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Composition of woody species in a dynamic forest–woodland–savannah mosaic in Uganda: implications for conservation and management

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Abstract. Forest–woodland–savannah mosaics are a common feature in the East African landscape. For the conservation of the woody species that occur in such landscapes, the species patterns and the factors that maintain it need to be understood. We studied the woody species distribution in a forest–woodland–savannah mosaic in Budongo Forest Reserve, Uganda. The existing vegetation gradients were analyzed using data from a total of 591 plots of 400 or 500 m² each. Remotely sensed data was used to explore current vegetation cover and the gradients there in for the whole area. A clear species gradient exists in the study area ranging from forest, where there is least disturbance, to wooded grassland, where frequent fire disturbance occurs. Most species are not limited to a specific part of the gradient although many show a maximum abundance at some point along the gradient. Fire and accessibility to the protected area were closely related to variation in species composition along the ordination axis with species like *Cynometra alexandri* and *Uvariopsis congensis* occurring at one end of the gradient and *Combretum guenzi* and *Lonchocarpus laxiflorus* at the other. The vegetation cover classes identified in the area differed in diversity, density and, especially, basal area. All vegetation cover classes, except open woodland, had indicator species. *Diospyros abyssinica*, *Uvariopsis congensis*, *Holoptelea grandis* and all *Celtis* species were the indicator species for the forest class, *Terminalia velutina* and *Albizia grandbracteata* for closed woodland, *Grewia mollis* and *Combretum mole* for very open woodland and *Lonchocarpus laxiflorus*, *Grewia bicolor* and *Combretum guenzi* for the wooded grassland class. Eleven of the species occurred in all cover classes and most of the species that occurred in more than one vegetation cover class showed peak abundance in a specific cover class. Species composition in the study area changes gradually from forest to savannah. Along the gradient, the cover classes are distinguishable in terms of species composition and vegetation structure. These classes are, however, interrelated in species composition. For conservation of the full range of the species within this East African landscape, the mosaic has to be managed as an integrated whole. Burning should be varied over the area with the forest not being burnt at all and the wooded grassland burnt regularly. The different vegetation types that occur between these two extremes should be maintained using a varied fire regime.

Introduction

Large areas of East Africa are covered with forest–woodland–savannah (FWS) mosaics. Fire, both of natural and anthropogenic origin, is typical for the woodland–savannah part of the mosaic (Walter 1985). The fresh grass that regrows after fire is advantageous for the many ungulates of East Africa and many of these ecosystems are, therefore, managed mainly for wildlife conservation. Forests, on the other hand, are managed for timber production, for woody species conservation, as water catchment areas, and for their aesthetic values. Consequently the forest and the woodland–savannah areas, even where they occur together as a mosaic, are often treated as independent conservation entities.

Uganda is has large tracts of FWS mosaics. Several of these FWS mosaics have been enlisted for demarcation as conservation areas because of their high biodiversity value (Forest Department Uganda 1999), yet surveys in such areas have focused on the forest and have not taken the woodland areas into account. Although forests are arguably richer in species (Sheil and Burslem 2003), this does not do justice to the specific flora and fauna found in woodlands that are adjacent to or within the forests.

In our study area, Budongo Forest Reserve, fire has been used as a management tool in the woodland areas for hundreds of years (Paterson 1991). The local people, resident on the outskirts of the forest reserve, set most of the fires. Changes in management of the area, which resulted in more active policing of the protected area and the establishment of a gate entrance to the only access route, have led to less use of fire in the woodland areas. As a consequence, forest vegetation is now colonizing the woodland areas (van Straaten 2003). It is unknown to what extent accessibility to the protected area acts as a controlling factor. As specific floristic information for the area is lacking, it is as yet unknown what the effects of continuing reforestation will be on the tree diversity of Budongo Forest Reserve. In this paper, we explore the current status of the forest in terms of species composition and diversity, and how it is distributed in space.

Studies that have explored the species interrelationship within FWS mosaics are rare (Hovestadt et al. 1999). Most studies have concentrated on species distribution within the forest (Eggeling 1947; Sheil et al. 2000; Mwami and McNeilage 2003; Eilu et al. 2004) or the woodland–savannah (Swaine et al. 1992; Schwilk et al. 1997; Schwartz and Caro 2003; Li et al. 2004). Previous data of Budongo forest (Eggeling 1947) stimulated the emergence of the important Intermediate Disturbance Hypothesis (Connell 1978), which states that in a landscape, species diversity is highest in areas with an intermediate level of disturbance. In areas of high disturbance and areas of low or no disturbance, species diversity is low. At the time of Eggeling's (Eggeling 1947) study, frequent burning had arrested the forest succession into the woodland. Eggeling's gradient mainly reflects succession within the forested area. With the increased control of burning over the years, resulting in variation of burning

with some areas burnt more often than others, forest succession into the woodland became possible. Hence, an added component of our study is the extension of a historically important succession gradient, exploring its range into the woodland areas.

In our study, special emphasis was placed on how the existing vegetation types can be characterized in terms of the woody plants and the implication of the observed species patterns to conservation of woody plants in such landscapes. The hypothesis made is that all the vegetation types that exist within the study area, and the species they support, are an integral part of a compositional/successional gradient that stretches across the FWS mosaic. We asked the following questions: Is it possible to quantify the gradient? What species are specific for certain areas? How does the species composition vary along the succession gradient? Can the gradient be explained in relation to environmental variables?

A further question we address is whether a satellite image classification of the area can be used to adequately map the vegetation and its composition in the area. For this we made use of discrete vegetation cover classes, obtained from a classification carried out using a combination of spectral information and environmental variables' information (Nangendo et al., submitted). The vegetation classes are considered a proxy of the vegetation types found in the area. Standard vegetation indices (NDVI and Tasseled Cap vegetation index) based on the same image were also compared in their ability to explain the observed gradient. Finally, we discuss the conservation and management implications of our results.

Materials and methods

Study area

The work was carried out in the northern part of Budongo Forest Reserve in north-western Uganda. The area is located between 1°35' and 1°55' N and 31°18' and 31°42' E. It receives between 1397 and 1500 mm of rain annually on 100 to 150 days. There are two main forest blocks: the main Budongo Forest block and the Kaniyo-Pabidi Forest block (Figure 1). A woodland area, interspersed with forest patches, commonly referred to as Kaniyo-Pabidi woodland, separates these two blocks.

The underlying geology of the Budongo Forest is Precambrian origin consisting of high-grade metamorphic rocks of the 2.9 billion-year-old granulite group (van Straaten 1976). The soils over 90% of the study area are orthic Ferralsols: highly weathered, deep, well drained soils with low pH. The remaining 10% of the area has typically shallow soils, called Lithosols. These soils are mainly found on hilltop regions and are predominantly underlain by rocks. In river valleys, eutric Fluvisols are present.

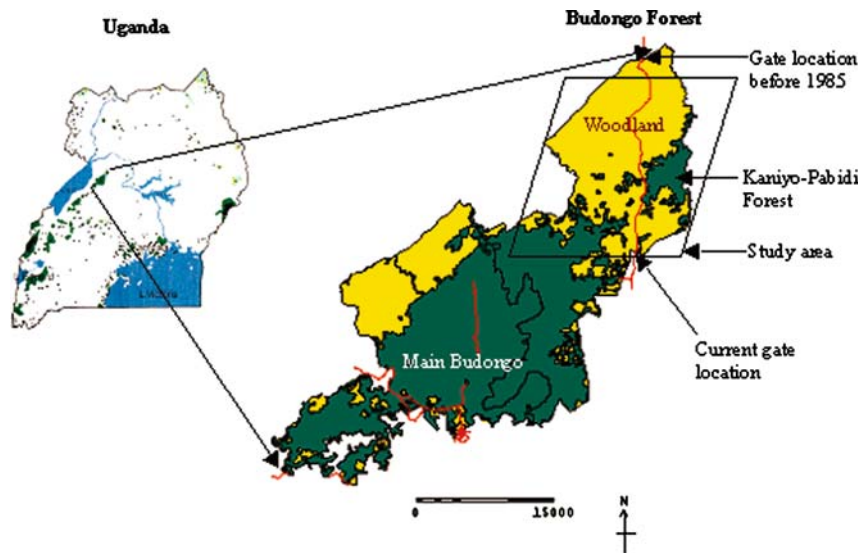


Figure 1. Map of study area location.

In the woodlands, fire has been prevalent for hundreds of years (Paterson 1991). The woodland burning was initially carried out by the local people for purposes of hunting and refreshing grass for both domestic and wild ungulates (Buechner and Dawkins 1961). With the transfer of the control of the woodlands from the local people (Bunyoro Kingdom) to the central government (Forest Department) in 1968, measures to control burning were put in place (Forest Department Uganda 1997). These were not very effective, however, until the establishment of the joint management between Forest Department and Uganda Wildlife Authority in the mid 1980s. Fewer, and smaller, areas are now burnt and the burning is also less frequent. The woodland is therefore heterogeneous and made up of vegetation patches at varying stages of recovery since they were last burnt.

Data collection

Data was collected from 591 plots, 266 of which had an area of 400 m² and 326 with an area of 500 m². All data were collected during the same period (August–October 2002). Along a transect, perpendicular lines were laid every 300 m. Along each perpendicular line, data were collected at every 75 m. For sites 1–5, a plot size of 400 m² was used (Figure 2), while for sites a–e, it was 500 m². Based on a 2002 satellite image of the study area, sites 1–5 were located in areas that showed a similar spectral reflectance, whereas sites a–e were located in areas that showed varying spectral reflectance. The variation

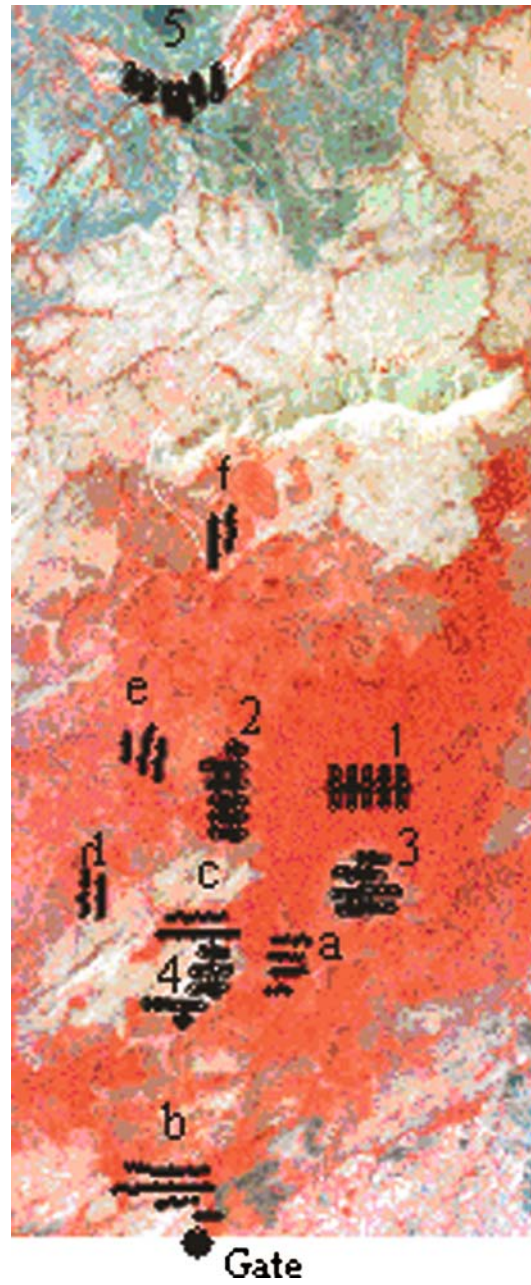


Figure 2. The location of the data collection points. 1, 2, 3, 4 and 5 are locations where the plots were 400 m² and a, b, c, d, e and f are locations where the plot size was 500 m².

of the site locations was to ensure that we capture as much as possible of the species variation within the area. In each plot, the following data were collected:

- Plot coordinates
- Species names, diameter at breast height (DBH) for all woody plants ≥ 10 cm DBH, measured at 130 cm. If the tree was buttressed and abnormal at 130 cm, the diameter was measured just above the buttress where the stem assumes a near cylindrical shape.
- Canopy cover percentage, using a canopy densiometer (Robert E: Lemmon, Forest Densiometers, Oklahoma, USA), following the provided guidelines. Four measurements were taken in each plot and an average of these measurements was calculated to determine the final canopy cover of the plot.
- A fire indicator value. The fire indicator value was based on several factors (1) the degree of scorching on the woody stems i.e. if it was fresh or old, (2) if there existed remains of burnt grass in the undergrowth and (3) whether fresh ash was found in the area. The last two factors were used to confirm areas with recent fire. Plots with fresh fire scorching on the woody stems, remains of burnt grass or ash were recorded as 'recent burns' and labelled class 2. Plots with old signs of fire were labelled class 1 (old fires) and plots with no sign of fire were labelled class 0 (no fire).

Species identification was based on Eggeling and Dale (1952) and Hamilton (1991). Samples of the species that could not be clearly identified in the field by the botanists on the team (Israel Tinka and Hezekias Dumba) were sent to the Uganda National Herbarium, Makerere University, where they were identified.

Data preparation

A Detrended Correspondence Analysis (DCA) (Multi-Variate Statistical Package MVSP 3.11, Kovach Computing Services, UK) was run using the two data sets i.e. for the 400 m² plots and the 500 m² plots. When the plot scores of DCA axis one and two were plotted together, using a separate symbol for each plot size, the data for the two sets fell within the same range i.e. they showed near to identical results and complemented each other. As the plots also overlap spatially, it was therefore decided to pool the two data sets. Expressing density as the number of trees per 1000 m², the abundance values were calculated for each plot. Plots with less than 10 individuals were removed from the data. As the larger plots have more individuals and thus capture more species on average than the smaller plots, rare species, defined as those having a total of less than 25 individuals, were also removed from the data set. The final dataset consisted of 491 plots with 45 species.

From the DBH values measured in the field, basal area (BA, m² ha⁻¹) was calculated for each plot, including all trees of the actual plot data.

Remote sensing

Values of the Normalized Difference Vegetation Index (NDVI), which is well correlated with vegetation biomass (Tucker 1979) and Tasseled Cap vegetation index (TC), which has a good correlation with forest stand density (Crist et al. 1986), were extracted for each plot from the respective vegetation index maps calculated using a 2002 Landsat ETM+ satellite image. These values were used for further analyses. Vegetation indices provide values that are indicative of the spectral reflectance of the vegetation at a given place. Depending on the satellite image bands selected and the ratios used, each vegetation index measure will result in a different value for a specific plot. Because there is a high variation in reflectance over a forested area, the resultant pixel values for a given index vary from point to point resulting in continuous values over the forested area.

NDVI used two bands, red and near infrared. Tasseled Cap incorporates more information by using six different light bands (blue, green, red, near infrared and far infrared). Depending on the ratios of combination of the six bands, different multispectral features are obtained (Crist and Cicone 1984). The first three features usually account for most of the variation in a single date image (Collins and Woodcock 1996). These three have been labelled brightness, greenness and wetness, respectively. All three were used in this study.

Vegetation cover class values for each plot were extracted from a vegetation cover map of the area obtained from an earlier classification (Nangendo et al., submitted) of a Landsat ETM+ image using both spectral and environmental information. All 592 plots were separated into the discrete cover classes (forest, closed woodland, open woodland, very open woodland and wooded grassland). Having used a Landsat satellite image, with a pixel size of 30 m, in the classification, the minimum area belonging to a specific cover class is 900 m². Species composition, diversity and forest structure were analyzed in consideration of the cover class in which each plot fell with the assumption that these vegetation cover classes were representative of the major vegetation variation within the area.

Accessibility

We used distance from the southern forest boundary to each plot as a surrogate for accessibility, by the local people, to the sampled areas. The conservation area gate marks the southern boundary between the conservation area and the local people's settlements. From here on, distance will be referred to as 'distance from gate.' During fieldwork, it was observed that because of the gate control, the local people entered the protected area at other points along the boundary of the protected area, instead of using the road. Having recorded the coordinate of the gate location, an east–west line was established at this point

and distance for each plot was calculated based on this line. This provided the plot distance relative to the conservation area gate.

Analysing the gradient

We used Detrended Correspondence Analysis to explore the species distribution within the study area. To determine which variables best explained the gradient in species composition, the plot scores on the DCA axes were related to the site variables using stepwise regression.

Linking remote sensing with the gradient

Two approaches were used in analysing remote sensing outputs. First, plot values obtained from vegetation indices (such as TC), which are continuous classifiers, were compared to DCA plot scores. To identify the vegetation index that best explained the gradient, a non-linear regression method was used since the scatter plot of the DCA vs. the index values showed a non-linear relationship. Second, discrete classes obtained from an earlier classification (Nangendo et al., submitted) were analyzed for differences in terms of species composition and diversity and, in basal area. Although the same satellite image was used for the classification and for the creation of the index maps, the plots used for the classification are not the same as those used in the analysis.

Differences in composition

We used the Multiple-Response Permutation Procedure (MRPP) and Indicator Species Analysis of PC-ORD (McCune and Mefford 1999; McCune et al. 2002) to test for differences in composition between the different vegetation units. MRPP, a non-parametric procedure was used for testing the hypothesis that no difference existed in composition between two or more groups of plots. For distance in composition between the plots, Relative Sørensen (Bray–Curtis) was used because it takes into account both composition (presence–absence of species) and abundance. For weighting option: $C_1 = n_1 / \sum n_1$ was used, which is the most widely used and recommended measure. C_1 is the weight and is dependent on the number of items in a group, say J , and n_1 is the number of items in group J . The software uses 9999 permutations in the test. Two tests were carried out based on *a priori* selection: cover classes and fire classes. An Indicator Species Analysis was also carried out on the basis of these two classifications.

Indicator species Analysis combines information on the concentration of species abundance in a particular group (transect) and the faithfulness of occurrence of the species in that group. A perfect indicator species of a

particular group should always be present and should also be exclusive to that group (not occurring in other groups). From the analysis, an indicator value is obtained for each species in each group (Dufrêne and Legendre 1997; McCune and Mefford 1999; McCune et al. 2002). The indicator values are tested for statistical significance using a Monte Carlo randomization. Species diversity was expressed as species dominance, which was calculated using the Simpson Index (SI) (Magurran 1988), and Fisher's α ($F\alpha$), (Fisher et al. 1943). These indices have low sensitivity to plot size differences (Magurran 1988). Differences between plots in different fire and cover classes with respect to SI, $F\alpha$ and BA were tested with ANOVA using SPSS (SPSS 10, SPSS Inc. USA).

To check for variation in species abundance and diversity in relation to disturbance, graphs of number of species per 100 m² and Fisher's α per plot were made. Having the assumption, which was also backed by field observation, that disturbance was lowest in the forest class and highest in the wooded grassland class, plots were arranged according to vegetation cover classes. The order of plot arrangement was; forest (1–147), closed woodland (148–310), open woodland (311–459), very open woodland (460–555) and wooded grassland (556–592). Within each vegetation cover class the plots are randomly ordered.

Results

Species distribution

A total of 26,076 individuals from 121 species, 89 genera, and 38 families were recorded on the 591 plots. The most species-rich family was Moraceae with 11% of all species found (13), followed by Euphorbiaceae and Mimosaceae with 8% each (10). The most species-rich genus was *Ficus* with 5% of all species (6), followed by *Acacia*, *Albizia*, *Celtis* and *Combretum* with 3% each (4). Nine species or 7% of all species could not be identified to genus level. A full species list with abundances is given in Appendix 3. The most abundant genus, in terms of total individuals encountered, was *Combretum*, with close to 16% of all individuals, followed by *Terminalia* (14%), *Grewia* (13), *Stereospermum* (6%), and *Uvariopsis* (6%).

The DCA analysis on combined and trimmed data (491 plots and 45 species) ordered the plots mainly along 1 axis (Figure 3a). This axis had a relatively high eigenvalue (0.465) suggesting significant woody species variation along this axis. The eigenvalue for the second axis was 0.172. With 491 plots included, axis 1 explained 11.8% of the variation. There was, however, one outlier plot strongly influencing the second axis. This outlier plot was dominated by *Sapium ellipticum*, a species that rarely occurred in the study area. After removing this plot, axis 1 explained 12.5% of the variation and axis 2 an additional 4.6%. Plots with a low axis score (close to 0) are found in the forest area, plots with a high score (>7) are found in the most open areas. As most of

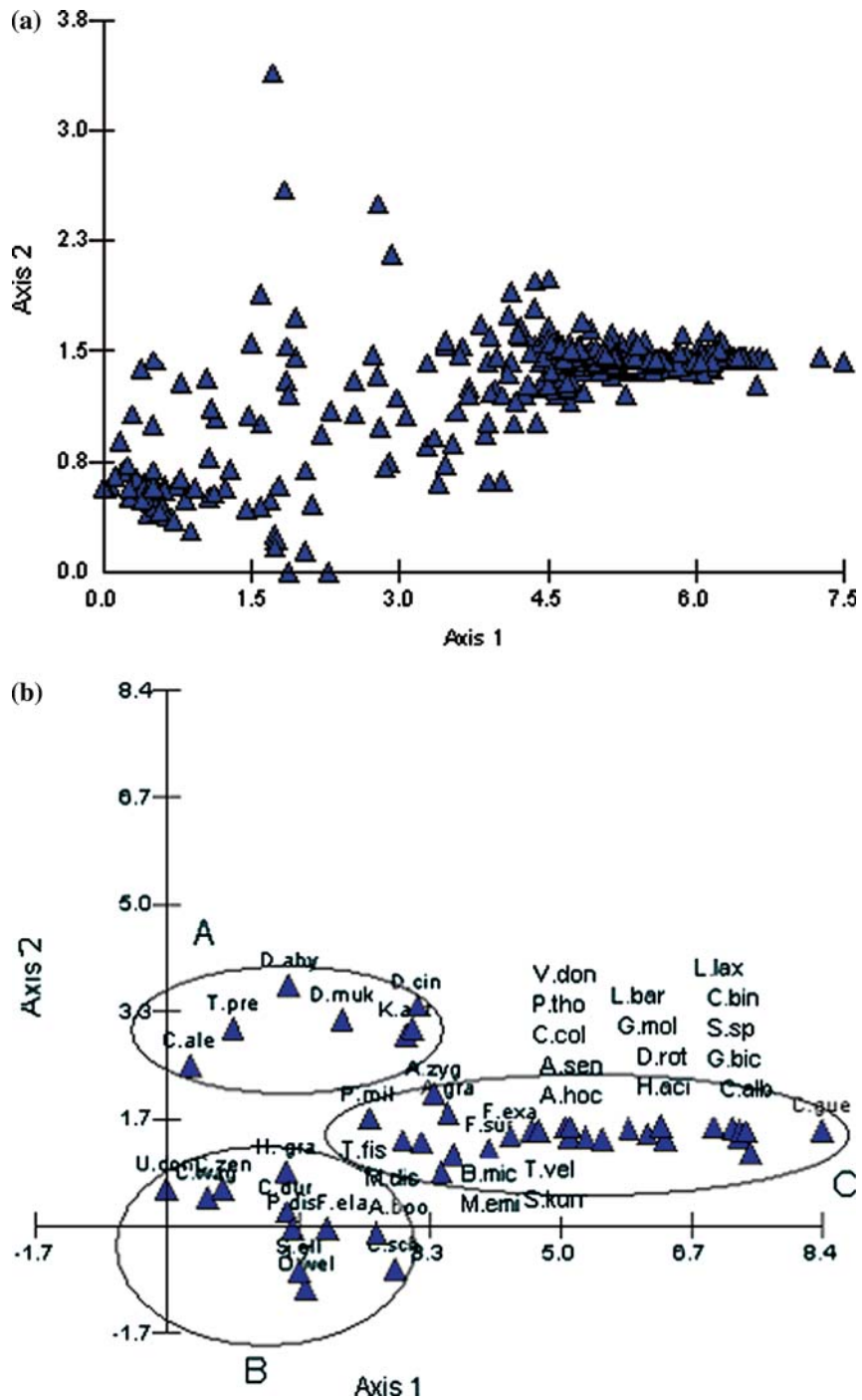


Figure 3. DCA graph showing (a) plot composition variation along the first two ordination axes (b) species composition variation along the first two ordination axes.

the discussion here on will pertain to axis 1, the main gradient, we will abbreviate 'DCA axis 1 plot scores' to 'DCA scores.'

The species plot (Figure 3b) also shows most of the variation along the first axis. The effect of the second axis is only evident close to zero along axis 1, the forest side, where there appear to be two groups (the same can be said for the plot scores). Based on this interpretation the species can be divided into three groups; A, B and C (Figure 3b). Groups A and B occur within the forest area and group C, probably starting at the forest edge, stretches through to the woodland area. Species found in group A include *Cynometra alexandri*, *Diospyros abyssinica* and *Khaya anthotheca*. Group B species include *Uvariopsis congensis*, *Celtis wightii*, *Holoptelea grandis* and *Funtumia elastica*. And species found in group C include *Albizia grandibracteata*, *Terminalia velutina*, *Grewia mollis*, *Combretum molle* and *Lonchocarpus laxiflorus*.

Fire indicator best explained the gradient in species composition followed by slope and then distance from gate. Using the stepwise regression analysis, fire alone had r^2 of 0.324 with a standard error of 1.395. Including slope in the model the r^2 was raised to 0.354 and the standard error reduced to 0.365. When distance from gate was included, the r^2 increased to 0.359 and the standard error was reduced to 1.361. Vegetation cover type was not significant and so it does not appear in the results table. Relating the site variables individually to DCA (results not shown) showed that while all the other variables had a positive correlation with the DCA, distance from gate had a negative correlation.

Species composition and vegetation indices

All the vegetation-indices explained well the DCA variation. TC-wetness and TC-greenness showed the best relationship with DCA scores with r^2 of 0.73 and 0.70, respectively. TC-brightness had the lowest value ($r^2 = 0.46$). NDVI had an r^2 of 0.64.

Species distribution in discrete vegetation cover classes

The classes derived from the analyses of the satellite image differed considerably in their DCA scores (Figure 4a and b). Plots of the 'No-fire' class had consistently low DCA scores, whereas the plots from the class 'Recent-fire' have high DCA scores. Plots from the class 'Old-fire' were intermediate. The Fire classes also differed considerably in their TC-greenness values. Consequently a combination of DCA scores and TC-greenness value segregated the fire classes well.

A similar result was found for the cover classes. These classes are segregated both by their DCA scores and TC-greenness values (Figure 4b).

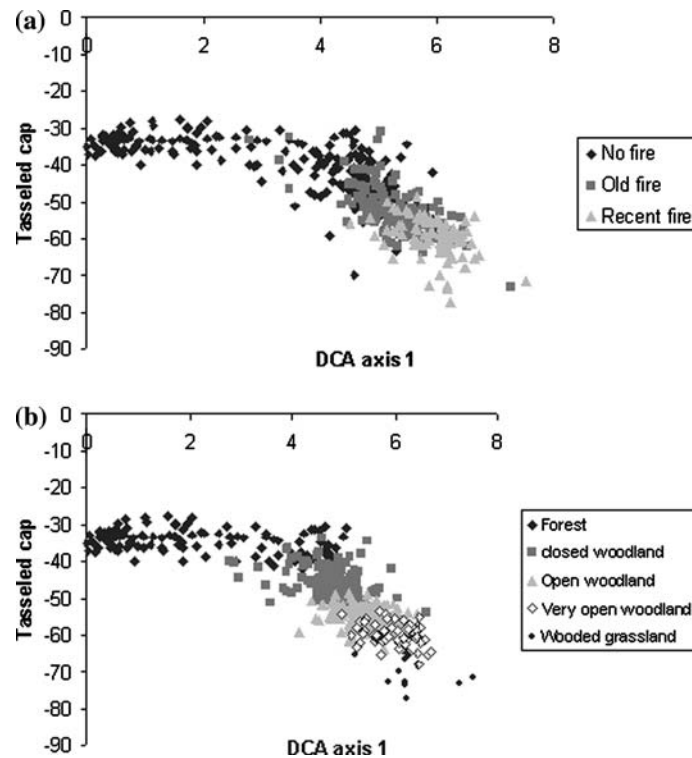


Figure 4. DCA axis 1-Tasseled Cap relationship as subdivided by (a) fire regimes and (b) vegetation cover classes.

Plots of different fire classes also differed significantly in their species composition (MRPP, $A = 0.061$, $p \ll 0.0001$). *Uvariopsis congensis*, *Celtis wightii*, *Diospyros abyssinica*, *Phyllanthus discoideus*, *Celtis zenkeri*, *Alstonia boonei*, *Cynometra alexandri* and *Trichilia prieuriana*, all exclusively occur in the No-fire class i.e. relative abundance (RA) equals 100% for each of the species. The indicator species analysis also identified the above named species as indicators for the No-fire class i.e. significant p values (Appendix 1). Although no species had 100% relative frequency in any class, *Terminalia velutina* and *Grewia mollis* had very high relative frequency, 90 and 87%, in Old-fire and Recent-fire classes, respectively. For the Old-fire class, species that had significant species indicator values include *Terminalia velutina*, *Stereospermum kunthianum* and *Piliostigma thoningii*. And for the Recent-fire, species that had significant species indicator values include *Grewia mollis*, *Annona senegalensis*, *Combretum molle*, *Lonicocarpus laxiflorus* and *Grewia bicolor*.

Plots of different cover classes also differed significantly in their species composition (MRPP, $A = 0.148$, $p \ll 0.0001$). Of the species exclusively found in the no fire area, *Uvariopsis congensis*, *Celtis wightii*, *Celtis zenkeri*, *Cynometra alexandri* and *Trichilia prieuriana* were also exclusively found in the

forest area. In addition, *Pterygota mildbreadii* was also exclusively found in the forest (Appendix 2). *Funtumia elastica*, *Uvariopsis congensis* and *Celtis wightii* had the highest relative frequency in the forest class; 55, 54 and 50%, respectively. Species with the highest relative frequency in the closed woodland are *Terminalia velutina* and *Grewia mollis* with 97 and 70%, respectively. In the open woodland plots, *Terminalia velutina* and *Grewia mollis* still had the highest relative frequency of 85 and 88%, respectively. In the very open woodland, *Grewia mollis* occurred in 99% of the plots while in the wooded grassland, *Stereospermum kunthianum* had the highest relative frequency of 67%. Overall, *Grewia mollis* in the very open woodland had the highest relative frequency i.e. it occurred in 99% of the closed woodland plots.

Whereas in the forest some of the species that had the highest relative frequency are part of those that had the highest relative abundance, it is different for the other cover classes. In the closed woodland, the species with the highest relative abundance were *Bridelia michrantha* (70%), *Albizia grandibracteata* (55%) and *Maesopsis eminii* (55%). In the open woodland there were no species with relative abundance above 50%. The highest was *Ficus exasperata* with 48%. In the very open woodland, *Combretum molle*, *Securinega virosa* and *Dombeya rotundifolia* had the highest relative abundance with 74, 71 and 75%, respectively. *Combretum guenzi* exclusively occurred in the wooded grassland. Other species with high relative abundance in the wooded grassland were *Combretum binderanun*, *Grewia bicolor*, *Lonchocarpus laxiflorus* and *Hymenocardia acida* with 78, 66, 58 and 50%, respectively.

Most of the species identified as belonging to groups A and B e.g. *Cynometra alexandri*, *Khaya anthotheca*, *Diospyros abyssinica*, *Uvariopsis congensis* and *Holoptelea grandis* (Figure 3b) were also identified through indicator species analysis as good indicators for the No-fire class. Of these, *Diospyros abyssinica*, *Uvariopsis congensis*, *Holoptelea grandis* and all *Celtis* species were also good indicators of the forest class (Appendix 2). The species in group C belonged both to Old-fire and Recent-fire classes. Considering the cover classes, *Terminalia velutina* and *Albizia grandibracteata* were good indicators for closed woodland, *Grewia mollis* and *Combretum mole* for very open woodland and *Lonchocarpus laxiflorus*, *Grewia bicolor* and *Combretum guenzi* were good indicators for the wooded grassland class. Several of these species e.g. *Uvariopsis congensis*, *Terminalia velutina* and *Grewia mollis* have distinctively high abundance in specific areas along the gradient (Figure 5).

Although the closed woodland had the largest area sampled followed by the open woodland, the forest had the highest number of species and genera identified (Appendix 3). The lowest number of species and genera was found in the wooded grassland. The highest ratio of species to genera was in very open woodland (1.4) and the lowest in wooded grassland (1.2). Eleven species occur in all classes and most species occur in more than one cover class but their abundance varies greatly between classes. Forest and closed woodland classes had an equal number of families and wooded grassland class had the lowest number of families.

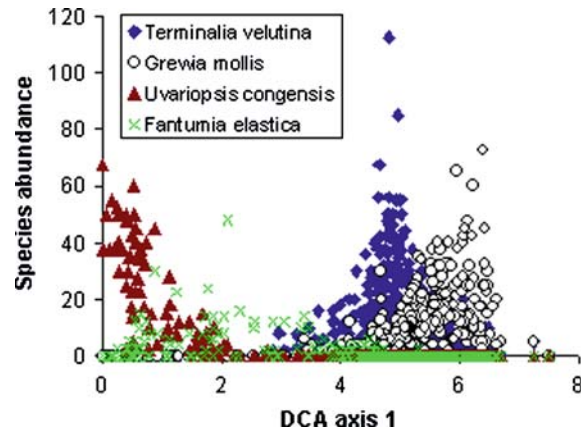


Figure 5. Relationship between DCA axis 1 and some of the most abundant species whose maximum abundance occur in different areas along the gradient. The selected species also display a variation in their distribution range.

The Simpson index of all vegetation classes differed only slightly except that of wooded grassland (Figure 6a). The wooded grassland had the highest value and the highest standard error. The forest class had the highest mean Fisher's α (Figure 6b) followed by the closed woodland class. These two classes were significantly different from all other classes but not from each other. The open woodland was also significantly different from the wooded grassland. The wooded grassland had the lowest Fisher's α .

The basal area (Figure 6c) decreased from the forest, which had the highest value, to the wooded grassland, which had the lowest. The forest also showed the highest variation. All cover types were significantly different from each other. The mean stem density values for the forest, closed woodland and open woodland were very close (Figure 6d) and there was no significant difference between them. The very open woodland also had a high mean value although slightly lower than the other 3. The wooded grassland is much lower than all others. The very open woodland and the wooded grassland are each significantly different from all others. So while many individual trees may be found in each cover type, they vary in size with the forest having larger trees than any of the other cover types. Details of the species occurring in each cover type and their abundance are indicated in Appendix 3.

Discussion

Variation in species composition along the gradient

The species composition along the gradient gradually changes from species that attain maximum abundance in areas of minimum disturbance e.g.

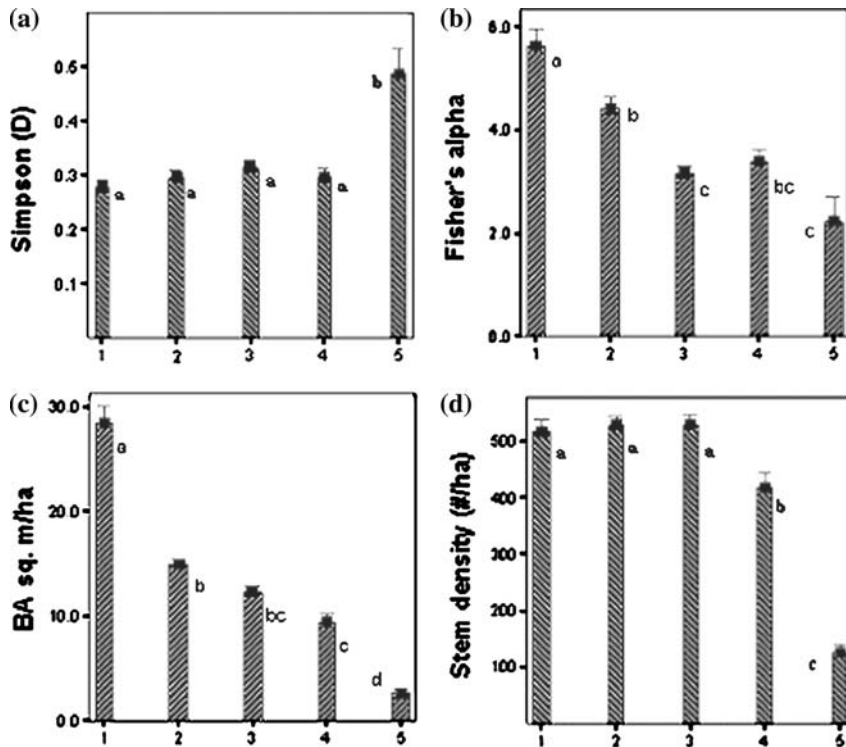


Figure 6. comparison of cover class mean and standard deviation for (a) Simpson index, (b) Fisher's α , (c) basal area and (d) stem density. The class numbers consistently represent 1, forest; 2, closed woodland; 3, open woodland; 4, very open woodland; and 5, wooded grassland. The letters beside each bar indicate significance differences. Bars, for a specific variable, which have the same letter mean that they are not significantly different (ANOVA: $p = 0.05$).

Cynometra alexandri and *Uvariopsis congensis* to species that attain maximum abundance in areas with frequent disturbance e.g. *Grewia mollis*. On the other hand, species like *Terminalia velutina* attain maximum abundance in the moderately disturbed areas (Smart et al. 1985). Many species, as evidenced by the species abundance plot (Figure 5), are wide ranging although they have a clear optimum, which occurs at species specific locations along the gradient. Identification of a vegetation type should, therefore, be based on species abundance proportions rather than species incidence alone. This variation in species tolerance range has also been observed in a Mexican dry forest (Balvanera et al. 2002). In another study (Nangendo et al., submitted), it was observed that the wide-ranging species often have their different development sizes (seedlings, saplings and trees) in species specific locations along the gradient.

Relationship between site variables and the observed gradient

Of the environmental variables recorded, fire best explained the gradient. This is evidenced by the high correlation between DCA and fire (Table 1) and the fact that the compositional gradient could be divided using the fire regime (Figure 4a). Areas that had recent fires, and are probably most frequently burnt, had species that characteristically display fire resistant traits e.g. a thick bark, peeling off of the old bark and good sprouting ability after a fire (Gashaw et al. 2002; Saha and Howe 2003; Vesik and Westoby 2004). The occurrence of some species is thus influenced by their fire-tolerance level (Cauldwell and Zieger 2000) with increasingly more of the less fire resistant species in the Old-fire class. Here, seed dispersal (a factor not explored in this study) may have an important role. A number of the species that occurred in the Old-fire class were most abundant in the No-fire class. Their seeds were probably dispersed into the Old-fire class areas e.g. by wind and, when conditions became favorable, they got established. Hence we suggest that the existent fire regime influences their low occurrence (Huston 1994).

Although water is often a limiting factor for plant survival, in humid FWS mosaics, water distribution is not a critical controlling factor (Favier et al. 2004). Despite the variation in rainfall over Budongo Forest Reserve, with the northern part receiving less rain than the south (Plumptre 1996), the north still receives over 1200 mm a year (Forest Department Uganda 1997) which is sufficient for forest maintenance. Also elephants that previously restricted forest expansion (Laws et al. 1975) are no longer present. The species turnover could possibly be explained by an additive effect of the environmental variables considered in this study, the historical impact by elephants and probably other factors that were not considered in this study e.g. seed dispersal mechanisms, which have been shown to favor establishment of species with higher dispersal ability in the post disturbance period (Hovestadt et al. 1999; Ohsawa et al. 2002). However, just like in other studies where FWS occur (Elliott et al. 1999; Hovestadt et al. 1999), fire plays a major role in controlling species distribution pattern but it does not explain all the variation (Weiher 2003). Accessibility to the protected areas, where local people mainly utilize areas closest to them (Acharya 1999; Obiri et al. 2002), also showed a significant relationship with the species composition gradient.

Vegetation variation and composition as mapped using satellite image classification

The image classification provided a good representation of the vegetation types. Each cover class had significant indicator species and differences in structural and species diversity existed among the cover classes (Figure 6). Although the best differentiating factor was basal area, where each cover class was significantly different from the others, indicator species have also been

shown (Cousins and Lindborg 2004) to correspond well with the succession gradient. Classification of mosaic areas using remotely sensed data could therefore be a good start for identification of the vegetation types that exist within them. This would require less time (Schmidt et al. 2004) as compared to when only field surveys would have been used.

Our study has shown that although the forest significantly differed in species diversity and vegetation structure, especially basal area, there was a systematic decrease in variation from forest to wooded grassland (Figure 5). A major gradient stretching from the forest to the wooded grassland is evident (Dezzeo et al. 2004) and species composition and forest structure vary along this gradient. Most of the areas sampled by Eggeling (1947) and followed up in Sheil et al. (2000) had not had disturbance for a long time. Areas sampled in this study, however, cover both areas with ranging times since last disturbance and areas that are still experiencing frequent disturbance. Thus, in this study we observe a wider range of vegetation variation.

Although subtle variations in vegetation structure may be evident in some landscapes, the species composition variation is often more complex (Muhlenberg et al. 1990). In our study, the observed gradual change in species composition along the gradient and the compositional interrelationship between the vegetation cover classes indicate that the FWS mosaic is a single, interacting, integrated unit.

The effect of continuing reforestation on the biodiversity of Budongo

Eggeling (1947), also followed up in Sheil (1999), identified successional stages within the forest, with ironwood (*Cynometra alexandri*) at the climax end of the spectrum and the colonizing (woodland) forest as the starting point. In their study, the lowest woody plant diversity occurred in the ironwood forest. In our study, although diversity is low at the ironwood end of the gradient, it is even lower on the wooded grassland side of the gradient (plot results not shown) indicating a drop on either end of the gradient. The highest diversity is within the forest area and it gradually reduces until the lowest level, which occurs in the wooded grassland. The colonizing forest, identified by Eggeling (1947) as the starting point of the succession, occurs somewhere towards the middle of the current gradient. The current study has, therefore, extended the succession gradient to further into the wooded grassland and yet still conforms with the Intermediate Disturbance Hypothesis (IDH) (Connell 1978).

Another DCA run, after combining a resampled set of Eggeling's data with data used in this study, revealed more of the similarities between the two gradients. It, additionally, emphasized the existence of more than one succession path in the forest (Eggeling 1947; Sheil et al. 2000) and the variation within the forest (Plumptre 1996). To incorporate Eggeling's data, resampling from the original data set was carried out. Having known the plot size and the number of individuals collected from each of his plots, the number of

individuals expected to occur in a 500 m² plot was calculated. The calculated number of individuals was then randomly sampled from the original individuals of the respective plot. The abundance of each species in each plot was then raised to that which would occur in an 1000 m² plot. After crosschecking the species names for possible changes in naming, the data were combined with the rest of the tree data used in this study and a DCA was carried out. All Eggeling's plots, considering the first axis, occurred at one end of the gradient but in line with the rest of the plots (Figure 7). Eggeling's observation of compositional convergence (Eggeling 1947) is still evident in his plots (see dotted lines in Figure 7).

Plumtre (1996) identified a north–south compositional gradient. In our study, the variation along the second axis of Figure 7 is an indicator of this gradient. Eggeling's plots collected from the southern part of the forest occur separate from most of our plots, which were collected from the northern part of the forest.

Succession always starts with very few species, then progresses awhile along one line with more species coming in as conditions become more favorable (Huston 1994). In our study, few species were observed in the wooded grassland end of the gradient and species numbers increased as one moved towards the forest (Figure 3b). Although the forest side of the gradient had more species, other species occur away from the forest environment. The diversity of an area is influenced by the type, frequency and intensity of the disturbance (Trapnell 1959; Petraitis et al. 1989). Hence, if the whole succession gradient occurs in an area, there would be more species (Connell 1978; Huston 1994) than if one or a few stages of the succession gradient were conserved. So while the areas that have high species numbers e.g. forest

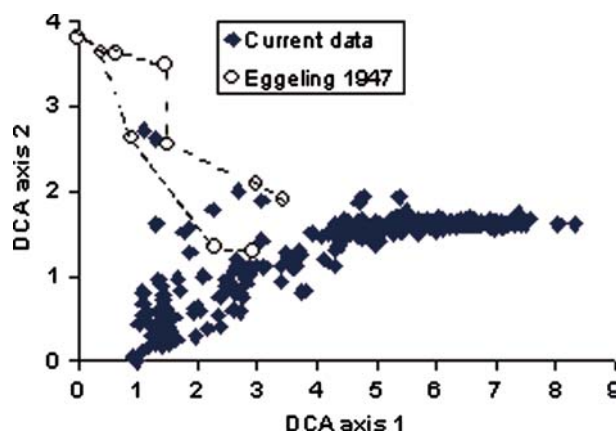


Figure 7. DCA graph obtained after combining a resampled set of Eggeling's data to the data used in this paper. Axis 1 had an eigenvalue of 0.38 and explained 9.8% of the variation. The second axis had an eigenvalue of 0.19 and explained 4.9%.

ought to be preserved (Sheil and Burslem 2003), the woodland areas should not all be allowed to become forest since that would mean losing the woodland dependant species. And the highest number of species can only be conserved when complementary areas are included in the conservation plan (Howard et al. 1998). The maintenance of the high diversity of Budongo, being an isolated forest with no immediate source of additional forest species, may be more attributed to the existence of all stages of the succession gradient (Richardson-Kageler 2004; Shea et al. 2004) than acquisition of more forest species from elsewhere, which, additionally, often takes a long time (Chapman et al. 1997). Hence, if reforestation of Budongo Forest Reserve would continue to the extent that the woodland areas would be lost, the biodiversity of the reserve would probably decrease. For purposes of conserving woody plants in a dynamic landscape, it is thus important that each vegetation type represented is included and maintained within the conservation area (Bengtsson et al. 2003). In the area under study, fire disturbance is a requirement for species coexistence (Shea et al. 2004).

In areas where fire may be applied, the vegetation type and its development stage may affect the potential for ignition and spread of the fire (Everett et al. 2000). Although no evidence exists of fires having destroyed tropical rain forests in Uganda, it has been observed elsewhere that tropical forests can burn (Cochrane and Schuize 1999; Cochrane and Laurance 2002; Laurance 2003). This, however, mainly occurs in the presence of very dry conditions, in fragmented forest landscapes and when fire is carelessly applied in or adjacent to logged over areas. Fire also remains a highly debated conservation management tool (Mentis and Bailey 1990; Trollope et al. 1995; van Wilgen et al. 1998). It is therefore important that fire be used cautiously and, probably learning and using burning methods that have been used in the past (Goma et al. 2001) will be a prerequisite. In this respect, conservationists need to focus more attention on the current vegetation management practices of local people surrounding conservation areas (Leone and Lovreglio 2004) since they have been noted to use fire destructively (Condit et al. 1998; Wheeler 1971).

In Africa FWS mosaics are prevalent in areas surrounding the Congo basin forests, including Uganda. These areas have been defined as transitional zones between the moist tropical forest and the drier savanna landscape typical of much of Africa. On the northern side, the transition occurs at about 8° N with the exception of Togo and Benin and part of Ivory Coast (Gautier and Spichiger 2004). Many FWS mosaics occur in Uganda because of its location in a zone of overlap between the ecological communities characteristic of the dry East African savannas and the West African rainforests (Howard 1991). The observations made in this study and their management implications are, therefore, relevant to many areas in Africa and in much of the tropical world where such landscapes occur.

Conclusions and recommendations

- Species composition in the area gradually changes from the forest to savannah.
- Although many of the species occurred in more than one vegetation cover class, each class had species that can be used to identify it. These are the classes where such species had a significantly higher relative abundance as compared to other classes.
- The gradient could be divided into sections using vegetation cover classes and the fire indicator. These cover classes were compositionally separable and vegetation structure significantly differed between the classes.
- Among the environmental variables, fire best explained the compositional variation along the gradient.

Areas with such a dynamic FWS mosaic need a purposeful management that takes into account the relationship between the observed vegetation pattern and how this has been generated over time (Alados et al. 2004). Since each vegetation cover class was compositionally separable from the others, a portion of each of these classes needs to be conserved. An area where all cover classes occur would be preferable since many species tend to occur in more than one cover class and another study (Nangendo 2005) showed that the juveniles and adults of some species do not occur in the same vegetation patches.

A well balanced management, including a controlled fire management system that will prevent forest from colonizing the whole area yet allowing the existence of varying disturbance regimes is a prerequisite for maintaining species diversity (Crow and Perera 2004).

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Appendix 1. The Indicator Species Analysis output based on fire indicator classes.

Species names	RA-0	RF-0	RA-1	RF-1	RA-2	RF-2	IV	<i>p</i>	Fire class
<i>Terminalia velutina</i>	39	66	52	90	9	47	46.7	0.001	1
<i>Grewia mollis</i>	14	47	37	80	49	87	42.4	0.001	2
<i>Combretum collinum</i>	23	37	39	56	38	49	21.7	0.046	
<i>Uvariopsis congensis</i>	100	26	0	1	0	0	25.7	0.001	0
<i>Annona senegalensis</i>	18	33	35	59	47	55	25.7	0.005	2

Appendix 1. Continued.

Species names	RA-0	RF-0	RA-1	RF-1	RA-2	RF-2	IV	<i>p</i>	Fire class
<i>Albizia grandibracteata</i>	64	41	31	22	5	6	26.2	0.001	0
<i>Stereospermum kunthianum</i>	22	28	44	50	34	47	21.9	0.003	1
<i>Combretum molle</i>	1	5	31	24	68	49	33.7	0.001	2
<i>Lonchocarpus laxiflorus</i>	10	12	19	22	71	45	31.7	0.001	2
<i>Vitex doniana</i>	38	33	36	36	26	25	12.8	0.585	
<i>Funtumia elastica</i>	94	31	6	3	0	0	28.9	0.001	0
<i>Lanea barteri</i>	27	25	41	32	32	29	13.1	0.174	
<i>Celtis wightii</i>	100	24	0	0	0	0	24.2	0.001	0
<i>Acacia hockii</i>	22	19	46	29	32	23	13.4	0.033	
<i>Piliostigma thonningii</i>	25	18	53	31	23	15	16.2	0.004	1
<i>Caloncoba schweinfurthii</i>	86	23	14	6	0	0	20.2	0.001	0
<i>Holoptelea grandis</i>	99	22	1	1	0	0	21.6	0.001	0
<i>Maesopsis eminii</i>	62	21	38	12	0	0	12.8	0.003	0
<i>Diospyros abyssinica</i>	100	10	0	0	0	0	9.6	0.001	0
<i>Ficus sur</i>	43	15	48	15	9	3	7.1	0.245	
<i>Grewia bicolor</i>	8	5	23	9	69	18	12.8	0.001	2
<i>Khaya anthotheca</i>	86	15	14	2	0	0	12.6	0.001	0
<i>Dombeya mukole</i>	79	8	17	3	5	1	6.4	0.013	0
<i>Bridelia micrantha</i>	87	12	9	1	4	1	10.7	0.001	0
<i>Celtis durandii</i>	86	12	14	2	0	0	9.9	0.003	0
<i>Combretum binderanum</i>	2	0	37	6	61	9	5.6	0.012	2
<i>Margaritaria discoidea</i>	71	11	29	2	0	0	7.6	0.004	0
<i>Phyllanthus discoideus</i>	100	10	0	0	0	0	9.6	0.001	0
<i>Albizia zygia</i>	56	2	20	2	24	3	1.3	0.829	
<i>Celtis zenkeri</i>	100	10	0	0	0	0	10.4	0.001	0
<i>Pterygota mildbreadii</i>	70	5	30	1	0	0	3.8	0.059	
<i>Hymenocardia acida</i>	11	3	27	5	62	9	5.7	0.008	2
<i>Olea welwitschii</i>	95	9	5	1	0	0	8.8	0.001	0
<i>Oncoba spinosa</i>	37	5	14	1	49	6	2.8	0.326	
<i>Tapura fisheri</i>	80	9	20	2	0	0	7.1	0.009	0
<i>Securinega virosa</i>	0	0	38	5	62	10	6.4	0.004	2
<i>Dichrostachys cinerea</i>	73	5	27	1	0	0	3.9	0.064	
<i>Alstonia boonei</i>	100	9	0	0	0	0	8.8	0.001	0
<i>Cynometra alexandri</i>	100	5	0	0	0	0	5	0.007	0
<i>Ficus exasperata</i>	37	3	63	3	0	0	2.2	0.272	
<i>Combretum gueinzii</i>	0	0	73	1	27	1	0.5	0.749	
<i>Sapium ellipticum</i>	81	2	19	1	0	0	1.2	0.403	
<i>Carpolobia alba</i>	0	0	21	3	79	6	4.5	0.006	2
<i>Dombeya rotundifolia</i>	8	2	25	5	67	8	5.4	0.012	2
<i>Trichilia prieuriana</i>	100	5	0	0	0	0	5.4	0.007	0

It indicates the concentration of each species in each class (Relative abundance, RA), the faithfulness of occurrence of the species in that class (Relative frequency, RF), the highest species indicator value across the classes (IV) the statistical significance of the indicator value (*p*) and the class in which a particular species had the highest indicator value (Fire class). For species that were not significant indicators for any class, fire class was left blank. RA is expressed as a proportion of a particular species in a particular class relative to its abundance in other classes. RF is expressed as the percentage of sample units in a class that contain that species.

p is significant at 0.01.

0, No fire; 1, old fire; and 2, recent fire.

Appendix 2. The Indicator Species Analysis output based on vegetation cover classes.

Species	RA-1	RF-1	RA-2	RF-2	RA-3	RF-3	RA-4	RF-4	RA-5	RF-5	IV	P	Cover cord
<i>Terminalia velutina</i>	12	30	44	97	31	85	8	57	5	44	42.8	0.001	2
<i>Grewia mollis</i>	2	16	16	70	32	88	48	99	1	11	47	0.001	4
<i>Combretum collinum</i>	11	18	20	52	38	64	22	43	10	22	24.3	0.042	
<i>Uvariopsis congensis</i>	100	54	0	0	0	0	0	0	0	0	54.4	0.001	1
<i>Annona senegalensis</i>	6	14	23	52	30	58	42	64	0	0	26.9	0.02	
<i>Albizia grandibracteata</i>	28	26	55	60	14	15	3	3	0	0	32.9	0.002	2
<i>Stereospermum kunthianum</i>	7	11	26	51	22	45	17	39	29	67	19.2	0.063	
<i>Combretum molle</i>	0	2	2	6	15	23	74	66	8	22	48.4	0.001	4
<i>Lonchocarpus laxiflorus</i>	0	0	2	10	14	36	26	47	58	56	32	0.001	5
<i>Vitex doniana</i>	5	11	33	51	23	36	16	24	23	22	16.8	0.095	
<i>Funtumia elastica</i>	89	55	11	11	0	0	0	0	0	0	49.4	0.001	1
<i>Lanea barteri</i>	2	3	23	30	35	40	34	43	6	11	14.7	0.095	
<i>Celtis wightii</i>	100	50	0	1	0	0	0	0	0	0	49.4	0.001	1
<i>Acacia hockii</i>	7	10	16	22	31	37	17	21	29	11	11.6	0.15	
<i>Ptilostigma thonningii</i>	5	8	18	24	22	31	10	16	45	44	19.8	0.024	
<i>Caloncoba schweinfurthii</i>	74	38	24	13	2	2	0	0	0	0	27.9	0.005	1
<i>Holoptelea grandis</i>	94	42	6	3	0	0	0	0	0	0	39.8	0.001	1
<i>Maesopsis eminii</i>	45	23	55	28	0	0	0	0	0	0	15.7	0.033	
<i>Diospyros abyssinica</i>	96	18	3	1	1	1	0	0	0	0	17.7	0.005	1
<i>Ficus sur</i>	18	10	43	20	31	14	8	4	0	0	8.8	0.133	
<i>Grewia bicolor</i>	0	0	3	3	11	13	20	20	66	56	36.9	0.001	5
<i>Khaya anthotheca</i>	71	20	23	10	6	1	0	0	0	0	14.2	0.03	
<i>Dombeya mukole</i>	82	14	5	2	11	4	3	1	0	0	11.1	0.04	
<i>Bridelia micrantha</i>	26	7	70	16	2	1	3	1	0	0	11.3	0.046	
<i>Celtis durandii</i>	93	23	7	3	0	0	0	0	0	0	21.5	0.005	1
<i>Combretum binderanum</i>	0	0	1	1	9	5	11	10	78	22	17.4	0.005	5
<i>Margaritaria discoidea</i>	61	14	39	9	0	0	0	0	0	0	8.3	0.078	
<i>Phyllanthus discoideus</i>	97	18	3	1	0	0	0	0	0	0	17.8	0.011	1
<i>Albizia zygia</i>	67	3	12	2	7	1	15	4	0	0	2.1	0.469	

Appendix 2. Continued.

Species	RA-1	RF-1	RA-2	RF-2	RA-3	RF-3	RA-4	RF-4	RA-5	RF-5	IV	P	Cover cord
<i>Celtis zenkeri</i>	100	22	0	0	0	0	0	0	0	0	21.6	0.006	1
<i>Pterygota mildbreadii</i>	100	13	0	0	0	0	0	0	0	0	12.8	0.025	
<i>Hymenocardia acida</i>	0	0	3	2	20	9	27	7	50	22	11.2	0.045	
<i>Olea welwitschii</i>	92	17	8	3	0	0	0	0	0	0	15.4	0.016	
<i>Oncoba spinosa</i>	48	9	6	1	12	3	33	6	0	0	4.2	0.166	
<i>Tapura fisheri</i>	90	18	10	2	0	0	0	0	0	0	16.6	0.014	1
<i>Securinega virosa</i>	0	0	8	1	21	3	71	14	0	0	10.1	0.03	
<i>Dichrostachys cinerea</i>	63	6	18	4	12	1	8	1	0	0	4	0.138	
<i>Alstonia boonei</i>	86	14	14	3	0	0	0	0	0	0	12.4	0.033	
<i>Cynometra alexandri</i>	100	10	0	0	0	0	0	0	0	0	10.4	0.022	
<i>Ficus exasperata</i>	6	1	46	5	48	4	0	0	0	0	2.2	0.454	
<i>Combretum gueinzii</i>	0	0	0	0	0	0	0	0	100	22	22.2	0.001	5
<i>Sapium ellipticum</i>	82	2	18	1	0	0	0	0	0	0	2	0.174	
<i>Carpolobia alba</i>	0	0	32	1	38	4	30	4	0	0	1.4	0.607	
<i>Dombeya rotundifolia</i>	0	0	8	2	17	4	75	13	0	0	9.7	0.04	
<i>Trichilia prieuriana</i>	100	11	0	0	0	0	0	0	0	0	11.2	0.03	

It indicates the concentration of each species in each class (Relative abundance, RA), the faithfulness of occurrence of the species in that class (Relative frequency, RF), the highest species indicator value across the classes (IV) the statistical significance of the indicator value (p) and the class in which a particular species had the highest indicator value (Cover cord). For species that were not significant indicators for any class, cover cord was left blank. RA is expressed as a proportion of a particular species in a particular class relative to its abundance in other classes. RF is expressed as the percentage of sample units in a class that contain that species.

p is significant at 0.01.

1, Forest; 2, closed woodland; 3, open woodland; 4, very open woodland; and 5, wooded grassland.

Appendix 3. The 121 woody species identified in the field, their abundance per class.

Family	Species	Number of individuals				
		Fo	cw	Ow	Vow	Wg
Mimosaceae	<i>Acacia hockii</i> De Wild.	20	55	97	25	7
Mimosaceae	<i>Acacia seyal</i> Delile	.	.	.	1	.

Appendix 3. Continued.

		Number of individuals				
Mimosaceae	<i>Acacia sieberiana</i> Dc. Var. woodii (Burt Davy) Keay & Brenan	1	6	.	3	.
Mimosaceae	<i>Acacia</i> spp.	2
Euphorbiaceae	<i>Acalypha neptunica</i> Müll. Arg. Var.	9
Mimosaceae	<i>Albizia coriaria</i> Oliver	9	8	2	.	.
Mimosaceae	<i>Albizia grandibracteata</i> Taub.	120	257	57	7	.
Mimosaceae	<i>Albizia</i> spp.	.	.	1	.	.
Mimosaceae	<i>Albizia zygia</i> (DC.) Macbr.	33	5	3	3	.
Apocynaceae	<i>Alstonia boonei</i> de Wild	24	5	.	.	.
Sapotaceae	<i>Aningeria altissima</i> (A. Chev.) Aubr. & Pellegr.	15	2	1	2	.
Annonaceae	<i>Annona senegalensis</i> Pers.	35	157	194	129	1
	<i>Balemetea gramofolia</i>	1
Rubiaceae	<i>Belonophora glomerata</i>	2	1	.	.	.
Sapindaceae	<i>Blighia unijugata</i> Baker	2	6	.	.	.
Euphorbiaceae	<i>Bridelia micrantha</i> (Hochst.) Baill.	15	49	1	1	.
Euphorbiaceae	<i>Bridelia scleroneuroides</i> Pax.	.	2	5	2	.
Elacourtiaceae	<i>Caloncoba schweinfurthii</i> Glig.	107	42	3	.	.
Polygalaceae	<i>Carpolobia alba</i> G. Don	.	9	12	4	.
Caesalpinioideae	<i>Cassia siamea</i> Lam.	2	13	.	.	.
Caesalpinioideae	<i>Cassia</i> spp.	.	1	.	.	.
Ulmaceae	<i>Celtis durandii</i> Engl.	59	6	.	.	.
Ulmaceae	<i>Celtis mildbraedii</i> Engl.	7
Ulmaceae	<i>Celtis wightii</i> Planch.	204	1	.	.	.
Ulmaceae	<i>Celtis zenkeri</i> Engl.	43
Moraceae	<i>Chlorophora excelsa</i> (Welw.) Benth	.	3	.	.	.
Sapotaceae	<i>Chrysophyllum albidum</i> G. Don	6
Rutaceae	<i>Citropsis articulata</i> (Wild. Ex Spreng) Swingle & M. Kellerm	1
Annonaceae	<i>Cleistopholis patens</i> (Beth.) Engl. & Diels	1
	<i>Closophila magida</i>	1
Rubiaceae	<i>Coffea canephora</i> Pierre ex Froechner.	5
Rubiaceae	<i>Coffea euginiodes</i>	5
Sterculiaceae	<i>Cola gigantea</i> A. Chev.	13
Combretaceae	<i>Combretum binderanum</i> Kotschy	.	3	16	14	17
Combretaceae	<i>Combretum collinum</i> Fresen.	107	240	431	137	12
Combretaceae	<i>Combretum gueinzii</i> Sond.	.	.	2	.	21
Combretaceae	<i>Combretum molle</i> R. Br. Ex G. Don	4	18	92	243	6
Boraginaceae	<i>Cordia millenii</i> Baker	7	7	.	.	.
Aralliaceae	<i>Cussonia arborea</i> Hochst. Ex A. Rich.	.	1	4	12	.
Caesalpiniaceae	<i>Cynometra alexandri</i> CH Wright	29
Mimosaceae	<i>Dichrostachys cinerea</i> (L.) Wright & Arn	19	8	3	1	.
Ebenaceae	<i>Diospyros abyssinica</i> (Hiern) F. White	90	3	1	.	.
Sterculiaceae	<i>Dombeya mukole</i> Sprague	56	3	6	1	.
Sterculiaceae	<i>Dombeya rotundifolia</i> (Hochst.) Planch.	2	3	6	12	.
Mimosaceae	<i>Entada abyssinica</i> Steud. Ex A. Rich	.	.	1	.	.
Meliaceae	<i>Entandrophragma angolense</i> (Welw.) C. DC.	3

Appendix 3. Continued.

		Number of individuals				
Meliaceae	<i>Entandrophragma cylindricum</i> (Sprague) Sprague	1
Papilionaceae	<i>Erythrina abyssinica</i> Lam. Ex DC	1	4	1	3	.
Leguminosae	<i>Erythrophleum suaveolens</i> (Guill. & Perr.) Brenan	8
Rutaceae	<i>Fagaropsis angolensis</i> (Engl.) HM. Gardner	5	1	.	.	.
Moraceae	<i>Ficus capensis</i> Thunb	1	1	.	.	.
Moraceae	<i>Ficus casuarina</i>	.	1	.	.	.
Moraceae	<i>Ficus exasperata</i> Vahl	1	10	8	.	5
Moraceae	<i>Ficus mucoso</i> Welw ex Ficalho	1	5	1	.	.
Moraceae	<i>Ficus polita</i> Vahl	9	5	1	.	.
Moraceae	<i>Ficus saussureana</i> DC.	.	1	.	.	.
Moraceae	<i>Ficus</i> spp.	1
Moraceae	<i>Ficus sansibarica</i> Warb.	1
Moraceae	<i>Ficus sur</i> Forssk	17	41	26	3	.
Apocynaceae	<i>Funtumia elastica</i> (Preuss) Stapf	227	32	.	.	.
Rubiaceae	<i>Gardenia Jovis-tonantis</i> (Welw.) Hiern.	.	1	1	1	.
Tiliaceae	<i>Grewia bicolor</i> Juss.	.	10	27	26	17
Tiliaceae	<i>Grewia mollis</i> Juss.	58	424	761	531	6
Simaroubaceae	<i>Harrisonia abyssinica</i> Oliv.	.	1	.	.	.
Ulmaceae	<i>Holoptelea grandis</i> (Hutch.) Mildbr.	99	10	.	.	.
Euphorbiaceae	<i>Hymenocardia acida</i> Tul.	3	3	22	15	3
Meliaceae	<i>Khaya anthotheca</i> (Welw.) C. DC.	50	16	4	.	.
Meliaceae	<i>Khaya grandifolia</i> C. DC.	1
Bignoniaceae	<i>Kigeria africana</i> (Lam.) Benth	.	.	5	1	.
Anacardiaceae	<i>Lanea barteri</i> (Oliv.) Engl.	5	78	107	48	2
Anacardiaceae	<i>Lanea welwitschii</i> (Hiern.) Engl.	.	3	.	1	.
Rhamnaceae	<i>Lasiodiscus mildbraedii</i> Engl.	1
Sapindaceae	<i>Lepisanthes senegalensis</i> (Juss. Ex Poir.)	6	5	.	.	.
Papilionaceae	<i>Lonchocarpus laxiflorus</i> Guill. & Perr.	.	20	116	108	34
Capparidaceae	<i>Maerua duchensii</i>	12
Rhamnaceae	<i>Maesopsis eminii</i> Engl.	47	61	.	.	.
Meliaceae	<i>Mahogany</i> spp.	8
Euphorbiaceae	<i>Margaritaria discoidea</i> (Baill.) Webster	29	21	.	.	.
Rignonaceae	<i>Markhamia platycalyx</i> (Baker) Sprague	2	1	.	.	.
Celastraceae	<i>Maytenus undata</i> (Thunb.) Blakelock	.	1	4	7	4
Papilionaceae	<i>Mildbraediodendron excelsum</i> (Harms)	3
Moraceae	<i>Milicia excelsa</i> (Welw.) CC Berg	2	2	.	.	.
Rubiaceae	<i>Mitragyna stipulosa</i> (DC.) O. Ktze	1
Moraceae	<i>Morus lactea</i> (Sim) Mildbr.	.	1	.	.	.
Moraceae	<i>Myrianthus holstii</i> Engl.	4
Oleaceae	<i>Olea welwitschii</i> (Knobl.) Gilg & Schellenb.	36	4	.	.	.
Flacourtiaceae	<i>Oncoba spinosa</i> Forsk.	24	3	5	8	.
Palmae	<i>Phoenix reclinata</i> Jacq.	12
Euphorbiaceae	<i>Phyllanthus discoideus</i> Muell.	46	2	.	.	.
Caesalpiniaceae	<i>Piliostigma thonningii</i> (Schum.)	21	66	75	18	12
Verbenaceae	<i>Premna angolensis</i> Guerke	18	2	.	.	.
Proteaceae	<i>Protea madiensis</i> Oliv.	.	.	.	9	.
Anacardiaceae	<i>Pseudospondias microcarpa</i> (A. Rich.) Engl.	4	2	.	.	.

Appendix 3. Continued.

		Number of individuals				
Sterculiaceae	<i>Pterygota mildbraedii</i> Engl.	40	2	.	.	.
Euphorbiaceae	<i>Ricinodendron excelsum</i>	8	2	.	.	.
Violaceae	<i>Rinorea dentata</i> (P. Beauv.) Kuntze	1
Violaceae	<i>Rinorea ilicifolia</i> (Welw. Ex Oliv.)	13
Capparidaceae	<i>Ritchiea albersii</i> Gilg	1
Rubiaceae	<i>Rothmannia urcelliformis</i> (Hiern)	.	.	4	5	6
	Bullock exRobyns					
Celestraceae	<i>Salacia elegans</i> Welw. Ex Oliv.	.	.	3	2	5
Euphorbiaceae	<i>Sapium ellipticum</i> Pax.	20	1	.	.	.
Oleaceae	<i>Schrebera arborea</i> A. Chev.	9
Polygalaceae	<i>Securidaca</i> spp.	.	4	10	19	.
Euphorbiaceae	<i>Securinea virosa</i> (Roxb. Ex Willd.) Baill	2	3	5	.	.
Bignoniaceae	<i>Spathodea campanulata</i> P. Beauv.	4	12	.	.	.
Umbelliferae	<i>Steganotaenia araliacea</i> Hochst.	2	2	2	9	.
Bignoniaceae	<i>Stereospermum kunthianum</i> Cham.	41	162	126	55	18
Apocynaceae	<i>Tabernaemontana holstii</i> K. Schum	13	1	.	.	.
Chailletiaceae	<i>Tapura fisheri</i>	32	6	.	.	.
Rutaceae	<i>Teclea nobilis</i> Del.	11	10	2	.	.
Combretaceae	<i>Terminalia velutina</i> Rolfe	308	1288	824	103	14
Euphorbiaceae	<i>Thecacoris lucida</i>	.	.	.	4	.
Ulmaceae	<i>Trema orientalis</i> (L.) Blume	1	2	.	.	.
Meliaceae	<i>Trichilia prieuriana</i> A. Juss	23
Meliaceae	<i>Trichilia</i> spp.	3
Meliaceae	<i>Turrae floribunda</i>	1	.	1	.	.
Annonaceae	<i>Uvariopsis congensis</i> Robyns & Ghesq.	663
Rubiaceae	<i>Vangueria apiculata</i> K. Schum	.	2	.	.	.
Compositae	<i>Vernonia amygdalina</i> Delile	1	2	.	.	.
Verbenaceae	<i>Vitex doniana</i> Sweet.	20	143	92	29	6
Rhamnaceae	<i>Zizyphus abyssinica</i> Hochst. Ex A. Rich	1	.	1	.	.
Total individuals		3042	3394	3172	1602	196
Total species		95	77	48	39	18
Total genera		73	60	35	28	15
Total families		33	33	23	19	13
Total area (sq. m)		65300	71000	65500	42100	16500

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