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RESEARCH ARTICLE

Medicinal *Vitex* species (Lamiaceae) occupy different niches in Haut-Katanga tropical dry woodlands

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Abstract

Background and aims – Sustainable management of the medicinal plant resources provided by tropical forests is of utmost importance to human populations in developing countries. Trees and shrubs of the genus *Vitex* (Lamiaceae) are of great medicinal importance in Haut-Katanga (SE D.R. Congo), frequently used to treat tropical diseases. However, the security of supply is threatened, particularly by urban sprawl and mining. A conservation strategy for medicinal plants is urgently needed. In this context, we try to better understand the ecological factors (mostly soil) explaining the distribution of three medicinal species of *Vitex* (Lamiaceae) (*V. fischeri*, *V. madiensis*, and *V. mombassae*) that co-occur in the tropical dry woodlands in the region of Lubumbashi.
Material and methods – In 114 plots (10 m radius), comprising at least one species of *Vitex*, all woody species with a DBH ≥ 10 cm were inventoried and soil samples were collected. Multivariate Regression Trees (MRT) combined with indicator species index IndVal and Redundancy analysis (RDA) were used to characterise habitats and woody plant communities associated to each *Vitex* species and to explain the variability of plant community composition.
Key results – Four habitats were identified, and the three *Vitex* species differ significantly in ecological range. *Vitex fischeri* is a specialist of a most distinctive community on high Mg and low Al soil (termite mounds). *Vitex mombassae* is indicative of one habitat, corresponding to low altitude (< 1230 m) plots. *Vitex madiensis* has a broader range, being a generalist of all habitats except termite mounds.
Conclusion – These results emphasise the importance of a detailed knowledge of species ecology to design species-specific conservation strategies, even for congeneric species occurring in sympatry in the same landscape.

Keywords

aluminium, conservation, indicator species, medicinal, miombo, niche, soil, termite mound, tropical dry woodlands, woody species

INTRODUCTION

The provision of medicinal plants is one of the important ecosystem services or nature contribution to people supplied by tropical forests and woodlands. Indeed, 70% of the population in sub-Saharan Africa uses plant medicinal resources as the access to the 'modern' healthcare system is very limited due to the lack of suitable infrastructure and the low incomes (Foulon and Some 2005; OMS 2011). In addition, medicinal plants are also known to develop value chains and contribute to the income of some households, especially those in rural

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areas (OMS 2011). Unfortunately, the African and global IPBES assessments have shown a decline in the supply of medicinal resources due to direct and indirect factors (Archer et al. 2018).

The same situation occurs in the Haut-Katanga province (D.R. Congo) where medicinal woody plants, widely used by the urban and rural dwellers, are declining rapidly because of the reduction of woodland or their intensive exploitation (Cabala et al. 2017). This is the case for *Vitex fischeri* Gürke var. *fischeri*, *Vitex mombassae* Vatke, and *Vitex madiensis* Oliv. subsp. *milanjiensis* (Britten) F.White (Lamiaceae) around Lubumbashi (the main city in Haut-Katanga province). These three medicinal species occur in dry woodlands and their leaves are used by the local population to treat certain diseases (Amuri et al. 2017). Pharmacological and phytochemical studies using modern scientific approaches have demonstrated that these congeneric species possess anticancer, antibacterial, antifungal, and antidiabetic properties (Meena et al. 2010; Amuri et al. 2017). Nevertheless, recent surveys showed that the traditional practitioners are facing increased scarcity of *Vitex* materials around Lubumbashi (Amuri et al. 2017). The cause of the increased scarcity is due to woodland destruction and degradation caused by intense wood harvest for charcoal, mining activities, anarchical urbanisation, and shifting cultivation (Cabala et al. 2017; Sikuzani et al. 2017; Nge 2021).

The development of a conservation program of the three *Vitex* species has become a priority to ensure a sustainable supply of these vital ecosystem services and to support the healthcare system in this region. Resource management of these three sympatric medicinal species under high anthropogenic impact is therefore crucial and requires a good understanding of the species' autecology and synecology. Indeed, the development of conservation programs for *Vitex* is crucial, in a context of steadily decreasing woodland area. Thus, the implementation of an adequate conservation strategy can only be achieved through a thorough understanding of the deterministic processes responsible for the variability of plant communities associated with *Vitex* species.

Previous studies in the Katangan miombo woodland have highlighted the importance of habitat heterogeneity at multiple spatial scales in tree community assemblages and species coexistence (Duvigneaud 1958; Schmitz 1971; Harms et al. 2001; Muledi et al. 2017, 2020; Zellweger et al. 2020). Duvigneaud (1958) highlighted the influence of topography and geological substrate, on the floristic composition of miombo woodlands in Katanga. The phytosociological study of Schmitz (1971) based on the Zurich-Montpellier approach recognised the existence of distinct species assemblages in relation to edaphic factors. Recently, based on more robust statistical methods, Muledi et al. (2017, 2020) revealed the importance of soil heterogeneity in predicting the distinct assemblages and performances of tree communities within the miombo at a fine spatial scale, with distinct edaphic habitats associated to specific communities and indicator species at scales of ca 100 m.

Despite their key role in traditional tropical medicine, the ecology of *Vitex* species, their assemblage with other species into communities, and their dependence on specific abiotic conditions (soil, topography) remain unstudied and therefore poorly understood. It is in this context that we try to better understand the ecological mechanisms explaining the distribution of three medicinal *Vitex* species (*V. fischeri*, *V. madiensis*, and *V. mombassae*) that co-occur in the dry woodlands of Katanga (SE D.R. Congo).

The genus *Vitex* (Lamiaceae, formerly Verbenaceae) comprises about 250 species found in tropical and subtropical regions (Verdcourt 1992; Mabberley 2017). A total of 21 species of *Vitex* occur in D.R. Congo (Meerts 2018). Three species (*V. fischeri* var. *fischeri*, *V. mombassae*, and *V. madiensis* subsp. *milanjiensis*) are widespread in the Haut-Katanga province (Meerts and Hasson 2016). *Vitex mombassae* is widely distributed in eastern and southern tropical Africa; *V. fischeri* var. *fischeri* occurs mostly in eastern tropical Africa, while *V. madiensis* subsp. *milanjiensis* has a Zambezian distribution. All three species occur in dry tropical woodlands and secondary shrub savanna, especially in *Brachystegia-Julbernardia* miombo woodlands (Meerts 2018; Paton and Meerts 2020).

Here, we address the following specific questions: (a) Do the three *Vitex* species occur in distinct plant communities and occupy different ecological niches? (b) What are the ecological factors discriminating the different communities?

MATERIAL AND METHODS

Study area

The study was conducted on the plain of Lubumbashi (Haut-Katanga province in the D.R. Congo), covering an area of 2500 km^2 (11°25'57.23"S, 27°16'3.11"E; 11°53'18.98"S, 27°15'56.31"E; 11°53'21.63"S, 27°44'25.86"E; 11°25'37.70"S, 27°44'29.59"E), with the post office downtown used as the centroid (Supplementary file 1). The climate is CW6 (Peel et al. 2007) with an average annual temperature of 20.3°C and a 1200 mm average annual rainfall between November and April.

Considered as the centre of endemism in the northern part of the Zambezian region, the plain of Lubumbashi is dominated by the humid miombo woodland (Kuper 2004; Cabala et al. 2017), i.e. a particular type of dry tropical woodlands characterised by trees of 15 to 20 m tall, mainly from the Fabaceae family, dominated by the ectomycorrhizal genera *Brachystegia*, *Julbernardia*, and *Isoberlinia* (Duvigneaud 1958; Schmitz 1971; Malaisse 1978; Werger and Coetzee 1978; Malaisse 1997). Miombo comprises semi-deciduous woodlands with a continuous herbaceous layer mostly composed of seasonal C4 grasses

and sedges, and is subjected to periodic bushfire (Frost et al. 1986; Malaisse 1997). Miombo woodlands do not occur in permanently or seasonally waterlogged soil, where they are replaced by riparian forest and dambo savannahs, respectively (Schmitz 1971; Meerts and Hasson 2016).

The geological substrate of the region is dominated by dolomitic shale and siltstone of the neoproterozoic Nguba and Roan groups (Batumike et al. 2006), and soils are ferralitic, deep, with poorly differentiated horizons and diffuse or gradual transitions. Red and yellow ferralitic soils are the most common, characterised by an acidic pH and low nutrient content (Ngongo and Sys 1993; Ngongo et al. 2009).

Vegetation inventory strategy

A total of 200 1-ha plots were defined along four main roads (Kasenga, Kafubu, Kipushi, and Likasi), covering the different degraded states of the landscape (miombo woodland, degraded miombo, shrub savannah, post-cultivation wasteland, and agricultural land) as described by André et al. (2018) based on vegetation crown cover and height. On each road axis, 50 one-hectare quadrats were systematically delineated (at an equidistance of 1 km) along the five secondary roads. The sampling strategy structured by the road network (Supplementary file 1) is adapted from Chidumayo (2016) and is partly due to logistical constraints. All plots were carefully scanned for the presence of *Vitex* individuals. In each 1-ha plot where at least one species of *Vitex* was present (i.e. 114 1-ha plots), a 10 m radius circular plot was installed, with its centre corresponding to the highest density of *Vitex* in the quadrat. In each of these circular plots, all trees and shrubs with a diameter at breast height (DBH) ≥ 10 cm were inventoried and identified to species level. The identification of woody species associated with *Vitex* was carried out using standard floras (Flora Zambeziaca and Flore d'Afrique centrale), the determination keys of Meerts and Hasson (2016) and the Upper Katanga tree checklist (Meerts 2016). The three *Vitex* species were identified with Meerts (2018) and Paton and Meerts (2020). The nomenclature of the families was adapted from APG IV (2016). The coverages of the shrub and tree layers (Cs and Ct, respectively) were estimated using the transect intercept method (Fiala et al. 2006). All further analyses are based on the species composition of the 114 circular plots with at least one *Vitex* individual.

Soil and topographic variables

Soil samples were systematically collected from each 10 m radius plot (0–20 cm soil layer). The soil samples were analysed according to the standard protocol of Pansu and Gautheyrou (2006). The bioavailable mineral elements (Al, Ca, K, P, Fe, Mg, Mn, Cu, and Zn) were extracted with 1 M ammonium acetate-EDTA at pH 4.65. Elemental concentrations were determined by ICP-OES with CCD detector (Varian, Vista MPX). Soil organic matter was measured by the loss on ignition method at 550°C. Soil pH was determined with an electrode pH meter in a soil-water solution (5 g soil to in 25 ml water).

Plot elevation was obtained in the field with a GPS (Edge 830), and height above the nearest drainage (HAND) was obtained for all circular plots at a one arc-second (ca 30 m) resolution (100 river head threshold cells) from the digital elevation model SRTM (Donchyts et al. 2016), using Google Earth Engine (Gorelick et al. 2017).

Data analysis

Absolute abundance (number of individuals of a species in a habitat) and relative abundance (ratio of the number of individuals of a species in a habitat to the total number of individuals of the species across all habitats) were calculated per habitat following Cottam and Curtis (1956).

We used multivariate statistical methods focused on both prediction and explanation to model the relationships between species and ecological variables and define species assemblages and specialist and indicator species of particular habitats. First, we used Multivariate Regression Trees (MRT; De'ath 2002) to define abiotic habitats that best predicted discontinuities in species assemblages and tested for the specialist and indicator nature of all species within the resulting habitats using the IndVal index (Dufrêne and Legendre 1997). We also applied a constrained ordination approach (redundancy analysis, RDA) to test the abiotic variables which we hypothesised could explain the observed variation in species composition among the studied plots. The candidate explanatory variables to be included in both the MRT and RDA were chemical soil variables, plot elevation (E), height above the nearest drainage (HAND), average tree height (H), and the tree and shrub ground cover (Ct and Cs, respectively), used to describe vegetation structure. Elevation was used as a proxy for geological variations in the region (see Batumike et al. 2006), whereas HAND was used as a proxy for local topography-related water constraints on the woody community (Nobre et al. 2011), as miombo woodland composition is known to vary with topography, due to its effect on soil depth and drainage (Duvigneaud 1958). However, miombo woodlands do not occur in waterlogged soils where they are replaced by other vegetation types (e.g. riparian forest and dambo savannahs). Within miombo woodlands, an important source of variation in soil water availability is termite mound activity (i.e. higher available water reserves in mounds), a factor included in our design, since we sampled vegetation both on and off termite mounds. Tree height and ground cover of tree layer were used as proxies of recent anthropogenic disturbance (logging, charcoal, agriculture), because recently disturbed plots have sparser and lower woody cover (Sikuzani et al. 2019). See Supplementary file 2 for variation range of all ecological variables.

To avoid unstable models due to collinearity issues, we calculated pairwise Pearson correlations across all explanatory variables and, for the variable pairs with r > +0.7 and r < -0.7, one of the two variables was removed from the model (Dormann et al. 2013) (see Supplementary file 3). The resulting set of variables used in the MRT and RDA were: Ct, Cs, HAND, E, Al, K, P, Fe, Mg, Mn, Co, and Cu. Variables removed from correlated pairs were reconsidered in the result discussion section.

Testing for distinct habitats and indicator species

Multivariate Regression Trees (MRT) is a form of constrained clustering method (De'ath 2002) that we used to optimise the detection of distinctive habitats and associated woody plant communities related to *Vitex* species. MRT sequentially split community data on the basis of a threshold value for one of the environmental variables, to be optimised, and minimises within-cluster dissimilarity (De'ath 2002). MRT optimises predictive power using cross-validation, unlike constrained ordinations such as redundancy analyses that emphasise explanatory power, hence ensuring a reduced set of environmental variables best predicting species assemblages into a number of distinct habitats. The final tree partition was therefore selected by minimising the relative error (Borcard et al. 2018).

The indicator species associated with each habitat were defined using the IndVal index. This index is calculated by considering both the fidelity and specificity of the species (Dufrêne and Legendre 1997). Specialist species were defined as those whose relative abundance in a given habitat was greater than 70% (criterion adapted from Harms et al. 2001). MRT and IndVal index calculations were performed using the packages mvpart (De'ath 2006) and labdsv (Roberts 2007).

Explaining community composition variability

Redundancy analysis (RDA) was used as a complementary approach to the combination of MRT and IndVal indices, to explain the variability of plant community composition from the heterogeneity of ecological factors. Explanatory variables were standardised to mean zero and unit standard deviation prior to the analysis. The statistical significance of the overall association between the community matrix and the environmental variable matrix, as well as each of the constrained RDA axis, were tested using 999 permutations of the model residuals (Anderson and Legendre 1999; Borcard et al. 2018). The adjusted R^2 was used to measure the unbiased amount of variation of the community matrix explained by the explanatory matrix (Legendre and Legendre 2012).

A Hellinger transformation was performed on the matrix of tree species abundance per plot using the R package vegan (Oksanen et al. 2013) before performing the multivariate analyses, to standardise the data by reducing the relative importance of the highest abundance

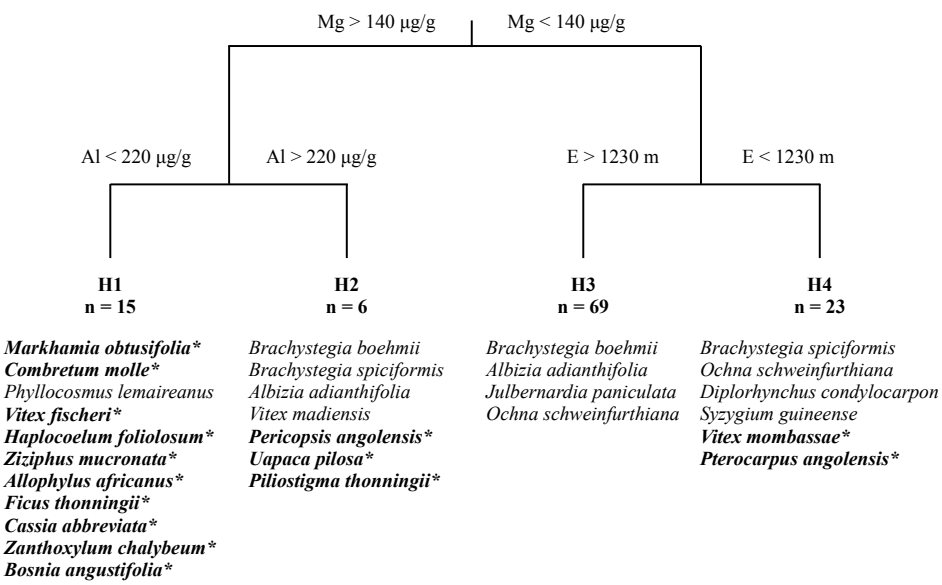

Figure 1. Habitats and corresponding community assemblages as defined by multivariate regression trees. The dominant species (highest absolute abundance) in each habitat are ranked in decreasing order of abundance and the indicator species are in bold with an asterisk indicating a significant p value ($p < 0.05$; 4999 permutations). Optimised habitat discrimination was performed using the following environmental variables: elevation (E), aluminium concentration (Al), and magnesium (Mg). Statistical values for the MRT analysis included: relative error = 0.891, cross-validation error = 1.03, standard error = 0.0249. n represents the number of plots within each habitat.

Table 1. IndVal values of indicator species for habitats associated with *Vitex*. * p < 0.05; ** p < 0.01; *** p < 0.001.

Species	MRT-Habitats	IndVal
Vitex fischeri	1	0.70***
Haplocoelum foliolosum	1	0.58***
Allophylus africanus	1	0.50***
Ziziphus mucronata	1	0.46***
Combretum molle	1	0.43***
Markhamia obtusifolia	1	0.40**
Cassia abbreviata	1	0.27**
Ficus thonningii	1	0.22*
Zanthoxylum chalybeum	1	0.20**
Boscia angustifolia	1	0.18*
Pericopsis angolensis	2	0.31*
Uapaca pilosa	2	0.24**
Piliostigma thonningii	2	0.15*
Vitex mombassae	4	0.32**
Pterocarpus angolensis	4	0.26*

values and the weights given to rare species (Legendre and Gallagher 2001; Borcard et al. 2018). The RDA was performed using the rda function from the R package vegan (Oksanen et al. 2013).

Comparison of habitats' abiotic features

We used permutation ANOVAs to test for differences in each environmental variable among the habitats defined by the MRT approach in order to better characterize them. To do so, the PERMANOVAs consisted of one environmental variable (e.g. Ca content) being modelled as a function of the factor 'habitat' (four levels, one per habitat; see Results), where each observation consisted of the corresponding variable value in one plot. If the ANOVA for a given environmental variable indicated that the variable differed significantly among habitats (based on 999 permutations), permutation t-tests were used to compare each pair of habitats and define the pairs that differed significantly. Permutation ANOVAs and t-tests were performed using the R functions anova.1way (Legendre 2007) and t.perm (Legendre 2005). These permutation tests were chosen to accommodate the unbalanced nature of the sampling design (i.e. varying number of plots per habitat; see details in Supplementary file 4) as well as any deviations from the assumptions of parametric tests in the model residuals. We used the false discovery rate correction to adjust p values and control for the inflated type I error rate that typically arises from multiple tests (Benjamini and Hochberg 1995). A level of significance of 0.05 (prior to correction) was used throughout the study.

All analyses were performed in the statistical environment R v.4.0 (R Core Team 2021) (see Supplementary file 4 for the R code).

RESULTS

Habitats and indicator species

A total of 82 species were inventoried, belonging to 32 families and 62 genera (Supplementary file 5). We inventoried 286 individuals of *Vitex* across all plots. Cluster partitioning of the MRT analyses in relation to environmental variables identified four habitats with an explanatory power of 11% (Fig. 1). Habitats were defined by three environmental variables (Mg and Al soil contents, and elevation). The discrimination of H1 (15 plots) and H4 (23 plots) was carried out on the basis of the Mg concentration at a threshold of 140 $\mu g.g^{-1}$. Above this Mg concentration, H1 and H2 (6 plots) were separated based on soil Al concentration at a threshold value of 220 $\mu g.g^{-1}$. The elevation at a threshold of 1230 m separated H3 (69 plots) H4 (Figs 1, 2). Significant variation among the habitats was found for the following variables: tree cover, elevation, Al, Fe, K, Mg, Mn, pH, and P (Supplementary file 6).

H1 was characterised by a very distinct floristic composition (Supplementary file 5), with 29 species only occurring in this habitat. Fabaceae were rare (9%) in this habitat. The species were grouped into two categories according to leaf phenology: deciduous (*Cassia abbreviata*, *Lannea discolor*, and *Zanthoxylum chalybeum*) and evergreen (*Allophylus africanus*, *Boscia mossambicensis*, *Markhamia obtusifolia*, and *V. fischeri*). *Markhamia obtusifolia* and *Combretum molle* were the most abundant species.

In the other three habitats, the Fabaceae was the most frequent family (48%). H2 had a low number of species (30 species) with an average tree height of 8.5 m. The average cover of the tree and shrub layer was 53% and

43%, respectively. *Brachystegia boehmii* and *B. spiciformis* were the most abundant species in H2. However, H3 and H4 were characterised by a dense shrub layer (52%) and a sparse tree layer (28%) with 66 and 54 species, respectively. The trees observed in H3 and H4 had an average height of 6.5 m. *Brachystegia boehmii* and *Albizia adianthifolia* were the abundant species in H3 and *B. spiciformis* and *Ochna schweinfurthiana* in H4.

Significant indicator species associated with each habitat were identified by permutations of the IndVal index in the habitat where the species was more abundant (Supplementary file 5). A total of 15 indicator species were detected in habitat H1, H2, and H4 (Table 1). No indicator species was found for H3. Two species of *Vitex* were indicative of distinct habitats. *Vitex fischeri* was indicative of H1 and *V. mombassae* of H4. In addition, *V. fischeri* had high absolute abundance in H1 and *V. mombassae* in H4. Both species had low abundance values in H2 and H3. In contrast, *V. madiensis* was equally frequent in H2, H3 and H4, and absent in H1 (Table 2).

A total of 45 specialist species were detected in all habitats. *Vitex fischeri* was a specialist in H1 and *V. mombassae* in H4. In contrast, *B. boehmii*, *B. spiciformis*, *Julbernardia paniculata*, and *V. madiensis* were generalists of H2, H3, and H4 (Supplementary file 5).

Relationship between species and environmental variables

A constrained ordination (RDA) was used to further describe and quantify the relation between community composition and environmental heterogeneity. The RDA between environmental variables and species abundances indicated a significant explanation of species composition

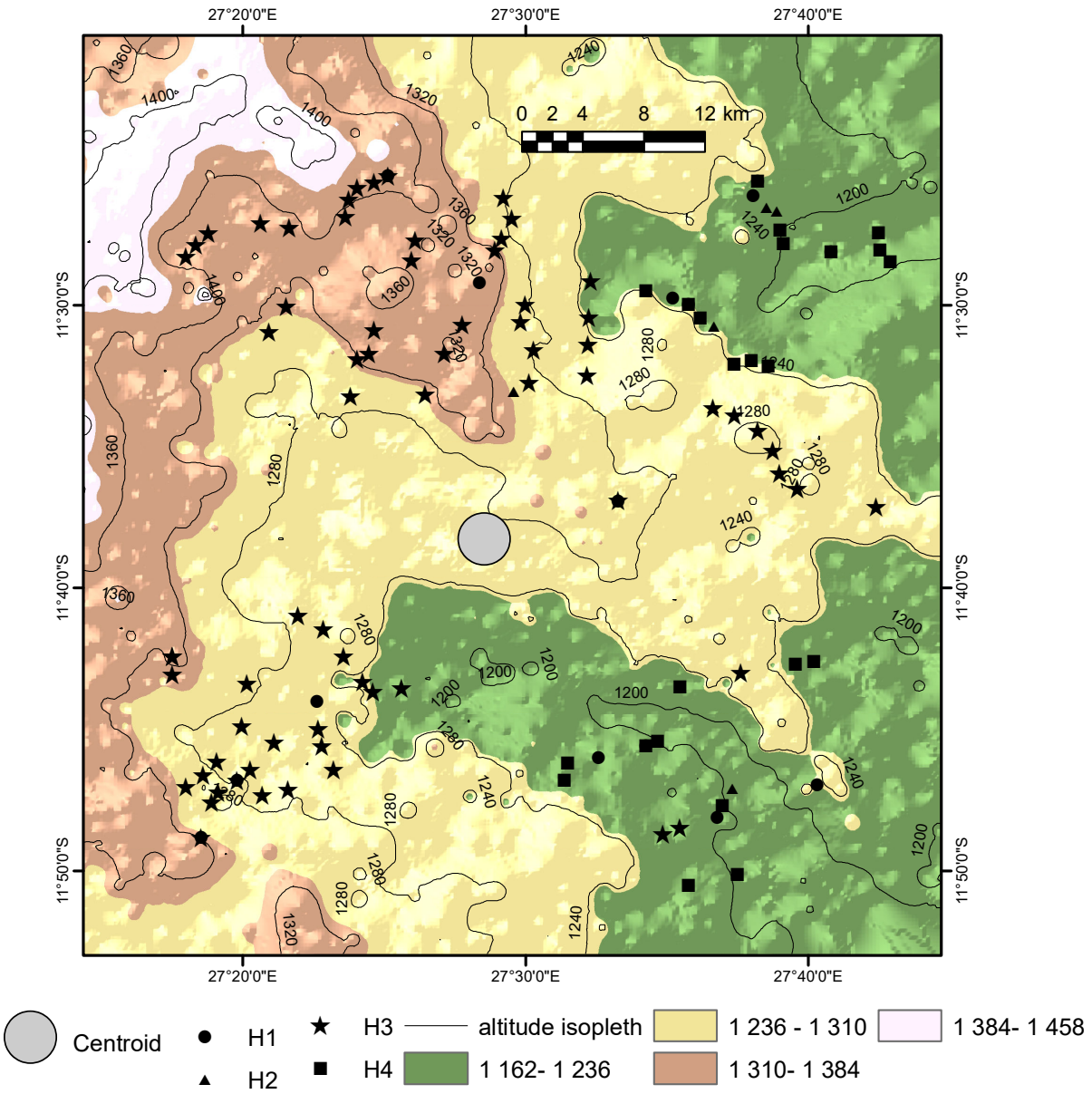

Figure 2. Spatial distribution of sampling points. The 4 MRT habitats are represented by different symbols. Topographic relief highlighted by different colours. The centre of the city of Lubumbashi is indicated by a grey disc.

Table 2. Absolute abundance (ABA) and relative abundance (REB) of the three species of *Vitex* in the four habitats.

Species	ABA				REB (%)			
	H1	H2	H3	H4	H1	H2	H3	H4
Vitex fischeri	39	3	3	0	88	6	6	0
Vitex madiensis	0	58	59	51	0	35	35	30
Vitex mombassae	0	7	13	56	0	9	17	74

variability by the environment ($p < 0.001$), although the overall explanatory power was relatively limited (adjusted $R^2 = 0.111$). The first two constrained axes explained 10.6% of the total variability. Axis 1 expressed on the constrained coordinated (7.6% of the variance) had major contributions from Mg, pH, K, Mn, and organic matter content (negative correlations), and Al and E (positive correlations) (Fig. 3A). Axis 2 (3% of variance) was mostly correlated with E (positively) and P (negatively), separating plots of lower elevation and higher P soil concentrations from higher elevations plots of lower P elevations (Fig. 3A).

The projection of the 4 MRT habitats in the ordination plane showed that habitats H1 and H2 were clearly different from the other two (H3 and H4). H1 was characterised by soil with high Mg concentration on axis 1, and H2 was located on fertile soils with high P concentration on axis 2. However, H3 and H4 formed a continuum located in intermediate altitude areas on poor soils with high Al concentrations (Fig. 3A). *Vitex fischeri* and *V. mombassae* were indicators of specific habitats (H1 and H4, respectively), while *V. madiensis* had a wide ecological range, occurring in H2, H3, and H4 (Fig. 3B).

DISCUSSION

Plant community of the three *Vitex*

The development of a conservation strategy requires a good knowledge of the species autecology. In this paper, we characterised the autecology of three congeneric, sympatric species of the genus *Vitex* that co-occur in the dry woodlands of southern D.R. Congo. The three species are important conservation targets due to their medicinal properties. In this paper, we assessed if they are associated to distinct plant communities and if their distribution can be accounted for by variation in environmental factors. The three species were found to occur in four habitats. We first examine if these habitats correspond to previously described vegetation units.

Habitat 1 corresponds to termite mound vegetation. The Katangan dry tropical woodlands are characterised by the presence of *Macrotermes* mounds, which harbour a highly distinctive vegetation (Malaisse 1978; Mushagalusa et al. 2018). We found *Vitex fischeri* to be a specialist of such vegetation, while the other two species almost never

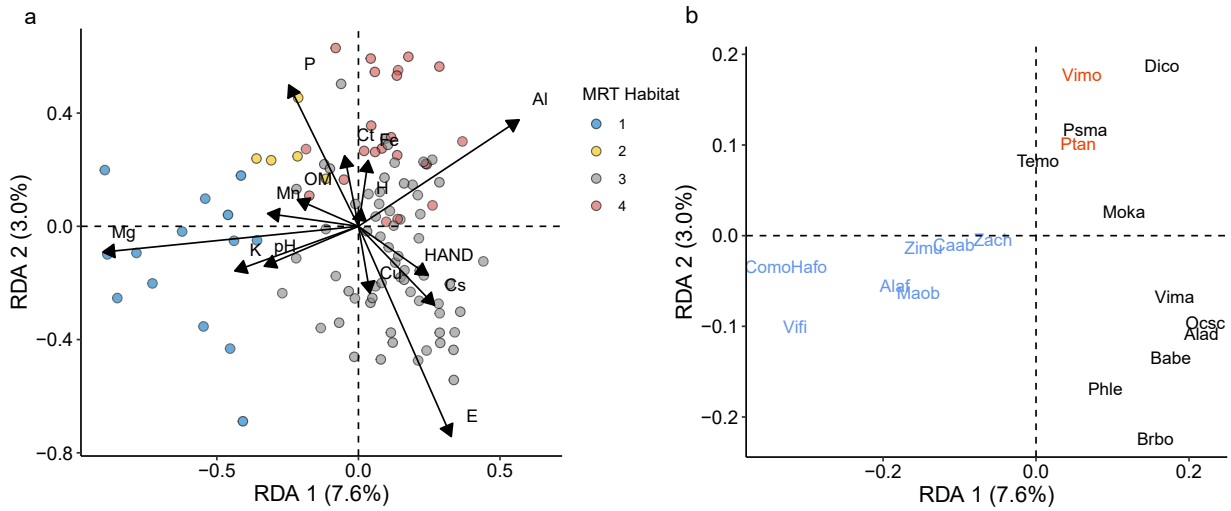

Figure 3. Ordination diagram showing the result of the redundancy analysis (RDA) in the constrained space. **A**. Projection of environmental variables and plots. Only significant variables ($p < 0.05$) are displayed; adjusted R^2 value = 0.098. The 4 habitats of the MRT are represented by different colours (H1: blue, H2: yellow, H3: grey, and H4: orange). **B**. Projection of species with goodness of fit ≥ 0.1 in the ordination plane formed by axes 1 and 2. Indicator species are coloured in the same way as their respective habitat and species in black have a goodness of fit = 0.1. The indicator species of H2 are not shown because they have goodness of fit values below 0.1. Elevation (E), shrub cover (Cs), tree cover (Ct), organic matter (OM). See Supplementary file 5 for species acronyms.

occur in it. Noticeably, the ectomycorrhizal tree genera characteristic of miombo woodlands (*Brachystegia*, *Isoberlinia, Julbernardia*) are lacking altogether in the termite mound community.

The other two species occur in the woodlands surrounding the termite mounds. Such woodlands are characterised by a high frequency of Fabaceae (*Julbernardia paniculata*, *Albizia adianthifolia*) and, in particular, the abundance of several species of *Brachystegia*. Based on the phytosociological classification of Schmitz (1971), the three communities comprising *V. madiensis* and *V. mombassae* belong to the Xerobrachystegion alliance. *Vitex* communities occur on soils that are neither extremely dry as suggested by the absence of species considered by Duvigneaud (1958) as indicative of shallow soils on rock outcrops (such as *Brachystegia microphylla*) nor with drainage impeded by lateritic crust as indicated by the lack of *B. utilis* and *B. stipulata*.

Modelling species-habitat associations

Our work further supports previous results pointing to the importance of topography and soil heterogeneity for the assemblage and dynamics of tree communities in miombo woodlands (Chidumayo 1987; Kanschik and Becker 2001; Mapaure 2001; Backéus et al. 2006; Munishi et al. 2011; Mwakalukwa et al. 2014; Muledi et al. 2017, 2020).

Here, we used complementary multivariate constrained analyses (MRT and RDA) to model soil-plant relationships associated with the three sympatric congeneric *Vitex* species at a regional scale. We highlighted four distinct habitats as well as associated specialist and indicator species and provided a detailed characterisation of the physico-chemical features of these habitats.

In this study, the four habitats presented statistically different values of nine environmental variables (see Supplementary file 6) and the discriminatory environmental variables of the habitats associated with the *Vitex* species were Mg, Al, and elevation. It is evident that even at fine spatial scales, heterogeneity in the edaphic and topographic environment facilitates the specialisation of species to contrasting habitats (Harms et al. 2001; Muledi et al. 2017). Thus, *V. fischeri* was a specialist and indicator in H1 characterised by high Mg and low exchangeable Al content (Supplementary file 6). The strong affinity of this species to high termite mounds was demonstrated by Mushagalusa et al. (2018). Compared to the surrounding matrix soils, termite mounds contain higher levels of clay-exchangeable base cations and the core of the mound constitutes a reservoir of available water (Turner et al. 2007; Mujinya et al. 2013). In a reciprocal transplant experiment, Mushagalusa et al. (2018) showed that termite mounds specialists are drought-sensitive species that do not resist the dry season when growing off termite mounds.

The other two *Vitex* species (*V. madiensis* and *V. mombassae*) were associated to base cation-poor soils with high aluminium concentration. *Vitex madiensis* was mainly a generalist of H2, H3, and H4. These results corroborate the observations of Chidumayo and Ellegaard (1993) who reported the presence of *V. madiensis* in several different habitats in the Zambezian region. In contrast, *V. mombassae* was a significant indicator and specialist of H4 located at lower elevations compared to H1, H2, and H3. The influence of elevation is surprising considering the narrow variation range in the study region (1178–1377 m) and could be mediated by geomorphological context. Batumike et al. (2006) suggested that geological variability on a regional scale may impact the pedology of the Lubumbashi plain, but also its topography. Duvigneaud (1958) pointed to topographical patterns in the floristic composition of Katangan dry woodlands, possibly due to variation in drainage. However, our results do not show a significant contribution of drainage on the structuring of the four habitats (Supplementary file 6). The significant effect of elevation could be mediated by geological background, because the different bedrocks tend to occupy slightly different elevation ranges (Supplementary files 7 and 8). Therefore, soil factors not analysed in this study and related to lithology, such as soil granulometry, could play in role in defining the ecological niche of *V. mombassae*.

The model generated from the MRT based solely on variability in soil chemistry, elevation, HAND, and structural variables predicted 10% and explained 11% of the spatial distribution of tree communities, while the RDA explained 9.9% using the same environmental variables. The explanatory and predictive powers observed in our study are lower than the range of variation (19% to 49%) of community-habitat associations in tropical forests (e.g. Mapaure 2001; Jones et al. 2008; Legendre et al. 2009; Chang et al. 2013; Punchi-Manage et al. 2013; Vleminckx et al. 2015; Muledi et al. 2017). The proportion unexplained by our variables could be attributed to stochastic processes (Legendre and Legendre 2012), or unmeasured environmental variables (Diniz-Filho et al. 2012; Baldeck et al. 2013). In addition, the woodland landscape of the Lubumbashi plain is subject to periodic anthropogenic activities that cause new filters responsible for species dispersal limitation (Cabala et al. 2017). These results suggest that the age of the forest land use succession plays an additive role in the community assemblages of these three *Vitex* species. In this paper, anthropogenic disturbance was indirectly assessed through the height and total cover of the woody layer. These variables do not appear to be key drivers of the discrimination of the four habitats, and all three *Vitex* species occur across a broad range of landscape degradation. A future paper will specifically examine the response of *Vitex* populations to anthropogenic disturbance.

These results emphasise the importance of a detailed knowledge of species ecology to design species-specific conservation strategies, for congeneric species occurring sympatrically in the same landscape. The designation of protected areas should include the different habitats

needed to conserve the three species. In particular, *V. fischeri* is associated to termite mounds, a habitat that is threatened by brick manufacturing. *Vitex mombassae* occurs mostly at lower elevations which are under pressure by shifting agricultural practices, while *V. madiensis* occupies a broader range of habitats, except termite mounds.

Future work on these *Vitex* species will be necessary to further understand their ecology as well as how it translates into potential differences in terms of secondary compounds of medical interest. Examples of future questions are whether the broad-niched *V. madiensis* is phenotypically more variable than the other two species, and whether populations occurring in different habitats show a different compositions of pharmacologically relevant compounds.

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SUPPLEMENTARY FILES

Supplementary file 1
Geographic map showing the spatial distribution of plots in the study area.
Link: https://doi.org/10.5091/plecevo.89394.suppl1

Supplementary file 2
Variation of environmental variables in the whole dataset.
Link: https://doi.org/10.5091/plecevo.89394.suppl2

Supplementary file 3
Pearson correlation coefficients between environmental variables.
Link: https://doi.org/10.5091/plecevo.89394.suppl3

Supplementary file 4
R code.
Link: https://doi.org/10.5091/plecevo.89394.suppl4

Supplementary file 5
Abundance of woody species associated with the three *Vitex* species in the four habitats.
Link: https://doi.org/10.5091/plecevo.89394.suppl5

Supplementary file 6
Comparison of environmental variables between the four habitats.
Link: https://doi.org/10.5091/plecevo.89394.suppl6

Supplementary file 7
Distribution of the four habitats in relation to geological substrate.
Link: https://doi.org/10.5091/plecevo.89394.suppl7

Supplementary file 8
Box plots of elevation as a function of geological substrate.
Link: https://doi.org/10.5091/plecevo.89394.suppl8