

A preliminary survey of epiphytes in some tree canopies in Zambia and the Democratic Republic of Congo

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Abstract

The vertical distribution of the density and richness of vascular and nonvascular epiphytes on some mature trees was studied in two 1 km² plots in Miombo Woodland in Zambia (n = 20) and the Democratic Republic of Congo (D.R.C.) (n = 20). The aim was to assess the diversity of arboreal epiphytes and to investigate general distribution patterns of epiphytes along some individual mature phorophytes. Species richness was low on both sampling sites (24 in D.R.C. and nineteen in Zambia) with *Orchidaceae* being the richest family. Epiphyte density for both sampling plots was high with 92% of the available surface area being occupied. Lichens showed the highest density of 67.2% followed by moss 18.4%, orchids 7.9% and ferns 6.5%. Species richness and density showed a clear zonation within the canopy. Richness and density peaked in the upper and mid-canopy and was positively correlated with available surface area, branch aspect and to some extent bark pH, but not with bark texture. This study demonstrated that tree canopies can harbour a diversity of epiphyte species, and the findings constitute baseline information in such environments.

Key words: Africa, density, epiphyte, Miombo, richness, tree

Résumé

Nous avons étudié la distribution verticale de la densité et de la richesse des épiphytes vasculaires et non vasculaires sur certains arbres matures de deux parcelles d'un kilomètre carré, dans une forêt à miombo en Zambie (n = 20) et en République Démocratique du Congo (RDC) (n = 20). Le but était d'évaluer la diversité des épiphytes corticoles et d'analyser le schéma de distribution générale

des épiphytes en même temps que quelques phorophytes individuels matures. La richesse en espèces était faible aux deux sites d'échantillonnage (24 en RDC et 19 en Zambie), et les *Orchidaceae* étaient la famille la plus riche. La densité des épiphytes était élevée dans les deux parcelles: 92% de la surface disponible était occupée. Les lichens présentaient la plus forte densité avec 67.2%, suivis par les mousses, 18.4%, puis par les orchidées, 7.9%, et les fougères, 6.5%. La richesse en espèces et la densité montraient un zonage net dans la canopée. La richesse et la densité présentaient un pic dans la canopée supérieure et moyenne et étaient positivement liées à la superficie disponible, à l'aspect des branches et, dans une certaine mesure, au pH de l'écorce mais pas à sa texture. Cette étude montre que la canopée des arbres peut abriter toute une diversité d'espèces épiphytes, et ces résultats constituent une base de référence pour de tels environnements.

Introduction

Deciduous and semi-deciduous dry forests in Africa contribute substantially to the global plant diversity (Chidumayo & Gumbo, 2010); however, little is still known about their importance to epiphytic canopy organisms. Epiphytes are vascular and nonvascular plants that live on other plants (i.e. phorophytes), such as trees, for physical support; however, they do not gain nutrient or water supply directly from the host (Kress, 1986). These organisms are major contributors to the biomass and the alpha and beta diversity of a forest (Hsu, Horng & Kuo, 2002), provide a diverse range of habitats and food resources for other organisms (Davidson, 1988; Nadkarni & Matelson, 1989; Fischer & Araujo, 1995) and regulate mineral (Pike, 1978) and nutrient cycling (Díaz *et al.*, 2010). Regardless of their importance, research on vascular and in particular nonvascular epiphytes in Africa

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remains sporadic. Early studies include work done by Sanford (1968, 1969), Johansson (1974, 1978), Sermolli (1985), Akinsoji (1990) and Barthelemy (1992). Later work comprises that of Kürschner (1995), Zapfack *et al.* (1996), Biedinger & Fischer (1996), Schaijes & Malaisse (2001), Nkongmeneck, Lowman & Atwood (2002), Mucunguzi (2007), Nyandwi (2008), Zapfack & Engwald (2008), Addo-Fordjour *et al.* (2009), Droissart *et al.* (2011, 2012).

Most of these studies, however, focused on specific epiphytic groups (e.g. pteridophytes and orchids) with the only exception being Biedinger & Fischer's (1996) study on vascular and nonvascular epiphytes in Rwanda and Zaïre [now known as Democratic Republic of Congo (D.R.C.)]. Besides, other studies only mentioned epiphytes briefly as part of a wider vegetation survey (Poulsen *et al.*, 2005; Hemp, 2006). This deficiency and/or absence of epiphyte research in most African countries might be associated with the generally low epiphyte diversity observed in many studies. For example, some epiphytic plant species from the families *Bromeliaceae* and *Cactaceae* are partially or entirely absent in Africa (Zapfack & Engwald, 2008).

In addition, it has become evident that the biomass, species richness and composition of some epiphytes change with height in the canopy (Johansson, 1974; Gauslaa, Lie & Ohlson, 2008; Fritz, 2009). Moreover, epiphytes are highly dependent on their host for physical support; their spatial and physical segregation from terrestrial resources constrains them in any means to a more dependent lifestyle. Bark texture, the instability of the substrate, nutrient availability of the suspended soil, atmospheric nutrient, litter fall, leaching, branch type and aspect can play key roles in their diversity, abundance and distribution (Marmor, Törro & Randlane, 2010). Although many important abiotic and biotic factors that affect epiphyte distributions in tree canopies have been identified, there still appears to be a sparse number of studies in Africa that assess these trends.

Vascular and nonvascular epiphytes in Zambia and southern D.R.C. have received little research attention, making this study an important contributor to epiphyte research in Africa. The two woodland sites were chosen because of their comparable woodland structure, distribution of mature trees within the sample area and topography. This study aimed (i) to assess the vascular and nonvascular epiphytic diversity on selected mature trees of two woodland plots, (ii) to compare the epiphyte

distribution, diversity and abundance (iii) and to investigate the vertical distribution, abundance and density of different groups of epiphytes along an elevation gradient of individual host trees (phorophytes).

Materials and methods

Study area

The two 1-km² woodland plots were located at the Nsobe Game Ranch (latitude 13°22'39.90"S, longitude 28°45'02.82"E) 60 km south of Ndola and approximately 60 km north of Kapiri Mposhi in Zambia, and the Kamoia Exploration Camp (latitude 10°76'81.92"S, longitude 25°25'42.73"E) approximately 25 km west of the town of Kolwezi and about 270 km from the provincial capital Lubumbashi, D.R.C. (Fig. 1). The woodlands were defined as open, mesic Miombo and transitional Miombo dry forest (Chidumayo & Gumbo, 2010). The topography of both sample sites was slightly undulated with a mean elevation of 1363 m. At the Zambian site, mean annual temperature was 24°C, with a mean annual precipitation of 1000 mm and a mean annual humidity of 61% (Phiri, 2005). At the D.R.C. site, mean annual temperature was 28°C with a mean annual precipitation of 1270 mm and a mean annual humidity of 67% (INPL, 2010). To capture the flowering period of many species and because of logistical time constraints, data were collected at the end of the rainy season between January and March 2010.

Sampling

A total number of 40 mature trees were sampled. The twenty trees per plot were chosen according to physical and morphological properties, abundance and climbing accessibility. A total number of three tree species from two genera were sampled. The twenty trees in Nsobe constituted *Brachystegia longifolia* Benth. (n = 5) and *Brachystegia boehmii* Taub. (n = 15) species, whereas the other twenty trees in Kamoia were represented by *Marquesia macroura* Gilg. (n = 20) species.

Data were obtained using single-rope techniques, dual-rope techniques and adopted industrial climbing techniques. These systems have been extensively used in canopy science and have been described in more detail elsewhere (Lowman & Rinker, 2004; Batke, 2012). Data such as branch height from the upper surface of the branch to the ground, circumference and aspect of the

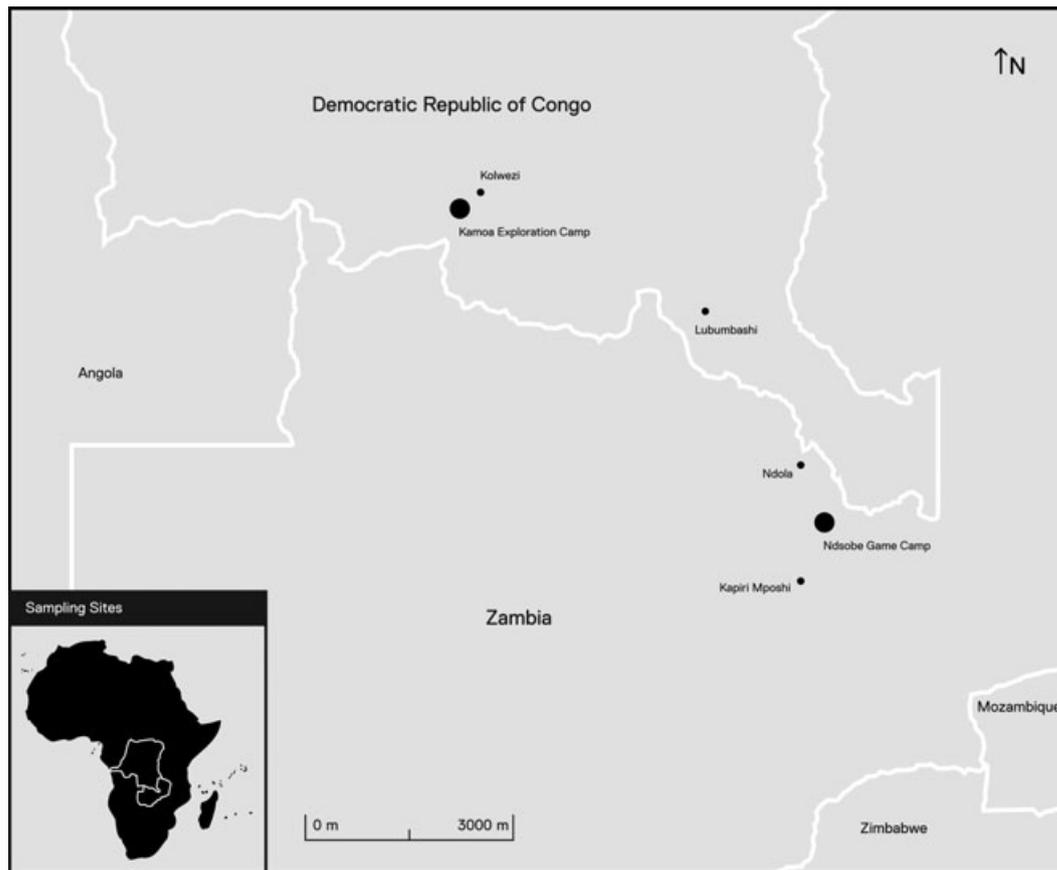


Fig 1 Sampling site in Ndsobe Game Camp, Zambia (latitude $13^{\circ}22'39.90''\text{S}$, longitude $28^{\circ}45'02.82''\text{E}$), and the Kamao Exploration Camp, D.R.C. (latitude $10^{\circ}76'81.92''\text{S}$, longitude $25^{\circ}25'42.73''\text{E}$). Sites are marked with a large black dot. Small dots symbolize nearby towns (see text for further description)

branch, branch and bole length, diameter at breast height (DBH) and total height of the tree, bark texture, species percentage cover and bark pH were collected for every phorophyte. Variables were decided upon following considerations from the literature (Sanford, 1968; Johansson, 1978; Gradstein *et al.*, 2003; Lowman & Rinker, 2004). Only species data for bryophytes, lichens, orchids and ferns were collected.

The bole was divided into four different aspects (north, east, south and west). Total percentage cover for every species at every aspect was estimated. Because some of the epiphytes had multilayered growth patterns, the percentage abundance sometimes exceeded 100%. Percentage cover was estimated to the nearest 5%, with 5% being the lowest. Total height of the bole was measured, and DBH was obtained at a standard height of 137 cm. A 10 g bark sample was collected for later pH analysis.

The texture of the bark was recorded for every aspect, that is, (i) smooth, (ii) flaky, (iii) lightly fissured and (iv) deeply fissured.

Every branch with a circumference >35 cm was sampled. To reduce the damage to the tree that might have occurred when following standard procedure (Gradstein *et al.*, 2003), smaller branches were not sampled. In addition, damaged and infected branches were excluded from the collection process. The total length of every branch was measured, and circumference was obtained from the middle of every branch. Moreover, the height from the top edge of the branch to the ground was measured using a tape measure. Branch aspect was determined by following the general direction of the branch using a standard compass (1 = N/NE, 2 = E/SE/W/NW, 3 = S/SW). Species percentage cover and bark texture were recorded as described earlier. In addition, the type

of branch, that is, primary, secondary, etc., was recorded for later analysis. All species were collected and later identified to genus/species level.

Data analysis

For the analysis, individual phorophytes were divided into five dynamic height-zones. Zone 1 (*D*) consisted of the bole. Zones 2–5 were classed into percentages, each zone being 25% (i.e. all branches = 100%). Zone 2 accounted for all branches between 0% and 25%, zone 3 between 25% and 50%, zone 4 between 50% and 75% and zone 5 between 75% and 100%. Branches below the 'branch-canopy' were added to zone 2 (i.e. all minus values). Total surface area of every bole and branch was calculated according to Eq. 1 as:

$$S_i = \pi dh \quad (1)$$

where S_i is the total surface area, d the diameter and h the total length of the branch/bole. This formula assumes that the branch/bole is circular in section (Swank & Schreuder, 1974). Bole and branch areas for every individual phorophyte were summed to calculate the total available surface area. The same was done for every zone.

Species surface density was calculated for every site, phorophyte, zone and species of epiphyte using surface area and estimated percentage cover according to Eq. 2 as:

$$\rho_A = A(n)/100 \quad (2)$$

where ρ_A is the species surface density, A the total available surface area and n the summed estimated percentage cover for all epiphytes, divided by 100. All percentage cover data were adjusted previous to implementation, that is, proportionally adjusted for all branches, which allowed confining the sample size to the actual available area. Species were then divided into four groups, that is, fern, lichen, moss and orchid.

Species diversity between the sites was calculated using Shannon's Diversity index, Simpson's Diversity index and Pielou Evenness index. The vegetation data were explored using Nonmetric Multidimensional Scaling (NMS) ordination and vegetation clustering (McCune & Mefford, 2011). Moreover, a Spearman's rank correlation was used to obtain significant levels for the nonparametric measurements identified by the NMS (Velleman &

John, 1996). The ordination and nonparametric correlation analyses were carried out separately between the two sample sites because the clustering suggested a strong independence of the vegetation types in Zambia and the D.R.C. However, the ordination visualization was performed with the combined data set. For the analysis, five factors were tested including phorophyte DBH, height of the tree, surface area, bark pH and number of branches. Altitude was not included in the analysis because it would have reduced the explanatory power of other variables (Wolf, 2005).

Density, group and zone were compared using a balanced analysis of variance (ANOVA). Species number and density association between different zones and sites was performed using regression analysis (Minitab, 2010). Finally, area and density calculations were carried out in Microsoft Excel (with Microsoft excel spreadsheet).

Results

Composition and diversity

A total of 29 species of epiphytes from twelve families were identified (Table 1) including three species of fern, ten species of lichen, five species of moss and eleven species of orchids. Species differences between sites (Table 1) and group differences between sites (Table 2) were observed, the D.R.C. being the most species-rich site with $n = 24$ and $n = 19$ for Zambia. Ferns and lichens were equally rich on both sampling sites ($n = 8$). However, mosses and orchids had a higher richness at the D.R.C. site (Table 2). Species diversity and evenness did not significantly differ ($df = 38$, $P < 0.05$) between sampling sites. Both sites showed a similar overall species diversity and evenness (Table 3).

Host morphology

Trees within and between sampling sites varied significantly in their morphology (Table 4) ($df = 38$, $P < 0.05$). The trees sampled in Zambia were taller than those in the D.R.C., but they had a smaller mean DBH (1.83 and 2.13 m, respectively). Mean number of branches in Zambia was lower ($n = 20.2$) when compared to the D.R.C. ($n = 29.0$) ($df = 38$, $P < 0.05$). Total available phorophyte surface area in both sites was 332.9 m² of which 306.2 m² (92%) was occupied by epiphytes. There were only marginal differences between the sites, with

Table 1 Species list for both sample sites

Epiphyte species	Family	Group	Present/Absent	
			D.R.C.	Zambia
<i>Nephrolepis undulata</i> J.Sm.	Oleandraceae	Fern	X	
<i>Pleopeltis excavata</i> (Willd.) Sledge	Polypodiaceae	Fern	X	X
<i>Pyrrosia schimperiana</i> (Kuhn) Alston	Polypodiaceae	Fern		X
<i>Bryoria fuscescens</i> Gyeln.	Parmeliaceae	Lichen	X	X
<i>Cladonia</i> spp. ^a	Cladoniaceae	Lichen	X	
<i>Diploicia canescens</i> (Dickson) A. Massal	Physciaceae	Lichen	X	X
<i>Lecanora chlarotera</i> Nyl.	Lecanoraceae	Lichen		X
Unidentified		Lichen	X	X
<i>Parmelia perlata</i> (L.) Ach.	Parmeliaceae	Lichen	X	X
<i>Phaeophyscia orbicularis</i> (Neck.) Moberg	Physciaceae	Lichen	X	X
<i>Pseudevernia furfuracea</i> (L.) Zopf	Parmeliaceae	Lichen	X	X
<i>Usnea florida</i> (L.) Weber ex F.H. Wigg	Parmeliaceae	Lichen		X
<i>Usnea subfloridana</i> Stirt.	Parmeliaceae	Lichen	X	
<i>Campylopus robillardae</i> var. <i>perauriculatus</i> (Broth.)	Dicranaceae	Moss	X	X
<i>Fabronia pilifera</i> Hornsch.	Fabroniaceae	Moss	X	X
<i>Macromitrium sulcatum</i> (Hook.) Brid.	Orthotrichaceae	Moss	X	
<i>Octoblepharum albidum</i> Hedw.	Calymperaceae	Moss	X	X
<i>Schlotheimia ferruginea</i> Bridel.	Orthotrichaceae	Moss	X	
<i>Bulbophyllum brevidenticulatum</i> De Wild.	Orchidaceae	Orchid	X	
<i>Calyptrochilum christyanum</i> (Rchb. f.) Summerh.	Orchidaceae	Orchid		X
<i>Cyrtorchis crassifolia</i> Schltr.	Orchidaceae	Orchid	X	
<i>Polystachya fusiformis</i> Lindl.	Orchidaceae	Orchid	X	
<i>Polystachya heckmanniana</i> Kraenzl.	Orchidaceae	Orchid	X	X
<i>Polystachya modesta</i> Rchb. f.	Orchidaceae	Orchid	X	X
<i>Polystachya vaginata</i> Summerh.	Orchidaceae	Orchid	X	
<i>Polystachya kermesina</i> Kraenzl.	Orchidaceae	Orchid	X	
<i>Rangaeria muscicola</i> (Rchb. f.) Summerh.	Orchidaceae	Orchid	X	X
<i>Tridactyle bicaudata</i> Schltr.	Orchidaceae	Orchid		X
<i>Tridactyle translucens</i> Summerh.	Orchidaceae	Orchid	X	X
Total			24	19

Species marked with an 'X' indicates whether the species was present.

^aOnly identified to genus.

Table 2 Density (%) and number of total epiphyte species divided into groups for both sample sites

Group	Density (%)		No. species	
	D.R.C.	Zambia	D.R.C.	Zambia
Fern	7.63	5.35	2	2
Lichen	71.26	62.89	8	8
Moss	13.40	23.68	5	3
Orchid	7.68	8.07	9	6
Total	100	100	24	19

Zambian epiphytes occupying a total of 44.7% and D.R. C. epiphytes 47.3% of the total available area (Table 5). Mean surface area varied between different canopy zones

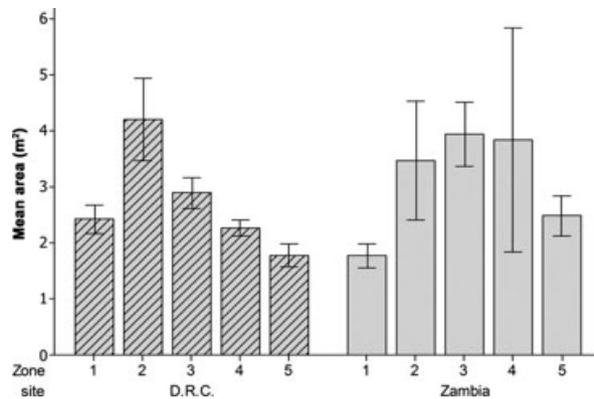
(Fig. 2). Phorophytes in the D.R.C. had a higher surface area in zone 2, followed by a gradual reduction towards the upper and the lower zones. In Zambia, however, phorophytes had more surface area in the mid-canopy, that is, zones three and four.

Distribution, richness and density

Epiphytic groups, that is, fern, lichen, moss and orchids, varied only marginally in density between sites ($F_{1,199} = 0.06$, $P > 0.05$) but significantly between groups within sites (Table 2). The group with the highest density on both sites was lichen (a total of 67.2%), with species such as *Phaeophyscia orbicularis*, *Parmelia perlata* and

Table 3 Average species richness (S), evenness (E), Shannon's Diversity index (H) and Simpson's Diversity index (D') between D.R.C. and Zambia

Site	Mean	SD	Sum	Min.	Max.	S	E	H	D'
D.R.C.	6.878	10.56	199.4	0	32.45	13.6	0.884	2.298	0.8856
Zambia	4.498	7.537	130.4	0	23.05	11.6	0.877	2.137	0.8648

**Fig 2** Mean phorophyte surface area and standard error between different zones of Zambia and the D.R.C.

Diploicia canescens being the most common varieties. Moss had the second highest density (18.4%) followed by orchids (7.9%) and ferns (6.5%).

Density of all groups in zone 1 was relatively low but exponentially increases in zones two, three and four where it then decreases in zone 5 again (Fig. 3). Significant differences between groups within and between zones were observed (fern: $F_{4,199} = 2.41$, $P < 0.05$; lichen: $F_{4,199} = 20.67$, $P < 0.05$; moss: $F_{4,199} = 4.48$, $P < 0.05$; orchids: $F_{4,199} = 4.72$, $P < 0.05$). Moreover, species richness showed a similar pattern to species density. Richness was highest in zones three and four and lowest in zones one, five and two (not shown).

Total available surface area between different zones was significantly correlated with overall changes in species density and species richness ($F_{3,6597} = 233$,

$R^2 = 9.6$, $P < 0.05$). Also, density and species richness were positively correlated at both sites (Tables 6 and 7), but differences in zones were observed (zone 1: $F_{1,38} = 13.73$, $P < 0.05$; zone 2: $F_{1,38} = 0.24$, $P > 0.05$; zone 3: $F_{1,38} = 11.70$, $P < 0.05$; zone 4: $F_{1,38} = 12.39$, $P < 0.05$; zone 5: $F_{1,38} = 11.70$, $P > 0.05$).

Other components

Figure 4 shows that bark pH and the number of branches were the most important variables. In the D.R.C., the ordination coefficient (two dimensions) indicated that axis 1 accounted for the highest similarity (Table 8). At this site, the physical properties of the phorophyte (i.e. number of branches, area, DBH and height) showed significant ($P < 0.05$, $r_s = 0.447$) positive correlation. Axis 2 had no significant correlation ($P > 0.05$, $r_s = 0.447$) to any of the variables. For the Zambian site composition data, the NMS recommended a three-dimensional solution (Table 9). However, axis 1 was not statistically significant following Monte Carlo procedure ($P > 0.05$) and was therefore excluded from further analysis (Kent, 2012). Bark pH on axis 2 and number of branches on axis 3 explained most of the similarity of the epiphyte composition between the phorophytes in Zambia. However, the results were not statistically significant ($P > 0.05$, $r_s = 0.447$) (Table 9).

Bark pH was significantly different between Zambia and the D.R.C. ($df = 38$, $P < 0.05$). Phorophytes in Zambia had a mean pH of 5.66 ± 0.05 , whereas phorophytes in the D.R.C. had a lower mean pH of 3.37 ± 0.03 . Species richness was significantly negative correlated

Table 4 Mean differences in phorophyte traits between Zambia and the D.R.C.

	Zambia			D.R.C.		
	DBH (m)	Height (m)	No. branches	DBH (m)	Height (m)	No. branches
Mean	1.83	15.68	20.20	2.13	14.25	29.00
SE	0.10	0.50	1.71	0.07	0.33	1.14

Significant values at $P < 0.05$ are given in bold.

Table 5 Total available, occupied and unoccupied area per site based on species density

	Zambia m ² (%)	D.R.C. m ² (%)	Total m ² (%)
Available area	161.3 (48.5)	171.5 (51.5)	332.9 (100)
Occupied area	148.7 (44.7)	157.5 (47.3)	306.2 (92.0)
Unoccupied area	12.6 (3.9)	14.0 (4.0)	26.7 (8.0)

with bark pH when analysed with the combined data set ($F_{1,38} = 6.18$, $R^2 = 13.99$, $P < 0.05$), but species surface density was not ($F_{1,38} = 0.05$, $R^2 = 0.1$, $P > 0.05$).

At branch level, bark texture varied only slightly between different phorophytes with a greater range at the D.R.C. site. Lightly fissured was the most frequent bark texture on both sites (83.3%), followed by deeply (7.2%), smooth (5.3%) and flaky (4.2%) bark. Though, neither species density nor species richness was statistically correlated with bark texture at the sites (Tables 6 and 7). The branch aspect was positively correlated with epiphyte richness at the Zambian site and negatively at the D.R.C. site (Tables 6 and 7). Richness was highest on north-west-facing branches in Zambia and north-east-facing branches in the D.R.C. The lowest richness on both sites was observed on north-facing branches. Density showed no correlation with branch aspect.

Discussion

A total of 29 species of epiphytes were encountered with *Orchidaceae* being the most diverse family. This number

does not seem particularly high when compared to epiphyte studies in tropical parts of the world (Gentry, 1982; Benzing, 1990), but is comparable with studies undertaken in other dry forests elsewhere (Werner & Gradstein, 2009) and tropical rainforest in Africa (Addo-Fordjour *et al.*, 2009). Biedinger & Fischer (1996), for example, found in two dry forests in Rwanda three species of orchids, 24 species of lichen and no species of fern and moss. The observed low epiphyte diversity along gradients of increased aridity is thought to be a reflection of the epiphytes specialization to moist environments and the lower nutrient capital available to the epiphytes in dry forests (Sanford, 1968; Benzing, 1990). Although the diversity is commonly reduced at dry and highly exposed sites, the abundance and density of epiphytes is often higher (Benzing, 1987, 1990). All sampled phorophytes in Zambia and the D.R.C., for example, had over 90% of epiphyte cover. Most of the high cover was attributed to moss and lichen species (approximately 85%), which could be a reflection of their colonial life form, that is, turf, mats and cushions (Sillett & Antoine, 2004). Vascular epiphytes (i.e. orchids and ferns) on the other hand are more perpendicular in their growing habit and often require less phorophyte surface area per individual than nonvascular epiphytes. Moreover, their mode of reproduction (sexual and asexual) (Löbel & Rydin, 2009) and affinity to higher solar radiation (Purvis, 2000) allow nonvascular epiphytes to occupy a wider niche, whereas vascular epiphytes are more niche restricted by physiological tolerance limits (Werner & Gradstein, 2008). For example, epiphytes sensitive to drought, such

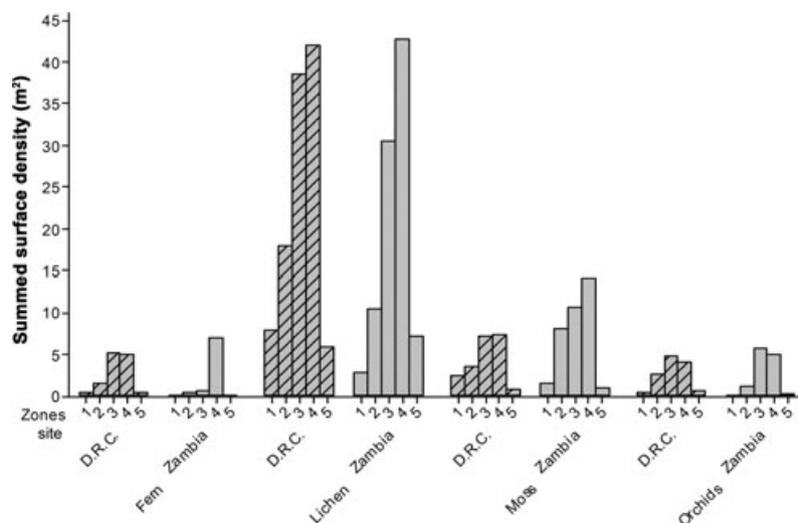
**Fig 3** Surface density of epiphytic group zones in Zambia and the D.R.C.

Table 6 Spearman's rank correlation coefficient for branches in Zambia

	Texture	Aspect	Density	Richness
Texture	1			
Aspect	-0.926	1		
Density	-1.831	0.189	1	
Richness	-0.905	2.021	2.399	1

The critical value for a two-tailed Student's *t*-test at α 0.05 was 1.96. Significant values are given in bold.

Table 7 Spearman's rank correlation coefficient for branches in the D.R.C.

	Texture	Aspect	Density	Richness
Texture	1			
Aspect	1.697	1		
Density	-1.298	-1.822	1	
Richness	-0.899	-2.621	9.209	1

The critical value for a two-tailed Student's *t*-test at α 0.05 was 1.96. Significant values are given in bold.

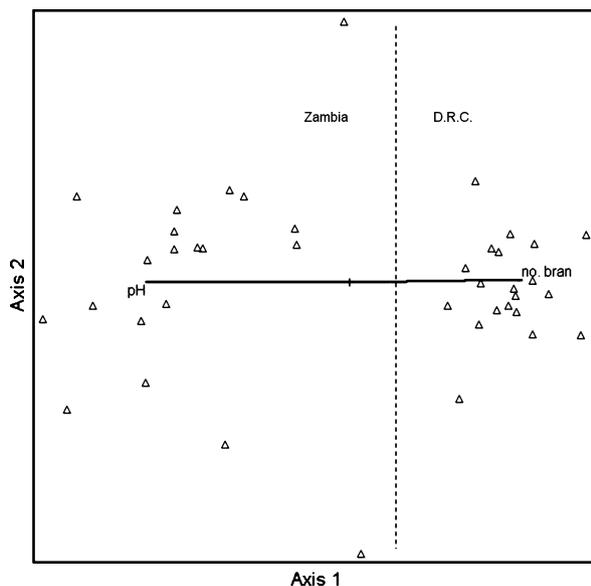


Fig 4 Nonmetric Multidimensional Scaling (NMS) ordination plot for Zambia and the D.R.C. combined. Per cent of cumulative variance in distance matrix was $R^2 = 0.807$ and $R^2 = 0.931$ for axes one and two, respectively. Bark pH (pH) and number of branches (no. bran) were the most important environmental variables in explaining the species composition between sites. Bark pH was more important at the Zambian site, whereas number of branches was a stronger force at the D.R.C. site

as many orchids, were more frequently encountered on intermediate exposed branches (S.P. Batke, Personal observation).

The difference in epiphyte richness between the two sample sites could be the result of four processes. First, epiphytes at the D.R.C. site grew in more moist conditions compared to epiphytes at the Zambian site. Second, phorophytes in the D.R.C. had a larger canopy with more branches, particularly in the lower canopy (Fig. 2 and Table 4). Third, the woodland at the Zambian site was characterized by more disturbances, possibly resulting in a more open vegetation, higher light irradiation and lower humidity (Muñoz *et al.*, 2003). Finally, Wolf (2005) pointed out that the distance between the sample sites could explain 20–30% of the variance in epiphyte composition and diversity between sample sites. Although different species of host trees have been investigated, the effect of epiphyte-host specificity is most certainly negligible (Callaway *et al.*, 2002). The NMS ordination (Fig. 4) suggested that the site variation in epiphyte composition and richness in the D.R.C. was driven by the physical properties of the phorophyte (Table 8). However, at the Zambian site, the variation in epiphyte composition between individual phorophytes could not be explained by the measured variables (Table 9). It is more than likely that all of the above-mentioned processes affect the difference in epiphyte composition between the sites; however, the results are inconclusive. Further studies should therefore explore additional factors including nutrient availability to the epiphyte, microclimatic climate variations within the phorophyte, competition, epiphyte dispersal and geographical relationships between sample sites.

At both sample sites, epiphytes showed a clear zonation in the canopy with density and richness being highest at mid- and upper canopy (Fig. 3). This trend is similar to that found in other studies (Wolf, 1994; Schuettpelz & Trapnell, 2006) but contradicts Addo-Fordjour *et al.* (2009). It has frequently been suggested that in epiphytes, density and richness are driven by environmental conditions such as solar radiation (Steege & Cornelissen, 1989; Werner & Gradstein, 2009) and different exposure gradients (Théry, 2001). Though, the 'mid-height' peak in epiphyte richness and density (Mucunguzi, 2007) could simply be because of fluctuating available physical support rather than changes in climate regimes (Hietz & Hietz-Seifert, 1995; Sillett & Bailey, 2003). Most studies that investigated the distribu-

Table 8 Spearman's rank correlation coefficient for the D.R.C.

	Axis 1	Axis 2	DBH	Height	Area	pH	No. branches
Axis 1	1						
Axis 2	-0.15	1					
DBH	0.644	-0.168	1				
Height	0.402	-0.387	0.472	1			
Area	0.666	-0.226	0.96	0.669	1		
pH	-0.097	0.288	0.156	-0.043	0.131	1	
No. branches	0.903	0.069	0.605	0.279	0.624	-0.003	1

The critical value for a two-tailed r_s at α 0.05 was 0.447. Significant values are given in bold.

Table 9 Spearman's rank correlation coefficient for Zambia

	Axis 2	Axis 3	DBH	Height	Area	pH	No. branches
Axis 2	1						
Axis 3	0.002	1					
DBH	-0.005	0.286	1				
Height	0.197	0.177	0.417	1			
Area	0.075	0.266	0.942	0.674	1		
pH	-0.413	-0.365	-0.017	-0.211	-0.096	1	
No. branches	0.177	-0.441	-0.089	0.141	0.008	0.026	1

The critical value for a two-tailed r_s at α 0.05 was 0.447. Significant values are given in bold.

tion of epiphytes (Normann *et al.*, 2010) mostly ignored area as a factor in explaining epiphyte richness and density (Rodrigode, Borgo & Menezes, 2009), and others found only small effects (Löbel, Snäll & Rydin, 2006). In this study, surface area seems to be of high importance and was strongly correlated to species density and richness but explained only a small fraction of the variation in the data. These highlight how important other factors than area are. Orchids, for example, had their highest density in zone 3, as compared to the other groups that had their highest densities in zone 4 (Fig. 3). Orchids are known for their sensitivity to high solar exposure and their desiccation intolerances (Benzing, 1990; Lowman & Rinker, 2004). Epiphytes, as most plants, can only exploit available resources outside their current realized niche when conditions are most favourable. Any differences in their niche optima need to be avoided by the epiphyte.

The aspect of the branch, the slope and the roughness of the bark are thought to be often important factors in shaping epiphyte communities within phorophytes (Marmor, Törre & Randlane, 2010; Nadkarni, 1994; Affeld *et al.*, 2008). Tree bark in particular is one of the most commonly used substrates of epiphytes and can affect

the epiphyte's ability to establish, attach and grow. Many studies have shown that different bark traits such as texture and pH affect epiphyte richness and composition (Wyse & Burns, 2011). Lightly and deeply fissured bark accommodates often more species and higher densities of epiphytes because bark with deeper fissures provides a better 'holding surface' for epiphytes. Flaky bark on the other hand does not support many epiphytes because of the instability of the substrate. For both sample sites, bark texture, however, was not significantly correlated to epiphyte richness and density (Tables 8 and 9). This is not surprising given that most branches had lightly fissured bark (83.3%), which weakened the effect of bark texture on the epiphyte.

On both sites, epiphyte richness showed significant correlation with branch aspect (Tables 8 and 9). Branches at the Zambian site showed a positive significant correlation and branches at the D.R.C. site a negative significant correlation with species richness. In Zambia, epiphytes had a higher richness on north-west-facing branches, and in the D.R.C., epiphyte richness was highest on north-east-facing branches. Moreover, on both sites, richness was lowest on north-facing branches. The low

species richness on north-facing branches could be the result of different stress conditions (Steege & Cornelissen, 1989) in terms of exposure differences. Annual mean solar radiation is strongest from the north (Tukiainen, 2012) and could therefore explain the difference in observed species richness. Other branches provide possibly better growing conditions to epiphytes; however, detailed data are lacking.

It is clear that epiphytes are less diverse in dry woodlands when compared to tropical forest. However, they account for an important proportion of the African epiphyte flora, with many species still being discovered (Fischer, Killmann & Lebel, 2009; Fischer *et al.*, 2010). Groups of epiphytes show a clear pattern of zonation, where density and species richness increased with height in the canopy. These changes are mainly associated with the size of the host, with larger trees hosting more epiphytes. Although the number of phorophytes under investigation was relatively low, this study provides an important baseline against which future changes can be monitored. Understanding the relationships between epiphytes and their host trees will be of fundamental importance in future conservation efforts regarding dry woodland management in Africa.

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