

Part II

Patterns of Liana Demography and Distribution: From local to Global

LIANA ABUNDANCE AND DIVERSITY IN CAMEROON'S KORUP NATIONAL PARK

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OVERVIEW

The lianas (≥ 1 cm stem diameter) in an 18-ha plot of lowland rainforest in southern Cameroon were surveyed to document the structure and species composition of the liana flora, and to compare the abundance and diversity of lianas to that of trees in the same area. The liana crowns were concentrated in the middle and lower canopy of the forest. We found a total of 256 species in 77 genera and 31 families. When compared to trees of the same diameter, lianas are both less abundant than trees (9023 versus 119,027) and less speciose (256 versus 409). We also found that the tree community in the mid/lower canopy is fairly strongly dominated by a single species (*Oubanguia alata*), while several liana species share dominance, each comprising a smaller portion of the dominance structure. As a result, liana diversity measured by several commonly used indices equals or exceeds that of the trees. This creates a forest canopy where trees and lianas both make large but different contributions to fruit and pollen/nectar resources. The liana community adds at least ten angiosperm families that are not represented in the Korup tree flora, broadening the phylogenetic diversity of the forest. About 80% of the 77 liana genera in the plot are unknown as trees, adding further to diversity above the species level. Lianas in Korup are overwhelmingly dispersed by animals or by ballistic means, which contrasts with the high incidence of wind dispersal among neotropical liana species.

INTRODUCTION

Data on liana density have become more common from forests worldwide. However, it still remains a challenge to find accurate or extensive data on the species comprising the liana community in tropical forests. While comparisons among tree communities are slowly emerging from large-plot consortia (DeCáceres et al. 2012), liana data are still largely lacking and this is especially true for African forests. Here, we describe a study of lianas conducted in the Korup National Park, located in Cameroon's Southwest Region, adjacent to the Nigerian border (Fig. 2.1). We focus on liana abundance, species richness, dominance, and diversity, with comparisons to these attributes for the tree community in the same area. For our study, lianas are narrowly

defined as climbers that develop secondary wood and are rooted in the soil. Rattan palms, hemiepiphytes/stranglers, and other categories of climbing plants that do not meet the narrow definition were included in the census in Korup but excluded from this account.

The study site is near the town of Mundemba at 160 m a.s.l., 5.074° N, 8.855° E, 30 km inland from estuarine mangrove swamps, and 70 km from the Atlantic Ocean in the Bight of Bonny. Following botanical and primatological studies in Korup National Park in the 1970s and 1980s (Gartlan & Struhsaker 1972; Gartlan et al. 1986; Newbery & Gartlan 1996; Usongo & Amubode 2000), a long-term forest monitoring plot was established in 1996. Each census of the 50-hectare plot (1000 × 500 m) includes all trees and saplings at least 1-cm diameter at breast height (dbh): all tagged, measured, mapped, and identified (Thomas et al. 2003; Kenfack et al. 2007; <http://www.ctfs.si.edu/site/Korup/>). Two complete tree censuses have been conducted, in 1997–1999 and in 2008–2009. In 2000–2002 and 2011–2012, two liana censuses for stems ≥ 1 cm were conducted in 18 ha of the 50-ha plot. The 18-ha liana census area is in lower elevation forest on gentle topography at the southern end of the 50-ha plot, in a mosaic of swampy creeks and uplands (Figs. 2.1B, 2.1C).

Proximity to the ocean, the presence of surrounding hills, and the onshore wet winds during much of the year create a very wet climate, with a mean annual rainfall of 5272 mm (1973–1994 data), as measured 20 km away (Chuyong et al. 2004). Korup experiences a short dry season with 3 months (December–February) averaging less than 100 mm precipitation. The remaining 9 months all average well over 100 mm precipitation, with average monthly rainfall peaking at over 900 mm in July and August. Because of the 3-month dry season, Korup vegetation is classified as moist tropical evergreen forest. However, the length and intensity of the wet season are unusual among tropical moist forests, and “wet seasonal evergreen forest” might be a better description. Mean daily maximum temperature is 32.6 °C, with a diurnal range of about 10 °C. Month-to-month and season-to-season variation is less than the diurnal range. Mean daily maximum temperatures are highest in February (32.8 °C), a dry season month with low cloud cover, and lowest in August in the middle of the wet season (27.8 °C).

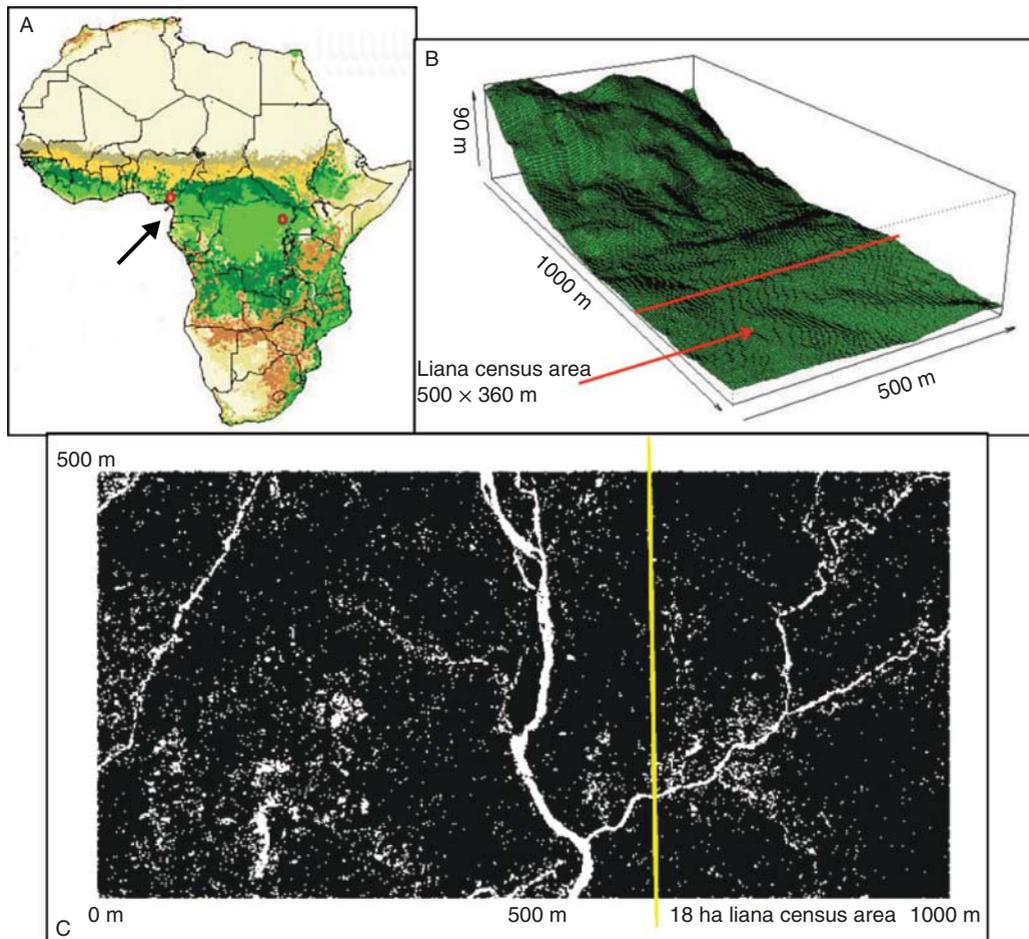


Fig. 2.1 (A) Africa, showing study area in western Cameroon (arrow); additional dot is Ituri Plot in DR Congo. (B) 3-D map of the Korup Forest Dynamics Plot showing the location of the liana census area at the flatter south end. (C) 50-ha Korup Forest Dynamics Plot showing the location of the 18-ha liana census area (right of vertical line) and pale areas of sparse tree cover, including rock outcrops (lower left) and creeks/swamps elsewhere. (Source: Fig. 2.1 A, adapted from United States Geological Survey vegetation map. Reproduced with permission.)

Distribution patterns of the Korup tree species have been studied relative to the major African phytochoria (Kenfack et al. 2007), based on the three main blocks of African moist tropical forest described by White (1979, 1983). The large Congolian forest block falls largely in the basin of the Congo River, the Lower Guinean forest covers the coastal belt from southeastern Nigeria through Gabon, and the Upper Guinea forest is distributed mostly in Liberia, the Ivory Coast, and Ghana. The 50-ha plot is located at the western end of the

Lower Guinea forest and the tree flora shows strong floristic affinities with this forest block. Approximately 33% of the tree species in the plot are known only from the Lower Guinea forest (Kenfack et al. 2007), and though we have not yet completed this analysis for lianas, we expect to find similar affinities for the liana flora.

Trees are less dense in the wetlands (Fig. 2.1C) and in treefall gaps. Korup experiences thunderstorms, especially during the onset of the wet season, resulting

in blow-downs or lightning strikes. These disturbances tend to be small, limited to a few trees or large branches, and the large tropical storms that cause widespread forest damage in other parts of the tropics are unknown in Korup (Thomas et al. 2003; Egbe et al. 2012). In the general area of Korup, large gaps result from shifting cultivation, rather than from storms. The Korup plot shows no signs of former cultivation, and is currently protected within a national park, so large canopy gaps favoring the establishment and growth of lianas and pioneer tree species are absent. Consequently, conditions in the plot are less conducive to the establishment of lianas than in most other tropical forests. Many liana species in Korup produce shade-tolerant tree-like saplings, which survive in the dark, forest understory, where they compete with tree saplings and with understory trees (unpublished data).

Liana field census methods followed those of Gerwing et al. (2006). Liana individuals were defined as plants with visible (even if shallowly buried) living connections between stems. We mapped the rooting position, measured the stem diameter at 1.3 m from the rooting position, and identified all individual lianas in the field as far as possible. Field botanists were responsible for allocating individual lianas to morphospecies, although 10% of the individuals remain unassigned to a morphospecies because of problems locating the foliage. Identification numbers for the tree(s) that hosted the crown of each liana were noted, where the host could be determined. We made herbarium collections for each morphospecies and the taxonomic identification of the multiple voucher specimens per morphotype is ongoing. For analyses of liana floristics and diversity we use data for individuals that have been assigned at least to morphospecies, while for calculations of overall density and basal area we use all individuals.

Soils in the plot are mostly well-drained ultisols, with the exception of wetlands. Seasonally torrential rainfall has moved much of the clay fraction from the upper horizons downward or washed it into the creeks, resulting in sandy clay with very low levels of nutrients because of low ion exchange capacity (Newbery et al. 1997).

The 18-ha liana census area has a fairly continuous canopy at 15–25 m, except in the wetlands, and is dominated by the tree *Oubanguia alata* Bak. f. (Lecythidaceae), which contributes 15.4% of the trees ≥ 20 cm dbh. Scattered larger trees emerge through this canopy, principally *Lecomtedoxa klaineana* (Pierre

ex Engl.) Pierre ex Dubard (Sapotaceae), with 10.3% of the trees ≥ 50 cm dbh. The largest tree is an individual of *Desbordesia glaucescens* (Engl.) Tiegh. (Irvingiaceae) at 197 cm diameter. However, five of the ten largest trees are *Lecomtedoxa klaineana*, so this species is one of the major dominants in terms of biomass.

The liana data presented here are based on the second (2011–2012) census in Korup, which includes the most accurate identifications of the largest number of individuals. Comparisons with data from the first 2001–2002 liana census are made where appropriate. The tree data reported here are drawn from the 2008/2009 second tree census. Analyses are presented as summary statistics for the complete set of 18 hectares that were censused, with all calculations performed with software available in Microsoft Excel or in open source R packages.

RESULTS

In the 18-ha survey area we found a liana density of 547 ha^{-1} for individuals ≥ 1.0 cm dbh (Table 2.1, s.d. = 105.2, range 388–721 ha^{-1}). For individual lianas ≥ 5 and ≥ 10 cm diameter respectively, hectare-level densities are 76 and 8.5 individuals. The largest liana encountered had a diameter of 37 cm in 2012 (not yet identified to morphospecies). Liana densities at Korup are low compared to other African sites, especially for smaller lianas (see Table 2.1).

Between the two censuses (2001–2002 and 2011–2012) the liana density in the 18-ha plot declined by about 16%. Ewango et al. (2010b) found an even more dramatic decline in liana density (33%) in the Ituri forest (D.R. Congo) over three censuses in 13 years (see also Bongers & Ewango, Chapter 3 in this volume). Our results on liana community decline will be detailed in a separate publication.

Liana crowns are concentrated in the middle/lower canopy of the study area, in the “*Oubanguia alata* stratum,” so called because of the dominance by this mid-canopy tree species. Almost 50% of the liana individuals are hosted by trees between 10 and 30 cm dbh, most of which are less than 30 m tall. About 90% of the liana stems are hosted by trees smaller than 40 cm dbh. Trees larger than 20 cm dbh consistently show a 50% occupancy rate by liana crowns. For trees 10–20 cm dbh, the crown occupancy rate is only 26%, for trees 5–10 cm dbh occupancy is 7%, and occupancy is less than 1% for trees 1–5 cm in dbh. However, the number

Table 2.1 Liana density and basal area (m² per hectare) by stem minimum diameters for Korup and two other central African forests. Korup values include means and standard deviation for 18 ha.

Liana density and basal area per ha	Diameter minimum (cm)			
	1	2	5	10
Korup density	517+/-240	312+/-160	91	10
Ituri density		677		13.5
Ebom density		408	113	10

Korup basal area	0.60+/-0.28	0.56+/-0.27		
Ituri basal area		0.71		
Ebom basal area		0.3 - 1.6		

Source: Ituri (Democratic Republic of the Congo): Ewango et al. (2010a); Ebom (Cameroon): Parren (2003)

of trees in each diameter class decreases inversely with the log of the tree size, so larger trees host far fewer liana individuals in total, even when the occupancy rate is similar.

Liana density, richness, and diversity at the family, genus, and species level are shown in Tables 2.2–2.5. A total of 31 families, 77 genera and 256 species were recorded. These numbers are probably underestimates, at least for the number of species, since the 10% of liana individuals that are as yet unidentified likely include additional taxa. At the 1-ha scale, fifteen 100×100 m plots supported an average of 104.9 liana species, with a standard deviation of 13.4. At the family level, the Loganiaceae has the greatest density of individuals, with 1736 lianas in 15 species, all in the single genus *Strychnos*. The Rubiaceae includes the highest diversity of both genera and species, with 1170 individuals in 51 species and 15 genera. At the genus level, *Strychnos* also includes the highest density, with 1736 lianas from 15 species. *Salacia* (Celastraceae) and *Dichapetalum* (Dichapetalaceae) are the most speciose genera, with 17 species each. Dominance in abundance of individuals at the species level is shared between *Raphiostylis beninensis* (Icacinaceae) with 669 lianas, and *Strychnos camptoneura*, with 622 lianas, each representing over 7% of the individuals censused. The next most abundant species, *Strychnos urceolata*, is represented by 281 individuals. At the family level, about 50% of the liana families are unrepresented or only very poorly represented in the tree flora. This percentage increases to 94% unrepresented in the tree flora at the genus level and of course 100% for species, showing that lianas add significant floristic diversity to the Korup forest canopy at all taxonomic levels.

We have characterized liana diversity and dominance using several indices and by rank order of abundance (Table 2.5, Fig. 2.2). We compared liana to tree diversity within Korup using three minimum diameter limits for the trees in the 18 ha of the liana census. When we include all trees and saplings ≥1 cm diameter, trees/saplings are about 13 times more abundant than lianas (119,027 vs. 9023 respectively). Including just trees ≥5 cm diameter results in trees being about 2.5 times more abundant than lianas (22281 vs. 9023 respectively). And including trees ≥9 cm diameter only, the trees and all lianas ≥1 cm diameter are about equal in abundance (9066, 9023, respectively). These ratios of tree-to-liana abundance suggest a lower abundance of lianas at Korup than censused at BCI in Panama where trees >5 cm are similar in number to lianas >1 cm (see values in Schnitzer et al. 2012; Schnitzer et al., Chapter 7 in this volume).

Species richness in the 18-ha plot is related, of course, to the number of individuals censused. Trees ≥1 cm include 409 species, more species than lianas with the same minimum diameter (268 species). At 5 cm diameter and larger, trees include roughly equal species richness (309 species) to all lianas ≥1 cm diameter. The 5-cm diameter tree to 1-cm diameter liana density equivalence was also suggested by Gerwing and Farias (2000), based on estimated similarity of crown sizes in Brazil. In Korup, trees ≥9 cm dbh include fewer species (244 species) than lianas ≥1 cm, although they include similar numbers of individuals (9066 vs. 9023, respectively). Lianas add diversity through the presence of many species, none of which is overwhelmingly dominant in Korup (Fig. 2.2). Although we have not estimated crown volumes for lianas and trees, our results suggest that the species richness of lianas in

Table 2.2 Summary of the Korup liana data by family for all 31 families. Families in italics are well represented among the canopy tree flora (defined here as trees ≥ 5 cm diameter). The 17 families in bold are absent – or almost absent – in the tree canopy.

Rank order	Family	Individuals	Species	Genera
1	Loganiaceae	1736	15	1
2	<i>Rubiaceae</i>	1170	51	15
3	<i>Fabaceae</i>	914	23	7
4	<i>Icacinaeae</i>	867	6	5
5	<i>Apocynaceae</i>	827	27	9
6	Dichapetalaceae	727	21	1
7	<i>Annonaceae</i>	479	16	6
8	Connaraceae	438	24	8
9	Convolvulaceae	350	4	1
10	Celastraceae	348	19	1
11	Dioscoreaceae	140	5	1
12	Combretaceae	130	10	1
13	Linaceae	130	4	1
14	Dilleniaceae	124	2	1
15	Vitaceae	98	5	1
16	<i>Euphorbiaceae</i>	69	2	2
17	Aristolochiaceae	46	3	1
18	Malpighiaceae	46	2	1
19	<i>Rutaceae</i>	25	2	1
20	Menispermaceae	23	2	2
21	Verbenaceae	22	1	1
22	<i>Gentianaceae</i>	17	1	1
23	<i>Melastomataceae</i>	15	1	1
24	Piperaceae	11	1	1
25	<i>Anacardiaceae</i>	9	1	1
26	Curcubitaceae	7	1	1
27	Ancistrocladaceae	5	1	1
28	<i>Malvaceae</i>	5	2	2
29	<i>Passifloraceae</i>	4	2	1
30	<i>Lauraceae</i>	3	1	1
31	<i>Polygalaceae</i>	2	1	1
	TOTALS	8787	256	78

the Korup 18-ha plot is equivalent to or exceeds that of the trees, when a species richness number is used that takes into account the size of the canopy of lianas versus trees, regardless of their supporting tissues.

Evenness is greater in lianas and small trees than in larger trees, because of the dominance of the tree *Oubanguia alata*. The effective diversity (the numbers equivalent of a diversity index), calculated as the exponent of the Shannon-Weiner index (see Table 2.5), is 87 for lianas and 70 for trees, in spite of the higher total species richness values of the trees. The use of effective diversity for comparison is strongly recommended when comparisons of different areas or life forms is

made (Jost 2007). It is clear that, in Korup, the lianas make a major contribution to the species diversity of the forest canopy, even though their stem density is relatively low.

DISCUSSION

As in many tropical forests studied to date (Bongers & Ewango, Chapter 3 in this volume; Parthasarathy et al., Chapter 4 in this volume; Burnham & Romero-Saltos, Chapter 5 in this volume; Nogueira et al., Chapter 6 in this volume; Schnitzer et al., Chapter 7 in this volume;

Table 2.3 The 20 most abundant liana genera in the Korup plot, out of the 77 total. With the exception of *Strychnos* and possibly *Millettia*, these genera are not represented among the tree species in the plot, nor in the immediate vicinity where tree observations are easily made during field surveys.

Rank order	Genus	Individuals	Species
1	<i>Strychnos</i> (Loganiaceae)	1736	15
2	<i>Rhaphiostylis</i> (Icacinaceae)	695	1
3	<i>Landolphia</i> (Apocynaceae)	647	14
4	<i>Dichapetalum</i> (Dichapetalaceae)	548	17
5	<i>Millettia</i> (Fabaceae)	403	5
6	<i>Neuropeltis</i> (Convolvulaceae)	350	4
7	<i>Salacia</i> (Celastraceae)	310	17
8	<i>Leptactina</i> (Rubiaceae)	277	2
9	<i>Agelaea</i> (Connaraceae)	176	7
10	<i>Leptoderris</i> (Fabaceae)	174	4
11	<i>Monanthes</i> (Annonaceae)	174	3
12	<i>Atractogyne</i> (Rubiaceae)	171	2
13	<i>Friesodielsia</i> (Annonaceae)	171	3
14	<i>Dioscorea</i> (Dioscoreaceae)	140	1
15	<i>Iodes</i> (Icacinaceae)	135	1
16	<i>Combretum</i> (Combretaceae)	130	10
17	<i>Hugonia</i> (Linaceae)	130	4
18	<i>Sherbournia</i> (Rubiaceae)	129	6
19	<i>Tetracera</i> (Dilleniaceae)	124	2
20	<i>Dioclea</i> (Fabaceae)	119	2

Ibarra-Manríquez et al., Chapter 8 in this volume), the liana community adds substantial species richness to the Korup forest. We documented the presence of 268 species of lianas in addition to the tree flora of 409 species known from a forested area of only 18 hectares. The additional diversity added by lianas is contributed to a large degree by species from families scarcely, if at all, represented among the tree community.

Phylogenetic diversity, then, is increased by the liana community through the addition of families such as Aristolochiaceae, Convolvulaceae, Celastraceae, Dichapetalaceae, Dioscoreaceae, Loganiaceae, and Menispermaceae, which are absent or almost absent from the tree flora (Celastraceae and Loganiaceae are both also present as scarce small trees).

Dominant species of lianas in neotropical forests have been reported as comprising 7–17% of the individuals, similar to the 14.7% combined value for the two dominant liana species in Korup (Perez-Salicrup et al. 2001; Burnham 2002; Mascaro et al. 2004). The two dominant liana species in Korup are animal dispersed, adding support to the supposition of an intact faunal community in the area (Ndenecho 2011). In contrast with the wind-dispersed dominant lianas in Yasuní, Ecuador (e.g., *Machaerium cuspidatum*, *Combretum laxum*), the dominants in Korup are largely animal dispersed. For example, Korup lianas bear seeds embedded in a tangy, fleshy pulp and then enclosed in a durable fruit (*Strychnos* spp., *Landolphia*, *Atractogyne*), or they bear fruits with a fleshy external appendage (*Rhaphiostylis*), or each carpel is a succulent apocarp (*Friesodielsia*). Indeed, the nine most abundant species in Korup appear to be animal dispersed, a phenomenon also reported from the Ituri forest in DR Congo (Ewango 2010a), whereas six of the top ten dominant lianas in Ecuador are wind dispersed (Burnham & Romero-Saltos, Chapter 5 in this volume). Among the largest diameter trees in Korup (upper canopy or emergents), there are only two wind-dispersed species among the 20 most abundant species, the remainder being animal, ballistic, or unknown, but not wind dispersed. Among mid-canopy Korup trees, none of the 20 most abundant species are wind dispersed (data from Thomas et al. 2003). The predominance of animal dispersal among trees and lianas in Korup may be at odds with a general impression of lianas, as more wind dispersed than trees in tropical forests (Gentry 1983, 1991). The high annual precipitation in Korup may contribute to favoring this difference, in spite of a three-month dry season. Similar patterns in Nigerian forests may have been found as early as 1957 by Keay, who found old secondary growth forest to have 56% wind-dispersed trees and 48% wind-dispersed lianas (see van der Pijl 1982). Reports from two tropical rainforest sites in DR Congo (Ewango 2010a; Beaune et al. 2013) show 74% and 79.2% of the liana species (Ituri and Salonga, respectively) are animal dispersed. Tree dispersal by

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Table 2.4 The 20 most abundant liana species in the Korup plot, of the 256 species total, along with their inferred dispersal agent based on fruit morphology.

Rank order	Individuals	Species	Inferred dispersal agent
1	669	<i>Rhaphiostylis beninensis</i> (Hook. f ex Planch.) Planch. ex Benth.	Animal
2	622	<i>Strychnos camptoneura</i> Gilg & Busse	Animal
3	281	<i>Strychnos urceolata</i> Leeuwenb.	Animal
4	276	<i>Leptactina latifolia</i> K.Schum.	Animal
5	256	<i>Strychnos johnsonii</i> Hutch. & M.D.Moss	Animal
6	231	<i>Dichapetalum affine</i> (Planch. Ex Benth.) Breteler	Animal
7	229	<i>Strychnos tricalisoides</i> Hutch. & M.D.Moss	Animal
8	180	<i>Landolphia</i> sp. "LANDPR"	Animal
9	167	<i>Atractogyne gabonii</i> Pierre	Animal
10	152	<i>Fabaceae</i> sp. "MILL"	Unknown
11	148	<i>Friesodielsia enghiana</i> (Diels) Verdc.	Animal
12	145	<i>Neuropeltis velutina</i> Hallier f.	Wind
13	141	<i>Millettia</i> sp. "MILLLE"	Ballistic
14	139	<i>Neuropeltis</i> sp. "NEUR"	Wind
15	135	<i>Iodes africana</i> Welw. Ex Oliv.	Animal
16	131	<i>Salacia longipes</i> (Oliv.) N.Halle	Animal
17	129	<i>Dioscorea smilacifolia</i> (De Wild.)	Wind
18	127	<i>Landolphia dulcis</i> (Sabine ex G.Don) Pichon	Animal
19	120	<i>Leptoderris ledermannii</i> Harms	Ballistic
20	118	<i>Dioclea</i> sp. "DIOC"	Ballistic

Table 2.5 Diversity indices for lianas and three size classes of trees (minimum dbh in cm) from 18 hectares of forest in Korup National Park. Comparison to values from Ituri (DR Congo) provided, when known, in column 6 (Ewango 2010a). Ituri data comes from two non-contiguous 10-ha plots (500 m apart). The Shannon-Wiener exponential eH' is the effective species number calculated considering frequency values (see Jost 2006, 2007).

	Trees ≥ 1	Trees ≥ 5	Trees ≥ 9	Lianas ≥ 1	Ituri lianas ≥ 2
Area in hectares	18	18	18	18	20
Number of individuals	119027	22281	9066	9023	15008
Minimum diameter cm	1	5	9	1	2
Number of species	409	309	244	268	195
Shannon evenness index	0.71	0.67	0.65	0.8	
Shannon-Wiener index H'	4.26	3.86	3.59	4.47	3.1
Shannon-Wiener exponential eH'	70.7	47.38	36.27	87.36	
Inverse Simpson's index D	30.23	17.14	11.06	48.38	11.4
Fisher's alpha	53	50.77	46.17	51.9	17.9

animals in the Salonga National Park, DR Congo is even higher (84%, Beaune et al. 2013).

Lianas add substantial diversity to the Korup forest, adding a community of dominant taxa that are relatively homogeneously distributed, contrasting with

the tree community in which one species is strongly dominant. The effect of this difference is to increase species richness but also to increase true diversity, as reflected in the frequency with which a new species is found in the forest. How does this affect the fauna

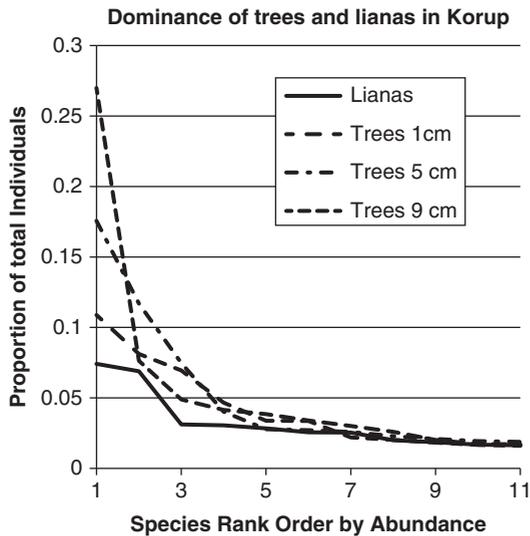


Fig. 2.2 Proportional abundance by species from the data used to compute the diversity indices in Table 2.5 (11 most abundant species). The highest level of species dominance is found among the largest diameter trees and lowest dominance is in the liana flora.

relying on resources in the area? The patterns of liana dispersal contrast with those in neotropical forests, but are in line with other African sites, suggesting that dispersal may be phylogenetically controlled to a larger degree than previously recognized. Liana management worldwide has become a prominent issue over recent years, and the clear contribution of lianas to intact forests suggests that the specific differences among lianas may help guide management. Species-specific attributes and interactions should be a high priority among liana biologists in the future.

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REFERENCES

- Beaune, D., Bretagnolle, F., Bollache, L. et al. (2013) Seed dispersal strategies and the threat of defaunation in a Congo forest. *Biodiversity and Conservation*, **22**, 225–238.
- Burnham, R.J. (2002) Dominance, diversity and distribution of lianas in Yasuni, Ecuador: who is on top? *Journal of Tropical Ecology*, **18**, 845–864.
- DeCáceres, M., Legendre, P., Valencia, R. et al. (2012) The variation of tree beta diversity across a global network of forest plots. *Global Ecology and Biogeography*, **21**, 1191–1202.
- Condit, R. (1998) *Tropical Forest Census Plots*, Springer Verlag, New York.
- Condit, R., Ashton, P., Baslev, H. et al. (2005) Tropical tree alpha-diversity: Results from a worldwide network of large plots. *Biologiske Skrifter*, **55**, 565–582.
- Chuyong, G. B., Condit, R., Kenfack, D., et al. (2004) Korup forest dynamics plot, Cameroon. In *Forest Diversity and Dynamism: Findings from a Network of Large-scale Tropical Forest Plots* (eds. U E.C. Losos & E.G., Leigh, Jr.). University of Chicago Press, Chicago.
- Egbe, E.A., Chuyong, G.B., Fonge, B.A. & Namuene, K.S. (2012) Forest disturbance and natural regeneration in an African rainforest at Korup National Park, Cameroon. *International Journal of Biodiversity and Conservation*, **4**, 377–384.
- Ewango, C.E.N., Bongers, F., Poorter, L., et al. (2010a) Structure and composition of the liana assemblage of a mixed rain forest in the Congo Basin. In *The Liana Assemblage of a Congolian Rainforest: Diversity, Structure and Dynamics* (C.E.N. Ewango). PhD thesis, University of Wageningen.
- Ewango, C.E.N., Poorter, L., Sosef, M.S.M., et al. (2010b) Thirteen years of dynamics of the liana assemblage in a Congo Basin rain forest. In *The Liana Assemblage of a Congolian Rainforest: Diversity, Structure and Dynamics*. (C.E.N. Ewango). PhD thesis, University of Wageningen.
- Gartlan, J.S., Newbery, D.M.C., Thomas, D.W. & Waterman, P.G. (1986) The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve, Cameroon. *Vegetatio*, **65**, 131–148.
- Gartlan, J.S. & Struhsaker, T.T. (1972) Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. *Journal of Zoology (London)*, **168**, 221–266.
- Gentry, A.H. (1983) Dispersal ecology and diversity in Neotropical forest communities. *Sonderbände des naturwissenschaftlichen Vereins in Hamburg*, **7**, 303–314.
- Gentry, A.H. (1991) Breeding and dispersal systems of lianas, in *The Biology of Vines* (eds F.E. Putz & H. Mooney), Cambridge University Press, Cambridge, pp. 393–423.
- Gerwing, J.J. & Farias, D.L. (2000) Integrating liana abundance and forest stature into an estimate of total above-ground biomass for an eastern Amazonian forest. *Journal of Ecology*, **16**, 327–356.

- Gerwing, J.J., Schnitzer, S.A., Burnham, R.J. et al. (2006) Censusing lianas in tropical forests. *Biotropica*, **38**, 256–261.
- Hawthorne, W.D. & Jongkind, C. (2006) *Guide to the Woody Plants of Western Africa*, Royal Botanic Gardens, Kew, London.
- Jost, L. (2006) Entropy and diversity. *Oikos*, **113**, 363–375.
- Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**, 2427–2439.
- Kenfack, D., Thomas, D.W., Chuyong, G. & Condit, R. (2007) Rarity and abundance in a diverse African forest. *Biodiversity and Conservation*, **16**, 2045–2074.
- Mascaro, J., Schnitzer, S.A. & Carson, W.P. (2004) Liana diversity, abundance and mortality in a tropical wet forest in Costa Rica. *Forest Ecology and Management*, **190**, 3–14.
- Ndenecho, E.N. (2011) *Local Livelihoods and Protected Area Management: Biodiversity Conservation Problems in Cameroon*, African Books Collective, Langaa Research & Publishing Common Initiative Group, Bamenda, Cameroon.
- Newbery, D.M.C., Alexander, I.J. & Rother, J.A. (1997) Phosphorus dynamics in a lowland African rain forest: the influence of ecto-mycorrhizal trees. *Ecological Monographs*, **67**, 367–409.
- Newbery, D.M.C. & Gartlan, J.S. (1996) A structural analysis of rain forest at Korup and Douala-Edea, Cameroon. *Proceedings of the Royal Society of Edinburgh*, **104B**, 177–224.
- Parren, M.P.E. (2003) Lianas and logging in West Africa. PhD dissertation. Wageningen University, Tropenbos-Cameroon Series 6. Tropenbos International, Wageningen, the Netherlands.
- Perez-Salicrup, D.R., Sork, V.L. & Putz, F.E. (2001) Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica*, **33**, 34–47.
- Schnitzer, S.A., Mangan, S.A., Dalling, J.W. et al. (2012) Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS One*, **7**(12), e52114. doi: 10.1371/journal.pone.0052114
- Thomas, D.W., Kenfack, D., Chuyong, G.B. et al. (2003) *Tree Species of Southwestern Cameroon: Tree Distribution Maps, Diameter Tables, and Species Documentation of the 50-Hectare Korup Forest Dynamics Plot*, Center for Tropical Forest Science of the Smithsonian Tropical Research Institute and Bioresources Development and Conservation Programme-Cameroon, Washington, DC.
- Usongo, L.I. & Amubode, F.O. (2000) Nutritional ecology of Preuss' red colobus monkey (*Colobus badius preussi* Rahm 1970) in Korup National Park, Cameroon. *African Journal of Ecology*, **39**, 121–125.
- Van der Pijl, L. (1982) *Principles of Dispersal in Higher Plants*, Springer-Verlag, Berlin.
- White, F. (1979) The Guineo-Congolian Region and its relationships to other phytochoria. *Bullétin du Jardin Botanique National de Belgique*, **49**, 11–55.
- White, F. (1983) *The Vegetation of Africa*, UNESCO, Paris.