




## Article

# Habitat Conditions and Tree Species Shape Liana Distribution in a Subtropical Forest

Buhang Li <sup>1</sup>, Yingming Zhang <sup>2</sup>, Fuchen Luan <sup>2</sup>, Zuoqiang Yuan <sup>3</sup> , Arshad Ali <sup>4</sup> , Chengjin Chu <sup>1</sup>   
and Yue Bin <sup>5,6,\*</sup>

<sup>1</sup> State Key Laboratory of Biocontrol and Department of Ecology, School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, China

<sup>2</sup> Guangdong Chebaling National Nature Reserve, Shaoguan 512500, China

<sup>3</sup> School of Ecology and Environment, Northern Polytechnical University, Xi'an 710072, China

<sup>4</sup> Forest Ecology Research Group, College of Life Sciences, Hebei University, Baoding 071002, China

<sup>5</sup> Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

<sup>6</sup> Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou 511458, China

\* Correspondence: binyue@scbg.ac.cn

**Abstract:** Lianas are woody plants that require external support to reach the canopy. They are expanding in forests worldwide, possibly due to climate change and forest disturbance. Most studies on lianas have been conducted in tropical forests. Lianas are less explored in subtropical forests. We aimed to document the density and diversity of lianas, to test how habitat condition and the distribution of tree species affect the distributions of lianas based on data from a fully mapped 20 ha plot in subtropical China. We analyzed habitat association by fitting a generalized linear model with family-level liana abundance as response variable and family identity, and its interaction terms with topographic variables (slope, convexity, elevation, and sin(aspect)), as explanatory variables. We focused on the spatial associations of three liana species and 82 tree species with  $\geq 100$  individuals using the pair correlation function and redundancy analysis. We found a total of 1305 lianas, falling into 26 species, and 16 families, in the 20 ha plot. They accounted for 1.5% of individuals, 11.7% of species, and 0.4% of total basal area of woody plants in the plot. There were large variations in distributions of liana with respect to the four topographic variables among families, contrasting with former findings suggesting that lianas favor dry and hot habitats. The three most abundant liana species showed non-random associations with tree species, and they tended to positively associate with similar tree species but negatively associate with different tree species. The distribution of tree species explained 21.8% of variance in liana distribution. Our study suggested that both habitat conditions and tree composition intervene in determining liana distributions and that habitat heterogeneity may be a mechanism for liana diversity maintenance. Our study provides a basic understanding of liana diversity and distribution in this subtropical forest and contributes to future planning of liana studies and diversity conservation in subtropical forests under climate change.

**Keywords:** liana; vines; woody vines; habitat association; habitat preference; habitat suitability; species association; host specificity; host preference; subtropical forests



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## 1. Introduction

Lianas are woody plants that rely on other plants for support to reach the canopy. In recent decades, one of the most prominent changes in tropical forests is the expansion of lianas [1,2]. Prolonged dry seasons under climate change are considered to favor the growth and expansion of lianas, since lianas grow much faster than trees during the dry season [3]. Though lianas constitute part of species diversity [4–6] and provide shelters and food sources for animals in forests [7,8], the expansion of lianas, however, has detrimental effects on tree growth, survival, and reproduction, (reviewed by Estrada-Villegas and Schnitzer [9])

and can potentially alter forest composition, structure, and functions [8–11]. Given that the causes of climate change and the risks of liana expansion may probably last [1,2], an understanding of diversity, distribution, and species association of lianas in forests is essential so that proper conservation measures can be implemented when necessary.

Liana distributions in tropical forests are influenced by habitat conditions, but no consensus has been reached currently. In a Panamanian forest, lianas grew seven times faster than trees during the dry season [3], suggesting lianas have comparative advantage over trees in drier habitats, and may be more abundant under such habitat conditions in forests [3,10]. On the other hand, evidence showed that lianas were more abundant in concave sites with high moisture supply [12]. Though it was demonstrated that liana species generally lack ecophysiological structures for releasing potentially toxic compounds due to anaerobiosis [13], in a savanna–forest transition zone in central Brazil, flooded forests had high liana abundance dominated by *Combretum laxum* [14]. Similarly, in southern Amazonia, lianas were more abundant in habitats with impeded drainage [15]. These results suggest that some liana species may prefer high moisture supply. Further studies are needed to understand how liana distributions are affected by habitat conditions.

Besides habitat condition, tree species also affect the distribution of lianas [11,16–18]. Since lianas rely on tree species for support, liana species may show preference for certain tree species [18]. Though lianas do not establish species-specific associations with trees, some tree species are more likely to have lianas on them, such as White oaks in northern temperate forests in the USA [18], *Liquidambar styraciflua* (sweet gum) in floodplain forests in the southeastern United States [19,20], and *Allophylus edulis* and *Cordia ecalyculata* in a subtropical Atlantic forest [21]. As lianas are fast growing and maintained by disturbance [8], their distributions should tend to avoid shade-tolerant species. However, a field study found that shade-tolerant tree species held a high level of liana prevalence [11]. The first step to understand why some tree species attract more lianas is to document the tree–liana spatial associations.

In subtropical forests, lianas are less prominent in communities and hence have received much less attention than in tropical forests (however, see Cai and Song, 2000; Kusumoto et al., 2008) [5,12]. Under the regulation of a subtropical monsoon climate, precipitation in the Chinese subtropical zone shows strong seasonality, with a dry season lasting about half a year [22]. Winter is relatively mild, and with the lowest temperature around  $-5^{\circ}\text{C}$ , subtropical forests are also suitable habitats for lianas. Recent studies showed that the rainfall pattern in subtropical areas in China has shifted towards more heavy rains in the wet seasons, and more no-rain days and fewer light-rain days in the dry season since around 1980, and vegetation may be affected because soil moisture declined significantly from 1950 to 2009 [23]. Such change in precipitation pattern suggests the risk of increasing liana expansion for subtropical forests in China. However, in subtropical forests, lianas are often ignored during forest censuses. As a result, poorly known are the liana species diversity and what shapes liana distributions in subtropical forests.

In this study, we included lianas in our census conducted in a 20 ha plot in a subtropical forest in China. Based on these data, we aim to provide primary knowledge of species diversity of lianas, to test whether liana distribution is related to habitat conditions reflecting gradients of drought, and whether lianas are specifically associated with certain tree species in a subtropical forest. In doing so, we tried to answer the following questions: (1) How much do lianas contribute to forest diversity? (2) How do habitat conditions shape the distribution of lianas? (3) How do tree species influence the distribution of lianas? Our primary goal was to provide primary knowledge of liana diversity and distribution in this forest but the results of this study were useful for the conservation of species diversity in subtropical forests and could also set the basis for future studies on the temporal dynamics of lianas in the context of ongoing climate change.

## 2. Materials and Methods

### 2.1. Study Site and Forest Plot

This study was conducted in the Chebaling National Nature Reserve, which was established in 1981 and is located in the southeast part of Shixing, Shaoguan, Guangdong, China ( $114^{\circ}09'04''$ – $114^{\circ}16'46''$  E,  $24^{\circ}40'29''$ – $24^{\circ}46'21''$  N). The altitude of this nature reserve ranges from 330 to 1256 m a.s.l. The climate regime belongs to the subtropical monsoon climate, with an annual average temperature of  $19.6^{\circ}\text{C}$  and an annual precipitation of 2126 mm. Precipitation is relatively centered on a rainy season from April to October. The dry season lasts from November to March for the next year. The nature reserve is covered by subtropical evergreen broadleaved forests. Broadleaved, evergreen tree species from Fagaceae, Lauraceae, Thestarae, Hamamelidaceae, and Magno-Listarae dominate the forest communities in this reserve.

In September 2017, a 20 ha forest dynamic plot (the CBL plot) was established in the nature reserve. The plot was first divided into 500 quadrats with projected areas of  $20\text{ m} \times 20\text{ m}$ . The elevations at the corners of all  $20\text{ m} \times 20\text{ m}$  quadrats were recorded. Elevation, slope, convexity, and aspect for all quadrats were calculated based on the recorded elevations [24]. Every woody stem, including trees and lianas, with diameter at breast (DBH) height  $\geq 1\text{ cm}$  was mapped, tagged, measured for DBH, and identified to species [25]. All rooted stems of lianas were measured and they were considered as individuals following Schnitzer et al. [26].

### 2.2. Data Analyses

We summarized information on abundance (i.e., the total number of individuals) and diversity at both the species and family levels for the lianas in the plot. These data for lianas were compared with the corresponding data for tree species in the plot.

For analyzing liana distribution with respect to topographic variables, we calculated elevation, slope, aspect, and convexity for each  $20\text{ m} \times 20\text{ m}$  quadrat, following Harms et al. [24]. We set zero aspect for a quadrat facing right towards the east. The value of  $\sin(\text{aspect})$  for a quadrat is associated with the amount of sunshine captured by it. A quadrat facing the south ( $\pi/2$ ) received the largest amount of sunshine ( $\sin(\pi/2) = 1$ ), while a quadrat facing the north received the least ( $\sin(3\pi/2) = -1$ ). Thus, the  $\sin(\text{aspect})$  axis suggested increasing insolation and drier habitat condition. If lianas prefer drier habitat conditions in this forest, liana abundance would increase along the  $\sin(\text{aspect})$  axis. We expected that the light captured should be more informative for liana distribution than the angle itself. Therefore, we used  $\sin(\text{aspect})$  instead of the value of aspect in subsequent analysis.

We grouped data of lianas to the family level, and combined families with  $<30$  individuals together to form a group (Others). We then fit a generalized linear model with the number of lianas of each group in each  $20\text{ m} \times 20\text{ m}$  quadrat as the response variable, while Family and its interactions with the linear and quadratic terms of elevation, slope, convexity, and  $\sin(\text{aspect})$  as explanatory variables, assuming a Poisson distribution for the response with a “log” link function [12]. The model was then subjected to a stepwise procedure to exclude non-significant variables. The significance of an interaction term of a topographic variable suggested significant variation among families in coefficients for that topographic variable.

We analyzed the distributions of liana species with  $\geq 100$  individuals with respect to tree species with  $\geq 100$  individuals using the bivariate pair correlation function,  $G_{12}(r)$ . A total of 3 liana species and 82 tree species were involved in this analysis.  $G_{12}(r)$  is defined as the expected number of individuals of species 2 in the rings with radius  $r$  of an individual of species 1, divided by the density of species 2 in these rings [27]. Values greater than 1 for  $g(r)$  indicate positive associations, while smaller than 1 suggests negative associations.  $G(r) = 1$  when the spatial association is random. We examined whether the deviation from one was significant by comparing the observed  $G_{12}(r)$  value with the confidence envelope obtained from 99 random toroidal shifts. Both  $G_{12}(r)$  and the confidence envelopes were estimated using the *spatstat* package on R 2.4.1 [28,29].

Only a few liana–tree associations were positive at some scales but negative at other scales. Excluding these liana–tree associations, we classified the remaining liana–tree associations into three types: “positive” for those positive at  $\geq$ one scale and random at other scales; “negative” for those negative at  $\geq$ one scale and random at other scales; “random” for those random throughout the range of scales studied. For simplicity, a tree species with positive and negative associations with a liana species was defined as the liana species’ attractor and detractor, respectively.

In order to obtain an integrative result for liana–tree association, we also analyzed their spatial distribution with redundancy analysis (RDA) using the *vegan* package implemented on the R platform [30]. As rare species often have an unduly large influence on the analysis, we included only the three liana species and tree species with  $\geq 100$  individuals in this analysis. We constructed two matrices,  $X$  and  $Y$ .  $X_{ij}$ ,  $Y_{ij}$  were the abundance of liana species  $j$  and tree species  $j$  in quadrat  $i$ , respectively. We first fit a null model with only the intercept term and a full model with all 82 tree species included. Then, variable selection was conducted using the *step* function based on Akaike Information Criterion (AIC, [31]). The significance of the final model was tested using 999 permutation tests.

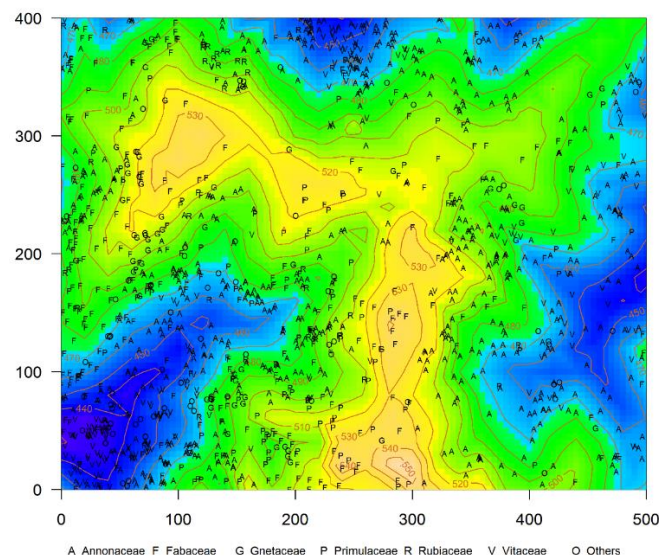
### 3. Results

#### 3.1. Diversity and Distribution of Lianas

There were a total of 1305 lianas, falling into 26 species and 16 families in the 20 ha CBL plot. They accounted for 1.5% of individuals, 11.7% of species, and 0.4% of the basal area in the plot. Among these stems, 387 (22 species) were  $\geq 5$  cm and 1249 (from 25 species) were  $\geq 2$  cm in diameter. Within the 20 m  $\times$  20 m quadrats, the number of liana stems ranged from 0 to 23 and the number of liana species ranged from 0 to 5. The ten most abundant quadrats collectively had 144 liana individuals from 12 species, corresponding to a density of 360 ha<sup>−1</sup>. *Fissistigma oldhamii* (Fisold) was the most abundant species, followed by *Ampelopsis cantoniensis* (Ampcan) and *Callerya dielsiana* (Caldie) (Table 1). Other species had fewer than 100 individuals in the plot. At the family level, Annonaceae had the largest number of lianas individuals but only Ampcan was in this family, followed by Fabaceae (257 individuals from 4 species) and then Vitaceae (183 individuals from 2 species) (Figure 1). The remaining families had  $\leq 100$  individuals and  $\leq 2$  species in the plot. The ranking based on basal area was the same as that based on number of individuals for the first three species and families.

**Table 1.** The liana species in the 20 ha Chebaling plot.

Species Code	Latin Binomial	Family	Abundance
Todasi	<i>Toddalia asiatica</i>	Rutaceae	6
Uncrhy	<i>Uncaria rhynchophylla</i>	Rubiaceae	16
Maccoc	<i>Maclura cochinchinensis</i>	Moraceae	6
Fisold	<i>Fissistigma oldhamii</i>	Annonaceae	610
Ampcan	<i>Ampelopsis cantoniensis</i>	Vitaceae	182
Kadcoc	<i>Kadsura coccinea</i>	Schisandraceae	1
Embrib	<i>Embelia ribes</i> var. <i>pachyphylla</i>	Primulaceae	6
Strcat	<i>Strychnos cathayensis</i>	Loganiaceae	3
Morpar	<i>Morinda parvifolia</i>	Rubiaceae	17
Melfus	<i>Melodinus fusiformis</i>	Apocynaceae	11
Actcal	<i>Actinidia callosa</i>	Actinidiaceae	12
Actlat	<i>Actinidia latifolia</i>	Actinidiaceae	1
Milnit	<i>Milletia nitida</i>	Fabaceae	2
Parlae	<i>Parthenocissus laetevirens</i>	Vitaceae	1
Elagla	<i>Elaeagnus glabra</i>	Elaeagnaceae	1
Rhanap	<i>Rhamnus napalensis</i>	Rhamnaceae	9
Versol	<i>Vernonia solanifolia</i>	Asteraceae	1
Aketri	<i>Akebia trifoliata</i>	Lardizabalaceae	1
Emblae	<i>Embelia laeta</i>	Primulaceae	49
Dalhan	<i>Dalbergia hancei</i>	Fabaceae	29
Staobo	<i>Stauntonia obovatifolia</i>	Lardizabalaceae	18
Muspub	<i>Mussaenda pubescens</i>	Rubiaceae	1
Caecri	<i>Caesalpinia crista</i>	Fabaceae	68
Embrud	<i>Embelia rudis</i>	Primulaceae	32
Caldie	<i>Callerya dielsiana</i>	Fabaceae	158
Gnepar	<i>Gnetum parvifolium</i>	Gnetaceae	64



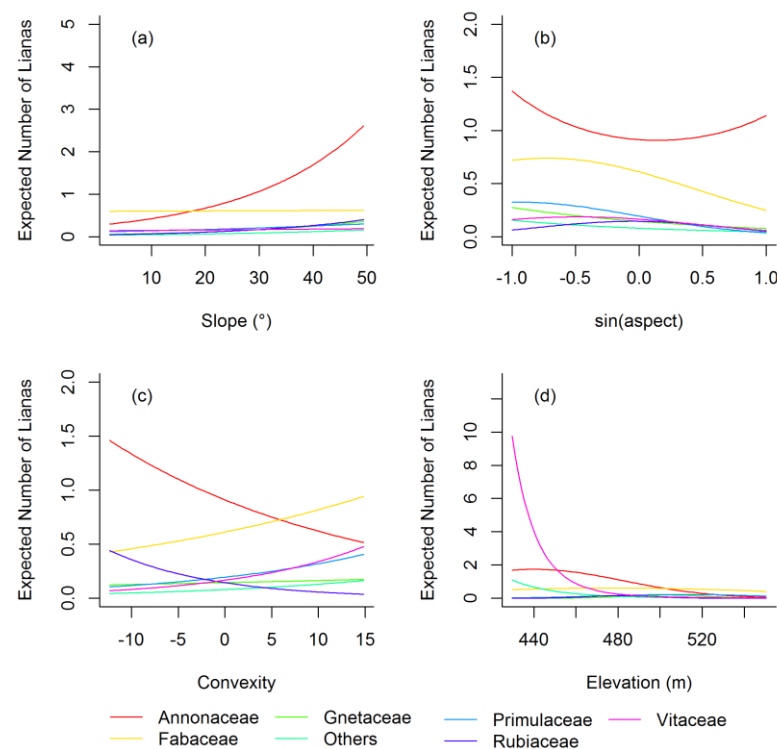
**Figure 1.** The distribution of liana individuals in a 20 ha subtropical forest dynamic plot in Chebaling (CBL), China. Color and numbers on the contour lines denote elevation. Capital letters show the locations of lianas and indicate their families.

### 3.2. Liana Distribution in Relation to Topographic Variables

The final model kept Family, and its interactions with the linear forms of all four topographic variables, and the quadratic forms of  $\sin(\text{aspect})$  and elevation (Table 2, Figure 2). The coefficients of slope for all families were positive. However, discernable increases within the ranges of slope in the plot were observed only for Annonaceae and Rubiaceae (Figure 2a). The coefficients of convexity were positive for all families except Annonaceae and Rubiaceae, indicating that most liana families had more individuals in convex habitats (Figure 2c). Though Annonaceae, Gnetaceae, and Others had positive coefficients for the quadratic term of  $\sin(\text{aspect})$ , only Annonaceae exhibited a concave curve with an inflection point at  $\sin(\text{aspect}) = 0.146$  (Figure 2b).

**Table 2.** The contribution of each variable to the reduction in deviance in the final model for liana abundance as a function of Family and its interactions with the linear and quadratic terms of four topographic variables, which were slope,  $\sin(\text{aspect})$ , convexity, and elevation using a generalized linear model assuming a Poisson distribution for the response variable. “Family” was a factor, with levels of Annonaceae, Fabaceae, Gnetaceae, Primulaceae, Rubiaceae, Vitaceae, and Others. The level of Others included all families of lianas with fewer than 30 individuals in the plot.

	Degree of Freedom	Deviance	Residue Degree of Freedom	Residue Deviance
NULL			3499	5073.9
Family	6	1082.1	3493	3991.8
Family: slope	7	98.89	3486	3892.9
Family: $\sin(\text{aspect})$	7	116.96	3479	3775.9
Family: convexity	7	126.24	3472	3649.7
Family: elevation	7	442.45	3465	3207.2
Family: $\sin^2(\text{aspect})$	7	25.37	3458	3181.9
Family: elevation <sup>2</sup>	7	49.98	3451	3131.9



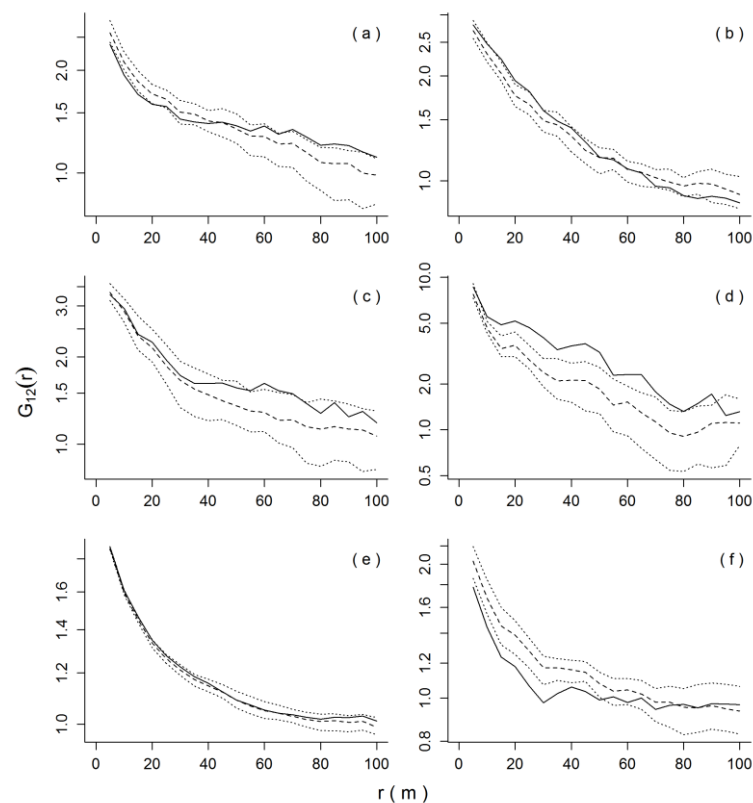
**Figure 2.** The expected number of lianas in relation to topographic variables under their observed ranges in the 20 ha subtropical forest dynamic plot in China. These curves were all obtained by the final generalized linear model fitted for lianas abundance in a 20 m  $\times$  20 m quadrat with a log link function against the family which the lianas belong to, and the interactions of family with slope, sin(aspect), convexity, and elevation of the quadrat. A Poisson distribution was set for the response variable.

Fabaceae, Primulaceae, Gnetaceae, and Others exhibited decreasing number of lianas within the main, if not the whole, range of sin(aspect) (Figure 2b), and all families except Annonaceae showed decreasing number of lianas when sin(aspect) > 0, suggesting that most liana families did not distribute more individuals in habitats facing the south (Figure 1b). Rubiaceae and Vitaceae had inflection points relatively close to zero (Rubiaceae,  $-0.047$ ; Vitaceae,  $-0.478$ ), forming convex curves with mild peaks (Figure 2b).

All families except Vitaceae and Others had negative coefficients for the quadratic term of elevation and their inflection points were within the range of elevation for the plot, showing convex curves for the expected number of lianas with respect to elevation (Figure 2d). In most cases, the curves were mild. The inflection point for Annonaceae was close to the lower limit, resulting in a decreasing trend for the main range of elevation (Figure 2d). Vitaceae and Others showed decreasing number of lianas with increasing elevation (Figure 2d).

### 3.3. Lianas' Spatial Association with Tree Species

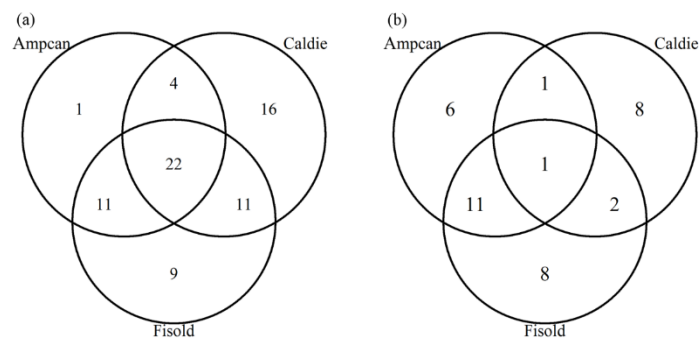
In a total of 246 liana–tree associations, only 20 were positive at some scales while negative at others (Figure 3a,b). Ten such associations were observed for Fisold, six for Ampcan, and four for Caldie. All three liana species showed more positive than negative associations with tree species (Caldie 53 vs. 22; Ampcan 38 vs. 19; Fisold 53 vs. 22).



**Figure 3.** Examples of pair correlation functions for liana species and tree species: negative at some scales while positive at others (a,b), positive associations at <five scales (c) and at  $\geq$ five scales (d), negative associations at <five scales (e) and  $\geq$ five scales (f).

Though in general, the majority (144/246, 58.5%) of liana–tree associations were positive, the  $G_{12}(r)$  curves usually did not deviate from the upper confidence envelopes much (Figure 3). Among these associations, a considerable proportion (61/144) of  $G_{12}(r)$  curves deviated from random toroidal shift at fewer than five scales examined (Figure 3c,e). This proportion was even larger for negative associations. Almost all (49/53, 92.5%)  $G_{12}(r)$  curves for negative associations deviated from random toroidal shift at more than five scales examined. The four exceptions were *Ilex dasyphylla*, *Elaeocarpus chinensis*, *Machilus grijsii* with Fisold, and *M. grijsii* with Ampcan (Figure 3f as an example).

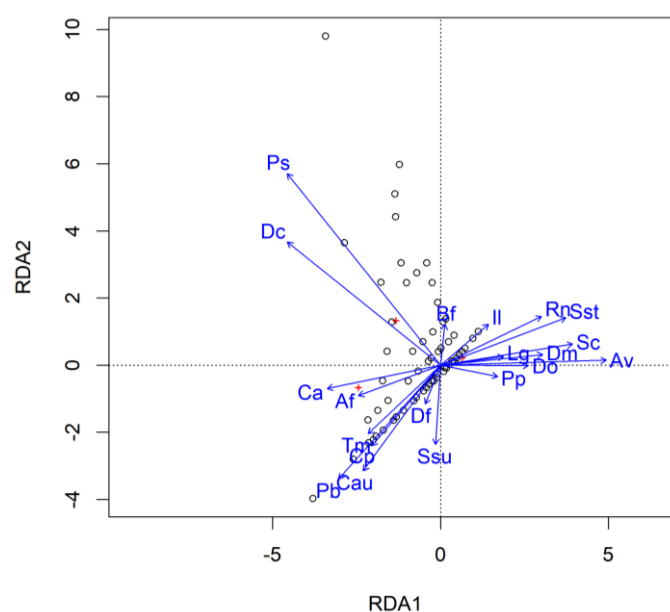
Most tree species (74/82) showed positive associations with at least one liana species. Among them, 64.9% (48) were positively associated with  $\geq 2$  liana species and 22 with all three liana species (Figure 4a). These 22 species made up 41.5% of the attractors of Caldie and Fisold, and 57.9% of those of Ampcan.



**Figure 4.** Venn diagram for the number of tree species associated with three liana species in a subtropical forest. Panel (a) shows the number for positive associations and panel (b) for negative associations.

Only 37 tree species showed negative associations with liana species and 22 of them were negatively associated with only one species (Figure 4b). Compared with attractors, liana species tended to have different sets of tree detractors. An exception was that the majority (63.2%) of detractors of Ampcan were also detractors of Fisold, and vice versa (54.4%). Caldie shared only two detractors with Ampcan and three detractors with Fisold.

The final model of the RDA analysis retained only 20 tree species (Figure 5), explaining 21.8% of the total variance (total Inertia = 5.989, constrained Inertia = 1.302) in distributions of the three liana species. RDA axes 1 and 2 contributed to 68.3% and 19.1% of the variance explained by the model, respectively. RDA axis 3 explained the remaining 12.5%. The permutation test showed that the model was significant ( $p < 0.001$ ).



**Figure 5.** Redundancy analysis for the distribution of three liana species with respect to 20 tree species in a 20 ha subtropical forest dynamic plot in Chebaling (CBL), China. Tree species (explanatory variable), liana species, and sites are indicated by arrows, red crosses, and open circles, respectively. RDA axis 1 and 2 contributed to 68.3% and 19.1% of the variance explained by the model, respectively. Tree species: Ps: *Phoebe sheareri*; Dc: *Daphniphyllum calycinum*; Pb: *Phoebe bournei*; Ca: *Choerospondias axillaris*; Sc: *Schoepfia chinensis*; Tm: *Tarenna mollissima*; Lg: *Lithocarpus glaber*; Rn: *Rapanea neriifolia*; Do: *Daphniphyllum oldhamii*; Sst: *Symplocos stellaris*; Cp: *Cinnamomum parthenoxylon*; Av: *Antidesma venosum*; Pp: *Photinia prunifolia*; Il: *Ilex lohfauiensis*; Ssu: *Styrax suberifolius*; Dm: *Diospyros morrisiana*; Bf: *Beilschmiedia fordii*; Cau: *Cinnamomum austrosinense*; Df: *Diplospora fruticosa*; Af: *Alniphyllum fortunei*.

#### 4. Discussion

Our study is one of the first studies that examined liana diversity and distribution based on large-scale permanent forest dynamic plots in subtropical China. Liana density and diversity in this plot were substantially lower than those reported in tropical areas, such as Brazil, Malaysia, and Ecuador [14,32–34]. Though liana density and diversity varied greatly in tropical forests (reviewed by Schnitzer and Bongers [8]), they were all much greater than those observed in the CBL plot, the subtropical forest plot we studied.

Differences in sampling protocol were the most important factor for such larger differences in liana density and diversity observed in CBL versus other forests [12,14,21,32,33]. Similar to de Oliveira et al. [14] and Kusumoto et al. (2008)'s studies [12], our study was conducted in a single 20 ha plot, whereas some liana surveys were conducted by sampling separated quadrats [14,21,32,33,35]. The latter approach could cover much larger environmental gradients and therefore recorded higher species diversity for a given area. Additionally, as lianas were the focus of these studies, sites with high density might have been chosen so as to better document the diversity or effects of lianas in these ar-

eas [14,21,32,33]. Large-scale sampling covered continuous large areas, such as 20 ha in our study and 16 ha in Kusumoto et al. (2008)'s study [12], and included many quadrats without lianas. If sampled over the top ten most abundant quadrats, the density was 360 ha<sup>-1</sup> in CBL, much higher than the density for the whole plot and much closer to the densities (about 1000 ha<sup>-1</sup>) for the Argentinian subtropical forest and other tropical forests [14,21,32,33]. As such, the difference in sampling methods was an important reason for the difference in recorded liana density and diversity between our and Kusumoto et al.'s studies (2008) [12] and others [14,21,32,33].

The difference in latitude or air temperature among these studies was another reason for the observed variation in liana density and diversity in our study and other subtropical forests. It is well known that liana diversity decreases with increasing latitude and increases with temperature at both local and global scales [3,6,36]. Variation in liana species richness was best explained by minimum temperature and frost events along a latitudinal gradient of temperate rainforest in South America [37]. Reduced liana density and diversity for colder zones may result mainly from embolisms in the wide vessel elements of lianas due to freezing [3,38,39]. Therefore, it is not surprising that tropical forests harbor much higher liana density and diversity than the CBL. Though Campanello et al. [21] and Kusumoto et al. (2008)'s [12] studies were also conducted in subtropical areas, the average temperatures for the coldest month for these two sites were about 18 °C, much higher than that of our study forest (10 °C) [12] (<https://www.worlddata.info/america/argentina/climate-misiones.php>, accessed on 20 April 2022; <https://www.osgeo.cn/post/f31b7>, accessed on 20 April 2022). Possibly owing to their warmer climate, liana diversity and density in these two forests were higher or similar to those of the studied forest plot, although our forest has a half-year annual dry season, which was thought to promote liana expansion [40].

Liana diversity and density decreased with increasing latitude and moisture supply in both tropical and temperate forests [3,8,41]. The mechanism driving these large-scale liana distributions might also operate at local scales. Accordingly, we expected lianas in this subtropical forest to exhibit preference for drier and hotter habitats. However, we found large variations among families in liana distribution with respect to topographic variables related to moisture supply and temperature. In our study, liana abundance increased with convexity for five of the seven families, consistent with the expectation of more lianas in drier habitats. However, the most abundant family, Annonaceae, exhibited the reversed trend, with more individuals in concave habitats than convex habitats. Similar to Annonaceae, total liana abundance was higher in concave sites than convex sites in a watershed in southwestern Japan [12]. In Central Brazil, liana density was remarkably higher in flooded forests which were also concave in topography [14]. Furthermore, decreasing liana abundances with sin(aspect) at the right half of the sin(aspect) axis were observed for all except one family (Annonaceae), in contradiction with the expectation that lianas prefer drier and hotter habitat conditions in this forest. Similarly, we expected quadrats at high elevations to be drier and have more lianas. However, five families of lianas showed convex while the remaining two groups (Vitaceae and Others) showed decreasing relationships with elevation, suggesting that most lianas were distributed in relatively low-to-medium elevations, which tend to have higher moisture supply. In general, our analysis of habitat preference revealed differentiated habitat conditions preferred by different liana families, consistent with previous fine-scale studies [34,42]. In a Bornean lowland tropical forest with alluvial, sandstone, and kerangas habitat types, 30 of 42 (71%) liana species showed significant habitat association with at least one habitat type, and liana species composition differed greatly among the three habitat types [34]. In the northern part of Okinawa Island, southern Japan, liana distributions in relation to topography also varied among species [42]. Taken together, at fine scales, topographic preference of lianas varied with liana taxonomic identity and habitat heterogeneity may help maintain liana diversity in local forest communities. What needs to be kept in mind when interpreting this result is that these topographic variables are not direct measures of temperature and

moisture content or humidity, though topographic variables are among the most important factors influencing water availability [43,44] and solar radiation [45] at fine scales.

Previous studies suggested that the lianas and trees do not establish species-specific interactions [46–48]. Consistent with this, our study found that 22 tree species in this forest associated positively with all three most abundant liana species studied and made up large proportions of tree species positively associated with them. Though liana–tree associations were not species-specific, some tree species were more likely to be hosts of lianas [11]. For example, white oak in northern temperate forests in the USA [18], *Liquidambar styraciflua* (sweet gum) in floodplain forests in the southeastern United States [19,20], and *Allophylus edulis* and *Cordia ecalyculata* in a subtropical Atlantic forest [21]. Our point pattern analysis also found that tree species differed in the number of liana species positively associated with them. Furthermore, the liana species that affiliated to a tree species were not random, either. For example, *Acer rubrum* was more likely than other trees to have *Vitis aestivalis* (summer grape) present, and both *Pinus banksiana* and *Quercus velutina* (black oak) were more likely to have *V. riparia* (riverbank grape) present [18]. Our study also found that 1, 9, and 16 tree species showed positive associations only with Ampcan, Fisold, and Caldie, respectively. On the other hand, some trees, such as *Acer saccharum*, were less likely than expected to host a liana [18]. In our study, tree species tended to negatively associate with different liana species. Particularly, there was only one tree species negatively associated with all three liana species. Former studies found that trees with smooth bark, long leaves, low wood density, high trunk/branch flexibility, high level of self-pruning, and tall, branch-free bole-height were more able to resist liana colonization or to shed lianas, resulting in lower liana colonization [16,17,49–51]. Therefore, there might be a functional basis underlying the liana–tree associations. Whatever the mechanisms are, distribution of trees explained only 21.8% of variance in liana distribution in the RDA analysis, indicating relatively weak liana–tree associations in this subtropical forest. Our analysis provided preliminary knowledge on possible liana preference of tree species. Direct surveys of liana colonization are needed for those tree species showing significant associations with liana species to test whether they are more/less likely to be infested by lianas. An analysis based on direct surveys and related traits of trees and lianas is essential to reveal the mechanisms for liana–tree interactions [11].

## 5. Conclusions

Liana habitat preference varies with their taxonomic identity at local scales, and there were significant spatial association between liana species and tree species. Liana species tend to have similar tree attractors but different tree detractors. Our study indicates that both fine-scale habitat conditions and tree species composition intervene in determining the diversity and distribution of lianas in subtropical forests. Habitat heterogeneity in terms of both topography and tree species may contribute to liana diversity maintenance. This study provides a primary understanding of liana diversity and distribution in subtropical forests and contributes to future planning on liana studies and diversity conservation in subtropical forests in scenarios of liana proliferation under climate change.

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