



Trait divergence of woody species in relation to affinity for termite mounds in Upper Katanga (DR Congo)

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Abstract

Question: Do functional traits vary in relation to affinity for termite mounds in trees of dry tropical woodlands?

Location: North of the Zambezi Region, Plain of Lubumbashi, Upper Katanga, DR Congo.

Methods: In four woodland sites, the occurrence of a total of 3,454 stems, on and off *Macrotermes* mounds has been recorded. Twenty-one functional traits including foliar concentrations of nutrients, specific leaf area (SLA), and leaf dry matter content (LDMC) were determined in 36 species. Intraspecific variation of traits was examined in one species (*Dalbergia boehmii*) occurring both on and off mounds.

Results: Most species had a narrow niche, with 22 species (31%) showing a strong positive affinity for termite mounds (>90% of occurrences) (T species), and 43 species (61%) showing strong negative affinity (<10% of occurrences) (NT species). Strong divergence of traits was found between T and NT species. Affinity for termite mounds was positively correlated to SLA and foliar concentrations of B, Ca, Fe, K, Mg, and negatively correlated to LDMC and leaf thickness. Intraspecific variation in *D. boehmii* showed the same pattern, though with a smaller amplitude.

Conclusions: Strong environmental filters are structuring the vegetation of dry tropical woodlands, with termitophilous species expressing a syndrome of faster resource capture and use, in line with the higher nutrient and water availability of termite mound soil. Broad-niched species are either more plastic, or have evolved locally adapted populations.

KEYWORDS

dry tropical woodland, edaphic specialization, intraspecific variation, miombo, niche, nutrients, termite, trait divergence, Zambezi region

1 | INTRODUCTION

Increasing evidence indicates that edaphic heterogeneity contributes to plant community diversity in the tropics (John et al., 2007; Mori, Schiatti, Poorter, & Piedade, 2019). In dry tropical woodlands

and savannahs of Africa, dramatic edaphic heterogeneity is driven by the activity of termites, with a remarkably general pattern of higher concentrations in base cations and clay in termite mounds (Erpenbach & Wittig, 2016; Jouquet, Traore, Choosai, Hartmann, & Bignell, 2011; Muvengwi, Ndagurwa, Nyenda, & Mbiba, 2016; Sileshi, Arshad, Konaté, & Nkunika, 2010). Termite mound soil also has larger stores of available water compared to surrounding soil

Abbreviations: NT, non-termitophilous; T, termitophilous.

(Bonachela et al., 2015; Jouquet, Dauber, Lagerlof, Lavelle, & Lepage, 2006; Konaté, Le Roux, Tessier, & Lepage, 1999; Sileshi et al., 2010; Turner, 2006).

Early botanical surveys in different regions of tropical Africa have repeatedly reported the distinctiveness of the plant cover of termite mounds (e.g. Fanshawe, 1968; Wild, 1952). More recent vegetation studies have confirmed that termite mounds harbour distinct plant communities, even though the degree of divergence in plant community composition depends on the regional climate and the geochemical context (Erpenbach, Bernhardt-Romermann, Wittig, Thiombiano, & Hahn, 2013; Joseph, Seymour, Cumming, Cumming, & Mahlangu, 2012; Muvengwi, Witkowski, Davies, & Parrini, 2017; Sileshi et al., 2010; Van der Plas, Howison, Reinders, Fokkema, & Olf, 2013).

In Upper Katanga (i.e. the northernmost part of the Zambeian region), *Macrotermes* termite mounds reach unrivalled density (3–5/ha) and size (up to 8 m high and 25 m in diameter), covering up to 8% of soil surface (Goffinet & Freson, 1972; Malaisse, 1978a, 1978b). Their soil has higher concentrations of base cations and clay (Erens et al., 2015; Mujinya et al., 2013), consistent with previous findings in other regions in Africa. Several authors have reported the original plant cover of *Macrotermes* mounds in Katanga (Duvigneaud, 1958; Malaisse, 1978a, 1985; Malaisse & Anastassiou-Socquet, 1977; Schmitz, 1971), based on floristic inventories.

In the last decade, a growing number of studies have analysed the distinct species assemblages of termite mound plant communities using ordination methods (Davies et al., 2014; Erpenbach et al., 2013; Muvengwi et al., 2016; Seymour et al., 2016; Vander Plas et al., 2013). However, to our knowledge, the affinity of individual species for termite mounds has not been tested based on large-scale censuses on whole regional floras (but see Joseph, Seymour, Cumming, Cumming, & Mahlangu, 2014). Also, the mechanisms underlying the distinct plant cover of termite mounds are poorly understood. Recently, in a reciprocal transplant experiment, Cuma Mushagalusa et al. (2018) found evidence for local adaptation in termite mound species. Seedlings of termite mound species transplanted to the surrounding woodland soil experienced higher mortality during the dry season, suggesting that they are more susceptible to water stress (Cuma Mushagalusa et al., 2018).

Functional traits have been increasingly popular to gain insight into the mechanisms of assemblage of plant communities (Kraft, Valencia, & Ackerly, 2008; McGill, Enquist, Weiher, & Westoby, 2006). The analysis of trait value distribution within and between communities allows assessing the strength of different filters acting on the assembly of communities (Cornwell & Ackerly, 2009; Mori et al., 2019). Since termite mounds have higher water and nutrient availability compared to the surrounding woodland matrix, we anticipate that termitophilous (T) and non-termitophilous (NT) species should exhibit divergent values of a number of functional traits. In particular, traits related to the leaf economics spectrum should be shifted to values reflecting higher rates of resource use (Grime et al., 1997; Wright et al., 2004). Only few previous studies have explored correlations between species traits and affinity for termite

mounds. Thus, Van der Plas et al. (2013), in the *Acacia* savannahs of South Africa, found larger concentrations of Na, Mg, and B in termite mound species but no difference for specific leaf area (SLA). Joseph et al. (2014) found larger foliar concentrations of N and P, larger SLA and higher frequency of evergreenness on mounds. Higher frequency of fleshy-fruited species on mounds has also been reported (Fleming & Loveridge, 2003; Joseph et al., 2012). In DR Congo, Colonval-Elenkov and Malaisse (1975) found higher frequency of spiny species in the woody flora of termite mounds.

In this paper, for the first time, we assessed the affinity of a large number of woody species for termite mounds in Upper Katanga, based on exhaustive population censuses on and off termite mounds at four different sites. We then measured functional traits in 36 species and tested whether species' trait values were correlated to affinity for termite mounds. For one species with a broad ecological amplitude, i.e. occurring on and off mounds, we examined intraspecific variation in functional traits and tested whether populations on and off mounds show distinct trait values.

2 | MATERIALS AND METHODS

2.1 | Study region

The study was conducted in the region of Lubumbashi (Province of Upper Katanga, DR Congo). The mean annual temperature is 20.3°C and the average annual precipitation is 1,200 mm, distributed mainly from November to April. The climate is Sudanian, corresponding to Cwa in Köppen's classification (Peel, Finlayson, & McMahon, 2007). Upper Katanga represents the northern part of the Zambeian centre of endemism (Malaisse, 1996; White, 1983). The vegetation consists of dry tropophilous woodlands, locally known as miombo, from the name of the most characteristic trees, i.e. *Brachystegia* (Fabaceae Caesalpinioideae) (Duvigneaud, 1958; Malaisse, 1978b; Schmitz, 1971; Werger & Coetzee, 1978). The miombo of Upper Katanga is of the wet type, corresponding to regions with rainfall >1,000 mm. Wet miombo is characterised by larger canopy height (ca. 20 m) and by a higher frequency of evergreen species (Malaisse, 1997). The landscape shows a flat topography, regularly punctuated (~3/ha) by termite mounds (up to 8 m high) (Goffinet & Freson, 1972; Mujinya et al., 2013). The geological substrate is dominated by dolomitic shales and siltstones from the Neoproterozoic Nguba and Roan Groups (Batumike, Kampunzu, & Cailteux, 2006). The soils are mostly haplic and xanthic Ferralsols characterised by low pH and nutrient content and a sandy loam to clay loam texture (Ngongo et al., 2009).

2.2 | Study sites

Four sites have been sampled in the Plain of Lubumbashi, i.e. Mikembo (11°28'36,43" S, 27°39'58,00" E, 1,181 m a.s.l.); Kiswishi (11°32'15,68" S, 27°28'06,40" E, 1,319 m a.s.l.); Kipopo (11°32'11,12" S, 27°19'29,8" E, 1,314 m a.s.l.) and Kaluwe (11°32'18,68" S, 27°7'8,63" E). These sites were selected due to their relatively well-preserved miombo vegetation. In the four sites,



the vegetation consists of dry tropical woodland with *Brachystegia* but with differences in the relative frequency of dominant species, i.e. Kipopo: *Brachystegia spiciformis*, *Julbernardia paniculata*, *J. globiflora*; Kiswishi: *Diplorhynchus condylocarpon*, *Strychnos spinosa*; Mikembo: *Marquesia macroura*, *Julbernardia paniculata*; Kaluwe: *Diplorhynchus condylocarpon*, *Combretum collinum* (nomenclature after Meerts [2016]). These four sites represent the floristic variation of miombo woodlands in the Plain of Lubumbashi (*Mesobrachystegion* and *Berlinio-Marquesion* in the phytosociological terminology of Schmitz [1971]).

2.3 | Species sampling

At each site, within a 12-ha area, 40 termite mounds have been sampled. In the surrounding matrix, 40 circular plots 15 m in diameter (i.e. similar to the average diameter of termite mounds in Upper Katanga [Goffinet & Freson, 1972]) have been sampled. In each plot, all stems of woody species (diameter at breast height (DBH) > 5 cm; meso- and microphanerophytes, lianas excluded) have been counted and identified to species.

The affinity of each species for termite mounds has been expressed as a “termitophily index” (IndT) calculated as $\text{IndT} = X_t / (X_t + X_m)$ where X_t and X_m are the number of occurrences of the species on and off termite mounds, respectively.

2.4 | Traits

For each individual, height has been measured with a clinometer (Suunto, Vantaa, Finland) after the method of Rondeux (1999) and girdle at breast height was determined with a measuring tape. Diameter at breast height was calculated as $\text{girdle}/3.14$.

Functional-trait measurements were performed at the site Mikembo for which extensive soil analyses are available. For 36 species (14 T, 22 NT) represented by at least 10 individuals, leaves were sampled in December 2016 and January 2017. For *Dalbergia boehmii*, a species present at the same frequency on and off termite mounds (“neutral species”), traits were measured on 10 individual trees on and off mounds in order to explore intraspecific trait variation. Leaves were sampled on adult trees, on branches exposed to the sun, following Perez-Harguindeguy et al. (2013). For each individual, two leaves were collected and weighed (fresh mass) and photographed. The leaves were oven-dried at 50°C for 48 h and their dry mass determined to the nearest 0.0001 g. Leaf area (LA) was determined from pictures using ImageJ (<http://imagej.nih.gov/ij/>). SLA was determined as LA/dry mass. Dry matter content was determined as the ratio between dry and fresh mass. Leaf thickness was estimated as the ratio of fresh mass and LA, after Vile et al. (2005).

Mineral element concentrations in leaves were determined by dry ashing at 500°C. Ashes were dissolved in nitric acid 65%, and Al, B, Ca, Fe, K, Mg, Mn, P and Zn contents were determined by inductively coupled plasma–optical emission spectrometry (Vista MPX CCD Simultaneous; Varian).

Twig density was determined on 20-cm long cuttings of twigs (20–30 mm in diam.). Diameter was determined with calipers to the nearest mm. Twig dry mass (oven-dried at 50°C to constant weight) was determined at 0.0001 g. Assuming a cylindrical shape, twig density was calculated as $\text{DM}/(\pi r^2 L)$, where r is the radius, L is the length and DM the dry mass of the twig. Wood density could not be determined using standard protocols because we were not allowed to bore tree boles at the study site.

Finally, the following qualitative traits were recorded for each species: spinescence (present/absent), leaf phenology (evergreen, brevideciduous (leaves shed at the end of the dry season a few days before bud break), deciduous) and diaspore type (fleshy i.e. drupe or berry, dry i.e. achene or seed).

2.5 | Soil analyses

To determine soil chemical properties and texture, samples were collected at the site Mikembo Sanctuary, a reference site for miombo ecology in DR Congo (Bauman et al., 2016; Ilunga Muledi et al., 2017). In the woodland matrix, soil was sampled in 102 plots of 25 m × 25 m, randomly selected from a grid of 160 plots as explained by Ilunga Muledi et al. (2017). In each plot, five cores were sampled at 0–15 cm depth (one core at the centre and four cores on the two diagonals, 5 m from each corner). In 48 termite mounds, one sample was collected at mid-height of the slope (0–15 cm depth; see Cuma Mushagalusa et al. [2018] for soil analysis methods). To determine the water holding capacity, we used samples collected from two termite mounds (Kasapa and Kimbeimbe) described by Mujinya et al. (2011, 2013) and Erens et al. (2015) (see details of sampling design therein). See Cuma Mushagalusa et al. (2018) for water holding capacity determination methods.

2.6 | Data analysis

The total stem counts on the termite mounds and matrix plots were 1743 and 1711, respectively. We used a Fisher exact test to evaluate whether the count ratio of species X on and off termite mounds (i.e., X_t/X_m) differed significantly from the count ratio computed for the whole woody community (after exclusion of species X), that is, $(N_t - X_t)/(N_m - X_m)$. A significantly higher ratio of the species of interest with respect to that of the rest of the community indicates a positive association of species X with termite mounds, compared to the rest of the community. Such species can conveniently be referred to as “termitophilous” (T). A significantly lower ratio indicates a negative association of the species with termite mounds, which can be referred to as “not termitophilous” (NT). Species neither associated to the matrix nor to termite mounds are referred to as “neutral”. The Fisher exact test was performed in each site separately and for all sites pooled. Only species represented by at least five individuals were considered in the study.

Trait comparisons were performed in the subsample of species that were significantly NT or T in all four study sites (T: 13 species, NT: 14 species). First, a permutational multivariate analysis of



variance (PERMANOVA) was performed in order to assess whether T and NT species are functionally different, when using all the traits together. This approach has the advantage that it explicitly considers among-trait covariation, therefore capturing potential signals related to the well-documented evolutionary functional trade-offs (e.g. Chave et al., 2009; Díaz et al., 2015; Dwyer & Laughlin, 2017; Westoby, Falster, Moles, Vesk, & Wright, 2002; Wright et al., 2004). Secondly, χ^2 tests and Wilcoxon rank sum tests were used to compare qualitative and quantitative traits between T and NT species, respectively. The corresponding p -values were adjusted for multiple tests using Benjamini and Hochberg's false discovery rate correction (Benjamini & Hochberg, 1995). Thirdly, a Principal Components Analysis was done based on all quantitative traits (including the termitophily index) for the 36 species (14 T, 22 NT) for which functional traits were measured, in order to visually assess whether T and NT species occupy distinct multidimensional functional trait spaces and to assess multivariate correlation patterns between functional traits and the termitophily index.

Finally, in order to explore the intraspecific trait variation of *Dalbergia boehmii* (Fabaceae subfam. Faboideae), a neutral species, the quantitative functional traits of the individuals on and off termite mounds were compared using Wilcoxon rank sum tests. The p -values were adjusted using the false discovery rate correction (Benjamini & Hochberg, 1995).

All analyses were performed using the R statistical environment (R Core Team, 2018), except PCA and PERMANOVA which were performed using PAST (Hammer, Harper, & Ryan, 2001).

3 | RESULTS

3.1 | Soil

Soil data were reported extensively by Cuma Mushagalusa et al. (2018). We here give only a brief overview of the differences between mounds and matrix (Appendix S1). Soils from termite mounds and matrix were significantly different for all parameters ($p < 0.01$, except K: $p > 0.05$). Termite mounds had higher concentrations of available Ca (10-fold difference), Mg (6-fold), Mn (5-fold), and organic matter (1.5-fold). In contrast, the matrix soil had higher concentrations of Al (3-fold), P (2-fold), and Fe (1.3-fold). The pH was higher in termite mound soils (6.0 vs 5.0) and so were clay (37.5% vs 24.6%) and silt (25.1% vs 18.6%) contents.

At both sites, available water content was much higher (2–4 times) for the termite mound samples than for the surrounding matrix soils (0.067–0.125 m^3/m^3 vs 0.035–0.042 m^3/m^3 , respectively). For pF curves and bulk density data, see Cuma Mushagalusa et al. (2018).

3.2 | Species affinity for termite mounds

A total of 3,454 stems representing 96 woody species (micro- and mesophanerophytes, lianas excluded) were recorded in the four study sites (1743 on termite mounds and 1711 in the surrounding

matrix). The termitophily index (I_t) defined as the frequency of occurrence on termite mounds, was calculated for 70 species represented by five individuals or more (four sites pooled) (Appendix S2). I_t showed a markedly bimodal distribution (Figure 1). Based on the Fisher exact test, 22 species were significantly positively associated to termite mounds ("termitophilous" species), 43 were negatively associated to mounds, and five species were neutral, i.e. neither positively nor negatively associated to mounds. The affinity for termite mounds was remarkably consistent across sites (Table 1).

3.3 | Comparison of traits between T and NT species

The comparison of traits was performed on the subsample of species significantly T or NT in each of the four study sites (T: $n = 13$; NT: $n = 14$) (Table 1).

PERMANOVA (17 traits) shows a very highly significant functional divergence between the two groups of species ($F = 4.525$; $p = 0.0006$).

A significant difference was found in eight of the 17 traits examined (Table 2). Termitophilous species had significantly larger foliar concentrations of B (ca. 45% larger), Ca (+48%), Fe (+49%), K (+29%) and Mg (+35%), had larger SLA (+30%, only marginally significant), and thinner leaves (–20%). No significant difference was found for Al, Cu, P, Mn, Zn, height, DBH, and twig density. Regarding the qualitative traits, the proportion of species with fleshy propagules was significantly higher among T species (10/13) compared to NT species (5/14) (Table 3).

Figure 2 shows the first two axes of the PCA computed from the quantitative traits. The first and second axes described 26% and 15% of the overall trait variability. The first axis is positively correlated to the termitophily index, SLA, and foliar concentrations of Ca, Mg, K, and B, and negatively correlated to leaf thickness and

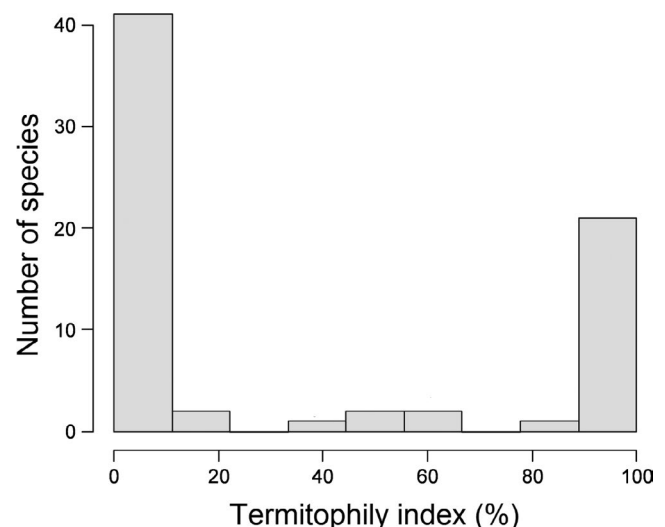


FIGURE 1 Distribution of the termitophily index values (i.e. the percentage of occurrences on termite mounds) among woody species in four dry tropical woodlands in Upper Katanga, DR Congo

**TABLE 1** Affinity of woody species for termite mounds in four sites in the Plain of Lubumbashi (DR Congo)

Species	Kipopo	Kiswishi	Kaluwe	Mikembo	Four sites pooled
<i>Albizia antunesiana</i>	-	-	NT*	-	NT** (8%)
<i>Allophylus africanus</i>	T***	T***	T**	T***	T*** (99%)
<i>Anisophyllea boehmii</i>	-	-	-	NT**	NT*** (5%)
<i>Balanites aegyptiaca</i>		-		T**	T** (100%)
<i>Baphia bequaertii</i>		NT*			NT* (0%)
<i>Bobgunnia madagascariensis</i>			-	-	NT** (0%)
<i>Boscia mossambicensis</i>	T***	T***	T***	T***	T*** (100%)
<i>Brachystegia boehmii</i>	NT***	NT**	NT***	NT***	NT*** (0%)
<i>Brachystegia longifolia</i>			NT*	-	NT** (0%)
<i>Brachystegia spiciformis</i>	NT***	NT***	NT***	NT***	NT*** (0%)
<i>Brachystegia taxifolia</i>		NT*		NT**	NT*** (0%)
<i>Brachystegia wangermeeana</i>	NT***	NT***	NT***	NT***	NT*** (0%)
<i>Bridelia duvigneaudii</i>	-	-		-	N (56%)
<i>Cassia abbreviata</i>	T***	T*	T*	T***	T*** (100%)
<i>Combretum adenogonium</i>		-			NT* (0%)
<i>Combretum collinum</i>	NT**	-	NT***	NT***	NT*** (1%)
<i>Combretum molle</i>	T***	T***	T***	T***	T*** (99%)
<i>Commiphora glandulosa</i>	T*	-	T*	T**	T*** (100%)
<i>Dalbergia boehmii</i>	N	N		N	N (44%)
<i>Dichrostachys cinerea</i>			-	N	N (50%)
<i>Diospyros lycioides</i>		-	-	T*	T** (100%)
<i>Diospyros mespiliformis</i>	T***	T*	T*	T***	T*** (98%)
<i>Diplorhynchus condylocarpon</i>	NT***	NT***	NT***	NT***	NT*** (5%)
<i>Ekebergia benguelensis</i>				-	NT* (0%)
<i>Erythrina abyssinica</i>	N	-	N	N	N (47%)
<i>Erythrophleum africanum</i>			-	-	NT* (0%)
<i>Euclea racemosa</i>	T***	T***	T**	T***	T*** (100%)
<i>Feretia aeruginescens</i>			-	T**	T** (100%)
<i>Ficus thonningii</i>		N	-		N (60%)
<i>Friesodielsia obovata</i>				T*	T* (100%)
<i>Garcinia huillensis</i>	-	-	-		NT* (13%)
<i>Gymnosporia senegalensis</i>			-	T**	T** (100%)
<i>Haplocoelum foliolosum</i>	T***	T***	T***	T***	T*** (99%)
<i>Harungana madagascariensis</i>			NT*		NT* (0%)
<i>Hexalobus monopetalus</i>	-	NT**	NT*	-	NT*** (0%)
<i>Hymenocardia acida</i>	-	-		NT***	NT*** (0%)
<i>Hymenodictyon parvifolium</i>	-	-		T***	T*** (100%)
<i>Julbernardia globiflora</i>	NT***	NT***	NT***	NT***	NT*** (1%)
<i>Julbernardia paniculata</i>	NT***	NT***	NT***	NT***	NT*** (1%)
<i>Lannea discolor</i>	T***	T***	T**	T***	T*** (87%)
<i>Markhamia obtusifolia</i>	T***	T***	T***	T***	T*** (99%)
<i>Marquesia macroura</i>	NT***	NT***	NT***	NT**	NT*** (0%)
<i>Monotes katangensis</i>	NT***	NT*	NT***	NT***	NT*** (2%)
<i>Multidentia crassa</i>			-	-	NT* (0%)
<i>Pappea capensis</i>			-	T**	T*** (100%)

(Continues)



TABLE 1 (Continued)

Species	Kipopo	Kiswishi	Kaluwe	Mikembo	Four sites pooled
<i>Parinari curatellifolia</i>	NT*	NT*	-	NT*	NT*** (8%)
<i>Pericopsis angolensis</i>	NT***		NT**	NT**	NT*** (12%)
<i>Philenoptera katangensis</i>	NT***	NT**	NT***	NT**	NT*** (2%)
<i>Pseudolachnostylis maprouneifolia</i>	NT**	NT***	NT**	NT***	NT*** (7%)
<i>Psorospermum febrifugum</i>			-	-	NT** (0%)
<i>Pterocarpus angolensis</i>	NT***	NT***	NT**	NT***	NT*** (0%)
<i>Pterocarpus tinctorius</i>				NT***	NT*** (5%)
<i>Strychnos cocculoides</i>		NT*	-	-	NT*** (0%)
<i>Strychnos innocua</i>	NT*			-	NT*** (0%)
<i>Strychnos potatorum</i>	T***		T***	T***	T*** (100%)
<i>Strychnos spinosa</i>	NT***	NT***	NT***	NT***	NT*** (0%)
<i>Syzygium guineense</i>	-	NT*	NT*	-	NT*** (0%)
<i>Terminalia mollis</i>				-	NT* (0%)
<i>Thespesia garckeana</i>		T*	-	T*	T*** (100%)
<i>Uapaca kirkiana</i>	NT*	NT***	-		NT*** (0%)
<i>Uapaca nitida</i>	NT***	NT*	NT***	NT***	NT*** (0%)
<i>Uapaca pilosa</i>	NT***	NT**	NT***	NT***	NT*** (0%)
<i>Uapaca sansibarica</i>			NT*	-	NT** (0%)
<i>Uvariastrum hexaloboides</i>		-		-	NT** (0%)
<i>Vitex doniana</i>	-		-		NT* (0%)
<i>Vitex fischeri</i>	T***	T**	T***	T**	T*** (97%)
<i>Vitex mombassae</i>	NT**	NT**	NT**	NT*	NT*** (0%)
<i>Zanthoxylum chalybeum</i>	T***	T***	T***	T***	T*** (100%)
<i>Ziziphus abyssinica</i>	NT***		NT***	NT***	NT*** (2%)
<i>Ziziphus mucronata</i>	T***	T***	T***	T***	T*** (100%)

For each species, a Fisher exact test was used to compare the ratio of the number of occurrences on mounds (X_t) and in the matrix (X_m) to this same ratio computed over the whole community, regardless of species (N_t, N_m). A non-significant test indicates a neutral species (N), a significant test with $N_t > N_m$ indicates a termitophilous species (T) and a significant test with $N_t < N_m$ indicates a termitofuge species (NT). *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$. The test is performed at each site and for the four sites pooled. The percentage in brackets is the "termitophily index", i.e., the proportion of occurrences of the species on termite mounds. Empty cells indicate the absence of the species in the corresponding site; (-) indicates that the species is present with less than five occurrences. Nomenclature follows Meerts and Hasson (2016) and Meerts (2016). For species occurrence counts, see Appendix S2

LDMC. The second axis is positively correlated to foliar concentrations of Al, Cu, Fe, and Zn. The two groups of species (T, NT) form two almost non-overlapping scatter plots, T species being shifted towards positive scores on PC1.

3.4 | Intraspecific variation in a broad-niched species

Dalbergia boehmii (Fabaceae), a "neutral" species, was represented across the four sites by 62 occurrences on termite mounds and 80 occurrences in the matrix. Its traits were compared between populations in the two types of habitats. Individuals on termite mounds had significantly larger values of B (+27%), Ca (+37%), Mg (+19%, only marginally significant), SLA (+11%), LA (+22%) and smaller values of Mn content (-43%), twig density (-10%), leaf thickness (-10%), and LDMC (-11%) (Table 4). The other traits did not show significant differences.

4 | DISCUSSION

4.1 | Two groups of species with non-overlapping realised niches

Termite mounds offer a striking example of dramatic short-distance variation in soil conditions in tropical Africa. Termite mounds harbour original plant communities, contrasting with the surrounding matrix (Erpenbach et al., 2013, 2017; Muvengwi et al., 2017; Seymour et al., 2016; Van der Plas et al., 2013). However, the mechanisms underlying that pattern are unclear. Functional traits can provide key insights into the mechanisms shaping species niche (McGill et al., 2006). Here for the first time we have assessed affinity for termite mounds in a whole regional flora, in order to explore the relations between the realised niche and species' functional traits. A striking result is the existence in the dry tropical woodlands



of Upper Katanga of two groups of species with almost non-overlapping realised niches. Here, 43 of 70 species occurred on termite mounds at frequencies <10%, and 22 species occurred on termite mounds at frequencies >90%. The scarcity of broad-niched species (i.e. with intermediate frequency of occurrence) is particularly striking (only eight of 70 species). We are aware of only one previous study (Joseph et al., 2014) reporting that only a minority of species (three of 36 in their study) are present both on mounds and in the matrix.

4.2 | Trait divergence

The bimodal distribution frequency of the termitophily index suggests that very strong filters determine the structuring of that vegetation pattern. This is confirmed by the strong divergence in functional traits between the two species groups. T and NT species do indeed occupy distinct positions in the leaf economics spectrum as defined by Wright et al. (2004) and McGill et al. (2006). Thus, T species tend to have larger SLA, lower LDMC, thinner leaves and larger foliar concentrations of nutrients. This suite of traits points to a syndrome of faster resource capture and faster growth rate, typical of species adapted to resource-rich habitats (Colgan, Martin, Baldeck, & Asner, 2015; Grime et al., 1997; Wright et al., 2004). Only few previous studies compared functional traits of termitophilous and non-termitophilous species (Holdo & McDowell, 2004; Joseph et al., 2014; Van der Plas et al., 2013). Termitophilous species generally had higher foliar mineral element concentrations. Higher SLA was found by Joseph et al. (2014) but not by Vander Plas et al. (2013). In Upper Katanga as well as across all tropical Africa, termite mound soil has higher concentrations of base cations (Ca, Mg, K) and larger stores of available water compared to the surrounding matrix (Garba, Cornelis, & Steppe, 2011; Konaté et al., 1999; Turner, 2006). Miombo woodlands are limited both by soil nutrients and by water, especially in the dry season (Frost, 1996). The low SLA values of matrix species in our study are accounted for both by thicker leaves and by higher LDMC. Thus, NT species apparently express foliar traits conferring more conservative resource use.

The foliar traits of termitophilous species point to a faster growth rate and higher uptake rate of water and nutrients. Such traits might incur a cost in terms of poor survival in resource-limited conditions, i.e. in the matrix. Recently, in a reciprocal transplant experiment, Cuma Mushagalusa et al. (2018) found that drought stress in the dry season was the main factor explaining poor survival of termitophilous species away from their native habitat. Thus, our results on functional traits are consistent with the contrasting niche affinities of the two species groups. Due to the larger frequency of evergreens, the environment on termite mounds might not only be determined by substrate, but also by shading, reducing temperatures and so reducing evaporation and water stress (Joseph et al., 2016).

The differences in foliar concentrations of nutrients parallel the differences in nutrients concentrations in the soil. Therefore, it is unclear if foliar mineral element composition tracks the composition of the soil (i.e. phenotypic plasticity) or if part of the difference is constitutive,

TABLE 2 Comparison of functional traits and foliar mineral element concentrations between termitophilous and non-termitophilous species

	T (n = 13)	NT (n = 14)	W	p
Leaf area (cm ²)	124 ± 148	85.5 ± 66.8	87	ns
LDMC (%)	37.2 ± 4.5	39.6 ± 3.4	131.5	ns
Leaf thickness (g cm ²)	0.021 ± 0.004	0.028 ± 0.008	146.5	*
SLA (cm ² g ⁻¹)	132 ± 37	101 ± 20	46	•
DBH (cm)	32.0 ± 7.1	30.9 ± 13.7	80.5	ns
Height (m)	14.7 ± 6.4	16.8 ± 5.5	118	ns
Twig density (m ³ kg ⁻¹)	0.67 ± 0.20	0.66 ± 0.07	88	ns
Al (µg g ⁻¹)	309 ± 356	142 ± 155	58	ns
B (µg g ⁻¹)	33.2 ± 15.5	18.0 ± 9.8	36	*
Ca (µg g ⁻¹)	13,278 ± 6,054	6,857 ± 4,434	26	**
Cu (µg g ⁻¹)	12.9 ± 8.9	8.8 ± 4.5	66	ns
Fe (µg g ⁻¹)	116 ± 99	59.4 ± 39.5	42	*
K (µg g ⁻¹)	11,640 ± 2,160	8,244 ± 2,923	27	**
Mg (µg g ⁻¹)	4,628 ± 1,322	2,979 ± 1,007	30	*
Mn (µg g ⁻¹)	187 ± 88	186 ± 88	90	ns
P (µg g ⁻¹)	1,223 ± 257	1,240 ± 385	92	ns
Zn (µg g ⁻¹)	32.8 ± 22.2	21.2 ± 11.2	60	ns

Species included: T: *Allophylus africanus*, *Boscia mossambicensis*, *Cassia abbreviata*, *Combretum molle*, *Diospyros mespiliformis*, *Euclea racemosa*, *Haplocoelum foliolosum*, *Lannea discolor*, *Markhamia obtusifolia*, *Vitex fischeri*, *Zanthoxylum chalybeum*, *Ziziphus mucronata*; NT: *Brachystegia boehmii*, *Brachystegia spiciformis*, *Diplorhynchus condylocarpon*, *Julbernardia globiflora*, *Julbernardia paniculata*, *Marquesia macrourea*, *Monotes katangensis*, *Philenoptera katangensis*, *Pseudolachnostylis maprouneifolia*, *Pterocarpus angolensis*, *Strychnos spinosa*, *Uapaca nitida*, *Uapaca pilosa*, *Vitex mombassae*.

Mean ± SD. W: Wilcoxon test. See Appendix S4 for species trait value data. Significance after Benjamini–Hochberg correction for multiple tests: ***p < .001; **p < .01; *p < 0.05; •p < .1; ^{ns}p > .1.

reflecting contrasting leaf structures. In principle, reciprocal transplant experiments are a suitable strategy to address this issue. However, such experiments could be strongly limited in practice due to the high mortality rate suffered by seedlings of termitophilous species grown on the soil matrix, and vice versa (Cuma Mushagalusa et al., 2018).

Apart from traits related to the leaf economics spectrum, we found only few consistent differences between T and NT species. Propagules of T species were more often fleshy compared to NT species, consistent with an earlier report by Joseph et al. (2014). This difference reflects the larger contribution of a few families with dry propagules in the matrix, i.e. Fabaceae and Dipterocarpaceae. Interestingly, termitophilous species are not a homogeneous group for leaf phenology, comprising both deciduous (*Cassia abbreviata*, *Commiphora glandulosa*, *Lannea discolor*, *Zanthoxylum chalybeum*) and evergreen species (*Allophylus africanus*, *Boscia mossambicensis*, *Diospyros mespiliformis*, *Euclea racemosa*). The mechanisms allowing for coexistence of these two strategies on termite mounds deserve further investigation.

Trait		Number of species		χ^2	p
		T (n = 13)	NT (n = 14)		
Spinescence	Present	3	1	1.356 (df = 1)	ns
	Absent	10	13		
Propagule	Fleshy	10	5	4.636 (df = 1)	•
	Dry	3	9		
Leaf phenology	Evergreen	4	2	2.967 (df = 2)	ns
	Brevideciduous	5	10		
	Deciduous	4	2		

See Appendix S4 for species trait value data. Significance after Benjamini–Hochberg correction for multiple tests: *** $p < .001$; ** $p < .01$; * $p < .05$; • $p < .1$; ^{ns} $p > .1$.

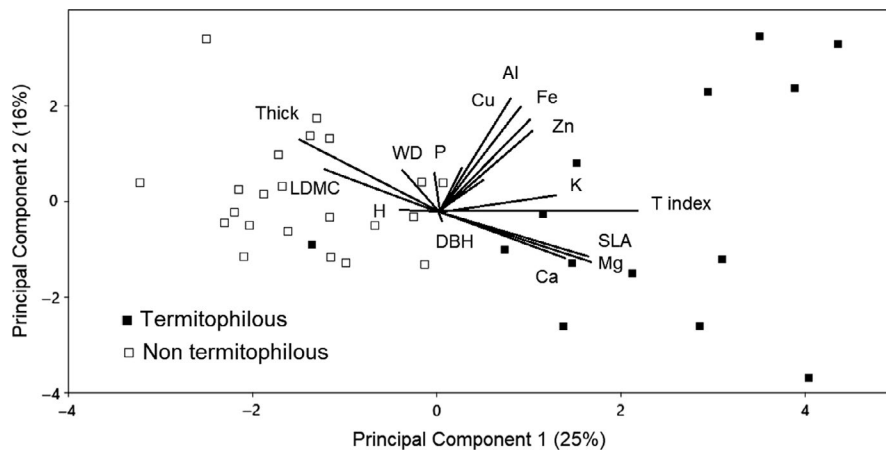


FIGURE 2 Principal Components analysis on 18 variables (17 functional traits, and termitophily index) based on 36 species present in all four study sites. Projection of variables and species on PC1 and 2. DBH: diameter at breast height, H: height, LA: leaf area, LDMC: leaf dry matter content, SLA: specific leaf area, Thick: leaf thickness, T index: termitophily index, WD: twig density

Traits	On mounds (n = 20)	Off mounds (n = 20)	W	p
Leaf area (cm ²)	134 ± 24	104 ± 15	21	*
LDMC (%)	37.7 ± 2.9	42.1 ± 1.8	125.5	**
Leaf thickness (g cm ⁻²)	0.018 ± 0.001	0.021 ± 0.002	122.5	**
SLA (cm ² g ⁻¹)	142 ± 9	126 ± 78	13	**
Twig density (m ³ kg ⁻¹)	0.53 ± 0.03	0.59 ± 0.05	126	***
Al (μg g ⁻¹)	40.9 ± 18.7	41.8 ± 16.1	86	ns
B (μg g ⁻¹)	30.4 ± 6.1	22.2 ± 8.8	32	*
Ca (μg g ⁻¹)	6,344 ± 1721	3,990 ± 1,452.4	29.5	*
Cu (μg g ⁻¹)	16.1 ± 3.6	15.4 ± 5.3	62	ns
Fe (μg g ⁻¹)	58.1 ± 9.5	58.5 ± 20.7	62	ns
K (μg g ⁻¹)	7,150 ± 1,467	6,421 ± 1,375	55	ns
Mg (μg g ⁻¹)	3,153 ± 795	2,532 ± 465	35	•
Mn (μg g ⁻¹)	115 ± 32	202 ± 130	109	*
P (μg g ⁻¹)	1,151 ± 139	1,448 ± 452	103.5	•
Zn (μg g ⁻¹)	34.0 ± 9.7	36.7 ± 11.1	85	ns

Comparison of functional traits and foliar mineral element concentrations between individuals on and off mounds. Mean ± SD. See Appendix S5 for trait data. W: Wilcoxon test. Significance symbols after Benjamini–Hochberg correction for multiple tests: *** $p < .001$; ** $p < .01$; * $p < .05$; • $p < .1$; ^{ns} $p > .1$.

TABLE 4 Intraspecific variation of traits in *Dalbergia boehmii*, a species present both on and off termite mounds

Traits not considered in this study may also contribute to the different ecological niche of T and NT species. In particular, mutualistic interactions with mycorrhizae might be involved. The dominant

trees in the woodland matrix belong to three families, i.e. Fabaceae, Dipterocarpaceae and Phyllanthaceae, which are ectomycorrhizal (Högberg & Pearce, 1986). In contrast, among the T group, no species



is known to host ectomycorrhizae, while several are documented to have endomycorrhizae (e.g. *Cassia abbreviata*, *Combretum molle*, *Commiphora glandulosa*, *Diospyros lycioides*, *Diospyros mespiliformis*, *Lannea discolor*, *Markhamia obtusifolia*, *Strychnos potatorum*, *Ziziphus mucronata* [Bâ, Duponnois, Diabaté, & Dreyfus, 2011; Högberg, 1982]). Further work is needed to test whether matrix species are excluded from termite mounds due to their failure to form mycorrhizae.

4.3 | Intraspecific variation in a broad-niched species

Surprisingly few species were equally frequent both on and off mounds. *Dalbergia boehmii* is such a “neutral species”, and presented clear intraspecific trait differences between populations established in the two types of habitats. Interestingly, the intraspecific trait pattern matches the differences found between the two groups of species. Termite mound populations of *D. boehmii* had higher foliar mineral nutrient concentrations (especially Ca, B, Mg), larger SLA, and thinner leaves. Thus, the traits of the T population are shifted towards a syndrome of enhanced nutrient capture rate. Very few previous studies have examined intraspecific variation in relation to affinity for termite mounds. Van der Plas et al. (2013) found only small variation within species, while Muvengwi, Ndagurwa, Nyenda, and Mlambo (2014) found larger foliar P, K, and Ca in individuals growing on mounds (average of 15 species), i.e. a pattern similar to our results. Interestingly, the amplitude of the intraspecific variation is smaller compared to the amplitude in interspecific comparisons. This could indicate that the within-species difference is mostly accounted for by the direct influence of soil (i.e. phenotypic plasticity), while the difference between species is in part constitutive (genetically fixed) in addition to a direct effect of growth conditions. “Neutral” species in miombo woodlands may occupy a broad niche either by extensive phenotypic plasticity, or by local adaptation, or a combination of both mechanisms. The existence of short-distance adaptation to local soil conditions within a species cannot be formally excluded. However, due to the spatial distribution of the termite mounds scattered in the matrix (3 mounds/ha, covering ca. 8% of soil surface), very steep selection gradients acting on functional-trait values are needed to counteract gene flow. Reciprocal transplant experiments between the two types of populations are needed to address this question.

5 | CONCLUSION

Strong ecological filters are structuring the woody vegetation of dry tropical woodlands in Katanga. Short-distance variation in soil nutrients and moisture due to the activity of termites determine the existence of two mutually exclusive groups of narrow-niched species, with positive and negative affinity for termite mounds, respectively. Strong trait divergence is observed between the two groups, pointing to different resource use strategies. Interestingly, the few broad-niched species show large intraspecific variation in functional traits, with the same pattern as the interspecific variation. Future

work is needed to examine whether broad-niched species are more plastic than narrow-niched ones or, alternatively, whether they have evolved locally adapted populations on termite mounds.

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AUTHOR CONTRIBUTIONS

FC conducted the field experiment, participated in soil chemical analyses, contributed to data analysis and writing of the paper; PM wrote the research project, designed the experiment and contributed to writing the manuscript; DB conducted most data analyses and commented on a draft; MS supervised the research in DR Congo.

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DATA AVAILABILITY STATEMENT

Data are stored in Appendices S2–S5 and in the free-access online repository https://github.com/davbauman/Cuma_et_al_2019_JVS

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

APPENDIX S1. Soil analyses in the experimental site (0–15 cm depth).

APPENDIX S2. Species occurrence on and off termite mounds at the four sites.

APPENDIX S3. Woody species with fewer than five occurrences in the dataset, not included in the test of affinity for termite mounds (Table 1).

APPENDIX S4. Trait values and termitophily index of the 36 species included in the PCA.

APPENDIX S5. Trait values of *Dalbergia boehmii* on and off termite mounds.

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