

Reduced abundance of late-successional trees but not of seedlings in heavily compared with lightly logged sites of three East African tropical forests

Jasper Mbae Kirika^{*,†,‡}, Katrin Böhning-Gaese^{‡,§}, Bonny Dumbo[#] and Nina Farwig^{*,†,1}

* Department of Ornithology, National Museums of Kenya, Nairobi, Kenya

† Institut für Zoologie, Abt. V. – Ökologie, Johannes-Gutenberg Universität Mainz, Becherweg 13, 55128 Mainz, Germany

‡ Johann Wolfgang Goethe Universität, Department of Biological Sciences, Siesmayerstr. 70, D-60323 Frankfurt (Main), Germany

§ Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, D-60325 Frankfurt (Main), Germany

P.O. Box 143, Kakamega, Kenya

(Accepted 7 May 2010)

Abstract: Logged forests form an increasingly large proportion of tropical landscapes but disproportionately few studies have studied the impact of forest disturbance, e.g. lightly vs. heavily logged, on tree and seedling communities simultaneously. We sampled all trees (on 1 ha) and all recently germinated seedlings (on 90 m²) in three lightly and three heavily logged sites in each of the following three East African tropical forests: Budongo Forest and Mabira Forest in Uganda and Kakamega Forest in Kenya. We analysed species richness, diversity, abundance and community composition of late- and early-successional trees and seedlings. We recorded no difference in species richness or diversity of late-successional or early-successional trees between lightly and heavily logged sites. However, the abundance of late-successional species was lower in heavily than lightly logged sites. Moreover, there was no difference in species richness or diversity of trees among the three forests. Yet, abundances of late-successional trees were higher in Budongo Forest than in Mabira Forest and Kakamega Forest. Species richness, diversity and abundance of seedlings did not differ between lightly and heavily logged sites. Only the abundance of seedlings of late-successional species differed among the forests with more individuals in Budongo Forest than in Mabira Forest. This was corroborated by non-metric multidimensional scaling (NMDS) showing clear differences in composition of tree and seedling communities among the three forests. Thus, both, the tree and seedling communities differed significantly among the three forests but not between lightly and heavily logged sites.

Key Words: canopy openness, early-successional trees, forest regeneration, late-successional trees, selective logging, tropical forest

INTRODUCTION

Global forest destruction has accelerated in the last few decades particularly in the tropics where between 25% and 50% of the forest have been converted to other land-uses (Lewis 2006, Pimm & Raven 2000). While many studies have addressed the impact of clear-cutting and fragmentation on biodiversity and ecological processes (Lewis 2006, Turner 1996), local forms of forest disturbance such as selective logging have been investigated less intensively but can have complex effects

on forest ecosystems (Lewis 2006). Even if only 3–10% of trees in a selectively logged forest are removed, around 50% of the trees are damaged as a result of falling trees bringing down neighbouring trees (Struhsaker 1997). This damage leads to reduction in canopy cover and creation of large gaps, changing tree distributions (Struhsaker 1997). Furthermore, large gaps promote the survival of early-successional species and reduce the number of late-successional species (Laurance *et al.* 1998).

In the long term, species persistence in selectively logged areas depends on the availability of seeds, seedlings and saplings (Martínez-Ramos & Soto-Castro 1993). Seedling communities of long-lived tree species may therefore indicate the regeneration potential of forests. Logging of forests has been demonstrated

¹ Corresponding author. Email: farwig@staff.uni-marburg.de Present address: Dept. Ecology – Conservation Ecology, Faculty of Biology, Philipps-Universität Marburg, Karl-von-Frisch-Str. 8, 35032 Marburg, Germany.

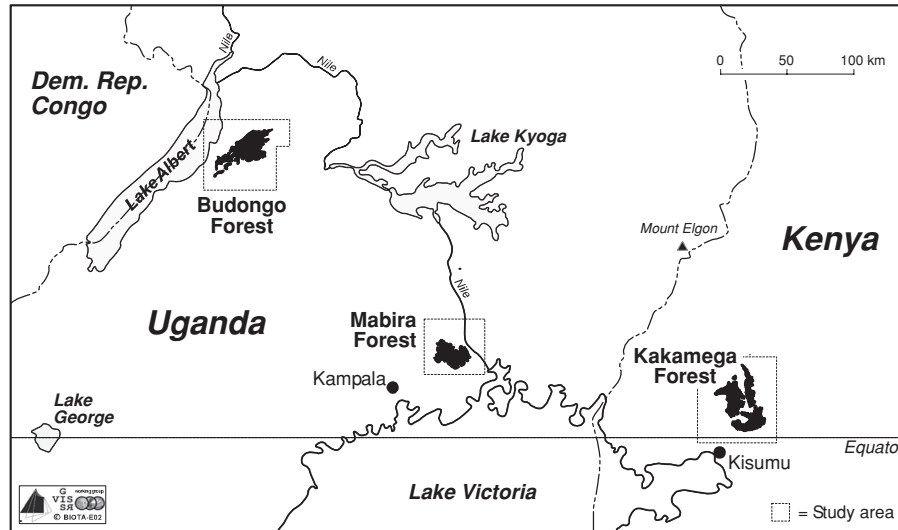


Figure 1. Map of Kenya and Uganda showing the location of Budongo, Mabira and Kakamega Forests. Courtesy of G. Schaab.

to affect seedling diversity and abundance through reduced availability of seeds (Makana & Thomas 2004, Plumptre 1996), increased seedling predation (Struhsaker 1997), decreased survival and growth of seedlings (Ramirez-Marcial 2003) and reduced overall sapling recruitment (Terborgh *et al.* 2008). Elevated hunting of mammals in forests has been shown to affect the seedling composition (Peres & van Roosmalen 2002, Terborgh *et al.* 2008). In addition, changes in abiotic conditions such as light, temperature and humidity have an impact on seedling establishment (Ellison *et al.* 1993, Makana & Thomas 2005). There is evidence that the density and species diversity of seedlings is lower in heavily compared with lightly logged forests (Farwig *et al.* 2008a). These impacts of selective logging on seedling communities, in the long term, probably lead to changes in tree communities (Hurt & Pacala 1995, Terborgh *et al.* 2008).

Most studies on effects of selective logging on tree communities and long-term patterns of seedling establishment have been carried out within a restricted study area (Chapman & Chapman 1997, Farwig *et al.* 2008a, Makana & Thomas 2005, Terborgh *et al.* 2008). Yet, it is vital to understand whether selective logging shows comparable effects on larger spatial scales, i.e. among different forests within a larger region. A study on the impact of differences in logging histories in three East African tropical forests showed reduced numbers of frugivorous birds and diminished seed dispersal of a small-seeded tree in heavily compared with lightly logged sites in each of the three forests (Kirika *et al.* 2008a). Also, the density of seedlings of the focal tree tended to be lower in heavily disturbed compared with lightly logged sites (Kirika *et al.* 2008a). Thus, it is reasonable to

hypothesize that selective logging might modify also the seedling community on this regional scale.

In this study, we tested: (1) whether differences in logging histories led to modifications in the tree communities due to selective logging of late-successional species and (2) whether modified tree communities and reduced numbers of frugivorous birds in highly disturbed forest sites led to changes in the composition of the seedling communities due to reduced recruitment of late-successional species. We therefore tested the impact of differences in logging histories on species richness, diversity, abundance and composition of late-successional and early-successional trees and seedlings in three East African tropical forests.

METHODS

Study areas

The study was carried out in three East African tropical forests, Budongo Forest and Mabira Forest in Uganda and Kakamega Forest in Kenya (distances: Budongo-Mabira 190 km, Budongo-Kakamega 385 km, Mabira-Kakamega 195 km, Figure 1). The three forests have been subjected to varying levels of past and present anthropogenic disturbances with selective logging having the most prominent impact on forest structure, especially canopy openness (Bleher *et al.* 2006). Prior to the investigation, we selected lightly and heavily logged sites within each forest. In addition, Budongo Forest has one site that could be classified as never logged, primary forest that we used as a control site. We used this undisturbed site only for descriptive statistics, but did not include it

in the statistical comparison among the three forests to avoid an unbalanced design.

Budongo Forest (1°35'N–1°55'N, 31°8'E–31°42'E, 1100 m asl, 428 km² of forest cover) is the most western of the three forests and closest to the Congo–Guinean rain-forest belt (Figure 1). Average annual precipitation is about 1410 mm with rainfall mostly between April and May and between August and October. Budongo Forest is described as a medium-altitude, semi-deciduous forest, with a tendency for *Cynometra alexandri* C. H. Wright to become monodominant (Plumptre 1996). Selective logging and treatment with arboricides has created a mosaic of forest types of which mixed forest is now the most common type (Plumptre 1996). The forest has over 260 species of trees (Howard 1991, Sheil 1996). The study was carried out in compartment N3 (logged in 1947–1952), a lightly logged site, and W22 (logged in 1963–1964 and again in 1996–1997), a heavily logged site. In addition we sampled trees and seedlings in N15 (never logged), a never logged, primary forest stand. For more details on Budongo Forest see Eggeling (1947), Howard (1991) and Plumptre (1996).

Mabira Forest (0°23'N–0°35'N, 32°50'E–33°7'E, 1150 m asl, about 306 km² forest cover) is located in Mukono district of central Uganda and lies between Budongo and Kakamega Forest (Figure 1). Annual precipitation is 1640 mm. The vegetation can be broadly classified as medium-altitude, moist semi-deciduous forest (Howard 1991). Mabira Forest reserve has been subjected to extensive encroachment, pit-sawing, charcoal burning and hunting in the past and present. The forest has 189 tree species (Boffa *et al.* 2008). The study sites in Mabira Forest were identified from land-use maps and geographic information system coverage compiled by the Forest Department. Within the forest we selected lightly logged sites (Buwola area), characterized by relatively undisturbed forest with only localized pit-sawing activity, and heavily logged sites (Najjembe area) located close to settlement areas and characterized by intense selective logging. For more details on Mabira Forest see Howard (1991) and Naidoo (2004).

Kakamega Forest (0°10'N–0°21'N, 34°47'E–34°58'E, 1550–1650 m asl) is a mid-altitude tropical forest and is considered to be the easternmost outlier of the Congo–Guinean rain-forest belt (Kokwaro 1988) (Figure 1). Kakamega Forest receives an average annual rainfall of 1910 mm. The main forest area covers about 85 km² of near-natural forest that is surrounded and interspersed by secondary forest, clearings and glades, as well as tea and timber plantations (Lung & Schaab 2006). Kakamega Forest has over 112 species of trees many of which are of Congolese lowland forest affinities (Althof 2005). Areas managed by the Kenya Wildlife Service have low levels of human disturbance, especially of selective logging,

whereas those managed by the Kenya Forest Service have high levels of disturbance (Bleher *et al.* 2006). We selected study sites under the management of the Kenya Wildlife Service as lightly logged (Buyangu area, northern part of main forest block) and those under the management of the Kenya Forest Service as heavily logged sites (Isecheno area, southern part of main forest block). For more details on Kakamega Forest see Bleher *et al.* (2006) and Kokwaro (1988). The selected little and heavily logged sites within each forest correspond to the ones in Kirika *et al.* (2008a).

Data collection

We established in Budongo Forest twelve 1-ha plots (six plots in primary forest as control plots, three plots in lightly logged sites and three plots in heavily logged sites, distance range: 0.3–4.7 km) and in each of the two other tropical forests, Mabira and Kakamega Forests, six 1-ha plots (three plots in lightly logged sites and three plots in logged disturbed sites, distance range: 0.4–6.3 km, 0.4–13.5 km, respectively). Note that the 1-ha plots with the same logging histories within a forest are located relatively close to each other (range 0.3–1.6 km) while distance among heavily and lightly logged plots was on average 5 km. Unfortunately, we could not avoid this design due to logistical reasons. The three forests have only very few access roads and we were forced to select sites that were within reasonable walking distance from these roads. Still 300 m as a minimum distance between plots of the same logging histories should be sufficient to treat them as independent replicates (Farwig *et al.* 2008a, Makana & Thomas 2005).

Censuses of the tree and seedling communities of the three forests were carried out in two sessions from November 2004 to March 2005, and from October 2005 to March 2006 (Budongo: November 2004 to January 2005 and October to November 2005, Mabira: January to February 2005 and February to March 2006, Kakamega: February to March 2005 and December 2005 to January 2006). During each session we sampled tree and seedling communities of six plots in Budongo (three plots in primary forest, and either two in lightly logged and one in a heavily logged sites or vice versa) and three plots in Mabira and Kakamega (two in lightly logged and one in a heavily logged sites or vice versa).

Plots of 100 × 100 m in size were laid out at least 100 m from the forest edge in order to reduce edge effects. Each of the 1-ha plots consisted of five line transects of 100 m length. Within each plot we selected nine point locations with three points placed along the first line transect (at 10, 50 and 90 m), three points along the third line transect and three along the fifth line transect. Additionally, we established ninety 1-m² subplots following the design by Harms *et al.* (2000). The

1-m² subplots were established in groups of three with six groups along each line transect (at 0, 20, 40, 60, 80 and 100 m) and placed at a distance of 2 m perpendicularly to the transect.

To quantify logging history we visually estimated canopy openness at each point location by looking vertically through a 5-cm-long tube with a diameter of 5 cm and estimating the percentage of the diameter through which the sky was visible. We then calculated the average over the nine measurements for each plot.

We identified and counted all trees >10 cm diameter at breast height (dbh) on the 1-ha plots by walking along five line transects separated from each other by 20 m, and recording all trees within 10 m to the left and 10 m to the right of the line transect (thereby covering a total area of 1 ha). We defined all woody plants with a dbh >10 cm as trees. Trees were identified using Beentje (1994) and Hamilton (1991). All trees were later classified as late-successional or early-successional depending on the ability to survive in forest shade following Lwanga (2003), Sheil *et al.* (2000) and E. Fischer (pers. comm.).

We quantified the seedling community on the ninety 1-m² subplots. During mapping wire frames were laid down to demarcate the area. All recently germinated seedlings of tree species were identified to species level and their numbers were counted. We defined as seedlings all plant individuals that had cotyledons and/or first or second sets of true leaves and absence of a woody stem. Species identification was carried out by a local taxonomist (B. Dumbo) from 20 y of experience in identifying tree and seedling species in Kenya, Uganda, Rwanda and Democratic Republic of Congo. Seedlings were classified into the same successional classes as the trees.

Data analysis

We calculated rarefied species richness (Hurlbert 1971), species diversity (Simpson index) and total abundance separately for late- and early-successional species per 1-ha plots for trees and over the ninety 1-m² subplots per hectare for seedlings. We tested the effect of selective logging, distinguishing between lightly and heavily logged sites (fixed effect) and of forest (random effect) on canopy openness, rarefied species richness, species diversity, and abundance of late- and early-successional trees and seedlings. For analysis, canopy openness was arcsine-square-root-transformed and abundance was log ($x + 1$) transformed. We use the species sampled in the primary forest site in Budongo Forest to evaluate how many of the tree and seedling species in this site were unique to this site and did not occur in lightly or heavily logged forest sites.

We used non-metric multidimensional scaling (NMDS) using Bray–Curtis index based on abundance data) and

Multi Response Permutation Procedure (MRPP) to assess differences in the tree and seedling composition among the three forests and two disturbance regimes. NMDS produces a two-dimensional graphical representation of the sample units according to the association among species and are not constrained by predictors (McCune & Grace 2002). MRPP is similar to multivariate analyses of variance without requirement of multivariate normality and homogeneity of variance. MRPP compares the observed within-group average distances with the average distances that would have resulted from all the other possible combinations of the data under the null hypothesis using 999 permutations. A chance-corrected estimate of the proportion of the distances explained by group identity (A) is calculated that is analogous to a coefficient of determination in a linear model. All analyses were done in Program R version 2.9.0 using the package *vegan*.

RESULTS

Canopy openness

Canopy openness differed significantly between lightly and heavily logged sites but not among the three forests (mixed-effect ANOVA: disturbance: $F_{1,2} = 20.0$, $P < 0.001$; forest: $F_{2,12} = 0.72$, $P = 0.51$; forest \times disturbance: $F_{2,12} = 2.07$, $P = 0.16$). Lightly logged sites in the three forests had on average 27.3% canopy openness while heavily logged sites in the three forests had rather open canopies with an average value of 50.0%. Control plots in primary forest sites in Budongo Forest had on average 18.3% canopy openness.

Trees

We recorded 160 tree species in the three forests, with 127 classified as late-successional and 33 as early-successional species (Appendix 1). Difference in logging history had no significant effect on late-successional or early-successional tree species richness or diversity (Table 1, Figure 2a, b). Further, species richness and diversity of late- and early-successional trees did not differ among the three forests (Table 1). The number of late-successional individuals was significantly higher in lightly compared with heavily logged sites (Table 1). In contrast, differences in logging history did not affect the number of early-successional tree individuals (Table 1). Budongo Forest had the largest number of late-successional tree individuals (Table 1). The number of late-successional tree individuals was lower in Kakamega Forest and Mabira Forest compared with Budongo Forest (Table 1) whereas the number of early-successional trees did not differ among the three forests (Table 1).

Table 1. Species richness, Simpson diversity and abundance of late- and early-successional trees (on 1 ha) and seedlings (on 90 m²) in lightly logged (ld) and heavily logged (hd) sites of Budongo (BF), Mabira (MF) and Kakamega Forest (KF) as well as results for differences in logging histories, forest and the interaction term logging × forest from mixed-effect ANOVAs. Shown are untransformed abundance data (mean ± SD) but F-values and their significance refer to transformed data, N = 18; degrees of freedom: logging 1, 2, forest 2, 1, 2, logging × forest 2, 1, 2, ns = not significant, *P < 0.05, ***P < 0.001.

	BF ld	BF hd	MF ld	MF hd	KF ld	KF hd	Logging	Forest	Logging × Forest
Late-successional trees									
Species richness	26 ± 4	28 ± 4	25 ± 2	25 ± 8	23 ± 1	22 ± 4	0.01 ns	1.61 ns	0.21 ns
Simpson diversity	0.87 ± 0.04	0.90 ± 0.04	0.87 ± 0.04	0.85 ± 0.04	0.86 ± 0.03	0.87 ± 0.05	5.33 ns	0.58 ns	0.09 ns
Abundance	598 ± 111	499 ± 77	314 ± 73	251 ± 74	268 ± 40	186 ± 32	21.48*	27.8***	0.30 ns
Early-successional trees									
Species richness	5 ± 1	5 ± 1	5 ± 1	5 ± 1	5 ± 0	5 ± 0	0.14 ns	0.17 ns	1.16 ns
Simpson diversity	0.85 ± 0.04	0.87 ± 0.01	0.87 ± 0.02	0.85 ± 0.07	0.86 ± 0.03	0.87 ± 0.03	0.10 ns	0.07 ns	0.64 ns
Abundance	61 ± 26	35 ± 18	77 ± 52	122 ± 67	121 ± 39	68 ± 28	0.34 ns	2.68 ns	1.87 ns
Late-successional seedlings									
Species richness	3 ± 2	4 ± 2	4 ± 0	4 ± 1	3 ± 1	4 ± 2	7.00 ns	0.83 ns	0.23 ns
Simpson diversity	0.50 ± 0.35	0.70 ± 0.29	0.67 ± 0.05	0.75 ± 0.10	0.55 ± 0.25	0.61 ± 0.21	6.20 ns	0.58 ns	0.18 ns
Abundance	246 ± 167	169 ± 73	39 ± 6	32 ± 26	104 ± 128	118 ± 122	2.89 ns	4.26*	0.08 ns
Early-successional seedlings									
Species richness	2 ± 0	1 ± 1	1 ± 1	1 ± 1	1 ± 1	1 ± 1	0.00 ns	1.09 ns	1.09 ns
Simpson diversity	0.57 ± 0.14	0.72 ± 0.25	0.71 ± 0.26	0.19 ± 0.33	0.41 ± 0.52	0.38 ± 0.12	0.42 ns	1.14 ns	1.96 ns
Abundance	6 ± 3	5 ± 7	2 ± 2	14 ± 13	262 ± 352	21 ± 20	0.01 ns	1.84 ns	1.03 ns

Seedlings

We recorded seedlings of 68 species in the three forests; of these 55 were late-successional and 13 were early-successional species (Appendix 1). For seedlings neither species richness nor diversity, nor number of individuals of late- or early-successional species were affected by differences in logging histories (Table 1, Figure 2c, d). Further, species richness and diversity of late- and early-successional seedlings did not differ among the three forests (Table 1). However, the number of late-successional individuals was lower in Mabira Forest than in Budongo Forest (Table 1).

NMDS of tree and seedling communities

The NMDS enabled us to plot sites and predictors in a two-dimensional species space (Figure 3a, b, convergent solutions found, two dimensions, trees: stress = 10.9, seedlings: stress = 21.5). The MRPP showed significant differences among the forests both for the tree and seedling communities (trees: A = 0.22, P = 0.001, seedlings: A = 0.10, P = 0.001) while tree and seedling communities did not differ between heavily and lightly logged sites (trees: A < 0.01, P = 0.28, seedlings: A < 0.01, P = 0.37). On the right side of the NMDS plot for tree communities are the plots located in Budongo Forest, in the middle the plots located in Mabira Forest and on the left the plots located in Kakamega Forest (Figure 3a). Placement of lightly and heavily logged sites differed among the three forests, being interspersed in Kakamega Forest, and distinctly different along the second NMDS axis in Mabira and Budongo Forest, although the effect was not significant (Figure 3a). The pattern of the NMDS plot for seedlings is not as distinct as for trees (Figure 3a, b). Plots located on the right side of the scaling plot are located in Budongo Forest, plots located towards the lower left are located in Mabira Forest and plots located towards the upper left are located in Kakamega Forest (Figure 3b). Plots of lightly and heavily logged areas are interspersed (Figure 3b).

DISCUSSION

Our results show significant differences in canopy openness between lightly and heavily disturbed sites that are similar among the three forests. Heavy logging significantly reduced the abundance of late-successional tree species. However, tree species richness or diversity was not affected by differences in logging histories concurring with a previous study conducted in Kakamega Forest (Farwig *et al.* 2008a). This could be explained by quick colonization of canopy openings through early-successional species in the course of forest succession

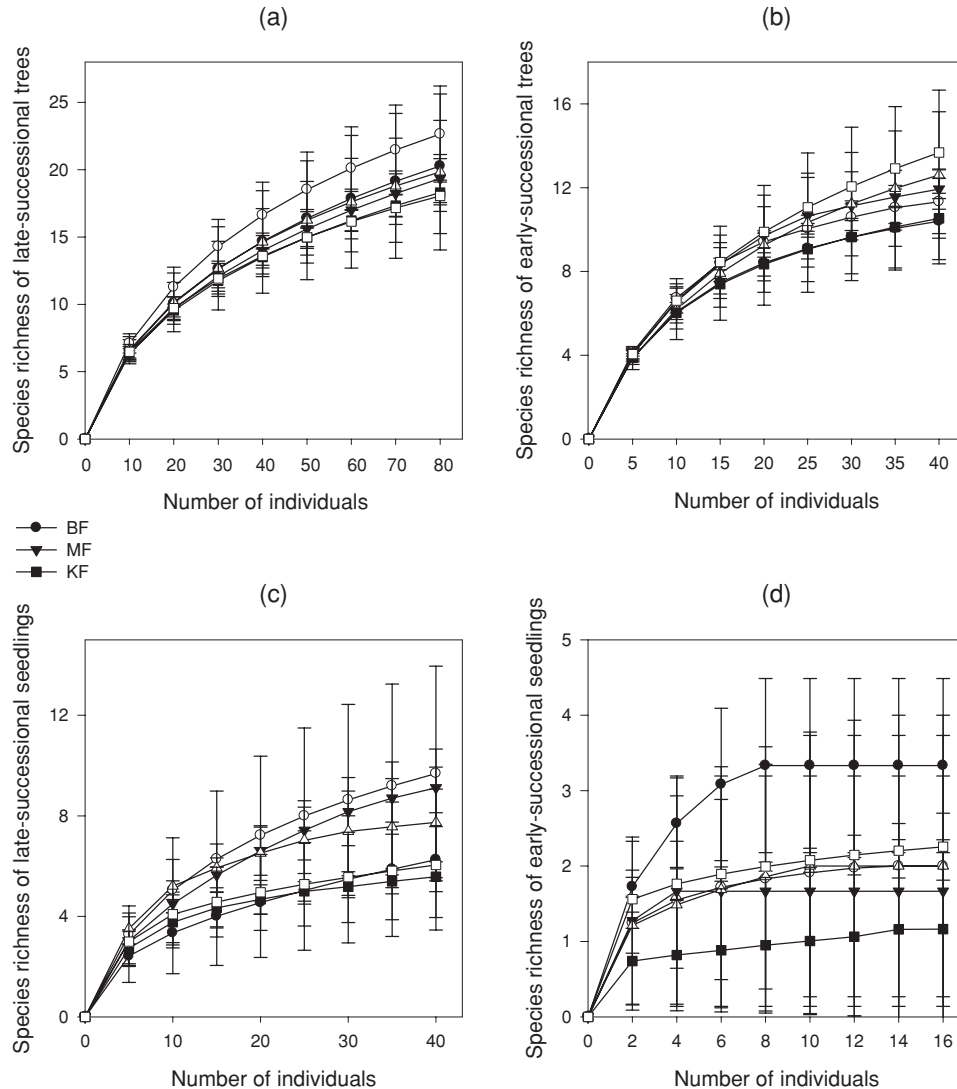


Figure 2. Rarefaction curves (mean \pm 1 SD) for late-successional trees (a), early-successional trees (b), late-successional seedlings (c) and early-successional seedlings (d) in Budongo Forest (BF), Mabira Forest (MF) and Kakamega Forest (KF). Closed symbols indicate lightly logged sites and open symbols indicate heavily logged sites.

(Kariuki & Kooyman 2005) maintaining an overall high tree species richness. The number of late-successional individuals was lower in heavily than in lightly logged sites, probably because specific trees had been selectively logged (Baranga 2007, Bleher *et al.* 2006, Laurance *et al.* 2006, Plumptre 1996, J. M. K. pers. observation). Other explanations for changes in the density of tree species may be higher mortality of certain tree species, microclimatic changes or increased hunting (Laurance *et al.* 2004, 2006; Nascimento *et al.* 2006, Terborgh *et al.* 2008). For instance, several studies have shown that reduced numbers of large-vertebrate seed dispersers resulted in shifts in relative abundance of tree species (Peres & van Roosmalen 2002, Terborgh *et al.* 2008). However, the abundance of animal- and wind-dispersed species did not differ between lightly and heavily logged sites in this study (data not shown). Thus, the most likely explanation

for reduced densities of late-successional trees in heavily logged sites seems to be selective logging of these tree individuals.

In contrast to the tree community, seedling species richness, diversity and number of individuals seemed unaffected by differences in logging histories. Similarly, selective logging did not affect diversity and abundance of seedlings of most tree species in central Amazonia (Magnusson *et al.* 1999) and in Kibale Forest, Uganda (Chapman & Chapman 1997). It appears that selective logging has fewer negative effects on early seedling establishment than on the adult tree community. One reason for relatively similar seedling establishment in differently logged sites could be that seed production of adult trees is increased in heavily disturbed sites, thus resulting in enhanced seed rain and seedling establishment. Some studies report increased seed

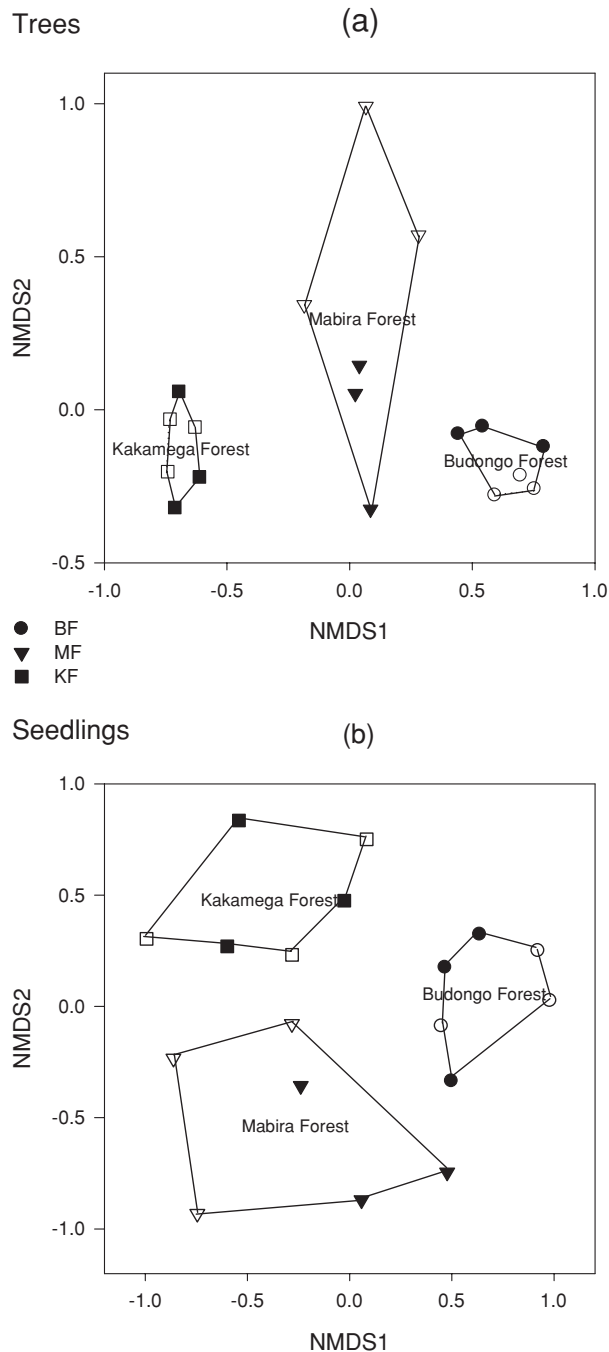


Figure 3. NMDS biplot ordination for tree (a) and seedling (b) communities of Budongo Forest (BF), Mabira Forest (MF) and Kakamega Forest (KF). Closed symbols indicate lightly logged sites and open symbols indicate heavily logged sites. Solid lines connect sites by forest.

production of trees in logged sites (Herrerías-Diego *et al.* 2006). However, *Celtis durandii* did not differ in seed production between heavily and lightly logged areas in the same three forests (Kirika *et al.* 2008a). Relatively increased seedling establishment might also be caused by better seed dispersal by frugivorous birds and mammals in heavily logged versus lightly logged sites. Whereas one study indeed provides support for enhanced fruit removal

of *Prunus africana* in intensively logged sites (Farwig *et al.* 2006), fruit removal of *Ficus thonningii* and of *C. durandii* is reduced in heavily than in lightly logged forest stands (Kirika *et al.* 2008a, 2008b). Such diminished fruit removal rates might be linked to reduced animal diversity and abundance in selectively logged forest due to hunting (Peres & van Roosmalen 2002, Terborgh *et al.* 2008). For instance, Peres & van Roosmalen (2002) showed that the abundance of late-successional seedlings could be linked to the abundance of large-vertebrate seed dispersers. Also, Terborgh *et al.* (2008) demonstrated that hunting alters tree recruitment with large-seeded species showing depressed recruitment. However, abundance of late- and early-successional seedlings as well as animal- and wind-dispersed species did not differ among lightly and heavily logged sites in our study (data not shown).

Still, comparable numbers of recently germinated seedlings in differently logged forest stands such as found in our study might not necessarily result in abundant forest regeneration. Whereas seedling establishment was not affected by selective logging in Kibale forest, a negative effect of disturbance on sapling densities could be detected (Chapman & Chapman 1997). Thus, it is possible that selective logging is impairing recruitment into the sapling stage. We did not sample saplings in our study. However, it might be possible that in our study sites early-successional species out-compete late-successional species in sites where the canopy is more open. In general, forest gaps seem to maintain high density and diversity of early-successional trees and species dispersed by abiotic means (Lawton & Putz 1988, Terborgh *et al.* 2008). In contrast, gaps do not appear to promote high species diversity of late-successional, shade-tolerant species (Hubbell *et al.* 1999, Schnitzer & Carson 2001). Even though we did not reveal negative effects of forest disturbance on seedling densities, there might be cryptic genetic effects. For example, in *Prunus africana*, the genetic diversity of seedlings declined in heavily logged sites in comparison to that of adult trees (Farwig *et al.* 2008b). The most plausible explanation for similar numbers of recently germinated seedlings seems to be the ability of the forest trees to recover their reproductive capacity.

In another study, species richness at the seedling size class was lower in heavily logged than in lightly logged sites comparing only study sites within Kakamega Forest (Farwig *et al.* 2008a). The difference between our results and those of Farwig *et al.* (2008a) could be due to the different sampling regimes adopted by the two studies. We sampled each seedling plot only once, thus, estimating species richness only for a 'snapshot' in time. In contrast, Farwig *et al.* (2008a) sampled seedling plots over several years reporting higher richness and density of seedlings on the same area than in the present study. Also other studies revealed strong differences in among-year germination and seedling survival rates (Hampe 2008, Lehouck *et al.* 2009). This highlights the importance of taking samples

over several years to understand effects of disturbance on forest regeneration.

The results of both the mixed-model ANOVAs and the NMDS ordinations in combination with MRPP demonstrated for trees and seedlings clear differences among the three forests. These differences in species composition among the three forests seem to mirror the overall composition of the forest species pools, i.e. the decreasing gradient of species richness from west to east, from closer to more distant to the Congo–Guinean rainforest belt (Wagner *et al.* 2008). Similarly, a previous study on frugivore assemblages in these three forests showed significant differences among the forests (Kirika *et al.* 2008a). These studies stress the importance of comparative studies in several forests to reveal a more general understanding of effects of selective logging.

In general, this study suggests that different intensities of selective logging of tropical forests may still result in similar numbers of recently germinated seedlings. However, this should be viewed with caution since in this study we focused on species richness of the complete tree and seedling community not taking into account habitat specialization or threat status of the specific species. Although differences in logging histories seem to have no effect on tree and seedling species richness in this study, there is evidence suggesting that common species benefit at the expense of species specialized to primary forests (Tabarelli & Peres 2002). For instance, reduced regeneration has been frequently reported for important timber species in Africa (Hall *et al.* 2003, Mwima *et al.* 2001, Struhsaker 1997). In our study, five tree species (*Chrysophyllum muerense*, *Heisteria pavifolia*, *Suregada procera*, *Rinorea dentata*, *Xylopia parvifolia* and *Zanthoxylum leprieurii*) and seedlings of two species (*Memecylon jasminoides* and *Celtis zenkeri*) were only found in the primary forest. Thus, our findings should not diminish the importance of preserving undisturbed forest areas, which include distinct species and communities different from logged forests (Laurance & Bierregaard 1997, Martin *et al.* 2004). Nevertheless, our results suggest that recently germinated seedlings can establish in selectively logged forests which might contribute to the regeneration and resilience of disturbed forest ecosystems. However, further research is required to determine whether the seedling communities of disturbed forests are able to persist over time.

ACKNOWLEDGEMENTS

This study was funded by the German Federal Ministry of Education and Research within the framework of BIOTA East Africa (O1LC040 subproject E11). We thank the Kenyan Ministry of Education and Research for the permission to carry out research in Kakamega Forest and

the Kenya Wildlife Service and the Kenya Forest Service for granting us access to their reserves. We thank the Ugandan Council for Science and Technology and the Forest Department for permission to work in Budongo and Mabira Forest reserves. We thank the Paper Club of the Department of Ecology, University of Mainz, and four anonymous reviewers for helpful comments on an earlier version of the manuscript.

LITERATURE CITED

- ALTHOF, A. 2005. *Human impact on flora and vegetation of Kakamega Forest, Kenya*. Ph.D. dissertation, University of Koblenz-Landau.
- BARANGA, D. 2007. Observations on resource use in Mabira Forest Reserve, Uganda. *African Journal of Ecology* 45:2–6.
- BEENTJE, H. 1994. *Kenya's trees, shrubs and lianas*. National Museums of Kenya, Nairobi, Kenya. 722 pp.
- BLEHER, B., USTER, D. & BERGSDORF, T. 2006. Assessment of the threat status and management effectiveness in Kakamega Forest, Kenya. *Biodiversity Conservation* 15:1159–1177.
- BOFFA, J.-M., KINDT, R., KATUMBA, B., JOURGET, J.-G. & TURUYOMURUGYENDO, L. 2008. Management of tree diversity in agricultural landscapes around Mabira Forest Reserve, Uganda. *African Journal of Ecology* 46:24–32.
- CHAPMAN, C. A. & CHAPMAN, L. J. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29:396–412.
- EGGELING, W. J. 1947. Observations on the ecology of the Budongo rainforest, Uganda. *Journal of Ecology* 34:20–87.
- ELLISON, A. M., DENSLOW, J. S., LOISELLE, B. A. & BRENES, M. D. 1993. Seed and seedling ecology of neotropical Melastomataceae. *Ecology* 74:1733–1749.
- FARWIG, N., BÖHNING-GAESE, K. & BLEHER, B. 2006. Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests. *Oecologia* 147:238–252.
- FARWIG, N., SAJITA, N., SCHAAB, G. & BÖHNING-GAESE, K. 2008a. Human impact diminishes seedling species richness in Kakamega Forest, Kenya. *Basic and Applied Ecology* 9:383–391.
- FARWIG, N., BRAUN, C. & BÖHNING-GAESE, K. 2008b. Human disturbance reduces genetic diversity of an endangered tropical tree, *Prunus africana* (Rosaceae). *Conservation Genetics* 9:317–321.
- HALL, J. S., HARRIS, D. J., MEDJIBE, V. & ASHTON, P. M. S. 2003. The effects of selective logging on forest structure and tree species composition in a Central African forest: implications for management of conservation areas. *Forest Ecology and Management* 183:249–264.
- HAMILTON, M. B. 1991. *Uganda forest trees*. Makerere University Press, Kampala, Uganda. 279 pp.
- HAMPE, A. 2008. Fruit tracking, frugivore satiation, and their consequences for seed dispersal. *Oecologia* 156:137–145.
- HARMS, K. E., WRIGHT, S. J., CALDERÓN, O., HERNÁNDEZ, A. & HERRE, E. A. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495.
- HERRERÍAS-DIEGO, Y., QUESADA, M., STONER, K. E. & LOBO, J. A. 2006. Effects of forest fragmentation on phenological patterns and

- reproductive success of the tropical dry forest tree *Ceiba aesculifolia*. *Conservation Biology* 20:1111–1120.
- HOWARD, P. C. 1991. *Nature conservation in Uganda's tropical forest reserves*. IUCN, Gland. 313 pp.
- HUBBELL, S. P., FOSTER, R. B. & O'BRIEN, S. T. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557.
- HURLBERT, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577–586.
- HURTT, G. C. & PACALA, S. W. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176:1–12.
- KARIUKI, M. & KOOYMAN, M. R. 2005. Floristic changes and regeneration patterns for a 12-year period during the 3rd and 4th decades following selection logging in a subtropical rainforest. *Austral Ecology* 30:844–855.
- KIRIKA, J. M., FARWIG, N. & BÖHNING-GAESE, K. 2008a. Local disturbance of tropical forests diminishes frugivores and seed removal of a small-seeded Afrotropical tree. *Conservation Biology* 22:318–328.
- KIRIKA, J. M., BLEHER, B., BÖHNING-GAESE, K., CHIRA, R. M. & FARWIG, N. 2008b. Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thomningii* trees. *Basic and Applied Ecology* 9: 663–672.
- KOKWARO, J. O. 1988. Conservation status of the Kakamega Forest in Kenya. The Eastern most relic of the equatorial rainforest of Africa. *Monographs in Systematic Botany from the Missouri Botanical Garden* 25:471–489.
- LAURANCE, W. F. & BIERREGAARD, R. O. (eds) 1997. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago. 616 pp.
- LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M., LAURANCE, S. G., HUTCHINGS, R. & LOVEJOY, T. E. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12:460–464.
- LAURANCE, W. F., OLIVEIRA, A. A., LAURANCE, S. G., CONDIT, R., NASCIMENTO, H. E. M., SANCHEZ-THORIN, A. C., LOVEJOY, T. E., ANDRADE, A., D'ANGELO, S., RIBEIRO, J. E. & DICK, C. W. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428:171–175.
- LAURANCE, W. F., NASCIMENTO, H. E. M., LAURANCE, S. G., ANDRADE, A. C., FEARNSIDE, P. M., RIBEIRO, J. E. L. & CAPRETZ, R. L. 2006. Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87:469–482.
- LAWTON, R. O. & PUTZ, F. E. 1988. Natural disturbance and gap phase regeneration in a wind exposed tropical cloud forest. *Ecology* 69:754–777.
- LEHOUCK, V., SPANHOVE, T., GONSAMO, A., CORDEIRO, N. & LENS, L. 2009. Spatial and temporal effects on recruitment of an Afromontane forest tree in a threatened fragmented ecosystem. *Biological Conservation* 142:518–528.
- LEWIS, S. L. 2006. Tropical forests and the changing earth system. *Philosophical Transactions of the Royal Society London B* 361:195–210.
- LUNG, T. & SCHAAB, G. 2006. Assessing fragmentation and disturbance of west Kenyan rainforests by means of remotely sensed time series data and landscape metrics. *African Journal of Ecology* 44:491–506.
- LWANGA, J. S. 2003. Forest succession in Kibale National Park Uganda; implications for forest restoration and management. *African Journal of Ecology* 4:9–22.
- MAGNUSSON, W. E., DE LIMA, O. P., REIS, F. Q., HIGUCHI, F. N. & RAMOS, J. F. 1999. Logging activity and tree regeneration in an Amazonian forest. *Forest Ecology and Management* 113:67–74.
- MAKANA, J. & THOMAS, J. C. 2004. Dispersal limits the natural recruitment of African mahoganies. *Oikos* 106:67–72.
- MAKANA, J. & THOMAS, J. C. 2005. Effects of light gaps and litter removal on seedling performance of six African timber species. *Biotropica* 37:227–237.
- MARTIN, P. H., SHERMAN, R. E. & FAHEY, T. J. 2004. Forty years of tropical forest recovery from agriculture: structure and floristics of secondary and old growth riparian forests in the Dominican Republic. *Biotropica* 36:297–317.
- MARTÍNEZ-RAMOS, M. & SOTO-CASTRO, A. 1993. Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio* 108:299–318.
- MCCUNE, B. & GRACE, J. B. 2002. *Analysis of ecological communities*. MjM Software, Gleneden Beach. 304 pp.
- MWIMA, P. M., OBUA, J. & ORYEM-ORIGA, H. 2001. Effect of logging on the natural regeneration of *Khaya anthotheca* in Budongo Forest Reserve, Uganda. *International Forestry Review* 3:131–135.
- NASCIMENTO, H. E. M., ANDRADE, A. C. S., CAMARGO, J. L. C., LAURANCE, W. F., LAURANCE, S. G. & RIBEIRO, J. E. L. 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conservation Biology* 20:853–860.
- NAIDOO, R. 2004. Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Animal Conservation* 7:93–105.
- PERES, C. A. & VAN ROOSMALEN, M. 2002. Primate frugivory in two species-rich Neotropical forests: implications for the demography of large-seeded plants in overhunted areas. Pp. 407–421 in Levey, D., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI Publishing, Wallingford.
- PIMM, S. L. & RAVEN, P. 2000. Extinction by numbers. *Nature* 403:843–845.
- PLUMPTRE, A. J. 1996. Changes since sixty years of selective timber harvesting in Budongo forest reserve, Uganda. *Forest Ecology and Management* 89:101–113.
- RAMIREZ-MARCIAL, N. 2003. Survival and growth of tree seedlings in anthropogenically disturbed Mexican montane rain forests. *Journal of Vegetation Science* 14:881–890.
- SCHNITZER, S. A. & CARSON, W. P. 2001. Tree fall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913–919.
- SHEIL, D. 1996. *The ecology of long term change in a Ugandan rain forest*. D. Phil. thesis, University of Oxford.
- SHEIL, D. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecology* 155:183–199.
- SHEIL, D., JENNINGS, S. & SAVIL, P. 2000. Long-term permanent plot observations of vegetation dynamics in Budongo, a Ugandan rain forest. *Journal of Tropical Ecology* 16:765–800.

- STRUHSAKER, T. T. 1997. *Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation*. University Press of Florida, Gainesville, 419 pp.
- TABARELLI, M. & PERES, C. A. 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: Implications for forest regeneration. *Biological Conservation* 106:165–175.
- TERBORGH, J., NUNEZ-ITURRI, G., PITMAN, N. C. A., VALVERDE, F. H. C., ALVAREZ, P., SWAMY, V., PRINGLE, E. G. & PAINE, C. E. T. 2008. Tree recruitment in an empty forest. *Ecology* 89:1757–1768.
- TURNER, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33:200–209.
- WAGNER, P., KÖHLER, J., SCHMITZ, A. & BÖHME, W. 2008. The biogeographical assignment of a west Kenyan rain forest remnant: further evidence from analysis of its reptile fauna. *Journal of Biogeography* 35:1349–1361.

Appendix 1. Species list of trees and seedlings recorded during the study. Given for each species are succession type (early or late) and presence (+) or absence (–) in the three forests. PF = primary forest, LD = lightly logged and HD = heavily logged.

Trees	Succession type	Budongo			Mabira		Kakamega	
		PF	LD	HD	LD	HD	LD	HD
<i>Acacia abyssinica</i> Benth.	early	–	–	–	+	–	–	–
<i>Alangium chinense</i> (Lour.) Harms	early	+	+	+	+	+	+	+
<i>Albizia grandibracteata</i> Taub.	late	–	–	–	–	+	–	–
<i>Albizia gummifera</i> (J. F. Gmel.) C. A. Sm.	late	+	+	+	+	+	+	+
<i>Alchornea laxiflora</i> (Benth.) Pax & K. Hoffm.	late	+	+	+	+	–	–	–
<i>Allophylus abyssinica</i> (Hochst) Radlkofer	late	–	–	+	–	–	–	–
<i>Allophylus dummeri</i> Baker f.	late	+	+	–	–	–	–	–
<i>Alstonia boonei</i> De Wild.	late	+	+	+	+	+	–	–
<i>Aningeria altissima</i> (A. Chév.) Aubrév. & Pellegr.	late	+	+	+	+	–	+	+
<i>Antiaris toxicaria</i> (Pers.) Lesch.	late	+	+	+	+	+	+	+
<i>Baphia wollastonii</i> Baker f.	late	+	–	+	+	–	–	–
<i>Beilschmiedia ugandensis</i> Rendle	late	–	–	–	–	+	–	–
<i>Bequaertiodendron oblanceolatum</i> (S. Moore) Heine & J. H. Hemsl.	late	+	+	–	+	+	+	+
<i>Bersama abyssinica</i> Fres.	early	–	–	–	–	–	–	+
<i>Bischofia javanica</i> Blume	early	–	–	–	–	–	–	+
<i>Blighia unijugata</i> Bak.	late	+	+	+	+	+	+	+
<i>Bridelia micrantha</i> (Hochst.) Baill.	early	–	–	–	–	+	–	–
<i>Broussonetia papyrifera</i> (L.) Vent.	early	–	+	–	+	+	–	–
<i>Caloncoba schweinfurthii</i> Gilg	late	+	+	+	–	–	–	–
<i>Canarium schweinfurthii</i> Engl.	late	+	+	–	+	+	–	–
<i>Casearia engleri</i> Gilg	early	+	–	–	–	–	–	–
<i>Casearia battiscombei</i> R. E. Fries.	late	+	–	+	–	–	+	+
<i>Casearia gladiiformis</i> Mast	late	+	+	–	+	+	+	+
<i>Cassipourea ruwensorensis</i> (Engl.) Alston	late	–	+	–	–	–	+	+
<i>Celtis africana</i> Burm. f.	late	–	–	–	+	+	+	+
<i>Celtis durandii</i> Engl.	late	+	+	+	+	+	+	+
<i>Celtis mildbraedii</i> Engl.	late	+	+	+	+	+	+	+
<i>Celtis philippensis</i> Blanco	late	+	+	+	+	+	–	–
<i>Celtis zenkeri</i> Engl.	late	+	+	+	+	+	–	–
<i>Chaetachme aristata</i> Planch.	late	–	–	–	+	+	+	+
<i>Chrysophyllum albidum</i> G. Don	late	+	+	+	+	+	+	+
<i>Chrysophyllum muerense</i> Engl.	late	+	–	–	–	–	–	–
<i>Chrysophyllum perpulchrum</i> Mildbr. ex Hutch. & Dalziel	late	+	+	+	–	–	–	–
<i>Chrysophyllum viridifolium</i> J. M. Wood & Franks	late	–	–	–	+	+	+	+
<i>Clausena anisata</i> (Willd.) Benth.	early	+	–	+	+	+	+	+
<i>Cleistopholis patens</i> (Benth.) Engl. & Diels	early	+	–	–	–	–	–	–
<i>Coffea canephora</i> Pierre ex A. Froehner	late	–	–	–	–	+	–	–
<i>Cordia africana</i> Lam.	late	–	–	–	–	–	+	+
<i>Cordia mellenii</i> Bak.	late	+	+	+	+	+	–	–
<i>Craibia brownii</i> Dunn	late	+	+	–	–	+	+	–
<i>Croton macrostachyus</i> Hochst. ex Delile	early	+	–	–	+	+	+	–
<i>Croton megalocarpus</i> Hutch.	early	–	+	–	–	–	+	+
<i>Croton sylvaticus</i> Hochst.	early	+	+	+	–	+	+	+
<i>Cynometra alexandri</i> C. H. Wright	late	+	+	+	–	–	–	–
<i>Deinbollia kilimandscharica</i> Taub.	late	–	–	–	–	–	–	+
<i>Desplatsia dewevrei</i> (De Wild. & T. Durand) Burret	late	+	+	+	–	–	–	–

Appendix 1. Continued.

Trees	Succession type	Budongo			Mabira		Kakamega	
		PF	LD	HD	LD	HD	LD	HD
<i>Diospyros abyssinica</i> (Hiern) F. White	late	–	+	–	+	+	+	+
<i>Dovyalis macrocalyx</i> (A. Rich.) Warb.	late	–	–	–	–	+	+	–
<i>Dracaena steudneri</i> Engl.	early	–	–	–	–	+	–	–
<i>Drypetes ugandensis</i> Hutch.	late	+	+	+	+	–	–	–
<i>Drypetes gerrardii</i> Hutch.	late	–	–	–	–	–	+	+
<i>Ehretia cymosa</i> Thonn.	late	+	+	+	+	+	+	+
<i>Ekebergia capensis</i> Sparrm.	late	–	–	+	–	–	–	–
<i>Entandrophragma angolense</i> (Welw.) C.DC.	late	–	–	–	+	+	–	–
<i>Entandrophragma utile</i> (Dawe & Sprague) Sprague	late	+	+	+	–	–	–	–
<i>Erythrina abyssinica</i> D.C.	early	+	–	–	–	–	–	–
<i>Erythrophleum suaveolens</i> (Guill. & Perr.) Brenan	late	+	+	–	–	+	–	–
<i>Fagaropsis angolensis</i> (Engl.) Dale	early	+	–	+	+	+	–	+
<i>Ficus cyathistipula</i> Warb.	late	–	–	–	–	–	+	–
<i>Ficus exasperata</i> Vahl	late	+	+	+	+	+	+	+
<i>Ficus lutea</i> Vahl	late	–	–	–	–	+	+	+
<i>Ficus mucoso</i> Welw. ex Ficalho	late	–	–	–	–	+	–	–
<i>Ficus natalensis</i> Hochst.	late	+	–	–	+	+	–	–
<i>Ficus</i> spp.	late	–	–	–	–	–	–	+
<i>Ficus sur</i> Forssk.	late	–	+	+	+	+	+	+
<i>Ficus sycomorus</i> L.	late	+	+	–	+	–	–	–
<i>Ficus thomningii</i> Bl.	late	–	–	–	–	+	+	+
<i>Ficus urceolaris</i> Welw. ex Hiern.	early	–	–	–	+	–	–	–
<i>Ficus vallis-choudae</i> Del.	late	–	–	–	–	+	+	–
<i>Funtumia africana</i> (Benth.) Stapf	early	+	+	+	+	+	+	+
<i>Glyphaea brevis</i> (Spreng.) Monachino	late	+	+	+	+	+	–	–
<i>Grewia mildbraedii</i> Burret	late	–	+	+	+	+	–	–
<i>Harungana madagascariensis</i> Poir.	early	–	–	+	–	–	+	+
<i>Heinsenia diervilleoides</i> K. Schum.	late	–	–	–	–	–	+	+
<i>Heisteria parvifolia</i> Sm.	late	+	–	–	–	–	–	–
<i>Holoptelea grandis</i> (Hutch.) Mildbr.	late	+	+	+	+	+	–	–
<i>Khaya anthotheca</i> C.DC.	late	+	+	+	+	+	–	–
<i>Kigelia africana</i> (Lam.) Benth.	late	–	–	–	–	–	+	+
<i>Klainedoxa gabonensis</i> Pierre ex Engl.	late	+	–	+	–	–	–	–
<i>Lannea welwitschii</i> (Hiern) Engl.	late	–	–	–	+	+	–	–
<i>Lasiodiscus mildbraedii</i> Engl.	late	+	+	+	+	–	–	–
<i>Lepisanthes senegalensis</i> (Poir.) Leenh.	late	–	+	+	+	–	+	–
<i>Lovoa trichilioides</i> Harms	late	–	–	–	–	+	–	–
<i>Lychnodiscus cerospermus</i> Radlk.	late	+	+	+	+	–	–	–
<i>Macaranga schweinfurthii</i> Pax	late	–	–	–	–	+	–	–
<i>Macaranga spinosa</i> Müll. Arg.	early	+	–	–	–	+	–	–
<i>Maerua decumbens</i> (Brongn.) DeWolf	late	–	–	+	+	+	–	–
<i>Maesa lanceolata</i> Forssk.	early	–	–	–	–	+	–	–
<i>Maesopsis eminii</i> Engl.	early	+	+	+	+	+	–	+
<i>Majidea zanguebarica</i> Kirk ex Oliv.	late	+	–	–	+	+	–	–
<i>Mallotus oppositifolius</i> (Geisel.) Müll.-Arg.	late	+	+	–	–	–	–	–
<i>Mammea africana</i> G. Don	late	+	+	+	–	–	–	–
<i>Manilkara butugi</i> Chiov.	late	–	–	–	–	–	+	–
<i>Margaritaria discoidea</i> (Baill.) Webster	early	+	+	+	+	+	–	–
<i>Margaritaria</i> sp.	late	–	–	–	+	+	–	+
<i>Markhamia lutea</i> (Benth) K. Schum.	early	–	+	–	+	+	+	+
<i>Mildbraediendron excelsum</i> Harms	late	+	+	–	–	–	–	–
<i>Milicia excelsa</i> (Welw.) C.C. Berg	late	–	+	+	+	+	–	+
<i>Milletia eetveldeana</i> (Micheli) Hauman	early	–	–	–	+	–	–	–
<i>Monodora angolensis</i> Welw.	late	+	–	+	+	–	+	–
<i>Monodora myristica</i> (Gaertn.) Dunal	late	+	+	+	–	–	–	–
<i>Morus mesozygia</i> Stapf	late	+	+	+	+	+	+	+
<i>Myrianthus holstii</i> Engl.	late	+	+	+	+	+	–	–
<i>Ochma bracteosa</i> Robyns & Lawalrée	late	+	–	–	–	–	–	–
<i>Olea capensis</i> L.	late	–	–	–	–	–	+	+
<i>Oncoba spinosa</i> Forssk.	late	–	–	–	–	–	+	–
<i>Ouratea densiflora</i> De Wild. & T. Durand	late	–	–	+	–	–	–	–

Appendix 1. Continued.

Trees	Succession type	Budongo			Mabira		Kakamega	
		PF	LD	HD	LD	HD	LD	HD
<i>Oxyanthus speciosus</i> DC.	late	+	–	–	+	+	+	+
<i>Pancovia turbinata</i> Radlk.	late	–	+	+	–	–	+	–
<i>Parkia filicoidea</i> Welw. ex Oliv.	late	+	–	–	+	–	–	–
<i>Piptadeniastrum africanum</i> (Hook. f.) Brenan	late	–	–	–	–	+	–	–
<i>Polyalthia suaveolens</i> Engl. & Diels	late	+	+	+	–	–	–	–
<i>Polyscias fulva</i> (Hiern) Harms	early	–	–	–	+	+	+	+
<i>Premna angolensis</i> Gürke	late	–	+	–	–	–	+	–
<i>Prunus africana</i> (Hook. f.) Kalkm.	late	–	–	–	–	+	+	+
<i>Pseudospondias microcarpa</i> (A. Rich.) Engl.	late	+	+	+	+	+	+	–
<i>Psidium guajava</i> L.	early	–	+	+	–	–	–	–
<i>Pterygota mildbraedii</i> Engl.	late	+	+	–	+	+	–	–
<i>Pycnanthus angolensis</i> (Welw.) Warb.	late	+	+	–	–	–	–	–
<i>Raphia farinifera</i> (Gaertn.) Hyl.	early	+	–	–	–	–	–	–
<i>Rauvolfia vomitoria</i> Afzelius	early	–	+	+	–	+	–	–
<i>Rawsonia lucida</i> Harv. & Sond.	late	+	+	–	+	–	+	–
<i>Ricinodendron heudelotii</i> (Baill.) Pierre ex Pax	late	+	+	+	–	–	–	–
<i>Rinorea ardisiiflora</i> Kuntze	late	+	+	+	–	–	–	–
<i>Rinorea dentata</i> (P Beauv.) O Ktze	late	+	–	–	–	–	–	–
<i>Ritchiea albersii</i> Gilg	late	–	+	–	+	–	–	+
<i>Rothmannia urcelliformis</i> (Hiern) Robyns	late	–	–	+	–	+	+	–
<i>Rytigynia umbellulata</i> (Hiern) Robyns	late	–	–	–	–	+	–	–
<i>Sapium ellipticum</i> (Krauss) Pax	late	–	–	–	+	+	+	+
<i>Schrebera arborea</i> A Chev.	late	–	–	+	+	+	+	–
<i>Spathodea campanulata</i> P. Beauv.	early	–	–	–	–	+	+	+
<i>Sterculia dawei</i> Sprague	late	+	–	+	+	+	–	–
<i>Strombosia scheffleri</i> Engl.	late	+	+	+	+	–	–	+
<i>Strychnos usambarensis</i> Gilg	late	+	–	–	–	–	+	+
<i>Suregada procera</i> (Prain) Croizat	late	+	–	–	–	–	–	–
<i>Syzygium guineense</i> (Willd.) DC.	late	–	–	–	–	–	+	+
<i>Tabernaemontana pachysiphon</i> Stapf	late	+	+	+	+	+	–	–
<i>Tabernaemontana stapfiana</i> Britten	late	+	–	–	+	+	–	–
<i>Tapura fischeri</i> Engl.	early	+	+	+	+	+	–	–
<i>Tarema pavettooides</i> (Harv.) Sim.	late	–	–	–	–	+	–	–
<i>Teclea nobilis</i> Del.	late	+	+	+	+	–	+	+
<i>Terminalia ivorensis</i> A. Chev.	late	–	–	–	–	+	+	–
<i>Tetrapleura tetraptera</i> (Schumach. & Thonn.) Taub.	late	+	+	+	+	+	–	–
<i>Tetrarchidium didymonstemon</i>	early	+	+	–	–	–	–	–
<i>Treculia africana</i> Desc.	late	–	–	–	+	+	–	–
<i>Trema orientalis</i> (L.) Bl.	early	–	–	–	–	+	+	–
<i>Trichilia emetica</i> Vahl	late	+	+	–	+	+	+	+
<i>Trichilia prieuriana</i> A. Juss.	late	+	+	+	+	+	–	–
<i>Trichilia rubescens</i> Oliv.	late	+	+	+	+	–	–	–
<i>Trilepisium madagascariense</i> DC.	late	+	+	+	+	+	+	+
<i>Turraea floribunda</i> Hochst.	late	+	–	–	–	–	+	+
<i>Turraea holstii</i> Gürke	late	+	+	+	+	+	–	–
<i>Turraeanthus africanus</i> (Welw. ex C.DC.) Pellegr.	late	+	+	+	–	+	–	–
<i>Uvariopsis congensis</i> Robyns & Ghesq.	late	+	+	+	+	+	–	–
<i>Vangueria apiculata</i> K. Schum.	early	–	–	–	+	–	+	+
<i>Vitex doniana</i> Sweet	late	–	–	–	–	–	–	+
<i>Vitex fischeri</i> Gürke	late	+	+	–	–	–	–	–
<i>Xylopia parviflora</i> De Wild. & T. Durand	late	+	–	–	–	–	–	–
<i>Zanthoxylum gillettii</i> (De Wild.) Waterm.	late	+	–	+	–	–	–	+
<i>Zanthoxylum leprieurii</i> Guill. & Perr.	late	+	–	–	–	–	–	–

Appendix 1. Continued.

Seedlings	Succession type	Budongo			Mabira		Kakamega	
		PF	LD	HD	LD	HD	LD	HD
<i>Alangium chinense</i>	late	–	+	–	+	+	–	–
<i>Albizia gummifera</i>	late	–	+	+	+	+	+	+
<i>Allophylus abyssinica</i>	late	–	–	–	+	+	+	+
<i>Alstonia boonei</i>	late	–	–	–	+	–	–	–
<i>Aningeria altissima</i>	late	+	+	+	–	–	+	+
<i>Antiaris toxicaria</i>	late	+	+	+	+	+	+	+
<i>Argomuellera macrophylla</i> Pax	late	+	+	+	+	–	–	–
<i>Baphia wollastonii</i>	late	–	–	–	–	–	–	–
<i>Bequaertiodendron oblanceolatum</i>	late	+	+	+	+	+	+	+
<i>Blighia unijugata</i>	late	–	–	+	+	+	–	+
<i>Bridelia micrantha</i>	early	–	+	–	–	–	–	–
<i>Casearia battiscombei</i>	late	–	–	–	–	–	–	+
<i>Cassipourea ruwensorensis</i>	late	–	–	–	–	+	–	–
<i>Celtis africana</i>	late	–	–	–	–	–	+	–
<i>Celtis durandii</i>	late	+	+	+	+	+	+	+
<i>Celtis mildbraedii</i>	late	+	+	+	+	+	+	–
<i>Celtis philippensis</i>	late	–	–	–	+	–	–	–
<i>Celtis zenkeri</i>	late	+	–	–	–	–	–	–
<i>Chaetachme aristata</i>	late	–	–	+	+	–	–	–
<i>Chrysophyllum albidum</i>	late	+	+	+	–	–	+	+
<i>Chrysophyllum perpulchrum</i>	late	–	+	+	–	–	–	–
<i>Chrysophyllum viridifolium</i>	late	–	–	–	+	–	–	–
<i>Clausena anisata</i>	early	–	–	–	–	+	–	–
<i>Coffea eugenioides</i> S. Moore	late	–	–	–	–	–	+	–
<i>Cordia africana</i>	late	–	+	–	–	–	–	–
<i>Croton macrostachyus</i>	early	–	–	–	+	–	–	–
<i>Croton sylvaticus</i>	early	–	–	+	–	–	+	+
<i>Cynometra alexandri</i>	late	+	+	+	–	–	–	–
<i>Diospyros abyssinica</i>	late	+	+	+	–	–	+	+
<i>Dovyalis macrocalyx</i>	late	–	–	–	–	–	–	+
<i>Erythrococca trichogyne</i> (Müll. Arg.) Prain	late	–	–	–	–	+	–	–
<i>Ficus asperifolia</i> Miq.	late	–	–	+	+	–	–	–
<i>Ficus exasperata</i>	late	–	+	–	+	–	–	–
<i>Funtumia africana</i>	early	–	+	+	–	–	+	+
<i>Khaya anthotheca</i>	late	+	+	+	–	–	–	+
<i>Lasiodiscus mildbraedii</i>	late	+	+	+	–	–	–	–
<i>Lecaniodiscus fraxinifolius</i> Bak.	late	+	–	–	–	–	–	–
<i>Maesa lanceolata</i>	early	–	+	–	–	+	–	–
<i>Maesopsis eminii</i>	early	–	+	+	–	–	–	–
<i>Margaritaria discoidea</i>	early	–	+	–	+	–	–	–
<i>Markhamia lutea</i>	early	–	–	–	–	–	–	–
<i>Memecylon jasminoides</i> Gilg	late	+	–	–	–	–	–	–
<i>Monodora angolensis</i>	late	+	–	–	+	+	–	–
<i>Morus mesozygia</i>	late	–	–	–	–	–	–	+
<i>Myrianthus holstii</i>	late	+	+	+	–	–	–	–
<i>Ouratea densiflora</i> De Wild. & Dur.	late	+	–	+	–	–	–	–
<i>Pancovia turbinata</i>	late	+	–	–	–	–	–	–
<i>Peddiea fischeri</i> Engl.	late	–	–	–	–	–	+	–
<i>Polyalthia suaveolens</i>	late	+	–	+	–	–	–	–
<i>Polyscias fulva</i>	early	–	–	–	–	–	–	+
<i>Prunus africana</i>	late	–	–	–	+	+	+	+
<i>Psidium guajava</i>	early	–	–	+	–	–	–	–
<i>Psychotria peduncularis</i> (Salisb.) Steyerl.	late	–	–	–	–	+	–	–
<i>Pterygota mildbraedii</i>	late	–	–	–	–	+	–	–
<i>Rawsonia lucida</i>	late	–	+	+	–	–	–	+
<i>Rinorea ardisiiflora</i>	late	+	+	+	–	–	–	–
<i>Rinorea brachypetala</i> (Turcz.) O. Ktze.	late	+	+	+	–	–	–	–
<i>Rinorea dentata</i>	late	+	–	+	+	–	–	–
<i>Rinorea ilicifolia</i> (Welw. ex Oliv.) Kuntze	late	–	–	+	+	+	–	–
<i>Sterculia dawei</i>	early	–	–	–	–	+	–	–

Appendix 1. Continued.

Seedlings	Succession type	Budongo			Mabira		Kakamega	
		PF	LD	HD	LD	HD	LD	HD
<i>Strombosia scheffleri</i>	late	+	+	+	+	+	-	+
<i>Strychnos usambarensis</i>	late	-	-	-	+	-	+	-
<i>Tabernaemontana pachysiphon</i>	late	+	-	-	-	+	-	-
<i>Teclea nobilis</i>	late	-	+	-	+	+	+	+
<i>Trilepisium madagascariense</i>	late	+	-	+	+	+	+	+
<i>Turraea floribunda</i>	late	-	-	+	-	-	+	-
<i>Uvariopsis congensis</i>	late	-	-	+	+	-	-	-
<i>Vangueria apiculata</i>	early	-	-	+	-	-	-	-