

Proximity to the host is an important characteristic for selection of the first support in lianas

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Keywords

Host diameter; Host distance; Rooting point; Stem density; Stem infestation; Support type; Tree families

Nomenclature

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Introduction

Lianas depend on support to reach optimal conditions for reproduction and growth (Putz & Mooney 1991). Host availability and host growth form both influence the success of liana establishment. Certain features of host plants have been suggested to affect their susceptibility to liana infestation. For example, slow-growing trees are more likely to be liana hosts than pioneers (Putz 1984; Schnitzer et al. 2000; Schnitzer & Carson 2001), which may be mainly due to the time to accumulate lianas (Schnitzer et al. 2000). Rough bark structure can promote support for root climbers, whereas smooth or flaky bark can cause lianas to slide down the stem (Putz 1984; Talley et al.

Abstract

Question: Lianas depend on support to reach optimal growing conditions. They can infest trees unevenly, and host selection may depend on functional characteristics of the potential hosts, such as growth rate, bark type or tree architecture. In this context we hypothesized that (1) simple proximity to the rooting point of the liana is the overriding property predicting the probability of selection as the host; (2) the distance to the host decreases with increasing stem density in the surrounding community; (3) host distance becomes more variable with liana age (~diameter), as some larger lianas probably have already lost their first host, whereas small lianas should use the nearest available stem to climb; and (iv) liana infestation of plant families is proportional to family abundance.

Location: Montane forest in southwest China.

Methods: We surveyed lianas (\geq 0.5-cm diameter) in 17 plots consisting of 153 subplots, recording the rooting point of lianas and the closest used host and nearest possible support, species identity and diameter of both liana and host.

Results: Of the analysed host–liana pairs, half of all lianas used the host that was closest to their rooting points. Distance to the nearest support was the most important predictor for host distance. Tree stem density had no major influence on liana–host distance. The variance in host distance did not increase with liana diameter. Liana infestation of plant families increased with family abundance.

Conclusion: We conclude that the proximity of a host is the most important of the tested factors determining climbing host selection in lianas, however we only considered stem, not crown, infestation.

1996). Certain climber guilds, such as tendril climbers, are limited to small stems that they can twist around, and are correlated with small host tree diameters, whereas the proportion of root climbers increases with tree diameter (Carrasco-Urra & Gianoli 2009; Leicht-Young et al. 2010). Lianas facilitate the access into a tree for other lianas (Putz & Chai 1987; Nabe-Nielsen 2001). Tree architecture, notably first branching height, is also important for quality of support (Balfour & Bond 1993; Campbell & Newbery 1993; Campanello et al. 2007). There are several studies in temperate and tropical forests showing that tree species are differently attacked by lianas (Clark & Clark 1990; Allen et al. 1997; Nesheim & Økland 2007; Van der Heijden et al. 2008; Leicht-Young et al. 2010; Sfair et al. 2010), whereas other studies consider that host species identity might be not relevant (Malizia & Grau 2006; Carrasco-Urra & Gianoli 2009). If trees are unevenly affected by infestation, liana-host interactions alter forest structure and composition due to negative impact on certain host groups, and by indirectly promoting the growth of others, e.g. pioneer-like trees (Van der Heijden et al. 2008), which are often less infested.

Studies of liana-host interactions have so far focused on forest structure, including tree diameter, tree species and light availability, but have not considered the distance between the rooting point of the liana and its climbing support (Muñoz et al. 2003; Malizia & Grau 2006; Ladwig & Meiners 2010; Leicht-Young et al. 2010). For an established liana sapling, the distance to the next available trellis in the surrounding environment should be the most important factor determining host selection. However, many liana species can explore their habitat by extending long shoots laterally on the ground, and therefore have more options to reach a spot with a suitable host and other favourable conditions (e.g. light availability). Lianas can use several hosts until they reach the canopy (Perez-Salicrup & De Meijere 2005), and once a liana lies on top of the canopy a host as climbing support becomes irrelevant, and the first climbing support (hereafter termed the 'climbing host') might have already died. Therefore climbing host-liana interactions should be more easily detected in small-stemmed, actively climbing lianas.

Here we attempt to disentangle the relative importance of spatial proximity on climbing host selection by liana species. We surveyed all lianas (≥ 0.5 -cm diameter) in 153 subplots within 17 plots and in a montane forest in southwest China (Roeder et al. 2015), recording the Euclidean distance between the rooting points in liana–host pairs, the host order as a measure of the spatial configuration, the diameter of the liana and its climbing host as a measure of the age of the liana–host relationship, the life form of the climbing host, and the species identity of the climbing host. We hypothesized that proximity is the overriding characteristic determining climbing host selection by lianas. On the basis of this hypothesis we made the following predictions:

- 1. Distance between lianas and their climbing hosts decreases in denser forests.
- 2. The distance between lianas and their climbing hosts becomes more variable with liana age, as some larger lianas have already lost their first host whereas small lianas should use the first available stem to climb.
- 3. Lianas climb their nearest neighbours.
- 4. Liana infestation of plant families is porportional to family abundance: Common tree families are also common hosts.

Methods

Study site

Seventeen (17) previously established plots were surveyed for lianas, distributed over ca. 120 km² in montane rain forest around the township of Mengsong (Yunnan, South West China on the border of Myanmar, 21°28–34′ N, 100°26–31′ E). The forest ranges from old growth to young disturbed forest at an elevation from ~1200–1800 m a.s.l. The area is a transition zone between tropical and subtropical climate, with average temperature of 18 °C and mean annual precipitation of 1700 mm at middle elevation (Xu et al. 2009).

Inventory

One plot consisted of nine subplots in a 3 \times 3 grid, spaced 50-m apart; each subplot had a 5-m radius (Appendix S1b). As part of an earlier study, a tree inventory was conducted in the previous year (Sept 2010-2011; E. Paudel & RD Harrison, unpubl. data) tagging and recording DBH rooting point (distance at 10 cm accuracy and angle from centre) and species identity for all tree stems >2 cm stem DBH. The liana survey was conducted in Nov 2011 to Feb 2012 (for more details see Roeder et al. 2015), including diameter, rooting point and species of each liana >0.5-cm diameter in all subplots. We followed liana census protocols (Gerwing et al. 2006; Schnitzer et al. 2008), e.g. we used the last rooting point of the liana before ascending to the canopy, and stems with no obvious connection were treated as apparent genets. For each liana we noted the life form of the first plant to which they attached and climbed (tree, bamboo, liana, bush, other or none (freestanding lianas)) and if available the host ID tag. If lianas were growing on several trees or other plants simultaneously, and a single closest host could not be clearly assigned, the climbing host was classified as 'many'. If lianas had several ramets (clonal shoots), a single host could be assigned if all ramets used the same host, or if one or few main ramets were ascending on a tree and other ramets stand free (e.g. Smilax sp.). Tree stems <2 cm DBH, bamboos and shrubs were not permanently marked and therefore we had no rooting point data. Our survey focused on first visible host, therefore trees or other plants that were not recorded as climbing hosts might still carry lianas, which used them as secondary hosts. Forest tree density was calculated as the number of all tree and liana stems >2 cm in a 5-m radius circle.

We calculated the Euclidean distance to each liana's present climbing host from the survey data; we did not measure the host distance directly in the field since tree data were already available. We did not include lianas that were classified as having 'many' hosts, because of the difficulty in discerning the primary climbing host. In total, we include 746 liana–host pairs. Euclidean distance was:

$$dist = \sqrt[2]{d_{liana} + d_{host} - 2 \times d_{liana} \times d_{host} \cos \alpha}$$

where α was the angle between liana and host calculated as $\alpha = 180 - |(|\alpha_{\text{liana}} - \alpha_{\text{host}}| - 180)|$, d_{liana} is distance of liana from circle centre, d_{host} is distance of host.

For calculation of the nearest possible support, we used a subset of these data. Because we sampled lianas in fixed circular subplots, lianas near the edge of the subplots were likely to have their nearest climbing host outside the edge of the circle. Therefore we only considered lianas found within an inner 3.6-m circle, as including the full data set would have biased the results towards shorter distances (Appendix S2). This inner circle radius was chosen because 1.4 m was the mean host distance of all liana-host pairs. This reduced our liana sample to n = 451 individuals. To calculate the ordinal position of the climbing host of the liana, we calculated Euclidean distances between each liana (3.6-m circle) and all its woody neighbours (5-m circle, tree and lianas >2 cm) in the subplot and then ordered these from shortest to longest, yielding the ordinal position of the actual host.

Statistical analysis

We tested for differences in liana structure between support groups (many hosts, no host or one-first host) with non-parametric Kruskal–Wallis test and subsequent Wilcoxon test, since the sample sizes of the three groups were very unbalanced. This data set included all liana stems (n = 2410).

To test our first prediction that liana-host distance decreases in denser forests, we modelled liana-host distance as a function of forest density and also included liana and host stem diameters as predictors (as representatives for age of the lianas and hosts). We used the subset of data only containing liana-host pairs (n = 746). To examine if host distance is influenced by the proximity of the nearest available support (prediction 3), we used the same model as described above and included nearest neighbour as an additional predictor for host distance (3.6-m inner circle, n = 451 lianas). Both models were also run only including small liana stems (<2-cm diameter). We used linear mixed effects model (lmer in R package *lme4*) including plot as a random factor. Distance to host, host diameter, liana diameter and distance to nearest neighbour were all In-transformed to normalize their distributions prior to regression. P-values for the coefficients of the mixed effects models were obtained using the likelihood ratio test.

To test whether distance between host and liana becomes increasingly variable with liana age (prediction 2), we split lianas into seven diameter classes, following centimeter steps (0.5-1.0 cm, then five classes in cm steps, >6 cm) and tested if the variance of distance to host (variability) increased with increasing liana diameter class (Spearman's correlation). We did the same with only four diameter classes (0.5-1.0, 1-2, 2-4, >4 cm) for higher sample sizes within each class. We used diameter as a surrogate for liana stem age.

To address our fourth prediction, that liana use of tree families is proportional to the abundance of the tree family, we plotted tree stem abundance per family over all plots against abundance per family used as host (linear regression, log-transformed data) and added the prediction interval (95%). All analysis was done with R 2.14.2 (R Foundation for Statistical Computing, Vienna, AT). Raw data are available as Supplements 3 and 4 (CSV files).

Results

Support type

From 2410 measured liana stems, 45% used one tree as first support, 6% other lianas, 6% bushes, 3% bamboo, 34% could not be assigned to a specific host and 5% had no support (Fig. 1). Lianas with many hosts had the highest mean basal area ($\chi^2 = 23.9$, *P* < 0.001), including all clones (19.6 ± 3.6 cm², ±SE), followed by lianas with one or no host (15 ± 1.6 cm² or 7.6 ± 2 cm², respectively). Lianas with many hosts also had a higher



Fig. 1. Type of support used by lianas: Support type used by lianas in a montane forest, SW China (n = 2410 liana individuals) as a first present host.

mean diameter for the main stem $(1.6 \pm 0.06 \text{ cm})$ than the other two groups $(1.4 \pm 0.04 \text{ cm}, 1.1 \pm 0.09 \text{ cm};$ $\chi^2 = 22.9$, P < 0.001). All groups differed significantly from one another. Ramet numbers were very similar in all groups $(1.21-1.26 \text{ ramets per liana individual}; \chi^2 = 9.4$, P = 0.009) and significantly different only between one host (1.2 ramets) and many hosts (1.26 ramets). Significance of all tests was increased by the very high sample size (n = 2410).

Distance to support plant

The mean distance to the host was 1.4 m (median distance 0.95 m, n = 746). More than three quarters of lianas (81%) used a host that grew <2 m away from their rooting point. When only small liana stems (<2 cm) were considered, the proportion was similar (83% <2 m from host; Fig. 2). Distance to climbing host was not affected by liana diameter, host diameter or by forest density (Table 1), whether for all lianas or for lianas <2 cm. Our first predic-



Fig. 2. Frequency of liana–host distance classes: 52% (385) of the lianas used hosts within <1-m distance around them, 81% (606) of lianas hosts were within <2-m distance. n = 746 lianas.

tion was not fulfilled. The variability (variance) of host distance did not increase with increasing liana diameter class, whether for seven DBH classes (median DBH of each DBH class vs variance of host distance, $\rho = 0.286$, P = 0.56) or four DBH classes ($\rho = 0.8$, P = 0.33). Thus there was no support for our second prediction.

Ordinal rank of climbing host (nearest neighbour)

Out of the 451 lianas in the inner circle (3.6 m) that were assigned to one host, almost half (49%) used the closest plants as support. For small liana stems (<2 cm) the share was similar (53%; Fig. 3). The distance to the nearest neighbour was the most important predictor for host distance: Host distance increased with distance to the closest neighbour (P < 0.0001 for coefficient in the mixed model; Table 2). Therefore we had support for our third prediction. For this reduced data set, forest density was also a significant predictor within the model: host distance increased in denser forests (Table 2), but not for lianas <2 cm. However there was no direct correlation between forest density and host distance (Pearson's r = 0.018, P = 0.709).

Host plant family

Liana infestation of plant families was positively related to family abundance: more common tree families were also more abundant as hosts (regression, log-transformed data, $r^2 = 0.85$, P < 0.001; Fig. 4). The prediction interval (95% CI) included all but three families: Myrtaceae (n = 73) and Ebenaceae (n = 10) contributed fewer liana hosts, and Lamiaceae (n = 4) more liana hosts than the predicted range.

Discussion

Host-liana relations are dynamic, because lianas can use several hosts in space (Perez-Salicrup & De Meijere 2005)

Table 1. Results of the linear mixed effect model. Response variable was In-transformed distance between liana and host. Two predictors were also In-
transformed, plot was used as random effect, 5-m circle was the actual subplot, and this analysis included 746 lianas in total. The data set was subset using
only liana stems <2 cm. P-values were obtained from maximum likelihood ratio (LRT).</th>

Fixed Effects	5-m circle, all lianas ($n = 746$)			5-m circle, small lianas <2 cm ($n = 595$)		
	Estimate t	SE	P (LRT)	Estimate t	SE	P (LRT)
Intercept	-0.148	0.159		-0.124	0.161	
Liana Diameter (In)	-0.031	0.062	0.625	-0.010	0.100	0.938
Host Diameter (In)	0.029	0.052	0.579	0.008	0.055	0.871
Stem Density in Plot	-0.001	0.004	1	0.001	0.004	0.937
Random Effect	Variance			Variance		
Plot	0.014			0.017		
Residuals	1.008			0.849		

Table 2. Results of the linear mixed effect model. Response variable was In-transformed distance between liana and host. Some other predictors were also In-transformed. The inner 3.6-m circle was used for analysis of the nearest available stem as potential liana host, including 451 lianas. Plot was used as random effect. The data set was subset using only liana stems <2 cm. *P*-values were obtained from maximum likelihood ratio (LRT).

	3.6-m circle, all lianas ($n = 451$)			3.6-m circle, small lianas <2 cm ($n = 352$)		
Fixed Effects	Estimate t	SE	P (LRT)	Estimate t	SE	P (LRT)
Intercept	-0.119	0.150		-0.015	0.161	
Liana Diameter (ln)	0.059	0.059	0.313	-0.039	0.099	0.699
Host Diameter (In)	0.089	0.050	0.075	0.027	0.057	0.620
Distance Nearest Stem (In)	0.733	0.038	2.2e-16***	0.675	0.042	2.2e-16***
Stem Density in Plot	0.011	0.004	0.012 *	0.009	0.005	0.061
Random Effect	Variance			Variance		
Plot	0.026			0.035		
Residuals	0.523			0.479		

*P < 0.05, ***P < 0.001.



Fig. 3. Rank of host among all plants: The order of liana host among all possible support plants (other liana and trees) in a plot, ranked by distance to liana. Lianas of an inner 3.6-m radius circle entered the analysis, n = 451.

and time. In our study, over a third of the lianas could not be assigned to one specific first host, but were using several trees or other plants as closest support. This might mean that lianas were using several plants in parallel from the start to climb towards the canopy, or that the first hosts (in time) had already died. A survey in the Mexican lowland forest revealed that lianas use between one and seven host trees to reach the canopy (Perez-Salicrup & De Meijere 2005), and in a study of Asian lowland forest on average 1.4 trees and up to four trees (Putz & Chai 1987).

Distance to host

Proximity to the host was very important for host choice: Half of the analysed lianas used the closest stem as their first host, more than three-quarters of individual lianas



Fig. 4. Tree stems per family: Correlation of tree stems per family used as liana host (n = 450) and all tree stems per family summed over all plots (n = 2305). R^2 and 95% prediction interval (dashed line) are given for log-transformed data. Several tree families were not used as host (host = 0), therefore +1 was added to keep the log scale or transformation.

used a host within 2-m distance and the distance of nearest neighbour was correlated to the distance from the host. This implies that liana trunk infestation patterns in forests are mainly determined by where liana seeds land and germinate, or to where lianas extend vegetatively. After establishment, liana species exhibit several behaviours to find hosts, including horizontal circling of a shoot, or growing towards dark objects and others (e.g. Darwin 1865; Strong & Ray 1975). For these strategies, proximity to the next support also plays an important role. Van der Heijden et al. (2008) showed that proximity to a liana-infested tree increases the likelihood of tree infestation and was the most important predictor for trunk and crown infestation. A study of temperate understorey climbers, which included the distance to the nearest possible support. found no influence of the latter on size and a minor influence on species distribution, however these plants stood free, had no host and did not yet climb (Collins & Wein 1993). Our study is the first one to include rooting points of both host and lianas. Other variables that we included as predictors had no or inconsistent influences on host selection (forest density). High forest density can correlate positively with liana abundance, suggesting lianas have an abundant trellis (Nabe-Nielsen 2001; Ibarra-Manríquez & Martínez-Ramos 2009), or negatively, suggesting e.g. a lack of light (Castagneri et al. 2013). Host distance could therefore also be shorter in dense forests (more options) or longer (search for light). We did not test for other host features, such as bark roughness, branch height, etc., and preferences for host types (e.g. canopy trees) may still occur when lianas climb onto further hosts. Our hypothesis that distances to host increases with liana size, because initial hosts may die, was not supported. In fact, some of the longest distances were covered by very thin lianas. It appears that because lianas can grow very long shoots and since they do not need to be self-supporting, shoot length and diameter might not need to be strongly related.

Preferences for tree families

We found a clear relationship between tree families used as host and tree family abundance in the plots: common families were also common as hosts. We therefore assume that most tree families did not differ in their susceptibility to liana infestation. Many studies have identified non-random host selection in temperate and tropical systems (Clark & Clark 1990; Allen et al. 1997; Muñoz et al. 2003; Nesheim & Økland 2007; Ladwig & Meiners 2010; Leicht-Young et al. 2010; Sfair et al. 2010); however in most studies very few species out of the species pool of host and lianas had higher or lower than average infestation rates. These host taxa often had special features, such as being pioneer species, sub-canopy species (Clark & Clark 1990; Nesheim & Økland 2007) or emergent trees with long branch-free boles, e.g. Dipterocarpaceae (Campbell & Newbery 1993). Other studies in temperate and tropical forest did not find any association between liana and host tree species (Perez-Salicrup & De Meijere 2005; Malizia & Grau 2006; Carrasco-Urra & Gianoli 2009). Low infestation rates of single taxa, e.g. species, genus or family, could still be present in our data set, but we had too few replicates for some families to properly evaluate their susceptibility. One low-infested family (outside prediction interval) with acceptable sample size was Myrtaceae, with two rather small trees (Syzygium brachythyrsum, Decaspermum fruticosum). This could indicate that lianas avoid these sub-canopy species. However, these trees could still be infested as a secondary host, or one of multiple hosts (we did not check this). Since host diameter had no influence in the previous

analysis, and the abundance pattern was so strong, we assume that encounter by chance (being close, being common) had an overriding effect on climbing host choice in our study.

Lianas can influence their host trees and therefore forest dynamics, for example by strangling the tree trunk or overgrowing the canopy, slowing host growth or increasing death rate. Since our data set included only the current first host, we cannot draw any conclusions about crown infestation. Proving host specificity in lianas is only possible with intense surveys of both trunk and canopy (Van der Heijden et al. 2008) as well as inclusion of absence data (which tree has no liana at trunk, no liana in the canopy).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Study area in Yunnan, SW China, and distribution of the plots.

Appendix S2. The analysis of the nearest neighbour included only lianas that grew in the inner 3.6-m circle.

Appendix S3. Liana–host data as CSV.

Appendix S4. Family data as CSV.