

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
<i>Vitex fischeri</i>	39	3	3	0	88	6	6	0
<i>Vitex madiensis</i>	0	58	59	51	0	35	35	30
<i>Vitex mombassae</i>	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

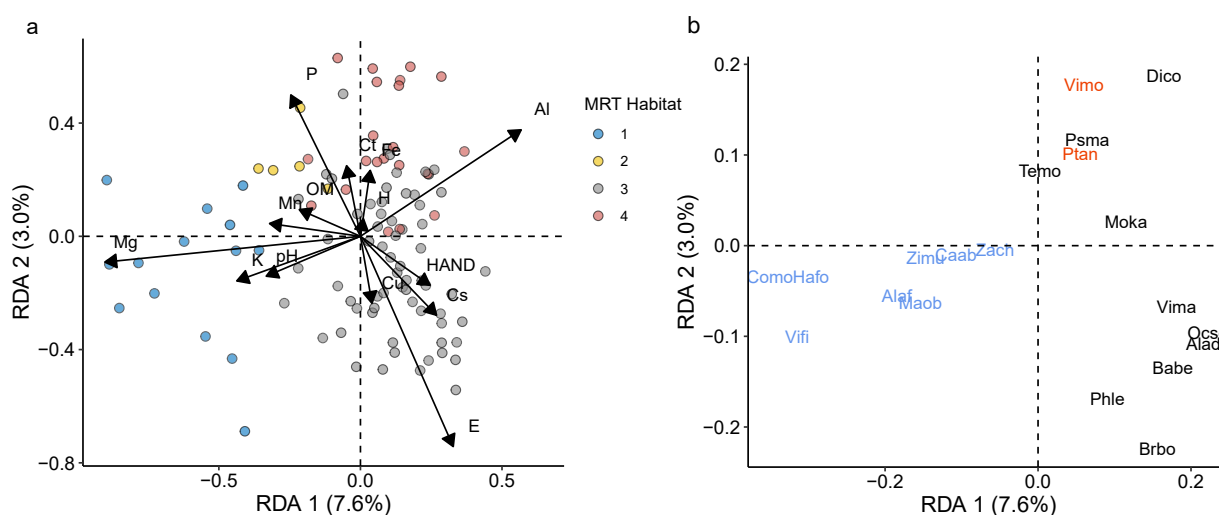


Figure 3. Ordination diagram showing the result of the redundancy analysis (RDA) in the constrained space. **A.** Projection of environmental variables and plots. Only significant variables ($p < 0.05$) are displayed; adjusted R^2 value = 0.098. The 4 habitats of the MRT are represented by different 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 Zambebian 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 a 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>