

## Patterns of tree-liana interactions: distribution and host preference of lianas in a tropical dry evergreen forest in India

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**Abstract:** Lianas are structurally dependent life-form that rely mostly on trees to access the forest canopy. The complex interactions between lianas and trees are often effected by host species' traits. Lianas are evolved with various climbing mechanisms that aid them attach and infest the host trees. Liana infestation on trees now seems to be common in many tropical forests, where they are abundant. The present study was aimed to investigate the patterns of liana-tree interactions in tropical dry evergreen forest of Point Calimere Wildlife Sanctuary (PCWS), south-east India. This study also analyzes the impact of various tree functional traits on liana colonization success in the PCWS. All trees  $\geq 10$  cm girth at breast height (gbh) was measured along with lianas ( $\geq 1$  cm diameter at 1.3 m from the rooting point) they hosted. Overall, 57.9% of trees in the study sites carried at least one liana. The infested trees hosted an average of  $1.53 \pm 0.49$  (range; 0–8) lianas per tree. At PCWS, the trees with medium girth-class, moderate wood specific density, rough bark and those with pronounced summer leaflessness are more prone to be infested by lianas. The preference of lianas under different climbing mechanisms in selecting host trees remained similar, although their proportion differed slightly in the present study. Liana infestation on host trees can be highly dynamic under the current scenario of increasing liana abundance and biomass in tropical forests world over for which, we recommend the need for documenting the patterns of tree-liana interactions, by employing a standard protocol to facilitate global comparisons.

**Key words:** Bark texture, climbing mechanism, liana infestation, tree-liana interaction, tropical forest, wood specific density.

### Introduction

Lianas are woody climbers that are found in abundance in tropical forests, where they comprise up to 35% of woody species richness and 32% of woody stems (De Walt *et al.* 2015; Schnitzer *et al.* 2012). Unlike trees, lianas are incapable of independent vertical growth, and rely on other supports, mostly trees to ascend the forest canopy (Gentry 1991). Lianas begin their life as self-supporting plants, but with the flexible stems, they grow only up to 1.5 m in height (Caballe 1998; Putz 1984a), after which specialized climbing structures develop to ascend through the host trees (Carsten *et al.* 2002). Lianas are evolved with varied climbing

structures and strategies that aid in attaching to the host trees (Rowe & Speck 2015). The lianescent habit of climbing plants was marked with continuous changes throughout the history of evolution (Gentry 1991; Spicer & Grover 2010).

There are several attributes that encourage or deter liana colonization on host trees, including host tree growth rate, effect of bark texture (Carsten *et al.* 2002; Clark & Clark 1990; Putz 1984a) (Sfair *et al.* 2016) bole diameters (Carrasco-Urra & Gianoli 2009; Nesheim & Okland 2007) and wood specific density (van der Heijden *et al.* 2008). Several other features of host trees such as stem flexibility, leaf size and bark exfoliation rates also influence the fate of liana colonization success (Putz

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**Table 1.** Liana ( $\geq 1$  cm dbh) and tree ( $\geq 10$  cm gbh) species diversity in two 1-ha plots (PC1 – Point Calimere 1; PC2 – Point Calimere 2) in Point Calimere wildlife sanctuary.

Variable	Study plot		Total for 2 ha (Mean $\pm$ SD)
	PC1	PC2	
Species richness			
Trees	37	26	40 (32 $\pm$ 7.7)
Lianas	28	31	38 (30 $\pm$ 2.12)
Density			
Trees	790	771	1561 (781 $\pm$ 13.4)
Lianas	672	720	1392 (696 $\pm$ 33.9)

1995). Host plant species, particularly the tropical canopy trees differ substantially in liana load (Parren & Doumbia 2004). Lianas are generally detrimental or antagonistic on their hosts by damaging them directly by producing mechanical scratches and by passive strangling (Kennard 1998). Lianas also affect light availability by forming dense leaf layer over tree crown (Avalos *et al.* 1999), thereby limiting the light availability for the host trees. In addition, several other studies have shown the negative influence of lianas on host tree growth rates (Putz 1984b), fecundity (Stevens 1987) and regeneration and survival (Ingwell *et al.* 2010; Schnitzer & Carson 2010; Schnitzer *et al.* 2000; Toledo-Aceves & Swaine 2008). Thus, trees that are free from lianas derive selective advantage (Putz 1984b) over liana-laden trees.

Since, lianas are increasing in abundance and basal area in many tropical forests (Schnitzer & Bongers 2011), the interaction between lianas and trees are expected to be temporally dynamic (Toledo-Aceves 2015). Although studies on lianas have widely attracted researchers at least over the last two decades, little is known about the patterns of liana-tree interactions. The tropical dry evergreen forest (TDEF) on the Coromandel Coast of India are one of the liana-dense forests in Asian tropics (DeWalt *et al.* 2015) that lack intense studies on liana-tree interactions. Trees and lianas form the major proportion of flowering plants in TDEF ecosystem (Parthasarathy *et al.* 2008; Vivek & Parthasarathy 2015) as there is no distinctive shrub and herb layer. Therefore, the outcome of interaction between trees and lianas will define the structure and function of these forests. Hence, the present study was aimed to investigate the patterns of liana-tree interactions in Point Calimere Wildlife Sanctuary (PCWS), the largest existing TDEF site in India.

We asked the following questions:

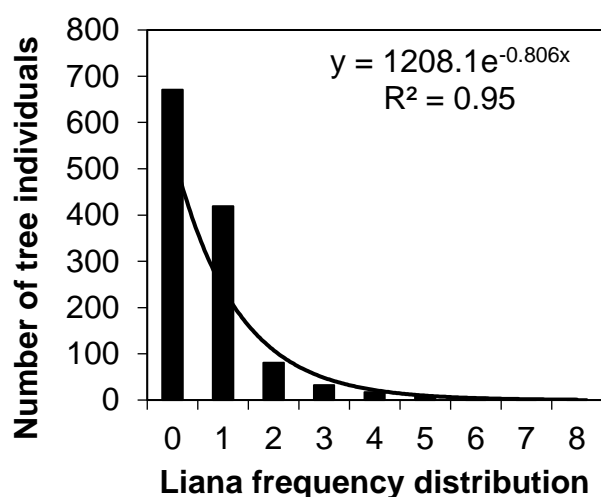
1. How many trees in the tropical dry evergreen forest hosted/did not host lianas?
2. How tree species differ in their susceptibility to liana infestation?
3. Do host-tree girth and other traits (bark type, wood specific density and physiognomic type) play a significant role in hosting/avoiding lianas?
4. Does the host selection of lianas differ by climbing mechanism?

This study will be helpful in predicting how the liana-tree interactions will influence biodiversity, tropical forest dynamics and future of this and similar tropical forest ecosystems.

## Materials and Methods

### *Study area*

Study was conducted in two 1-ha plots (Point Calimere 1 (PC1) and Point Calimere 2 (PC2)) located within the Point Calimere Wildlife Sanctuary (PCWS), south-east India, during January to June 2014. The PCWS is located in Nagapattinam district of Tamil Nadu, where the Bay of Bengal meets the Palk Strait. This sanctuary was created in 1967 to protect the diminishing population of blackbucks (*Antelope cervicapra*). The vegetation here is classified as tropical dry evergreen forest (TDEF; type 7/C1 of Indian forest classification (Champion & Seth 1968). The TDEF is a geographically restricted forest type that occurs as numerous patches dotted along the Coromandel Coast of India. Among which, the PCWS is probably the largest existing and relatively undisturbed TDEF site in India. The vegetation is dominated by trees of short-stature (6–12 m) and mostly two-three layered. The rainfall here is tropical dissymmetric type with most of the rainfall received during the North-East monsoon (October–



**Fig. 1.** Frequency distribution of lianas on host trees in Point Calimere wildlife anctuary.

December) and a little inconsistent rainfall during the South-West monsoon (June–July). The mean annual rainfall in the nearest town Nagapattinam is 1346 mm yr<sup>-1</sup>. The mean annual maximum and minimum temperature are 34.9 °C and 22.3 °C in Nagapattinam. Like other TDEF sites, PCWS experiences 6–8 months of dry season annually.

#### *Plot design and inventory*

Research was carried out in two 1-ha plots in PCWS. To facilitate the inventory, each 1-ha plot was subdivided into one-hundred 10 m × 10 m quadrats. All trees ≥ 10 cm girth at breast height (gbh) was measured along with lianas (≥ 1 cm diameter at 1.3 m from the rooting point) they hosted. Since, PCWS is relatively short-statured, we examined the association between lianas and trees without explicitly taking the site of infestation (i.e. either trunk/crown or both) into account. Hence, liana infestation here refers to the presence of lianas in host trunk/crown or both. Lateral infestation of trees by large lianas is also very common in this forest, but we took only the first incidence (i.e. the primary host) into account. All the inventoried tree and liana species were recognized to species-level using regional floras (Gamble & Fischer 1915–1935; Matthew 1991) and confirmed with the specimens lodged in the herbarium of Department of Ecology and Environmental Sciences, Pondicherry University.

#### *Tree and liana functional traits*

All the tree and liana functional traits including bark type (smooth, rough and slightly rough), and climbing mechanism were assessed through direct observations in the field. The wood specific density (WSD) of each tree species was taken from available literature (Mani & Parthasarathy 2007). For few species (data unavailable), we calculated the wood specific density as oven-dry weight (105 °C, 48 h) divided by volume. We categorized tree girth into five different classes (10–30, 30–60, 60–90, 90–120 and ≥ 120 cm gbh). Based on their leafing phenology, each tree species was designated as evergreen/brevi-deciduous/deciduous physiognomic types (PT).

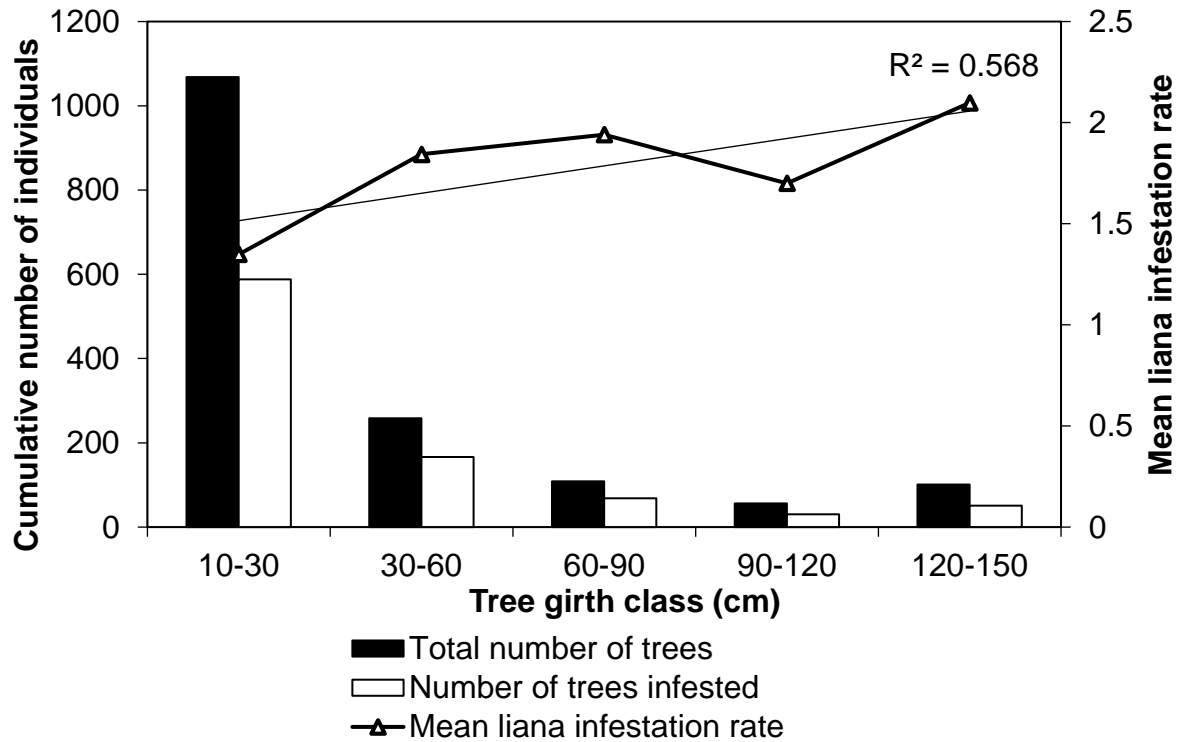
#### *Statistics*

All the statistical analyses were conducted using SPSS (Version 20). We used one-way analysis of variance (ANOVA) to check whether there is any significant difference between lianas under different climbing mechanisms and the tree functional traits. Contingency table Chi-square tests were used to test the significant difference in the frequencies of presence/absence of lianas among the different tree variables including tree girth class, physiognomic type, bark type and wood specific density. Simple linear regression was performed to understand the influence of host-tree girth class on lianas under different climbing mechanisms.

## **Results**

#### *Liana and tree community*

We inventoried a total of 1392 (696 ± 33.9 ha<sup>-1</sup>) liana individuals ≥ 1 cm dbh (diameter at breast height) representing 38 (30 ± 2.12) species, and 1561 (781 ± 13.4 ha<sup>-1</sup>) tree individuals ≥ 10 cm gbh (girth at breast height) that belonged to 40 (32 ± 7.7) species from the two 1-ha study plots in PCWS (Table 1). The commonest liana species in the studied forest include *Carissa spinarum* (170 individuals) and *Jasminum angustifolium* (166) (Table S1). Among trees, *Memecylon umbellatum* (295 individuals), *Manilkara hexandra* (135) and *Atalantia monophylla* (121) comprised the major proportion of trees (35.3%) in the study sites (Table S2).



**Fig. 2.** Proportion of liana infestation on different tree girth-class and linear regression between mean liana infestation rates and different tree girth classes in Point Calimere wildlife sanctuary.

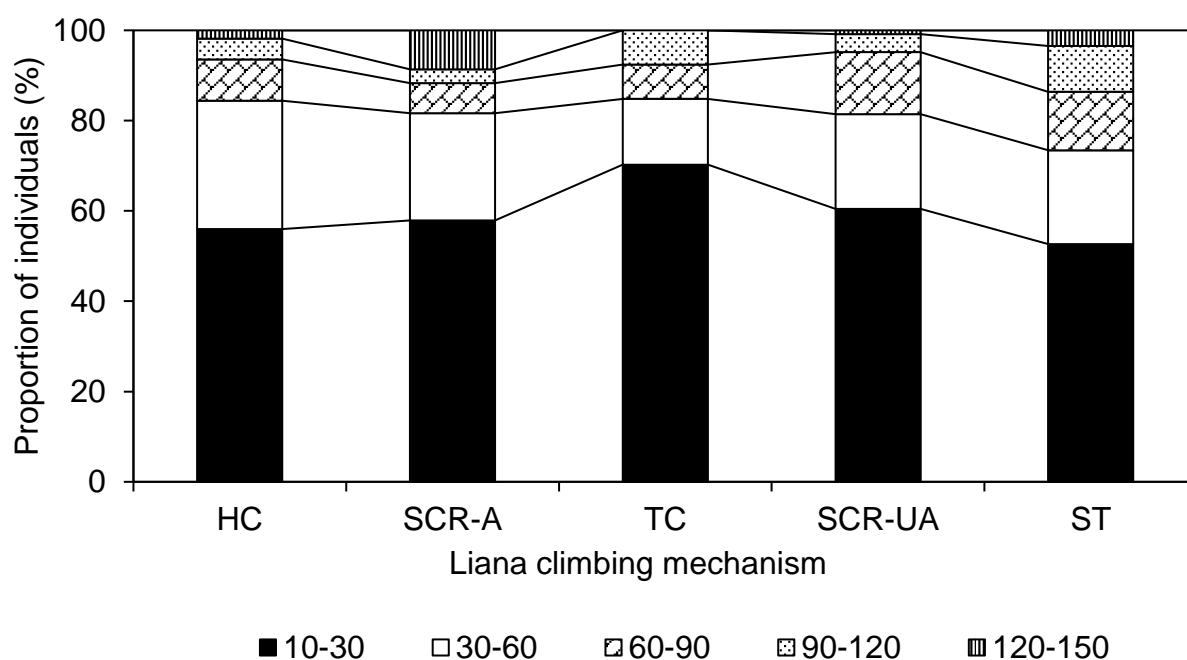
#### *Liana-tree interactions*

Of the total 1561 trees enumerated, 904 trees carried at least one liana (data pooled for two 1-ha study plots) and thus 57.9% of trees in the study plots were liana-infested. The infested trees hosted an average of  $1.53 \pm 0.49$  lianas per tree (Table 2). The frequency distribution of lianas on host trees ranged from 0–8 and the number of trees carrying lianas decreased exponentially ( $r = 0.95$ ) with the increase in frequency distribution (Fig.1). *Pongamia pinnata* lodged the highest frequency of liana load, ranging from 0–8 liana individuals, whereas six tree species including *Cassia auriculata* and *Mallotus philippensis* are devoid of lianas (Table S2). For further analysis, we included only the lianas and trees having  $\geq 30$  individuals. *Pongamia pinnata* was the most infested host species (77% of the total abundance) followed by *Azadirachta indica* (74%) and *Canthium dicoccum* (73%) (Table S2). *Tarenna asiatica* was the least preferred host species (34% of the total abundance). Meliaceae, Sapotaceae and Fabaceae are the most colonized tree families (77%, 69% and 66% of their total abundance respectively) by lianas (Table S3). The severely infested tree species in the study plots

include *Pongamia pinnata* that carried at least 1.9 lianas per infested individual followed by *Azadirachta indica* (1.9) and *Cassia fistula* (1.8) (Table S2). Some of the dominant tree species including *Memecylon umbellatum* and *Glycosmis mauritiana* are among the least infested hosts that carried less than 1.4 lianas on an average per infested tree (Table S3). However, *Memecylon umbellatum* (223 liana individuals) along with *Manilkara hexandra* (162) and *Cassia fistula* (122) carried most number of lianas in the study plots (Table S2).

#### *Tree functional traits and liana colonization*

In the present study, each tree in the plot was analyzed for the presence/absence of lianas. Contingency table Chi-square tests revealed that the host tree traits play a significant role ( $P < 0.05$ ) in hosting/avoiding lianas in the frequencies of presence/absence of lianas among different tree variables including tree girth class (GC;), bark type (BT;), wood specific density (WSD;), physiognomic type (PT;) and ecological guild (EG;) (Table 2). Host tree species in the mid-girth class (30–60 cm gbh)



**Fig. 3.** Distribution of lianas on different tree girth classes (10–30; 30–60; 60–90; 90–120;  $\geq 120$  cm gbh) by climbing mechanism (ST – stem twiner; TC – tendrill climber; HC – hook climber; SCR-A – armed-scrambler; SCR-UA – unarmed-scrambler) in Point Calimere wildlife sanctuary.

registered the highest per cent (64.3%) liana infestation and trees of lowest (10–30 cm gbh) and highest girth class ( $\geq 120$  cm gbh) registered the lowest (Fig. 2). The lowest girth class also registered the least mean liana infestation rates (1.3 lianas per infested individual) and there was a positive correlation ( $r = 0.568$ ) between the liana infestation rates and tree girth classes in the study plots (Fig. 2). Host trees with WSD value between 0.60–0.90 g cm<sup>-3</sup> were more susceptible to liana infestation (61.7% infested), whereas trees with high WSD (0.90–1.20 g cm<sup>-3</sup>) are less susceptible to be the hosts of lianas (Table 3). The total number of lianas carried and the mean liana infestation rates did not show any correlation with tree wood specific density. At PCWS, 60% of the deciduous tree species carried at least one liana followed by evergreen species (56.5%) (Table 3). The mean liana infestation rate was also highest ( $1.7 \pm 0.7$  liana per infested tree) in deciduous species followed by brevideciduous ( $1.53 \pm 0.7$ ) and evergreen species ( $1.49 \pm 0.4$ ) (Table 4).

Among 40 tree species, trees with rough bark registered maximum number of individuals (60.3%) laden with lianas followed by slightly rough (56.8%) and smooth-barked trees (51.2%). Trees in the

rough-barked category carried 49.5% of the total lianas at an average of  $1.62 \pm 0.5$  lianas per infested stem. Trees in slightly rough-barked category carried  $1.48 \pm 0.3$  and smooth-barked category carried  $1.42 \pm 0.3$  lianas per infested stem (Table 3).

#### *Host preferences of lianas by climbing mechanisms: Tree girth class vs climbing mechanisms of lianas*

We recognized five different climbing mechanisms (HC – hook climber; ST – stem twiner; TC – tendrill climber; SCR-A – armed-scrambler; SCR-UA – unarmed-scrambler) employed by lianas in the TDEF (Fig. 3). We also analyzed the preferential host tree girth class of each climbing mechanism. There was no significant difference between the host tree girth class and the lianas under different climbing mechanisms ( $F_{2, 12} = 1.59$ ,  $P > 0.05$ ). Irrespective of the climbing mechanism, the major proportion of lianas fell within the lowest gbh class and it is exceptionally high in tendrill climbers (70.2% of the total abundance; Fig. 3). Tendrill climbers rarely infested the higher-girthed trees, whereas unarmed-scramblers and twiners had significant levels of infestation in middle and higher girth classes.

**Table 2.** Summary of contingency table Chi-square tests to ascertain significance of difference in the frequencies of presence and absence of lianas.

Variable	Value	df	*Asymptotic Sig. (2-sided)
Girth-class	24.364	4	0.000
Bark type	27.469	2	0.000
Wood specific density	23.512	2	0.000
Physiognomic type	30.939	2	0.000
Ecological guild	22.505	2	0.000

\*Asymptotic significances are displayed. The significance level is 0.05

### *Tree functional traits vs climbing mechanisms of lianas*

The percent infestation of lianas employing five different climbing mechanisms on three different bark categories did not differ significantly ( $F_{2, 12} = 1.15$ ,  $P > 0.05$ ) in the study sites. Lianas under the five different climbing mechanisms tend to be more frequent on the rough-barked trees followed by trees under slightly-rough and smooth-barked category (Fig. 4a). Particularly, the stem twiners preferred more of rough-barked trees (54.8% of the total individuals). On the other hand, smooth-barked trees are the least preferred hosts (17.9%) for stem twiners. Whereas, the proportion of tendril climbers and the scramblers (armed and unarmed) on the smooth-barked trees was higher than that of the stem twiners, and hook climbers (Fig. 4a). Trees with medium-WSD values are more prone to be colonized by lianas, irrespective of climbing mechanisms. Especially, the hook climbers showed maximum affinity (88% of individuals) towards hosts with moderate-WSD values (Fig. 4b). The proportion of infestation by lianas under different climbing mechanisms on host trees of different physiognomic types did not significantly ( $F_{2, 12} = 6.16$ ,  $P > 0.05$ ). Hook climbers had the highest proportion of individuals infesting evergreen trees (Fig. 4c). The proportion of liana infestation on non-evergreen hosts (deciduous and brevi-deciduous) was greater in SCR-UA, TC and SCR-A (31.4%, 27.5% and 24.7% of the total individuals, respectively).

## Discussion

Although there are studies that reported the patterns of tree-liana interactions in tropical forests, the application of different methodologies in inventorying trees and lianas, for example, the

differences in attributes considered, girth-class threshold, point of measurement and sites of liana infestation, confound comparisons across the study sites (Perez-Salicrup & de Meijere 2005; van der Heijden *et al.* 2008). Yet, we made an attempt to compare the percentage of liana infestations (Table 5); our results (57.9%) are on par with the infestation rate reported from south-east Asian tropics (Campbell & Newbery 1993; Putz & Chai 1987; Putz *et al.* 1984b) and higher than the previous studies (Chittibabu & Parthasarathy 2001; Muthuramkumar & Parthasarathy 2001) reported from peninsular Indian study sites but, lower than those reported from many Neotropical forests (Alvira *et al.* 2004; Campanello *et al.* 2007; Gerwing 2001; e.g. Killeen *et al.* 1998; Perez-Salicrup *et al.* 2001, 2005) (Table 5). Such disparities in results are not surprising, because the percentage of liana infestation on host trees seems to be determined by the abundance of lianas and trees in the study sites. Hence, the Neotropical sites with greater abundance of lianas are expected to have higher proportion of liana-laden trees. Similarly, the mean liana infestation rates in the study sites (1.53 lianas per infested tree) are at least six-fold lesser than that of the values reported (9.3 lianas per infested tree) by Alvira *et al.* (2004) in lowland tropical forest of Bolivia. Therefore, the per cent liana infestation and the mean liana infestation rates are likely to be governed by the composition of the woody species in the respective study sites.

The mean liana infestation rates in the study sites varied among species and among individuals of the same species. For example, some species such as *Pongamia pinnata* and *Azadirachta indica* are severely infested, while species like *Tarennia asiatica* and *Borassus flabellifer* (toddy palm) are least infested. This shows the difference in needs of

**Table 3.** Liana infestation rates (LIR) in different tree variables at Point Calimere wildlife sanctuary.

Tree variable	Total number of tree individuals	Total number of trees infested (%)	Total no. of lianas carried	Mean liana infestation (LIR)
<b>Bark type</b>				
Rough	696	420 (60.3)	679	1.62 ± 0.5
Slightly rough	477	271 (56.8)	401	1.48 ± 0.3
Smooth	388	199 (51.2)	290	1.42 ± 0.3
<b>Wood specific density (g cm<sup>-3</sup>)</b>				
0.30 – 0.59	250	117 (46.8)	166	1.42 ± 0.7
0.60 – 0.89	1180	729 (61.7)	1118	1.53 ± 0.4
0.90 – 1.20	131	59 (45.0)	86	1.46 ± 0.2
<b>Physiognomic type</b>				
Brevi-deciduous	103	57 (55.3)	87	1.53 ± 0.4
Deciduous	233	140 (60.0)	247	1.76 ± 0.7
Evergreen	1225	693 (56.5)	1036	1.49 ± 0.4

lianas and functional traits associated with the host plants that support/deter liana infestation (Alvira *et al.* 2004). Similarly, the frequency of liana distribution varied within the individuals of same species (e.g. *Pongamia pinnata*; 0–8) with similar functional traits, which is still unclear and may be explained by the unexplored attributes in the present study like branch-free bole height (Reddy & Parthasarathy 2006), allelopathic effect of the host (Tally *et al.* 1996) and environmental factors (Leicht-Young *et al.* 2010).

#### *Tree functional traits*

Trees are the most usual hosts that are colonized by lianas (Carsten *et al.* 2002). The unique physical networks between trees and lianas are often controlled by host species' traits (Leicht-Young *et al.* 2010). As expected, the host trees with mid- and high WSD values are more prone to be infested by lianas, whereas trees with low-WSD are less infested in the studied forest. In general, tree species with low wood-density grow faster than those with high WSD values (Chave *et al.* 2006; Enquist *et al.* 1999; King *et al.* 2005; Muller-Landau 2004). Further, studies have demonstrated the possible effect of lianas on slow-growing trees, with high WSD than the fast growing trees (e.g. van der Heijden *et al.* 2008). Similarly, the mean liana infestation rate was also higher in trees with moderate and high WSD values, which further justifies the influence of wood specific density on liana infestation. However, the total number of lianas carried and the mean liana infestation rates did not show any correlation with WSD values,

indicating the effect of intra-specific variations in WSD among individuals of same species rather than the species-specific averages (Putz 1984b). Among the three plant physiognomic types distinguished, the deciduous trees marked with highest mean liana infestation rates are more vulnerable to liana infestation followed by brevi-deciduous and evergreen species. This is interesting, although lianas are generally shade-tolerant (Baars & Kelly 1996; Carter & Teramura 1988) and can wait for favorable light conditions (Greenberg *et al.* 2001; Leicht & Silander 2006), they can thrive even better, where there is abundant light and little competition from trees (Putz 1984b). Lianas are known for their ability to exploit aboveground resources in seasonal forests, utilizing the prevailing high solar radiation in the dry seasons (Schnitzer 2005; Yong *et al.* 2012). The TDEF with pronounced dry season (6–8 months) is known for tree leaflessness associated with the deciduous trees at least for three month time period, which offers competitive advantage for lianas during the dry season.

Host trees with rough bark are often colonized by lianas than the slightly-rough and smooth-barked trees in PCWS as trees with rough bark offers suitable surface grip for attachment of lianas, whereas lianas may not be able to climb trees with smooth barks, for lack of suitable attachment sites for their climbing structures (Campanello *et al.* 2007; Putz 1980). Host trees in moderate-girth classes registered the highest proportion of individuals encountered with the presence of lianas. Our results are in par with the findings of Perez-Salicrup (2001) in seasonal moist forests of Bolivia

**Table 4.** Percentage of liana infestation reported from various tropical forests (dbh = diameter at breast height; gbh = girth at breast height).

Location	Percentage of infested trees	Gbh threshold (cm)	Reference
Tropical dry evergreen forest, south-east India	57.9	10 gbh	Present study
Tambopata nature reserve, Peru	49.8	10 dbh	Van der Heijden <i>et al.</i> (2008)
Subtropical semi-deciduous forest, Argentina	82.4	10 dbh	Campanello <i>et al.</i> (2007)
Tropical dry evergreen forest			
Tropical rain forest, Mexico	63.3	10 dbh	Perez-Salicrup (2005)
Subtropical humid forest, Bolivia	73	10 dbh	Alvira <i>et al.</i> (2004)
Tropical evergreen forests, Eastern Ghats, India	10	30 gbh	Chittibabu & Parthasarathy, (2001)
Tropical evergreen forests, Western Ghats, India	28	30 gbh	Muthuramkumar & Parthasarathy (2001)
Seasonal evergreen forest, Brazil	90	5 dbh	Gerwing (2001)
Seasonal moist forest, Bolivia	86.3	10 dbh	Perez-Salicrup <i>et al.</i> (2001)
Tropical dry forest, Bolivia	77	20 dbh	Carse <i>et al.</i> (2000)
Seasonal dry forest, Bolivia	75	10 dbh	Killeen <i>et al.</i> (1998)
Wet evergreen forest, Lambir, Malaysia	52.3	10 dbh	Putz & Chai (1987)
Moist forest, Similajau, Malaysia	53.8	10 dbh	Putz <i>et al.</i> (1984)

and Ding & Zang (2009) in tropical lowland forests of China. The positive correlation between the mean liana infestation rates and the tree girth classes suggests that rate of liana infestation increases with increase in girth class, and this can be attributed to the sufficient time lapse provided by larger trees for lianas to locate them as supports (Alvira *et al.* 2004; Perez-Salicrup 2005; van der Heijden *et al.* 2008). Moreover, large trees and those which already possess lianas are often more likely to be colonized (Nabe-Nielsen 2001; Perez-Salicrup & de Meijere 2005). Overall, in PCWS, small-stemmed trees with low WSD and smooth bark are least preferred by lianas. Also, evergreen trees suffered lesser liana infestation than the deciduous and brevi-deciduous trees. On the other hand, trees that possess rough bark, moderate-sized stems and those with moderate-WSD values are often more infested. These varying host preferences of lianas may result in differential impacts on host trees within the forest (Ladwig & Meiners 2010).

The role of tree functional traits in determining the liana colonization success is evident from the present study. However, the independent effect of each trait is difficult to distinguish (van der Heijden 2008), because it involves wide array of characteristics that allow trees to avoid or shed lianas, but no single feature gives complete shield

from lianas (Putz 1984b). Previous studies have considered various tree morphological traits and architectural patterns as attributes and influencing factors of tree-liana interactions. However, the attributes considered in the studies differed from place to place and produced contrasting results. For example, Black & Harper (1979) proposed “buttress-liana” hypothesis and proved that buttressed trees have negative influence on liana infestation; in contrast, Boom & Mori (1982) falsified the hypothesis in Brazilian tropical wet forests. In contrast to many studies, Carse *et al.* (2000) reported that there is no single major characteristic that facilitates or repels liana colonization in Las Trancas. Few other studies also have failed to find any association between liana and tree traits, suggesting that instead, spatial factors may influence the susceptibility of trees for liana infestation (Malizia & Grau 2006; Perez-Salicrup *et al.* 2001). Leicht-Young *et al.* (2010) suggested the possible role of environmental factors in the initial and tree characteristics in the later stage of infestation. Therefore, the factors influencing tree-liana interactions appear to be regional and depend on spectrum of unexplored variables including the local environmental factors, forest vegetation and disturbance regimes.

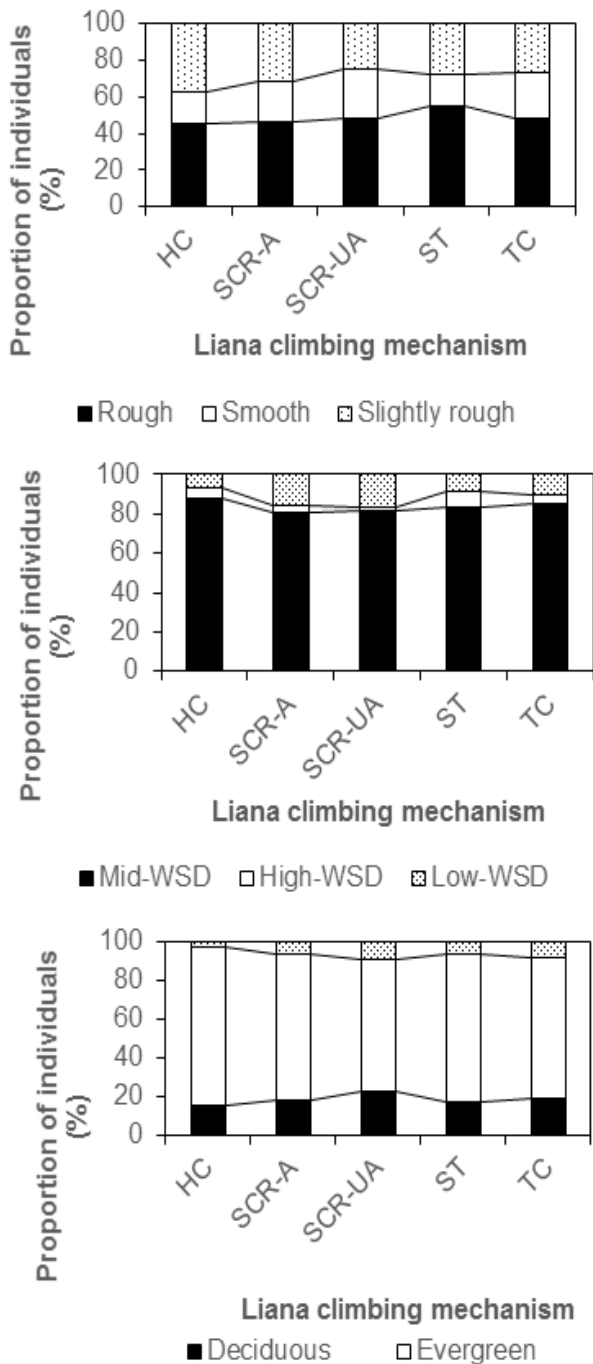


*Climbing mechanism vs liana infestation*

The present study is one of the very few studies (Vivek & Parthasarathy 2016) that deal with the differential needs in host preferences of lianas employing different climbing mechanisms. At PCWS we explored the preferential host tree girth class of each climbing mechanism. The reason for most lianas climbing on the smaller supports, irrespective of climbing mechanisms may be due to the greater abundance of smaller trees in the studied sites. However, it is exceptionally higher in tendrill climbers because, the smaller trees may possibly serve as suitable host for tendrill climbers by providing relatively smaller branches for them to enfold and move further (Carsten *et al.* 2002). This shows that the host-size biomechanical constraints are higher for tendrill climbers than lianas with other climbing means (Gianoli 2015). Simple linear regression revealed the decrease in the proportion of liana infestation by climbing mechanisms with the increase in tree size-class especially in the case of stem twiners. This is in conformity with the previous studies reported from tropical (Putz 1984b; Putz & Chai 1987) and subtropical forests (Carsten *et al.* 2002) which showed the decrease in relative abundance of twiners with the increasing tree dbh. Contrary to our expectations, the demand of lianas under different climbing mechanisms in selecting the hosts remained similar, but their proportion differed marginally. This may be due to the intense competition among lianas of different climbing mechanism in finding their supports (Vivek & Parthasarathy 2016). Nevertheless, co-occurrence studies on lianas of different climbing mechanisms are expected to give a better knowledge (Addo-Fordjour *et al.* 2016) which is not discussed in the present study.

**Conclusion**

As elsewhere in the tropics, liana infestation on trees now seems to be common in the TDEFs. In these complex associations, lianas are believed to have detrimental effects on their hosts as evidences are accruing (Alvarez-Cansino *et al.* 2015; Campanello *et al.* 2007; Toledo Aceves & Swaine 2008) that lianas compete penetratingly for resources with co-occurring trees, reducing their fecundity, regeneration, growth, diversity and survival even. Therefore, the trees that remain free from lianas may derive competitive advantage (Alvira *et al.* 2004; Campbell & Newbery 1993; Putz 1984a, b; Schnitzer *et al.* 2000). This competition



**Fig. 4.** Variation in proportion of liana infestation by different climbing mechanism (HC – hook climbers; ST – stem twiners; TC – tendrill climbers; SCR-A – armed-scrambler; SCR-UA – unarmed-scrambler) of lianas on different tree functional traits (a. Bark – rough; smooth and slightly rough; b. Wood specific density – 30–59.9– low WSD; 60–90 – medium WSD; 90–120– high WSD; c. Plant type: BD – brevi-deciduous; D – deciduous; E – evergreen).

between lianas and trees may be intensified by biotic and abiotic stresses generated by both natural and anthropogenic disturbances. The present study sites with pronounced dry season (6–8 months) are therefore expected to witness intense competition among the woody life-forms at least for the belowground resources which is a limiting factor in many seasonal forests. For instance, long-term monitoring studies over two decades in tropical dry evergreen forest sites revealed that tree density decreased by about 30% and liana density on the other hand increased by 30% (Parthasarathy *et al.* 2015) during the same period. This drastic increase in liana abundance, not only in the TDEF but also in many tropical forests would pose a serious threat for tropical forest dynamics and functioning. For example, lianas with their deleterious effects on trees may reduce whole forest carbon storage, as lianas cannot compensate for the tree biomass they displace (Schnitzer & Bongers 2011; e.g., van der Heijden & Phillips 2009). Therefore, it has become crucial now to understand the potential liana impacts on the tree community, for which it is a pre-requisite to study the patterns of liana-tree interactions and intensity of liana burden on the host trees (Ladwig & Meiners 2010). Such studies may provide greater insight and a better understanding of the maintenance of high biodiversity and to check the global carbon stocks. Thus, we recommend the following:

1. A need for greater insight in analyzing the patterns of tree-liana interactions, as it seems to be governed not only by a spectrum of tree functional traits but also by site environmental characteristics coupled with legacies of anthropogenic impact, which might contribute to disparities in patterns of tree-liana interactions across the tropics.

2. A need for developing a standard protocol to document the patterns of liana-tree interactions so as to facilitate global comparison, which is of paramount importance in the present scenario.

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## Supporting Information

Additional Supporting information may be found in the online version of this article.

**Table S1.** List of liana species with their climbing mechanism, density and total abundance enumerated in four sites (KT, PC 1, PC 2 and SN) of tropical dry evergreen forest.

**Table S2.** Functional traits, abundance (2 ha) and percentage of liana colonization on host tree species in two 1-ha plots of Point Calimere wildlife sanctuary.

**Table S3.** Percent colonization and mean liana infestation on tree families in Indian tropical dry evergreen forest.