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Plant communities of a semi-deciduous tropical rainforest in north-western Uganda: role of soil and anthropogenic factors

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with 2 figures and 3 tables

Abstract: Forest plant communities were described using two floristic data sets (accompanied by data on soil and former management practices) from the Budongo Forest Reserve (BFR), Uganda – a semi-deciduous tropical rainforest. The first data set featured species basal-area data for woody species, while the other data set featured abundance for woody plants of stem diameter ≥ 2.0 cm. Four forest community types: *Pseudospondias microcarpa* Swamp Forest, *Funtumia elastica-Pouteria altissima* Forest, *Lasiodiscus mildbraedii-Khaya anthotheca* Forest, and *Cynometra alexandri-Rinorea ilicifolia* Forest were distinguished. Each community is characterised by a group of species, however, there are a considerable number of species shared by all four communities. The forest communities show clear separation along gradients of screened soil characteristics (i.e. Organic matter, Na, N, Ca, Mg, and Si), corroborating the results suggested by the canonical correspondence analysis (CCA). For the species basal-area data, Axes 1 and 2 of the CCA explained 18 % in species, and 34 % of the variance in species-environment relations. Whereas, for the abundance data, the amount of information accounted for by the first two axes was 25 % and 44 %, in species variance and species-environment relations, respectively. Axis 1 of CCA was strongly correlated with soil nutrients, while Axis 2 was correlated with logging and arboricide treatment. Accordingly we interpret Axis 1 as an edaphic gradient, while Axis 2 is depicting an anthropogenic disturbance gradient.

Abbreviations: ANOSIM – Analysis of Similarity, BFR – Budongo Forest Reserve, CCA – Canonical correspondence analysis, DRH – diameter at reference height, SIMPER – SIMilarity PERcentage.

Keywords: ANOSIM, arboricide treatment, CCA, cluster analysis, logging, SIMPER, species diversity, tropical semi-deciduous forest.

Nomenclature: Polhill (1952 et seq.), Hamilton (1991).

Introduction

Biological communities are frequently exposed to environmental changes that cause measurable responses in the properties of the community such as composition and structure (Klug & Cottingham 2001). Plant species differ in their tolerance to and requirements of environmental factors so that their distribution or abundance varies along environmental gradients (Swaine 1996). The gradients in plant abundance associated with physical gradients may be different for each species, creating a vegetation mosaic integrated across the landscape (Patten & Robin 1995). Forest plant communities are largely influenced by the dominant species, so that the most abundant woody species may serve as a good proxy for understanding the structure and dynamics of a plant community as a whole (Eyre 1980). An understanding of the association of a particular species with other species further helps to explain the distribution of that species (Thrash 1998), whereas the description of patterns of species distributions is an important step in generating hypotheses (Jonsson & Moen 1998). Such knowledge is therefore very important in the management of ecosystems of high environmental and conservation value such as the Budongo Forest Reserve (BFR), in north-western Uganda (see Tweheyo 2003).

However, the long-term survival of the populations of wild animals in BFR requires the development and implementation of management practices (and strategies) based on the conservation of habitats suitable for a variety of the resident fauna. This requires a clear understanding of the structure and dynamics of the community types (Sagers & Lyon 1997, Witkowski & O'Connor 1996). The knowledge of the BFR forest community types has been, however, limited – relying only on broad and much generalised descriptions (Eggeling 1947, Langdale-Brown et al. 1964, Howard 1991).

Eggeling (1947) classified the vegetation of BFR into four forest types, such as the *Cynometra* Forest, the Mixed Forest, the Colonising Woodland, and the Swamp Forest. This classification scheme did not incorporate an understorey component and relied only on the overstorey dominant tree species (≥ 10 cm at DBH). Yet, some woody plants with a DBH much smaller than 10 cm (that may be treelets) may con-

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tribute significantly to the overall species diversity, and influence forest composition and structure (Pitman et al. 2001). Indeed, studies that have sampled for woody species smaller than 10 cm at DBH have shown that species diversity (based on woody species) is substantially contributed to by treelets (see Valencia et al. 1994, Galeano et al. 1998, Mwavu 2007). In addition, whereas some studies have looked at the influence of environmental factors on the distribution of plant species (Walaga 1994, Sheil 1996, Eilu et al. 2004), there has not been consideration of the importance of soil nutrients such as silicon.

Over the last three decades, BFR has become increasingly affected by rising demands for timber (Sheil 1996), wood-fuel, building materials, bushmeat, and for other non-timber products such as rattan canes (Turyareeba 2000) as well as land for agriculture (Mwavu & Witkowski 2008a). Much of BFR has also been silviculturally treated by planting some 'favoured' trees, such as *Khaya* and *Entandrophragma*, or poisoning 'unwanted' ones, such as *Cynometra alexandri* (Synnott 1985), cutting and control of lianas, creepers and other impeders including *Ficus* (Dawkins 1955, Sheil 1996). It has also been argued that the present structure, diversity and dynamics of a forest ecosystem are determined by both physical conditions and chance factors (Connell 1978, Denslow 1980, Masaki et al. 1999). Indeed, local biotic and abiotic ecological interactions strongly influence ecological processes and have long been focussed on to explain the distribution patterns of plant species (Turner 1989, Verheyen & Hermy 2001). Therefore, the vegetation classification generated by Eggeling (1947) and Langdale-Brown et al. (1964), representing plant community types defined by a qualitative inventory of dominant tree species rather than by quantitative data from the entire local flora, may not adequately explain the current vegetation patterns within BFR.

The study was aimed at carrying out an exploratory analysis to classify and describe the main forest community types of BFR, and to relate these community types to soil and historical management practice types, using multivariate analysis techniques. The classification and description of the main forest types enables a better understanding of the driving variables involved in the natural reforestation process (Nansen et al. 2001). This understanding can contribute to setting an ecological framework to guide utilisation and restoration, and implementation of suitable management strategies for BFR.

Materials and Methods

Study area

Budongo Forest Reserve is an equatorial tropical rainforest, with some areas protected as a nature reserve. The forest is situated between 1°37' and 2°03' N and 31°22' and 31°45' E, and is located at an average altitude of 1050 m. It is broadly classified as mid-altitude semi-deciduous moist tropical rainforest, since several of the dominant trees (incl. representatives of the genera *Celtis, Maesopsis* and *Ficus*) are at least briefly deciduous (Eggeling 1947, Langdale-Brown et al. 1964), with a noticeable exception of *Cynometra alexandri* (Sheil 1996). The deciduous habit is noticeable during the two dry seasons of the year (June–August, December–February). According to Sheil (1996) the canopy trees are generally high and emergent stems occasionally reach over 60 m. BFR has a generally wet climate, with a monthly mean rainfall of 138.5 ± 66.7 mm. It has a relatively constant minimum temperature with a monthly mean of 20.86 ± 0.9 °C (Tweheyo 2003). BFR is the largest forest reserve in Uganda, covering about 825 km^2, 53 % of which is continuous tropical forest while the remaining area of the reserve is comprised of tropical grasslands (Howard 1991). Like all Uganda's natural forest reserves, BFR is managed primarily for economic, conservation and environmental benefits. It was planned to be sustainably managed from the start of mechanical logging operations in the 1920's. Consequently, a number of management plans have been implemented. The management operations have included logging (both mechanical and pitsawing) and a refining operation using arboricides (e.g. 2,4,5-trichloro-phenoxyacetic acid and 2,4-dichloro-phenoxyacetic acid) during the 1950's and 1960's aimed at killing trees that were regarded as 'weed species' (Plumptre & Reynolds 1994). Therefore, most of the forest's compartments have been treated with arboricides, and today some 77 % of the forest has been more or less logged at least once, except for a few that from the onset were set aside to be left untouched and managed as nature reserve.

Field data collection and analyses

Vegetation data

The forest was stratified into four major habitats identified by Howard (1991) and using data on historical management practice (HMP) types. These forest habitats were dominated by *Khaya, Celtis, Senna,* and *Cynometra*, respectively. Within each habitat transects were laid to capture all the historical management practice types, and to cover as much habitat variation in each assumed community type as possible from valley bottoms to ridge tops to enable the sampling of various slope and topographic positions. A rectangular 50 × 100 m (0.5 ha) plot consisting of five contiguous (50 × 20 m) sub-plots was employed for vegetation sampling. Along each transect at least three 0.5 ha sampling plots were laid, following topographic position categories, such as lower slope (usually with swamp at the foot), mid-slope, upper-slope, and flat top or ridge The sampling plots were oriented at right angles to topographic gradients with the long side parallel to the contour. For each plot the HMP type was recorded on a presence/absence (1 or 0) scale. A total of 32 plots, 6 in the nature reserve areas, 19 in logged and arboricide treated, and 7 in logged but not arboricide treated areas were laid. The variation in the number of plots per HMP type is related to the corresponding size of the area in the forest.

Within each plot the identity of each woody species, number of individuals with ≥2.0 cm stem diameter (hereafter referred to as DRH: Diameter at Reference Height) were recorded and measured. We adopted DRH instead of the usual diameter at breast height (DBH), because of the differences in growth habit and stem irregularities for most individuals. We used 2.0 cm as the minimum stem-diameter cut-off to include more species, as many of them rarely exceed a 10 cm stem-diameter at maturity. Indeed, woody plant species diversity and richness in BFR is substantially contributed to by treelets (for definition see Valencia et al. 1994) and shrubs that rarely attain a stem diameter size of ≥10 cm (Mwavu 2007). Diameters of all canopy tree and pole stems were measured at breast height (1.3 m above the ground), unless there were irregularities at this height, using a diameter tape. For trees with large buttresses or prop roots, their diameters were measured above these protrusions. Basal area per stem was calculated as $BA = \pi(DRH/2)^2$, on the assumption that, stem cross-section area is a circle (Ibarra-Manríquez & Martínez-Ramos 2002). For each shrub, all stems were counted, the diameter of 3 'average' stems measured and then used to extrapolate the composite DRH value of the whole shrub to enable the computation of its basal area in the same manner as done for the trees. The values of the basal area for each taxon sampled were used in both the classification and ordination analyses. Initial plant species identification was done in the field with reference to plant identification guides (Hamilton 1991), the Flora of Tropical East Africa (Polhill 1952 and subsequent volumes), and the help of an expert. Trees were identified using a combination of characters, including general growth form, bark texture, slash colour and smell, occurrence of exudates as well as leaf traits (White 1994). Specimens of shrubs and trees which could not be confidently identified in the field were sampled and subsequently identified in the Botany Department Herbarium (MHU), Makerere University, Kampala, Uganda.

Soil variables

Soil samples were collected with a soil auger (2 cm diameter, 15 cm deep cores) from 10 randomly chosen locations within each of the 0.5 ha samples and placed into polyvinyl bags, then bulked, and sub-sampled, air-dried, cleaned by removing stones and root fragments, and finally passed through 20 mm and 2 mm sieves. The pH of soil was determined in a 1:1 soil-water suspension using the Glass Electrode Method (McLean 1982), while organic matter (OM) content was indirectly estimated through the determination of the organic carbon (C) content by the Walkley-Black procedure (Nelson & Sommers 1982), and total nitrogen (N) was determined by the Kjedahl method (Bremner & Mulvaney 1982). Analyses for % organic matter, pH, and total N were performed by the Soil Science Department Laboratory, Makerere University, Kampala, Uganda. The major (e.g. Na^+, K^+, Mg^{2+}, and Ca^{2+}) and minor elemental constituents of the soil samples were determined using the X-Ray Fluorescence Spectrometry method (Feather & Willis 1976, Thomsen 2002) in the School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa.

Data analyses

Three data matrices were created namely; (1) the matrix of plots × species featuring basal-area values, (2) matrix of plots × species featuring counts of individuals (abundance), and (3) matrix of plots × environmental (soil variables and HMP type) factors. The HMP type data was treated as a nominal variable. The traits depicting the mineral constituents of the soils were log-transformed.

Classifications

The species basal area and abundance (i.e. number of individuals of a species in a 0.5 ha plot) data sets were separately classified employing a clustering approach in order to identify forest types (i.e. groups of plots similar in species composition). Prior to the cluster analysis the original abundance values were code-replaced into a 0–9 scale (i.e. <5 = 1, 5–9 = 2, 10–19 = 3, 20–49 = 4, 50–99 = 5, 100–199 = 6, 200–299 = 7, 300–499 = 8, 500+ = 9). The code-replaced abundance values were also used to construct a synoptic table showing the species composition of the distinguished communities. Species which occurred 1–5 times but failed to show any obvious link to one or two communities were disregarded. We used Incremental Sum of Squares Clustering technique (ISS), known also as Ward's method (see Podani 2000, 2001). Chord Distance was applied as the resemblance measure in order to remedy for unequal species richness of the classified plots (the Chord Distance employs intrinsic standard normalization). The basal-area data were used as indicators of the importance (dominance) of tree and shrub cover (Nelder & Howitt 1991, Caratti et al. 2004). Comparisons between the communities were made using the ANOSIM (ANalysis Of SIMilarity) permutation test sub-routine within the CAP 3.1 software (Seaby et al. 2006). A significance level of 0.05 (5 %) was used to distinguish the communities from one another. Species contributing to the similarities within communities were determined using a SIMilarity PERcentage analysis (SIMPER; Clarke 1993). Species abundance and basal area per plot data were used separately in the SIMPER test. The SIMPER estimates the contribution of individual taxa to similarity among or within clusters, and it is used to determine the extent to which individual species contribute to the patterns detected by the cluster analyses and ANOSIM. The analysis breaks down the contribution of each species to the observed similarity (or dissimilarity) between samples. The method uses the Bray-Curtis Similarity, comparing in turn each sample in Group 1 and Group 2. The species primarily responsible for observed similarity within the clusters (i.e. make up 90 % of the similarity within the communities) as revealed in the results of SIMPER analysis were used in describing each cluster. Only species with >2.0 % contribution to the similarity within the cluster (in terms of average abundance and average basal area) were considered.

Ordinations

Species basal-area and abundance data for each 0.5 ha plot together with the corresponding plot × environmental variables data matrix were subject to Canonical Correspondence Analysis (CCA) to reveal the relations between the species composition and environmental variables. The software package CANOCO version 4.5 was employed (ter Braak & Šmilauer 2002). The environmental factors included in the CCA featured soil variables (pH, Ca, Mg, Na, P, Li, Si, Ti, Fe, OM and N) and HMP types (i.e., nature reserve, logged only and logged and arboricide treated). The vegetation samples were plotted in an ordination diagram with the soil variables shown by vectors (arrows), while management by filled triangles. The length of the arrows is proportional to their importance and the directions of the arrows show their correlation with the axes. Statistical significance of the relationship between species and the whole set of environmental variables was evaluated using a Monte Carlo randomisation procedure with 999 permutations under reduced model (ter Braak & Šmilauer 2002). This is a direct test of whether the included environmental variables have significant effect on the species composition. It was calculated firstly for Axis 1 and then for the combination of the first four canonical axes. The CCA generated intraset correlations (i.e., correlations between environmental variables and ordination axes) were used to infer the relative importance of each environmental variable for prediction of species composition and distribution (ter Braak 1995).

Results

Classification

A total of 269 species from 171 genera and 51 families were recorded. Based on species basal-area and abundance data from 32 half-hectare sampling plots, the cluster analysis yielded four community groups, some of them having sub-communities. The dendrograms showed several common features such as clearly revealing clusters of samples dominated by *Cynometra alexandri* and by *Senna spectabilis* as well as a cluster interpreted as the Swamp Forest (see Fig. 1 featuring the abundance-data analysis; the clustering of the basal-area data is not shown). The ANOSIM test indicated the separation of plots based on the

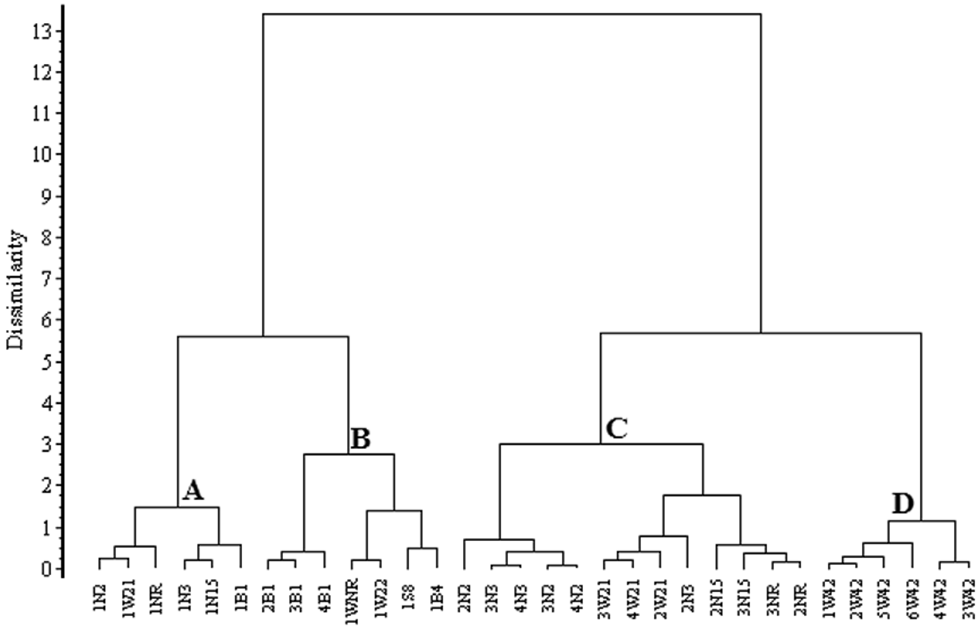

Fig: 1. Cluster analysis dendrogram based on code-replaced abundance per species per plot data for woody species of stem diameter ≥2.0 cm from 32, 0.5 ha plots in BFR NW Uganda. It is based on the Incremental Sum of Squares (ISS) clustering method with the Chord distance. The abbreviations for the plots stand for plot and compartment number in BFR (i.e. 1N2, 2N2 and 3N2 are plots 1, 2 and 3 sampled along the same transect in compartment N2).

four communities to be significant ($R_{ANOSIM} = 0.76$, $p = 0.001$; $R_{ANOSIM} = 0.71$, $p = 0.001$ for species abundance and basal area, respectively). However there were visible differences in the clustering of plots for the other communities. We ascribe these differences to the continuous nature of the forest vegetation. In such cases the fine differentiation between natural clusters (well-defined forest communities) is rather of quantitative than qualitative nature. Hence, any importance values beyond mere abundances would add information leading to clearer cluster definition. Therefore in the sequel we concentrate on the interpretation of the clustering based on code-replaced abundance data (for a simplified synoptic table see Table 1) and SIMPER analysis results.

We distinguish the following four communities (A–D):

A. Pseudospondias microcarpa Swamp Forest

The plots clustered within this community were all sampled from seasonally flooded (swamp) habitats. This community is characterised by *Pseudospondias microcarpa* (A. Rich.) Engl., *Raphia farinifera* (Gaertn.) Hylander, *Euphorbia teke* Schweinf. ex Pax, *Neoboutonia melleri* (Muell. Arg.) Pain, *Leea guineensis* G. Don. and *Baphia wollastonii* Bak. f. (Table 1). The SIMPER analysis showed that there were 26 and 38 (for basal area and abundance data, respectively) species making up 90 % of the similarity within this community. The five species contributing most to the similarity (based on abundance data) were *P. microcarpa*, *Cynometra alexandri* C.H. Wright, *Khaya anthotheca* (Welw.) C. DC., *Cleistopholis patens* (Benth.) Engl. & Diels. and *Glyphaea brevis* (Spreng.) Manachino. If basal-area data were considered, the top 5 species included *Lasiodiscus mildbraedii* Engl., *Acalypha neptunica* Muell. Arg., *G. brevis, Mallotus oppositifolius* (Geisel.) Muell. Arg. and *P. microcarpa.* This suggests that generally *Pseudospondias microcarpa* defines this community. The species richness for this plant community spans 78–106. However, two sub-communities, characterised by *B. wollastonii* and *Leea guineensis,* respectively were distinguished (Table 1).

B. Funtumia elastica-Pouteria altissima Forest

This community comprises plots that were sampled from distant locations of the forest (Table 1). The SIMPER analysis identified 24 and 37 species (basal-area and abundance data, respectively) contributing to 90 % of the observed similarity. The five species contributing most to similarity on the basis of abundance were *Senna spectabilis* (DC.) Irwin & Barneby, *Funtumia elastica* (Preuss) Stapf., *A. neptunica*, *Alchornea laxiflora* (Benth.) Pax & K. Hoffm. and *Teclea nobilis* Del.. The most important ones identified by SIMPER on the basis of basal-area data include *Senna spectabilis*, *Funtumia elastica, Cola gigantea* A. Chiev., *Khaya anthotheca* and *Pouteria altissima* (A. Chiev) Aubrev. & Pellgr. The species richness for this plant community spans 67–94. Two sub-communities, the *Piptadeniastrum africanum* sub-community and *Senna spectabilis* sub-community were identified.

The *Senna spectabilis* sub-community is characterised by *Senna spectabilis* which is both dominant (in terms of basal area) and most frequent. The species richness in the plots classified within this forest type spans 67–85. The associated upper-storey and understorey varied with location of the plots. Plots from the forest interior included interior forest species such as *L. mildbraedii* and *Argomuellera macrophylla* Pax Laka, while those sampled towards the forest edges were associated with typical savanna woodland species such as *Albizia coriaria* Oliv., *Combretum collinum* Fres., *Combretum molle* G.Don and *Terminalia glaucescens* Benth. (Table 1).

The *Piptadeniastrum africanum* sub-community is characterised by the dominant *Khaya anthotheca,* followed by *Pouteria altissima*, *Trilepsium madagascariensis* DC., *C. gigantea* and *Funtumia elastica.* The most frequent species include *Acalypha neptunica*, *Acalypha ornata* Hochst. ex A. Rich., *Alchornea laxiflora* and *Pouteria altissima*. The plot species richness for this sub-community spans 83–94. This community has been, presumably, shaped by past anthropogenic activities. The Uganda Forest Department (now: National Forest Authority) records indicated that *K. anthotheca* dominance here is a result of enrichment planting and its protection from illegal and legal harvesting).

C. Lasiodiscus mildbraedii-Khaya anthotheca Forest

This community comprises up-slope plots from forest compartments of various management practice history, including mechanical logging, arboricide treatment, and pitsawing (between 1995 and 1997). It also contains plots from protected parts of the forest which have not experienced arboricide treatment, legal logging, or pitsawing. The latter plots form a sub-cluster (Fig. 1). The sub-units within this community (see Fig. 1, Table 1) are considered only as variants and not sub-communities because their differentiation is more quantitative (in terms of abundance of the species involved) than qualitative (presence of species or species groups). The SIMPER analysis identified 19 and 23 species (basal area and abundance data, respectively) making up 90 % of the observed similarity within this community. The top five species contributing most to similarity on the basis of abundance were *L. mildbraedii*, *Celtis mildbraedii* Engl., *A. neptunica, A. ornata* and *Rinorea ardisiiflora* (Welw. ex Oliv.) Kuntze, while those on the basis of basal area include *Cynometra alexandri*, *Celtis mildbraedii*, *Funtumia elastica, Alstonia boonei* De Wild, *Celtis zenkeri* Engl. and *Khaya anthotheca.* The species richness patterns are highly variable spanning

59–111. In some places, the forest floor is densely covered with *Leptaspis zeylanica*, a species characteristic of closed (including old mixed) forests, but not of the unlogged *Cynometra* Forest (Synnott 1985). This community comprises plots that are all from an area with no history of arboricide treatment and mechanical logging, except for pitsawing. The sub-units within this community (Fig. 1, Table 1) are considered only as variants and not sub-communities because their differentiation is more quantitative (in terms of abundance of the species involved) than qualitative (presence of species or species groups). The SIMPER analysis showed that species making up 90 % of the similarity within this community were 4 and 11 for the basal area and abundance data respectively. The top three species in terms of basal-area were *Cynometra alexandri*, *Celtis mildbraedii* and *Lasiodiscus mildbraedii*. On the basis of abundance, the five species contributing most to the similarity were; *Thecacoris lucida* (Pax) Hutch., *A. ornata, A. neptunica, L. mildbraedii* and *Argomuellera macrophylla*. In areas where *Cynometra alexandri* formed a closed upper-storey canopy, the forest floor was devoid of a herbaceous layer, and the understorey was dominated by *T. lucida*. In habitats where recent human disturbance was evident, the understorey was dominated by shrubs such as *A. neptunica*, *A. ornata*, and *Argomuellera macrophylla*. Species richness of this community spans 24–59.

Results of the analyses of SIMilarity PERcentages (SIMPER procedure from CAP 3.1) for the identified communities showed that species making up 90 % of the observed similarity within each community spans 4–26, and 11–38 for the basal area and abundance data, respectively. In both cases *Cynometra alexandri-Rinorea ilicifolia* Forest community had the lowest, while *Pseudospondias microcarpa* Swamp Forest community had the highest number of species. This suggests that *Pseudospondias microcarpa* Swamp Forest community is characterised by high species richness, while the *Cynometra alexandri-Rinorea ilicifolia* Forest community (*Cynometra alexandri* dominated) and *Senna spectabilis* sub-community are characterised by low species richness. These results corroborate the CCA results as revealed by the location of the above communities in relation to the number of species isolines (Figs. 2a & b). Separation of species composition among clusters is evident but considerable overlap is also evident, with over 48 species present in all four communities (A–D; Table 1). Notable among the 48 species are *A. neptunica*, *A. ornata*, *C. mildbraedii* and *F. elastica* that were relatively frequent in all four communities and could be regarded as generalists (Table 1). A few species however, were exclusively associated with particular plots because of their unique environmental conditions. For example, *Pseudospondias microcarpa*, *Raphia farinifera*, *Euphorbia teke*, and *Neoboutonia melleri* were exclusively associated with the Swamp Forest community.

Ordination

The relative influence of the measured environmental variables on species variance can be inferred from the CCA ordination diagram (Figs. 2a & 2b), and the intra-set correlations (Table 2). In relation to soil variables, the following trends can be observed in Fig. 2. For both data sets Fe, Si, and OM are the most important soil variables determining variation in species composition along axis 1. Ca, N, and to lesser extent P, also contribute to this variation. On the other hand, Mg and Ti are the most important soil variables determining variation in species composition along axis 2. Na also contributes to this variation. Although the overall correlations of environmental variables were more similar among the species data sets, their relative importance as controlling factors of community species composition vary. For example, pH is more strongly correlated with Axis 1 in the abundance data than in the basal-area data (Table 2). The logged only, and logged and arboricide treatment historical management practice types were strongly correlated with axis 2 (Table 2, Fig. 2). Thus Axis 1 can be seen as representing an edaphic gradient, while Axis 2 can be interpreted as an anthropogenic disturbance gradient.

Reasonably high amounts of variance in the species data and the variance in species-environmental factor relations were explained by Axes 1 and 2 of the CCA for both data sets, although higher for the abundance than for the basal area (Table 3). For both data sets, the variance in species-environmental factors relation was higher than 50 %, suggesting a relatively great influence of environmental factors on species composition and distributions. In addition, the variances explained (sum of all canonical eigenvalues) as a portion of the total inertia were relatively high (0.53 and 0.56 for basal area and abundance, respectively), suggesting how well the measured variables explained species composition. The summary of the Monte Carlo permutation test results showed significance for the first canonical axis ($F = 1.71$, $p = 0.028$) and the combination of the first four canonical axes ($F = 1.53$, $p = 0.002$) for the ordination of the species presence/absence data. The ordination of the species basal area data did not show significance for Axis 1 ($F = 1.71$, $p = 0.116$), but did show significance for all the canonical axes ($F = 1.35$, $p = 0.001$).

The CCA of the species abundance and basal area data sets to a great extent reflected the categorization of plant community clusters identified in the hierarchical cluster analysis for the respective data sets (Fig. 2). Although the sample plots were relatively highly dispersed in the ordination space, those that comprised *Pseudospondias microcarpa* Swamp Forest, *Cynometra alexandri-Rinorea ilicifolia* Forest and the *Senna spectabilis* sub-community (plots on the far right) were distinctly delineated (Figs. 2a & b). Along CCA axis 1, *Pseudospondias microcarpa* Swamp Forest and *Funtumia elastica-Pouteria*

Table 1. Synoptic table of the studied forest communities. The Plot Code carries the identity of each sample plot. The "Cluster No." corresponds to the clusters identified by the clustering analysis (see Fig. 1). The values in the body of the table are the code-replaced abundance values (see section on Materials and methods for the code replacement rules). The meaning of the diagnostic (Diag.) codes: G: general taxon (occurring in all 4 communities); Example 1: "G, B1, D1" means that the taxon occurs in all 4 communities, but it appears as differentiating also among sub-communities within Community B and D. Example 2: "G, C1-2" means that the taxon is a general one (see above), but it discriminates between sub-communities C1 and 2 against sub-community C3. Example 3: "AB,A1" taxon occurs in both communities A and B and is (at the same time) discriminating sub-communities within the community A. Example 4: "B" means that the taxon is characteristic of the community B. Example 5: "B1" means that the taxon is characteristic of the community B and is (at the same time) discriminating between sub-communities within the community B. Example 6: "ABC,(A),C1-2" means that the taxon occurs in 3 communities (A,B,C), while it show preference to community A and is also discriminating sub-communities C1 and C2 against C3. The taxa indicated by asterisk are alien to the region.

A: *Pseudospondias microcarpa* Swamp Forest
A1: *Baphia wollastonii* Sub-Community
A2: *Leea guineensis* Sub-Community
B: *Funtumia elastica–Pouteria altissima* Forest
    B1: *Piptadeniastrum africanum* Sub-Community
    B2: *Senna spectabilis* Sub-Community
C: *Lasiodiscus mildbraedii–Khaya anthotheca* Forest
    C1: *Ficus exasperata* Variant
    C2: *Glyphaea brevis* Variant
    C3: *Rothmannia urcelliformis* Variant
D: *Cynometra alexandri–Rinorea ilicifolia* Forest
    D1: *Rothmannia urcelliformis* Variant
    D2: *Ochna holstii* Variant

Plot Code	**Diag.**	**1N2**	**1W21**	**1NR**	**1N3**	**1N15**	**1B1**	**2B1**	**3B1**	**4B1**	**1WNR**	**1W22**	**1S8**	**1B4**	**2N2**	**3N3**	**4N3**	**3N2**	**4N2**	**3W21**	**4W21**	**2W21**	**2N3**	**2N15**	**3N15**	**3NR**	**2NR**	**1W42**	**2W42**	**5W42**	**6W42**	**4W42**	**3W42**
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Acalypha neptunica	**G**	4	5	5	5	4	5	6	5	7	5	5	2	1	5	6	6	6	7	6	5	5	6	7	7	4	4	5	4	6	6	6	5
Acalypha ornata	**G**	4	3	3	3	2	4	5	4	6	3	4	.	.	4	8	7	6	7	6	5	4	6	5	5	5	4	7	6	8	5	5	6
Alchornea laxiflora	**G**	3	6	3	6	3	4	4	5	6	5	6	1	4	1	2		4	2	4	5	4	4	2	4	1		1	.	2	6	4	3
Celtis mildbreadii	**G**	1	.	5	2	3	2	1	3	5	4	4	.	.	4	6	7	5	5	5	6	6	7	6	6	7	7	4	3	4	1	4	7
Funtumia elastica	**G**	3	3	3	5	3	3	4	4	5	6	6	5	2	6	6	6	6	5	6	5	5	6	2	3	3	4	1	.	3	1	.	3
Antiaris toxicaria	**G**	1	1	1	1	2	2	5	3	3	1	1	1	1	3	3	3	4	3	.	3	3	4	1	2	1	1	.	.	3	1	1	.
Celtis zenkeri	**G**	.	1	2	2	1	2	3	5	3	3	3	1	.	3	4	4	4	4	3	4	4	3	3	2	4	3	4	4	2	2	2	4
Chrysophyllum albidum	**G**	1	2	2	2	.	1	2	3	2	4	2	1	1	2	1	3	1	1	2	2	2	1	2	1	2	2	1	1	1	.	1	3
Cynometra alexandri	**G**	3	4	4	3	2	4	.	.	2	4	5	.	.	5	5	4	5	4	4	5	3	4	4	4	4	3	4	4	4	4	4	5
Lychnodiscus cerospermus	**G**	3	1	3	1	2	2	3	4	3	.	1	1	1	1	4	3	1	2	3	2	3	3	3	2	3	4	.	.	1	.	1	1
Tapura fischeri	**G**	1	2	1	1	.	1	3	3	1	3	2	2	1	3	1	3	2	2	3	4	3	3	2	1	1	.	4	2	2	1	2	1
Teclea nobilis	**G**	2	1	1	3	.	1	4	5	3	2	2	3	4	1	2	1	3	2	2	2	3	2	2	1	.	1	1	1	3	3	2	4
Rinorea ardisiflora	**G**	2	1	5	1	.	.	1	.	5	3	3	.	.	4	7	8	7	5	4	4	2	6	5	4	5	6	5	4	2	.	2	1
Trichilia prieureana	**G**	3	1	2	1	1	.	3	5	3	2	1	.	3	2	.	.	.	.	2	3	3	1	4	4	3	3	1	.	2	1	1	1
Celtis wightii	**G**	2	4	1	.	1	.	1	1	.	3	1	.	4	1	.	.	1	.	1	2	2	.	1	4	1	1	3	2	1	4	1	5
Vitex amboniensis	**G**	1	1	1	1	1	1	.	1	.	.	1	.	.	.	1	1	1	.	.	1	1	1	.	.	.	1	1	.	.	1	.	.

Table 1. (cont.)

Plot Code	Diag.	1N2	1W21	1NR	1N3	1N15	1B1	2B1	3B1	4B1	1WNR	1W22	1S8	1B4	2N2	3N3	4N3	3N2	4N2	3W21	4W21	2W21	2N3	2N15	3N15	3NR	2NR	1W42	2W42	5W42	6W42	4W42	3W42
Cluster No.		A1	A1	A1	A2	A2	A2	B1	B1	B1	B2	B2	B2	B2	C1	C1	C1	C1	C1	C2	C2	C2	C2	C3	C3	C3	C3	D1	D1	D1	D1	D2	D2
Melanodiscus sp.	**G**	1	.	1	1	1	1	3	4	3	1	1	1	2	.	1	1	1	.	1	1	.	1	2	1	.	1	.	.	1	.	1	1
Albizia zygia	**G**	1	.	.	.	.	1	2	1	1	1	1	1	2	1	1	.	.	1	1	.	.	.	1	.	.	.	.	.	1	2	.	.
Bridelia micrantha	**G**	1	.	1	1	1	1	1	1	.	1	.	3	1	1	.	.	.	.	2	.	.	1	.	.	.	.	.	.	1	.	1	.
Chaetacme aristata	**G**	1	2	.	.	.	1	1	2	.	.	.	.	1	1	.	.	.	.	1	.	.	.	1	.	.	.	.	.	1	3	2	3
Citropsis articulata	**G**	2	.	1	.	.	1	.	.	1	1	1	.	.	.	1	2	.	1	1	.	1	1	.	1	.	1	.	.	1	1	.	.
Coffea euginoides	**G**	2	1	.	1	.	.	1	2	1	2	.	.	1	.	.	.	.	.	.	1	.	.	1	1	1	.	.	.	1	1	.	2
Ehretia cymosa	**G**	1	1	1	1	.	.	1	.	1	1	1	.	.	.	1	1	.	.	1	2	.	1	1	.	.	.	.	.	1	1	.	.
Monodora angolense	**G**	1	.	.	.	.	.	1	2	1	1	.	1	1	1	1	1	1	.	1	.	1	.	.	.	.	1	.	.	1	.	.	2
Vangueria apiculata	**G**	.	.	.	2	.	1	.	.	.	.	.	.	4	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Aeglopsis eggelingi	**G**	.	.	1	1	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.
Dictyandra arborescens	**G**	.	.	1	1	.	1	.	2	.	1	.	.	.	1	1	1	1	1	1	.	1	1	1	.	.	.	1	.	3	.	.	.
Drypetes ugandensis	**G**	.	.	3	.	1	1	2	4	3	.	.	1	1	1	3	2	.	1	1	1	1	1	1	2	.	1	1	.	.	.	1	.
Pavetta molundensis	**G**	1	1	.	4	.	1	1	2	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Diospyros abyssinica	**G, A1**	1	1	.	.	.	.	.	.	.	1	.	.	4	1	.	.	.	.	1	3	1	1	.	.	3	1	.	.	.	.	1	4
Tetrapleura tetraptera	**G, B1, D1**	1	1	.	.	1	1	2	1	1	.	.	.	.	.	1	2	1	1	1	1	1	2	1	1	.	1	1	.	1	.	.	.
Rinorea brachypetala	**G, B1, D1**	3	5	5	1	1	4	.	4	4	.	.	.	.	1	4	5	2	3	1	.	4	3	2	7	4	5	2	3	.	4	.	.
Mimusops bagshawei	**G, B1**	2	.	.	1	1	3	3	3	3	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	.	1	.	.	.	1	1	1
Holoptelea grandis	**G, B1**	1	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.	.	1	1	1	.	.	.	1	.	.	.	.	1
Lasiodiscus mildbraedii	**G, B2**	7	8	6	5	4	1	.	.	.	4	5	.	.	6	8	7	7	6	5	7	6	8	8	6	8	6	6	6	6	9	3	5
Argomuellera macrophylla	**G, B2**	2	1	1	2	2	3	.	.	.	3	3	.	.	2	3	4	1	.	2	4	4	4	.	5	4	3	4	5	5	5	6	5
Celtis gomphophylla	**G,C1-2**	1	1	1	1	1	.	.	.	1	3	2	1	.	5	3	4	2	.	2	4	3	3	.	.	1	1	.	.	2	.	.	.
Grewia sp.	**G,C1-2**	2	1	1	2	1	.	1	3	1	.	.	1	.	1	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	1	1
Margaritaria discoidea	**G,C1-2**	.	1	1	1	2	.	1	.	1	2	1	1	1	1	1	1	.	1	1	3	.	3	.	.	.	.	.	.	1	.	.	2
Markhamia lutea	**G,C1-2**	2	2	.	2	3	1	1	.	.	1	2	3	.	1	1	.	.	.	1	1	.	.	.	.	.	.	1	.	1	.	1	2
Oncoba spinosa	**G, C1-2, D1**	.	2	.	1	.	1	.	1	.	1	1	.	.	.	1	.	1	.	1	.	.	1	.	.	.	.	.	.	1	1	.	.
Ochna holstii	**G, C2, D2**	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	3
Khaya anthotheca	**G, D1**	4	4	3	2	2	4	5	4	4	2	.	4	1	3	4	4	4	2	4	3	4	2	2	2	1	3	1	.	1	1	.	.
Blighia unijugata	**G, D1**	2	1	.	2	1	2	4	2	1	1	1	2	.	3	3	2	3	4	1	.	1	2	1	1	.	1	1	1	1	.	.	.
Morus mesozygium	**G, D1**	1	.	1	1	1	1	3	2	2	1	.	2	.	1	1	1	1	1	.	1	.	1	2	2	1	1	.	1	1	.	.	.
Albizia glaberrima	**G, D1**	1	.	.	2	1	1	1	.	.	1	1	1	.	1	1	.	1	1	1	1	1	2	.	.	1	.	1	.	.	1	.	.
Ricinodendron heudelotii	**G, D1**	.	.	1	.	1	1	.	1	.	.	1	.	.	1	1	1	.	.	1	.	1	1	.	.	.	.	.	.	1	1	.	.
Rothmannia urcelliformis	**G, D1**	.	1	.	.	1	.	1	2	2	1	1	.	1	1	.	.	.	.	.	.	.	1	1	2	2	1	1	1	1	1	.	.
Treculia africana	**A, C2**	2	.	2	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.
Neoboutonia melleri	**A**	2	.	3	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eurphobia teke	**A**	3	1	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Raphia farinifera	**A**	4	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 1. (cont.)

Plot Code	Diag.	1N2	1W21	1NR	1N3	1N15	1B1	2B1	3B1	4B1	1WNR	1W22	1S8	1B4	2N2	3N3	4N3	3N2	4N2	3W21	4W21	2W21	2N3	2N15	3N15	3NR	2NR	1W42	2W42	5W42	6W42	4W42	3W42
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Baphia wallastonii	**A1**	.	3	3	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mitragyna stipulosa	**A1**	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spondianthus preussii	**A1**	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pleiocarpa pycnantha	**A1**	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leea guineensis	**A2**	1	.	.	5	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Zanthoxylum gillettii	**A2**	1	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Syzygium cordatum	**A2**	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dovyalis macrocalyx	**AB,A1**	1	.	1	.	.	.	.	1	.	2	.	1	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
Parkia filicoidea	**AB,A1**	1	.	2	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linociera johnsoni	**AB**	1	3	.	1	1	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Syzygium guineensis	**AB**	1	1	.	1	.	.	.	.	1	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sapium ellipticum	**AB**	1	1	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spathodea campanulata	**AB,B2**	.	1	.	1	.	1	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Olea welwitschii	**AB,B2**	.	2	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Senna spectabilis	**B**	.	.	.	.	.	.	1	.	2	8	9	7	8	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Pachystela brevipes	**B**	.	.	1	.	.	.	3	2	2	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Rytigynia usambarensis	**B**	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Piptadeniastrum africanum	**B1**	.	.	.	.	.	1	1	2	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
*Citrus citrus**	**B1**	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Albizia coriaria	**B2**	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Rytigynia sp.	**B2**	.	.	1	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*Psidium guajava**	**B2**	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*Mangifera indica**	**B2**	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Combretum collinum	**B2**	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Antidesma membranaceum	**B2**	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Combretum molle	**B2**	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Maytenus gracilipes	**B2**	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tabernaemontana holstii	**ABC**	3	2	4	4	4	2	4	1	2	3	1	2	1	4	4	3	3	2	4	2	4	4	3	1	2	3	.	.	.	.	.	.
Aningeria altissima	**ABC**	1	1	1	1	1	2	4	6	4	2	1	4	2	1	1	2	1	1	4	3	2	3	1	3	2	1	.	.	.	.	.	.
Trichilia rubescens	**ABC**	2	2	4	4	5	3	1	1	3	5	1	3	.	5	4	2	2	1	3	3	2	4	2	1	1	3	.	.	.	.	.	.
Trilepisium madagascariensis	**ABC**	1	1	2	2	2	3	1	3	4	1	.	1	1	2	2	2	1	1	2	2	2	3	3	2	1	2	.	.	.	.	.	.
Entandrophragma utile	**ABC**	1	1	1	1	1	1	2	3	1	1	.	.	.	1	1	1	1	1	2	.	1	1	.	1	1	1	.	.	1	.	.	.
Trichilia dregeana	**ABC**	1	1	1	.	1	2	2	1	2	1	.	.	.	4	3	4	4	4	1	1	.	3	1	2	1	1	.	.	.	.	.	.
Bequaertiodendron oblanceolatum	**ABC**	1	.	1	1	2	1	4	4	2	1	.	.	1	1	1	1	2	2	1	2	1	1	1	.	1	1	.	.	.	.	.	1
Chysophyllum perpulchrum	**ABC**	1	1	3	1	.	2	1	3	3	1	.	.	.	4	2	3	3	1	1	1	1	2	2	2	3	3	.	.	.	.	.	.

Table 1. (cont.)

Plot Code	Diag.	1N2	1W21	1NR	1N3	1N15	1B1	2B1	3B1	4B1	1WNR	1W22	1S8	1B4	2N2	3N3	4N3	3N2	4N2	3W21	4W21	2W21	2N3	2N15	3N15	3NR	2NR	1W42	2W42	5W42	6W42	4W42	3W42
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Myrianthus holstii	**ABC**	1	1	4	4	4	4	2	3	3	.	.	4	.	4	4	1	1	1	2	1	2	3	2	1	1	1	.	.	.	.	.	.
Belonophora hypoglauca	**ABC**	2	1	3	1	.	1	1	2	2	1	1	.	1	1	.	.	.	1	1	2	3	1	3	3	3	4	.	.	.	.	.	.
Guarea cedrata	**ABC**	.	1	3	1	1	.	.	2	1	1	1	.	.	3	1	1	2	1	2	1	1	3	1	1	1	2	1	.	.	.	.	.
Coffea canephora	**ABC**	.	3	1	1	.	.	1	4	3	1	.	2	1	1	1	1	1	1	1	1	2	1	1	.	.	.	.	.	1	.	.	.
Greenwayodendron suaveolens	**ABC**	.	.	1	1	1	.	.	1	2	.	.	.	1	1	2	2	1	.	1	1	1	4	1	1	2	1	1	.	.	.	.	.
Erythrophleum suaveolens	**ABC**	1	1	1	1	.	.	.	3	1	1	1	.	1	1	.	1	1	1	1	1	1	1	1	.	1	.	.	.	.	.	.	.
Entandrophragma angolense	**ABC**	1	1	1	1	.	1	2	1	.	.	.	.	1	1	.	.	1	1	1	.	1	1	1	.	1	.	.	.	.	.	.	.
Maesopsis eminii	**ABC**	.	.	1	.	.	.	1	.	1	.	1	1	.	1	1	3	1	.	1	2	2	1	1	1	1	1	.	.	1	.	.	.
Cordia millenii	**ABC**	1	1	1	.	.	1	.	1	1	1	.	.	.	1	1	.	1	.	2	1	3	1	1	.	1	.	.	.	.	.	.	.
Oxyanthus speciosus	**ABC**	1	2	1	1	2	.	.	1	2	1	.	2	.	2	.	1	1	.	1	.	1	.	1	1	.	.	.	.	.	.	.	.
Memecylon jasminiodes	**ABC**	1	.	1	1	1	.	1	4	.	1	.	.	1	1	.	.	1	.	.	.	.	1	1	1	1	1	1	.	.	.	.	.
Mammea africana	**ABC**	.	1	1	1	1	3	.	.	.	1	.	.	.	4	3	1	1	1	2	.	1	2	.	.	2	.	.	.	.	.	.	.
Kigelia africana	**ABC**	2	3	1	4	2	2	1	1	1	2	.	.	1	.	2	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.	.	.
Ficus sur	**ABC**	1	1	.	.	.	.	1	.	1	.	2	1	.	1	1	1	1	.	1	1	1	4	1	.	.	.	.	.	.	.	.	.
Caloncoba crepiniana	**ABC**	2	.	1	.	.	1	.	.	1	.	1	5	3	4	1	.	2	.	1	4	.	1	1	.	.	.	.	.	.	.	.	1
Lannea welwitschii	**ABC**	1	.	1	.	.	1	.	1	1	.	1	1	1	.	.	.	.	.	4	.	1	1	1	.	.	.	.	.	.	.	.	.
Mildbraediodendron excelsum	**ABC**	1	.	1	.	.	.	1	1	.	1	.	.	.	1	.	1	1	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.
Pycnanthus angolensis	**ABC**	1	2	2	.	1	2	1	.	1	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Klainedoxa gabonensis	**ABC**	1	.	1	.	.	1	1	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Xylopia parviflora	**ABC**	.	.	.	1	1	.	.	1	.	.	.	.	1	.	.	1	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Strombosia scheffleri	**ABC**	1	.	.	.	.	.	.	.	1	1	.	.	.	1	.	.	.	.	1	.	.	1	.	1	.	.	.	.	.	.	.	.
Mallotus oppositifolius	**ABC,(A),C2-3**	5	6	4	4	5	5	.	.	.	1	.	.	.	.	.	.	.	.	4	.	1	1	1	2	2	2	.	.	.	1	.	.
Ouratea densiflora	**ABC,(A)**	4	3	4	6	3	1	1	3	2	1	.	.	.	3	3	.	.	.	.	.	2	1	1	1	.	.	.	.	.	.	.	1
Pseudospondias microcarpa	**ABC,(A)**	4	4	3	4	4	4	2	.	.	1	.	1	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Glyphaea brevis	**ABC,(A),C2-3**	4	6	4	5	6	6	2	2	3	.	.	.	1	.	.	.	.	1	3	2	1	2	.	.	.	.	.	.	.	.	.	.
Desplatsia dewevrei	**ABC,B1**	1	1	2	3	1	.	.	1	1	.	.	.	.	3	1	.	3	.	.	1	2	3	1	.	1	.	.	.	.	.	.	.
Entandrophragma cylindricum	**ABC,B1**	.	.	2	.	.	1	1	3	3	.	.	.	.	1	1	1	2	1	1	.	.	2	1	1	2	1	1	.	.	.	.	.
Alstonia boonei	**ABC,B2**	2	.	2	1	1	1	.	.	.	2	1	1	.	3	1	2	1	.	1	2	2	2	1	.	1	1	.	.	1	.	.	.
Clausena anisata	**ABC,C1**	1	.	1	1	.	.	1	.	1	1	1	.	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cola gigantea	**ABC,C1-2**	1	1	.	1	1	1	3	3	1	1	.	1	4	1	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.
Cleistopholis patens	**ABC,C1-2**	5	2	4	1	2	.	.	1	.	3	1	.	.	1	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.
Rauvolfia vomitoria	**ABC,C1-2**	1	.	1	.	.	1	.	.	1	.	1	3	.	1	1	1	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.
Croton macrostachyus	**ABC,C1-2**	.	.	.	.	.	2	1	.	1	.	.	3	2	3	1	2	3	3	.	.	1	2	.	.	.	.	1	.	.	.	.	.
Lovoa swynnertonii	**ABC,C1-2**	1	.	.	.	1	.	2	2	1	.	.	.	1	.	1	1	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.
Canarium schweinfurthii	**ABC,C1-2**	.	.	.	.	1	.	.	.	1	.	1	1	.	1	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.
Rothmannia whitfieldii	**ABC,C1-2**	1	.	.	.	.	2	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.

Table 1. (cont.)

Plot Code	**Diag.**	**1N2**	**1W21**	**1NR**	**1N3**	**1N15**	**1B1**	**2B1**	**3B1**	**4B1**	**1WNR**	**1W22**	**1S8**	**1B4**	**2N2**	**3N3**	**4N3**	**3N2**	**4N2**	**3W21**	**4W21**	**2W21**	**2N3**	**2N15**	**3N15**	**3NR**	**2NR**	**1W42**	**2W42**	**5W42**	**6W42**	**4W42**	**3W42**
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Croton sylvaticus	**ABC,C2-3**	.	.	1	1	1	.	1	1	1	3	3	.	1	.	.	.	.	.	1	1	3	1	.	1	1	1	.	.	.	.	.	.
Leptonychia mildbreadii	**ABC,C2-3**	1	1	1	1	.	1	2	3	1	1	1	1	.	.	.	.	.	.	2	1	2	.	.	.	1	.	.	.	.	.	.	.
Teclea grandifolia	**ABC,C2-3**	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	1	.	1	.	.	.	.	.	.	.	.
Zahna golungensis	**ABC,C2-3**	1	1	.	.	.	.	1	3	2	.	1	.	1	.	.	.	.	.	.	1	.	.	1	1	.	1	.	.	.	.	.	.
Lindackeria schweinfurthii	**ABC,C2-3**	1	.	2	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	1	1	1	.	1	.	.	.	.	.	.	.	.	.
Trema orientalis	**ABC,C2-3**	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	2	.	2	.	.	.	.	.	.	.	.	.
Chrysophyllum muerense	**ABC,B1**	.	1	.	.	.	2	2	6	2	.	.	1	.	1	1	.	.	.	.	2	.	.	.	2	.	1	.	.	.	.	.	.
Alchornea floribunda	**ABC,B1,C3**	.	.	.	2	.	.	4	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.
Dracaena fragrans	**ABC,C2**	1	1	1	1	.	.	.	.	.	1	1	.	.	.	.	.	.	.	1	2	1	1	.	.	.	.	1	.	.	.	.	.
Antidesma laciniatum	**ABC,C2**	2	.	2	3	2	.	1	1	2	.	.	3	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
Rinorea oblongifolia	**AC,A1,C2-3**	.	1	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	5	4	.	.	.	.	6	.	.	.	.	.	.
Staudtia kamerunensis	**AC.A1**	1	.	1	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.
Ficus orttonofolia	**AC,A1 ,C2**	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	1	.	.
Allophyllus dummeri	**AC,C2**	1	1	.	2	1	1	.	.	1	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.
Sterculia dawei	**AC,C2-3**	1	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.
Zanthoxylum rubescens	**AC**	1	.	1	2	1	.	.	.	.	.	.	1	.	.	1	1	.	1	.	1	1	.	1	.	.	.	1	.	.	.	.	.
Erythrina excelsum	**AC**	1	.	1	1	2	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	.	.
Claoxylon hexandrum	**AC**	.	.	1	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	1	.	.	.	.	1	.	.	.	.	.	.
Macaranga pynaertii	**AC**	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.
Alangium chinense	**AC**	.	.	1	1	4	3	.	.	.	.	.	.	.	.	1	.	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.
Picralima nitida	**AC,A2**	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Desplatsia chrysochlamys	**AC,A2,C1-2**	.	.	.	2	1	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Monodora myristica	**AC,A2,C1-2**	.	.	.	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.
Ochna membranacea	**C,C1-2**	.	.	1	.	.	.	.	.	.	.	.	.	.	3	1	.	1	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.
Ficus asperifolia	**C,C1-2**	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Randia longiflora	**C,C1-2**	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Majidea fosteri	**C**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	1	1	.	1	.	.	.	.	.
Lindackeria ruwenzoriensis	**C**	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Croton megalocarpus	**C**	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Coffea spathycalyx	**C**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Cedrella cedrata	**C,C2**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.
Alchornea hirtella	**C,C2-3**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.
Gardenia vogelli	**C,C2-3**	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.	.
Englerophytum natalense	**BC,B2**	.	.	.	.	.	.	.	.	.	1	.	2	2	3	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.

Table 1. (cont.)

Plot Code	**Diag.**	**1N2**	**1W21**	**1NR**	**1N3**	**1N15**	**1B1**	**2B1**	**3B1**	**4B1**	**1WNR**	**1W22**	**1S8**	**1B4**	**2N2**	**3N3**	**4N3**	**3N2**	**4N2**	**3W21**	**4W21**	**2W21**	**2N3**	**2N15**	**3N15**	**3NR**	**2NR**	**1W42**	**2W42**	**5W42**	**6W42**	**4W42**	**3W42**
Cluster No.		**A1**	**A1**	**A1**	**A2**	**A2**	**A2**	**B1**	**B1**	**B1**	**B2**	**B2**	**B2**	**B2**	**C1**	**C1**	**C1**	**C1**	**C1**	**C2**	**C2**	**C2**	**C2**	**C3**	**C3**	**C3**	**C3**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**
Fagaropsis angolensis	**BC,C1**	.	.	.	.	.	.	1	1	.	4	.	2	2	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Ficus exasperata	**BC,C1-2**	.	.	.	.	.	.	1	.	1	.	.	1	.	4	1	1	2	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Pancovia turbinata	**BC,C1-2**	.	.	.	.	.	1	.	2	1	.	.	.	.	2	1	1	1	1	.	.	.	2	.	.	.	.	.	.	.	.	1	.
Uvariopsis sp.	**BC,C1-2**	.	.	.	.	.	1	.	.	.	.	1	.	1	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Ficus mucuso	**BC,C1-2**	.	.	.	.	.	.	.	.	1	.	1	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.
Aphania senegalensis	**BC**	.	1	.	.	.	.	.	1	1	1	1	1	1	.	.	1	1	1	1	.	.	.	.	1	2	.	.	.	.	.	.	1
Milicia excelsa	**BC**	.	.	.	.	.	.	1	.	.	1	.	1	1	1	.	1	.	1	.	1	.	.	.	1	.	.	.	.	1	.	.	.
Zanthoxylum leprieurii	**BC**	.	.	1	.	.	.	.	.	1	.	1	.	1	2	.	1	.	.	1	.	1	1	.	.	.	1	.	.	.	.	.	.
Tetrorchidium didymostemon	**BC**	.	.	.	1	.	.	.	.	1	1	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.
Antidesma venosum	**BC**	.	.	.	.	.	.	.	.	.	.	.	.	4	2	3	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Uvariopsis congensis	**BCD**	.	.	.	.	.	.	1	1	.	1	4	.	.	1	.	.	1	.	.	4	.	.	.	1	.	.	.	1	.	.	.	1
Drypetes gerrardii	**BCD**	.	.	.	.	.	.	1	.	.	1	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	3	5
Maerua duchesnei	**BCD**	.	.	.	.	.	.	.	1	1	3	1	.	.	1	1	.	1	2	1	1	1	.	1	4	1	.	1	3	3	3	5	6
Rawsonia lucida	**BCD**	1	.	.	.	.	.	1	1	.	.	1	.	.	1	4	1	.	.	.	.	.	1	1	3	.	.	3	3	3	4	1	6
Lovoa trichilioides	**BCD,B1,D1**	1	.	.	.	.	.	2	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	1	.	.	.
Suregada procera	**BCD,C3**	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	2	.	1
Thecacoris lucida	**CD**	.	.	1	7	.	.	.	.	.	.	1	.	.	1	.	.	5	6	.	.	5	3	3	5	4	3	8	8	7	5	3	6
Whitfieldia elongata	**CD,C2-3**	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	2	1	.	3	1	4	1	3	1
Strychnos mitis	**D**	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	1	2	.	.	1	5
Maytenus undata	**D**	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	2
Dialium excelsum	**D**	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	1	1	1	1
Rinorea ilicifolia	**D**	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	4	1	7	1	.
Balsamocitrus dawei	**D**	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	3
Manilkara dawei	**D**	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	4	.	.	.	1	1
Dombeya mukole	**D**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	2	2
Ficus pseudomangifera	**D,D1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.

Table 2. Intra-set correlations between environmental variables (i.e., pH, Ca, Mg, Na, P, Li, Si, Ti, Fe, OM, N and historical management practices) and the first four axes of CCA. OM: Organic matter; Li: Lithium; Log.arbt: Logged and arboricide treated (see Materials and Methods section).

Variable	Basal area data				Abundance data			
	CCA Axes				CCA Axes			
	1	2	3	4	1	2	3	4
pH	0.418	-0.063	0.049	-0.157	0.587	-0.132	-0.132	-0.231
Si	-0.685	0.116	0.287	-0.080	-0.696	0.051	0.276	-0.154
Ti	0.202	0.234	-0.439	-0.226	-0.053	-0.454	-0.522	0.200
Fe	0.593	-0.307	-0.473	-0.004	0.642	0.125	-0.542	0.099
Mg	0.073	-0.307	0.339	0.178	0.252	0.480	0.391	-0.066
Ca	0.603	0.161	0.142	0.018	0.669	-0.085	0.203	0.006
Na	-0.156	0.497	0.714	0.247	-0.113	-0.340	0.804	0.070
P	0.327	-0.523	-0.168	0.008	0.453	0.424	-0.216	-0.143
Li	0.603	-0.159	-0.155	0.180	0.636	0.171	-0.082	0.179
OM	0.559	0.109	0.326	0.586	0.637	-0.048	0.403	0.483
N	0.654	0.215	0.086	-0.017	0.636	-0.130	0.254	0.003
Logged only	0.290	0.224	-0.106	0.219	0.266	0.062	0.130	0.068
Log.arbt	0.178	0.685	-0.430	0.071	0.136	-0.589	-0.223	0.084

Table 3. Summary table of Canonical Correspondence Analysis results for the first four axes, based on species basal-area and abundance data, and environmental data from 32, 0.5 ha plots representing the major historical management practice types in Budongo Forest Reserve, NW Uganda.

Axes	1	2	3	4	Total Inertia
a) Basal area data					
Eigenvalues	0.437	0.42	0.329	0.226	4.785
Species-environmental correlations	0.9	0.943	0.949	0.943	
Cumulative percentage variance					
of species data:	9.1	17.9	24.8	29.5	
of species-environment relation:	17.3	33.9	47	55.9	
Sum of all eigenvalues					4.785
Sum of all canonical eigenvalues					2.523
b) Abundance data					
Eigenvalues	0.422	0.333	0.225	0.151	3.085
Species-environmental correlations	0.923	0.909	0.929	0.899	
Cumulative percentage variance					
of species data:	13.7	24.5	31.8	36.7	
of species-environment relation:	24.5	43.9	57	65.8	
Sum of all eigenvalues					3.085
Sum of all canonical eigenvalues					1.72

altissima forest communities are generally clearly differentiated from the others, while along axis 2 it is *Cynometra alexandri-Rinorea ilicifolia* forest community. Generally, *Pseudospondias microcarpa* Swamp Forest is associated with high levels of Na and Si; while *Funtumia elastica-Pouteria altissima* Forest is associated with high levels of OM, Ca and N; and *Cynometra alexandri-Rinorea ilicifolia* forest community with high levels of Mg. The relatively high dispersion of plots in some clusters in the ordination space corroborates the cluster analysis (Fig. 1), and the SIMPER results that showed that the within community average similarity was fairly low and spans 33–55 %.

Discussion

The classification of the vegetation of BFR showed that the forest is formed by overlapping plant communities, which were identified both by the cluster analysis and CCA ordination, and scrutinised by ANOSIM and SIMPER analyses. However, there were some differences in the grouping of samples into clusters for the abundance and basal area data sets.

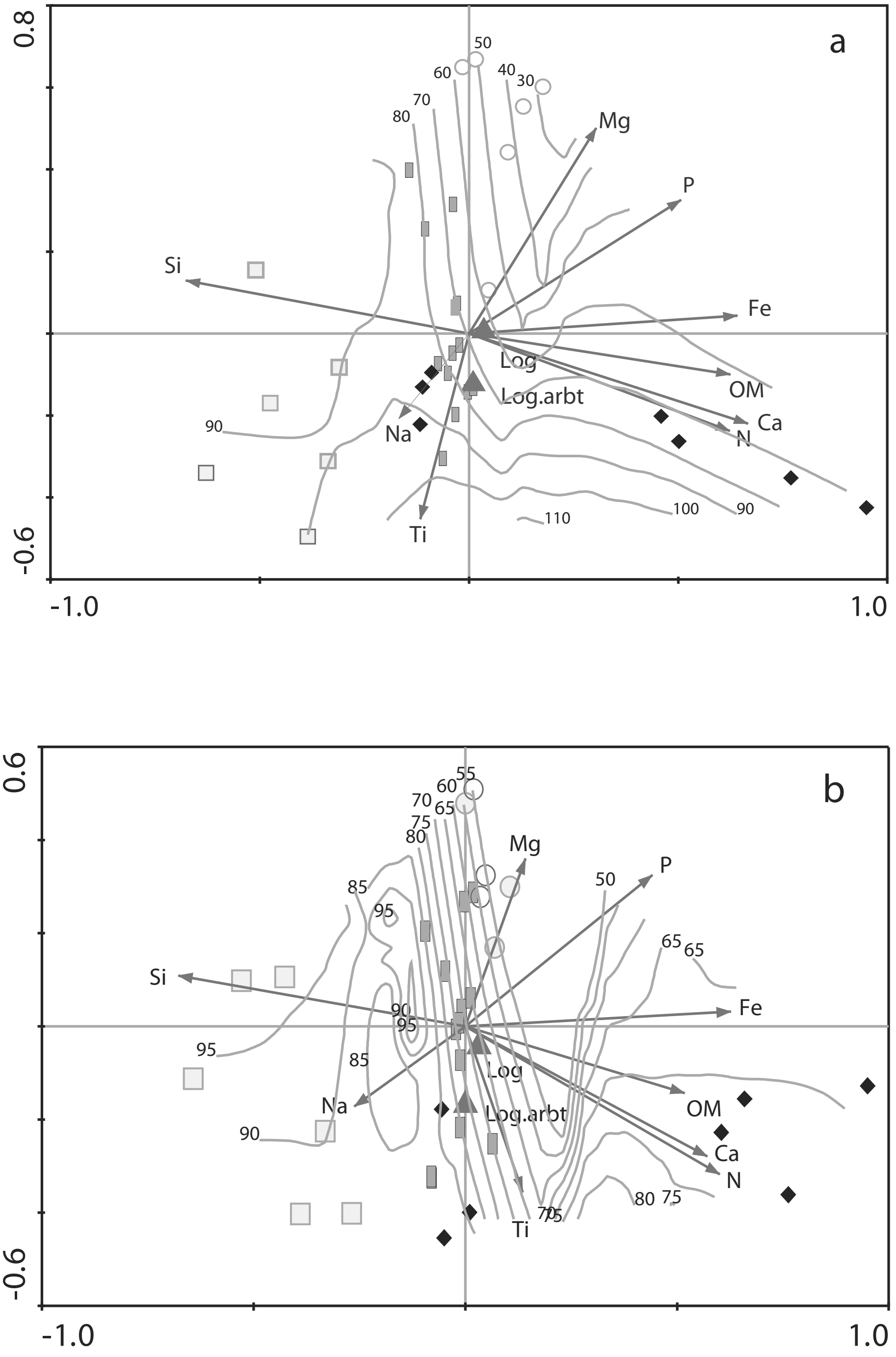

Fig: 2. CCA ordination diagram with soil variables (arrows), historical management practice types nominal variables (▲) and sampling plots grouped into 4 forest Communities (A-D) using species (a) abundance, (b) basal area data; first axis is horizontal, second axis vertical. The isolines of number of species are also plotted in the CCA ordination diagram. A= empty square, B= diamond, C= filled box, and D= empty circle. Sample labels and environmental variables pH and Li → have been suppressed for clarity.

The relatively poor agreement between the clusters for the two data sets is not surprising. Several communities may show similarity in physiognomy (resulting from sharing dominant species), and differ in abundance of other species. The dominant species were not necessarily the most abundant and frequent ones in the communities, except for the *Senna spectabilis* sub-community. Thus it might be misleading to classify woody plant communities using basal area alone, particularly in environments where relatively small stature plant species are frequent and anthropogenic disturbance is pronounced. A few large trees (e.g. *Alstonia boonei, Cynometra alexandri*) may contribute substantially to the total basal area of a plant community, yet they may be rare or scattered (hence, less important in terms of frequency). The high degree of dispersion of plots within communities as featured in the dendrogram (Fig. 1) and ordination diagram (Fig. 2) is usually indicative of internal heterogeneity of the cluster (Miranda et al. 2002).

The relatively high number of shared species among the communities is not surprising, because of the patchy and heterogeneous nature of the environment within the communities as a result of opening of canopy gaps due to natural and human disturbance (Mwavu 2007). The opening of canopy gaps as found in BFR is a recurring source of environmental heterogeneity in forest habitats that favours the coexistence of species with different life histories, contributing to the maintenance of community diversity (Barkham 1992, Valverde & Silvertown 1998). Indeed, some of the species (e.g. *Cynometra alexandri*, *Celtis mildbraedii*, and *Lasiodiscus mildbraedii)* all highly abundant and occurring in all the four communities have been by classified by Walaga (1994) as 'generalists' with respect to the soil variation in BFR. Similarly, Terborgh & Andersen (1998) in their study of the distribution of tree species in a variety of habitats, found about 15 % of the species to have been habitat specialists, while the majority were generalists. On the other hand, many canopy trees shed their leaves during the dry season, consequently, increasing light availability. This allows the germination of seeds and growth of many light demanding species, even in areas of dense upper-canopy that would otherwise not have been possible.

The cluster analysis results are corroborated by the CCA biplots, which demonstrate that plant communities in this forest intergrade and are not highly discrete probably due to the individualistic nature of species responses to environmental factors. However, clear separation of *Pseudospondias microcarpa* Swamp Forest as well as the *Senna spectabilis* and the *Cynometra alexandri* Communities, compares to some extent with the findings of Eggeling (1947) and Howard (1991). These three communities were identified by Eggeling (1947) on the basis of a successional gradient, while Howard (1991) also distinguished the *Senna spectabilis* Forest Community. Results of the present study, however, contrast with earlier classifications in that the *Maesopsis eminii* Forest described by Eggeling (1947) was not identified. *Maesopsis eminii* is an early successional species that has been ascribed to a period when the Budongo Forest was spreading unhindered, except for being contained by natural factors such as unfavourable soils or elephant herbivory (e.g. Laws et al. 1975, Walaga 1994). However, in the last two decades, large herbivores such as elephants, have disappeared from the interior of the forest (Laws et al. 1975, Sheil & Salim 2004). Nonetheless, increasing anthropogenic disturbances, including mainly timber (targeting mahogany species and *Maesopsis eminii*) and pole harvesting, have become more common phenomenon in most parts of the forest, except in some patches in the nature reserve area (Mwavu & Witkowski 2008b). Consequently, the successional pathways, as postulated by Eggeling (1947), have been disrupted. Shifts in relative densities of various woody species have also been observed, with some previously absent species now ranked as widespread (Sheil et al. 2000). Indeed, disturbances, both human-induced and natural, are known to shape forest communities by influencing their composition, structure, and functional processes (Dale et al. 2001, van Germerden et al. 2003). However, different levels and types of disturbance have differential impact on forest communities (Halpern & Spies 1995). The occurrence of *Senna spectabilis* in the BFR interior and on its edges, and the dominance of *Cynometra alexandri* (even in areas where it was treated with arboricides over 40 years ago), are to a great extent directly or indirectly results of human interventions. *Senna spectabilis* was commonly planted as an ornamental (Synnott 1985), and is now naturalised widely in colonising forest and forest edges. The dominance of *C. alexandri* may be attributed to it having not been targeted for timber harvesting, hence, enjoying a competitive advantage over other species that have been constantly targeted for timber over the years.

The CCA ordination to a great extent illustrates the position of the forest communities and the link between the community species composition and the measured environmental variables operating in BFR. The CCA Axes 1 and 2 for both data sets had eigenvalues >0.33, which denotes a fair separation of species along both axes (ter Braak 1987). As a rule of thumb, an eigenvalue >0.30 indicates a strong gradient (ter Braak 1995). The relatively strong bias in the spatial distribution of tree species in relation to edaphic variation as observed in BFR, has similarly been widely reported for tropical forest trees in Ghana (Swaine 1996), neotropical rainforests (Clark et al. 1998, Svenning 2001) and the mixed dipterocarp forest in Malaysia (Lee et al. 2002). Soil characteristics such as texture, nutrient status, depth, and soil moisture regime are important factors that determine competitive relationships and growth rates of plants in a wide variety of environments, consequently, determining spatial or temporal species distribution (Tilman 1982) and composition of a community (Barbour et al. 1987). A number of studies (e.g. Duivenvoorden 1995, Swaine 1996, Clark et al. 1998, Sheil et al. 2000, Svenning 2001) demonstrated that species distributions were also strongly aggregated with respect to variation in topography, soil water, and soil nutrient status. In BFR, some of the soil nutrients (e.g. Si, Na, Mg, N and Ca) are clearly correlated with distinct forest communities. A study by Walaga (1994) on the development of climax vegetation in BFR similarly reported significant correlations between local patterns of tree species distribution and soil variables (K, N, Mg, Ca and silt content). The fact that in the present study apart from soil nutrients no other measured environmental variable was strongly correlated with Axis 1 of the CCA, suggests the strong influence of soil nutrients on the species distributions in BFR. For instance, *Pseudospondias microcarpa*, *Eurphorbia teke* and *Neoboutonia melleri,* characteristic of the swamp forest are spatially aggregated on silicon-rich soils in the seasonally flooded lower-slope areas. However, clear correlations between forest vegetation and Si, Fe, Ti, and Li as shown in BFR was not previously well known. Nevertheless, it is reported that plants lacking in silica (Si) are more susceptible to biotic and abiotic stresses, can exhibit abnormal growth, and are structurally weak (EPSTEIN 1994, MARSCHNER 1995). This suggests that plants growing on silica rich soils are more likely to survive and contribute to the high species richness of the forest community as shown for the *Pseudospondias microcarpa* Swamp Forest in BFR. It has been suggested for Borneo's mixed dipterocarp forests that availability of soil nutrients, particularly phosphorus and magnesium, directly influence species distributions and community composition (BAILLIE et al. 1987, POTTS et al. 2002). Phosphorus is widely reported to be the principal nutrient limiting tree growth and productivity in tropical forests (SOLLINS 1998, TIESSEN 1998, CLEVELAND et al. 2002). Other studies (including LICHTER 1998 and FRELICH et al. 2003) have similarly reported on the influence of soil nitrogen on the structure of forests (especially their understorey component). While according to SOLLINS (1998) phosphorus availability, aluminium toxicity, drainage, water holding capacity, and availability of K, Ca, Mg, N and micronutrients such as B and Zn are reportedly the soil properties most likely to influence species composition and structure of lowland tropical rainforests.

The distribution of plant communities along edaphic gradients, as shown in BFR, supports the individualistic hypothesis of community organization (GLEASON 1926). Similarly, this study suggests that small spatial scale variability in soil nutrients (at the scale of hundreds of meters) structures the plant communities of BFR. Indeed, elsewhere it has been reported that species composition and forest structure can vary quite dramatically with small scale edaphic and topographic gradients (NEWBERRY & PROCTOR 1984, BAILLIE et al. 1987, DAVIES & BECKER 1996). On the other hand the wide and abundant occurrence of *Cynometra alexandri* across a variety of soil types and nutrient status contradicts OSMASTON's (1959) characterisation of *Cynometra* consociation as an edaphic climax. However, it confirms WALAGA's (1994) suggestion that *Cynometra alexandri* is a generalist with no soil preferences, and therefore OSMASTON's (1959) theory, as regards its dominance only under certain soil conditions, is not operational in BFR.

Although there is strong evidence that soil nutrients and anthropogenic gradients influence the composition and structure of plant communities in BFR, there may be other abiotic and biotic factors whose influence cannot be disentangled in this study. For instance, the plots of the Swamp Forest community, although located far apart, in terms of species composition resembled each other more than the adjacent up-slope plots along the same transect, suggesting a strong relationship between the habitat and floristic composition (see also TERBORGH et al. 1996). It appears that *Pseudospondias microcarpa* and *Senna spectabilis* show a degree of habitat specialization, suggesting that the *Pseudospondias microcarpa* Forest and *Senna spectabilis* Forest are organised by niche-assembly processes (CLARK et al. 1999, HUBBELL 2001). Species neighbourhood effects may also contribute to the differences in species community composition found in BFR. For instance, the *Cynometra alexandri* Forest had the lowest species richness, followed by the *Senna spectabilis* sub-community. A secondary effect of the closed canopy of these forest types is that it limits the understorey development leading to a simplified forest structure and lower diversity of plants (FRANKLIN et al. 1993).

The floristic data show that some of the most ecologically important and speciose woody plant families (e.g. Euphorbiaceae and Fabaceae), are similarly among the ten most important in other Albertine Rift forests (i.e., Kalinzu, Bwindi, Kasyoha and Kibale Forests), as well as the dry forests of Madagascar (MWAVU 2007, and reference therein). The BFR exhibits single-species dominance in the *Cynometra alexandri* forest community type, which is also characteristic of almost all primary lowland rainforests (i.e., Bugoma, Kalinzu, Kibale, Semliki, and Zoka Forests; see EGGELING 1947). However, in Kalinzu and Kibale Forests, *Cynometra alexandri* is replaced as the climax dominant by *Parinari exclesa* Sabine (CHAPMAN & CHAPMAN 2004). Similarly Bwindi and Kasyoha forests of the Albertine Rift are *Parinari* dominated forests (HOWARD 1991). Although the flora of BFR has affinities to the Guineo-Congolian forests and the East African montane forests, they are different in terms of the most dominant canopy and sub-canopy species. In BFR, *Cynometra alexandri* and *Lasiodiscus mildbraedii* are the persistent dominant canopy and sub-canopy species respectively. Whereas in the Bumbesa and Yangambi forests of the Democratic Republic of Congo (formerly Zaire), *Gilbertiodendron dewevrei* and *Isolana thonnari* are the most persistent canopy and sub-canopy species respectively (CONNELL & LOWMAN 1989). Great floristic similarity of the BFR is shared with remnants of tropical lowland forests of Kenya, such as Kakamega Forest (e.g. FASHING et al. 2004) and especially with the geographically close and famous Ituri Forest of eastern Congo (e.g. MAKANA & THOMAS 2006 for a recent reference). The palaeo-ecological links between the tropical lowland forests of Congo, Uganda and Kenya relates to the existence of a putative relictual region termed 'Congolia' whereto the tropical forests would have retreated during the Late Glacial Maximum (LEAL 2004). Phytogeographically BFR falls under the broad category of Lowland Forest (HEDBERG 1951, HAMILTON 1974, 1975).

Conclusions

The numerical classification and ordination in this study have proven to be effective in the description of the forest communities and forest community-environment relationships in this semi-deciduous tropical rainforest. Although the cluster analysis clearly shows the existence of four plant community groups, the present BFR is more of a mosaic of community types with varying dominant and abundant species, because of the considerable overlap in species composition and local environment. The CCA ordination points to the importance of soil nutrients (i.e. OM, Na, N, Ca, Mg, Si, and Ti) and anthropogenic disturbances as controlling factors of forest community type patterns in BFR. Hence, there is evidence supporting the hypothesis that edaphic, habitat variation and anthropogenic factors that interrupt environmental vegetation gradation, directly contribute to the diversity and heterogeneous nature of the BFR plant communities. The impacts of human activities may play an important role in the conservation of the natural vegetation of this forest; hence, adequate management plans are urgently required for BFR. It will also be important to ensure adequate conservation of the various forest community types identified, to preserve its woody species diversity. Measurements of some other significant soil traits (e.g. soil moisture) that were not measured in this study may shed more light on the relationship between pattern of forest communities and environmental variables.

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