

Fine-scale habitats influence tree species assemblage in a miombo forest

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Abstract

Aims

Relationships between local habitat heterogeneity and tree communities in miombo woodlands have been very little studied. While some studies have addressed this topic at broad scales and based on few environmental parameters, this study aims at (i) detecting fine-scale habitats (≤ 10 ha) on the basis of a detailed characterisation of soil explicitly considering past anthropogenic disturbances, and an exhaustive census of the tree community, and at (ii) searching for indicator tree species corresponding to the resulting habitats.

Methods

The study was carried out in the miombo woodland of Mikembo Forest Reserve, Upper Katanga, The Democratic Republic of the Congo. A complete census of the tree community was conducted in a 10-ha forest dynamics plot comprising 160 adjacent quadrats of 25 × 25 m, with a total of 4604 trees (diameter at breast height > 10 cm). Thirty-six physicochemical soil parameters were measured. Studying the frequency distribution of soil charcoal content allowed identifying local signature of past human agriculture in the soil. Two strategies were used to define habitats: (i) a combination of principal component analysis (PCA) on soil variables and Ward clustering and (ii) multivariate regression trees (MRT) to search for key soil parameters allowing the best prediction of species composition. Tree-habitat associations were tested by means of a robust statistical framework combining the IndVal index and torus randomisations.

Important Findings

The forest contained 82 tree species and a significant proportion of wet miombo species (e.g. *Marquesia macroura*). We detected

a strong east–west edaphic gradient driven by soil texture; most chemical soil parameters followed this pattern. Five habitats were identified based on soil factors and floristic composition. Nine indicator species of these habitats were found. The key soil factors discriminating habitats were total calcium, available forms of phosphorus and clay content. Even though past agricultural practices were successfully detected in soils, they did not display any significant influence neither on habitat differentiation nor on the associated tree communities. Based on an unprecedented large number of soil parameters, fine-scale soil heterogeneity and niche partitioning were shown to contribute to the variability of the floristic composition in this forest. Our results indicated that considering the most variable environmental parameters, as in PCA, is a poor manner for defining habitats. In contrast, combining MRT with the IndVal index and torus randomisation has proved to be a much more robust and sensitive approach to highlight tree-habitat associations at this scale. The common dichotomous viewpoint of considering deterministic and neutral effects as acting at broad and fine scales, respectively, is not confirmed when measuring suitable environmental variables, even in a case where the physical environment does not exhibit strong heterogeneity.

Keywords: forest dynamics plot, indicator species, miombo, multivariate regression trees (MRT), soil, torus randomisation

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INTRODUCTION

Understanding the mechanisms structuring tree species distribution in tropical forests is a challenging issue in community ecology (Legendre et al. 2009; de Oliveira et al. 2014; Vleminckx et al. 2015). On one hand, niche differentiation allows, to a certain extent, to predict the species composition of a given community on the basis of measurable environmental parameters (Legendre and Legendre 2012). On the other hand, neutral processes (dispersion limitation, ecological drift) also influence continually the community in an unpredictable manner (Hubbell 2005; Nguyen et al. 2016). The current consensus among ecologists is that both deterministic and neutral processes act together to shape living communities (Chase 2014; Velázquez et al. 2015). So far, deterministic processes acting on tree communities have been associated to broad scales, related to large environmental gradients, while neutral processes are often considered as a matter of fine scales presenting relative homogeneity of edaphic or climatic parameters (Borcard et al. 2011). Although an influence of deterministic processes is deemed able to occur at fine scales in some cases (Legendre and Legendre 2012), such fine-scale environmental heterogeneity influence on tree species community has not been thoroughly investigated.

Miombo woodlands are the most common savanna type in the southern hemisphere, covering ca. 2.7 million km² (i.e. 10% of the African continent; Millington et al. 1994). The miombo is a semi-deciduous formation, with a tree layer characterized by the abundance of three genera of Fabaceae (subfamily Caesalpinioideae): *Brachystegia*, *Julbernardia* and *Isobertinia* (Campbell 1996; White 1983). The miombo plays an important role in the regulation of regional climate (Malmer and Nyberg 2008), carbon sequestration (Williams et al. 2007; Zahabu 2008) and the conservation of soil and water resources. These forests, although they occupy a larger area than tropical African rainforest (Campbell 1996), have received comparatively little attention and the deterministic processes influencing their woody species distribution remain mainly unknown.

Forest dynamics plots are essential tools to monitor forest composition and dynamics and to unravel the mechanisms promoting biodiversity and the coexistence of species (e.g. habitat heterogeneity, historical events), and design management strategies (Legendre et al. 2009). The structure and dynamics of miombo woodlands have received much attention in the Zambezian region (Campbell et al. 2007). However, this miombo is extremely variable in terms of floristic composition and comprises regions of dry and wet miombo (Backéus et al. 2006; Chidumayo 1987; Kanschik and Becker 2001). The structure and functioning of the wet miombo has been relatively little studied in comparison with the dry miombo. In order to fill that gap of knowledge, the first 10-ha forest dynamics plot was installed in 2009 in Upper Katanga (DRC) in order to monitor growth and dynamics of the tree community. Earlier work on the miombo revealed extensive

variation in floristic composition at the landscape scale, in part accounted for by variation in soil factors (Duvigneaud 1958; Munishi et al. 2011; Mwakalukwa et al. 2014; Schmitz 1971; Sys and Schmitz 1959). Duvigneaud (1958) explored soil–vegetation relationships in the miombo with the methods of geobotany using topo-lithological transects and proposed a system of ecological groups of indicator species in relation to soil drainage, depth and texture. He recognized four main types of miombo forests (i.e. plateau miombo in deep soil with *Brachystegia longifolia*, *Brachystegia spiciformis*, *Erythrophleum africanum*, miombo on slopes with compact gravelly yellow soil, with *Brachystegia utilis*, miombo on shallow rocky soil with *Brachystegia microphylla* and *Brachystegia bussei*, miombo on poorly drained lateritic crust, with *Isobertinia tomentosa* and *Brachystegia stipulata*). Based on the methods of Zürich–Montpellier, Schmitz (1971) published a phytosociological survey recognising three alliances (i.e. Berlinio–Marquesion (semi-evergreen miombo), Mesobrachystegion (mesic, usually deep soil) and Xerobrachystegion (shallow, dry stony soil)).

Until now, no study using modern statistical methods has investigated soil–vegetation relationships in the miombo of Katanga. Specifically, we investigate the existence of indicator tree species and species assemblages characterising habitats resulting from fine-scale soil heterogeneity. Since several studies highlighted the long-lasting influence of human activities on vegetation distribution patterns (Van Gemerden et al. 2003; Vleminckx et al. 2014), we also explicitly consider the effect of past human agricultural activities as potential driver of habitat and tree community differentiation. Detecting precise relationships between species and their habitat preferences allows establishing precise locations for species plantations (Dray et al. 2012). In addition, the detection of indicator species has been shown to be a requisite tool in the field of nature monitoring, conservation and management and is a more robust method of assessing ecologically meaningful habitats than the use of diversity indices (Dufrene and Legendre 1997). So far, the reported species assemblage observations have generally been studied at large scales in frameworks implicitly acknowledging miombo forests as relatively large homogeneous units (Campbell 1996; White 1983). Therefore, we addressed the following specific questions: (i) Is soil heterogeneity at fine scale (<10 ha) sufficient to characterize different habitats? (ii) Can we define species assemblages related to these fine-scale habitats? (iii) Are some tree species indicators of the defined habitats? (iv) Did past agricultural activities influence the soil parameters and the forest species composition?

MATERIAL AND METHODS

Study site

The study was undertaken in the Mikembo Forest Reserve (11°28'57" to 11°29'5"S, 27°40'12" to 27°40'28"E, ~1200 m above sea level), an 800-ha private nature protection area located in Upper Katanga, about 35 km northeast of

Lubumbashi, the Democratic Republic of the Congo (Fig. 1). The mean annual temperature is 20.3°C, and the average annual precipitation is 1200 mm, occurring mainly from November to March or April. The climate is Sudanian, corresponding to Cwa in Köppen's classification (Peel *et al.* 2007). Upper Katanga, also referred to as southern Katanga, represents the northern part of the Zambezi centre of endemism (Malaisse 1996; White 1983). The eastern part of Upper Katanga belongs in the Katango–Zambian sector (Duvigneaud 1958; Malaisse 1996; Werger and Coetzee 1978). The landscape showed a flat topography, but regularly punctuated (~3/ha) by termite mounds (up to 8 m high). The forest is located on geological substrates dominated by dolomitic shales and siltstones from Neoproterozoic Nguba and Roan Groups (Batumike *et al.* 2006). Soils of this region are mostly haplic and xanthic Ferralsols characterized by low pH and nutrient content and a sandy loam to clay loam texture (Baert *et al.* 2009). The vegetation is a mixed tropical dry season woodland with a mean canopy height of 14 m and basal area of ~20 m² ha⁻¹. The reserve was established in 2003, and since then, it has been protected from fire practices and fuel-wood cutting.

Inventory design

In 2009, a forest dynamics plot of 10 ha (200 × 500 m) divided into 160 quadrats of 25 × 25 m was installed (Fig. 1). The area was systematically inventoried for all living and dead trees ≥10 cm diameter at 130 cm (diameter at breast height, DBH) following Picard and Gourlet-Fleury (2008). Trees were tagged, mapped, identified to the species level and measured for DBH in 2014. Heights of the 25 largest trees were measured using a clinometer (Suunto Co., Finland) to achieve 100 trees measured per ha as recommended by Rondeux (1993). Family (Angiosperm Phylogeny Group 2009), genus and species were determined for all trees in the experimental plot following Meerts (2016). Thirty tree termite mounds were present in the dynamic plot but were not considered in this study (neither their tree community nor their soil parameters) due to their completely distinct floristic assemblage and ecological conditions. The identification of tree species was completed using Flora Zambeziaca and the Flore d'Afrique Centrale.

Soil sampling and analyses

Soil sampling was performed in 102 randomly chosen quadrats of the 160 of the dynamic forest plot (Fig. 1), with the constraint of selecting quadrats comprising no termite mound. In each of these quadrats, five soil cores were collected (four at 5 m from the corners, one in the centre) at 0–20 cm depth. A total of 36 soil variables were determined on these samples according to conventional protocols (Pansu and Gautheyrou 2006). For each soil sample, the stoniness index (SI) was estimated on the field after sieving (2-mm mesh) by a discreet quantitative index taking the values of 0 (no gravels), 1 (half of the sieve area or less covered by gravels) or 2 (all the sieve area covered). Undisturbed soil cores were taken for bulk density measurements (cylinder method). Soil texture (clay, silt and sand) was determined by wet sieving and the pipette method after organic matter (OM) destruction with H₂O₂ and clay dispersion by Na citrate. The pH-H₂O and the electrical conductivity were respectively measured with glass electrodes (Mettler-Toledo) and a conductimeter (VWR EC300) on a 1:5 soil:deionized water suspension. The pH-KCl and exchangeable Al (Al_{exch}) were determined on a soil suspension (1:5 ratio) of 1 M KCl and measuring the derivative of the titration curves for Al_{exch} (Radiometer Copenhagen TIM900). The ΔpH was obtained by calculating the difference between pH-KCl and pH-H₂O. The plant-available elements ((Ca, Mg, K, Al, Fe, Mn, B and Zn)_{avail}) were extracted with 0.5 M ammonium acetate 0.03 M EDTA at pH 4.65 and measured by inductively coupled plasma optical emission spectroscopy (ICP-OES) with CCD detector (Varian, Vista MPX). Bioavailable phosphorus (P_{Olsen}) was extracted with Na bicarbonate and determined by colorimetry, a second form (P_{EDTA}) was extracted with ammonium acetate EDTA and measured by ICP-OES. Total forms of elements ((Ca, Mg, K, Al, Fe, Mn, B, Mo, P and Zn)_{tot}) were taken in solution by complete dissolution of finely ground soil samples by a tri-acid attack (HCl–HNO₃–HF) in Teflon vials on a hot plate. The dry residue was re-dissolved in HNO₃ and total element concentrations were determined by ICP-OES. The effective cation exchange capacity (CEC) was calculated as the sum of exchangeable Ca, K, Mg concentrations and titrated Al (Al_{exch}), expressed in cmol_c kg⁻¹. The Al saturation

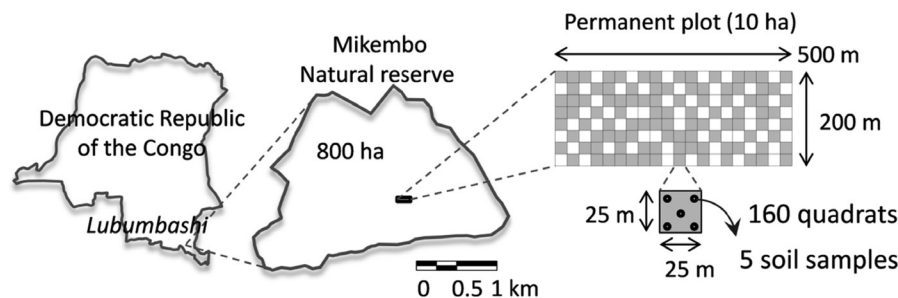


Figure 1: location of the study site at the Mikembo Reserve (Upper Katanga, DRC), schematic representation of the dynamic permanent plot and of a sampled quadrat. Sampled quadrats are in grey, soil samples location are filled circles.

rate (*Al-Sat*) of the exchange complex corresponds to the proportion of Al^{3+} on the total *CEC*. The soil carbon-to-nitrogen ratio (*C/N*) was computed after measuring soil nitrogen and carbon contents by flash combustion at 1350°C in a CN elemental analyser (Dumas method, ISO 10694). *OM* content was calculated by mass loss of a sample after dry ashing at 550°C. The extinction coefficient in visible light (*E4/E6*) allows to know the relative importance of humic and fulvic acids in the soil *OM* and is related to the humification stage. This coefficient was obtained measuring the absorbance at 465 and 665 nm of a soil extract with 0.5 M NaOH during 16 h after centrifugation (10 000 rmd/min). The soil charcoal content was measured as a proxy for past agricultural activities. This parameter was determined by loss on ignition of 1 g of soil sample after a hot H_2O_2 pre-treatment destructing *OM* but preserving charcoals. At the eastern end of the forest dynamics plot, and for a few hundred metres to the east beyond this limit, the forest was subjected to slash and burn cultivation. In order to assess whether the soil charcoal content was a good proxy of past agricultural practices, we measured the charcoal content in 16 additional quadrats beyond the eastern limit of the plot, covering a supplementary area of 6 ha with attested human disturbance. The frequency distribution of the charcoal content values clearly indicated a bimodal distribution pattern, pointing to a trace of human influence beyond the value of 2% of charcoals (see online supplementary Appendix S1). Beyond this threshold, a double amount of charcoal does not necessary indicate a double human activity. Therefore, we generated a binary variable (*Man*) taking the value of 1 beyond 2% of charcoal content in the soil (significant past human activity) and taking the value 0 otherwise.

Data treatment and statistical analyses

Species abundance as well as basal area were determined in each quadrat. For each species, relative frequency (*RF*; absolute frequency divided by the additive frequency (the sum of all species' frequencies, where the absolute frequency is the number of quadrats where the species is present divided by the total number of quadrats)), relative density (*RD*; number of individuals of a species divided by the number of all individuals in all species) and relative basal area (*RBA*; total species basal area divided by the total tree basal area of the plot) were calculated. These three indices were used to calculate the importance value index (*IVI*) based on the following equation: $IVI = RF + RD + RBA$ (Cottam and Curtis 1956). Box-Cox transformations of the soil data were conducted before analyses in order to stabilize the variances and bring the variables closer to a normal distribution. We used ordinary kriging to make interpolation on the soil data and to build a map at 6.25 m resolution for each variable (model parameters not presented here). Then, the mean value of each variable was calculated for each quadrat. Relations among all measured soil variables were evaluated with Pearson correlation coefficients, and with the coefficient of intra-class correlation

for the relations between the *Man* qualitative variable and the quantitative soil parameters (see online supplementary Appendix S3).

The habitats were defined using two different methods. First, principal component analysis (PCA) was applied to the matrix of soil variables. The selection of the significant axes of the PCA was performed by comparing the distribution of the rank-ordered axes with a broken stick distribution and using the Kaiser–Guttman criterion (Borcard et al. 2011). A cluster analysis based on the site scores of the PCA was used to determine the main habitats within the inventory plot (Ward's method), following Borcard et al. (2011) for the optimal cutting tree criteria. This procedure defined habitats on the basis of the most variable soil parameters, independently of the tree community. This method is commonly used for summarizing environmental parameters into one or two axes in order to use them as synthetic explanatory variables (e.g. Moraes et al. 2016; Swaine 1996; Toledo et al. 2012).

A second strategy was used to discriminate habitats by means of multivariate regression trees (MRT; De'ath 2002). This was carried out in order to model species–environment relationships and to highlight species assemblages (Wang et al. 2016; Zhang et al. 2016). This approach forms clusters of quadrats by repeating a splitting procedure based on species composition. Each split is characterized by a threshold value of one environmental variable and is made in a way that minimizes the dissimilarity within the clusters (within-group sum of squares). Among the numerous possible trees, the retained solution is the one that maximizes the predictive power. Therefore, MRT analysis focuses on prediction, making it a useful and powerful tool for ecosystem management and conservation. The result of the analysis is a number of species assemblages to which habitats defined by the threshold values of the environmental variables selected during the splitting procedure correspond. In addition, MRT was shown to outperform the commonly used redundancy analysis and canonical correspondence analysis (RDA and CCA, respectively) for explaining and predicting species composition. Moreover, MRT needs no model assumptions (linear in RDA, unimodal in CCA) and is indifferent to monotonic transformations of environmental variables, which makes this method very robust (De'ath 2002).

The IndVal index was then used to compute indicator values of individual species within the habitats defined by the PCA and clustering, and by the MRT approaches (Dufrene and Legendre 1997; Duff et al. 2014). The significance of the indices was tested using a torus-randomisation approach (Chuyong et al. 2011; De Cáceres et al. 2010; Harms et al. 2001; Vleminckx et al. 2015) in order to correct for spatial autocorrelation. This procedure allowed removing species-habitat associations while maintaining the original abundance spatial patterns. It was repeated 4999 times to build a null distribution of IndVal index values. The observed IndVal index value was then considered significant when it was higher than 95% of the null values. Classical permutations were also run for method comparison. Torus randomisation and permutation

tests were performed for each species displaying a minimum of 10 occurrences.

Statistical analyses were conducted using the R statistical software (v. 3.2.2). Data transformations and ordinary kriging were completed using package ‘car’ (Fox *et al.* 2011) and ‘gstat’ (Pebesma 2004), respectively. The PCA and cluster analyses were computed using package ‘vegan’ (Oksanen *et al.* 2008). The MRT analysis and IndVal index computation were conducted using the package ‘mvpart’ (De’ath 2006) and ‘labdsv’ (Roberts 2007), respectively. All R scripts were adapted from Borcard *et al.* (2011).

RESULTS

Floristic composition

A total of 4604 trees with DBH ≥ 10 cm was inventoried in the 10-ha forest dynamics plot. The list of identified species and families is provided in Table 1 with their abundances and *IVI* values; 82 tree species were identified. Mean species density was 43 ± 7 species/ha (range: 32 to 53). All the individual trees occurring on the termite mounds were excluded (8.5% of the total number of individuals). Among them were 14 species exclusively restricted to these mounds (Table 1). The remaining 68 tree species belonged to 32 families and 52 genera. Fabaceae was the most abundant family, comprising 60.4% of the trees. Within this family, Caesalpinioideae was the most abundant subfamily with 42.7% of the individuals followed by Faboideae (14.7%) and Mimosoideae (3.1%). Fabaceae were followed by Apocynaceae (9.3%), Dipterocarpaceae (7.7%) and Combretaceae (3.5%). Eleven species were represented by more than 100 individuals. *Julbernardia paniculata* was the most abundant species with 1240 individuals (26.9%). Other abundant species are *Diplorhynchus condylocarpon* (428), *Brachystegia wangermeeana* (305), *M. macroura* (298), *Julbernardia globiflora* (249), *Pterocarpus angolensis* (247), *Pterocarpus tinctorius* (178), *B. spiciformis* (128), *Pseudolachnostylis maprouneifolia* (119), *Uapaca nitida* (113) and *Albizia antunesiana* (111). The ranking of species according to *IVI* (Table 1) was slightly different. In particular, *B. wangermeeana* ranked third based on frequency and sixth when considering *IVIs*.

Habitats and species assemblages

The first four principal axes of the PCA accounted for 80% of the total inertia of the soil dataset (see online supplementary Appendix S4). In decreasing order, variables contributing the most to the axes were: Al_{avail} , K_{avail} , Mn_{tot} , charcoal content and Fe_{avail} (Axis 1), Al_{titr} , B_{tot} , pH_{KCl} and Ca_{avail} (Axis 2), P_{tot} , B_{avail} and K_{tot} (Axis 3). The site scores of the quadrats on the four principal axes were then used in a Ward clustering. All three cutting tree criteria pointed to an optimal division of the dendrogram into five groups (or habitats). Figure 2a describes the habitat membership of quadrats on a map of the forest plot and shows that the resulting habitats are spatially structured in well-defined patches. Table 2 presents the results of the

IndVal analysis. *Brachystegia wangermeeana* was mostly present in the fifth habitat (*h5*) and was the only significant indicator species (IndVal = 0.63, $P = 0.031$). No other species could be linked to any habitat based on the IndVal index. Except for *B. wangermeeana*, all significant values obtained with the classical full randomisation were not significant using the more appropriate torus-randomisation procedure (Table 2).

Figure 3 presents the dendrogram resulting from the MRT analysis. While the MRT analysis explained 25.7% (calculated as the reciprocal of the relative error) of the tree community variation, the best predictive model was obtained considering five groups of quadrats (Fig. 3), with a predictive power of 10.3% (the reciprocal of the cross-validated error). The five resulting groups are *H1* to *H5* (Fig. 3). Figure 2b shows the habitat membership of quadrats on a map of the forest plot. The resulting habitats are spatially structured as well-defined patches but show a different distribution in the forest compared to the habitats defined in Figure 2a. The MRT analysis first divided the tree community in two on the basis of Ca_{tot} at a threshold value of $12.4 \mu\text{g g}^{-1}$. Below this threshold, the community was split again into two communities based on P_{Olsen} (threshold value: $3.66 \mu\text{g g}^{-1}$). In addition, Al_{avail} produced a similar split at this node. Beyond the Ca_{tot} threshold value, the community was split twice, first by P_{EDTA} (threshold value: $2.85 \mu\text{g g}^{-1}$) and then by clay content (threshold value: 24.8%) for the sub-community corresponding to the lowest P_{EDTA} concentrations. Moreover, Fe_{avail} and P_{EDTA} gave identical results at this node. Beyond these four discriminant variables, the five habitats also differed significantly for many other soil parameters (see online supplementary Appendix S2). A significant signature of past human activities was detected for only five quadrats within the dynamic plot (corresponding partly to *H4* and *H5*). Ca_{tot} and P_{EDTA} were negatively correlated to past agricultural activities (see online supplementary Appendix S3), but considering the additional sampled area of 6 ha together with the quadrats of the dynamic plot made these correlations non-significant.

East–west variation in clay content and stoniness was the most evident gradient in the plot examined. This textural change was associated with chemical modifications along the gradient. *H1* and *H2* have a high SI (>0.6) and low clay content ($\sim 19\%$). This explains the relatively low *CEC* ($\sim 1.6 \text{ cmol}_c/\text{kg}$) resulting in low available element contents (*Mg*, *K*, *Mn*, *Al*); even though *Al* saturation was the highest within this group of habitats. High available *Al*, which can cause long-term *P* immobilisation, is likely to be responsible for the low concentrations of the two forms of available phosphorus (P_{EDTA} and P_{Olsen}). Total forms of elements were generally lower than in the other habitats except for *K*. Further, *H4* and *H5* are characterized by high clay content ($\sim 35\%$) and *CEC* values ($\sim 1.9 \text{ cmol}_c/\text{kg}$) and were inversely correlated to the SI (<0.2). Concentrations of most available cations were favoured by this large *CEC*. Total concentration of elements presented higher values than for the other habitats. Furthermore, *H3* presented intermediate characteristics compared to the previous groups

Table 1: table of the identified species and families of the forest plot

Species	Family	Abund.	No. quadrats	RF (%)	RD (%)	RBA (%)	IVI
<i>Julbernardia paniculata</i>	Fabaceae—Cesalpinioideae	1240	124	6.89	26.93	11.89	45.71
<i>Marquesia macrourea</i>	Dipterocarpaceae	298	91	5.06	6.47	27.10	38.63
<i>Diplorhynchus condylocarpon</i>	Apocinaceae	428	150	8.33	9.30	9.14	26.77
<i>Brachystegia spiciformis</i>	Fabaceae—Cesalpinioideae	128	87	4.83	2.78	7.56	15.18
<i>Brachystegia wangermeeana</i>	Fabaceae—Cesalpinioideae	305	65	3.61	6.62	4.35	14.58
<i>Pterocarpus angolensis</i>	Fabaceae—Faboideae	247	97	5.39	5.36	3.74	14.49
<i>Julbernardia globiflora</i>	Fabaceae—Cesalpinioideae	249	78	4.33	5.41	4.01	13.75
<i>Pterocarpus tinctorius</i>	Fabaceae—Faboideae	178	74	4.11	3.87	4.01	11.98
<i>Pseudolachnostylis maprouneifolia</i>	Phyllanthaceae	119	75	4.17	2.58	1.88	8.64
<i>Albizia antunesiana</i>	Fabaceae—Mimosoideae	111	72	4.00	2.41	1.53	7.94
<i>Pericopsis angolensis</i>	Fabaceae—Faboideae	76	53	2.94	1.65	3.25	7.84
<i>Combretum collinum</i>	Combretaceae	85	51	2.83	1.85	1.98	6.66
<i>Uapaca nitida</i>	Phyllanthaceae	113	49	2.72	2.45	1.43	6.60
<i>Combretum molle</i>	Combretaceae	72	44	2.44	1.56	1.59	5.60
<i>Strychnos innocua</i>	Loganiaceae	59	44	2.44	1.28	1.16	4.89
<i>Dalbergia boehmii</i>	Fabaceae—Faboideae	71	45	2.50	1.54	0.47	4.51
<i>Philenoptera katangensis</i>	Fabaceae—Faboideae	61	33	1.83	1.32	1.10	4.26
<i>Monotes katangensis</i>	Dipterocarpaceae	55	35	1.94	1.19	0.99	4.13
<i>Hexalobus monopetalus</i>	Annonaceae	50	42	2.33	1.09	0.49	3.91
<i>Ziziphus mucronata</i>	Rhamnaceae	54	27	1.50	1.17	1.10	3.78
<i>Haplocoelum foliolosum*</i>	Sapindaceae	55	21	1.17	1.19	1.40	3.76
<i>Parinari curatellifolia</i>	Chrysobalanaceae	39	30	1.67	0.85	0.93	3.44
<i>Bobgunnia madagascariensis</i>	Fabaceae—Faboideae	31	27	1.50	0.67	0.80	2.97
<i>Anisophyllea boehmii</i>	Anisophylleaceae	28	27	1.50	0.61	0.47	2.58
<i>Zanthoxylum chalybeum*</i>	Rutaceae	32	24	1.33	0.70	0.42	2.45
<i>Lannea discolor</i>	Anacardiaceae	27	21	1.17	0.59	0.42	2.17
<i>Ficus thonningii</i>	Moraceae	19	14	0.78	0.41	0.47	1.66
<i>Phyllocosmus lemaireanus</i>	Ixonanthaceae	21	19	1.06	0.46	0.14	1.65
<i>Boscia angustifolia*</i>	Capparaceae	18	13	0.72	0.39	0.50	1.61
<i>Albizia adianthifolia</i>	Fabaceae—Mimosoideae	19	17	0.94	0.41	0.25	1.60
<i>Allophylus africanus*</i>	Sapindaceae	21	14	0.78	0.46	0.35	1.58
<i>Uapaca kirkiana</i>	Phyllanthaceae	22	15	0.83	0.48	0.26	1.57
<i>Brachystegia taxifolia</i>	Fabaceae—Cesalpinioideae	16	11	0.61	0.35	0.40	1.36
<i>Ochna schweinfurthiana</i>	Ochnaceae	14	12	0.67	0.30	0.15	1.12
<i>Commiphora glandulosa*</i>	Burseraceae	11	11	0.61	0.24	0.21	1.06
<i>Erythrina abyssinica</i>	Fabaceae—Faboideae	10	9	0.50	0.22	0.33	1.05
<i>Albizia versicolor</i>	Fabaceae—Mimosoideae	10	8	0.44	0.22	0.37	1.03
<i>Erythrophleum africanum</i>	Fabaceae—Cesalpinioideae	10	8	0.44	0.22	0.35	1.01
<i>Hymenodictyon parviflorum</i>	Rubiaceae	14	10	0.56	0.30	0.14	1.00
<i>Uapaca pilosa</i>	Phyllanthaceae	12	11	0.61	0.26	0.08	0.95
<i>Diospyros mespiliformis*</i>	Ebenaceae	12	7	0.39	0.26	0.24	0.89
<i>Ekebergia benguelensis</i>	Meliaceae	10	9	0.50	0.22	0.07	0.79
<i>Ficus ingens</i>	Moraceae	7	6	0.33	0.15	0.23	0.71
<i>Senna abbreviata</i>	Fabaceae—Cesalpinioideae	8	8	0.44	0.17	0.08	0.70
<i>Thespesia garckeana*</i>	Malvaceae	8	5	0.28	0.17	0.24	0.69
<i>Hymenocardia acida</i>	Phyllanthaceae	12	6	0.33	0.26	0.09	0.68
<i>Markhamia obtusifolia</i>	Bignoniaceae	10	6	0.33	0.22	0.09	0.65
<i>Uvariastrum hexaloboides</i>	Annonaceae	7	5	0.28	0.15	0.11	0.54
<i>Vitex fischeri</i>	Lamiaceae	4	4	0.22	0.09	0.22	0.53

Table 1. Continued

Species	Family	Abund.	No. quadrats	RF (%)	RD (%)	RBA (%)	IVI
<i>Garcinia huilensis</i>	Clusiaceae	6	6	0.33	0.13	0.05	0.51
<i>Diospyros abyssinica</i> *	Ebenaceae	6	3	0.17	0.13	0.19	0.49
<i>Ochna puberula</i>	Ochnaceae	7	5	0.28	0.15	0.05	0.48
<i>Diospyros lycioides</i> *	Ebenaceae	5	5	0.28	0.11	0.08	0.47
<i>Senna singuana</i>	Fabaceae—Cesalpinioideae	6	5	0.28	0.13	0.05	0.45
<i>Commiphora edulis</i> *	Burseraceae	5	4	0.22	0.11	0.12	0.45
<i>Syzygium guineense</i>	Myrtaceae	5	5	0.28	0.11	0.06	0.45
<i>Pappea capensis</i> *	Sapindaceae	4	2	0.11	0.09	0.23	0.43
<i>Strychnos spinosa</i>	Loganiaceae	5	5	0.28	0.11	0.03	0.42
<i>Strychnos cocculoides</i>	Loganiaceae	5	5	0.28	0.11	0.02	0.41
<i>Annona senegalensis</i>	Annonaceae	4	4	0.22	0.09	0.06	0.37
<i>Schreberia trichoclada</i>	Oleaceae	4	4	0.22	0.09	0.06	0.37
<i>Gymnosporia senegalensis</i>	Celastraceae	4	4	0.22	0.09	0.05	0.36
<i>Euclea racemosa</i>	Ebenaceae	4	3	0.17	0.09	0.07	0.32
<i>Combretum celastroides</i> *	Combretaceae	3	2	0.11	0.07	0.03	0.20
<i>Azelia quanzensis</i>	Fabaceae—Cesalpinioideae	2	2	0.11	0.04	0.02	0.18
<i>Acacia sieberiana</i>	Fabaceae—Mimosoideae	1	1	0.06	0.02	0.10	0.18
<i>Craterosiphon quarrei</i>	Thymelaeaceae	2	2	0.11	0.04	0.02	0.17
<i>Psyrax mutimushii</i>	Rubiaceae	2	2	0.11	0.04	0.02	0.17
<i>Homalium abdessamadii</i>	Salicaceae	2	2	0.11	0.04	0.02	0.17
<i>Vitex mombassae</i>	Lamiaceae	2	2	0.11	0.04	0.01	0.17
<i>Bridelia duvigneaudii</i>	Phyllanthaceae	2	2	0.11	0.04	0.01	0.17
<i>Dichrostachys cinerea</i> *	Fabaceae—Mimosoideae	2	1	0.06	0.04	0.02	0.12
<i>Sterculia quinqueloba</i> *	Malvaceae	1	1	0.06	0.02	0.02	0.10
<i>Gardenia ternifolia</i>	Rubiaceae	1	1	0.06	0.02	0.01	0.09
<i>Dalbergia nitidula</i>	Fabaceae—Faboideae	1	1	0.06	0.02	0.01	0.08
<i>Vitex payos</i>	Lamiaceae	1	1	0.06	0.02	0.01	0.08
<i>Canthium crassum</i>	Rubiaceae	1	1	0.06	0.02	0.01	0.08
<i>Faurea rochetiana</i>	Proteaceae	1	1	0.06	0.02	0.00	0.08
<i>Vangueriopsis africana</i>	Rubiaceae	1	1	0.06	0.02	0.00	0.08
<i>Rourea orientalis</i>	Connaraceae	1	1	0.06	0.02	0.00	0.08
<i>Salacia rhodesiaca</i>	Celastraceae	1	1	0.06	0.02	0.00	0.08
<i>Vangueria infausta</i>	Rubiaceae	1	1	0.06	0.02	0.00	0.08
Total		4604		100.0	100.0	100.0	300.0

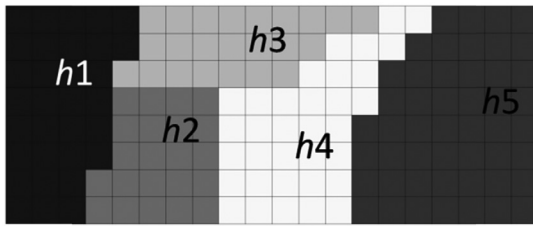
The basal area was calculated on the 10 ha of miombo woodland. Species are classified by decreasing IVI. Species marked with an asterisk (*) were exclusively encountered on termite mounds and were not included in the species-habitat association analyses.

described, in accordance with its central geographic location. Only total and available forms of *Ca* are inconsistent within the groups of habitat and the overall gradient described. Total concentrations in *Ca* are lower ($<12 \mu\text{g g}^{-1}$) in *H2* and *H5* located on the opposite sides of the plot. This corresponds to the first bifurcation of the regression tree (Fig. 3).

The IndVal index was computed and tested for each species on the basis of the habitats in order to detect potential indicator species and search for species assemblages (Table 2). *J. paniculata* and *B. wangermeeana* were both significantly associated with *H5*, *M. macroura* with *H3*, *Strychnos innocua* and *Hymenocardia acida* with *H4* and *J. globiflora*, *U. nitida*, *Brachystegia taxifolia* and *Lannea discolor* with *H1*. Within the

habitat, species were therefore associated with one another and were significant indicators of their respective soil conditions. Other species were detected as indicator with the classical randomisation test, but this later suffered from inflated type I error, too often considering species to be indicator species, while the torus randomisation was not significant (Table 2). Besides the relations between significant indicator species and habitats, other interesting features of the tree community are worth mentioning. The five dominant tree species of each habitat are listed in Fig. 3. In addition, *J. paniculata*, *D. condylocarpon* and both species of *Pterocarpus* were among the most abundant species of all (or nearly all) the *Hs* (see Fig. 3).

a) Habitats - PCA & Ward clusters



b) Habitats - MRT

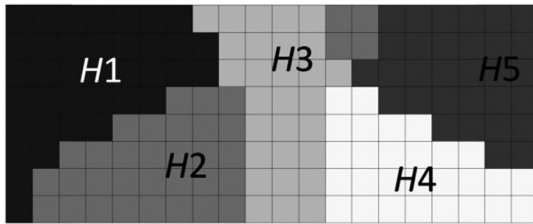


Figure 2: (a) map of the five habitats selected by PCA and Ward clustering (*h1* to *h5*); (b) map of the five habitats selected on the basis of the multivariate regression trees (*H1* to *H5*).

DISCUSSION

Mikembo forest as a typical wet miombo

Besides species widely distributed in the Zambebian region (e.g. *D. condylocarpon* and *J. paniculata*), the woody layer of Mikembo forest comprises a number of wet miombo species that are more or less restricted to the northern part of the Zambebian region (*M. macroura*, *B. wangermeeana*, *Anisophyllea boehmii*, *Craterosiphon quarrei* and *Uvariastrum hexaloboides*). All these species are evergreen or breviceduous, except *C. quarrei* which is deciduous. Based on Schmitz's (1971) phytosociological system, Mikembo forest is intermediate between Berlinio–Marquesion (rich in evergreen species) and Mesobrachystegion (poor in evergreen species).

Duvigneaud (1958) proposed ecological groups of indicator species for the miombo of Katanga. The most influential soil factors were drainage, soil depth, topography and soil texture. Soil chemical factors, however, were not measured. Based on his system, Mikembo forest lacks indicators of shallow rocky soil (e.g. *Brachystegia microphylla*) and of impaired drainage on shallow lateritic crust and yellow compact clayey soil (*Brachystegia utilis*, *B. boehmii*, *B. stipulata* and *Isoberlinia* div. sp.). In contrast, the floristic composition of Mikembo forest comprises indicators of deep red soil of plateau miombo (*Brachystegia spiciformis*, *J. paniculata*, etc.) and species with a broad ecological amplitude (*J. globiflora* and *M. macroura*). However, this does not agree very well with our observations since a large part of the plot is established on yellow soils with high gravel load. This discrepancy highlights the need for more detailed species preference characterisations and suggests that any generalisation of indicator status must be done with caution.

Modelling species-habitat associations and species assemblages

Very few studies used explanatory multivariate analyses in order to detect soil–plant relationships in the miombo woodland (Mapaure 2001), and this work is the first to use so many potentially relevant soil variables to do so. In other parts of the miombo ecoregion, statistical soil–vegetation analyses have generally considered larger spatial scales and much less ecological parameters (Backéus et al. 2006; Chidumayo 1987; Kanschik and Becker 2001; Munishi et al. 2011; Mwakalukwa et al. 2014).

In our study site, we observed variation in many edaphic factors (e.g. clay content, $Al-Sat$, P_{EDTA} , P_{Olsen} and Ca_{tot}). At the same time, a striking result is the high species richness of the forest. Eighty-two woody species have been recorded on a 10-ha area. In other floristic studies of miombo, similar species richness is generally found over considerably larger study areas (Backéus et al. 2006; Chidumayo 1987; Kanschik and Becker 2001; Munishi et al. 2011; Mwakalukwa et al. 2014). Our results suggest that this high floristic richness may be accounted for by fine-scale edaphic variation and niche differentiation. Indeed, our model based only on soil variability allowed a significant explanation of 26% of the community distribution. The remaining variation could be partially explained by using spatially explicit models (McIntire and Fajardo 2009) in order to account for other ecological processes (e.g. dispersal limitation, ecological drift). Furthermore, Bauman et al. (2016) detected a relation between the dominant ectomycorrhizal fungi of the Mikembo plot and functional traits related to the 'leaf economics spectrum' of host tree species. These results suggest a potential additive role of the soil microbiota in the tree community assembly in miombo woodlands.

To our knowledge, the present study is the first to explicitly test the potential of tree species as indicators of fine-scale habitats in miombo woodlands. To that end, two methods have been used. The first method identified five habitats based on soil factors only, giving more weight to the greatest environmental gradients, independent of their relevance for the tree community. Only one species was identified as an indicator of one of the habitats. In a second approach, vegetation data were used to weight environmental parameters according to their influence on species assemblages. Using a combination of MRT and IndVal analyses and correcting for spatial autocorrelation, five species assemblages were detected. Nine species were significant indicator species (out of a total of 38 species with 10 specimens or more). This is a remarkable result, considering that statistical significance was corrected for spatial autocorrelation using torus randomisation. Four of the five most frequent species, representing >50% of the total population, were significant indicators of soil conditions (i.e. *J. paniculata*, *J. globiflora*, *B. wangermeeana* and *M. macroura*). In previous studies at much larger scales, the factors that best explained spatial variation of the miombo were soil

Table 2: species IndVal value based on two different habitat definitions

Species	PCA and Ward		MRT	
	max_hab	IndVal	max_hab	IndVal
<i>Julbernardia paniculata</i>	1	0.337 ^{ns,*}	1	0.363 ^{****}
<i>Diplorhynchus condylocarpon</i>	2	0.246 ^{ns,*}	5	0.218
<i>Brachystegia wangermeeana</i>	5	0.628 ^{*,*}	1	0.574 ^{*,****}
<i>Marquesia macroura</i>	3	0.240 ^{ns,*}	3	0.312 ^{*,****}
<i>Julbernardia globiflora</i>	3	0.274 ^{ns,*}	5	0.325 ^{*,****}
<i>Pterocarpus angolensis</i>	1	0.210 ^{ns,*}	5	0.219 ^{ns,*}
<i>Pterocarpus tinctorius</i>	5	0.195 ^{ns,*}	4	0.197 ^{ns,*}
<i>Brachystegia spiciformis</i>	2	0.220 ^{ns,*}	3	0.234 ^{ns,*}
<i>Pseudolachnostylis maprouneifolia</i>	5	0.123	4	0.113
<i>Uapaca nitida</i>	3	0.198 ^{ns,*}	5	0.309 ^{*,****}
<i>Albizia antunesiana</i>	1	0.138	4	0.122
<i>Combretum collinum</i>	5	0.189 ^{ns,*}	1	0.172 ^{ns,*}
<i>Pericopsis angolensis</i>	2	0.112	5	0.097
<i>Dalbergia boehmii</i>	1	0.105	5	0.139 ^{ns,*}
<i>Strychnos innocua</i>	5	0.183 ^{ns,*}	4	0.335 ^{*,****}
<i>Monotes katangensis</i>	2	0.129	4	0.170 ^{*,*}
<i>Philenoptera katangensis</i>	1	0.069	4	0.133 ^{*,*}
<i>Hexalobus monopetalus</i>	3	0.122	3	0.100
<i>Parinari curatellifolia</i>	3	0.107	5	0.089
<i>Bobgunnia madagascariensis</i>	5	0.070	1	0.097
<i>Anisophyllea boehmii</i>	2	0.106	4	0.070
<i>Uapaca kirkiana</i>	2	0.093 ^{ns,*}	5	0.069
<i>Phyllocosmus lemaireanus</i>	3	0.080	5	0.081
<i>Combretum molle</i>	2	0.099 ^{ns,*}	3	0.069
<i>Albizia adianthifolia</i>	5	0.126 ^{ns,*}	1	0.069
<i>Brachystegia taxifolia</i>	3	0.079	5	0.130 ^{*,***}
<i>Lanea discolor</i>	3	0.135 ^{*,*}	5	0.146 ^{*,***}
<i>Ochna schweinfurthiana</i>	3	0.035	5	0.028
<i>Hymenocardia acida</i>	5	0.122 ^{ns,*}	4	0.214 ^{*,****}
<i>Uapaca pilosa</i>	2	0.086 ^{ns,*}	5	0.063

In the first approach, five habitats were obtained by Ward clustering of the first four soil PCA axes. In the second approach, five communities and corresponding habitats were obtained by multivariate regression tree. IndVal indices tested by torus randomisation and total randomisation. ns = non-significant, * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$, **** $P < 0.001$. The first and second symbols give the significance levels of the IndVal index based on the torus randomisation and total randomisation tests, respectively. No symbol is indicated when both tests were not significant. 'max_hab' stands for 'habitat in which the species displayed the highest IndVal value'. Species ranked by order of decreasing frequency. Species with <10 individuals are not considered.

pH, available Ca and texture (Kanschik and Becker 2001; Mapaire 2001; Mwakalukwa *et al.* 2014), topography and soil colour (Backéus *et al.* 2006), elevation and slope (Munishi *et al.* 2011; Mwakalukwa *et al.* 2014), rainfall (Kanschik and Becker 2001), fire and elephant herbivory (Mapaire 2001).

In this study, soil factors that best discriminated plant assemblages were Ca_{tot} , P_{Olsen} , P_{EDTA} and clay content. Soil texture and the associated soil chemical composition are determined by the bedrock (dolomitic shales vs. siltstones) in the Lubumbashi Plain (Batumike *et al.* 2006) suggesting that geological heterogeneity at the scale of the 10-ha plot may drive the observed variation in edaphic properties. In addition, Ca_{tot} content is the only variable that does not follow the textural gradient. Local

concentration of Ca could be driven by carbonate precipitates induced by the termite mound activity as shown by Mujinya *et al.* (2011). Phosphorus is known to be a limiting resource for miombo trees (Högberg 1986; Campbell 1996). However, fine-scale variation of floristic composition in response to variation in soil P availability does not seem to have been previously reported. This result suggests that niche differentiation for phosphorus availability may be one of the processes structuring miombo at a fine scale. These four soil variables predicted 10% of the variation in the community composition while the whole set of soil variables explained 26% of the tree composition variability. In previous studies, niche differentiation accounted for 19% to 48% of tropical plant community

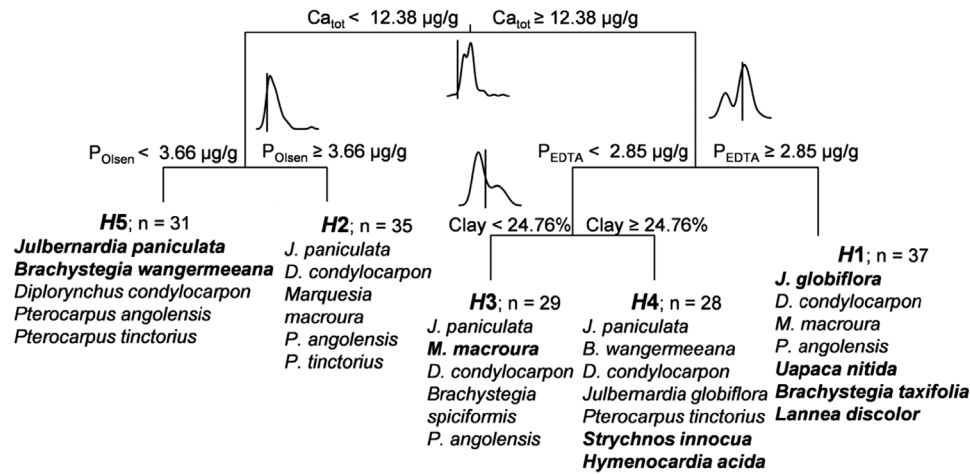


Figure 3: dendrogram resulting from the multivariate regression trees. Density plots represent the distribution of the corresponding soil parameters through the forest. The vertical bar indicates the splitting threshold value corresponding to the node. *n* indicates the number of quadrats of the cluster. The five dominant species of each habitat are listed in decreasing order of abundance. Species in bold are significant indicator species (4999 torus randomisations at the α level of 0.05). Statistics of the MRT analysis were as follows: relative error = 0.743, cross-validated error = 0.897, standard error = 0.0419.

composition variability (e.g. Chang et al. 2013; Jones et al. 2008; Legendre et al. 2009; Mapaure 2001; Punchi-Manage et al. 2013; Vleminckx et al. 2015). The explanatory power of species-habitat associations in the Mikembo plot is therefore of the same order of magnitude than in other tropical plant communities. Nonetheless, comparing the relative relevance of deterministic processes in different communities must be done with caution, since the magnitude of the detection of such processes depends upon the quality of the explanatory environmental data collected (Chang et al. 2013; Jones et al. 2008), the spatial properties of the sampling design (Garzon-Lopez et al. 2014) and the analytical methods used (Jones et al. 2008).

Mikembo forest has been subjected, at least in part, to slash and burn cultivation. Traces of human disturbance such as cultivation ridges were observed in the eastern portion of the examined plot (portions of H4 and H5, Fig. 2b). Traces of agriculture were localized in the quadrats with higher clay content and lower gravel load, probably because of easier soil tillage conditions. This preference probably explains the negative correlation between P_{EDTA} and past human activities. Indeed, clay content and P_{EDTA} displayed opposite gradients in the plot and were significantly negatively correlated. Since the five quadrats displaying significant human signature were located at the eastern end of the plot, most quadrats non-affected by human corresponded to intermediate or opposite values of the P_{EDTA} gradient. When testing the relationship between P_{EDTA} and *Man* in H4 and H5 only, i.e. considering an area of relatively homogeneous soil texture, no significant link could be detected, therefore supporting that the correlation of P_{EDTA} and past human activities is indirect and caused by the choice made by past growers for clayey soils with low gravel loads.

The fine-scale (here ~2 ha) variation of habitat distribution implies practical perspectives for management and restoration of miombo forests. (i) The choice of tree species in

restoration programmes should be guided by habitat diversity and by preliminary studies assessing potential preferences of species for specific habitat conditions. (ii) Conservation strategies should prioritize heterogeneity rather than the extent of the protected areas.

Effect of the observation scale

In this study, we sampled an unprecedented high number of physicochemical soil parameters at a very fine spatial degree of resolution. This may explain why such fine-scale habitat heterogeneity could be detected and related to species assemblages and indicator species. The results support the idea that previous studies may have not detected fine-scale niche differentiation due to (i) a sampling strategy designed to focus on broader scales, (ii) sampling of too few environmental variables (Chang et al. 2013). The present study did not match the common view of ecology that deterministic processes of tree species assemblage act at broad scales while neutral processes dominate at finer scales. Indeed, Chang et al. (2013) showed that this conception may have arisen from the low number and low resolution of environmental parameters measured in many studies. Therefore, we suggest that our analytical approach, both for soil sampling and data analyses, might allow highlighting similar fine-scale tree-habitat associations in other tropical forests, therefore helping to (i) better understand how environmental heterogeneity contributes to species assemblages at fine scales and (ii) establish well-calibrated conservation programs.

Conclusion

This study revealed fine-scale differentiation of the tree layer of a miombo forest in response to variation of soil factors. The explicit consideration of anthropogenic historical disturbances in the analyses indicated that the soil heterogeneity

responsible for habitat and tree community differentiation is mostly natural. Further work is needed to evaluate whether such local habitat heterogeneity can be extended to other miombo forests. Despite the small extent of the plot studied and of the apparent homogeneity of the environment, five contrasting habitats were highlighted and related to distinct indicator tree species. We advise further studies aiming at restoration and conservation purposes in miombo woodlands to adopt the methodology used here and to address fine-scale tree-habitat associations to guide practical decisions.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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