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1 **Liana abundance and relationships to sapling and tree hosts in an East African**

2 **Primary Forest**

3

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

5

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21

22 **ABSTRACT**

23 Lianas are an important structural component of tropical rain forests. Recent concern

24 regarding a putative global rise in liana abundance, and its implications for forest

25 conservation, calls for data collection across biomes. We here provide a first assessment and

26 baseline data for a geographical gap in liana surveys to date. We surveyed liana (DBH>1cm),

27 tree (DBH>10 cm) and sapling (DBH≤10cm) abundance and basal area, as well as liana-host

28 relationships, in a tropical East African primary forest.

29   We recorded a total of 347 liana stems (DBH > 1cm) in 0.31 ha, with an average basal area of

30   36.9 m^{2}ha^{-1}. Lianas were found to be widespread, with 24% of saplings and 57% of trees

31   colonised by at least one liana, independently of bark texture or host diameter. The dominant

32   liana colonization strategy was to associate with a single host, through stem twining. We

33   found no evidence of liana density being influenced by host density. We synthesised

34   published liana density data across continents and report that our estimate of liana density for

35   Kibale's primary forest fits within the expected range of liana densities for primary tropical

36   forests. This synthesis further highlights a neotropical sampling bias, which our findings

37   make a step towards addressing.

38

40

41   **INTRODUCTION**

42   Lianas are key structural and functional components of tropical forests (Schnitzer, Bongers,

43   Burnham, & Putz, 2015). An increase in liana density, biomass and productivity has been

44   reported for several neotropical forests (Phillips et al. 2002, Wright et al. 2004, Ingwell et al.

45   2010, Laurance et al. 2014). The main hypotheses for this increase point towards global

46   climate change, increase in the duration and severity of seasonal drought, and forest

47   fragmentation (Schnitzer & Carson 2010, Schnitzer & Bongers 2011), given that liana

48   abundance is known to rise in disturbed forest areas (Ledo & Schnitzer, 2014; Schnitzer &

49   Bongers, 2011).

50   When liana abundance increases, forest dynamics and succession can be affected.

51   Competition for above- and belowground resources can negatively affect tree recruitment,

52   regeneration, growth (Schnitzer & Bongers, 2002; Toledo-Aceves & Swaine, 2008; Schnitzer

53   & Carson, 2010; Martínez-Izquierdo et al., 2016), survival (Ingwell et al., 2010; Marshall et

54   al., 2016; Phillips et al., 2005; Martínez-Izquierdo et al., 2016; Visser et al., 2018) and

55   reproduction (García-León et al., 2018; Visser et al., 2018). Carbon cycling, storage and

56 sequestration are negatively affected by extremely high liana abundance (van der Heijden et

57 al. 2013, 2015), thus imposing challenges for conservation and functioning of tropical forests.

58 Some studies postulate that liana abundance is overall higher in South America than

59 elsewhere in the tropics, and that liana abundance has decreased in African forests (Caballé &

60 Martin, 2001; Ewango, 2010). However, comprehensive comparative analyses between

61 tropical regions are hampered by the limited number and geographic range of studies,

62 especially in Africa (Parthasarathy, Vivek, Muthumperumal, Muthuramkumar, & Ayyappan,

63 2015; Schnitzer et al., 2015). Furthermore, relatively few liana inventories based on plot

64 sampling are available (Schnitzer et al., 2015) and fewer perform analysis of liana-host

65 relationships (but see Pérez-Salicrup & de Meijere, 2005; Reddy & Parthasarathy, 2006;

66 Roeder et al., 2015). Given the implications of increasing liana density, it is important to

67 reduce the sampling gap concerning East African tropical forests, for which baseline data are

68 sparse.

69 We conducted a survey of liana abundance and liana-host relationships in the primary forest

70 of Kibale National Park, southwest Uganda, providing baseline data and contributing towards

71 filling a sampling gap. We further assessed whether host characteristics, such as diameter or

72 bark texture, influenced the probability of liana colonisation and climbing strategy (Carse,

73 Fredericksen, & Licona, 2000; Reddy & Parthasarathy, 2006).

74 We predicted that higher liana abundance would be associated with a lower density of

75 saplings, due to previous studies showing negative impact of high liana density on juvenile

76 tree survival (Ingwell et al., 2010), and recruitment (Martínez-Izquierdo et al., 2016). Finally,

77 we review the literature for data on liana abundance in primary forests across continents, and

78 place our data on a global context.

79

80 **MATERIALS AND METHODS**

81 **Study site**

82 The study was conducted in Kibale National Park (KNP) in South-Western Uganda (0°13' -

83 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,

112 snapped and dead trees or saplings were excluded.

113 Summary data and statistical analysis regarding lianas are exclusively based on stems with

114 DBH >1cm in order to be comparable with other studies.

115 When possible (92% of assessed lianas), individual liana stems were tracked to their hosts. In

116 such cases, liana and host characteristics were recorded with specific identification tags to

117 allow the analysis of liana-host relationships (Table S2).

118 Trees of the genus *Ficus* could be a source of bias to basal area calculations due to their large

119 size (ranging from 50 cm to 162 cm DBH). All analyses were repeated excluding the plots

120 with large *Ficus* trees, and qualitatively equal results were obtained. We therefore present

121 results based on the full data set.

122

123 **Statistical analysis**

124 Linear models were performed to assess correlations between host and liana abundance and

125 basal area (BA). Explanatory variables were density and BA of saplings, and density and BA

126 of trees. Response variables were liana density and liana basal area.

127 To test for associations between liana load and host characteristics, liana-host pairings were

128 assessed (Table S2). A generalised linear model, using strategy as binomial response variable

129 (1 for hooks and 0 for twining), and a logit link function was performed to test for a

130 correlation of host DBH with climbing strategy. To test whether bark roughness influenced

131 liana colonisation, we performed a two-sample t-test to assess whether bark of colonised trees

132 was rougher on average than that of trees lacking lianas. All statistical analyses were

133 performed in R version 3.4.3 (R Core Team, 2017).

134

135 **Liana density data review and global comparisons**

136 To enable the global contextualisation of our data, liana density data (defined as average liana

137 stems per hectare) were obtained from a literature review of published liana surveys. The data

138 were plotted on a world map with the software QGIS v2.18. Only studies with information

139 regarding forest type were considered, and with main focus on primary forests. When several

140   types of forest were surveyed for a single location only primary forest data were included.

141   Two exceptions were the forests from Cameroon and Gabon, which were included for further

142   comparison of liana densities among African sites, despite not being from primary forests.

143   See Table S3 for detailed data with corresponding reference, continent, country, location,

144   forest type, total area sampled and minimum DBH considered in the liana survey.

145

146   **RESULTS**

147   **Survey data for lianas in Kibale National Park**

148   In the 0.31 ha of sampled primary forest, a total of 1410 saplings, 199 trees and 347 lianas

149   >1cm DBH were recorded. Trees were present in 39 out of the 40 plots, ranging from 2 to 12

150   individuals, at an average density of 633 ± 41 stems ha^{-1} (mean ± SE), and average basal area

151   of 36.9 ± 8.6 m^2 ha^{-1}. Saplings were present in all sampled plots, ranging from 12 to 62

152   individuals, at an average density of 4488 ± 202, and average basal area of 4.07 ± 0.25 m^2 ha^{-}

153   ^{1} (Table S1).

154   Lianas were present in all of the sampled plots, with an estimated average density of

155   1105 ± 129 stems ha^{-1} and average basal area of 1.21 ± 0.19 m^2 ha^{-1}.

156   The majority of liana stems (91%) had diameter lower than 5 cm, with an average DBH of

157   3.15 ± 0.11 cm (Fig. S3). The maximum liana DBH recorded was 10.9 cm. Only 89 lianas

158   (25.6%) presented recognisable climbing strategy (twining or hooks); climbing strategies

159   could not be assessed from ground level for the majority of the records. Of those that could be

160   classified, stem-twining was the most common strategy (65%), followed by hooks (35%),

161   especially among lianas of < 2 cm DBH (Fig. S4).

162

163   **Liana-host interactions**

164   Liana colonisation rates were high, with 57% of trees and 24% of saplings carrying at least

165   one liana. From the subset of 318 lianas that could be assigned to specific hosts, 165

166   individual lianas (52%) colonized a single host stem, and only three (7%) colonised more

167   than two hosts simultaneously, with the most common strategy being single host colonisation.

168   While the majority of hosts were colonised by a single liana, liana load ranged from one to

169   nine on trees, and from one to four on saplings (Fig. 2A). The probability of liana

170   colonisation increased with sapling DBH (GLM, n= 1410, z= 7.43, P < 0.001), with 43% of

171   the saplings in the higher DBH size class (7.5-10 cm DBH) being colonised. Among

172   colonised saplings, 52% were colonised by lianas <2 cm DBH. For trees, DBH did not affect

173   probability of liana colonisation (GLM, n = 199, z = -1.28, P = 0.202). The majority of trees

174   (66%) hosted a single liana individual (Fig. 2A). Large lianas (DBH > 5 cm) colonize mainly

175   trees (Fig. 2B), and larger trees tend to be colonised by larger lianas (r = 0.21, n = 125, P =

176   0.018). Regarding saplings, however, host DBH showed no correlation with liana DBH (r =

177   0.005, n = 126, P = 0.96).

178   Bark texture of the trees had no influence on the probability of liana colonisation (GLM, z = -

179   1.25, P = 0.212), nor on the climbing mechanism adopted (GLM, z = 0.004, P = 0.997).

180   No correlation was found between host density or basal area and liana density or basal area,

181   either for trees or saplings (Table 1). Only two out of the six damaged trees were both

182   colonised and fallen, while the remaining four were snapped but showing no signs of liana

183   colonization. Among saplings, the majority of hosts showing signs of degradation were not

184   colonised by lianas, with only 23 out of 124 damaged saplings bearing liana stems.

185

186   **Global context of liana abundance**

187   When put in global context, the level of liana colonisation in Kibale primary forest is not

188   atypical given the average density for primary tropical forests (743±300) and its high

189   variability, expressed by the considerable standard error. Comparing our study site with other

190   African primary forests from Ghana (Addo-Fordjour et al., 2009a; Addo-Fordjour et al.,

191   2009b; Addo-Fordjour, Rahmad & Burnham, 2016) and DR Congo (Ewango, 2010) we see

192   similarity in average liana density with the Congolese forest and relatively higher liana

193   density compared to the Ghanian forest (Fig. 3). When comparing Kibale's primary forest

194   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^{2}ha^{-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.,

223   2018). Given that sapling density was always greater than tree density, it is likely that the

224   majority of stemming lianas will first encounter a sapling as their host, potentially hampering

225   its survival or growth (Visser et al., 2018).

226   Despite having found no association between liana abundance and sapling abundance, there is

227   strong experimental evidence of the negative effect of lianas on recruitment across tree

228   species (Martínez-Izquierdo et al., 2016). Lianas thus have the potential to compromise

229   regeneration in disturbed or secondary forests (Campbell et al., 2018; Marshall et al., 2016).

230   We believe that including saplings in future liana assessments would allow further

231   understanding of the impacts of lianas on forest succession and regeneration.

232

233   **Global patterns are subject to sampling bias**

234   It has been previously stated that liana abundance is overall higher in South America, and it

235   might be decreasing in African forests (Caballé & Martin, 2001; Ewango, 2010; Schnitzer et

236   al., 2015). However, when taking into account average values across continents, differences

237   in liana abundance do not appear substantial, nor do the African forests seem to deviate from

238   the observed range of densities (Fig. 3, see Table S3 for detailed data). Temporal data are

239   however unavailable for our study site.

240   Despite having spanned a relatively small sampling area (0.31 ha), Kibale's liana abundance

241   falls well within the range of primary forests across the tropics. Furthermore, we show that in

242   comparison with late secondary forests in Cameroon, with similar basal area of trees, the

243   herein reported liana density is relatively lower (Fig. 3). This is expected given that gaps and

244   edges are more frequent in secondary or disturbed forests and lianas are known to thrive in

245   such environments (Campbell et al., 2018; Ledo & Schnitzer, 2014; Schnitzer & Bongers,

246   2011).

247   The data distribution reinforces the idea that the currently discussed global rising of liana

248   abundance may be geographically limited, as it is mainly drawn from liana data from seasonal

249   neotropical forests (Parthasarathy et al., 2015; Schnitzer et al., 2015; Smith, Queenborough,

250   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).

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	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

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**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**

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**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).**

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**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**