Tree species composition and diversity in Miombo woodlands between co-managed and government-managed regimes, Malawi

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HIGHLIGHTS

- Tree species showed low similarity between management regimes due to site differences
- Fabaceae (31%), in subfamilies Caesalpinioideae and Papilionoideae, were dominant
- Species associations were driven by site differences and management regimes
- Eigenvalues ≥0.3 showed stable sub-communities
- Species rank importance distributions were related to stem abundance and diameters
- Disturbances stimulated regeneration and enhanced species richness and evenness

Abstract

Comparative information on the composition and diversity in tree species associations in Miombo woodland is limited. This study assessed how tree species associations across forest reserves of Miombo woodland in Malawi varied in composition and diversity concerning site factors and resource use disturbances under co-management versus government-management. Eighty nested circular plots, randomly selected in ArcGIS, were sampled to record stem diameter at breast height (DBH) of tree species: 0.04 ha for stems 5-29.9 cm DBH and 0.16 ha for stems ≥30 cm DBH. The recorded 109 tree species grouped into communities and 14 sub-communities, using stem counts by species in TWINSPAN analysis. Sub-divisions to level 5 showed eigenvalues ≥0.3, symbolising the stability of sub-divisions. North/South sub-divisions related to site factors; historical/current resource use influenced differences at levels 3 to 5. Species importance differed, indicating few important species in each sub-community. *Brachystegia* and *Julbernardia* species showed importance across sub-communities while *Uapaca sansibarica* in government-management. Disturbances stimulated high species diversity. Recommendations include the need for a policy review towards group-felling mature stands to stimulate regeneration and selective thinning of

suppressed stems in stand development stages to maintain species diversity, productive recovery, diverse resource use-value, and monitoring of harvesting impacts.

KEYWORDS: Co-management, government-management, Importance values, Malawi, Miombo woodland, species diversity, tree species composition

1. INTRODUCTION

Knowledge of the variation in the composition of tree species associations of a Miombo woodland ecosystem can provide a baseline against which management impact can be measured. A forest inventory can provide such baseline ecological information to assess management impact on tree species dynamics (Geldenhuys, 2010; Matthews & Whittaker, 2015).

Different management regimes have been introduced for managing Miombo and also improving livelihoods in Malawi (Government of Malawi, 2005, 2016). They include community management of customary forests, government-management of forest reserves (FRs), co-management of government-owned FRs, individual/household trees on farms, afforestation (private, estate, community), and community involvement in government plantations. The Forest Department is responsible for protecting government-managed FRs but has limited human and financial resources (Government of Malawi, 2010, 2016). Products have been illegally harvested from forest reserves in sub-Saharan Africa (Makero & Kashaigili, 2016; Chichinye et al., 2019; Gondwe et al., 2020). Co-management is an obligatory contract between the Forest Department and communities to legally use products according to a management plan (Government of Malawi, 2005). Effective and sustainable woodland management requires relevant policies, governance, participatory tools, capacity, and knowledge (Senganimalunje et al., 2015; Liu et al., 2017). However, knowledge is lacking on how contractual agreements and management regimes impact forest condition, tree species associations, common, rare, and over-exploited tree species (Geldenhuys, 2014; Matthews & Whittaker, 2015).

Miombo woodland (Miombo) has important ecological functions (Kalaba et al., 2013; Pullanikkatil et al., 2018; Handavu et al., 2019). In Malawi, the livelihood of most poor rural people (85%) depends on woodlands (Government of Malawi, 2018; Munthali et al., 2019). Over-exploitation, degradation and deforestation, and limited knowledge on resources management (Rudel, 2013; McNicol et al., 2015) could lead to 'The tragedy of the commons' (Hardin, 1968, 1998) with negative impacts on such resources and the environment (Schwartz & Caro, 2003; Giliba et al., 2011). However, most Miombo species sprout (Geldenhuys et al., 2013; Syampungani et al., 2016); deforestation only occurs with de-rooting, and degradation being a temporary change in stand structure (Geldenhuys, 2010; Gondwe et al., 2020). Criteria for effective sustainable resource management include the use that does not negatively affect the resource base but should improve the regeneration status of harvested tree species (Geldenhuys, 2010; Vinya et al., 2011; Jew, 2016).

Several studies have assessed tree species composition of Miombo and Undifferentiated woodland (Mwakalukwa et al., 2014; McNicol et al., 2015; Chichinye et al., 2019). Site condition and disturbance-recovery processes underlie variation in the distribution and composition of tree species associations, but such information is poorly understood (Geldenhuys, 2010; Munishi et al., 2011) to support harvesting practices that mimic natural disturbance-recovery processes to which the vegetation is adapted in stimulating regeneration of common and rare species (Geldenhuys, 2010).

Different plot shapes and sizes have been used to record most tree species and sizes, i.e. rectangular (Chinangwa et al., 2017; Halperin, 2017) and nested circular plots (Geldenhuys, 2010; Chichinye et al., 2019). Syampungani et al. (2016) used plotless sampling to record a fixed number of stems (>30 stems) to cover regeneration and large trees of most species. Circular plots ease plot establishment and minimise sampling errors (Chichinye et al., 2019). Nested plots optimise reliable and cost-effective recording similar numbers of stems of different sizes of most tree species, with a larger plot for fewer larger stems versus a smaller plot for abundant smaller stems (Pearson et al., 2005). Chichinye et al. (2019) and Nyirenda et al. (2019) used nested circular plots of 0.01 ha, 0.04 ha, and 0.2 ha, around the same mid-point, to respectively record regeneration counts (stems <5 cm DBH (stem diameter at 1.3 m above ground level)), and trees of 5.0-29.9 cm and ≥30 cm DBH.

Classification and ordination techniques identify tree species associations based on the similarity-dissimilarity between component species (Assédé et al., 2012; Matthews & Whittaker, 2015; Chichinye et al., 2019). The ecological importance of species within associations is calculated as Importance Value Index (IVI) based on their relative frequency, density, and basal area (Jew, 2016; Gonçalves et al., 2017; Chichinye et al., 2019). IVI is affected by the number and size of stems recorded, and the number of species included. Species abundance distributions (SADs) have been used to visually display the ranking of species within species associations (Magurran, 2004; Matthews & Whittaker, 2015). Jaccard Similarity Index has been used to calculate the percentage of shared species between 2 management regimes (Yue & Clayton, 2005; Chao et al., 2006). Such information is limited in comparing the effect of different resource management regimes (Bhadra & Pattanayak, 2016).

The objective of this study was to assess the variation in the composition of associations of Miombo tree species in terms of distribution, abundance, and diversity, and effect of the species pool, site conditions, and land-use disturbances related to management regime on such variation. The study questions were: (i) What differences exist in tree species pools between northern and southern FRs in Malawi, and between FRs under co-management (CM) versus government-management (GM)? (ii) What are the main tree species associations and indicator species for the different identified communities and sub-communities? (iii) How do site factors and land use disturbances (CM versus GM regimes) drive the variation in tree species composition, distribution, and diversity of the identified associations?

2. MATERIALS AND METHODS

2.1 Study areas

Four FRs of Miombo woodland in Malawi were purposively selected to compare the variation in tree species composition between CM and GM (Figure 1) (Hudak & Wessman, 2000; Banda et al., 2015; Kamangadazi et al., 2016):

- Northern Malawi: Kaning’ina GM; 11^{o} 27’S, 34^{o} 07’E; 1200–2000 mm rainfall/year; 15,000 ha; including some evergreen forest species (Banda et al., 2015) and Perekezi (CM in western part; 12^{0} 03’S, 33^{0} 37’E; 760–1270 mm rainfall/year; 15,370 ha), both gazetted as FRs in 1935;
- Southern Malawi: Thambani (GM; 15^{o}41’S, 34^{o}27’E; 1042–1269 mm rainfall/year; 10,670 ha) and Liwonde (CM; 15^{o} 06’S, 35^{o} 24’E; 840–960 mm rainfall; 34,175 ha;), respectively gazetted in 1927 and 1924.

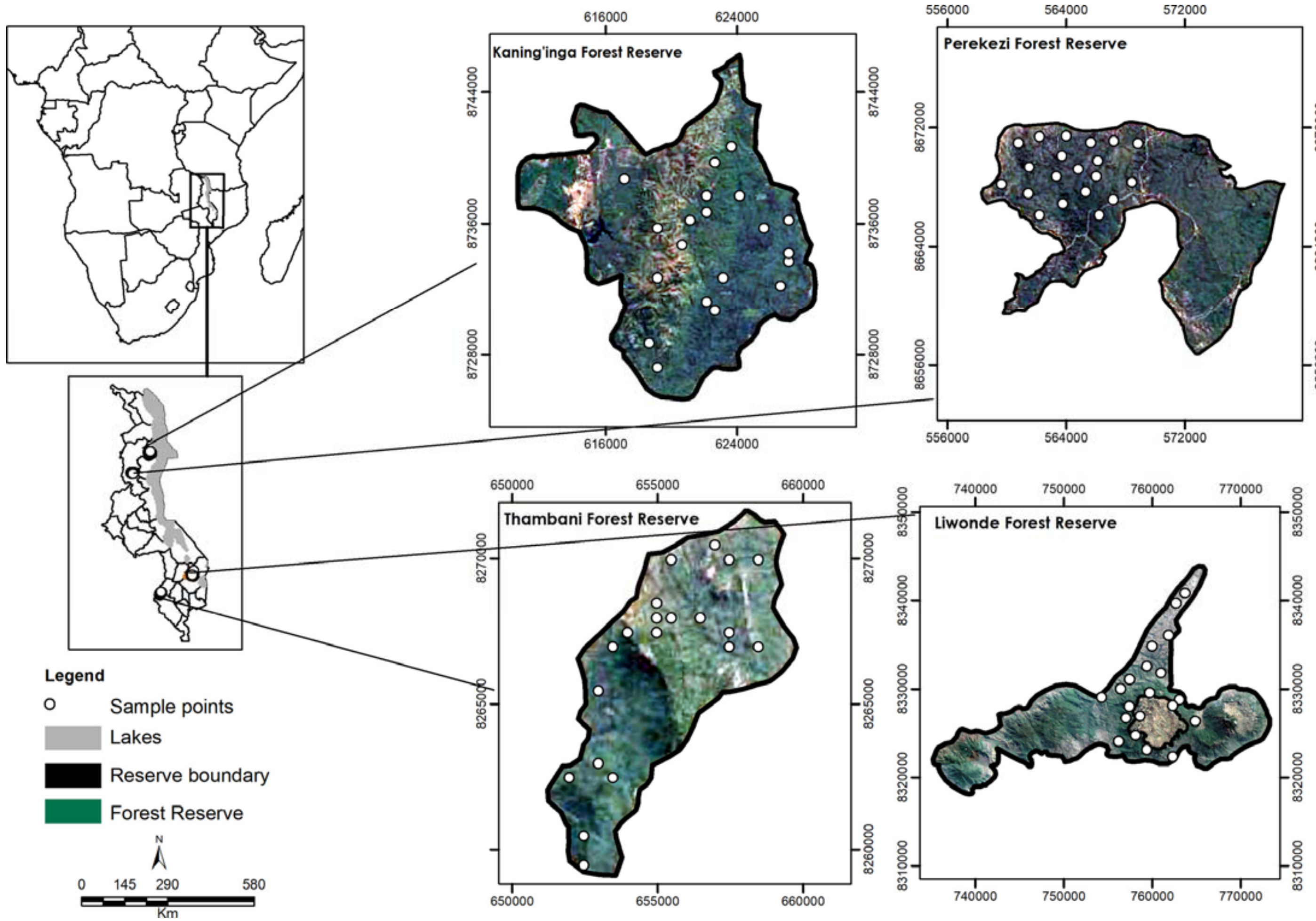

Figure 1. Location of the studied forest reserves, Kaning'ina and Perekezi in northern Malawi, and Thambani and Liwonde in southern Malawi. Sampled plots are indicated as dots. The eastern part of Perekezi was excluded from the study

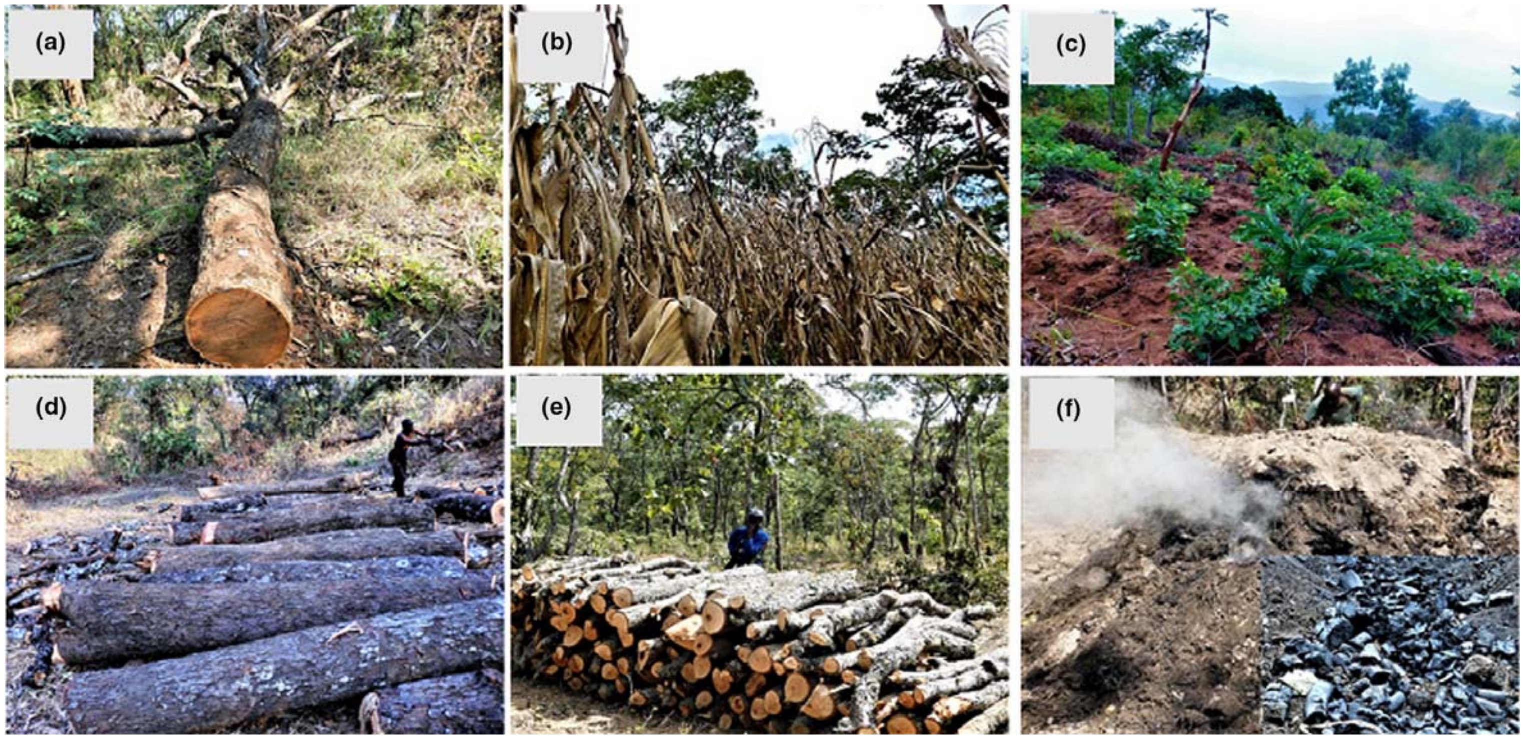

Figure 2. Examples of resource use within the different forest reserves, impacting on the condition of co-managed (CM) and government-managed (GM) Miombo woodland, Malawi. (a) Cutting trees for timber, and later for fuel wood in Kaning'ina (GM); (b) Clearing of trees in patches to grow maize in Liwonde (CM); (c) Two stages of woodland recovery in Liwonde, showing good sprouting of different tree species in crop fields, and development towards regrowth woodland in the background; (d) Confiscated off-loaded illegally cut stems in Thambani (GM); (e) Stems in Perekezi (CM) ready for making charcoal; (f) A charcoal kiln in Perekezi with an insert of mature charcoal.

Historically, all FRs were gazetted to conserve biodiversity and protect fragile woodland and water catchments (Government of Malawi, 1996, 2016). CM of FRs started in 1999. Both management regimes have been subjected to wood extraction, and Liwonde and Kaning'ina include patches of cultivation (Figure 2) (Government of Malawi, 2010).

2.2 Sampling design, plot establishment, and data collection

A 500-m grid superimposed over each FR, using Google Earth and ArcGIS, was used to randomly select 20 intersections as sampling points inaccessible parts of each FR (total of 80 plots; Figure 1) and were located in the field using a GPS 62sc.

Nested circular plots were used, with a large plot (0.16 ha; radius 22.6 m) to record stems ≥30 cm DBH, and the main plot (0.04 ha; radius 11.28 m) to record stems 5.0-29.9 cm DBH. All stems were recorded by species and DBH. It was assumed that trees with 5cm DBH could indicate the regeneration. A Taxonomist from the National Herbarium, Zomba, Malawi, identified all the species in the field, using 'Trees of Malawi' (Binns, 1972). Observed disturbances such as tree cutting, charcoal production, and fire, were recorded for each plot.

2.3 Data analysis

2.3.1 Tree species composition/pool of forest reserves

All the tree species were listed by their botanical names, family, species code, and the total number of stems recorded on plots in each FR (Appendix A). Species generally forming part of Afromontane evergreen forest were indicated. Species codes used in all analyses were abbreviations of botanical names in a standardised format (Geldenhuys, 2005). Author names of species are only indicated in Appendix A, following the Royal Botanic Garden lists (Brummitt &

Powell, 1992) supplemented with updates listed in Van Wyk et al. (2011) and Burrows et al. (2018).

Jaccard Similarity Index was calculated to compare the shared species listed in Appendix A, between CM and GM FRs in the North and South, using formula 1 (Chao et al., 2006):

Sj = a/(a +b + c)……………………………………………………………………………1

Sj = Jaccard Similarity Index (%); a = species count in CM and GM, b = species count in CM, c = species count in GM. An index value of ≥50% was considered high.

A rare species in this study was based on an arbitrary total count of ≤4 stems recorded on all plots across the 4 FRs in Appendix A.

2.3.2 Classification of tree species associations

Data from the 2 nested plots per sample point were pooled to use all stems ≥5 cm DBH as stem counts per species per plot in a Two-Way INdicator SPecies ANalysis with TWINSPAN 2.3 (Hill & Šmilauer, 2005), following procedures of Chichinye et al. (2019) and Nyirenda et al. (2019). Ten plots were not used in the analysis; 5 plots had no DBH data and 5 had ≤2 stems. A species x plot matrix with stem counts of all recorded tree species was condensed with CANOCO 4.5 (Cornell condensed format Windows version 2.3 program package). The TWINSPAN analysis used pseudo-species cut levels of 0, 2 and 5 (1 = 1-2, 2 = 3-5, 3 = >5 stems per species per plot). Eigenvalues ≥0.3 and the identified indicator species were considered ecologically important (Hill, 1979).

2.2.3. Tree species Importance Values and their ranking across sub-communities

The IVIi for species i in each sub-community was calculated as:

$\mathrm{IVIi} = (\mathrm{RFi} + \mathrm{Rdi} + \mathrm{RBAi})/3$ ……………………………………………………………2

where RFi (relative frequency of species i) was calculated as:

RFi = 100 x Fi/TF…………………………………………………………………………….3

where Fi is the number of plots (frequency) in which species i is present, and TF is the sum of all frequencies for all species.

Rdi (relative density of species i) was calculated as:

Rdi = 100 x di/Td ……………………………………………………………………......4

where di is the total number of stems of species i, and Td is the total number of stems of all species; RBAi (relative basal area of species i was calculated as:

RBAi = 100 x BAi/TBA ………………………………………………………………….5

where BAi is the total basal area of species i, and TBA is the total basal area of all species.

Ranked importance distribution curves (RIDCs) (Matthews & Whittaker, 2015) plotted the calculated IVI (as a percentage) for each species against its rank (highest to lowest IVI) within selected sub-communities. RIDCs are a combination of the frequency, abundance, and tree size (calculated as basal area) of each species across sub-communities (Table 1). Only 1 to 3 top-ranked species in tables have been inserted in graphs to demonstrate stem abundance and mean DBH in CM and GM sub-communities.

2.2.4. Tree species diversity

RIDCs have also been used to determine tree species diversity (Matthews & Whittaker, 2015) in the identified sub-communities. Species richness was regarded as the number of species in a sub-

Table 1. Grouping of plots (columns) based on the distribution and abundance of tree species (rows), into 14 sub-communities, showing differences between co-managed (CM) and government-managed (GM) regimes.

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Region          SS SSSSSSS SSSSSSSSSS SSSSSS SSSS NSSSSN NNNN NNNNNNNN NNNNN NNNS NNNNN NNNN NNNN N
Management      cg cgggggg cccccccccc cccccg gggg gggcgg cccc cccccccc ccccc gggg gcggg gggg gggg g
Disturbance     CS CISSISS CISSSCCCCI SCSSSI ISSI gIScSg cccc cccccccc ccccc gggS gcggg gggg gggg g
                51 4.59..1 4333444543 05445. 201. I10I.I IIII ISSIIISS IISSS 11I2 IS1II GIIS 11II I
                10 2162111 1768058265 633401 2411 290313 1333 22322303 34030 1145 13535 3443 2344 5
                .0 .0..059 .......... .....5 ..25 7..250 8706 70589133 90741 590. 78496 6133 8096 1
                .. .2..75. .......... .....9 ...7 7...12 .... ........ ..... 565. ..035 4810 1564 .
  29 Brid  cat  -- ---2--- ---311-1-- ---1-- ---- ------ ---- -------2 ----- ---- ----- ---- ---- -  000000
  61 Flac  ind  -3 ------- --1------1 ------ ---- ------ ---- -------- ----- ---- ----- ---1 ---- -  000000
  46 Dalb  nya  1- -----22 -1--211-33 -----2 ---- ------ ---- -------- ----- ---- ----- ---- ---- -  000001
  48 Dios  kir  -- ------- 32311----- ------ ---- ------ ---- -------- ----- ---- ----- ---- ---- -  000001
  78 Olax  obt  -- ------- 2-21--22-- ------ ---- ------ ---- -------- ----- ---- ----- ---- ---- -  000001
 105 Term  ser  -3 ------1 32-12121-- ------ 1--- ------ ---- -------- ----- ---2 ----- ---- ---- -  000001
  19 Brac  bus  -- -333223 32-313--31 ---2-1 ---- ------ ---- -------- ----- ---- ----- ---- ---- -  000010
  75 Mund  ser  -- --12--- --1------- ------ ---- ------ ---- -------- ----- ---- ----- ---- ---- -  000010
  87 Pseu  map  -1 3221-22 33223--2-3 ------ -22- 12---- ---- ----22-- ----- --1- ----- ---- ---- -  000010
  31 Burk  afr  -- -1-1-1- ----1---2- ------ --2- ------ ---- -------- ----- ---- ----- ---- ---- -  000011
  35 Comb  ade  12 -1----- ---------- ------ ---- -----1 ---- -------- ----- ---- ----- ---- ---- -  000011
  50 Dipl  con  -- -332--1 22-12--1-1 -23312 3121 2----- ---- -------- ----- ---- ----- ---- ---- -  0001
  32 Burt  nya  -- --11--- ---------- ------ 1--- -2---- ---- -------- ----- ---- ----- ---- ---- -  00100
  90 Pter  ang  -- 2123--1 ----1----- -----1 321- -22--- ---- -------- ----2 ---1 ----- ---- ---- -  00100
   9 Anno  sen  -1 ---1--- ---------- 2----- 23-2 1-2--- ---- -------- ----- ---- ----- ---- ---1 -  001100
  15 Bauh  pet  -- ------- -----11-2- 2--3-3 3-22 ------ ---- -------- ----- ---- ----- ---- ---- -  001100
  36 Comb  api  -1 ---1--- ------1--- ---3-3 ---- ------ ---- -------- ----- ---- ----- ---- ---1 -  001100
  40 Comb  zey  -- ------- ---------- -----2 22-2 2----- ---- -------- ----- ---- 1---- ---- ---- -  001100
  47 Dich  cin  -- ------- ------1--- ---2-- 1--2 ---2-- ---- -------- ----- ---- ----- ---- ---- -  001100
  91 Pter  rot  -- ------- ---------- ---1-- -2-- --2--- ---- -------- ----- ---- ----- ---- ---- -  001100
  18 Brac  boe  -- ------- ------1--- ----12 1-2- -212-- ---- --2----- ----- ---1 ----- ---- ---- -  001101
  99 Stry  mad  -- -----1- ---11----- 2-12-3 ---- ------ ---- -2------ ----- ---- ----- ---- ---- -  00111
  33 Catu  obo  -- ------- --1------2 ------ ---- 2----- ---- -------- ----- ---- ----- ---- --1- 1  0100
  69 Lann  dis  -- 3121--- 21212-2-21 --111- -2-- -11--- 2--- 23-22--2 2--2- ---- ----- ---- ---- -  0100
 114 Xime  ame  -- --1--1- --1------2 ------ ---- -1---- ---- -2------ ----- ---- ----- ---- ---- -  0100
  45 Dalb  nit  -- -122-3- ----2----- -----2 1--- ------ 2222 -------- ----- -1-1 ----- 1--- ---- -  0101
  67 Julb  glo  -- ------- -12------2 -----3 1--- 2-1--3 ---- ----2--- ---2- 2331 ----- ---- ---- -  0101
  42 Cuss  arb  -- ------- ---------- -1---- 11-- ---2-- ---- -------- ----- 1--- -2--- ---- ---- -  0110
 108 Uapa  kir  -- ---2--2 ---------- ------ ---1 ------ ---- -------- ----- ---- 3---- ---- 11-- -  0111
 109 Uapa  nit  -- -2----- ---------- ------ 1--- ------ ---- -------- ----- ---- 2--1- ---- -1-- -  1000
  84 Peri  ang  -- ------- 1--11-1--- ------ 221- 312--- ---- --2-3--2 ----- ---1 ----- ---- 2233 -  1001
  21 Brac  lon  -- --21-2- 23222---1- -----2 -113 231332 --2- 33233333 23--- -2-- ----- ---- ---- -  101
  55 Eryt  liv  -- ------- ---------- ------ ---- --22-- ---- -22----- 2---- ---- ----- ---- ---- -  101
  38 Comb  mol  -- ------- ---------- ------ -1-- --12-- 3--- -2---2-2 ---3- --1- ----- ---- 1--- -  11000
  20 Brac  flo  -- ------- ---------- ------ ---- 1----1 ---- 2------- 33-2- ---- -2--- ---- ---- -  110010
  22 Brac  man  -- ------- ---------- --1--- ---- ------ ---- ----3--3 ----- ---- ----- ---- ---- -  110011
  26 Brac  uti  -- ------- --------33 ------ ---- ---3-- ---- -33-3223 --333 211- ----- ---- ---- -  110011
  23 Brac  mic  -- ------- ---------- ------ ---- ------ 3-33 -------- ----- ---- ----- ---- ---- -  110100
  25 Brac  tax  -- ------- ---------- ------ ---- ------ 33-- -------- 3222- ---- ----- ---- ---- -  110100
  66 Isob  ang  -- ------- ---------- ------ ---- ------ ---- -------- 32-2- ---- ----- ---- ---- -  110100
  68 Julb  pan  -- ------- ---------- ------ 2--- ------ --23 2--33323 333-3 ---- ----- ---- --1- -  110100
  73 Mono  afr  -- ------- --11------ ------ ---- ------ --32 3-2-2--- -23-- ---- -2--- ---- ---- -  110100
  96 Senn  pet  -- ------- ---------- ------ ---- ------ ---- 22------ ----- ---1 ----- ---- ---- -  110100
  77 Ochn  sch  -- 1--1--- ---------- ------ ---- ------ 2--- --2----3 -2--2 ---- ----- ---2 ---- -  110101
  59 Ficu  syc  -- ------- ---------- ------ ---- ------ ---- -------2 ----- -1-- ----- ---- ---- 2  11011
  57 Faur  roc  -- ------- ---------- ------ ---- ------ --2- ------2- -2-22 ---- -212- 2--2 ---- -  11100
  58 Faur  sal  -- ---1--- ---------- ------ ---- ------ -23- 2-2----- ----- ---- -2132 1--- --1- -  11100
   3 Agar  sal  -- ------- ---------- ------ ---- ------ ---- -------- ----- ---- ----- 3333 -22- 2  111010
  11 Anti  ven  -- ------- ---------- ------ ---- ------ ---- -------- ----- ---- ----- ---- --22 1  111010
  65 Haru  mad  -- ------- ---------- ------ ---- ------ ---- -------- ----- ---- ----- --1- ---3 -  111010
  89 Psyc  mah  -- ------- ---------- ------ ---- ------ ---- -------- ----- ---- ----- ---- --2- 3  111010
 103 Syzy  gui  -- ------- ---------- ------ ---- ------ ---- ---2---- ----2 ---- -2--- --1- -23- -  111010
 110 Uapa  san  -- ------- ---------- ------ ---- ------ ---- -------- -333- 1-1- 33333 --33 3333 1  111010
  71 Marg  dis  -- ------- ---------- ------ ---- 1----- ---- -------- ----- -21- ----- ---- -2-- 3  111011
  82 Pari  cur  -- ----1-- ---------- ------ ---- 12---- ---3 -------- -3--3 32-3 2311- 21-2 123- -  111011
  24 Brac  spi  -- ---2--- ---------- ------ 122- 223--- -23- 32-322-3 32323 3122 22-2- --23 3333 -  1111
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                   0000111 0000000011 011111 0001 00011  0011 00000000 11111      0000  1111 0001
Sub-community       1.1   1.21      1.22       2.11  2.12   2.2   3.11    3.121   3.122  3.2  4.111 4.112 4.12 4.2
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Region: S = Southern forest reserves (FRs), N = Northern FRs; c = CM FRs (South), cc = CM FRs (N), g = GM FRs (South), gg = GM FRs (North); Disturbance: C = Clear-felled, I = Intact, S = Single-tree harvesting, G = Grassland fires. See Appendix A for complete species names of 8-digit species codes in column 3. Level of presence: No number = none, 1 = 1-2, 2 = 3-5, 3 = >5 stems plot^{-1}. The boxed lines highlight species groupings (see text). The following 23 species that occurred with ≤3 occurrences in 1 to 3 sub-communities, with no pattern, were deleted from the body of the table: *Albizia versicolor*, *Allophylus africanus*, *Brackenridgea zanguebarica*, *Bridelia bridelifolia*, *B. micrantha*, *Craterispermum schweinfurthii Combretum collinum*, *Coptosperma neurophyllum*, *Dalbergia boehmii*, *D. melanoxylon*, *Ekebergia benguelensis*, *Erythrina abyssinica*, *Mangifera indica*, *Philenoptera bussei*, *Piliostigma thonningii*, *Psorospermum febrifugum*, *Rothmannia engleriana*, *Securidaca longepedunculata*, *Strychnos spinosa*, *Turraea nilotica, Vangueria infausta*, *Vernonia amygdalina* and *Vitex doniana.*

community. The species ranking demonstrates the abundance of each species. The curves, flatness, and steepness explain the species distribution (evenness or no evenness) in CM and GM sub-communities.

3. RESULTS

3.1 Tree species composition/pools across forest reserves

The 109 recorded tree species belong to 38 families, 87 species in GM FRs (Kaning'ina 58, Thambani 52), and 69 in CM FRs (Perekezi 45, Liwonde 43) (Appendix A). The largest families in this study (number of species between brackets) were Fabaceae (34, with 3 subfamilies, Caesalpinioideae (17), Papilionoideae (12), and Mimosoideae (5), Combretaceae (7), Rubiaceae (7) and Clusiaceae (4)). Twenty-seven families had only 1 species recorded each. Kaning'ina FR (GM) included 8 tree species that are associated with Afromontane evergreen forest (Appendix A). The 42 tree species recorded with ≤4 stems over all sampled plots, were considered as rare: 20 species in Kaning'ina (GM North) with 4 evergreen forest species; 9 species in Perekezi (CM North); 11 species in Thambani (GM South); and 12 species in Liwonde (CM South).

The Jaccard Similarity Index of the number of shared species between CM FRs (23 unique species in North and 16 in South) and GM (36 unique species in North and 25 in South) was lowest in the North (27.2% of 81 species) than in the South (39.7% of 68 species), and for the combination of North and South (45.0% of 109 species).

3.2. Classification of species associations

TWINSPAN grouped the sampled plots into 4 communities and 14 sub-communities based on similarity/dissimilarity of the number of stems of their species, up to level 5 sub-divisions. All species recorded on the 70 plots were included in the TWINSPAN table and subsequent analyses (IVIs and RIDCs), but 23 species with 3 or fewer occurrences over 1 to 3 sub-communities, with no clear pattern, were excluded to maintain the value of seeing the grouping, distribution, and abundance of species driving the sub-divisions, across the identified sub-divisions on 1 page.

The blocked outlines highlight the grouping of key species determining the sub-divisions (Table 1). The middle horizontal block shows a small group of species occurring across the 4 identified communities, linking the northern and southern groupings. Most species in Communities 1 and 2 (South) occur mainly in the upper left block (with further groupings between and within the 2 communities) while in Communities 3 and 4 (North) most species occur mainly in the lower right block (with further groupings between and within the 2 communities). The strength of each sub-division, and eventual sub-communities, is determined by 1 or more species present in most stands of a sub-division, becoming indicator species for the specific sub-communities, indicated only by codes shown in Figure 2. For example, *Diplorhynchus condylocarpon* occurs in most stands of Communities 1 & 2 (South) and *Brachystegia spiciformis* occurs in most stands in Communities 3 & 4 (North), except in 4.2, causing the first sub-division at level 1; *Pterocarpus angolensis* and *Dalbergia nitidula* are indicator species for 1.21GM, and *Terminalia sericea* (stronger) and *Pericopsis angolensis* (weaker) are indicator species for 1.22CM. The upper, right block shows very few to no stems of relevant species occurring in most stands in the upper, left block. Similarly, the lower, left block (not outlined) shows few to no stems of relevant species occurring in the lower, right block.

The dendrogram shows the sub-division of communities into sub-communities at 5 levels, together with the eigenvalue (all >0.37, indicating stability) and indicator species at each sub-division (where relevant) (Figure 3). Sub-communities 1.1 and 4.2, with 1 or 2 plots with very few

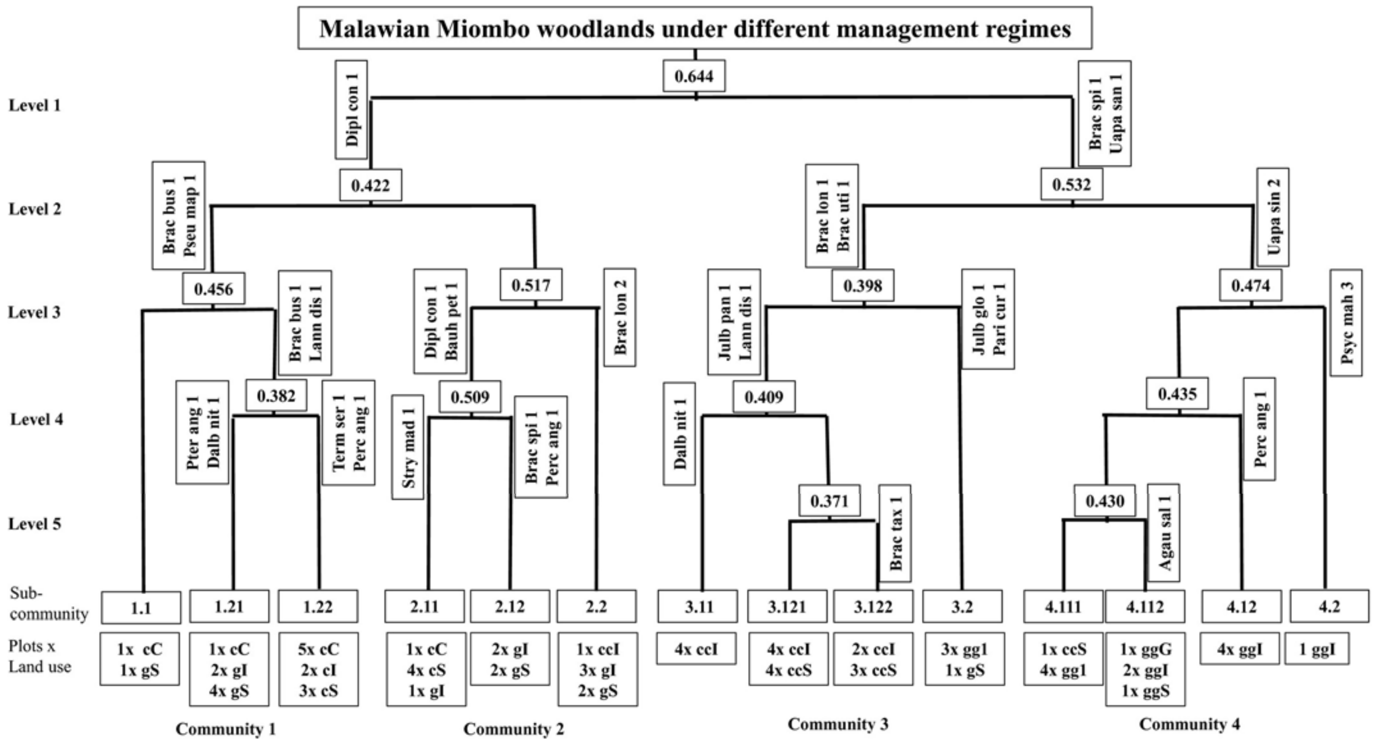

Figure 3. Dendrogram of the TWINSPAN sub-division to level 5 of plots (stands) sampled in 4 co-managed and government-managed forest reserves in Miombo woodlands in northern and southern regions of Malawi. Eigenvalue and number of plots involved are shown at each sub-division. Indicator species (maximum 2) are indicated for each branch of a division. Plot codes in boxes below sub-community names indicate the following: Co-management (c = plots in South, cc = plots in North); Government management (g = plots in South; gg = plots in North); Disturbance level is indicated as I = Intact, S = Selectively harvested, C = Clear-felled, G = Grassland fires. See Appendix A for the full names of species. Number at end of species code = level of presence by stem density of indicator species: 1 = 1–2 stems/plot, 2 = 3–5 stems/plot, and 3 = >5 stems/plot

stems, were regarded as outliers and excluded, but their species were present within the other 12 sub-communities (where their species were present). The species in these plots were included in the species pools and the Jaccard Similarity Index.

3.3. Tree species importance Values and their ranking across sub-communities

IVIs of the 109 tree species varied considerably across sub-communities with 26 species showing a total IVI ≥1.0 across the 12 sub-communities (Table 2a). Of the 83 species, 41 species have an IVI ≥2.0 in at least 1 sub-community (Table 2b), and 42 species have IVI ≤2.0 in any of the sub-communities where they were present (Table 2c). Four species had a total IVI ≥5: *B. spiciformis* (total IVI 8.7) showed IVIs of 5.6-26.3 in 9 sub-communities in CM and GM, mostly in the North. *B. longifolia* (total IVI 8.3) showed IVIs of 5.2-11.6 in 4 sub-communities of CM and GM, mostly in the South; *U. sansibarica* (total IVI 7.8) was absent from the South but showed high IVIs of 12.0-41.7 in 4 of the 5 sub-communities of presence in the North (3 GM). *B. utilis* (total IVI 5.6) showed IVIs of 6.6-16.6 in 2 sub-communities each in the South and North (CM and GM).

Several species showed a high IVI in 1 sub-community, with either medium to low IVI to absence in other sub-communities (Table 2a):

- Species with medium to high IVIs in CM and GM sub-communities are North and South: *Brachystegia longifolia*, *B. spiciformis,* and *B. utilis*; North: *Uapaca sansibarica*; South: *Bauhinia petersiana*, *Brachystegia boehmii*, *B. bussei*, *Julbernardia globiflora,* and *Pseudolachnostylis maprouneifolia*.
- Species with medium to high IVIs in CM sub-communities: North: *Brachystegia floribunda*, *B. manga*, *B. microphylla, B. taxifolia*, *Dalbergia nitidula*, *Isoberlinia angolensis*, *Julbernardia paniculata*, *Monotes africanus,* and *Syzygium guineense*; South:

Table 2: Importance Value Index (IVI, as %) of each tree species across the identified sub-communities belonging to government-managed (GM) and co-managed (CM) forest reserves. Species are arranged by total IVI values, in descending order (IVI ≥10 = high (indicated in bold), 5.0-9.9 = medium, 2.0-4.9 = low, 0.1-1.99 = very low).

Species code (See Appendix A for full names)	Sub-communities												
	1.21 GM	1.22 CM	2.11 CM	2.12 GM	2.2 GM	3.11 CM	3.121 CM	3.122 CM	3.2 GM	4.111 GM	4.112 GM	4.12 GM	Total IVI
(a) Species with total IVI of ≥1.0 across all sub-communities													
Brac spi	2.7	-	-	5.8	9.1	5.6	1.3	**12.7**	**16.2**	8.2	8.3	**26.3**	8.7
Brac lon	5.2	8.6	4.8	**11.6**	2.5	2.4	2.3	3.7	5.2	-	-	-	8.3
Uapa san	-	-	-	-	-	-	-	**12.0**	3.9	**41.7**	**27.1**	**16.5**	7.8
Brac uti	-	6.6	-	-	9.5	-	**16.6**	1.2	7.4	-	-	-	5.6
Brac bus	**34.6**	2.2	7.7	-	-	-	-	-	-	-	-	-	4.6
Julb pan	-	-	-	2.7	-	5.1	1.6	**15.8**	-	-	-	1.8	4.1
Brac mic	-	-	-	-	-	**41.1**	-	-	-	-	-	-	3.9
Pari cur	0.8	-	-	-	2.6	2.9	-	3.4	**11.6**	1.7	6.2	5.3	2.9
Peri ang	-	2.4	-	7.1	6.3	-	2.8	-	1.9	-	-	1.3	2.6
Julb glo	-	5.3	3.7	2.0	5.5	-	0.9	1.0	2.3	-	-	-	2.5
Lann dis	4.2	5.0	3.8	1.5	1.8	2.2	4.5	2.0	-	-	-	-	2.5
Pseu map	8.0	8.8	-	2.8	2.5	-	1.4	-	1.4	-	-	-	2.2
Dipl con	5.1	4.4	1.2	6.4	1.5	-	-	-	-	-	-	-	2.0
Brac tax	-	-	-	-	-	**14.5**	-	6.2	-	-	-	-	1.9
Faur sal	0.8	-	-	-	-	3.8	1.6	-	-	**14.4**	1.6	1.9	1.8
Brac boe	-	0.5	7.8	5.3	5.4	-	1.5	-	2.7	-	-	-	1.7
Mono afr	-	1.4	-	-	-	6.5	3.4	3.7	-	2.0	-	-	1.7
Pter ang	6.4	0.5	1.2	6.9	3.5	-	-	1.4	1.3	-	-	-	1.6
Agar sal	-	-	-	-	-	-	-	-	-	-	**19.1**	5.3	1.5
Brac flo	-	-	-	-	2.3	-	0.9	9.0	-	2.9	-	-	1.5
Eryt liv	-	-	-	-	5.5	-	3.2	3.7	-	-	-	-	1.4
Dalb nit	4.5	1.2	1.4	1.0	-	6.7	-	-	2.6	-	1.5	-	1.2
Brac man	-	-	2.2	-	-	-	6.4	-	-	-	-	-	1.2
Bauh pet	-	1.9	7.8	5.3	-	-	-	-	-	-	-	-	1.0
Comb mol	-	-	-	0.9	1.9	2.3	2.2	1.6	1.3	-	-	1.2	1.0
Faur roc	-	-	-	-	-	1.7	0.8	3.4	-	4.5	3.9	-	1.0

(b) Species (41) with total IVI <1.0, but with IVI ≥2.0 in at least one sub-community, indicated with IVI value and in which sub-community (between brackets): Albi ant 2.2 (3.11 CM), Albi ver 2.2 (2.11 CM), Allo afr 2.3 (2.2 GM), Anno sen 2.0 (2.2 GM), 6.7 (2.12 GM), Anti ven 2.5 (4.12 GM), Aphl the 3.6 (4.112 GM), Brac zan 2.2 (4.12 GM), Brid bri 3.0 (3.2 GM), Brid cat 2.6 (1.22 CM), Burk afr 2.4 (1.21 GM), 3.6 (2.12 GM), Burt nya 3.3 (1.21 GM), Comb api 9.3 (2.11 CM), Comb col 2.2 (2.12 GM), Comb zey 6.3 (2.12 GM), Copt neu 2.5 (1.21 GM), Cuss arb 2.0 (2.12 GM), Dalb nya 2.7 (1.21 GM), 2.9 (2.11 CM), 4.3 (1.22 CM), Dich cin 2.7 (2.12 GM), Dios kir 6.8 (1.22 CM), Dios zom 2.9 (3.2 GM), Garc sme **12.6** (4.112 GM), Garc buc 2.1 (3.2 GM), Isob ang 5.4 (3.122 CM), Mang ind 3.4, (3.2 GM), Marg dis 3.7 (3.2 GM), Mund ser 2.0 (1.21 GM), Ochna sch 2.5 (3.122 CM), Olax obt 3.3 (1.22 CM), Pedd afr 3.8 (4.112 GM), Phil bus 3.2 (2.11 CM), Pili tho 2.0 (2.2 GM), Pter rot 2.5 (2.12 GM), Roth eng 2.1 (3.2 GM), Sene gal 6.8 (2.11 CM), Stry mad 9.1 (2.11 CM), Syzy cor 2.6 (4.12 GM), 2.6 (3.121 GM), Syzy gui 5.0 (4.12 GM), Term ser 2.8 (3.2 GM), 5.2 (1.22 CM), Turr nil 2.8 (2.11 CM), Uapa kir 2.0 (1.21 GM), 2.1 (4.111 GM). 2.9 (4.12 GM), Uapa nit 4.2 (4.111 GM)

(c) Species (42) with total IVI <1.0, and all IVI values <2.0 in all sub-communities were present: Anis nat, Apod dim, Azan gar, Brid mic, Catu obo, Comb ade, Comb mos, Crat sc, Dalb boe, Dalb mel, Domb rot, Ekeb ben, Eryt aby, Eryt ema, Euca ter, Ficu syc, Flac ind, Frie obo, Garc hui, Gymn bux, Haru mad, Mult cra, Neob afr, Ormo kir, Ozor ins, Prot pet, Psor feb, Psyc mah, Rapa mel, Secu lon, Senn pet, Steg ara, Sten kun, Stry spi, Swar mad, Vach amy, Vang inf, Vern amy, Vite don, Xime ame, Zahn afr and Zizi muc.

Combretum apiculatum, *Diospyros kirkii*, *Lannea discolor*, *Senegalia galpinii*, *Strychnos madagascariensis,* and *Terminalia sericea*.

- Species with medium to high IVIs in GM sub-communities: North: *Agarista salicifolia*, *Faurea saligna,* and *Parinari curatellifolia*; South: *Annona senegalensis*, *Combretum zeyheri*, *Diplorhynchus condylocarpon*, *Erythrina livingstoniana*, *Garcinia smeathiana*, *Pericopsis angolensis,* and *Pterocarpus angolensis.*

The RIDCs show a sharp decline in relative importance up to ranks 2 to 3 (depending on sub-community) while a more gradual decline is observed for ranks 8 to 12, and then a levelling out with many species with very low relative importance. The table inserted within each Community shows the species ranked 1 to 3 in each sub-community, the relationship between IVI value (in the graph), stem number, and mean stem diameter (calculated from total basal area of all stems) (Figure 4).

3.4. Tree species diversity

RIDCs show a similar pattern with inverted J-shaped species distributions for all sub-communities with relatively flatter curves with high species richness and evenness in CM and GM sub-communities. Most CM and GM sub-communities have 28-34 species with high evenness (shorter distance between 2 adjacent species). In the South, sub-communities showed high species richness and evenness. In communities 3 and 4 (North), the lowest species richness occurs in 3.11CM and 4.111GM (each 15 species) and 4.112GM (18 species) with low evenness showing a strong decline (steep curve means 1 species is more dominant than others) from species rank 1 to 6. The dots represent species.

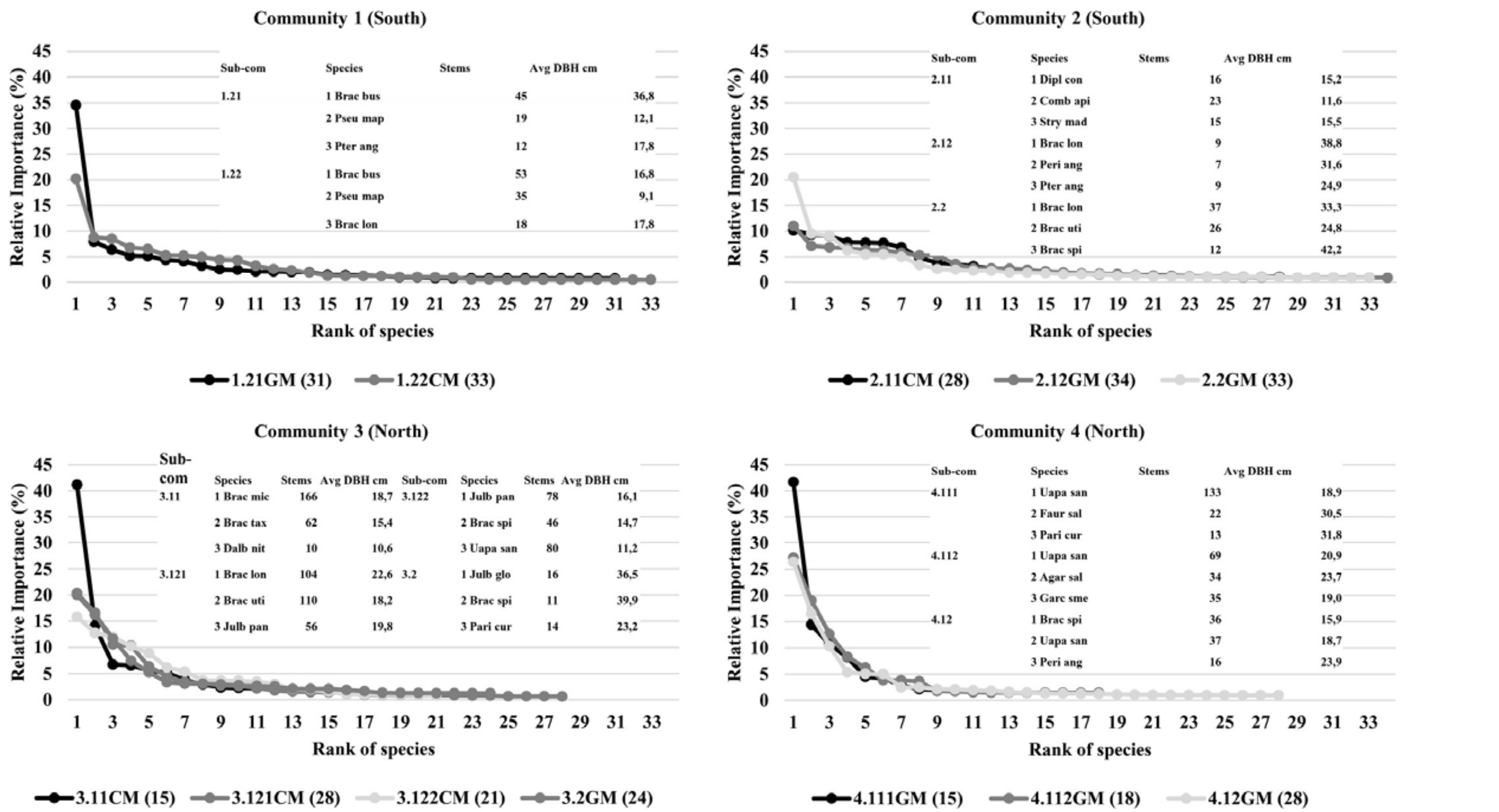

Figure 4. Rank importance distribution curves (RIDCs) for tree species within each sub-community of each community, allowing comparisons between co-managed (CM) and government-managed (GM) forest reserves with Miombo woodland, Malawi. The table inside each community diagram shows the top-ranked 3 species, with the number of stems and mean DBH for the selected tree species in each sub-community. The number of species in each sub-community is shown in legend after the name of each sub-community

4. DISCUSSION

4.1. Tree species composition/pools across forest reserves

The 109 recorded tree species varied in presence and abundance within each FR. Sharing of species was low (27.2% of 81 species) between Kaning'ina (GM) and Perekezi (CM) in the North, but relatively higher (39.7% of 68 species) between Thambani (GM) and Liwonde (CM), in the South. The study is in line with the observation by Nyirenda et al (2019) who reported low tree species similarity between GM FR's and communal Malawian Miombo woodland. GM FRs, North, and South had more non-shared species than CM FRs. Differences in species pools between FRs are attributed to differences in annual rainfall and landscape physiography. Sampling in Kaning'ina covered the eastern (moister) side of the ridge and at Perekezi the western (drier) side of the ridge. Topographical features in sampled parts differed between Thambani and Liwonde (section 2.1; Figure 1). Differentiation between dry and wet Miombo is based on annual rainfall (Frost et al., 2003) and anthropogenic disturbances. Therefore, the presence of several Afromontane evergreen forest tree species in Kaning'ina FR (Appendix A) may be attributed to higher rainfall, cooler slopes, and lower human disturbances (most plots were relatively intact, Table 1, Figure 3). Wooded grassland developing into the evergreen forest via woodland due to the protection of timber and fruit plantations against fire has been observed in South Africa (Geldenhuys & Venter, 2002). However, resource use may have contributed to lower species pools in CM FRs than in GM FRs (North and South) (Figure 2).

The high numbers of Fabaceae species, 30 (27.5%) in CM and 25 (22.9%) in GM are dominated by subfamilies Caesalpinioideae and Papilionoideae (Palgrave, 2002; Van Wyk et al., 2011; Burrows et al., 2018), dominating broad-leaved Miombo and Undifferentiated woodlands, with subfamily Mimosoideae dominating fine-leaved woodlands, an indication of their adaptive potential in the area. The listed 9 *Brachystegia* species, 2 *Julbernardia* species, and *Isoberlinia angolensis* are diagnostic species of Miombo woodland (White, 1983).

The 42 tree species recorded with ≤4 stems over all sampled plots (Appendix A) are not all rare or threatened. Individual species could be naturally rare, or have been over-utilised, under-sampled, or maybe sporadically present outside their natural habitat, or are becoming established because of changed conditions. Each species with low abundance need to be assessed to identify the truly rare species and which of those are threatened by uncontrolled use.

4.2. Classification of species associations

The sampled stands of tree species under different environmental factors and land use disturbances, grouped into species associations, with sub-divisions showing eigenvalues ≥0.3 in management regimes (Figure 3). This suggests that species associations of the sub-communities are ecologically important and stable (Hill, 1979). The observation confirms the findings of earlier studies that Miombo is a resilient and stable woodland ecosystem (Syampungani et al., 2016; Gonçalves et al., 2017). Indicator species of identified sub-communities (Figure 3) support field observations that one or more species are dominating each stand, despite utilisation intensity.

Level 1 and 2 sub-divisions, separating stands into Communities 1 and 2 (South) and Communities 3 and 4 (North) are attributed to different species pools associated with differences in rainfall and landscape physiography (section 4.1). Such variables, though not considered in the design of the study, may override the influence of the 2 management regimes. In the South, each community contains stands from both Liwonde (CM) and Thambani (GM). In the North, Community 3 included 17 CM and 4 GM stands, and Community 4 included 13 GM stands and one CM stand. The little overlap and differences in species composition between FRs at the community level (Table 1) may be attributed to site differences (Munishi et al., 2011). This suggests that the species pool and site variation need to be considered in assessing the impact of management regimes in the Miombo.

The first management-based sub-division was in the North at level 3 (Figure 2), with Community 3 separating into 3.1CM (with indicators *J. paniculata* and *L. discolor*) and 3.2GM (with indicators *J. globiflora* and *P. curatellifolia*). The abundant presence of the latter 2 species related to good regeneration after clear-felling Miombo, withstands in recovery stages after former intensive utilisation, like higher densities of *Brachystegia* species in 3.11CM, 3.121CM and 3.122CM (Table 1).

In the South, the first management-based sub-division was at level 4 (Figure 3), splitting into 1.21GM (indicators *Pterocarpus angolensis* and *D. nitidula*) and 1.22CM (indicators *T. sericea* and *Pericopsis angolensis*). The 4 species are used for timber and poles, but they all regenerate well after woodland clearing. Their higher abundance in some GM stands could relate to resource use disturbances before gazettement. Currently, canopy closure may impede their regeneration (Chichinye et al., 2019) as these are light-demanding species. Sub-community 2.1 sub-divided into 2.11CM (indicator species *Swartzia madagascariensis*) and 2.12GM (indicator species *Brachystegia spiciformis* and *Pericopsis angolensis*). The 3 indicator species show relatively low abundances.

Community 4 sub-divided at level 3 into 4.1GM (abundant *U. sansibarica*) and 4.2GM (with several evergreen forest species). The frequent high abundance of *U. sansibarica* in 4.1 sub-communities suggests young to intermediate regrowth after historical heavy resource use (Chidumayo, 1997; Lowore, 1999). Pure and mixed stands of *U. sansibarica* occurred in former abandoned cultivated and settlement areas, as evidenced by old ridging, and cemeteries. Field observations indicated that *U. sansibarica* regenerates from seed in small gaps, thus supporting observations at Dedza, Malawi, of its high stump mortality (Lowore, 1999). The presence of several evergreen forest species was discussed in section 4.1. Typical Miombo species are evenly distributed in Community 4, such as *Pericopsis angolensis* dominant in 4.12GM, and *B. spiciformis* across all sub-communities.

Most species in southern stands (CM and GM FRs) show no to a limited presence in the North (CM and GM FRs), and the same applies to species in the North (Table 1). For example, *Brachystegia boehmii* and *B. bussei* are limited to the South, *B. floribunda, B. manga, B. microphylla, B. spiciformis, B. taxifolia, B. utilis, Isoberlinia angolensis*, and *J. paniculata* are limited to the North, and *B. longifolia* and *J. globiflora* occur in South and North. The distribution patterns suggest that each species has specific ecological requirements, and their presence or absence may not relate to specific resource use impacts. No information on-site variables were collected, which could have helped to identify the site requirements of different species. This is because the dominance of *Brachystegia* species mixtures with *Julbernardia* and/or *Isoberlinia* species and other associated species depend on, site conditions (White, 1983; Chidumayo, 2013; Lupala et al., 2015).

4.3. Tree species importance values and their ranking across sub-communities

Variation in IVIs (Table 2) needs to be interpreted using the frequency, abundance, and tree size (calculated as basal area) of species across sub-communities (Table 1). This is demonstrated in stem number and mean stem DBH for species ranked 1 to 3 with RIDCs (Figure 4). Species vary in their importance in different stands; Figure 4 lists 20 species that were ranked in the top 3 important species across the 12 sub-communities. Each species IVI needs a more detailed assessment to know whether the frequency of occurrence using Table 1, stem density, and/or tree size contribute to its impact in the stand. A high stem density of smaller stems can cause higher intra-specific competition and exclusion of other species. Many large trees may affect light conditions in the understory. For example, many *B. bussei* stems (36.8 cm mean DBH) dominate 1.21GM, with fewer, smaller stems for species ranked 2 & 3. Few, small stems (11.5-15.5 cm mean DBH) of *D. condylocarpon, C. apiculatum,* and *S. madagascariensis* dominate 2.11CM, but 2.12GM and 2.2GM have large trees but they differ in stem number. Different *Brachystegia* and *Julbernardia* species mostly dominate Community 3 sub-communities, but the 3 CM sub-communities have smaller stems at high density, and the GM sub-community has a lower density of large trees. *U. sansibarica* has mostly small stems (<20 cm DBH) in 4.1GM sub-communities, with high stem numbers in 4.111GM (few larger stems of *Faurea saligna* and *P. curatellifolia*). Individual species may be associated with differences in site conditions (not studied), or strong sprouting response after cutting or stages of recovery after different intensities of disturbance (Geldenhuys, 2010). The higher density and ecological importance of several species in CM and GM sub-communities relate to stages of woodland recovery after historical and recent resource use (Geldenhuys, 2014; McNicol et al., 2015).

4.6 Tree species diversity

The RIDCs relatively inverted J-shaped and flatter curves (CM, GM, South), and the more inverted J-shaped (CM and GM) (North) (Figure 4) show patterns in many natural multi-species communities. Some sub-communities, CM, and GM (South, North) show high species richness and evenness with 1-3 ranked species showing relatively high abundance (Figure 4). These results are associated with early woodland recovery (section 4.3) following disturbances (Figure 2).

Mostly illegal activities have created a conducive environment for the proliferation of many species. In the North, the RIDCs with steep inverted J-shapes and 1 to 6 ranked tree species in 3.11CM, 4.111GM, and 4.112GM, showed high abundance and dominance; indicating low species richness and evenness. This pattern is common in mature woodlands suggesting low disturbances (Figure 4). With most canopy species being intolerant of shade, only the faster-growing trees will remain in the canopy, and stems of other species become suppressed or die, and species become dormant. Many species would regenerate with the clearing of the stand with good light conditions. Group-felling as with slash-and-burn traditional cropping systems and charcoal production would stimulate abundant and diverse species regeneration (Figure 2c) as also shown by Syampungani et al. (2016) and Chichinye et al. (2019).

5. CONCLUSIONS

The differentiation of tree species associations based on the distribution, abundance, and diversity of their species was influenced by available species, site factors, and recovery from resource use impacts under the 2 studied management regimes. Species similarity between management regimes was low. Additionally, species varied in importance in the identified communities and sub-communities. Site differences influenced the variation in the composition of the identified communities and sub-communities. Impacts of co-management and government-management are important at levels at which resource users operate to harvest timber, poles, firewood, and charcoal, and cultivate crops. Species importance ranking emphasised that few important species differed between co-managed and government-managed sub-communities. However, *Brachystegia* and *Julbernardia* species were dominant across CM and GM sub-communities while *Uapaca sansibarica* dominated in the government-management regime. The high species diversity in most sub-communities are associated with disturbances. The information suggested that regeneration after historical and current intensive resource use facilitated the recovery of the harvested tree species. Miombo resilience and stability in disturbed and undisturbed areas could form the basis for combining the continued flow of products and services with maintaining tree species communities.

Information obtained emphasises the need for appropriate disturbances, rather than protection, to maintain tree species diversity while recovering under resource use. This requires a policy review to improve resource use management. Regeneration of most Miombo canopy species targeted for resource use needs some disturbance. This requires a management system that provides for group-felling of mature stands to stimulate regeneration with better light conditions, and selective thinning of suppressed, damaged and deformed stems in stand development stages. Such a system will maintain species diversity, productive woodland recovery, and sustainable production of poles and timber of different dimensions. This also needs monitoring of harvesting impacts.

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CONFLICT OF INTEREST

The authors declare that they have no financial or personal relationships which may have inappropriately influenced them in authoring this article.

AUTHORS' CONTRIBUTIONS

M. F. K. Gondwe is a PhD student (University of Pretoria) responsible for research design, data collection, analysis, interpretation and wrote the manuscript.

C. J. Geldenhuys contributed to data collection, guided the analysis and interpretation, and reviewed the manuscript.

P. W. C. Chirwa and M. A. Cho contributed to the research conception, design and reviewed the manuscript.

E. S. P. Assédé contributed to perfecting the methodology, data analysis and reviewed the manuscript.

S. Syampungani contributed to drafting the manuscript and critically revised it.

DATA AVAILABILITY STATEMENT: Data is available within the article and/or its supplementary materials.

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