

Structure and composition of the liana assemblage of a mixed rain forest in the Congo Basin

Corneille E.N. Ewango^{1,2,3}, Frans Bongers², Jean-Remy Makana¹,
Lourens Poorter² & Marc S.M. Sosef^{3,4,*}

¹Wildlife Conservation Society, D.R. Congo Program, Centre de Formation et de Recherche en Conservation Forestière, Ituri Forest, PO Box 240, Kinshasa, D.R. Congo

²Department of Environmental Sciences, Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, NL-6700 AA, Wageningen, The Netherlands

³Biosystematics Group, Wageningen University, Gen. Foulkesweg 37, NL-6703 BL, Wageningen, The Netherlands

⁴Botanic Garden Meise, Nieuwelaan 38, BE-1860 Meise, Belgium

*Author for correspondence: marc.sosef@br.fgov.be

Background and aims – The Congo Basin lowland forest represents one of the largest tropical forest blocks in the world, but its liana assemblage has never been characterized. We evaluate liana floristics, diversity, and structure in the Ituri Forest, and determine the effects of forest structure and edaphic variation on liana species composition.

Methods – Two permanent 10-ha plots (200 × 500 m), 500 m apart, were established in mixed forest. All liana individuals ≥ 2 cm dbh were identified, measured, mapped, and marked. For 20 × 20 m subplots we distinguished terra firme and swamp, and we estimated canopy openness.

Key results – The combined 20-ha area contains 15,008 lianas (dbh ≥ 2 cm) representing 195 species, 83 genera, and 34 families. Per hectare, species number averaged 64, mean basal area was 0.71 m² and mean Fisher's alpha, Shannon index, and Simpson diversity index values were 17.9, 3.1 and 11.4, respectively. Ten dominant plant families represented 69% of total species richness, 92% of liana abundance and 92% of basal area, while ten dominant species accounted for 63% of abundance and 59% of basal area. A single species, *Manniophyton fulvum*, dominated the liana community (22% of all individuals). Forty-one species (21%) had one individual only. Twiners, zoochorous, light-demanding, and meso- or microphyllous species dominated. Liana abundance increased with abundance of medium-sized and large trees but was, surprisingly, independent of small-tree abundance. Canopy openness, habitat type, and tree size were the most important factors influencing abundance and distribution of liana individuals.

Conclusions – The Ituri liana assemblage stands out by showing an extreme one-species dominance. Species floristic composition is, however, generally similar to that in other tropical African forests.

Key words – Africa, Congo Basin, forest structure, floristic composition, functional traits, Ituri Forest Dynamics Plots, lianas, rain forest, species diversity.

INTRODUCTION

Lianas (woody climbers) are notoriously abundant in the tropics, contributing up to 25% of the woody stem density (Gentry 1991a, Schnitzer & Bongers 2002) and 12–40% of the overall species diversity of tropical forests (Smith 1970, Hall & Swaine 1981, Gentry 1991a, Schnitzer & Bongers 2002, Bongers et al. 2005). Apart from their direct contribution to diversity, lianas help maintaining diversity through their effects on forest structure and dynamics (Putz 1984, Schnitzer & Bongers 2002, Schnitzer et al. 2012) and thus on species composition of both plants and animals.

A number of studies have documented the functional aspects of lianas in tropical forests. First, lianas substantially contribute to canopy closure after tree fall, stabilizing the microclimate underneath, and contributing to whole-forest transpiration (Schnitzer & Bongers 2002, Andrade et al. 2005). Second, lianas contribute to the carbon budget of tropical forests (Lewis et al. 2009), representing as much as 10% of the fresh above-ground biomass (Putz 1984, Phillips et al. 2002, Gehring et al. 2004) and accounting for up to 40% of the leaf productivity (Hegarty & Caballé 1991, Gerwing & Farias 2000, Wright et al. 2004). Finally, by colonizing trees, lianas create structural stress on their hosts, compete for

light, water and soil nutrients, generally reducing tree growth (Whigham 1984, Schnitzer et al. 2005, Peña-Claros et al. 2008, Villegas et al. 2009, Ingwell et al. 2010, Dalling et al. 2012) and reproduction (Stevens 1987, Kainer et al. 2006, Nabe-Nielsen et al. 2009), while increasing rates of tree fall and limb breakage (Lowe & Walker 1977, Putz 1984).

The varying species composition of lianas in different forest types demonstrates that there are large ecological and functional differences across species. Although lianas have a similar growth form and are generally thought to be light demanding (Gilbert et al. 2006, Putz 1984), species do differ in for example climbing mechanisms (Putz 1984, Putz & Holbrook 1991) and light requirements (Baars et al. 1998, Gianoli et al. 2010, Gilbert et al. 2006, Putz 1984). Furthermore, flower size and diaspore type vary markedly across liana species (Bullock 1995, Cai et al. 2009, Gentry 1991b) and are correlated with a wide range of pollinators and propagule distributors. All this enables lianas to occupy a wide range of habitat types (Darwin 1867, Balfour & Bond 1993, Nabe-Nielsen 2001).

The abundance, species diversity, and distribution of lianas depends on several abiotic factors, including total rainfall, seasonality (DeWalt et al. 2010), soil fertility (Poulsen et al. 2005, Toledo 2010), landscape topography (Dalling et al. 2012), canopy structure (Ibarra-Manríquez & Martínez-Ramos 2002), disturbance regimes and successional stage (DeWalt et al. 2000, 2006, Schnitzer & Bongers 2002, Schnitzer et al. 2005). Putz (1984) and Balfour & Bond (1993) showed that trellis availability and canopy structure (i.e. canopy openness and tree architecture) together influence the distribution and abundance of lianas in different forest types. Spatial variation in water availability, often driven by topography, may also play an important role in these patterns (Nabe-Nielsen & Hall 2002, Kusumoto et al. 2008), while lianas always depend on other plants for support after the initial, self-supporting stages (Homeier et al. 2010, Nabe-Nielsen & Hall 2002).

Although the importance of lianas is broadly recognized, very few liana studies have been performed in the Congo Basin (Lebrun 1937, Makana et al. 1998). In this study we evaluate the community structure of the liana assemblage of the mixed lowland Ituri Forest, north-eastern Democratic Republic of Congo. Using data from two 10-ha forest plots we (1) describe the floristics, diversity and structure of the liana assemblage in this forest, (2) characterize liana functional traits (climbing mechanisms, regeneration guilds, leaf sizes, flower types and dispersal syndromes); and (3) determine the effect of forest structure on liana species abundance.

We tested the hypotheses that (1) the liana assemblage in the Ituri Forest accords in diversity and structure with lowland rain forests elsewhere, but floristically most closely resembles other such assemblages in central Africa, (2) the liana species abundance and species richness are related to local environmental parameters of canopy openness and soil drainage (Balfour & Bond 1993), while overall liana density is correlated with the number of available host trees.

MATERIALS AND METHODS

Study site

The study was carried out in the Okapi Faunal Reserve (Réserve de Faune à Okapis (RFO), 1°25'N 28°35'E; fig. 1) in the central part of the Ituri Forest, north-eastern D.R. Congo. Two 10-ha permanent forest plots were established near the Edoro Field Research area of the Centre de Formation et de Recherche en Conservation Forestière and the Wildlife Conservation Society (hereafter referred to as CEFRECOF/WCS). The Ituri Forest Dynamics Plots are part of the worldwide tropical forest network of the Center for Tropical Forest Science (CTFS; Condit 1998, Losos & Leigh 2004). The Edoro research area covers about 52 km² of primary mixed tropical forest at an altitude of 700–850 m a.s.l.

The climate of the region is Köppen's Am (Gerard 1960, Peel et al. 2007), i.e. tropical megathermal with a pronounced dry season. Mean annual precipitation is 1785 mm, with a bimodal seasonal distribution, with two wet seasons from March to June and August to November. In the dry season, December through February, monthly rainfall is less than 100 mm and the two driest months, January and February, have less than 50 mm. Mean annual temperature is between 17.9°C and 25.5°C (Hart & Carrick 1996, fig. 1). The soils consist mainly of highly weathered tropical oxisols, with texture ranging from sandy clay loam to sandy clay (Hart et al. 1989). Topography in each plot is gentle with only small internal differences in elevation: less than 20 m (Makana et al. 2004a, 2004b). The vegetation in the study area is mixed tropical lowland forest (*sensu* White 1983). In the two 10-ha plots three tree species, *Cynometra alexandri*, *Julbernardia seretii* (both Leguminosae), and *Cleistanthus michelsonii* (Phyllanthaceae), account for up to 30% of the basal area and density of stems ≥ 10 cm dbh (Hart 1985). The canopy is heterogeneous, 30–40 m in height, with frequent emergent trees. For a more detailed description of the study area, soils, and climate, see Hart (1985), Conway (1992) and Hart & Carrick (1996).

Data collecting

In December 1994, two permanent plots of 10 ha (200 × 500 m), 500 m apart, called Edoro-1 and Edoro-2 (fig. 1), were established in mixed forest. They had no large-scale recent disturbances, and each included about 1 ha of swampy area. Botanical and topographic data were collected following the plot standards of the CTFS network (Condit 1998). In each 10-ha plot, a grid of 250 contiguous 20 × 20 m quadrats was demarcated with 286 cement stakes and each quadrat was subdivided into 16 sub-quadrats of 5 × 5 m. All liana individuals ≥ 2 cm dbh were identified, measured, mapped and marked with a pre-numbered aluminum tag. Liana dbh was measured at 1.3 m distance along the stem from their rooting point. To facilitate comparison with other liana studies, we only included true liana species: woody climbing plants that germinate on the ground but lose their ability to support themselves as they grow, so they have to rely on external physical support to ascend to the canopy (Gerwing et al. 2006). We distinguished genets from ramets for each individual liana, based on rooting location and underground stem

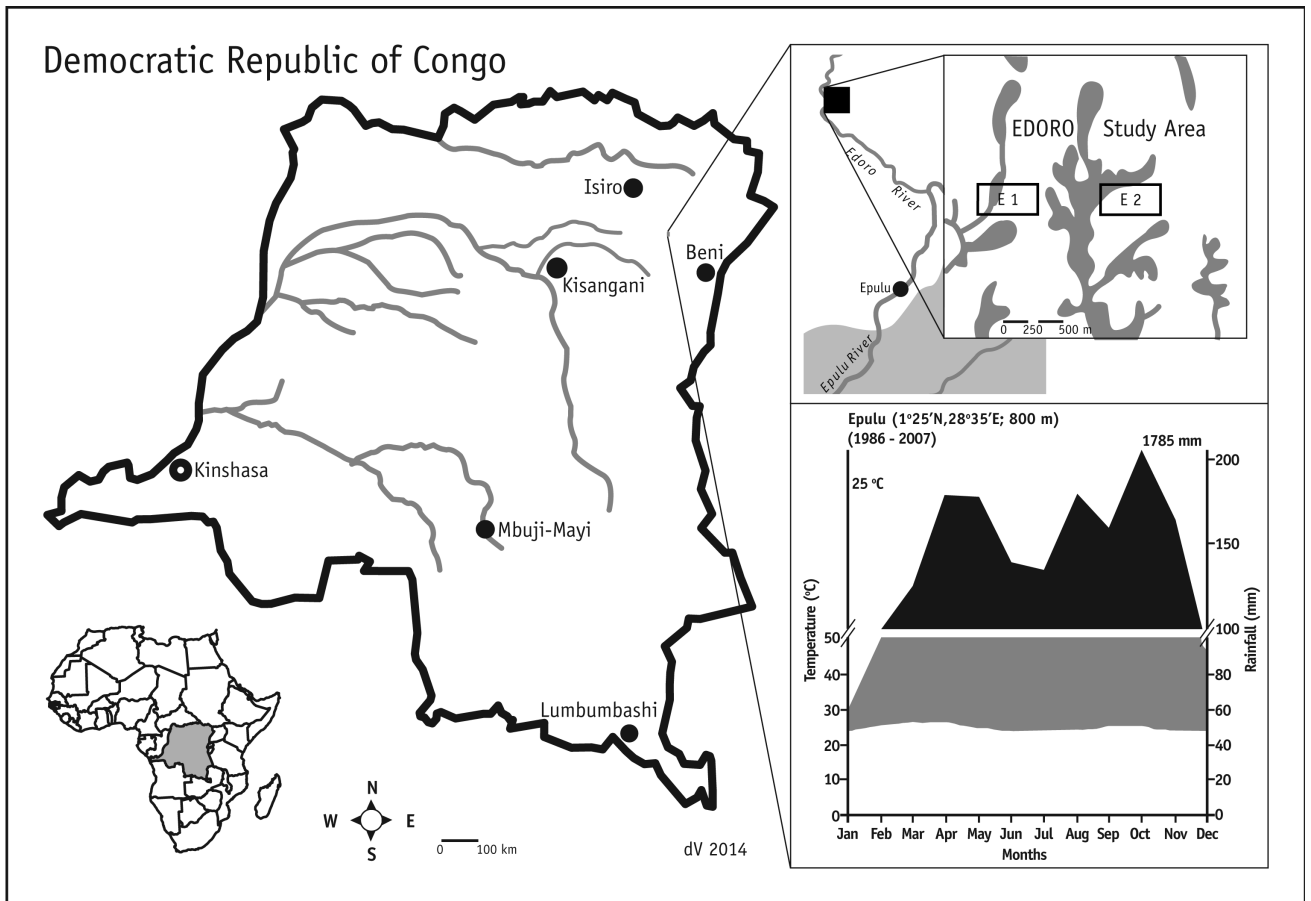


Figure 1 – Location of the two Edoro mixed forest dynamics plots in the Ituri Forest, eastern D.R. Congo. The grey areas crossing the Edoro plots is swamp forest. The climate diagram is from the Epulu site (Okapi Wildlife Reserve) with mean monthly temperatures (lower line) and mean monthly rainfall (grey and black surfaces) showing two wetter and two dryer periods. Weather records collected from 1986–2007.

connections (Parren et al. 2005). This was verified by removing litter. All multiple and non-rooted interconnected stems were assumed to belong to the rooted individual and were counted as an individual clone group. However, in some cases we could not reject with total certainty the possibility of below-ground connections and we adopted as a general rule that stems were treated as genets unless it was evident that they had connections with other stems.

Major habitat types were defined using visual evaluation of superficial soil water availability. Terra firme forest (TF) was defined as non-inundated terrain with sandy to loamy soils and a thin layer of organic matter, while swamp forest (SF) was defined as terrain with hydromorphic and alluvial soils, regularly flooded during rainy periods. At the study site, the canopy of SF is much lower, more open, and less homogeneous than that of TF. For each 5×5 m subquadrat we estimated canopy cover using a three-class semi-quantitative scale (0: cover = < 25%, 1: cover = 25–50%, 2: cover = 50–100%). Data were converted to their midpoint values and mean canopy openness ($1 - \%cover$; see Jennings et al. 1999) was used for further analysis.

If possible, we identified lianas to species in the field. All botanical identifications were based on both reproductive (flowers or fruits) and vegetative (leaves, bark and trunk) characteristics of specimens collected or observed in the

field. In most cases, either fertile or sterile material was collected for identification at the reference Herbarium of CE-FRECOF at Epulu. Collected material was later compared with identified collections at international herbaria, notably the National Herbarium of the Netherlands - Wageningen branch (WAG), the Botanic Garden Meise (BR) in Belgium and Missouri Botanical Garden (MO) in St. Louis. In each herbarium a set of voucher specimens was deposited. Family nomenclature follows the Angiosperm Phylogeny Group (APG, Stevens 2001); that of the species follows Lebrun & Stork (1991–1997).

Data analysis

We characterized liana floristic and structural components at three scales: fine (20×20 m quadrat), plot (10 ha) and community (20 ha). We used a conservative approach in calculating species numbers. Only morphospecies that clearly represented a distinct species were considered. When we were unsure of the species, but had no doubt about genus or family, we lumped all individuals into a morphogroup genus or family, respectively. Electronic appendix gives an overview of all species, morphospecies, and morphogroups. All analyses are based on identifications at three taxonomic ranks: species (all subspecific taxa lumped under the parent

Table 1 – The ten most abundant species, genera and families of lianas in Edoro mixed rain forest in Ituri, D.R. Congo.

Abundance, basal area and importance value in 20 ha of forest. Values between parentheses are percentages of abundances and basal area, and exponent values provide the rank order of taxa with decreasing abundance.

	Scientific name	Family	Stem abundance	Basal area (m ²)	Importance value (%)
Species	<i>Manniophyton fulvum</i>	Euphorbiaceae	3299 (21.9) ¹	2.2 (13.6) ¹	14.3 ¹
	<i>Rourea thomsonii</i>	Connaraceae	922 (6.1) ²	0.9 (5.6) ³	5.7 ²
	<i>Dichapetalum staudtii</i>	Dichapetalaceae	854 (5.7) ³	0.9 (5.3) ⁴	5.3 ³
	<i>Agelaea pentagyna</i>	Connaraceae	767 (5.1) ⁴	1.2 (6.3) ²	5.4 ⁴
	<i>Combretum racemosum</i>	Combretaceae	685 (4.6) ⁵	0.5 (3.2) ⁹	3.3 ⁵
	<i>Dichapetalum heudelotii</i>	Dichapetalaceae	638 (4.3) ⁶	0.7 (4.2) ⁷	3.8 ⁶
	<i>Agelaea paradoxa</i>	Connaraceae	636 (4.2) ⁷	0.5 (3.1) ¹⁰	3.9 ⁹
	<i>Agelaea rubiginosa</i>	Connaraceae	454 (3.0) ⁸	0.6 (3.7) ⁸	3.3 ⁸
	<i>Combretum marginatum</i>	Combretaceae	421 (2.8) ⁹	0.8 (4.9) ⁶	3.7 ¹⁰
	<i>Millettia psilopetala</i>	Leguminosae	390 (2.6) ¹⁰	0.9 (5.6) ⁵	3.7 ⁷
	10 most abundant		9066 (63.2)	9.0 (59.2)	55.8
	All other		5942 (36.8)	7.2 (40.8)	44.2
	Total for identified species		13534 (90.2)	14.4 (89)	88.2
	Total for non-identified morphogroups		1474 (9.8)	1.8 (11)	11.2
	Total (20 ha)		15008 (100)	16.2 (100)	100
	Number of identified species		195		
Genera	Genus	# species			
	<i>Manniophyton</i>	1	3299 (21.9) ¹	2.2 (13.6) ²	14.8 ¹
	<i>Agelaea</i>	3	2117 (14.1) ²	2.5 (15.3) ¹	12.9 ²
	<i>Dichapetalum</i>	7	1821 (12.1) ³	1.9 (11.6) ³	10.8 ³
	<i>Combretum</i>	7	1506 (10.0) ⁴	1.8 (11.2) ⁴	9.3 ⁴
	<i>Rourea</i>	2	971 (6.5) ⁵	1.0 (6.1) ⁶	6.5 ⁵
	<i>Millettia</i>	1	583 (3.9) ⁶	1.4 (8.5) ⁵	5.6 ⁶
	<i>Salacia</i>	3	490 (3.3) ⁷	0.7 (4.5) ⁷	4.2 ⁷
	<i>Strychnos</i>	14	480 (3.2) ⁸	0.4 (2.7) ⁹	3.4 ⁸
	<i>Landolphia</i>	13	303 (2.0) ⁹	0.5 (2.9) ⁸	2.9 ⁹
	<i>Cnestis</i>	2	212 (1.4) ¹⁰	0.2 (1.0) ¹⁰	1.6 ¹⁰
	10 most abundant	40 (21)	11782 (78.5)	12.5 (77.5)	72.2
	All other identified	155 (79)	3226 (21.5)	3.7 (22.5)	27.8
	Total for identified genera	195 (100)	14217 (94.7)	15.2 (93.8)	93.1
	Total for non-identified genera		791 (5.3)	1.0 (6.2)	6.9
	Total (20 ha)		15008 (100)	16.2 (100)	100
Families	Family	# species			
	Connaraceae	13	3482 (23.2) ¹	3.8 (23.5) ¹	19.7 ¹
	Euphorbiaceae	4	3420 (22.8) ²	2.34 (14.6) ²	16.3 ²
	Dichapetalaceae	7	1821 (12.1) ³	1.9 (11.6) ³	11.6 ³
	Combretaceae	7	1506 (10.0) ⁴	1.8 (11.2) ⁴	10.3 ⁴
	Celastraceae	22	1001 (6.7) ⁵	1.5 (8.9) ⁶	8.1 ⁶
	Leguminosae	15	820 (5.5) ⁶	1.8 (11.1) ⁵	8.1 ⁵
	Apocynaceae	30	654 (4.4) ⁷	0.7 (4.6) ⁷	5.2 ⁷
	Loganiaceae	14	480 (3.2) ⁸	0.4 (2.7) ⁸	4.1 ⁸
	Annonaceae	18	424 (2.8) ⁹	0.3 (1.8) ⁹	3.4 ⁹
	Malvaceae	5	245 (1.6) ¹⁰	0.2 (1.5) ¹⁰	2.1 ¹⁰
	10 most abundant	135	13853 (92.3)	14.9 (91.6)	89.1
	All other identified	60	1113 (7.7)	1.3 (8.4)	10.9
	Total for identified	195	14966 (99.7)	16.1 (99.4)	99.5
	Total for non-identified		42 (0.3)	0.1 (0.6)	0.5
	Total (20 ha)		15008 (100)	16.2 (100)	100

species), genus, and family. Morphogroups not identified to a named taxon (9.8% of all recorded stems) were excluded from further analyses.

To describe the liana community structure we calculated for each taxon the Importance Value Index (IVI), i.e. the average percentage of relative density, its occurrence frequency (based on 20 × 20 m plots) and its basal area (Mueller-Dombois & Ellenberg 1974). The total number of species, genera, and families were tallied for each plot (10 ha) and for the whole community (20 ha). We plotted each of these parameters following the method of Preston (1948), by counting the number of species within classes of abundance that doubled in size from one class to the next. For size-related species richness, stem abundance, and basal area we used diameter size class intervals of 2 cm.

We used three indices: Fisher's alpha, the Shannon index, and Simpson diversity (1/D where D is the standard Simpson Dominance) to calculate liana diversity in the 20-ha community. These indices were selected based on their discriminant ability, sensitivity to sample size, and popularity. Fisher's alpha is less sensitive to sample size and thus facilitates comparisons of diversity among sites that differ in abundance (cf. ter Steege et al. 2003, Parmentier et al. 2007). The Shannon index emphasizes the contribution of rare species, while the Simpson diversity index gives more weight to common species in a sample (Magurran 2004). We used EstimateS 8.0 (Colwell 2006) to compute the abundance-based coverage estimator (ACE) and Coleman non-parametric estimators of species richness (Chazdon et al. 1998, Colwell & Coddington 1994). These estimators differently approximate total species richness per plot. The Coleman estimator indicates site heterogeneity, while ACE estimates total species richness by considering singletons (species presented by one individual) and doubletons (species represented by two individuals).

In each 20 × 20 m quadrat, trees were categorized as small (1 cm ≤ dbh < 10 cm), medium (> 10 cm dbh ≤ 30 cm) and large (dbh > 30 cm), and the lianas as small (dbh ≤ 5 cm) or large (dbh > 5 cm). The hypothesis that tree abundance (in separate size classes) would affect the liana abundance (in separate size classes) was tested using backward multiple regression analysis (SPSS 15.0 for Windows; SPSS Inc., Chicago, USA). Terra Firme and Swamp Forest subplots were compared for canopy openness and for abundance of liana stems using T-tests.

We assigned functional traits/ecological characteristics (climbing mechanism, leaf size, regeneration light requirements, flower type, and primary dispersal syndrome) to each species, either by direct field observations and/or using data available in the primary literature (Évrard 1968, Gerard 1960, *Flore d'Afrique centrale* Various editors 1948–, etc.). Climbing mechanisms for all liana species were categorized as (1) stem twiner, (2) hook climber, (3) root climber, and (4) tendrill climber. Leaf size was classified following Raunkjær (1934) as lepto- (< 0.2 cm²), nano- (0.2–2 cm²), micro- (2–20 cm²), meso- (20–200 cm²), and macro-phyllous (200–2000 cm²). Regeneration light requirements were grouped into four classes (Evrard 1968): light demanding, partially light-demanding, partially shade-tolerant, and shade tolerant. Flower types were classified as conspicuous (with generally

bright coloured and large flowers [longer or wider than 1 cm] or with smaller flowers but mass-flowering) and inconspicuous (with whitish, pale, or green coloured and small flowers) (Bawa et al. 1985, Gentry 1982, 1991b). Three primary dispersal syndrome classes were used: anemochory (wind-dispersed fruits or seeds with plumose appendages or scarious wing-like appendages), zoochory (animal dispersed fruits with soft and fleshy outer layers or seeds with arils), and barochory (autochory or active seed dispersed by the plant itself, usually by explosive dehiscence, such as explosive pods). Dispersal by water does not seem to occur in our liana species.

RESULTS

Floristic and taxonomic diversity

A total of 15,008 stems were recorded in the two 10-ha plots. Of these stems 90.2% (13,534 stems) were identified to species level and represented 195 species (see electronic appendix for a complete list) in 83 genera and 34 families (table 1). Edoro-2 (169 species, 76 genera and 33 families) was slightly richer than Edoro-1 (137 species, 72 genera, 31 families). The ten most abundant species collectively accounted for 63.2% (9,066 stems) of all stems and 59.2% (9.0 m²) of all basal area. *Manniophyton fulvum* (Euphorbiaceae) had the highest Importance Value Index (14.3%): it accounted for 21.9% of all liana stems and 13.6% of the total basal area, and was distributed in 88.4% of the quadrats. The ten most important genera included 40 species (21%) and contributed 78.5% of all stems and 77.5% to the basal area. *Manniophyton* (Euphorbiaceae) was the most abundant genus, but *Agelaea* (Connaraceae) had the highest basal area (15.3%). *Landolphia* (13 species) was the most speciose genus but contributed only 2% to abundance and 2.9% to basal area. Ten of 34 families contained 47 genera, and contributed 92.3% to the number of stems, 91.6% to basal area and 89.1% to total Importance Value Index. The most speciose families were Apocynaceae (30 species), Celastraceae (22) and Annonaceae (18). *Laccosperma secundiflorum* (Arecaceae) was the only palm liana in the Ituri Forest liana assemblage.

Species richness and diversity

An average of 63.9 species, 40.6 genera and 21.9 families were recorded per hectare (table 2). Fisher's α was $17.9 \pm 1.3 \text{ ha}^{-1}$, Shannon index was $3.1 \pm 0.2 \text{ ha}^{-1}$ and Simpson index was $11.4 \pm 1.9 \text{ ha}^{-1}$. In the whole community (20 ha), we found that hectare-based species number estimates ranged from Coleman = 62.8 to ACE = 100.3. At the smaller scale of 20 × 20 m quadrats, all values were considerably lower (table 2). The estimated species number was up to twice as high as the observed number. The species accumulation curves (fig. 2A) did not attain an asymptote, even at the 20-ha sampling area. Rare species, defined as those found as singletons and doubletons remained numerous even in large samples.

Table 2 – Liana community floristic and structural attributes of Edoro mixed rainforest, Ituri, D.R. Congo (mean \pm SD).

Site	Edoro 1		Edoro 2		Edoro	
Attribute	20 \times 20 m N = 250	1 ha N = 10	20 \times 20 m N = 250	1 ha N = 10	20 \times 20 m N = 500	1 ha N = 20
Structural and taxonomic recorded characteristics						
Abundance	24.1 \pm 13.7	603.6 \pm 122.5	29.9 \pm 15.1	749.8 \pm 123.6	27.1 \pm 0.7	676.7 \pm 141.3
Basal area (m ²)	0.02 \pm 0.01	0.61 \pm 0.10	0.03 \pm 0.01	0.82 \pm 0.10	0.03 \pm 0.01	0.71 \pm 0.10
Number of species	9.1 \pm 3.5	54.8 \pm 7.8	11.6 \pm 3.5	73.1 \pm 2.1	10.2 \pm 0.2	63.9 \pm 10.9
Number of genera	8.4 \pm 3.1	39.0 \pm 3.9	9.4 \pm 2.8	42.3 \pm 2.6	9.1 \pm 0.1	40.6 \pm 3.7
Number of families	7.6 \pm 2.4	21.7 \pm 1.7	7.9 \pm 2.2	22.2 \pm 1.7	8.4 \pm 0.1	21.9 \pm 1.7
Species richness non-parametric estimators						
ACE	19.8 \pm 11.7	78.6 \pm 10.3	25.2 \pm 14.9	100.3 \pm 9.3	19.9 \pm 12.7	90.4 \pm 17.0
Coleman	13.4 \pm 2.6	62.8 \pm 4.2	16.5 \pm 2.9	85.9 \pm 4.7	15.3 \pm 2.9	80.1 \pm 4.8
Species diversity						
Fisher's Alpha	6.2 \pm 2.1	15.1 \pm 1.2	8.4 \pm 3.1	20.3 \pm 1.4	7.4 \pm 3.3	17.9 \pm 1.3
Shannon	1.9 \pm 0.4	2.9 \pm 0.1	2.1 \pm 0.3	3.2 \pm 0.1	1.9 \pm 0.4	3.1 \pm 0.2
Simpson	6.9 \pm 3.5	10.0 \pm 1.6	8.7 \pm 3.8	12.1 \pm 1.7	8.4 \pm 4.8	11.4 \pm 1.9

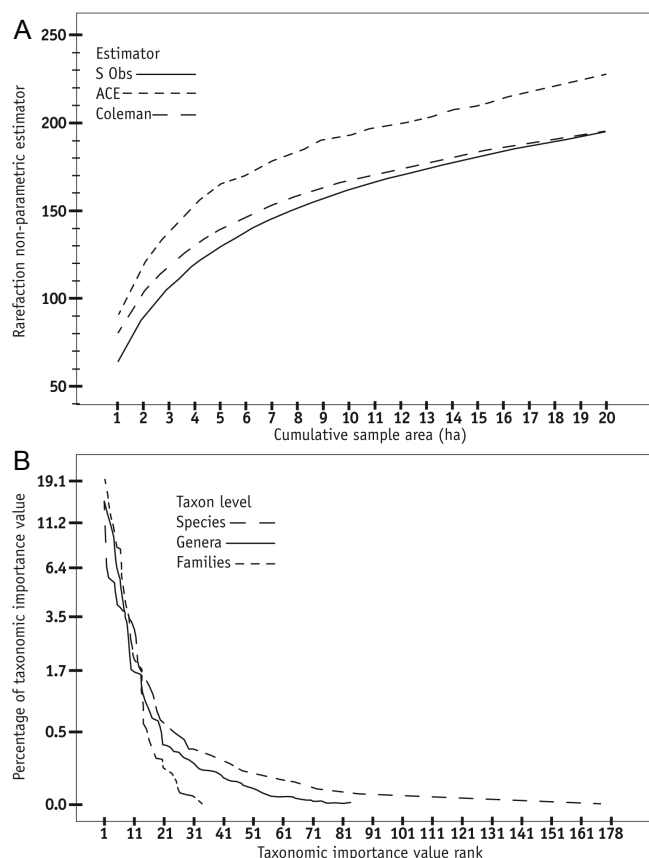


Figure 2 – A, species area curves for observed species richness (S Obs) and species richness estimators ACE and Coleman for lianas in the Edoro mixed forest of Ituri, D.R. Congo; **B**, rank-importance curves for species, genera and families for lianas in 20 ha of mixed rain forest in Ituri. Taxon importance is calculated as the percentage of the total community Importance Value Index and is natural log-transformed (IVI+1) for the graph. Y-axis shows the back-transformed IVI percentages. See electronic appendix for species IVI values.

Liana assemblage structure

Based on the twenty 1-ha plots, mean stem density was 677 ± 141.3 stems ha^{-1} , and mean basal area was 0.71 ± 0.10 m^2 ha^{-1} . Dominance-diversity curves (fig. 2B) show strong dominance of a few taxa and many taxa represented by only a few individuals. Taxonomic abundances (fig. 3) at the 20-ha level varied greatly. Forty-one species (21%) were only known as a single individual, while 56.9% of all stems were represented by species with less than eight liana stems (fig. 3A). In contrast, genera and families exhibited lognormal-like distributions (fig. 3B & C), indicating that taxa vary markedly in their abundances. Most liana individuals were small: nearly 79% were smaller than 4 cm in diameter, while only 2% of stems had a dbh of more than 10 cm (fig. 3E). On average, stems measured 3.4 cm in dbh. The largest stem measured was 19.5 cm dbh (*Landolphia owariensis*, Apocynaceae). Species richness (fig. 3D), abundance (fig. 3E), and total basal area (fig. 3F) decreased with increasing stem size. Large lianas (> 10 cm dbh) contributed 16.5% to the total liana basal area, and included 33 species. Species stem abundance, basal area, and frequency were positively correlated (abundance versus basal area, $r = 0.95$; abundance versus frequency, $r = 0.89$; basal area versus distribution, $r = 0.93$; all $N = 195$ and $P < 0.001$).

Species richness and abundance of lianas were positively correlated with richness and abundance of trees, although the correlation was very low ($r^2 = 0.02$ and 0.01 , $P < 0.01$ in both cases). Especially large-sized trees correlate positively with liana abundance in all size categories (table 3); medium-sized trees also had a positive correlation, but, surprisingly, small trees showed no correlation.

Swamp Forest subplots had more liana stems (38.9 ± 21.7 , $n = 85$) than Terra Firme subplots (mean 28.2 ± 13.4 SD, $n = 415$), possibly partly because canopy openness was higher in SF ($52.9\% \pm 18.7$) than in TF ($39.1\% \pm 12.9$) (T-tests, $p < 0.001$).

Liana characteristics

The functional and ecological characteristics are summarized for the total species assemblage as well as for the 10 most important families separately (fig. 4). Most liana species were stem twiners (69%), followed by tendrill climbers (16%) and hook climbers (14%). Liana species were predominantly mesophyllous (55%) or microphyllous (43%) in leaf size. Most species were light demanding (82%); only a few were either partially light-demanding or partially shade-

tolerant. Just over half of the species had conspicuous flowers (53% vs. 46% inconspicuous flowers). The seeds of most species were animal dispersed (74%), followed by wind dispersed (22%). Only a few species were barochorous (4%). With few exceptions, individual families generally exhibited trends in functional characteristics similar to the complete liana assemblage. Notable exceptions are as follows. Apocynaceae are mostly tendrill-climbers and Loganiaceae are only hook climbers. Dichapetalaceae are only shade-tolerant.

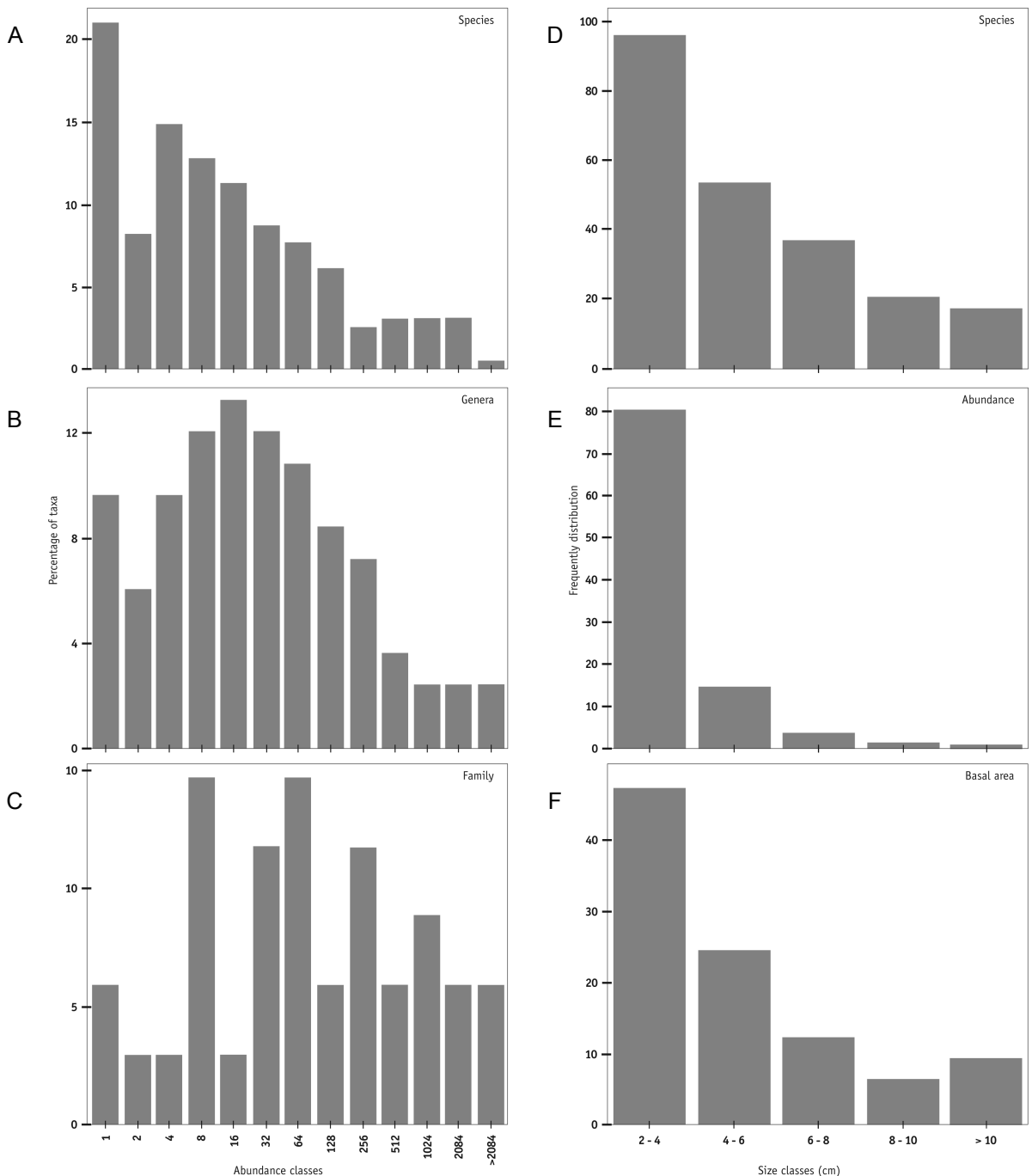


Figure 3 – Frequency distributions of: A, species (N = 195); B, genera (N = 83) and C, families (N = 34) in 20 ha of mixed rain forest in Ituri by abundance classes; and percentage of: D, total species number; E, stem abundance; F, basal area of lianas of different size classes. The abundance classes' interval doubles with each increasing interval, while size class intervals are 2 cm each (X-axis).

Table 3 – Pearson’s correlations of liana abundance with abundance of trees in different stem diameter at breast height size classes in the Ituri mixed forest (N = 500 quadrats).
r is the Pearson coefficient of correlation, *P* is significance level (** *P* < 0.01, *** *P* < 0.001, ns = not significant).

Stature category	Small trees (1-10 cm)		Medium trees (> 10–30 cm)		Large trees (> 30 cm)	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>P</i>
Small lianas (2–5 cm)	0.08	ns	0.15	**	0.25	***
Large lianas (> 5 cm)	0.04	ns	0.11	**	0.09	ns
All size-class lianas	0.08	ns	0.16	***	0.23	***

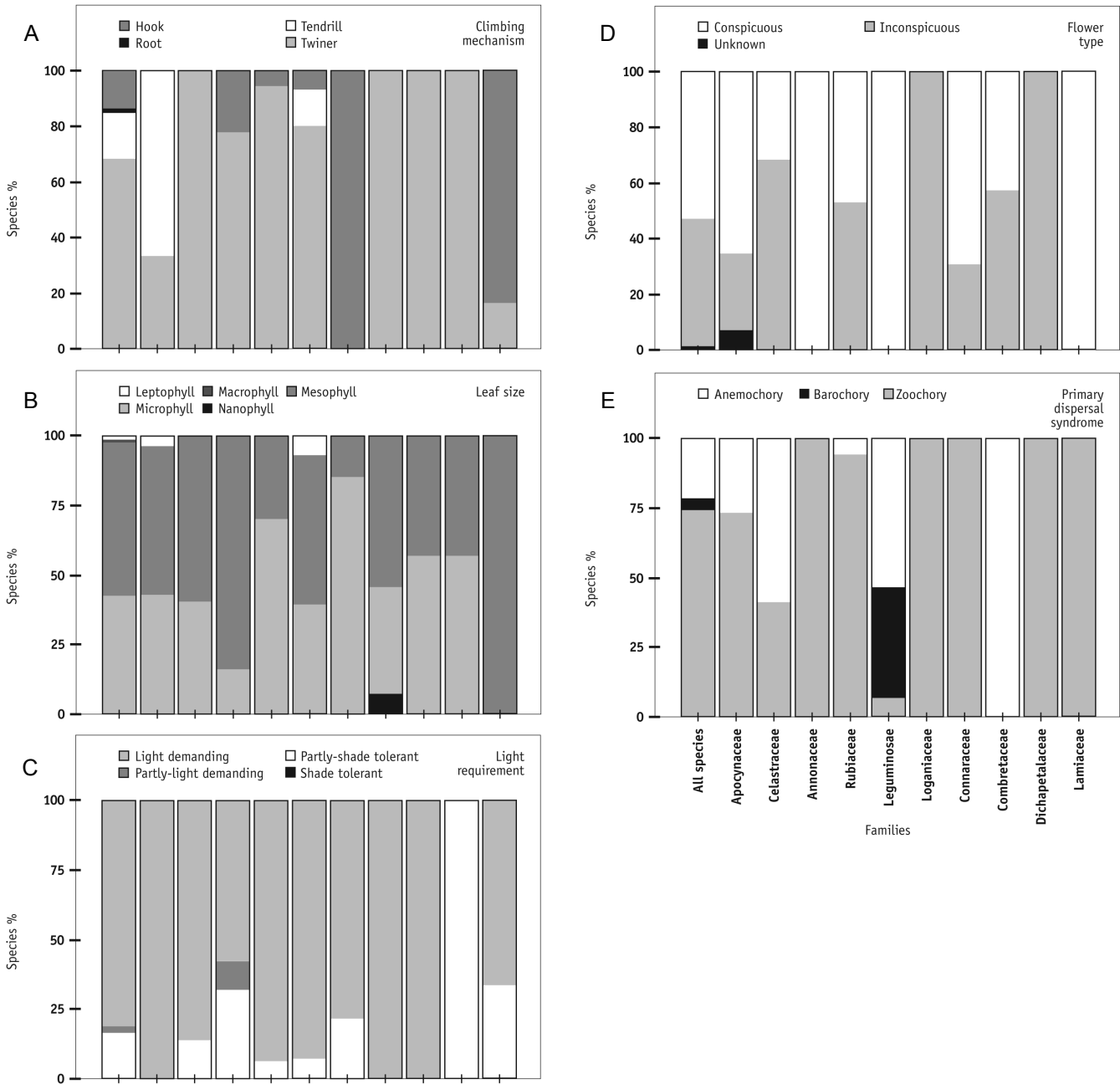


Figure 4 – Proportion (%) of species with different: A, climbing mechanism; B, leaf size; C, life light requirement; D, flower type; E, primary dispersal syndrome for all species (N = 195) and for the 10 most speciose families Apocynaceae (30 species), Celastraceae (22), Annonaceae (18), Rubiaceae (19), Leguminosae (15), Loganiaceae (14), Connaraceae (13), Combretaceae (7), Dichapetalaceae (7), and Lamiaceae (7).

Annonaceae, Connaraceae, Loganiaceae, Dichapetalaceae, Lamiaceae, and Rubiaceae species are entirely dispersed by animals, while all of our Combretaceae lianas are wind-dispersed.

DISCUSSION

Floristic composition

Nearly all individuals (98.2% of all stems) were identified to family, genus, or species. This is on par with Schnitzer et al. (2012) who identified 98.5% of all individuals in a 50-ha plot in Panama, Burnham (2002) who identified 93% of all stems to species or morphospecies in a census of twelve 1-ha plots within Yasuní Forest (Ecuador), and Kuzee & Bongers (2005) who identified 94% of their lianas in Ivory Coast, but is generally well above the results reported in most other studies.

The liana flora in our study plots was dominated by only a few widespread and more generalist species, among them, *Manniophyton fulvum*. Such dominance may be the result of effective dispersal capacity, prolific vegetative sprouting, lack of specific habitat requirements and low abundance of seed predators, or combinations of these. Although this species is generally thought to be light-demanding, we also observed it in shady environments. Dispersal generally is barochorous, though not always clear (Jongkind & Hawthorne 2005) as the comparatively large seeds are reputedly eaten by insects and birds (Jiofack Tafokou 2012), while no apparent predator is known to attack its seeds.

Species composition and family dominance of lianas in Ituri are largely the same as those found in most Central African tropical forests (Cameroon: Parren 2003, Tchouto 2004; Uganda: Eilu 2001). The most abundant families of Ituri (Connaraceae, Euphorbiaceae, Dichapetalaceae, Combretaceae, Celastraceae, Leguminosae and Apocynaceae) are widely distributed even in Upper Guinea (Addo-Fordjour et al. 2008, Jongkind & Hawthorne 2005, Kuzee & Bongers 2005, Muoghalu & Okeesan 2005, Natta & Sinsin 2005, Swaine et al. 2005), suggesting strong similarity among West and Central African lowland forests. However, in the Neotropics the assemblages show a distinctly different family composition, being generally rich in species of Bignoniaceae (Gentry 1991a), a family with only few liana representatives in African forests. The speciose families Apocynaceae, Euphorbiaceae, Leguminosae, and Rubiaceae (which also include many non-lianas) and Connaraceae, Celastraceae, Vitaceae (only including climbers) are important liana families in both Old- and New World floras (Gentry 1991a). The most common liana families in Asian forests are Annonaceae, Leguminosae, Loganiaceae, Rubiaceae, Dilleniaceae and Connaraceae (Appanah et al. 1993, Appanah & Putz 1984) suggesting a closer affinity to the Ituri Forest assemblage. However, the Ituri Forest is poor in palm lianas compared to the Neotropics and continental Asian forests.

Diversity and community structure

Mean liana species richness in the Ituri Forest (64 species ha⁻¹) is within the ranges of values reported for other low-

land forests in Africa and the Neotropics (Burnham 2002, DeWalt et al. 2010, Parren 2003, Romero-Saltos et al. 2001). It compares particularly well with Panama (65 species ha⁻¹, ≥ 2 cm dbh, Putz 1984), Brazilian Amazonia (70 species ha⁻¹, Laurance et al. 2001), and Cameroon (68 species ha⁻¹, Parren 2003), but figures from for example the Barro Colorado Island, Panama are slightly higher (75 species ha⁻¹, Schnitzer et al. 2012).

Species richness (observed number of species, ACE; fig. 2) and species diversity (Shannon index and Fisher α) indices increased with sample sizes, as predicted.

The Ituri Forest contains a few highly abundant lianas. *Manniophyton fulvum* accounts for 22% of all liana stems, with 3299 individuals in 20 ha, and it is nearly threefold more important than the next species (*Rourea thomsonii*). This single species dominance is exceptional, although a few other studies also reported hyperdominant liana species: *Moutabea aculeata* (Polygalaceae) accounted for 17% of stems at La Selva, Costa Rica (Mascaro et al. 2004); *Strophanthus barteri* (Apocynaceae) for 12% of stems in Ghana (Addo-Fordjour et al. 2008), *Machaerium cuspidatum* (Leguminosae) for 11% of stems in Yasuni National Park, Ecuador (Burnham 2002, Nabe-Nielsen 2001), *Maripa panamensis* (Convolvulaceae) for 11% of stems in both secondary and primary forests in Panama (DeWalt et al. 2000), and *Coccoloba excelsa* (Polygonaceae) accounted for 9.1% of all individuals in a 50-ha plot in Panama (Schnitzer et al. 2012). We speculate that the observed collapse of *M. fulvum*, a light-demanding species, indicates it took advantage of recent disturbances but is now declining due to gap closure (Ewango 2010).

Family dominance, however, was in accord with other studies in Africa (Bongers et al. 2005, Gentry 1991a), with Connaraceae, Euphorbiaceae, Dichapetalaceae, Combretaceae, Celastraceae and Leguminosae being the most important families. The 10 most abundant liana species (of 195) represent 63.2% of the stems, which may be characteristic of the Ituri Forest, because the tree assemblage shows a strong single-species dominance (Hart 1985).

Small lianas account for the highest species richness, abundance, and basal area (fig. 3D–F) and, compared to other tropical forests, the Ituri Forest is particularly poor in large liana stems. Again, we speculate that this is the result of disturbances in the recent past (Richards 1952, Whitmore & Burslem 1998, Ewango 2010). Alternatively, its high liana density may be related to the climate seasonality (cf. Schnitzer 2005, DeWalt et al. 2010, van der Heijden & Phillips 2009) under which large-diameter lianas are few (nutrient-poor soils have fewer lianas: DeWalt et al. 2006, Gentry 1991a).

Within the Ituri Forest, liana density (677 ± 141.3 stems ha⁻¹) is high compared to other African forests but not compared to Neotropical forests (Parren 2003, DeWalt & Chave 2004, DeWalt et al. 2010). Some Bolivian Amazon forests showed exceptionally high liana density (mean of 2471 lianas ha⁻¹ ≥ 2 cm dbh) and lianas accounted for as much as 44% of the total woody species (Pérez-Salicrup et al. 2001). The lianas in our forest, despite their high abundance, have a low biomass compared to other tropical rain forests (e.g. in

Brazil, Klinge & Rodriguez 1973; Venezuela, Putz 1983; Bolivia, Pérez-Salicrup et al. 2001, West Africa, Parren 2003), consistent with their relatively small size.

As predicted, liana abundance was influenced by forest structure within the plots and positively correlated with that of trees in the same quadrats (table 3), which suggests that lianas are dependent on mechanical support (trellis), and young lianas can only survive in areas with tree saplings. These grow up when a canopy opening is created, but stop growing once the canopy closes again (Whitmore 1984). High liana abundance is therefore expected to be associated with large densities of trees. Our weak but positive correlation between liana abundance and species richness then may be the direct result of the high abundance. Host tree identity and availability (Ibarra-Manríquez & Martínez-Ramos 2002, Phillips et al. 2005), forest disturbance (Hegarty & Caballé 1991), and seasonality (Gentry 1991a, Schnitzer 2005, DeWalt et al. 2010) are factors most strongly controlling the abundance, species richness, and distribution of lianas in other forests. Abundance was higher in SF plots than in TF plots. This may be related to the generally higher light levels in the more open swamp plots. Openness of the canopy creates higher irradiance at the forest floor, which is generally favourable for liana proliferation (Schnitzer & Carson 2001, Schnitzer et al. 2004). This small-scale pattern parallels observations done at larger spatial scales; lianas tend to be most abundant in drier forests with a seasonally open canopy (DeWalt et al. 2010, Gentry 1991a, Schnitzer 2005).

Functional characteristics of the liana community

In Ituri, twining is the dominant climbing mode (70% of the species, fig. 4A). Our findings corroborate with many other studies in tropical forests (DeWalt et al. 2000 in Panama, Addo-Fordjour et al. 2008 in Ghana, Cai et al. 2009 in China and Laurance et al. 2001 in Brazil). Because of their ability to ascend trees directly, twining species indiscriminately colonize a wide range of trees and species. By twining, lianas may be sufficiently flexible to sway along with trees when there is wind, and they avoid falling under the weight of the whole liana tangle. In the understory, herbivory has been reported as an ecological factor inducing twining in climbing plants (Gianoli & Molina-Montenegro 2005). Families with tough and heavy stems (≥ 5 cm dbh) tend to rely on safety. There seems to be an association between stem mechanical architecture and climbing mechanism; some families with heavy stems are exclusively twining (e.g. Celastraceae, Connaraceae, Combretaceae, and Rubiaceae) or hook-climbing (e.g. Loganiaceae), while other families that tend to have flexible stems also rely on tendrils (e.g. Apocynaceae, like some *Ancyclobotrys*, *Clitandra*, *Dictyophleba* and most *Landolphia* species).

Herbaceous climbers are generally light-demanding, since they establish and grow particularly well in large clearings (Putz 1984). In contrast, woody lianas often occur in very heterogeneous light habitats such as in old gaps, forest margins, and under irregular and broken forest canopies (Gilbert et al. 2006, Hegarty & Caballé 1991, Putz 1984). Most of our lianas are found in both deep shade and full-sun environments, and thus may possess broad intraspecific

physiological plasticity which promotes survival, growth, and competitive ability (Cai et al. 2008). Most liana species can start their life as a seedling in the understorey, and wait for a long time until they find support and get access to the canopy. Liana abundance in old-growth forest is therefore not so much determined by light availability, but rather by trellis availability (table 3, cf. Carter & Teramura 1988). Eighteen per cent of the Ituri liana species were classified as being (partially) shade tolerant. These species have the ability to remain self-supporting for a longer period, and can grow several meters tall before they have to rely on trees for support. If they do not find support, they can flower and reproduce as a self-supporting plant in the shaded understorey, for instance *Millettia psilopetala*, *Strychnos camptoneura*, *S. icaia*, *Trichoscypha reygartii*, and *Dichapetalum* spp.

About half of the species featured conspicuous flowers, while the other half featured inconspicuous flowers (fig. 4D). Species with conspicuous flowers are likely to be pollinated by birds, while less conspicuous flowers are likely to be visited by insects such as bees and flies, or are pollinated by wind. The prevalence of zoochory and animal-mediated pollination we observed (fig. 4) stresses the faunal dependence of the majority of liana species, as is the case for most other rain-forest plants (Bawa 1980, Bullock 1995), and which accords with other liana studies (Addo-Fordjour et al. 2008, Gentry 1991b, Senbeta et al. 2005). This is important for conservation: most lianas rely on animals for their seed dispersal and/or pollination, whilst animals rely on them for food and habitat (Ødegaard 2000, Schnitzer & Bongers 2002). Gentry (1991a) argued that animal dispersal is a characteristic feature of tropical rain-forest plants, as in such wind-still, closed-canopy forests seed dispersal is most effectively done by animals. In contrast, in semi-evergreen and dry evergreen forests, wind dispersal can be the dominant dispersal mechanism, where up to 60% of the species may be anemochorous (Cai et al. 2009, Muthuramkumar & Parthasarathy 2000, Parthasarathy et al. 2004). This can be explained by the fact that in dry forest with a seasonally open canopy, wind can disperse seeds more effectively if they are produced during the dry season.

CONCLUSIONS

We found that, in terms of structure and family composition, the liana community in Ituri Forest is congruent with other Guineo-Congolian forests, with prominent liana taxa being Dichapetalaceae, Connaraceae, Leguminosae, Apocynaceae and Loganiaceae. The most important taxa at Ituri Forest are also important in other African forests, and we conclude that the Ituri Forest liana composition accords with other tropical forest elsewhere. However, the Ituri Forest differs from other Guineo-Congolian forests because it has a high liana abundance and species richness, especially in small size classes, but a low basal area. In addition, the high dominance of a single liana species (*Manniophyton fulvum*) is exceptional. In the Ituri Forest the most important determinants of variations in liana abundance, species richness, and distribution are forest structure and habitat. Soil drainage, and possibly canopy openness play an important role since the more open

swamp forest had a higher liana abundance than the more closed terra firme forest.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of a list of liana species (dbh \geq 2 cm) recorded in the 20 ha plots in Ituri mixed forest.

ACKNOWLEDGMENTS

Fieldwork was supported by the National Geographic Society, the Conservation, Food and Health Fund (CFHF) and the Center for Tropical Forest Sciences/ Smithsonian Institution (CTFS/SI). Drs. John and Terese Hart initiated the Ituri Forest Dynamics Permanent Plots project. The many field assistants and technicians are thanked for their major effort in data collection; the autochthonous pygmies were crucial in this respect. The Management Authority of the Okapis Faunal Reserve kindly granted permission to perform this work within their reserve. Richard Tshombe, Robert Mwinyihali, Innocent Liengola and other staff members of the Centre de Formation et de Recherche en Conservation Forestière / Wildlife Conservation Society-DR Congo Program provided extensive aid in fieldwork. The assistance of plant taxonomy experts of the National Herbarium of the Netherlands-Wageningen Branch and the National Botanical Garden of Belgium (Meise) in specimen identification was highly appreciated. We are grateful to H. ter Steege, R. Burnham and an anonymous reviewer for their constructive comments on the manuscript. This study is part of a PhD fellowship C.E.N. Ewango received from Wageningen University.

REFERENCES

- Addo-Fordjour P., Anning A.K., Atakora E.A., Agyei P.S. (2008) Diversity and distribution of climbing plants in a semi-deciduous rain forest, KNUST botanic garden, Ghana. *International Journal of Botany* 4: 186–195. <http://dx.doi.org/10.3923/ijb.2008.186.195>
- Andrade J.L., Meinzer F.C., Goldstein G., Schnitzer S.A. (2005) Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees* 19: 282–289. <http://dx.doi.org/10.1007/s00468-004-0388-x>
- Appanah S., Gentry A.H., Lafrankie J.V. (1993) Liana diversity and species richness of Malaysian rain forests. *Journal of Tropical Forest Science* 6: 116–123.
- Appanah S., Putz F.E. (1984) Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *Malaysian Forester* 47: 335–342.
- Baars R., Kelly D., Sparrow A. (1998) Liane distribution within native forests remnants in two regions of the South Island, New Zealand. *New Zealand Journal of Ecology* 22: 71–85.
- Balfour D.A., Bond W.J. (1993) Factors limiting climber distribution and abundance in a southern African forest. *Journal of Ecology* 81: 93–99. <http://dx.doi.org/10.2307/2261227>
- Bawa K.S. (1980) Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* 11: 15–39. <http://dx.doi.org/10.1146/annurev.es.11.110180.000311>
- Bawa K.S., Bullock S.H., Perry D.R., Coville R.E., Grayum M.H. (1985) Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *American Journal of Botany* 72: 346–356.
- Bongers F., Parren M.P.E., Traoré D. (2005) Forest climbing plants of West Africa: diversity, ecology and management. Wallingford, Oxfordshire, CAB International.
- Bullock S.H. (1995) Plant reproduction in neotropical dry forests. In: Bullock S.H., Mooney H.A., Medina E. (eds) *Seasonally dry tropical forests*: 277–303. Cambridge, Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511753398.011>
- Burnham R.J. (2002) Dominance, diversity and distribution of lianas in Yasuni, Ecuador: who is on top? *Journal of Tropical Ecology* 18: 845–864. <http://dx.doi.org/10.1017/S0266467402002559>
- Cai Z.-Q., Poorter L., Han Q., Bongers F. (2008) Effects of light and nutrients on seedlings of tropical *Bauhinia* lianas and trees. *Tree Physiology* 28: 1277–1285. <http://dx.doi.org/10.1093/treephys/28.8.1277>
- Cai Z.-Q., Schnitzer S.A., Wen B., Chen Y.J., Bongers F. (2009) Liana communities in three tropical forest types in Xishuangbanna, South-West China. *Journal of Tropical Forest Science* 21: 252–264.
- Carter G.A., Teramura A.H. (1988) Vine photosynthesis and relationships to climbing mechanics in a forest understory. *American Journal of Botany* 75: 1011–1018. <http://dx.doi.org/10.2307/2443769>
- Chazdon R.L., Colwell R.K., Denslow J.S., Guariguata M.R. (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier F., Comiskey J.A. (eds) *Forest biodiversity research, monitoring and modeling: conceptual background and Old World case studies*: 285–309. Paris, Parthenon Publishing.
- Colwell R.K. (2006) EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, Version 8.0. Available at <http://viceroy.eeb.uconn.edu/estimates> [accessed 6 Oct. 2014]
- Colwell R.K., Coddington J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 345: 101–118. <http://dx.doi.org/10.1098/rstb.1994.0091>
- Condit R. (1998) *Tropical forest census plots*. Berlin, Springer Verlag.
- Conway D.J. (1992) A comparison of soil parameters in monodominant and mixed forest in Ituri Forest Reserve, Zaire. Honors Project. University of Aberdeen, Aberdeen, Scotland.
- Dalling J.W., Schnitzer S.A., Baldeck C., Harms K.E., John R., Mangan S.A., Lobo E., Yavitt J.B., Hubbell S.P. (2012) Resource-based habitat associations in a neotropical liana community. *Journal of Ecology* 100: 1174–1182. <http://dx.doi.org/10.1111/j.1365-2745.2012.01989.x>
- Darwin C. (1867) On the movements and habits of climbing plants. *The Journal of the Linnean Society, Botany* 9: 1–118.
- DeVries P.J. (1997) *The butterflies of Costa Rica and their natural history. II Riodinidae*. New Jersey, Princeton University Press.
- DeWalt S.J., Chave J. (2004) Structure and biomass of four lowland Neotropical forests. *Biotropica* 36: 7–19. <http://dx.doi.org/10.1111/j.1744-7429.2004.tb00291.x>
- DeWalt S.J., Schnitzer S.A., Denslow J.S. (2000) Density and diversity of lianas along a chronosequence in a Central Panamanian lowland forest. *Journal of Tropical Ecology* 16: 1–19. <http://dx.doi.org/10.1017/S0266467400001231>

- DeWalt S.J., Ickles K., Nilus R., Harms K.E., Burslem D.F.R.P. (2006) Liana habitat association and community structure in a Bornean lowland tropical forest. *Plant Ecology* 186: 203–216. <http://dx.doi.org/10.1007/s11258-006-9123-6>
- DeWalt S.J., Schnitzer S.A., Chave J., Bongers F., Burnham R.J., Cai Z., Chuyong G., Clark D.B., Ewango C.E.N., Gerwing J.J., Gortaire E., Hart T., Ibarra-Manríquez G., Ickes K., Kenfack D., Macía M.J., Makana J.-R., Martínez-Ramos M., Mascaro J., Moses S., Muller-Landau H.C., Parren M.P.E., Parthasarathy N., Pérez-Salicrup D.R., Putz F.E., Romero-Saltos H., Thomas D. (2010) Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* 42: 309–317. <http://dx.doi.org/10.1111/j.1744-7429.2009.00589.x>
- Eilu G. (2001) The diversity and distribution of climbers and trelises in some forests of the Albertine Rift, western Uganda. PhD thesis, Makerere University, Kampala, Uganda.
- Évrard C. (1968) Recherches écologiques sur le peuplement des sols hydromorphes de la cuvette centrale congolaise. Ministère belge de l'éducation nationale et culture. Publ. INEAC, Série scientifique 110.
- Ewango C.E.N. (2010) The liana assemblage of a Congolian rain-forest. PhD thesis, Wageningen University, Wageningen, the Netherlands.
- Gentry A.H. (1982) Patterns of Neotropical plant species diversity. *Evolutionary Biology* 15: 1–84. http://dx.doi.org/10.1007/978-1-4615-6968-8_1
- Gentry A.H. (1991a) The distribution and evolution of climbing plants. In: Putz F.E., Mooney A.H. (eds) *The biology of vines*: 3–50. Cambridge, Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511897658.003>
- Gentry A.H. (1991b) Breeding and dispersal systems of lianas. In: Putz F.E., Mooney A.H. (eds) *The biology of vines*: 393–424. Cambridge, Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511897658.017>
- Gehring C., Park S., Denich M. (2004) Liana allometric biomass equations for Amazonian primary and secondary forest. *Forest Ecology and Management* 195: 69–83. <http://dx.doi.org/10.1016/j.foreco.2004.02.054>
- Gerard P. (1960) Etude écologique de la forêt dense à Gilbertiendron dewevrei dans la région de l'Uélé. Brussels, Publication INEAC, Série Scientifique 87.
- Gerwing J.J., Farias D.L. (2000) Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* 16: 327–335. <http://dx.doi.org/10.1017/S0266467400001437>
- Gerwing J.J., Schnitzer S.A., Burnham R.J., Bongers F., Chave J., Dewalt S.J., Ewango C.E.N., Foster R., Kenfack D. (2006) A standard protocol for liana censuses. *Biotropica* 38: 256–261. <http://dx.doi.org/10.1111/j.1744-7429.2006.00134.x>
- Gianoli E., Molina-Montenegro M.A. (2005) Leaf damage induces twining in a climbing plant. *New Phytologist* 167: 385–390. <http://dx.doi.org/10.1111/j.1469-8137.2005.01484.x>
- Gianoli E., Saldaña A., Jiménez-Castillo M., Valladares F. (2010) Distribution and abundance of vines along the light gradient in a southern temperate rain forest. *Journal of Vegetation Science* 21: 66–73. <http://dx.doi.org/10.1111/j.1654-1103.2009.01124.x>
- Gilbert B., Wright S.J., Muller-Landau H.C., Kitajima K., Hernández A. (2006) Life history trade-offs in tropical trees and lianas. *Ecology* 87: 1281–1288. [http://dx.doi.org/10.1890/0012-9658\(2006\)87\[1281:LHTITT\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87[1281:LHTITT]2.0.CO;2)
- Hall J.B., Swaine M.D. (1981) Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation in Ghana. The Hague, W. Junk.
- Hart J.A., Carrick P. (1996) Climate of the Réserve de Faune à Okapi: rainfall and temperature in the Epulu sector 1986–1995. Unpublished CEFRECOF Working Paper No. 2, Kampala, Uganda.
- Hart T. (1985) The ecology of a single-species dominant forest and of a mixed forest in Zaïre, Africa. PhD thesis, Michigan State University, East Lansing, United States.
- Hart T.B., Hart J.A., Murphy P.G. (1989) Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *The American Naturalist* 133: 613–633. <http://dx.doi.org/10.1086/284941>
- Hegarty E.E., Caballé G. (1991) Distribution and abundance of vines in forest communities. In: Putz F.E., Mooney A.H. (eds) *The biology of vines*: 313–336. Cambridge, Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511897658.013>
- Homeier J., Englert F., Leuschner C., Weigelt P., Unger M. (2010) Factors controlling the abundance of lianas along an altitudinal transect of tropical forests in Ecuador. *Forest Ecology and Management* 259: 1399–1405. <http://dx.doi.org/10.1016/j.foreco.2010.01.008>
- Ibarra-Manríquez G., Martínez-Ramos M. (2002) Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecology* 160: 91–112. <http://dx.doi.org/10.1023/A:1015839400578>
- Ingwell L.L., Wright S.J., Becklund K.K., Hubbell S.P., Schnitzer S.A. (2010) The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* 98: 879–887. <http://dx.doi.org/10.1111/j.1365-2745.2010.01676.x>
- Jennings S.B., Brown N.D., Sheil D. (1999) Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry* 72: 59–74. <http://dx.doi.org/10.1093/forestry/72.1.59>
- Jiofack Tafokou R.B. (2012) Manniophyton fulvum Muell.Arg. In: Brink M., Achigan-Dako E.G. (eds) *Plant resources of Tropical Africa* 16. Fibres: 318–320. Wageningen, PROTA Foundation / CTA.
- Jongkind C.C.H., Hawthorne W.D. (2005) A botanical synopsis of the lianes and other forest climbers. In: Bongers F., Parren M.P.E., Traoré D. (eds) *Forest climbing plants of West Africa: diversity, ecology and management*: 19–39. Wallingford, Oxfordshire, CAB International.
- Kainer K.A., Wadt L.H.O., Gomes-Silva D.A.P., Capanu M. (2006) Liana loads and their association with Bertholletia excelsa fruit and nut production, diameter growth and crown attributes. *Journal of Tropical Ecology* 22: 147–154. <http://dx.doi.org/10.1017/S0266467405002981>
- Klinge H., Rodriguez, W. (1973) Biomass estimation in central Amazonian rain forest. *Acta Cientifica Venezolana* 24: 225–237.
- Kusumoto B., Enoki T., Watanabe Y. (2008) Community structure and topographic distribution of lianas in a watershed on Okinawa, south-western Japan. *Journal of Tropical Ecology* 24: 675–683. <http://dx.doi.org/10.1017/S0266467408005452>
- Kuzee M.E., Bongers F. (2005) Climber abundance, diversity and colonization in degraded forests of different ages in Côte d'Ivoire. In: Bongers F., Parren M.P.E., Traoré D. (eds) *Forest climbing plants of West Africa: diversity, ecology and management*: 73–91. Wallingford, Oxfordshire, CAB International.
- Laurance W.F., Pérez-Salicrup D., Delamônica P., Fearnside P.M., D'Angelo S., Jerozolinski A., Pohl L., Lovejoy T.E. (2001) Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82: 105–116. [http://dx.doi.org/10.1890/0012-9658\(2001\)082\[0105:RFFATS\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2001)082[0105:RFFATS]2.0.CO;2)

- Lebrun J. (1937) Observations sur la morphologie et l'écologie des lianes de la forêt équatoriale du Congo. Institut Royal Colonial Belge, Bulletin des Séances 8: 78–87.
- Lebrun J.-P., Stork A.L. (1991–1997) Énumération des plantes à fleurs d'Afrique tropicale. Vols 1–4. Genève, Conservatoire et Jardin botaniques de la Ville de Genève.
- Lewis S.L., Lopez-Gonzalez G., Sonké B., Affun-Baffoe K., Baker T.R., Ojo L.O., Phillips O.L., Reitsma J.M., White L., Comiskey J.A., Djuikouo M.K., Ewango C.E.N., Feldpausch T.R., Hamilton A.C., Gloor M., Hart T., Hladik A., Lloyd J., Lovett J.C., Makana J.-R., Malhi Y., Mbago F.M., Ndangalasi H.J., Peacock J., Peh K.S.-H., Sheil D., Sunderland T., Swaine M.D., Taplin J., Taylor D., Thomas S.C., Votere R., Wöll H. (2009) Increasing carbon storage in intact African tropical forests. *Nature* 457: 1003–1006. <http://dx.doi.org/10.1038/nature07771>
- Losos E.C., Leigh E.G. Jr. (2004) Tropical forest diversity and dynamism: findings from a large-scale plot network. Chicago, University of Chicago Press.
- Lowe R.G., Walker P. (1977) Classification of canopy, stem crown status and climber infestation in natural tropical forests in Nigeria. *Journal of Applied Ecology* 14: 897–903. <http://dx.doi.org/10.2307/2402820>
- Magurran A.E. (2004) Measuring biological diversity. Oxford, Blackwell Publishing.
- Makana J.-R., Hart T.B., Hart J.A. (1998) Forest structure and diversity of lianas and understory treelets in monodominant and mixed stands in Ituri Forest, Democratic Republic of the Congo. In: Dallmeier F., Comiskey J.A. (eds) Forest biodiversity research, monitoring and modeling. Conceptual background and Old World case studies: 429–446. London, The Parthenon Publishing Group.
- Makana J.-R., Hart T.B., Hibbs D.E., Condit R. (2004a) Stand structure and species diversity in the Ituri Forest Dynamics Plots: a comparison of monodominant and mixed forest stands. In: Losos E.C., Leigh E.G., Jr. (eds) Tropical forest diversity and dynamism: findings from a large-scale plot network: 159–174. Chicago, The University of Chicago Press.
- Makana J.-R., Hart T.B., Liengola I., Ewango C., Hart J.A., Condit R. (2004b) Ituri Forest Dynamics Plots, Democratic Republic of Congo. In: Losos E.C., Leigh E.G., Jr. (eds) Tropical forest diversity and dynamism: findings from a large-scale plot network: 492–505. Chicago, The University of Chicago Press.
- 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. <http://dx.doi.org/10.1016/j.foreco.2003.10.002>
- Mueller-Dombois D., Ellenberg H. (1974) Aims and methods of vegetation ecology. New York, John Wiley & Sons.
- Muoghalu J.I., Okeanos O.O. (2005) Climber species composition, abundance and relationship with trees in a Nigerian secondary forest. *African Journal of Ecology* 43: 258–266. <http://dx.doi.org/10.1111/j.1365-2028.2005.00585.x>
- Muthuramkumar S., Parthasarathy N. (2000) Alpha diversity of lianas in a tropical evergreen forest in the Anamalais, Western Ghats, India. *Diversity and Distributions* 6: 1–14. <http://dx.doi.org/10.1046/j.1472-4642.2000.00057.x>
- Nabe-Nielsen J. (2001) Diversity and distribution of lianas in a neotropical rain forest, Yasuni National Park, Ecuador. *Journal of Tropical Ecology* 17: 1–19. <http://dx.doi.org/10.1017/S0266467401001018>
- Nabe-Nielsen J., Hall P. (2002) Environmentally induced clonal reproduction and life history traits of the liana *Machaerium cuspidatum* in an Amazonian rain forest, Ecuador. *Plant Ecology* 162: 215–226. <http://dx.doi.org/10.1023/A:1020561923488>
- Nabe-Nielsen J., Kollmann J., Peña-Claros M. (2009) Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical timber trees. *Forest Ecology and Management* 257: 987–993. <http://dx.doi.org/10.1016/j.foreco.2008.10.033>
- Natta A.K., Sinsin B. (2005) Taxonomic diversity of climbers of riparian forests in Benin. In: Bongers F., Parren M.P.E., Traoré D. (eds) Forest climbing plants of West Africa: diversity, ecology and management: 123–136. Wallingford, Oxfordshire, CAB International.
- Ødegaard F. (2000) The relative importance of trees versus lianas as host for phytophagous beetles (Coleoptera) in tropical forests. *Journal of Biogeography* 27: 283–296. <http://dx.doi.org/10.1046/j.1365-2699.2000.00404.x>
- Parmentier I., Malhi Y., Senterre B., Whittaker R.J., Alfonso Alonso A.T.D.N., Balinga M.P.B., Bakayoko A., Bongers F., Chatelain C., Comiskey J.A., Cortay R., Kamdem M.-N.D., Doucet J.-L., Gautier L., Hawthorne W.D., Issembe Y.A., Kouamé F.N., Kouka L.A., Leal M.E., Lejoly J., Lewis S.L., Nusbaumer L., Parren M.P.E., Peh K.S.-H., Phillips O.L., Sheil D., Sonké B., Sosef M.S.M., Sunderland T.C.H., Stropp J., ter Steege H., Swaine M.D., Tchouto M.G.P., Van Gemenen B.S., Van Valkenburg J.L.C.H., Wöll H. (2007) The odd man out? Might climate explain the lower tree α -diversity of African rain forests relative to Amazonian rain forests? *Journal of Ecology* 95: 1058–1071. <http://dx.doi.org/10.1111/j.1365-2745.2007.01273.x>
- Parren M.P.E. (2003) Lianas and logging in West Africa. Tropenbos-Cameroon Series 6. Wageningen, Tropenbos International.
- Parren M.P.E., Bongers F., Caballé G., Nabe-Nielsen J., Schnitzer S.A. (2005) On censusing lianas: a review of common methodologies. In: Bongers F., Parren M.P.E., Traoré D. (eds) Forest climbing plants of West Africa: diversity, ecology and management: 41–57. Wallingford, Oxfordshire, CAB International.
- Parthasarathy N., Muthuramkumar S., Sridhar Reddy M. (2004) Patterns of liana diversity in tropical evergreen forests of peninsular India. *Forest Ecology and Management* 190: 15–31. <http://dx.doi.org/10.1016/j.foreco.2003.10.003>
- Peel M.C., Finlayson B.L., McMahon T.A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11: 1633–1644. <http://dx.doi.org/10.5194/hess-11-1633-2007>
- Peña-Claros M., Fredericksen T.S., Alarcón A., Blate G.M., Choque U., Leño C., Licona J.C., Mostacedo B., Pariona W., Villegas Z., Putz F.E. (2008) Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management* 256: 1458–1467. <http://dx.doi.org/10.1016/j.foreco.2007.11.013>
- Pérez-Saliciup D.R., Sork V., Putz F.E. (2001) Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica* 33: 34–47. [http://dx.doi.org/10.1646/0006-3606\(2001\)033\[0034:LATIAL\]2.0.CO;2](http://dx.doi.org/10.1646/0006-3606(2001)033[0034:LATIAL]2.0.CO;2)
- Phillips O.L., Vázquez Martínez R., Arroyo L., Baker T.R., Killen T., Lewis S.L., Malhi Y., Monteagudo Mendoza A., Neil D., Nuñez Vargas P., Alexiades M., Cerón C., Di Fiore A., Erwin T., Jardim A., Palacios W., Saldias M., Vinceti B. (2002) Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770–774. <http://dx.doi.org/10.1038/nature00926>
- Phillips O.L., Vázquez Martínez R.V., Monteagudo Mendoza A., Baker T.R., Nuñez Vargas P. (2005) Large lianas as hyperdynamic elements of the tropical forests canopy. *Ecology* 86: 1250–1258. <http://dx.doi.org/10.1890/04-1446>

- Poulsen A.D., Hafashimana D., Eilu G., Liengola I.B., Ewango C.E.N., Hart T.B. (2005) Composition and species richness of forest plants along the Albertine Rift, Africa. *Biologiske Skrifter* 55: 129–143.
- Preston F.W. (1948) The commonness, and rarity, of species. *Ecology* 29: 254–283. <http://dx.doi.org/10.2307/1930989>
- Putz F.E. (1983) Liana biomass and leaf area of a “Tierra Firme” forest in the Rio Negro Basin, Venezuela. *Biotropica* 15: 185–189. <http://dx.doi.org/10.2307/2387827>
- Putz F.E. (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713–1724. <http://dx.doi.org/10.2307/1937767>
- Putz F.E., Holbrook N.M. (1991) Biomechanical studies of vines. In: Putz F.E., Mooney H.A. (eds) *The biology of vines*: 73–98. Cambridge, Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511897658.005>
- Raunkiaer C. (1934) *The life forms of plants and statistical plant geography*. Oxford, Clarendon Press.
- Richards P.W. (1952) *The tropical rain forest, an ecological study*. Cambridge, Cambridge University Press.
- Romero-Saltos H., Valencia R., Macía M.J. (2001) Patrones de diversidad, distribución y rareza de plantas leñosas en el Parque Nacional Yasuní y la Reserva Étnica Huaorani, Amazonia ecuatoriana. In: Duivenvoorden J.F., Balslev H., Cavelier J., Grandez C., Tuomisto H., Valencia R. (eds) *Evaluación de recursos vegetales no maderables en la Amazonía noroccidental*: 131–162. Amsterdam, IBED, Universiteit van Amsterdam.
- Schnitzer S.A. (2005) A mechanistic explanation for the global patterns of liana abundance and distribution. *The American Naturalist* 166: 262–276. <http://dx.doi.org/10.1086/431250>
- Schnitzer S.A., Bongers F. (2002) The ecology of lianas and their role in forests. *Trends in Ecology & Evolution* 17: 223–230. [http://dx.doi.org/10.1016/S0169-5347\(02\)02491-6](http://dx.doi.org/10.1016/S0169-5347(02)02491-6)
- Schnitzer S.A., Carson W.P. (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82: 913–919. [http://dx.doi.org/10.1890/0012-9658\(2001\)082\[0913:TGA TMO\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2001)082[0913:TGA TMO]2.0.CO;2)
- Schnitzer S.A., Parren M.P.E., Bongers F. (2004) Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. *Forest Ecology and Management* 190: 87–98. <http://dx.doi.org/10.1016/j.foreco.2003.10.008>
- Schnitzer S.A., Kuzee M.A., Bongers F. (2005) Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology* 93: 1115–1125. <http://dx.doi.org/10.1111/j.1365-2745.2005.01056.x>
- Schnitzer S.A., Mangan S.A., Dalling J.W., Baldeck C.A., Hubbell S.P., Ledo A., Muller-Landau H., Tobin M.F., Aguilar S., Brassfield D., Hernandez A., Lao S., Perez R., Valdes O., Rutishauser Yorke S. (2012) Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS ONE* 7: e52114. <http://dx.doi.org/10.1371/journal.pone.0052114>
- Senbeta F., Schmit C., Denich M., Demissew S., Vlek P.L.G., Preisinger H., Woldemariam T., Teketay D. (2005) The diversity and distribution of lianas in the afro-montane rain forests of Ethiopia. *Diversity and Distributions* 11: 443–452. <http://dx.doi.org/10.1111/j.1366-9516.2005.00180.x>
- Smith R.F. (1970) The vegetation structure of a Puerto Rican rain forest before and after short-term gamma irradiation. In: Odum T.H., Pigeon R.F. (eds) *A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico*: 103–140. Oak Ridge, US Atomic Energy Commission.
- Stevens G.C. (1987) Lianas as structural parasites: the *Bursera simaruba* example. *Ecology* 68: 77–81. <http://dx.doi.org/10.2307/1938806>
- Stevens P.F. (2001–onwards). Angiosperm Phylogeny website [online]. Available from <http://www.mobot.org/MOBOT/research/APweb> [accessed 1 Jun. 2008].
- Swaine M.D., Hawthorne W.D., Bongers F., Toledo M.A. (2005) Climbing plants in Ghana Forests. In: Bongers F., Parren M.P.E., Traoré D. (eds) *Forest climbing plants of West Africa: diversity, ecology and management*: 93–108. Wallingford, Oxfordshire, CAB International.
- Tchouto M.G.P. (2004) *Plant diversity in a central African rain forest, implications for biodiversity conservation in Cameroun*. PhD thesis, Wageningen University, Wageningen, The Netherlands.
- ter Steege H., Pitman N., Sabatier D., Castellanos H., Van Der Hout P., Daly D.C., Silveira M., Phillips O., Vasquez R., Van Andel T., Duivenvoorden J., De Oliveira A.A., Ek R., Lilwah R., Thomas R., Van Essen J., Baider C., Maas P., Mori S., Terborgh J., Nuñez Vargas P., Mogollón H., Morawetz W. (2003) A spatial model of tree α -diversity and tree density for the Amazon. *Biodiversity & Conservation* 12: 2255–2277. <http://dx.doi.org/10.1023/A:1024593414624>
- Toledo M.V. (2010) *Neotropical lowland forests along environmental gradients*. PhD Thesis, Wageningen University, Wageningen, The Netherlands.
- van der Heijden G.M., Phillips O.L. (2009) Environmental effects on Neotropical liana species richness. *Journal of Biogeography* 36: 1561–1572. <http://dx.doi.org/10.1111/j.1365-2699.2009.02099.x>
- Various editors (1948–) *Flore d’Afrique centrale*. Meise, Jardin botanique national de Belgique.
- Villegas Z., Peña-Claros M., Mostacedo B., Alarcón A., Licona J.C., Leño C., Pariona W., Choque U. (2009) Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest. *Forest Ecology and Management* 258: 971–977. <http://dx.doi.org/10.1016/j.foreco.2008.10.031>
- Whigham D. (1984) The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). *Canadian Journal of Forest Research* 14: 37–39. <http://dx.doi.org/10.1139/x84-008>
- White F. (1983) *The Vegetation of Africa*. Paris, UNESCO.
- Whitmore T.C. (1984) *Tropical rain forests of the far East*. 2nd Ed. Oxford, Clarendon Press.
- Whitmore T.C., Burslem D.F.R.P. (1998) Major disturbances in tropical forests. In: Newbery D.M., Prins H.H.T., Brown N.D. (eds) *Dynamics of tropical communities: the 37th Symposium of the British Ecological Society*, Royal Holloway College, University of London, 1996: 549–565. Malden, Massachusetts, Blackwell Science.
- Wright J.S., Calderón O., Hernández A., Paton S. (2004) Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85: 484–489. <http://dx.doi.org/10.1890/02-0757>

Manuscript received 21 Feb. 2014; accepted in revised version 6 Oct. 2014.

Communicating Editor: Hans ter Steege.