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Structure and composition of the liana assemblage of Azagny National Park in the Southern Côte d'Ivoire

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The Azagny National Park represents one of the most important blocks of forest in Côte d'Ivoire, but its liana assemblage has never been characterized. Liana floristics, diversity, species composition and structure were evaluated. Fourteen plots of 1 ha (20 × 25 m) were established in different biotopes of the forest. All individual lianas of dbh ≥ 1 cm were identified, measured and marked. For each 1 ha plot, old growth forest from secondary forest was distinguished. In total, 5,436 lianas, representing 63 species, 47 genera, and 28 families were identified. The average number of species was 18.35, mean basal area was 0.21 m² and mean Fisher's alpha, Shannon index and Simpson diversity index values were 19, 2.81 and 0.72, respectively. Ten dominant plant families accounting for 83% of total species richness, 71% of liana abundance and 71% of basal area were also identified. Twiners, zoochorous, light-demanding and microphanerophyte species dominated. There were more large lianas in old growth forests than in secondary forests. The liana assemblage and species floristic composition is generally similar to that in other tropical African forests.

Key words: Lianas, old growth forest, secondary forest, species diversity, Azagny National Park, Côte d'Ivoire.

INTRODUCTION

Lianas (woody climbers) are notoriously abundant in the tropics, contributing up to 25% of the woody stem density (Gentry, 1991; Schnitzer and Bongers, 2002), and up to 12 to 40% of the overall species diversity of such forests (Gentry, 1991). Apart from their direct contribution to biodiversity, lianas help maintaining diversity through their effects on forest structure and dynamics (Putz,

1984; 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. Indeed, lianas substantially contribute to canopy closure after tree fall, stabilizing the microclimate underneath, and contributing to whole-forest transpiration (Schnitzer and Bongers,

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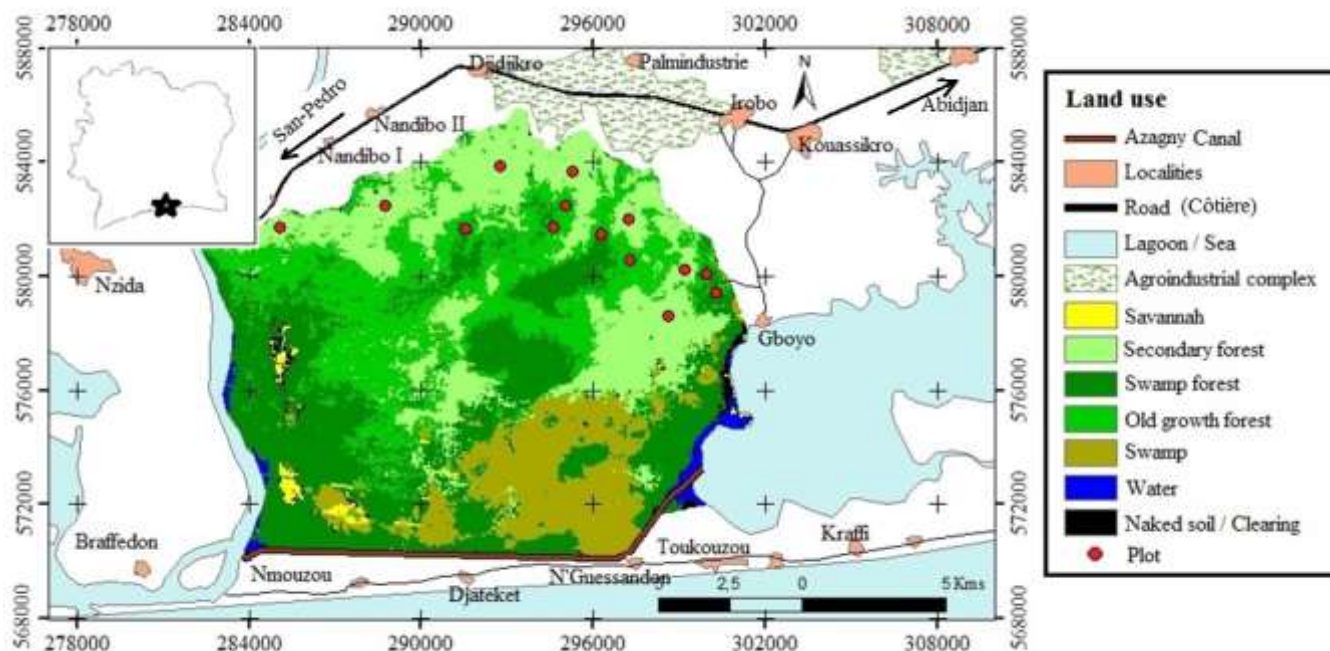


Figure 1. Location map of the Azagny National Park (ANP) in the South Côte d'Ivoire showing different types of biotopes.

2002). Lianas contribute also to the carbon budget of tropical forests (Lewis et al., 2009), representing as much as 10% of the fresh above-ground biomass (Putz, 1984), and accounting for up to 40% of the leaf productivity (Hegarty and Caballé, 1991). By colonizing trees, lianas create structural stress on their hosts, compete for light, water and soil nutrients, generally reducing tree growth (Dalling et al., 2012), and reproduction; while increasing rates of tree fall and limb breakage (Putz, 1984).

The varying species composition of lianas, in different forest types, demonstrates that there are large ecological and functional differences across species. Lianas have a similar growth form and are generally light demanding (Putz, 1984), but they do differ in, for example, climbing mechanisms (Putz and Holbrook, 1991) and light requirements (Kuzee and Bongers, 2005). Furthermore, dispersal type varies markedly across liana species (Cai et al., 2009), and are correlated with a wide range of pollinators and propagule distributors. All this enables lianas to occupy a wide range of habitat types (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 (Toledo, 2010), landscape topography (Dalling et al., 2012), canopy structure (Ibarra-Manríquez and Martínez-Ramos, 2002) and disturbance regimes.

Although the importance of lianas is broadly recognized in the tropical world, in Ivorian forests, very few liana studies have been undertaken (Etien and Traoré, 2005; Kuzee and Bongers, 2005; Tra Bi et al., 2005; Kouassi,

2007). The present study could help redress this lack. It aims to evaluate the community structure of the liana assemblage in a national park in the South Côte d'Ivoire. Using data from 14 forest plots of 1 ha each, we (1) describe the floristics, diversity and structure of the liana assemblage in this park; (2) characterize liana functional traits (climbing mechanisms, regeneration guilds, stem size and dispersal syndromes); and (3) determine the effect of forest structure on liana species abundance.

Hypotheses were tested that (1) the liana assemblage in the Azagny National Park (ANP) is similar in diversity and structure with rain forests elsewhere, but precisely similar other such assemblages in West Africa, and (2) there is a correlation between the number of species and of abundance between the two forest types.

MATERIALS AND METHODS

Study site

The Azagny National Park, located in the South of Côte d'Ivoire, between 5° 14' and 5° 31' north latitude, and 4° 76' and 5° 01' west longitude, covers an area of 21,850 ha (Kouamé et al., 2010) (Figure 1). It covers the Departments of Grand Lahou and Jacqueville, and is part of the phytogeographical region of "Upper Guinea", which stretches from Senegal to Togo.

Azagny National Park is a low lying and composed of vast swamp areas (about 9,000 ha), made of salt water, which does not show any sign of natural sinking (Kouamé et al., 2008). The water regime of the park gives its ecological specificity. Three quarters of its area are formed by the complex Bandama River, the Azagny

Canal and the Ebrié lagoon. Finally, the park is flooded to 45% throughout the year and 62% during the main rainy season. The climate of the region is sub-equatorial (Avenard et al., 1971). Few studies have been undertaken in this park concerning its diversity. In the same way, the history of the occupation of the park allows a variety of habitats to meet the objectives of this study.

Data collection

From September 2013 to December 2014, data was collected in the Azagny National Park. Fourteen plots of 1 ha, sub-divided into smaller plots (20 × 25 m), were surveyed. Seven different plots have been selected in old growth forests and seven in secondary forests, which are old fallows to allow comparisons.

In each 1 ha plot, a grid of 20 contiguous 20 × 25 m² quadrats was demarcated. All liana individuals of dbh ≥ 1 cm were identified and measured. Liana dbh was measured at 1.3 m distance along the stem from their rooting point. To facilitate comparison with other liana studies, true liana species was only included: 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; Schnitzer et al., 2008).

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 the Botanic Garden in Félix Houphouët-Boigny University. Family and species nomenclatures follow Lebrun and Stork (1991–1997).

Data analysis

Liana floristic and structural components at three scales were characterized: fine (20 × 25 m quadrat), plot (7 ha) and community (14 ha). All analyses are based on identifications at three taxonomic ranks: species, genus, and family. Morphogroups not identified to a named taxon (10.31% of all recorded stems) were excluded from further analyses.

To describe the liana community structure, for each taxon, the Importance Value Index (IVI), was calculated, that is, the average percentage of relative density, its occurrence frequency (based on 20 × 25 m plots) and its basal area (Mueller-Dombois and Ellenberg, 1974). The total number of species, genera, and families were tallied for each plot (1 ha) and for the whole community (14 ha).

Three indices were used: Fisher's alpha, the Shannon index, and Simpson diversity (1/D, where D is the standard Simpson Dominance), to calculate liana diversity in the 14 ha community. These indices were selected based on their discriminant ability, sensitivity to sample size, and popularity. Estimate S 8.0 was used to compute the abundance-based coverage estimator (ACE) and Coleman non-parametric estimators of species richness (Chazdon et al., 1998).

In each 20 × 25 m quadrat, the lianas were categorized as small (dbh ≤ 5 cm) or large (dbh > 5 cm). The hypothesis that the number of liana species would affect the liana abundance and that the abundance of species, by diameter class, depends on the type biotope, was tested using Wilcoxon test (R 2.15). Old growth forests and secondary forests subplots were compared for abundance of liana stems using t tests.

Functional traits/ecological characteristics (climbing mechanism, stem size, regeneration light requirements and primary dispersal syndrome) were assigned to each species, either by direct field observations and/or using data available in the primary literature

(Aké-Assi, 2001, 2002; Adou Yao, 2005; Vroh, 2013). Climbing mechanisms for all liana species were categorized as (1) stem twiner, (2) hook climber, (3) root climber, and (4) tendril climber. Stem size was classified following Raunkiaer (1934) as: mega-phanerophyte (> 30 m), meso-phanerophyte (8 to 29 m), micro-phanerophyte (2 to 7 m), and nano-phanerophyte (< 2 m). Regeneration light requirements were grouped into two classes: light demanding and shade tolerant. Three primary dispersal syndrome classes were used: anemochory, zoochory and barochory.

RESULTS

Floristic and taxonomic diversity

A total number of 5,436 stems were recorded in the fourteen 1 ha plots. Of these stems, 89.69% (4,876 stems) were identified to species level, and represented 63 species in 47 genera and 28 families. Secondary forest (41 species, 32 genera and 25 families) was slightly richer than old growth forest (39 species, 34 genera and 21 families). The ten most abundant species collectively accounted for 46.3% (2,258 stems) of all stems, and 57.6% (1.33 m²) of all basal area (Table 1). *Adenia lobata* (Passifloraceae) had the highest Importance Value Index (19.2%): it accounted for 6.9% of all liana stems and 5.4% of the total basal area, and was distributed in 6.9% of the quadrats. The ten most important genera included 16 species (25.4%), and contributed 54.7% of all stems and 58.3% to the basal area. *Adenia* (Passifloraceae) was the most abundant genus, but *Strophantus* (Apocynaceae) had the highest basal area (8.8%). *Cissus* (3 species) was the most speciose genus but contributed only 3.8% to abundance, and 2.5% to basal area. Ten of 28 families contained 27 genera, and contributed 71.0% to the number of stems, 70.9% to basal area, and 90.0% to total Importance Value Index. The most speciose families were Fabaceae (7 species), Apocynaceae (5 species), and Icacinaceae (5). *Calamus deerratus* (Arecaceae) was the only palm liana in the Azagny National Park liana assemblage.

Species richness and diversity

An average of 18.35 species, 13 genera and 11.28 families were recorded per hectare (Table 2). Fisher's α was $19.0 \pm 2.7 \text{ ha}^{-1}$, Shannon index was $2.81 \pm 0.25 \text{ ha}^{-1}$, and Simpson index was $0.72 \pm 0.01 \text{ ha}^{-1}$. In the whole community (14 ha), we found that hectare-based species number estimates ranged from Coleman = 50.3 to ACE = 74.8. At the smaller scale of 20 × 25 m quadrats, all values were considerably lower.

Liana assemblage structure

Based on the fourteen 1 ha plots, mean stem density was

Table 1. The ten most abundant species, genera and families of lianas in the Azagny National Park (ANP). Abundance, basal area and importance value in 14 ha of forest. Values between parentheses represent percentages of abundance and basal area.

	Scientific name	Family	Stem abundance	Basal area (m²/ha)	Importance value (%)	
Species	<i>Adenia lobata</i>	Passifloraceae	376 (6.9)	0.16 (5.4)	19.2	
	<i>Tiliacora dinklagei</i>	Menispermaceae	362 (6.7)	0.25 (8.3)	18.8	
	<i>Strophanthus gratus</i>	Apocynaceae	292 (5.4)	0.26 (8.8)	18.2	
	<i>Alchornea cordifolia</i>	Euphorbiaceae	246 (4.5)	0.11 (3.6)	13.3	
	<i>Piper guineense</i>	Piperaceae	260 (4.8)	0.10 (3.4)	12.4	
	<i>Pararistolochia leonensis</i>	Aristolochiaceae	186 (3.4)	0.11 (3.5)	9.9	
	<i>Calamus deerratus</i>	Arecaceae	146 (2.7)	0.11 (3.7)	8.4	
	<i>Macaranga bellei</i>	Euphorbiaceae	158 (2.9)	0.08 (2.8)	8.2	
	<i>Cnestis ferruginea</i>	Connaraceae	148 (2.7)	0.04 (1.3)	7.0	
	<i>Secamone afzelii</i>	Asclepiadaceae	84 (1.5)	0.11 (3.8)	6.9	
	10 most abundant	-	2258 (46.3)	1.33 (57.6)	48.1	
	All other	-	2618 (53.7)	0.98 (42.4)	51.9	
	Total for identified species	-	4876 (89.7)	2.31 (77.7)	84.8	
	Total for non-identified morphogroups	-	560 (10.3)	0.66 (22.3)	15.2	
	Total (14 ha)	-	5436 (100)	2.97 (100)	100	
	Number of identified species	-	63	-	-	
Genera	Genus	# Species				
	<i>Adenia</i>	2	474 (8.7)	0.2 (6.6)	23.71	
	<i>Tiliacora</i>	1	362 (6.7)	0.2 (8.3)	19.1	
	<i>Strophanthus</i>	1	292 (5.4)	0.3 (8.8)	18.6	
	<i>Clerodendrum</i>	3	318 (5.8)	0.1 (3.8)	15.9	
	<i>Alchornea</i>	1	246 (4.5)	0.1 (3.6)	13.7	
	<i>Piper</i>	1	260 (4.8)	0.1 (3.4)	12.7	
	<i>Pararistolochia</i>	1	186 (3.4)	0.1 (3.5)	10.2	
	<i>Cissus</i>	3	206 (3.8)	0.1 (2.5)	10.1	
	<i>Macaranga</i>	2	178 (3.3)	0.1 (3.1)	9.0	
	<i>Calamus</i>	1	146 (2.7)	0.1 (3.8)	8.6	
		10 most abundant	16 (25.4)	2668 (54.7)	1.4 (58.3)	54.8
		All other identified	47 (74.6)	2208 (45.3)	1.0 (41.7)	45.2
		Total for identified genera	63 (100)	4876 (89.7)	2.4 (77.0)	86.2
		Total for non-identified genera	-	560 (10.3)	0.7 (33.0)	13.8
		Total (14 ha)	-	5436 (100)	3.1 (100)	100
Families	Family	# Species				
	Apocynaceae	5	470 (8.6)	0.34 (11.5)	27.8	
	Passifloraceae	2	474 (8.7)	0.2 (6.6)	24.1	
	Euphorbiaceae	4	436 (8.0)	0.2 (6.7)	23.0	
	Fabaceae	7	512 (9.4)	0.3 (6.8)	22.8	
	Menispermaceae	3	438 (8.1)	0.1 (9.1)	22.7	
	Verbenaceae	3	318 (5.8)	0.1 (3.8)	16.2	
	Piperaceae	1	260 (4.8)	0.1 (3.4)	13.0	
	Aristolochiaceae	1	186 (3.4)	0.1 (3.5)	10.3	
	Vitaceae	3	206 (3.8)	0.1 (2.5)	10.2	
	Icacinaceae	5	160 (2.9)	0.1 (3.4)	9.3	
		10 most abundant	34	3460 (71.0)	1.7 (70.9)	90.0
		All other identified	29	1416 (29.0)	0.7 (29.1)	10.0
		Total for identified	63	4876 (89.7)	2.4 (77.0)	89.9
		Total for non-identified	-	560 (10.3)	0.7 (33.0)	10.1
		Total (14 ha)	-	5436 (100)	3.1 (100)	100

Table 2. Liana community floristic and structural attributes of Azagny National Park (ANP) (mean \pm SD).

Site	Old growth forest		Secondary forest		Azagny	
Attribute	20x25 N=140	1ha N=7	20x25 N=140	1ha N=7	20x25 N=280	1ha N=14
Structural and taxonomic recorded characteristics						
Abundance	19.6 \pm 7.02	392 \pm 133.8	19.22 \pm 9.23	384.6 \pm 173.5	19.41 \pm 8.2	388.3 \pm 143.9
Basal area (m ²)	0.01 \pm 0.01	0.30 \pm 0.12	0.006 \pm 0.005	0.12 \pm 0.09	0.01 \pm 0.009	0.21 \pm 0.13
Number of species	7.67 \pm 2.22	19.14 \pm 7.08	8.21 \pm 3.04	17.57 \pm 4.57	7.94 \pm 2.67	18.35 \pm 5.78
Number of genera	5.44 \pm 1.58	12.42 \pm 3.15	6.19 \pm 2.24	13.57 \pm 2.76	5.81 \pm 1.97	13 \pm 2.90
Number of families	5.2 \pm 1.55	10.57 \pm 2.93	5.86 \pm 2.18	12 \pm 2.16	5.53 \pm 2.02	11.28 \pm 2.58
Species richness non-parametric estimator						
ACE	19.48 \pm 10.77	74.88 \pm 11.34	15.84 \pm 5.12	66.22 \pm 3.26	17.66 \pm 7.95	70.58 \pm 7.27
Coleman	10.31 \pm 2.58	69.1 \pm 2.8	6.11 \pm 2.04	50.33 \pm 1.3	8.21 \pm 2.31	59.77 \pm 2.11
Species diversity						
Fisher's Alpha	9.27 \pm 2.2	22.17 \pm 4.2	6.68 \pm 2.45	15.8 \pm 0.9	7.97 \pm 2.32	19.0 \pm 2.57
Shannon	2.26 \pm 0.24	2.78 \pm 0.32	2.30 \pm 0.30	2.84 \pm 0.18	2.28 \pm 0.28	2.81 \pm 0.25
Simpson	0.77 \pm 0.8	0.72 \pm 0.01	0.73 \pm 0.7	0.73 \pm 0.006	0.75 \pm 0.07	0.72 \pm 0.01

388.3 \pm 143.9 stems ha⁻¹, and mean basal area was 0.21 \pm 0.13 m² ha⁻¹. Taxonomic abundances (Figure 2), at the 14 ha level, varied greatly. Six species (6%) were only known as two individuals; while 56% of all stems were represented by species with less than sixteen liana stems (Figure 2A). In contrast, genera and families exhibited lognormal-like distributions (Figure 2B and C), indicating that taxa vary markedly in their abundances. Most liana individuals were small: nearly 78% were smaller than 3 cm in diameter; while only 1% of stems had a dbh of more than 10 cm (Figure 2E). On average, stems measured between 2 and 3 cm in dbh. The largest stem measured was 17 cm dbh (*Leptoderris ledermannii*, Fabaceae). Species richness (Figure 2D), abundance (Figure 2E), and total basal area (Figure 2F) decreased with increasing stem size. Large lianas (> 11 cm dbh) contributed 8% to the total liana basal area and included 6 species.

The correlation test shows that the number of species is correlated positively with the abundance ($N = 0.86$, $p < 0.0001$). When the number of liana species increases, abundance also increases. There is no difference between the proportion of small lianas (dbh \leq 5 cm) patches of old growth forest (average 17.67 \pm 6.58), and those of the secondary forest (average 18.92 \pm 9.01). By contrast, for large lianas (dbh > 5 cm), there is a difference between old growth forest (mean 1.92 \pm 2.37) and secondary forest (average 0.30 \pm 0.8). There are more large lianas in old growth forest than in secondary forest. Secondary forest plots had more liana stems (mean 8.59 \pm 1.90) than old growth forest plots (mean 9.31 \pm 2.19), possibly partly because the secondary forest fallows are recent and continue to be pressured.

Liana characteristics

The functional and ecological characteristics are summarized for the total species assemblage, as well as for the 10 most important families separately (Figure 3). Most liana species were stem twiners (63%): *Secamone afzelii* and *Baisseba baillonii*, followed by hook climbers (18%): *Salacia debilis* and *Clerodendrum formicarum*, and tendril climbers (16%): *A. lobata* and *Cissus aralioides*. Liana species were predominantly micro-phanerophyte (84%) or nano-phanerophyte (10%), in stem size. Most species were light demanding (92%); only a few were either shade tolerant. The seeds of most species were animal dispersed (75%), followed by wind dispersed (22%). Only a few species were barochorous (3%). With few exceptions, individual families generally exhibited similar trends in functional characteristics to the complete liana assemblage. Notable exceptions are as follows: Fabaceae are mostly twiner-climbers and Vitaceae are only tendril climbers. Icacinaceae are only shade-tolerant. Icacinaceae, Menispermataceae, Araceae, Verbenaceae, Vitaceae and Rubiaceae species are entirely dispersed by animals; while all of the Apocynaceae and Dioscoreaceae lianas are wind-dispersed.

DISCUSSION

Floristic composition

Nearly all individuals (89.69% of all stems) were identified to family, genera, or species. The same result has been

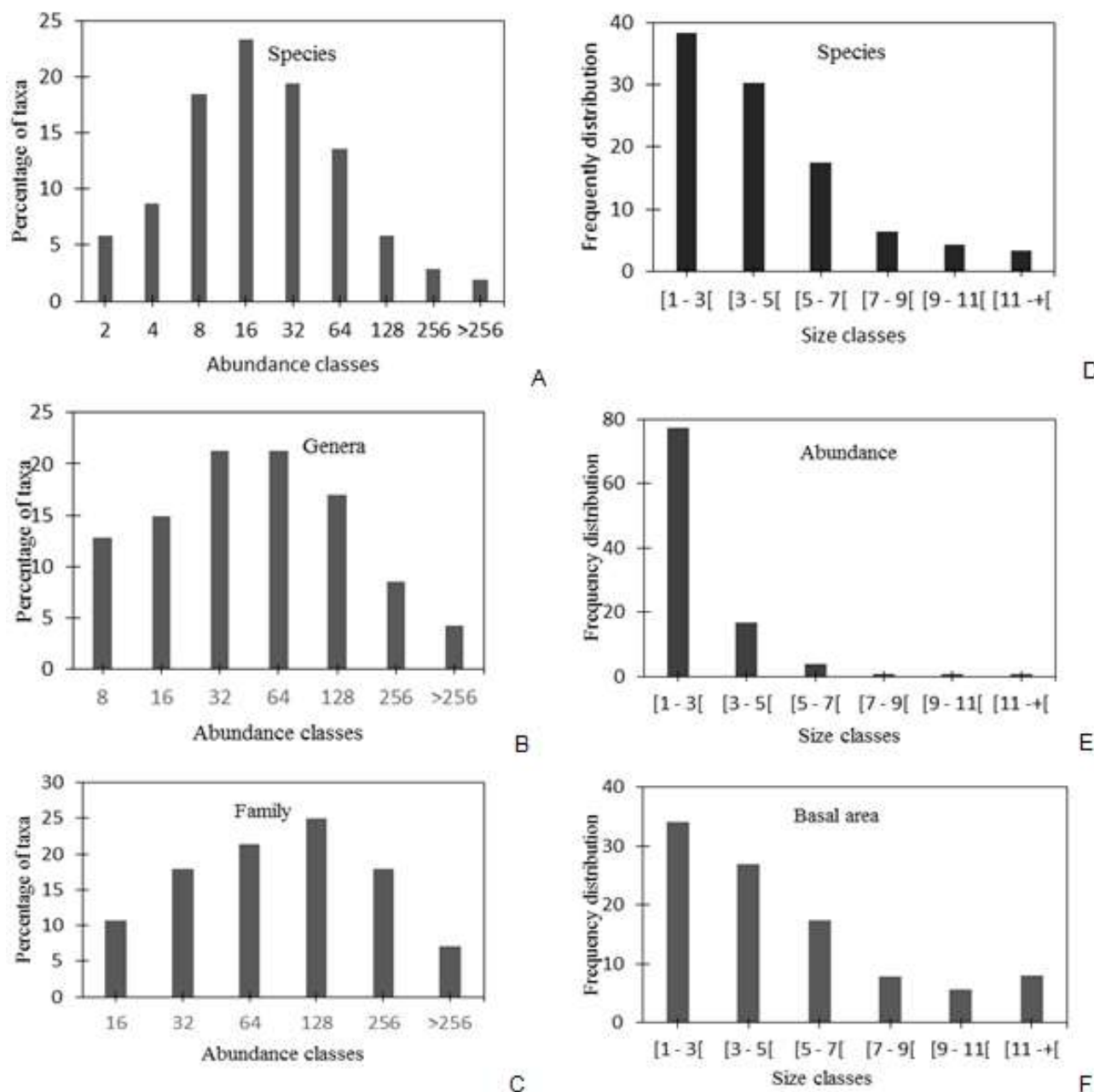


Figure 2. Percentage of: A, species (N = 63); B, genera (N = 47); and C, families (N = 28), in 14 ha of Azagny National Park (ANP) by abundance classes; and Frequency distribution of: D, total species number; E, stem abundance; F, basal area of lianas, of different size classes.

found by Ewango et al. (2015), who identified 90.2% of all individuals in a 20 ha plot in the Congo Basin. Our results are lower than those of Schnitzer et al. (2012), who identified 98.5% of all individuals in a 50 ha plot in Panama, and Kuzee and Bongers (2005), who identified 94% of their lianas in Côte d'Ivoire, but are 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, *A. lobata*. 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 (pioneer), it was also observed in shady environments (Kouamé et al., 2005).

Species composition and family dominance of lianas in Azagny are largely the same as those found in most

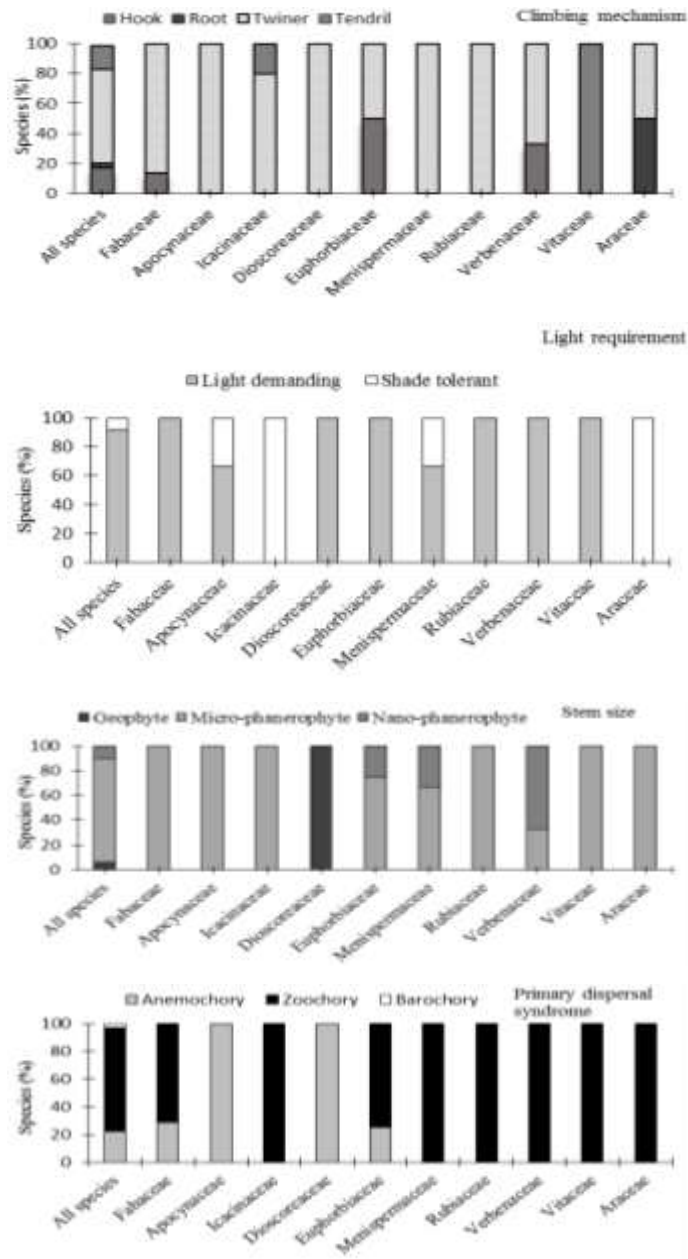


Figure 3. Proportion (%) of species with different: A, climbing mechanism; B, life light requirement; C, stem size, D, primary dispersal syndrome for all species (N = 63), and for the 10 most speciose families: Fabaceae (7 species), Apocynaceae (5), Icacinaceae (5), Dioscoreaceae (4), Euphorbiaceae (4), Menispermaceae (3), Rubiaceae (3), Verbenaceae (3), Vitaceae (3), and Araceae (2).

West African tropical forests Côte d'Ivoire (Etien and Traoré, 2005); Benin (Natta and Sinsin, 2005), and Togo (Kokou and Caballé, 2005). The most abundant families of Azagny (Apocynaceae, Passifloraceae, Euphorbiaceae, Fabaceae, Menispermaceae, Verbenaceae and Piperaceae) are widely distributed in West Africa (Kuzee and Bongers, 2005; Addo-Fordjour et al., 2008), even in

Central Africa Cameroon (Parren, 2003) and Democratic Republic of Congo (Ewango et al., 2015), suggesting a strong similarity among West and Central African lowland forests. The speciose families Apocynaceae, Euphorbiaceae, and Fabaceae (which also include many non-lianas) and Vitaceae, Passifloraceae, Dioscoreaceae (only including climbers) are important liana families in

both Old and New World floras (Gentry, 1991). The most common liana families in Asian forests are Menispermaceae, Fabaceae, Rubiaceae, Dilleniaceae and Icacinaceae (Appanah et al., 1993) suggesting a closer affinity to the Azagny Forest assemblage. However, the Azagny National Park is poor in palm lianas compared to the Neotropics and continental Asian forests.

Diversity and community structure

Species richness and species diversity (Shannon index and Fisher α) indices increased with sample sizes, as predicted. The Azagny National Park contains a few highly abundant lianas. *A. lobata* accounts for 7% of all liana stems, with 376 individuals, in 14 ha. These results are lower when compared with those of certain authors. *Strophanthus barteri* (Apocynaceae) represents 12% of stems in Ghana (Addo-Fordjour et al., 2008); while *Mariipa panamensis* (Convolvulaceae) represents 11% of stems in both secondary and primary forests in Panama (DeWalt et al., 2000).

Family dominance, however, was in accord with other studies in Africa (Gentry, 1991; Bongers et al., 2005), with Apocynaceae, Passifloraceae, Euphorbiaceae, Fabaceae, Menispermaceae, Verbenaceae, Piperaceae, Aristolochiaceae, Vitaceae and Icacinaceae being the most important families. The 10 most abundant liana species (of 63) represent 71% of the stems, which may be characteristic of the Azagny National Park.

Small lianas account for the highest species richness, abundance, and basal area (Figure 2D to F) and, compared to other tropical forests, the Azagny National Park is particularly poor in large liana stems. Again, it was speculated that this is the result of disturbances in the recent past (Konan, 2008). Alternatively, its high liana density may be related to the climate seasonality (DeWalt et al., 2010) under which large-diameter lianas are few (nutrient-poor soils have fewer lianas (Gentry, 1991).

Within the Azagny National Park, liana density (388.3 ± 143.9 stems ha^{-1}) is lower compared to other African forests (Parren, 2003; Ewango et al., 2015). Some Bolivian Amazonian forests showed exceptionally high liana density (mean of 2,471 lianas $\text{ha}^{-1} \geq 2$ cm dbh), and lianas accounted for as much as 44% of the total woody species (Pérez-Salicrup et al., 2001).

As predicted, the abundance of lianas was positively correlated with the number of species, which means that the number of species increases with abundance. The proportion of small vines (dbh ≤ 5 cm) is the same in both habitats. By contrast, there is a big difference in terms of large lianas (dbh > 5 cm) in both habitats. Forest disturbance (Hegarty and Caballé, 1991) and seasonality (Gentry, 1991; DeWalt et al., 2010) are factors most strongly controlling the abundance, species richness, and distribution of lianas in other forests. Abundance was

higher in secondary forests plots than in old growth forests plots. This is caused by the human activities that take place in secondary forests. These activities include agriculture, hunting and gathering of plant species (Konan, 2008).

Functional characteristics of the liana community

In Azagny, twining is the dominant climbing mode (63% of the species, Figure 3A). Our findings corroborate that of many other studies in tropical forests: Laurance et al. (2001) in Brazil; Sridhar Reddy and Parthasarathy (2003) in India; and Addo-Fordjour et al. (2008) in Ghana. Because of their ability to ascend trees directly, twining species indiscriminately colonize a wide range of trees and species. There seems to be an association between stem mechanical architecture and climbing mechanism; some families with heavy stems are exclusively twining (e.g. Fabaceae, Asclepiadaceae, Menispermaceae, and Apocynaceae) or hook-climbing (e.g. Verbenaceae); while other families that tend to have flexible stems, also rely on tendrils (e.g. Passifloraceae, like some *Adenia* and most Vitaceae species, *Cissus*).

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 (Putz, 1984; Hegarty and Caballé, 1991). 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. Eight per cent of the Azagny National Park liana species were classified as being 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, for instance *Piper guineense*, *Cercestis afzelii*, *Flagellaria guineensis* and *Xylopia acutiflora*.

The prevalence of zoochory shows the importance of animals in the liana's dissemination (Figure 3). The same result has been found by some authors as Bullock (1995) and Addo-Fordjour et al. (2008). 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 and Bongers, 2002).

Conclusion

It was found that, in terms of structure and family composition, the liana community in Azagny National Park is congruent with other Guineo-Congolian forests,

with prominent liana taxa being Apocynaceae, Fabaceae, Vitaceae, Rubiaceae and Euphorbiaceae. The most important taxa at Azagny National Park are also important in other African forests, and we conclude that the Azagny National Park liana composition accords with other tropical forest elsewhere. However, the Azagny National Park 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 the Azagny National Park, the most important determinants of variations in liana abundance, species richness, and distribution are forest structure and habitat. The secondary forest had greater liana abundance than the more closed canopy of the old growth forest. Human activity plays an important role in the liana abundance. However, further research on the use of lianas by the local populations is required.

Conflict of interests

The authors have not declared any conflict of interests.

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