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Liana abundance and relationships to sapling and tree hosts in an East African Primary Forest

Short running title: Liana and host survey for Ugandan primary forest

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ABSTRACT

Lianas are an important structural component of tropical rain forests. Recent concern regarding a putative global rise in liana abundance, and its implications for forest conservation, calls for data collection across biomes. We here provide a first assessment and baseline data for a geographical gap in liana surveys to date. We surveyed liana (DBH>1cm), tree (DBH>10 cm) and sapling (DBH≤10cm) abundance and basal area, as well as liana-host relationships, in a tropical East African primary forest.

We recorded a total of 347 liana stems (DBH > 1cm) in 0.31 ha, with an average basal area of 36.9 m^2ha^{-1}. Lianas were found to be widespread, with 24% of saplings and 57% of trees colonised by at least one liana, independently of bark texture or host diameter. The dominant liana colonization strategy was to associate with a single host, through stem twining. We found no evidence of liana density being influenced by host density. We synthesised published liana density data across continents and report that our estimate of liana density for Kibale's primary forest fits within the expected range of liana densities for primary tropical forests. This synthesis further highlights a neotropical sampling bias, which our findings make a step towards addressing.

Keywords: Liana; Primary forest; Saplings; Host; Uganda

INTRODUCTION

Lianas are key structural and functional components of tropical forests (Schnitzer, Bongers, Burnham, & Putz, 2015). An increase in liana density, biomass and productivity has been reported for several neotropical forests (Phillips et al. 2002, Wright et al. 2004, Ingwell et al. 2010, Laurance et al. 2014). The main hypotheses for this increase point towards global climate change, increase in the duration and severity of seasonal drought, and forest fragmentation (Schnitzer & Carson 2010, Schnitzer & Bongers 2011), given that liana abundance is known to rise in disturbed forest areas (Ledo & Schnitzer, 2014; Schnitzer & Bongers, 2011).

When liana abundance increases, forest dynamics and succession can be affected. Competition for above- and belowground resources can negatively affect tree recruitment, regeneration, growth (Schnitzer & Bongers, 2002; Toledo-Aceves & Swaine, 2008; Schnitzer & Carson, 2010; Martínez-Izquierdo et al., 2016), survival (Ingwell et al., 2010; Marshall et al., 2016; Phillips et al., 2005; Martínez-Izquierdo et al., 2016; Visser et al., 2018) and reproduction (García-León et al., 2018; Visser et al., 2018). Carbon cycling, storage and

sequestration are negatively affected by extremely high liana abundance (van der Heijden et al. 2013, 2015), thus imposing challenges for conservation and functioning of tropical forests. Some studies postulate that liana abundance is overall higher in South America than elsewhere in the tropics, and that liana abundance has decreased in African forests (Caballé & Martin, 2001; Ewango, 2010). However, comprehensive comparative analyses between tropical regions are hampered by the limited number and geographic range of studies, especially in Africa (Parthasarathy, Vivek, Muthumperumal, Muthuramkumar, & Ayyappan, 2015; Schnitzer et al., 2015). Furthermore, relatively few liana inventories based on plot sampling are available (Schnitzer et al., 2015) and fewer perform analysis of liana-host relationships (but see Pérez-Salicrup & de Meijere, 2005; Reddy & Parthasarathy, 2006; Roeder et al., 2015). Given the implications of increasing liana density, it is important to reduce the sampling gap concerning East African tropical forests, for which baseline data are sparse.

We conducted a survey of liana abundance and liana-host relationships in the primary forest of Kibale National Park, southwest Uganda, providing baseline data and contributing towards filling a sampling gap. We further assessed whether host characteristics, such as diameter or bark texture, influenced the probability of liana colonisation and climbing strategy (Carse, Fredericksen, & Licona, 2000; Reddy & Parthasarathy, 2006).

We predicted that higher liana abundance would be associated with a lower density of saplings, due to previous studies showing negative impact of high liana density on juvenile tree survival (Ingwell et al., 2010), and recruitment (Martínez-Izquierdo et al., 2016). Finally, we review the literature for data on liana abundance in primary forests across continents, and place our data on a global context.

MATERIALS AND METHODS

Study site

The study was conducted in Kibale National Park (KNP) in South-Western Uganda (0˚13’ - 0˚41’N, 30˚19’ - 30˚32’E) (Fig. 1). KNP is an area of high conservation significance

84 comprising approximately 776 km^2 of mid-montane evergreen tropical semi-deciduous forest,
85 varying in altitude between 1100 and 1590m *asl*, with plant species composition and diversity
86 intermediate between lowland and montane African moist evergreen forests. About 57% of
87 the park is comprised of old growth forest; the remaining area comprises anthropogenic
88 grassland, woodland, swamp forest, *Papyrus* swamp, and regenerating forest.
89 The typical year includes two rainy seasons: September-November, and March-May; and two
90 dry seasons: December-February, and June-August.Data collection occurred in August 2015
91 in the primary forest in Kanyawara area (Fig. 1).
92
93 **Plot characteristics**
94 Data were collected at the start of the wet season from 40 circular plots (5m radius),
95 comprising a total area of 0.31 ha of primary forest. Plot locations were chosen at random
96 within the study area, with plots separated by at least 20 m. The number of fallen trees with
97 original diameter at breast height (DBH) greater than 10 cm was also recorded.
98
99 **Liana, tree and sapling data collection**
100 Diameter at breast height (DBH; 1.3 m) was recorded for all lianas (DBH > 0.1 cm), trees
101 (DBH > 10.0 cm) and tree saplings (DBH > 1.0 cm) within each of the 40 plots (Gerwing et
102 al., 2006). Liana climbing strategy was classified as stem twining, bearing hooks or unknown.
103 Lianas were also associated with individual tree or sapling hosts.
104 Six out of 40 plots contained liana bundles (Fig.S1), comprising a total of 50 individual
105 lianas. These were excluded from further analysis due to the difficulty of determining suitable
106 measurement points. Snapped or dead lianas were also excluded.
107 For each tree in the plots, bark texture was classified on a scale from 1 to 3, following the
108 criteria of Carse et al. (2000), where “1” corresponds to smooth bark, “2” corresponds to bark
109 with some furrowing or scaling, and “3” corresponds to highly rough bark, heavily furrowed
110 (Fig. S2).
111 Summary data on basal area (BA) and density exclusively regards living stems; all fallen,

snapped and dead trees or saplings were excluded.

Summary data and statistical analysis regarding lianas are exclusively based on stems with DBH >1cm in order to be comparable with other studies.

When possible (92% of assessed lianas), individual liana stems were tracked to their hosts. In such cases, liana and host characteristics were recorded with specific identification tags to allow the analysis of liana-host relationships (Table S2).

Trees of the genus *Ficus* could be a source of bias to basal area calculations due to their large size (ranging from 50 cm to 162 cm DBH). All analyses were repeated excluding the plots with large *Ficus* trees, and qualitatively equal results were obtained. We therefore present results based on the full data set.

Statistical analysis

Linear models were performed to assess correlations between host and liana abundance and basal area (BA). Explanatory variables were density and BA of saplings, and density and BA of trees. Response variables were liana density and liana basal area.

To test for associations between liana load and host characteristics, liana-host pairings were assessed (Table S2). A generalised linear model, using strategy as binomial response variable (1 for hooks and 0 for twining), and a logit link function was performed to test for a correlation of host DBH with climbing strategy. To test whether bark roughness influenced liana colonisation, we performed a two-sample t-test to assess whether bark of colonised trees was rougher on average than that of trees lacking lianas. All statistical analyses were performed in R version 3.4.3 (R Core Team, 2017).

Liana density data review and global comparisons

To enable the global contextualisation of our data, liana density data (defined as average liana stems per hectare) were obtained from a literature review of published liana surveys. The data were plotted on a world map with the software QGIS v2.18. Only studies with information regarding forest type were considered, and with main focus on primary forests. When several

types of forest were surveyed for a single location only primary forest data were included. Two exceptions were the forests from Cameroon and Gabon, which were included for further comparison of liana densities among African sites, despite not being from primary forests. See Table S3 for detailed data with corresponding reference, continent, country, location, forest type, total area sampled and minimum DBH considered in the liana survey.

RESULTS

Survey data for lianas in Kibale National Park

In the 0.31 ha of sampled primary forest, a total of 1410 saplings, 199 trees and 347 lianas >1cm DBH were recorded. Trees were present in 39 out of the 40 plots, ranging from 2 to 12 individuals, at an average density of 633 ± 41 stems ha^{-1} (mean ± SE), and average basal area of 36.9 ± 8.6 m^2 ha^{-1}. Saplings were present in all sampled plots, ranging from 12 to 62 individuals, at an average density of 4488 ± 202, and average basal area of 4.07 ± 0.25 m^2 ha^{-1} (Table S1).

Lianas were present in all of the sampled plots, with an estimated average density of 1105 ± 129 stems ha^{-1} and average basal area of 1.21 ±0.19 m^2 ha^{-1}.

The majority of liana stems (91%) had diameter lower than 5 cm, with an average DBH of 3.15 ± 0.11 cm (Fig. S3). The maximum liana DBH recorded was 10.9 cm. Only 89 lianas (25.6%) presented recognisable climbing strategy (twining or hooks); climbing strategies could not be assessed from ground level for the majority of the records. Of those that could be classified, stem-twining was the most common strategy (65%), followed by hooks (35%), especially among lianas of < 2 cm DBH (Fig. S4).

Liana-host interactions

Liana colonisation rates were high, with 57% of trees and 24% of saplings carrying at least one liana. From the subset of 318 lianas that could be assigned to specific hosts, 165 individual lianas (52%) colonized a single host stem, and only three (7%) colonised more than two hosts simultaneously, with the most common strategy being single host colonisation.

While the majority of hosts were colonised by a single liana, liana load ranged from one to nine on trees, and from one to four on saplings (Fig. 2A). The probability of liana colonisation increased with sapling DBH (GLM, n= 1410, z= 7.43, $P < 0.001$), with 43% of the saplings in the higher DBH size class (7.5-10 cm DBH) being colonised. Among colonised saplings, 52% were colonised by lianas <2 cm DBH. For trees, DBH did not affect probability of liana colonisation (GLM, n = 199, z = -1.28, P = 0.202). The majority of trees (66%) hosted a single liana individual (Fig. 2A). Large lianas (DBH > 5 cm) colonize mainly trees (Fig. 2B), and larger trees tend to be colonised by larger lianas ($r = 0.21$, n = 125, P = 0.018). Regarding saplings, however, host DBH showed no correlation with liana DBH ($r = 0.005$, n = 126, P = 0.96).

Bark texture of the trees had no influence on the probability of liana colonisation (GLM, z = -1.25, P = 0.212), nor on the climbing mechanism adopted (GLM, z = 0.004, P = 0.997).

No correlation was found between host density or basal area and liana density or basal area, either for trees or saplings (Table 1). Only two out of the six damaged trees were both colonised and fallen, while the remaining four were snapped but showing no signs of liana colonization. Among saplings, the majority of hosts showing signs of degradation were not colonised by lianas, with only 23 out of 124 damaged saplings bearing liana stems.

Global context of liana abundance

When put in global context, the level of liana colonisation in Kibale primary forest is not atypical given the average density for primary tropical forests (743 ± 300) and its high variability, expressed by the considerable standard error. Comparing our study site with other African primary forests from Ghana (Addo-Fordjour et al., 2009a; Addo-Fordjour et al., 2009b; Addo-Fordjour, Rahmad & Burnham, 2016) and DR Congo (Ewango, 2010) we see similarity in average liana density with the Congolese forest and relatively higher liana density compared to the Ghanian forest (Fig. 3). When comparing Kibale's primary forest with non-primary African forests of similar tree density and basal area, in Gabon and

195 Cameroon (Caballé & Martin 2001, Parren & Bongers 2001), liana density is also within the
196 same range, despite the different forest types (Fig. 3).
197
198 **DISCUSSION**
199 We found lianas to be widespread and abundant in this Central African primary rain forest,
200 with 24% of saplings and 57% of trees colonised by lianas. We estimated liana density at
201 1105 ± 129 stems per hectare, with average BA of 1.21 ± 0.19 m^2ha^{-1}. Both liana density and
202 basal area were independent of host density and basal area. Our study covered 0.31 ha of
203 forest, within a single season, and thus might be insufficient to capture patterns occurring
204 across larger temporal or special scales (Martínez-Izquierdo et al., 2016). Nevertheless, we
205 provide baseline data on liana abundance, critically lacking for this region, and our results
206 show typical patterns of liana density for a primary tropical rain forest.
207
208 **Patterns of host-liana relationships**
209 Following the general pattern of other known African primary forests (Addo-Fordjour et al.,
210 2009a; Addo-Fordjour et al., 2009b; Addo-Fordjour, Rahmad, & Burnham, 2016; Mascaro,
211 Schnitzer, & Carson, 2004), 87% of lianas were small (1-5cm DBH), with stem-twining being
212 the main climbing strategy, independently of host DBH or bark texture. These seem to be
213 widespread patterns across tropical rain forests (Chittibabu & Parthasarathy, 2001; Ewango,
214 2010; Parthasarathy et al., 2015). The majority of lianas colonised a single host, a pattern also
215 previously described for Chinese (Roeder, Slik, Harrison, Paudel, & Tomlinson, 2015) and
216 Indian (Chittibabu & Parthasarathy, 2001) forests.
217 Our survey is one of the few known to assess sapling density and its relationship to lianas. We
218 found 24% of saplings to carry at least one liana. Lianas initially climb the nearest neighbour
219 plant for support as they are stemming, later reaching for taller hosts which allow them to
220 reach the canopy (Roeder et al., 2015; Rowe & Speck, 2005). This is supported by our finding
221 that large lianas colonise mainly trees and the larger the tree, the larger and older the lianas
222 colonizing it tended to be – a pattern also reported for an Australian forest (Campbell et al.,

2018). Given that sapling density was always greater than tree density, it is likely that the majority of stemming lianas will first encounter a sapling as their host, potentially hampering its survival or growth (Visser et al., 2018).

Despite having found no association between liana abundance and sapling abundance, there is strong experimental evidence of the negative effect of lianas on recruitment across tree species (Martínez-Izquierdo et al., 2016). Lianas thus have the potential to compromise regeneration in disturbed or secondary forests (Campbell et al., 2018; Marshall et al., 2016). We believe that including saplings in future liana assessments would allow further understanding of the impacts of lianas on forest succession and regeneration.

Global patterns are subject to sampling bias

It has been previously stated that liana abundance is overall higher in South America, and it might be decreasing in African forests (Caballé & Martin, 2001; Ewango, 2010; Schnitzer et al., 2015). However, when taking into account average values across continents, differences in liana abundance do not appear substantial, nor do the African forests seem to deviate from the observed range of densities (Fig. 3, see Table S3 for detailed data). Temporal data are however unavailable for our study site.

Despite having spanned a relatively small sampling area (0.31 ha), Kibale's liana abundance falls well within the range of primary forests across the tropics. Furthermore, we show that in comparison with late secondary forests in Cameroon, with similar basal area of trees, the herein reported liana density is relatively lower (Fig. 3). This is expected given that gaps and edges are more frequent in secondary or disturbed forests and lianas are known to thrive in such environments (Campbell et al., 2018; Ledo & Schnitzer, 2014; Schnitzer & Bongers, 2011).

The data distribution reinforces the idea that the currently discussed global rising of liana abundance may be geographically limited, as it is mainly drawn from liana data from seasonal neotropical forests (Parthasarathy et al., 2015; Schnitzer et al., 2015; Smith, Queenborough, Alvia, Romero-Saltos, & Valencia, 2017).

One difficulty regarding the interpretation of comparative data arises due to the different minimum DBH considered for liana surveys. We reiterate the need for following a standardised protocol, which would increase reproducibility and comparative value of the studies (Gerwing et al., 2006).

Extensive liana cutting has been advocated as a means of management (e.g. Marshall et al. 2016). However, local abiotic factors such as elevation (Fadrique & Homeier, 2016; DeWalt & Chave, 2004) and seasonality (Smith et al., 2017), within forests, can strongly shape liana dynamics and abundance. Thus, liana cutting strategies based on non-local data can instead be detrimental to biodiversity (Bongers, Schnitzer & Traore, 2002). It is therefore not only essential to include lianas in vegetation models (Verbeeck & Kearsley, 2015) but to further explore the abiotic and biotic factors that determine large-scale structural changes in liana density and composition across biomes.

Final remarks

We have contributed a first assessment of liana abundance and its relation to hosts in an East African primary forest. This provides baseline data to inform further monitoring efforts and contributes to filling a gap in the global coverage of liana surveys. Further spatial and temporal sampling, together with taxonomic information, will enable a broader understanding of liana distribution and contribution to local forest structure and dynamics.

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Table 1 Summary statistics of liana-host regression analysis; No correlations were detected between host density/basal area (BA), and liana abundance/basal area (BA).

	Liana density				Liana BA			
	Estimate	SE	*t* value	*P* value	Estimate	SE	*t* value	*P* value
Sapling density	0.012	0.117	0.099	0.922	0	0	1.005	0.322
Tree density	0.619	0.540	1.146	0.260	0.001	0.001	1.076	0.290
Sapling BA	-30.839	94.243	-0.327	0.746	-0.068	0.131	-0.521	0.606
Tree BA	-2.657	4.193	-0.634	0.531	-0.003	0.005	-0.594	0.556

Figure 1 Geographic location of sampling area. 40 random plots were sampled, comprising a total area of 0.3 ha of primary tropical forest in Kanyawara, Kibale National Park, Uganda. Map: Google Earth, Landsat/Copernicus

Figure 2 Liana load and size per host A Liana load (number of lianas recorded on a single host) distribution in trees (grey) and saplings (black). B Size of lianas and specific host colonization frequency: trees (grey) and saplings (black).

Figure 3 Global distribution of liana density; data from 15 studies comprising 29 primary tropical forests (yellow), one late secondary forest (Cameroon; brown) and one transition forest (Gabon; brown). Only four studies cover African primary forest (including the present study). Detailed data and corresponding references in Table S3, Map: Google Earth, Landsat/Copernicus