be due to a high disturbance pressure since seedling density (which instead is well represented by the ordination) is negatively correlated with disturbance. Destruction due to grazing and trampling and raised competition with weeds increases seedling mortality by depriving them of light and other resources, as seedlings of *Funtumia* are known to require a minimum availability light (Kitajima & Fenner, 2000). Long distance dispersal events are difficult to detect in the field, and species dispersed by wind are still very underrepresented in empirical research, especially in the tropics (Damschen et al., 2014; Bullock & Nathan, 2008), which makes these findings valuable for future research.

Distance to the national park and to the nearest crater forest also created the main gradient in density variation of *Ficus sycomorus*. The density of seedlings and saplings decreases with decreasing forest size, which could be explained by the edge effects becoming more prominent when a forest fragment becomes smaller, which negatively influences a late-successional species like *Ficus*. More counter-intuitively is the seemingly positive correlation of the density of young life stages with distance from the national park and the nearest crater forest. However, the density of young life stages of *Ficus* are not well represented by the ordination, so it is likely there are other factors than the included environmental variables influencing the density of these young recruits. On top of that, saplings were only found in one crater forest, which makes it difficult to derive a correlation with the environmental variables. The density of mature trees, on the other hand, is well explained by the ordination, with density clearly being higher in crater forests closer to the national park and neighbouring crater forests. Also pole density is higher in craters closer to the national park. The included environmental variables in the PCA contributed least to explain the variation in *Ficus* in comparison with the other tree species. This could be attributed by the fact that vertebrate dispersers were not included as variables in the PCA, and that the variation in *Ficus* is not directly related to the environmental variables, but rather indirectly following the presence/absence of possible seed dispersers. In other words, the lack of early life stages relatively to the density of adult trees and the low correlation with environmental variables, could be attributed to the overall negative response of seed dispersers to the effects of fragmentation, as demonstrated by their absence in crater forests that are more isolated, have a smaller forest size and a higher disturbance intensity. Research has shown that proximity to human residence (used as the proxy for disturbance here) may indeed affect regeneration indirectly by disturbing possible seed dispersers such as monkeys and large-bodied birds, and consequently disrupting seedling recruitment (Popradit et al., 2015). Looking at seed dispersers, we found a trend where they are mostly encountered in craters that are closer to the national park and less exposed to human disturbance. So the lack of seedlings and saplings of *Ficus* may be explained by the fact that seed dispersers were found to be less abundant or even absent in more isolated, disturbed and smaller forest fragments. The results show that red-tailed monkeys had a higher chance to be found in forests closer to the national parks and hornbills preferred to visit crater

forests with a low disturbance and larger size. Previous research has also demonstrated the correlation between, in particular, forest size and the red-tail population size and number of groups in a fragment (Tabuti, Ticktin, Arinaitwe, & Muwanika, 2009). Our results are supported by other studies in African forest fragments (Tanzania), where species dispersed by vertbrates had a recruitment level 40 times lower in small forest fragments in comparison to a continuous forest, while wind-dispersed and gravity-dispersed species remained unaffected in their recruitment (Cordeiro & Howe, 2001). If vertebrate seed dispersers are as crucial to the persistence of trees as this and other studies suggest (Montoya, Zavala, Rodríguez, & Purves, 2008), the combination of habitat destruction and the direct or indirect loss of seed dispersers is likely to have more drastic effects than the pure disturbance effects alone (Montoya, Zavala, Rodríguez, & Purves, 2008).

The variation in density of *Albizia grandibracteata* was mainly explainable by the size of the forest. All life stages, especially the early recruits, were negatively correlated with forest size, which reflects the strong pioneer traits of *Albizia*. This is in line with previous research which showed that pioneer species in particular exhibit higher densities in small fragments than in large fragments or continuous forest (Santo-Silva, Almeida, Tabarelli, & Peres, 2016). Smaller forests are associated with a reduced distance to the forest edge, consequently more prominent edge effects (e.g. increasing light levels) and an increased abundance of pioneers (Henle, Davies, Kleyer, Margules, & Settele, 2004). In line with this, all life stages were found to be positively correlated with increasing disturbance. Research has shown that the seedling and sapling distribution of a pioneer species is indeed mainly associated with canopy openness (Goodale et al., 2012). Based on these findings, the strong pioneer characteristics are considered to play an important role in the persistence of this species (Obiri, Hall, & Healy, 2010). *Albizia* is the only species of the four with a strong correlation between seedling and adult density in the crater forests. Possible explanations are its vegetative propagation, low dispersal capacities and a higher tolerance to conspecifics (Santo-Silva, Almeida, Tabarelli, & Peres, 2016). Vegetative reproduction is a common disturbance adaptation in the tropics, and consequently plays an important role in population persistence by minimizing dependence on seedling recruitment, and reducing the impacts of local disturbance and loss of pollinators (Bellingham, 2000; Lander, Harris, Cremona, & Boshier, 2019). Even though we have taken great care not to include vegetative shoots in the seedling and sapling count, it is likely that the count is slightly biased in the recruitment assessment. The density of all life stages, but especially adults and poles, decreases with distance from the national park, which is probably independent of species traits and points towards an increase in protective measures near the park instead. Lodges around the crater lakes increase the surveillance in the forests, and are located closer to the park's border. This proves that a certain degree of protection is important, as *Albizia* is highly targeted for harvest by local people and also showed signs of a reduced regeneration cycle despite its strong pioneer characteristics.

The most important environmental variables structuring the density variation of *Dombeya torrida* were distance to the national park and distance to the nearest neighbouring crater forest. The density of

adult trees and poles was negatively correlated with distance to the national park, again likely because of increased protection closer to the national park. Seedling and sapling density was positively correlated with the intensity of disturbance, which is in line with the expectations of the light-requirement of a moderate pioneer (Terborgh et al., 2008). Research has also emphasised that the regeneration of trees can be improved by mild disturbances (e.g. increased solar radiation on the forest floor and reduced competition from trees of the upper canopy) (Boring, Monk, & Swank, 1981), while severe disturbances however have been regarded as deleterious (Eilu & Obua, 2005). The fact that seedling density was poorly correlated to adult density is in line with the problematic regeneration pattern and possible loss of an essential pollinator.

Seedling density of *Funtumia*, *Ficus* and *Dombeya* was not correlated with adult tree density of the respective species, which together with previous findings can also be explained by competition theories such as Janzen-Connell, resulting in a lower number of conspecifics within an area close to an adult tree (Connell, 1971). However, research in an Afrotropical rainforest demonstrated that for animal-dispersed species, dispersal limitation outweighs inter-seedling competition as a force shaping the seedling plant community (Olsson, Nuñez-Iturri, Smith, Ottosson, & Effiom, 2019). So the loss of seedling dispersers due to hunting or due to migration to more intact habitat, is likely to be of greater importance for the poor recruitment of *Ficus* than competition theories.

Two other environmental variables which could be of importance for the presence of a species and its population structure, are the slope of the crater and the type of the soil. Because of the unique origin of the crater forests, the soil ranged from dark soil (ashes) of volcanic origin, to red-coloured soil. This can possibly influence the tree community composition, but because of logistic reasons we were not able to determine the influence. Regarding the slope effect, research has shown that erosion is an important disturbance measure, but slope effects alone do not significantly determine the density of young trees (Olupot & Chapman, 2006).

5.3 *Differential response of species with different functional traits to fragmentation*

Understanding the intrinsic traits of a species is central to our ability to predict species sensitivity and population responses to environmental perturbations. Three traits were taken into account: dispersal ability (dispersal distance), successional niche (pioneer characteristics) and economic value of a species.

Our results showed that **dispersal distance** did not significantly affect the density of any of the ontogenetic stages. A possible explanation for the absence of dependency of seedling density on a species' dispersal ability is an alteration in the dispersal distances ranking due to fragmentation. As mentioned before, mutualistic relationships between plants and frugivorous animals may become disrupted by fragmentation, and reduce the seed dispersal of trees that depend on biotic dispersal agents such as *Ficus sycomorus*. Research has shown that animal-dispersed seeds travelled double the distance,

in quantities twice as great, in continuous forests as in fragments (Cramer, Mesquita, Bentos, Moser, & Williamson, 2007). On top of that, seed dispersal depends on the characteristics of the matrix that has to be overcome, which is also of influence for the dispersal ranking (Frank, Drechsler, & Wissel, 1994; Henle, Davies, Kleyer, Margules, & Settele, 2004). A second reason for not finding a clear dependency is that the two species with the least dispersal capacity (*Albizia grandibracteata*, *Dombeya torrida*) are both pioneers, overcoming the low dispersal capability by being better adapted to disturbed conditions. Dispersal distance is thus not a determinant trait for the density of young recruits, but our results showed that a high dispersal capacity makes seedling recruitment less dependent on the available mature trees in the same forest. We found that a species in a fragment with a low density or even absence of mature trees *(Funtumia africana)*, is still recruiting thanks to the presence of a healthy seed source (national park) in proximity. This is supported by other studies, where dispersal failure was determined to be a main causal mechanism for the differences in species regeneration responses to the remaining forest cover in a fragmented area (Santo-Silva, Almeida, Tabarelli, & Peres, 2016; Montoya, Zavala, Rodríguez, & Purves, 2008). It has been demonstrated by multiple studies that long-distance dispersal increases the tree survival in dynamic landscapes, especially landscapes suffering from habitat fragmentation (Higgins & Richardson, 1999; Clark, Silman, Kern, Macklin, & HilleRisLambers, 1999; Soons & Ozinga, 2005). Species with a high dispersal power (depending on their dispersal agents (e.g., wind, animals (Poschlod, Kleyer, & Tackenberg, 2000))) generally had a lower risk of extinction in highly fragmented habitats (Frank, Drechsler, & Wissel, 1994; Henle, Davies, Kleyer, Margules, & Settele, 2004). However, in this and other studies, plant traits adapted to grow under changed conditions turn out to be more important for regional tree species survival than dispersal distance (Soons & Ozinga, 2005).

In this study we purely focused on the dispersal mechanism and corresponding dispersal distance ranking, but also several other plant traits such as seed morphology, releasing height, mass and digestion survival, relate to transport (Henle, Davies, Kleyer, Margules, & Settele, 2004). However, the four species studied were chosen to be very clear representatives of each dispersal mode.

The successional niche of a species had an effect on all ontogenetic stages, the more a species resembled a pioneer, the higher the density of each life stage was. This finding is supported by previous research where pioneers exhibited higher relative densities than shade-tolerant species in all ontogenetic stages (Santo-Silva, Almeida, Tabarelli, & Peres, 2016). The competitive ability of a plant species and its response to disturbance is generally considered to be a suitable indicator for fragmentation sensitivity, and this is confirmed by studies in fragmented tropical forests (Henle, Davies, Kleyer, Margules, & Settele, 2004; Laurance, 2000; Tabarelli, Mantovani, & Peres, 1999). The results of this study indeed showed that shade-tolerant species were present in significantly lower densities, which is likely related to their lower growth rate and the altered environment due to fragmentation such as modified light conditions, resulting in a competitive disadvantage under these conditions (Henle, Davies, Kleyer, Margules, & Settele, 2004). Tree

communities in edge-dominated forest fragments are therefore likely to undergo long-term shifts towards greater dominance of pioneer species.

We found, rather counter-intuitively, that the **(economic) value** of a species positively influenced the density of seedlings and saplings. This may be due to a bias in the choice of our species. We only took four species into consideration because of logistic reasons, which also causes certain traits to overlap. *Albizia grandibracteata* in particular appears to be harvested to a large extent by the local community, but at the same time this species has strong pioneer characteristics and can even initiate vegetative propagation after a mature tree has been cut. Conversely, of the four species, *Ficus* is the least preferred species to be harvested by the locals, but at the same time its regeneration was found to be very low, likely due to the absence of biotic dispersal vectors. Another explanation can be deducted from previous studies around Kibale National Park, where it was determined that although wood harvesting is mostly referred to as selective logging, much of the timber exploitation in the tropics nowadays resembles clear felling because of its intensiveness (Bedigian, 1998). In the mentioned studies this led to the removal and destruction of 50-80% or more of the trees in the considered forests, almost independent of species identity (Bedigian, 1998).

This study focused on four indigenous tree species which gives a good idea about the overall generation and differences between species, but a clear distinction between species effect and the effect of functional traits is in need of more replicates. However, overall we were able to find clear patterns between environmental effects, species traits and the regeneration pattern of each species.

5.4 *The nature of anthropogenic disturbance in the forest*

It is generally known that anthropogenic activities affect the regeneration of plant species to a large extent (Khumbongmayum, Khan, & Tripathi, 2006). This study was performed in an area subjected to human disturbances, which is also the reason why the landscape is fragmented to such a large extent in the first place. To know how tree regeneration responds to such disturbances, it is essential to study the prevalence and nature of the disturbances currently taking place. Studies have shown that the booming population in Uganda, growing at an annual rate of 3.6%, is to blame for a large part for the increasing anthropogenic pressure on the forests (Josephat, 2018). About 40% of the observed environmental degradation was found to be attributed by the population growth after an assessment of the environmental degradation and its causes (The National Service Delivery Survey (NSDS)) was carried out in 2015 (National Environment Management Authority, 2016/2017). Known threats to forests in Uganda include bushmeat hunting (which disrupts seed dispersal (Effiom, Nuñez-Iturri, Smith, Ottosson, & Olsson, 2013)), demand for charcoal and firewood as an alternative for the poor electricity provision, high demand for timber instead of steel and other substitutes, agricultural land use (usually unsustainable due to rural poverty), livestock grazing and the consequences of these activities such as soil degradation and

erosion (Josephat, 2018). The monitoring carried out by KFF was essential to help fill the current knowledge gap in the frequency and impact of human activities taking place in the crater forests.

This analysis of the monitoring data showed that the nature and the frequency of the ongoing disturbances in the forest fragments contributed to the current regeneration patterns of the tree species. The fact that we found a negative correlation between disturbance and young life stages of non-pioneer species (*Funtumia africana* and *Ficus sycomorus*) is in line with the nature of the dominant disturbances in the forest. Grazing by cattle, goats and sheep was the most prevalent type of disturbance, together with the gathering of firewood. Both activities mainly affect the forest understory, and thus seedlings and saplings, due to grazing, browsing and trampling. This is also confirmed by the size of the trees that were destroyed, the destroyed trees were very rarely large, most of the times small, and only to a certain extent of medium size. A previous study in a natural tropical forest showed that the level of human access is an important determinant of anthropogenic disturbance, resulting in a severe decline in the ratio of young life stages to adult trees and poles towards households (Popradit et al., 2015). This decline often results in a shortage of juveniles, which puts the species under the risk of extinction (Popradit et al., 2015). This matches our results, since density of households around each crater forest was chosen as a proxy for disturbance and was negatively correlated with the density of young life stages of the non-pioneers. Activities like burning, grazing, collecting herbs and premature and medicinal plants can make a forest stall when it happens too frequently or to a large extent (Popradit et al., 2015; Omeja, Lwanga, Obua, & Chapman, 2011). In previous forest research cattle grazing has been found to exhibit a negative effect on the regeneration of plants in all circumstances, and this effect is even stronger than the detrimental effect of selective logging (Zamorano-Elgueta et al., 2014). The finding that more trees were destroyed during the rainy season than in the dry season also points to the emergence of higher numbers of seedlings during that period.

The importance and positive impact of forest monitoring is confirmed by the clear downward trend in the number of destroyed trees over the monitoring period (2 years and 5 months). This implies the importance of instances such as lodges (Adamowicz, Naidoo, Nelson, Polasky, & Zhang, 2011), NGO's like Kyaninga Forest Foundation and local protective measures to increase surveillance and create awareness towards the importance of forest conservation and restoration. As is the case in many places, farmers are mainly interested in managing relatively few species, mostly not indigenous, while neglecting the benefits of a higher diversity of trees (Augusseau, Nikiéma, & Torquebiau, 2006). This again emphasizes the importance of sensibilization in the area. This and other studies confirm that particularly when there are no (effective) measures to limit disturbance or forest exploitation, forests surrounded by dense human populations are experiencing a general decline in numbers in all tree size classes (Olupot & Chapman, 2006).

The findings of this study reinforce and expand the existing knowledge about the effects of fragmentation on tropical tree communities, supported by empirical studies in diverse tropical forests. Many of the patterns we saw in the crater lake region are due to the interaction between the characteristics of the environment and the functional traits of the species, which is in agreement with previous studies (Khumbongmayum, Khan, & Tripathi, 2006). Finally, if we accept the differences between seedling and adult assemblages (both taxonomically and ecologically) in the crater forests as a prediction of changes in the tree community, the future tree composition in the ancient crater lake area will likely be drastically different from the one in the past and the one present today. Our study thus expands on growing evidence of rapid consequences of fragmentation on the shifts in tree community composition. However, the question remains in this study if the shortage of seedlings is caused by a limitation in seed dispersal or by post-dispersal processes such as seed survival, germination and seedling establishment, or both (Cordeiro, Ndangalasi, McEntee, & Howe, 2009).

5.5 *Management implications*

Tropical forests of the Albertine rift have received little attention in the past, but their importance in conservation is now increasingly recognised (Plumptre et al., 2007). The forests and lakes in the Albertine Rift region constitute a hotspot of flora and fauna in Africa, mainly because of the high level of endemism and species richness (Winterbottom & Eilu, 2006). A study on the tree species density and diversity in the Albertine Rift region in western Uganda focusing on four protected and intact forests, Bwindi Impenetrable National Park (Bwindi), Kasyoha-Kitomi Forest Reserve (Kasyoha), Kibale National Park (Kibale) and Budongo Forest reserve (Budongo), identified 5747 trees (diameter ≥ 10 cm) from 53 different families, 159 genera and 212 species (Eilu, Hafashimana, & Kasenene, 2004a). Most of the species found belonged to the Euphorbiaceae family (25 species) followed by the Rubiaceae (16 species) and Meliaceae (16 species). Based on these findings, the tree species richness in the Albertine Rift is relatively 'low' in comparison with studies from Neotropical forests (Turner, 2001). This makes protection even more urgent, as a relatively low species diversity combined with high disturbance makes the ecosystem functioning of the forests more vulnerable to becoming disrupted (Biswas & Mallik, 2011). Moreover, 47% of all identified species were limited to a single forest type and 41% occurred at densities of less than one individual per hectare (Eilu, Hafashimana, & Kasenene, 2004b). Regarding the families to which the tree species of this study belong to, it was found that the family to which *Ficus sycomorus* belongs, the Moraceae, and the family to which *Funtumia africana* belongs, the Apocynaceae, contain common species with high frequency and high local abundance in the protected and intact forests of the Albertine Rift in western Uganda (Eilu, Hafashimana, & Kasenene, 2004b). However, in our study we found *Ficus* and *Funtumia* to be the least abundant species, with a problematic population density structure and, especially for *Ficus*, a problematic regeneration. This again proves a

rapid conservation effort and management plan is requiered to ease the human pressure on the crater forests and to prevent species from disappearing.

The forests of the crater lake region afford great value, as timber or non-timber products, to the local communities. In reality, forest remnants outside Kibale National Park are usually not actively protected, and often privately managed by citizens who depend on them for the extraction of resources (Chapman & Chapman, 2003). To ensure sustainablility of woody plants extraction, there is a need for cooperation between all stakeholders to take conscious efforts to prevent harmful events such as grazing, forest fires, premature plant collection and soil erosion (Maua, MugatsiaTsingalia, Cheboiwo, & Odee, 2019). The main stakeholders in the crater lake region include the local community, County governments, the tourism sector and environmentalists (Maua, MugatsiaTsingalia, Cheboiwo, & Odee, 2019). A multiple-use-conservation approach is recommended, with undisturbed areas being strictly protected and designated for conservation purposes (acting as a repository), while peripheral areas can be allocated for sustainble use (Gurmessa, Soromessa, & Kelbessa, 2012).

Conservation actions could include a refinement of our knowledge of the usage of pioneer species' ability to facilitate the establishment of later successional species (Menalled, Kelty, & Ewel, 1998). It has been recommended that generalists and shade-intolerant species should be used for reforestation efforts on large scale degraded lands, while the partially shade-intolerant species are better suited for enrichment of forest gaps or fragment edges in order to achieve a higher diversity (Menalled, Kelty, & Ewel, 1998). Interesting is already the fact that *Albizia grandibracteata*, a pioneer and leguminous woody species, contributes towards a rapid recovery of soil nutrients (Blay, 2002). Detailed studies are required for species showing "none" or "poor" regeneration to fully identify the causes of this and the mechanisms that could enhance natural regeneration (Gurmessa, Soromessa, & Kelbessa, 2012). In addition, further research is recommended on the ecosystem functioning, establishment of new recruits, soil seed banks and the germination success of seeds (Gurmessa, Soromessa, & Kelbessa, 2012). A better understanding of the regeneration pattern in a reference forest such as Kibale National Park will also assist the understanding of regeneration in threatened areas like the crater lake region.

NGO's like Kyaninga Forest Foundation (KFF) are putting a lot of effort in participatory forest management programs involving local farmers to bring up awareness for the conservation and reforestation responsibility. They encourage people to plant native trees, and try to integrate tree planting in school programs, farming and land and river management. At the same time, the farmers become beneficiaries of the economic advantages derived from planting native trees, so that in the end everyone is benefitted by actions against forest loss (Gurmessa, Soromessa, & Kelbessa, 2012).

6. <u>Conclusion</u>

1. Regeneration, ontogenetic class abundances and seedling recruitment limitation varied substantially between the tree species, however, overall regeneration was found to be not optimal. Seedling recruitment was found to be limited due to a combination of restricted seed dispersal and low overall recruit survival. Of the non-pioneer species, *Ficus sycomorus* (an animal-dispersed species) is currently suffering from a very poor regeneration cycle, for which we found evidence this is likely due to a lack or absence of seed dispersers, while *Funtumia africana* (a wind-dispersed species) is still able to recruit seedlings in areas where adults are no longer present. We found a significantly better regeneration for *Albizia grandibracteata* (a strong pioneer), however, also for this species the number of seedlings was determined to be not optimal and young life stages were absent in some fragments containing mature trees. The 'fair' regeneration pattern could in addition be explained by the species' ability of initiating vegetative propagation. *Dombeya torrida* (a species with moderate pioneer traits) was found to have a poor regeneration pattern, likely due to the lack of vegetative propagation capacity. Consequently, despite being a pioneer, this species is also suffering tremendously under the current conditions and human activities in the forest.

2. Environmental characteristics of the fragmented crater lake region were found to contribute to the differences between species and their life stages, depending on their intrinsic traits. The density of each life stage did not depend on dispersal distance, but a higher dispersal capacity enabled species to overcome a limited seed production due to a lack of mature trees in a fragment. The seed source however, needs to be of good quality (high source density and high seed production) and located within a certain distance from the forest fragment. Having pioneer traits significantly increased the density of each ontogenetic stage, which is in line with the pioneer species positively reacting to the environmental effects of fragmentation such as decreasing forest size. However, we found evidence to suggest that even for pioneers a certain degree of protection is required for the species to persist. Shade-tolerant, late-successional species were found in significantly lower densities.

3. The most common disturbances in the crater forests (grazing and firewood collection) mainly affect the young life stages, which was also evidenced by the significantly higher number of small trees destroyed compared to large trees. In addition, the young life stages of species without real pioneer traits (*Funtumia africana* and *Ficus sycomorus*) were found to be negatively correlated to disturbance.

4. Future research suggested by this study includes a comparative study of regeneration in the crater lake area and a protected area like Kibale National Park. Besides this, a tree diversity

study is recommended to be able to take into account competitive interactions and more replicates of each functional trait-category.

5. Overall, the fate of the crater forests is likely to be a continued loss of diversity with destroyed trees being beyond replacement level, unless action is taken against detrimental activities in the forests. State, local and traditional institutions will need to cooperate in the design of management and conservation plans in order to prevent complete loss of the unique crater forest communities. The initiatives and activities of organisations such as KFF have already proven their effectiveness.

7. <u>Summary</u>

7.1 <u>English summary</u>

As tropical forest conversion continues to increase worldwide, conservationists are faced with the challenge of identifying which and how human-induced disturbances influence the population structure and communities in tropical forest ecosystems. In tropical Africa, the rapidly increasing human population size is putting pressure on the remaining unprotected forests due to an increasing exploitation of forest products (Josephat, 2018). Southwest Uganda is a key component of the Albertine Rift, a diverse region important for global conservation, but recently listed as a critically endangered area with a high level of fragmentation (Plumptre et al., 2007; Winterbottom & Eilu, 2006). A proper understanding of the current status of the forest remnants and the mechanisms behind it is needed to assess their conservation potential and predict the survival of present species. This in turn is important for the development of management plans and strategies to ensure the future of the remaining forests.

This dissertation study was carried out to quantify the current status of forest regeneration in the fragmented crater lake region in western Uganda, with particular focus on the interaction between species functional traits and environmental characteristics. Hence, in this study we considered both intrinsic, species-specific traits that determine a species' resilience against disturbance and extrinsic, environmental characteristics of the crater forest remnants. We therefore focused on four different tree species (*Funtumia africana*, *Ficus sycomorus*, *Albizia grandibracteata*, *Dombeya torrida*), all indigenous, representative for the area and having a range of functional traits. *Dombeya* performs gravity dispersal, *Albizia* spreads by ballistic mechanisms, *Funtumia* by wind and *Ficus* by vertebrates.

Here, the first objective was to determine if the current regeneration of the species in forest remnants surrounding the crater lakes is poor, fair or good, as the overall regeneration in the forest is suspected to be stagnating in recent years. To evaluate the regeneration potential of the four tree species, we determined the current population structure by quantifying the density of four ontogenetic stages or size classes (seedlings, saplings, poles and adults) using fixed-width strip transects in each crater forest. This way, not only a forest regeneration assessment was made, but this also enabled an evaluation of the conservation status and adds to overcoming the deficiency of field data on present species. We hypothesized that the overall tree density and current regeneration pattern would differ between species and their ontogenetic stages. The overall population structure of the crater forests showed a greater proportion of adults, followed by poles, saplings and seedlings. Consequently, the current overall regeneration pattern was found to be not optimal, with the population structure being highly dependent on the species identity. For *Ficus* the poor regeneration pattern was unexpected, since this species is dispersed over large distances by animals with the national park serving as a possible seed source. *Funtumia*, a wind-dispersed species, showed a reversed pattern in which seedlings were still found despite the very low density and distribution of adult trees, proving that the absence of large trees at

high harvesting pressures can be compensated by a high dispersal ability (in this case wind dispersal). However, the overall density was still very low, showing that disturbance in the first place must be addressed in order for the species to persist. *Albizia*, a strong pioneer species, and *Dombeya*, a moderate pioneer species, showed the highest densities in all size classes. However, the regeneration pattern of *Albizia* was only "fair", with vegetative propagation likely contributing to the better regeneration pattern in comparison to the other species. *Dombeya* in addition showed a poor regeneration pattern, demonstrating that even pioneer species are suffering under the current conditions and anthropogenic activities in the forests. These findings enabled us to make predictions on how the community will change, and even completely disappear under the current extinction debt if no action is taken.

Secondly we determined whether and to what extent differences between species and their ontogenetic stages can be attributed to the environmental characteristics of the considered forest fragments. The research was carried out in 21 crater forests, for which the following environmental variables were measured: distance from the national park (in all cases Kibale National Park except for one which was closer to Semuliki Wildlife reserve), distance to the nearest crater forest, presence of possible seed dispersers, forest size and a proxy for disturbance. The environmental characteristics of the fragmented crater lake region were hypothesized to have a differential effect on species and their life stages. Our results demonstrated clear correlations between the density of the ontogenetic stages and the environmental variables, with indeed differences between species and ontogenetic stages. The negative correlation between the density of young life stages of *Funtumia* and distance to the national park provides evidence for the importance of a healthy seed source for seed supply (and subsequently new recruits) to the crater forests. We demonstrated that the lack of young life stages of *Ficus* is likely due to the lack of seed dispersers present in the crater forests. Distance from the national park seemed to be overall the most important environmental variable shaping the density variation of the selected species, except for *Albizia*, for which the size of the forest was the most important environmental variable. Density of all life stages of *Albizia* increased with decreasing forest size and increasing disturbance which is typical for a strong pioneer, since this increases edge effects and pioneers are better adapted to disturbance. All species were negatively correlated with distance to the national park (where most of the lodges are located), which also points towards the need of a certain degree of surveillance and protection in the forests for each species. *Dombeya* showed similar correlations as *Albizia*, but seems to suffer more from the lack of protection in the crater forests. The reason for this is unclear, but probably due to either its lack of the ability of vegetative propagation, not reaching suitable germination sites in the highly disturbed forest due it its poor dispersal capacity (and suffering density-dependent effects) or due to the loss of an essential pollinator.

The third objective was to determine whether and to what extent differences between species and their ontogenetic stages can be attributed to their different life-history traits and economic value. The

traits we have focused on were dispersal ability (in terms of distance reached by the seeds), successional niche (in terms of pioneer characteristics) and local (economic) value of a species. Species traits were hypothesised to contribute to the differences in responses of species to fragmentation. **Dispersal distance** was found to not significantly affect the density of any of the ontogenetic stages. However, this might be due to an alteration in the dispersal distances ranking due to fragmentation effects. As was derived from the correlation between the young life stages and environmental factors, the otherwise long distance seed dispersal of *Ficus* seems to be disrupted by the lack of seed dispersers. However, as was demonstrated for *Funtumia*, a high dispersal ability is important to compensate for a low local density of mature trees in seedling recruitment. **Pioneer characteristics** positively affected the density of all life stages, which indicates that the tree community in small forest fragments is likely to undergo a long-term shift towards greater dominance of pioneer species. More counter-intuitively was the finding that the density of seedlings and saplings is higher for species with higher **economic value**. This may be due to a bias in the choice of our species. We only took four species into consideration because of logistic reasons, which causes certain traits to overlap. *Albizia* is a relatively highly valued species for harvest, but due to its pioneer characteristics the species showed a relatively high density of seedlings and saplings. Vice versa, *Ficus* is generally not targeted for harvest, while still few individuals of the young stages were found due to its disrupted seed dispersal.

Lastly, we evaluated the nature and prevalence of the anthropogenic activities taking place in the forests. To do this we used the data of a 2.5-year forest monitoring around Lake Kyaninga in an exploratory analysis to be able to develop management plans for the region. The current human activities were hypothesized to have a direct influence on the observed demographic distributions. Our analyses showed that the most prevalent disturbance is grazing, followed by firewood gathering. This mainly disturbs the ground vegetation, and thus seedlings and saplings, due to trampling, browsing and grazing. This is in line with the negative correlation between the density of young life stages of the non-pioneer species (*Funtumia* and *Ficus*) and disturbance. The importance of forest monitoring is confirmed by the downward trend in the number of destroyed trees over the monitoring period. This implies the positive impact of lodges, NGO's like Kyaninga Forest Foundation and local protective measures to increase surveillance and create awareness towards the importance of forest conservation and restoration.

In conclusion we were able to find clear patterns between environmental variables, species traits and the regeneration status of the species. We found evidence to suggest that the only way of retaining the diversity in the crater lake area, is to control human disturbance in the area. Particularly in the face of the booming human population, a collaborative effort of all stakeholders will be needed to ensure long-term persistence of the crater forests in western Uganda.

Door de wereldwijde toenemende druk op tropisch woud, staan conservationisten voor de uitdaging om te identificeren welke en hoe menselijke verstoringen de populatiestructuur en gemeenschappen in tropische bosecosystemen beïnvloeden. In tropisch Afrika oefent de snel toenemende menselijke populatie druk uit op de overgebleven onbeschermde wouden door een stijgende vraag naar woudproducten (Josephat, 2018). Zuidwest-Oeganda is een belangrijk onderdeel van de Albertine Rift, een diverse regio die van belang is voor instandhouding, maar recent opgelijst is als een kritiek bedreigd gebied met een hoge fragmentatiegraad (Plumptre et al., 2007; Winterbottom & Eilu, 2006). Het begrijpen van de huidige status van de bosfragmenten en de mechanismen die erachter zitten, is nodig om hun potentieel voor instandhouding te beoordelen en de overleving van aanwezige soorten te voorspellen. Dit is op zijn beurt belangrijk voor de ontwikkeling van beheerplannen en-strategieën om de toekomst van de resterende wouden te verzekeren.

Dit thesisonderzoek werd uitgevoerd om de huidige status van woudregeneratie in het gefragmenteerde kratermeergebied in West-Oeganda te kwantificeren, met bijzondere aandacht voor de interactie tussen functionele kenmerken van soorten en omgevingskenmerken. Daarom hebben we in deze studie zowel soortspecifieke (intrinsieke) eigenschappen (die de veerkracht van soorten tegen verstoring bepalen) als omgevingskenmerken (extrinsiek) van de kraterwouden beschouwd. We hebben ons hiervoor gericht op vier verschillende boomsoorten (*Funtumia africana*, *Ficus sycomorus*, *Albizia grandibracteata*, *Dombeya torrida*) die inheems zijn, representatief voor het gebied en een reeks aan functionele eigenschappen bezitten. *Dombeya* verspreidt zich via de zwaartekracht, *Albizia* verspreidt zich door middel van ballistische mechanismen, *Funtumia* via de wind en *Ficus* door vertebraten.

Het eerste doel van deze studie was bepalen of de huidige regeneratie van de soorten in de wouden rond de kratermeren slecht, redelijk of goed is, omdat vermoed wordt dat de algehele regeneratie in deze regio de afgelopen jaren stagneert. Om het regeneratiepotentieel van de vier boomsoorten te evalueren, bepaalden we de huidige populatiestructuur door de densiteit van vier ontogenetische stadia of grootteklassen (zaailingen, jonge boompjes, palen en volwassenen) te kwantificeren met behulp van transecten met een vaste breedte in elk kraterwoud. Op deze manier werd niet alleen de regeneratie in de wouden beoordeeld, maar maakte dit ook een evaluatie van de staat van instandhouding mogelijk en draagt dit daarenboven bij tot het verhelpen van het tekort aan veldgegevens over de soorten. Onze hypothese was dat de algehele boomdensiteit en het huidige regeneratiepatroon zou verschillen tussen de soorten en hun levensstadia. De totale populatiestructuur van de kraterwouden vertoonde een groter aandeel volwassenen, gevolgd door palen, jonge boompjes en zaailingen. Bijgevolg bleek het huidige algehele regeneratiepatroon niet optimaal te zijn, waarbij de populatiestructuur sterk afhankelijk bleek te zijn van de soortidentiteit. Voor *Ficus* was het niet-optimale regeneratiepatroon onverwacht, aangezien deze soort door dieren over grote afstanden verspreid wordt en het nationale park als mogelijke

zaadbron kan fungeren. *Funtumia*, een door de wind verspreide soort, vertoonde een omgekeerd patroon waarbij ondanks de zeer lage densiteit en verspreiding van volwassen bomen nog steeds zaailingen werden aangetroffen, wat bewijst dat de afwezigheid van adulte bomen onder hoge verstoring kan worden gecompenseerd door een hoog verspreidingsvermogen (in dit geval winddispersie). De totale densiteit was echter nog steeds erg laag, wat aantoont dat verstoring in de eerste plaats moet worden aangepakt om de soort in stand te houden. *Albizia*, een sterke pioniersoort, en *Dombeya*, een gematigde pioniersoort, vertoonden de hoogste densiteit in alle grootteklassen. Het regeneratiepatroon van *Albizia* was echter slechts 'redelijk', waarbij vegetatieve vermeerdering waarschijnlijk aan de basis lag van het betere regeneratiepatroon in vergelijking met de andere soorten. *Dombeya* vertoonde daarbovenop een slecht regeneratiepatroon, wat aantoont dat zelfs pioniersoorten lijden onder de huidige omstandigheden en de antropogene activiteiten in de wouden. Deze bevindingen stelden ons in staat voorspellingen te doen over hoe de gemeenschap zal veranderen en zelfs volledig zal verdwijnen onder de huidige 'extinction debt' als er geen actie wordt ondernomen.

Ten tweede hebben we bepaald of en in hoeverre verschillen tussen soorten en hun ontogenetische stadia kunnen worden toegeschreven aan de omgevingskenmerken van de beschouwde bosfragmenten. Het onderzoek werd uitgevoerd in 21 kraterwouden, waarvoor de volgende omgevingsvariabelen gemeten werden: afstand tot het nationale park (in alle gevallen Kibale National Park behalve voor een krater dat dichter bij het Semuliki Wildlife Reserve lag), afstand tot het dichtstbijzijnde kraterwoud, aanwezigheid van mogelijke zaadverspreiders, woudoppervlakte en een proxy voor verstoring. Onze hypothese was dat de omgevingskenmerken van de kraterwouden een differentieel effect zouden hebben op soorten en hun levensstadia. Onze resultaten toonden duidelijke correlaties tussen de densiteit van de ontogenetische stadia en de omgevingsvariabelen, die inderdaad verschilden tussen soorten en ontogenetische stadia. De negatieve correlatie tussen de densiteit van jonge levensstadia van *Funtumia* en de afstand tot het nationale park bewijst het belang van een gezonde zaadbron in de zaadtoevoer (en vervolgens nieuwe rekruten) naar de kraterwouden. We hebben aangetoond dat het gebrek aan jonge levensstadia van *Ficus* waarschijnlijk te wijten is aan het ontbreken van zaaddispersers in de kraterwouden. Afstand tot het nationale park leek over het algemeen de belangrijkste verklarende omgevingsvariabele te zijn van de densiteitsvariatie van de geselecteerde soorten, behalve voor *Albizia*, waarvoor de grootte van het woud de belangrijkste omgevingsvariabele was. De densiteit van alle levensstadia van *Albizia* nam toe met afnemende woudoppervlakte en toenemende verstoring, wat typisch is voor een sterke pionier, aangezien dit de randeffecten vergroot en pioniers beter zijn aangepast aan verstoring. Alle soorten waren negatief gecorreleerd met afstand tot het nationale park (waar de meeste lodges zich bevinden), wat ook wijst op de nood aan een zekere mate van bewaking en bescherming in de kraters voor elke soort. *Dombeya* vertoonde vergelijkbare correlaties als *Albizia*, maar lijkt meer te lijden onder het gebrek aan bescherming in de kraterwouden. De reden hiervoor is

onduidelijk, maar waarschijnlijk is dit vanwege ofwel het gebrek aan vegetatieve vermeerdering, het niet bereiken van geschikte kiemlocaties in het sterk verstoorde woud door het slechte verspreidingsvermogen (en het lijden aan densiteitsafhankelijke effecten) of door het verlies van een essentiële bestuiver.

Het derde doel was om te bepalen of en in hoeverre verschillen tussen soorten en hun ontogenetische stadia kunnen worden toegeschreven aan hun verschillende functionele eigenschappen en economische waarde. De eigenschappen waar we ons op gericht hebben waren dispersievermogen (in termen van bereikte afstand), successie-niche (in termen van pionierkenmerken) en lokale (economische) waarde. Er werd verondersteld dat soortenkenmerken zouden bijdragen aan de verschillen in reacties op fragmentatie. De **dispersieafstand** bleek de densiteit van geen van de ontogenetische stadia significant te beïnvloeden. Dit kan echter te wijten zijn aan een wijziging in de rangschikking van de verspreidingsafstanden als gevolg van fragmentatie-effecten. Zoals werd afgeleid uit de correlatie tussen de jonge levensstadia en omgevingsfactoren, lijkt de anders lange-afstandsverspreiding van *Ficus* te worden verstoord door het ontbreken van zaadverspreiders of een essentiële bestuiver. Hoewel, zoals aangetoond voor *Funtumia*, is een hoog verspreidingsvermogen belangrijk om te compenseren voor een lage lokale densiteit van adulte bomen. **Pionierkenmerken** hadden een positieve invloed op de densiteit van alle levensstadia, wat indiceert dat de bomengemeenschap in kleine woudfragmenten een verschuiving op de lange termijn zal ondergaan richting een grotere dominantie van pioniersoorten. Contra-intuïtiever was de bevinding dat de densiteit van zaailingen en jonge boompjes hoger was voor soorten met een hogere **economische waarde**. Dit kan te wijten zijn aan een bias in de keuze van onze soorten. We hebben slechts vier soorten in overweging genomen om logistieke redenen, waardoor bepaalde eigenschappen met elkaar overlappen. *Albizia* is een relatief geprefereerde soort om te kappen, maar vanwege zijn pionierkenmerken vertoonde deze een relatief hoge densiteit aan zaailingen en jonge boompjes. Vice versa, *Ficus* is over het algemeen niet het doelwit voor houtkap, terwijl er toch weinig individuen uit de jonge stadia werden gevonden vanwege de verstoorde zaadverspreiding.

Ten slotte hebben we de aard en frequentie van de antropogene activiteiten geëvalueerd die plaatsvinden in de kraterwouden. We gebruikten daarvoor de gegevens van een 2,5-jaar lange monitoring rond het meer van Kyaninga in een verkennende analyse om beheerplannen voor de regio te kunnen ontwikkelen. Er werd verondersteld dat de huidige verstoringen een directe invloed hebben op de waargenomen demografische distributies. Uit onze analyses bleek dat de meest voorkomende verstoring begrazing is, gevolgd door het verzamelen van brandhout. Dit verstoort voornamelijk de bodemvegetatie en dus zaailingen en jonge boompjes door vertrappen en grazen. Dit sluit aan bij de negatieve correlatie tussen de densiteit van jonge levensstadia van de niet-pioniersoorten (*Funtumia* en *Ficus*) en de verstoringsintensiteit. Het belang van bosmonitoring werd bevestigd door de dalende trend in het aantal vernietigde bomen gedurende de monitoringperiode. Dit impliceert de positieve impact van

lodges, NGO's als Kyaninga Forest Foundation en lokale beschermingsmaatregelen om de bescherming en het bewustzijn over het belang van woudbehoud en -herstel te vergroten.

Ter conclusie konden we duidelijke patronen zien tussen omgevingsvariabelen, soortkenmerken en de regeneratiestatus van de soorten. We hebben aanwijzingen gevonden dat de enige manier om de diversiteit in het kratermeergebied te behouden, is door de menselijke verstoring in het gebied te beperken. Met name in het licht van de snel groeiende menselijke populatie zal een gezamenlijke inspanning van alle belanghebbenden nodig zijn om ervoor te zorgen dat de kraterwouden in het westen van Oeganda op lange termijn blijven bestaan.

9. <u>Reference list</u>

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10. <u>Appendix</u>

Table S1 – Lake names from Figure 1.

N°	Lake/District
	Fort portal
1	Saaka
2	Kyaninga
3	Ekikoto
4	Kayihara
	Kasenda
5	Nyamirima
6	Nyinabulitwa
7	Nyabikere
8	Nkuruba
9	Lyantonde
10	Kifuruka
11	Nyinambuga
12	Rukwanzi
13	Katanda
14	Kanyango
15	Rwenjuba
16	Kasenda
17	Murusi
18	Kitere
19	Kanyamukali
20	Ntambi
21	Nyamugosani

Table S2 – Pairwise comparisons between the ontogenetic stages per species, using emmeans.

Species density	Contrast	Estimate	SE	df	t-value	p-value
Funtumia africana	Adult-Pole	0.6101	2.07	60	0.294	0.9910
	Adult-Sapling	0.0292	2.07	60	0.014	1.0000
	Adult-Seedling	-3.8101	2.07	60	-1.838	0.2661
	Pole-Sapling	-0.5809	2.07	60	-0.280	0.9922
	Pole-Seedling	-4.4202	2.07	60	-2.132	0.1548
	Sapling-Seedling	-3.8393	2.07	60	-1.852	0.2598
Dombeya torrida	Adult-Pole	17.57	16.2	60	1.082	0.7020
	Adult-Sapling	64.35	16.2	60	3.961	**0.0011****
	Adult-Seedling	60.62	16.2	60	3.731	**0.0023****
	Pole-Sapling	46.78	16.2	60	2.879	**0.0275***
	Pole-Seedling	43.05	16.2	60	2.649	**0.0492***
	Sapling-Seedling	-3.73	16.2	60	-0.230	0.9957
Ficus sycomorus	Adult-Pole	27.306	6.49	60	4.210	**< 0.001*****
	Adult-Sapling	31.316	6.49	60	4.828	**< 0.001*****
	Adult-Seedling	30.521	6.49	60	4.705	**< 0.001*****
	Pole-Sapling	4.009	6.49	60	0.618	0.9259
	Pole-Seedling	3.214	6.49	60	0.496	0.9598
	Sapling-Seedling	-0.795	6.49	60	-0.123	0.9993
Albizia grandibracteata	Adult-Pole	-3.86	19.2	60	-0.201	0.9971
	Adult-Sapling	39.11	19.2	60	2.035	0.1870
	Adult-Seedling	37.24	19.2	60	1.937	0.2237
	Pole-Sapling	42.97	19.2	60	2.235	0.1255
	Pole-Seedling	41.10	19.2	60	2.138	0.1530
	Sapling-Seedling	-1.87	19.2	60	-0.097	0.9997

Table S3 – p-values of one-way PERMANOVA pairwise comparisons (Bonferroni-corrected).

	Funtumia africana	*Dombeya torrida*	*Ficus sycomorus*	*Albizia grandibracteata*
Funtumia africana		**< 0.001**	**< 0.001**	**< 0.001**
Dombeya torrida	**< 0.001**		**0.0114**	1
Ficus sycomorus	**< 0.001**	**0.0114**		**0.0018**
Albizia grandibracteata	**< 0.001**	1	**0.0018**	

Table S4 – Scores of the variables on the ordination axes (axis 1-3) of the between-group PCA.

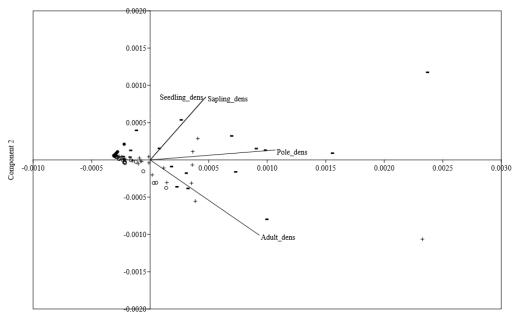| Variable	Axis 1	Axis 2	Axis 3
Seedling density	0.30118	0.5372	0.19486
Sapling density	0.30354	0.53807	0.48188
Pole density	0.68106	0.084695	-0.71242
Adult density	0.59441	-0.644	0.47147

Table S5 – The fraction of eigenvalues of each ordination axis (axis 1-4) for each PCA. This gives a measure of the percentage of variance in the data accounted for by each of the principal components, the explained variation.

Species in the PCA	Axis 1	Axis 2	Axis 3	Axis 4
Funtumia africana	0.8625	0.1075	0.0300	/
Dombeya torrida	0.8720	0.0662	0.0607	0.0011
Ficus sycomorus	0.9912	0.0083	0.0005	0
Albizia grandibracteata	0.6871	0.1833	0.1069	0.0227

Table S6 – The scores of the environmental variables for ordination axis 1 and 2 in each PCA plot. The scores show how well an environmental variable is correlated with the respective axes, this is also visualized in the PCA plot. The higher the value, the higher the correlation is (negative or positive).

Environmental variable	CorS.1	CorS.2
Funtumia africana		
Forest size	-0.2152	-0.1099
Disturbance	-0.1685	0.1896
Distance NP	-0.2520	-0.0063
Nearest crater	-0.0389	-0.1515
Dombeya torrida		
Forest size	-0.2319	0.1052
Disturbance	-0.0920	-0.1704
Distance NP	-0.3195	-0.1466
Nearest crater	-0.3348	-0.0275
Ficus sycomorus		
Forest size	-0.1407	0.0076
Disturbance	0.1030	-0.0378
Distance NP	-0.2851	-0.1723
Nearest crater	-0.2806	-0.0430
Albizia grandibracteata		
Forest size	-0.3351	0.0688
Disturbance	0.1258	0.0730
Distance NP	-0.3033	-0.1003
Nearest crater	-0.1200	-0.2727

Table S7 – The cumulative fit of the response variables for ordination axis 1 and 2 in the PCA. This shows which fraction of the variation in each response variable is explained by the respective axes.

	CFit1	CFit2
Funtumia africana		
Seedling density	0.9999	1.0000
Sapling density	0.0097	0.1094
Pole density	0.0094	0.9915
Adult density	0.0094	0.9915
Dombeya torrida		
Seedling density	0.0069	0.3681
Sapling density	0.2741	0.5591
Pole density	0.8982	0.9627
Adult density	0.9537	0.9867
Ficus sycomorus		
Seedling density	0.0731	0.0731
Sapling density	0.0322	0.0323
Pole density	0.0225	1.0000
Adult density	1.0000	1.0000
Albizia grandibracteata		
Seedling density	0.5574	0.5752
Sapling density	0.6831	0.8185
Pole density	0.9080	0.9248
Adult density	0.3607	0.9934

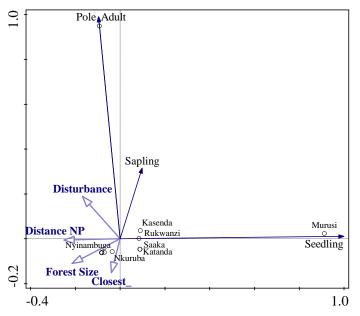**Figure S1** – Between-group PCA plot discriminating species by ontogenetic stage.

Figure S2 – PCA-plot showing the density of all life stages of *Funtumia africana* in relation to the environmental variables, as well as all surveyed sites (open circles). The sites where seedlings were found but adults were absent are named.