# Tree communities of different aged logged areas in an Afrotropical rainforest

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## Abstract

Predicting the recovery processes in tree communities after logging is critical when developing conservation strategies. We assessed the patterns in tree communities in logged and primary forests in Kibale National Park, Uganda, representing 9- to 19-year-old clear-cuts of former conifer plantations, 42- to 43-year-old logged forests and primary forests. Species density and diversity were lower and dominance higher in the 9- to 19-year-old forests compared to the 42- to 43-year-old forests or primary forests. The tree species density, diversity and dominance of 42- to 43-year-old forests did not differ significantly from primary forests. However, they had a lower stem density, and higher cover of *Acanthus pubescens*, a shrub known to arrest the succession in Kibale. The tree community compositions of 9- to 19-year-old, 42- to 43-year-old and primary forests differed from each other. A large group of tree species (21) were primary forest indicators, that is, they were either missing or relatively rare in logged forests. The results of this study show that even after four decades of natural recovery, logged Afrotropical forests can still be distinguished from primary forests in their tree community compositions, emphasizing the slow community recovery and the important role of primary forests when preserving the tree communities in tropical rainforests.

*Key words:* anthropogenic disturbance, biodiversity, forest recovery, Kibale National Park, succession, Uganda

## Résumé

Il est essentiel de pouvoir prédire les processus de restauration de communautés d'arbres après les coupes lorsque l'on développe des stratégies de conservation. Nous avons évalué les schémas de communautés d'arbres dans des forêts exploitées et primaires dans le Parc National de Kibale, en Ouganda, à savoir des coupes à blanc de 9 à 19 ans d'anciennes plantations de conifères, des forêts exploitées il y a 42–43 ans et des forêts primaires. La densité et la diversité des espèces étaient plus faibles et la dominance plus élevée dans les forêts de 9–19 ans que dans les forêts de 42–43 ans ou dans les forêts primaires. La densité, la diversité et la dominance des espèces d'arbres des forêts de 42–43 ans ne différaient pas significativement de celles des forêts primaires. Mais elles avaient une densité de troncs plus basse et une plus grande couverture d'*Acanthus pubescens*, un arbuste connu pour arrêter la succession à Kibale. La composition des communautés d'arbres des forêts de 9–19 ans, 42–43 ans et primaires différait de l'une à l'autre. Un grand groupe d'espèces d'arbres (21) étaient des indicateurs de forêt primaire, à savoir qu'ils étaient soit manquants, soit relativement rares dans les forêts exploitées. Les résultats de cette étude montrent que même après quatre décennies de rétablissement naturel, les forêts afrotropicales exploitées peuvent encore être distinguées des forêts primaires par la composition de leurs communautés d'arbres, ce qui montre bien la lenteur du rétablissement de ces communautés et le rôle important des forêts primaires lorsqu'il s'agit de préserver les communautés d'arbres dans des forêts pluviales tropicales.

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## Introduction

Tropical rainforests are subject to a wide range of natural and anthropogenic disturbances that vary in duration, intensity and frequency. These disturbances can determine

the distribution and abundance of tree species, and the ecological functions in forest ecosystems (Chazdon, 2003). However, the effects of anthropogenic resource extraction on the dynamics and recovery of tropical forests remain poorly studied. The important questions are as follows: How long does it take for human-disturbed forests to recover to their predisturbance states, are there differences in the rates by which forest structural aspects, species diversity and community compositions recover after disturbances, and in what directions, the succession can progress after human disturbances? The period required for disturbed natural forests to recover is known to vary widely depending on the site characteristics, duration, intensity and forms of disturbances (Uhl *et al.*, 1982; Saldarriaga *et al.*, 1988; Chapman & Chapman, 1999). However, the structural aspects of forests and species composition are known to recover at different rates (Dewalt, Maliakal & Denslow, 2003). In general, tree community recovery in tropical rainforests should show successional changes, where early-successional communities are followed by mid- and late-successional tree communities (Guariguata & Ostertag, 2001; Chazdon, 2003). Yet, in some cases, tree communities can show delayed recovery because of suppression of early-successional communities by thick colonizing vegetation, that is, 'arrested succession' (Chapman & Chapman, 2004). Furthermore, differences in local conditions, or past disturbances, could lead to 'polyclimax communities' (e.g. Begon, Townsend & Harper, 2006), and therefore, the successional pathways may vary.

Knowledge on the recovery of Afrotropical tree communities after human-induced disturbances is usually based on changes in species richness, density, basal area or diversity indices (Fashing *et al.*, 2004; Bonnell, Reyna-Hurtado & Chapman, 2011; Sassen & Sheil, 2013). In addition to inspecting these univariate indices, multivariate community analyses would be useful (see e.g. Chinea, 2002), because community compositions could recover at different rates compared to species richness, diversity or forest structural aspects. In this study, we assessed the natural recovery of forest structural aspects (stem density), as well as tree species richness, diversity, dominance and community compositions in Kibale National Park, Uganda, following anthropogenic disturbances. In Kibale forest, a shrub *Acanthus pubescens* Engl. (Acanthaceae) and a grass *Pennisetum purpureum* Schumach. (Poaceae) can dominate vegetation in logged areas and canopy gaps. When their growth is dense, succession of tree communities can be 'arrested' for a long time because establishment of trees into

the area is suppressed (Chapman & Chapman, 1999), due to associated changes in the light and nutrient availability (Duclos, Boudreau & Chapman, 2013). Alternatively, the shrubs could also facilitate forest regeneration by attracting seed dispersers (Omeja *et al.*, 2011). Given this background, understanding the recovery of tree community compositions in Kibale is particularly interesting.

In this study, we sampled communities of trees on study plots representing three age groups: 9- to 19-year-old clearcuts, 42- to 43-year-old logged forests and primary forests. Our specific study questions were as follows: (i) Does stem density, species density, diversity, dominance or community composition of trees differ among the three age groups? (ii) Do the cover of *A. pubescens* or *P. purpureum* (known to arrest the succession) differ among the three age groups, and does their cover explain the tree community composition? and (iii) Which tree species characterize the three age groups? We expected to find a recovery path forming a gradient from 9- to 19-year-old forests to 42- to 43-year-old forests and primary forests, that is, increasing stem density, species density and diversity and a shift in tree community composition. However, if 'arrested succession' takes place, such recovery pattern in community composition would not be strong and the cover of *A. pubescens* and *P. purpureum* should be important factors explaining the variation in tree community composition in Kibale.

## Material and methods

### Study area

This study was conducted in Kibale National Park (KNP), in western Uganda (Fig. 1) (0°13′–0°41′N and 30°19′–30°32′E) between April and October 2011. The park represents a medium-altitude rainforest, located east of the Ruwenzori Mountains, and covers approximately 795 km$^2$ (Wasserman & Chapman, 2003). Rainfall in KNP is highly variable, but generally bimodal, with peaks occurring in March–May and in September–November. The annual rainfall during the period 1903–2001 averaged 1547 mm year$^{-1}$, with annual mean daily minimum and maximum temperatures of 14.9 and 20.2°C, respectively, recorded during 1990–2001 (Chapman *et al.*, 2005).

Kibale forest was logged to varying intensities by pit sawyers between 1967 and 1969, creating numerous large gaps in the canopy (Kasenene, 1987). The plantations of mainly *Pinus caribaea* Morelet and *Cupressus lusitanica* Mill. were established in the grassland sites
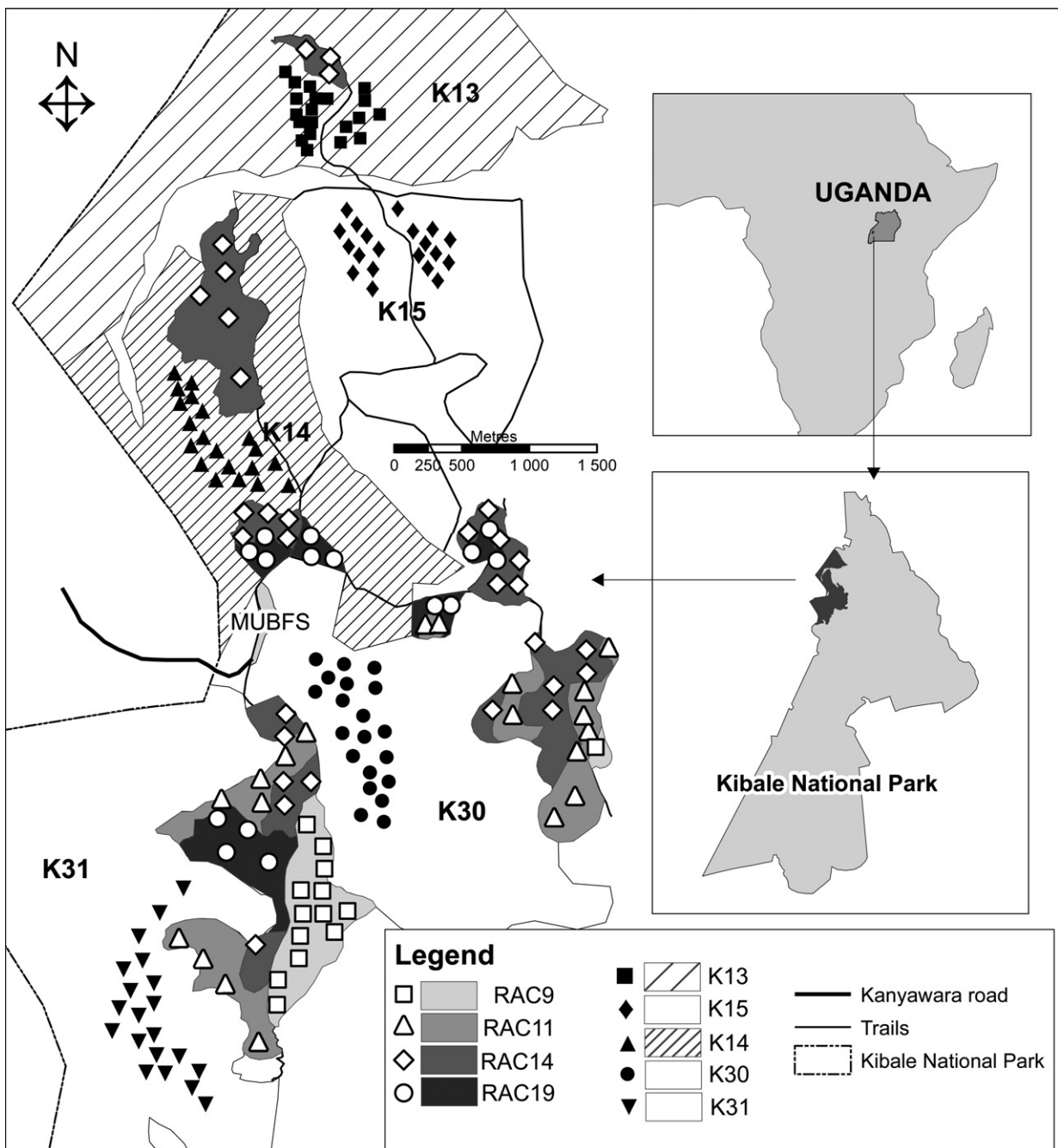
**Fig. 1** Map of Kanyawara area of Kibale National Park, Uganda, and the location of the study plots in differently aged forests. MUBFS = Makerere University Biological Field Station

which dominated many hill tops (deriving from past human activities; Brown & Harrop, 1962). These plantations were established mainly for timber production following the Lockwood Consultants recommendation of 1973 (Kasenene, 2007). The management and conservation status of KNP changed in 1993 (Chapman & Chapman, 1997) and the plantations were clear-cut between late 1980s and early 2000s, following a man-

agement decision to allow natural colonization of KNP by native trees. Prior to clear-cut, a diverse community of native tree species was found below the pine trees, while the tree communities under the cypress stands were impoverished (Fimbel & Fimbel, 1996).

### Study design

The Kanyawara forest area in KNP was classified and mapped *a priori* into nine different areas based on harvest history (Table 1). Seven of the study areas were logged, and two represented separate primary forest compartments (Table 1). The areas represent three age groups, including regenerating age class forests (9- to 19 years) of former clear-cuts of coniferous plantations (RAC9, RAC11, RAC14 and RAC19), natural forest compartments selectively logged 42–43 years ago (K13, K14 and K15) and primary forests (K30 and K31). In each area, location of 20 sampling plots was randomized based on the actual

sizes of RACs (RAC9–RAC19), and others (K13, K14, K15, K30 and K31) approximately on the same-sized areas as RACs, using a relative grid system. The ages since disturbance were determined prior to the study based on historical records (J.M. Kasenene, unpublished data). However, later some plots had to be reclassified after inspection of Landsat images (Table 1), which produced an uneven number of plots, ranging from 14 to 31, at the areas (see median distances to closest plot in Table 1). At each GPS location, the study plot was established with sides oriented to north (40 m) and east (20 m) (Fig. S1). If the plot extended into foot trails or inaccessible points such as steep slopes, it was reoriented perpendicular from that direction.

### Tree community measurements

Each study plot was nested, that is, divided into differently sized quadrats (Fig. S1). Within the largest quadrat of

**Table 1** Description of the nine studied areas in Kibale National Park, Uganda. In terms of management history, Kibale has been divided into regenerating age class areas (RAC) and compartments (K)

| Study area | Median years since harvesting | Area (ha)[a] | Management history[a] | Altitude range (m a.s.l.) | Number of plots | Median distance to nearest plot (m) |
|---|---|---|---|---|---|---|
| RAC9 | 9 | 60 | Conifer plantation clear-cut during 2002–2004 and left under natural regeneration | 1489–1568 | 14 | 164 |
| RAC11 | 11 | 104 | Conifer plantation clear-cut during 2000–2001 and left under natural regeneration | 1488–1599 | 20 | 225 |
| RAC14 | 14 | 171 | Conifer plantation clear-cut during 1995–1999 and left under natural regeneration | 1488–1607 | 31 | 179 |
| RAC19 | 19 | 61 | Conifer plantation clear-cut during 1987–1994 and left under natural regeneration | 1507–1613 | 15 | 166 |
| K13 | 43 | 622 | Heavily logged (50% basal area reduction) during 1968–1969, treated with arboricides and left under natural regeneration | 1453–1514 | 20 | 92 |
| K15 | 43 | 347 | Heavily logged (extraction of 21 m$^3$ ha$^{-1}$, equivalent of 40% basal area reduction) during 1968–1969, and left under natural regeneration | 1457–1525 | 20 | 120 |
| K14 | 42 | 405 | Lightly and selectively harvested in 1969 (extraction of 14 m$^3$ ha$^{-1}$) | 1460–1544 | 20 | 121 |
| K30 | | 282 | Primary *Parinari* natural forest. Two-three trees per km$^2$ felled by pit sawyers prior to 1970 with minimal impact on the compartment | 1469–1528 | 20 | 147 |
| K31 | | 754 | Unlogged primary natural forest | 1420–1494 | 20 | 153 |

[a]Age data for RAC9–19 obtained from Landsat images (http://earthexplorer.usgs.gov/), processed by Erdas Imagine 2011 (version 11.0.2) covering years between 1986 and 2004. Other information from Skorupa & Kasenene (1984), Kasenene (1987), Struhsaker (1997) and Kasenene (2007).

40 × 20 m, large trees (dbh ≥ 20 cm) were sampled, small trees or poles (dbh ≥10 and <20 cm) were sampled in a 20 × 20 m quadrat, saplings (dbh ≥5 and <10 cm) were sampled in a 20 × 10 m quadrat, and seedlings (dbh < 5 cm) were sampled in a 10 × 10 m quadrat (modified from Tabuti, 2007). Stems of all tree species were counted in each subplot, and the stem density (number $ha^{-1}$) for each species in each plot was estimated; first, the number of stems ($ha^{-1}$) in each subplot was estimated, and then, values of all subplots were summed together. Tree species were identified in the field, but in a few cases, samples were collected and identified at the Makerere University Herbarium. At each plot, the cover of *A. pubescens* and *P. purpureum* were estimated visually in percentages: 0%, <1%, <10%, <20%, <30% …100%.

### Data analysis

The sample-based species accumulation plots were generated for the nine study areas with EstimateS 9.1 (Colwell, 2013). The differences in total species richness were compared by calculating rarefied species richness (and their 95% confidence intervals) for each area.

For each study plot, we evaluated the following: (i) density (stems $ha^{-1}$), (ii) species density (i.e. species richness per plot, see Gotelli & Colwell (2011)), (iii) Simpson's diversity index (Simpson's $D = 1 - \Sigma((N_i \times (N_i - 1))/(N \times (N - 1)))$, where $N_i$ = number of stems in species $i$, and $N$ = total number of stems) and (iv) Berger–Parker dominance index (proportion of all stems represented by the most abundant species; Maurer & McGill, 2011). The values were calculated with Primer-E, version 6 (Clarke & Gorley, 2006). To determine whether the three age groups differ in these univariate measures, we fitted four ANOVA models, where the response variable was modelled with age group (fixed factor) using SPSS (IBM SPSS Statistics, version 19). Simpson's $D$ and Berger–Parker index were arcsine square-root-transformed prior to analyses. We also ran mixed models with age group (fixed factor) and study area (random factor); however, for species density and stem density, the random term was nonsignificant, whereas for Simpson's $D$ and Berger–Parker dominance, the effect of random term could not be estimated.

Differences in the presence/absence of *A. pubescens* in each plot among the age groups were tested with Fisher's exact test (no *P. purpureum* was detected in any study plot). Differences in *A. pubescens* cover among the age

groups were compared with nonparametric Kruskal–Wallis rank-sum test, because the distribution in cover was highly skewed. To test for associations between *A. pubescens* cover of each plot and its stem density, tree species density, diversity and dominance, Spearman correlations were calculated. These analyses were conducted with R (R Development Core Team, 2008) version 2.14.1.

We visualized the variation in tree community composition among the nine study areas with nonmetric multi-dimensional scaling (NMDS; conducted with program Primer-E, with 50 restarts). For this analysis, we square-root-transformed the abundance data to down-weight the influence of the most abundant species and calculated a Bray–Curtis similarity matrix between samples (plots), after adding a dummy variable 1. For clarity, also a graph representing distances among centroids of the different study areas was generated.

The PERMANOVA+ routine of program Primer-E (Anderson, Gorley & Clarke, 2008) was used to test whether and to what degree age group explains the variation in tree communities, on the basis of the Bray–Curtis similarity matrix. We conducted 999 random permutations using the 'unrestricted permutation of raw data' method. To test whether cover of *A. pubescens* explains the tree community composition, a distance-based linear model (DISTLM, conducted with program Primer-E) was fitted where the Bray–Curtis similarity matrix was modelled with cover of *A. pubescens* as the explanatory factor.

Finally, we identified the species characterizing each age group using the Dufrene–Legendre Indicator species analysis (Dufrêne & Legendre, 1997), calculated using package 'labdsv' (Roberts, 2013) in R. Species with index values >0.25 were considered as indicator species, following Dufrêne & Legendre (1997). To illustrate the patterns in ageing tree communities, we plotted the proportional abundances of the strongest indicator species against the age since harvesting (for each indicator species, the mean number of stems $ha^{-1}$ was calculated per age (since harvesting), the values were summed across the ages, and the proportion of the sum was then calculated for each age; due to the high number of indicator species, only the strongest indicators with index values >0.45 were plotted).

## Results

A total of 18,805 stems were sampled in the 180 study plots, representing 113 taxa (list in Table S1). All except

eight taxa were identified at species level (six were identified at genus level, and two remained unidentified). The species accumulation curves of the nine study areas continued to rise slowly, but approximately at the same rate, with the exception of the third youngest area (RAC14), which continued to rise more steeply (Fig. S2). Based on the rarefied species richness for fourteen samples (the largest shared number of plots across study areas), the total species richness was significantly higher in oldest harvested forests and primary forests (RAC19, K13, K14, K15, K30 and K31), compared to the two youngest areas RAC9 and RAC11 (Table S1).

*Stem density, species density, diversity and dominance patterns*

We found clear differences in univariate measures among the three age groups of forests (Fig. 2); the stem density (ANOVA; $F_{2, 177} = 6.6$; $P = 0.002$), species density

($F_{2, 177} = 60.8$; $P < 0.001$), Simpson's D ($F_{2, 177} = 17.0$; $P < 0.001$), and Berger–Parker index ($F_{2, 177} = 13.1$; $P < 0.001$) differed among the three age groups. Species density and Simpson's D were lower and dominance higher in the 9- to 19-year-old forests compared to 42- to 43-year-old or primary forests, while stem density was higher in primary forests compared to logged forests (Tukey's pairwise tests; Fig. 2). The mean values ($\pm$SE) of each univariate in each study area are shown in Fig. S3.

The frequencies of plots with *A. pubescens* differed among the age groups (Fisher's exact test, $P < 0.001$); *A. pubescens* being present on 40% of the 9- to 19-year-old, 32% of 42- to 43-year-old and 8% of primary forest plots. Also, the cover of *A. pubescens* differed among the age groups (Kruskal–Wallis test, $\chi^2 = 12.7$, df = 2, $P = 0.002$), being significantly higher in 9- to 19-year-old and 42- to 43-year-old forests compared to primary forests (pairwise Mann–Whitney U-tests, $P < 0.05$), but
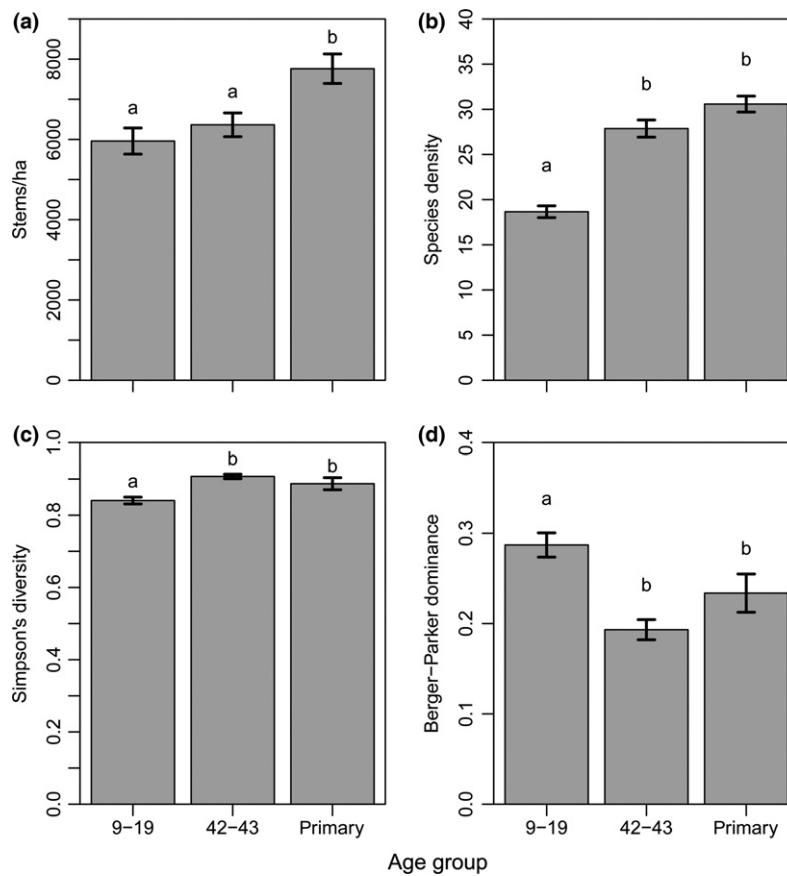


**Fig. 2** The mean values ($\pm$SE) of (a) species density per plot, (b) density of stems ha$^{-1}$, (c) Simpson's D and (d) Berger–Parker dominance in the three age groups in Kibale National Park, Uganda

not differing between the 9- to 19- and 42- to 43-year-old forests ($P = 0.49$). At plot level, the *A. pubescens* cover correlated negatively with stem density (Spearman's rho = $-0.45$, $P < 0.001$), tree species density (rho = $-0.38$, $P < 0.001$) and Simpson's $D$ (rho = $-0.18$, $P = 0.018$), but no association was found with dominance (rho = 0.09, $P = 0.22$).

*Composition of tree communities*

There were significant differences in tree community compositions among the three age groups (PERMANOVA, Pseudo-$F_{2, 177}$ = 21.8; $P < 0.001$) as illustrated by the NMDS ordinations (Fig. 3). According to the pairwise tests, all age groups differed from each other significantly ($P < 0.001$). The age group explained 38% of the variation in the tree community data. The cover of *A. pubescens* explained a significant, but marginal proportion of variation in tree community composition (DISTLM; $P < 0.001$, $R^2 = 0.05$).
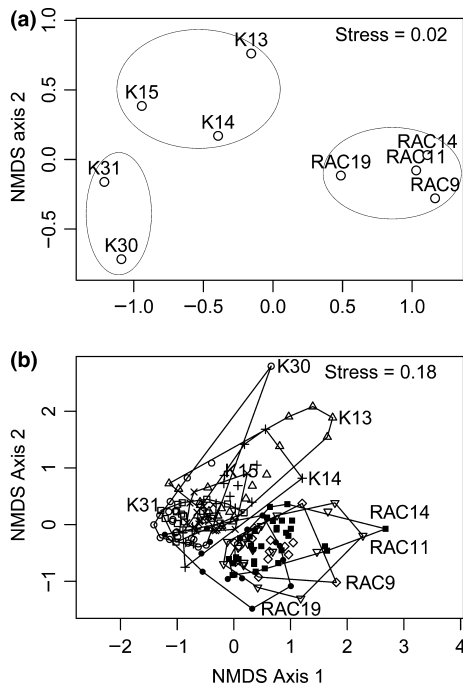


**Fig. 3** NMDS ordinations showing patterns in tree communities. (a) The centroids of the nine study areas (the three age groups circled) and (b) tree communities in the 180 study plots, polygons overlayed on top of ordination enclosing all points of each study area

*Indicator species*

A total of fourteen indicator tree species were identified for the 9- to 19-year-old forests, 16 for the 42- to 43-year-old forests and 21 for primary forests (Supporting Information, Table S1). *Albizia grandibracteata* Taub., *Celtis durandii* Engl. and *Clausena anisata* (Willd.) Hook.f. were the strongest indicators for 9- to 19-year-old forests; *Allophylus dummeri* Baker f., *Strombosia scheffleri* Engl. and *Euadenia eminens* Hook.f. for 42- to 43-year-old forests; and *Aphania senegalensis* Radlk., *Pleiocarpa pycnantha* Stapf and *Uvariopsis congensis* Robyns & Ghesq. for primary forests (the proportional abundances of the strongest indicators are plotted in Fig. S4).

## Discussion

Even after four decades of natural recovery, the tree community compositions of selectively logged areas in Kibale are still different from the nearby primary forests, that is, the recovery is still under way (see also Osazuwa-Peters, Chapman & Zanne, 2015). A large group of tree species were found to indicate the primary forests, suggesting that they were late-successional species and largely absent from the young regenerating forests studied. In East Africa, studies have found that tropical high altitude forests left under natural succession require a minimum recovery time frame of 50 years to reach an ecosystem equivalent to that of primary forests (Plumptre, 1996; Fashing *et al.*, 2004; Bonnell, Reyna-Hurtado & Chapman, 2011). However, other studies suggest that the recovery of tropical forests could take much longer, up to hundreds of years (Finegan, 1996; Liebsch, Marques & Goldenberg, 2008). Such understanding of forest recovery patterns in tropical forests is more timely than ever, because the level of anthropogenic disturbance in tropical forests continues to increase (Taylor *et al.*, 2008).

Our results demonstrate how the different characteristics of forests can recover at different rates; while species density, diversity and dominance of 43-year-old forests did not differ from those in primary forests, they exhibited lower stem densities, and significantly different tree community composition, compared to primary forests. The structural aspects and species composition of tropical forests are known to recover at different rates (Dewalt, Maliakal & Denslow, 2003). From practical management point of view, this means that when estimating the recovery patterns in tropical forests, forest structural

aspects, species richness, diversity and community compositions should all be assessed together. Forests which seem to have recovered with respect to their species richness or diversity may actually host rather different tree communities than primary forests.

Our results also revealed that the 42- to 43-year-old forests already exhibit a much further recovery state than the 9- to 19-year-old forests; their species density and diversity was significantly higher, dominance of the most abundant species lower, and the community composition significantly different, compared to the 9- to 19-year-old forests. To us, this suggests that there has been a turnover of species from pioneer to later-successional species, consistent with findings by Kasenene (2007). The increasing trend in species density and diversity along with age because disturbance is similar to those observed previously in Neotropical secondary forests (Guariguata & Ostertag, 2001; Chinea, 2002) and in Kibale, Uganda (Lwanga, 2003).

Based on the results of this study, it is difficult to judge whether communities of logged forests are 'approaching' primary forest communities along time, or whether 'polyclimax communities' are possible. Eggeling (1947) suggested that tropical forests are undergoing a compositional succession through time, and in Uganda, converging to low-diversity *Cynometra* forest as the end-point of succession. However, later analyses by Sheil (1999, 2001) have revealed that the time-series do not generally support Eggeling's predictions, and neither in our study sites primary forests were characterized with low diversity. Interestingly, the primary forest communities in our study (K30 and K31) differed significantly in their tree species composition (PERMANOVA test comparing the nine study areas, data not shown). This could be explained by differences in local conditions such as edaphic properties or physical and chemical soil properties, topography, slope, exposure or differences in timing, rate and intensity of past disturbances. For example, different types of mature forests in Congo are suggested to be a result of continuing vegetation responses to past disturbances (Hart, 2001).

Furthermore, our results do not allow a strong judgment of how important the 'arrested succession' is in shaping the tree communities in the studied areas. According to our results, *A. pubescens* was more frequent and showed higher cover in logged forests compared to primary forests. At plot level, its cover was negatively associated with stem density, species density and diversity of trees, but at the same time, its cover explained only a marginal proportion

of variance in tree community compositions. Clearly, some other factors rather than *A. pubescens* might have a central role in shaping the tree community compositions in Kibale.

As a conclusion, this study demonstrates that even after four decades of natural recovery, the tree community compositions of logged areas in Kibale are still different from the nearby primary forests, that is, the recovery is still under way. However, the 42- to 43-year-old forests already exhibit a much 'advanced' recovery state than the 9- to 19-year-old forests. Notably, the forest structural aspects, species richness, diversity and tree community composition show different recovery rates.

Our results provide valuable information on the recovery processes of tree community compositions in Kibale, which is one of the most intensively studied Afrotropical forests. Here, for example, the knowledge of the indicator tree species can be used in management interventions to facilitate the recovery processes, for example, in restoration planting efforts. On a more general level, our results also provide valuable information on rainforest recovery processes in Afrotropics. The time periods required for tree community compositions in human-disturbed forests to recover can take much longer than four decades. The slow recovery of many later-successional tree species to logged areas emphasizes the important role of primary forests when preserving the tree communities in tropical rainforests.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Nested study plot, SW corner (●) of all sub-plots located at the randomized GPS coordinate.

**Table S1.** Tree taxa, the age group they indicate (P = primary forest), and their estimated mean density (stems) per hectare in each forest area, in Kibale NP, Uganda.

**Figure S2.** Sample-based species-accumulation curves of trees in the nine areas in Kibale National Park, Uganda.

**Figure S3.** The mean values (±SE) of: (a) species density per plot, (b) density of stems ha$^{-1}$, (c) Simpson's $D$ and (d) Berger–Parker dominance in the nine forest areas in Kibale National Park, Uganda. (e) The cover of *Acanthus pubescens* shown as boxplots (the box representing the first and third quartile, whiskers extending to the most extreme data point which is ≤1.5 × (length of the box) away from the box).

**Figure S4.** The proportional abundances of the strongest indicator species (Dufrene Legendre Indicator species analysis), for the six ages, plotted against the years since harvesting.