

# How the diversity, abundance, size and climbing mechanisms of woody lianas are related to biotic and abiotic factors in a subtropical secondary forest, Taiwan

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**Abstract** Lianas are woody vines that play an important role in forest dynamics in tropical and subtropical areas. Their relationship to various biotic and abiotic conditions is, however, not yet wholly clear. We explored how the size, climbing mechanisms, diversity and abundance of woody lianas is related to host plant size, environmental factors and topography. Liana assemblages were examined in twenty 20 × 20 m plots in each of three topographic sites (valley, slope and ridge) in a subtropical secondary forest in southeastern Taiwan. The valley site had the highest abundance and species richness of lianas. The abiotic factors, soil pH and rock cover, were related to different topographic sites. Larger lianas were always found on larger host trees, while smaller lianas were found in smaller trees; no lianas with a DBH greater than 10 cm were found. Significantly more adhesive lianas were found on larger trees whereas twining and leaning-hook lianas were found in smaller trees. In conclusion, this study demonstrates that the species of liana is associated with the size and type of tree growing under different topographic conditions.

**Keywords** Climbing · Host tree · Liana · Rarefaction · Species richness · Topography

## Introduction

Woody lianas constitute an important part of tropical and subtropical forests (Schnitzer and Bongers 2002) and represent special evolutionary adaptations driven by competition for light (Tang et al. 2012). Their thin stems relying on the support of trees, wide vessels, poor secondary thickening, special adaptations for climbing, deep roots and high leaf area (Putz 1983) distinguish woody lianas from trees. They influence forest gap dynamics, increase the forest turnover rate and reduce forest recruitment, growth rate and biomass (Hegarty and Caballé 1991; Schnitzer and Bongers 2002, 2011). Most tropical and subtropical lowland and montane forests harbour several liana species; their distribution and performance is, however, affected by different biotic and abiotic factors.

Several environmental factors are correlated with abundance and distribution patterns of lianas across abiotic gradients. For example, the abundance and diversity of lianas decreases with decreasing rainfall and temperature (Parthasarathy et al. 2004; Schnitzer 2005). Various soil properties (such as soil type, soil pH, fertility and phosphorus concentration) might also affect the species richness of lianas (Nurfazliza et al. 2012). Topographic position and natural disturbances that produce tree-fall gaps might affect the diversity and regeneration of lianas (Letcher and Chazdon 2009).

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The distribution of lianas might also be influenced by a range of biotic factors, such as invading species decrease the abundance of lianas (Addo-Fordjour et al. 2009); larger host trees support a larger diversity of liana species and increase the basal areas of lianas (Homeier et al. 2010). Host tree availability is one of the factors which limit liana growth and is related to the attachment mechanisms of lianas (Putz 1984; Isnard and Silk 2009). Lastly, human disturbance may increase the cover of lianas of the host tree canopy and wind dispersal of seeds (Schnitzer and Bongers 2011).

Much of the information about the relationship between lianas, topography and soil conditions and liana-tree interactions described above has been collected in tropical forests. However, information about the relationship of lianas to different habitats and host trees in subtropical forests remains limited, especially in Taiwan. In particular, studies assessing the relationship between liana size and climbing mechanisms and the diameter and height of host trees or whether topography affects the distribution and abundance of lianas in southeastern Taiwan are still few and unclear.

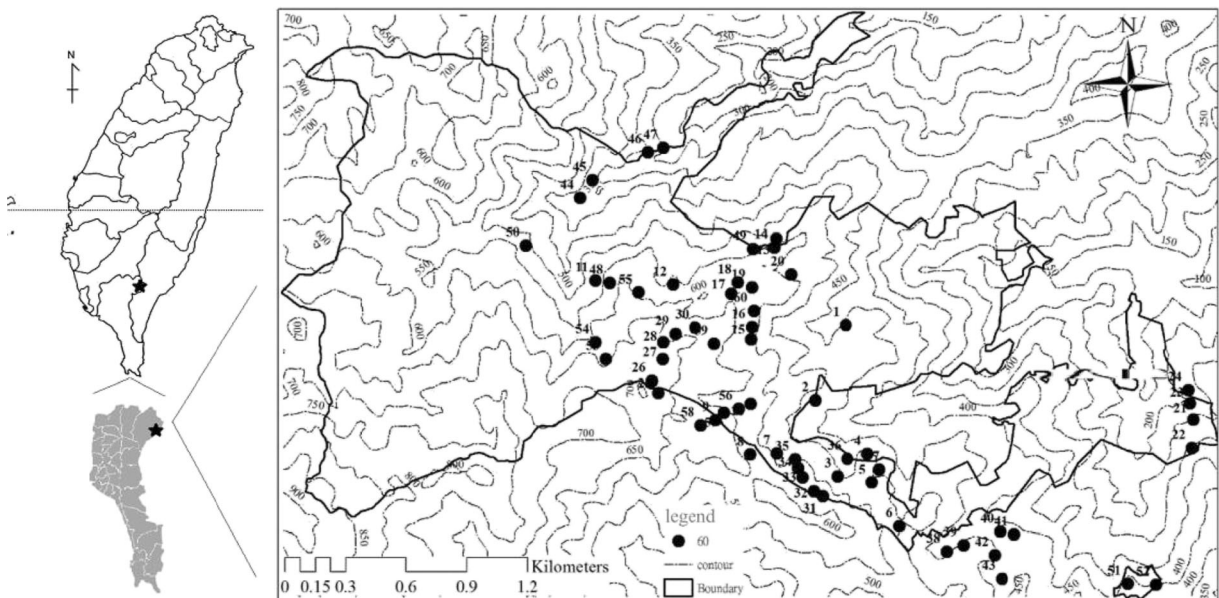
Our objective was to determine how diversity, abundance, size and climbing mechanisms of woody lianas in a subtropical forest are related to biotic and abiotic factors. The following questions were investigated: (1) What is the diversity and abundance of lianas in the area under study? (2) How are the diversity, abundance and size of lianas affected by topography and other abiotic

factors? (3) How are the size and climbing mechanisms of lianas related to the size of host trees? We conducted our study in a secondary subtropical forest in southeastern Taiwan which hosts 35% of 133 liana species documented in Taiwan to date (Yang et al. 2015).

## Material and methods

### Study area

The study area was located in the Tajen Experimental Forest Station (22°15' N, 120°49' E) at the boundary between the Pingtung and Taitung counties of Taiwan. The study area covered an area of 576 ha, with elevations ranging from 180 to 900 m a.s.l. (Fig. 1). This area lies within the southeastern climate region and has an annual rainfall of ca 3,500 mm, a mean annual temperature of around 20°C and no significant dry season. Due to the south-west monsoon in the summer and the north-east monsoon in the winter, precipitation occurs throughout the year. The dominant native tree species include: *Alniphyllum pterospermum*, *Beilschmiedia tsangii*, *Castanopsis cuspidata* var. *carlesii*, *Cyclobalanopsis championii*, *Machilus japonica* var. *kusanoi* and *Schima superba* var. *kankaoensis* (Yang et al. 2015). This area was clear-cut by intense logging activities in the early 1970s and was reforested between 1975 and 1981. The tree species that were planted



**Fig. 1** Map of southern Taitung County showing the location of 60 liana plots at the Tajen Experimental Forest Station, Taiwan

**Table 1** Only top ten species of tree and liana are shown about their frequency, average diameter at breast height (DBH), basal areas and largest DBH

| Species   | Family          | Frequency [%] | Average DBH [cm] | Basal area [m <sup>2</sup> ·ha <sup>-1</sup> ] | Largest DBH [cm] |
|---|-----------------|---------------|------------------|--|------------------|
| <b>Trees</b>  |                 |               |                  |  |                  |
| <i>Castanopsis cuspidata</i> var. <i>carlesii</i>     | Fagaceae        | 9.5           | —                | 3.21   | —                |
| <i>Schefflera octophylla</i>                          | Araliaceae      | 8.6           | —                | 2.99   | 51               |
| <i>Schima superba</i> var. <i>kankaoensis</i>         | Theaceae        | 4.1           | —                | 1.33   | —                |
| <i>Adinandra formosana</i>                            | Theaceae        | 4.1           | —                | —  | —                |
| <i>Cyclobalanopsis longinux</i>                       | Fagaceae        | 3.4           | —                | —  | —                |
| <i>Albizia falcata</i>                                | Fabaceae        | —             | 35.8             | —  | 53               |
| <i>Alniphyllum pterospermum</i>                       | Styracaceae     | —             | 27.9             | —  | —                |
| <i>Sapium discolor</i>                                | Euphorbiaceae   | —             | 27.7             | —  | —                |
| <i>Castanopsis fabri</i>                              | Fagaceae        | —             | 27.1             | 1.89   | 94               |
| <i>Machilus zuihoensis</i>                            | Lauraceae       | —             | 24.4             | —  | —                |
| <i>Aleurites montana</i>                              | Euphorbiaceae   | —             | —                | 1.44   | —                |
| <i>Lagerstroemia subcostata</i>                       | Lythraceae      | —             | —                | —  | 70               |
| <i>Bischofia javanica</i>                             | Euphorbiaceae   | —             | —                | —  | 64               |
| <b>Lianas</b>   |                 |               |                  |  |                  |
| <i>Mussaenda pubescens</i>                            | Rubiaceae       | 10.3          | —                | 0.018  | —                |
| <i>Stauntonia obovatifoliola</i>                      | Lardizabalaceae | 7.5           | —                | —  | —                |
| <i>Calamus formosanus</i>                             | Arecaceae       | 6.5           | 2.6              | 0.043  | —                |
| <i>Erycibe henryi</i>                                 | Convolvulaceae  | 5.8           | —                | 0.018  | —                |
| <i>Zanthoxylum nitidum</i>                            | Rutaceae        | 4.8           | —                | —  | —                |
| <i>Hiptage benghalensis</i>                           | Malpighiaceae   | —             | 3.0              | —  | —                |
| <i>Morinda umbellata</i>                              | Rubiaceae       | —             | 2.7              | 0.040  | 8.0              |
| <i>Ampelopsis brevipedunculata</i> var. <i>hancei</i> | Vitaceae        | —             | 2.6              | —  | —                |
| <i>Erycibe henryi</i>                                 | Convolvulaceae  | —             | 2.2              | 0.031  | —                |
| <i>Kadsura japonica</i>                               | Schisandraceae  | —             | —                | —  | 9.1              |
| <i>Tetrastigma formosanum</i>                         | Vitaceae        | —             | —                | —  | 8.8              |
| <i>Tetrastigma umbellatum</i>                         | Vitaceae        | —             | —                | —  | 8.8              |
| <i>Fissistigma glaucescens</i>                        | Annonaceae      | —             | —                | —  | 8.0              |

included: *Albizia falcata*, *Aleurites montana*, *Alnus formosana*, *Fraxinus griffithii* and *Liquidambar formosana*. However, few of these species remain today. After 35 years regrowth by 2016, this area had become a secondary forest that had self-regenerated with regional native species.

#### Field investigations

Few studies have assessed which biotic and abiotic factors affect the diversity and distribution of lianas in southeastern Taiwan. We examined the distribution of lianas in three sites with different topography (ridge,

**Table 2** Species richness, abundance, basal area and average diameter at breast height (DBH) of lianas in valley, slope and ridge habitats

| Habitats | Species richness | Abundance [individuals/0.8 ha] | Basal area [cm <sup>2</sup> /0.8 ha] | Average DBH [cm] |
|----------|------------------|--------------------------------|--------------------------------------|------------------|
| Valley   | 42               | 728.0                          | 1,878.89                             | 1.53             |
| Slope    | 39               | 359.0                          | 2,068.98                             | 1.63             |
| Ridge    | 29               | 529.0                          | 1,206.34                             | 1.32             |

**Table 3** Density [individuals/0.04 ha] and important index values (IVI) of liana species (DBH  $\geq$  0.5 cm) distributed in valley, slope and ridge habitats

| Scientific name                                     | Valley  |      | Slope   |      | Ridge   |      |
|---|---------|------|---------|------|---------|------|
|   | Density | IVI  | Density | IVI  | Density | IVI  |
| <i>Mussaenda pubescens</i>                          | 70      | 27.7 | 112     | 37.5 | 73      | 41.6 |
| <i>Stauntonia obovatifoliola</i>                    | 53      | 24.9 | 69      | 22.4 | 41      | 26.7 |
| <i>Erycibe henryi</i>                               | 34      | 19.7 | 39      | 19.0 | 29      | 31.7 |
| <i>Morinda umbellata</i>                            | 31      | 19.5 | 47      | 24.3 | 25      | 36.1 |
| <i>Derris laxiflora</i>                             | 12      | 15.5 | 2       | 0.9  | 7       | 8.4  |
| <i>Fissistigma glaucescens</i>                      | 23      | 13.3 | 57      | 24.4 | 20      | 21.9 |
| <i>Hiptage benghalensis</i>                         | 13      | 12.3 | 1       | 0.9  | 9       | 8.4  |
| <i>Cayratia corniculata</i>                         | 25      | 11.9 | 17      | 6.6  |         |      |
| <i>Zanthoxylum nitidum</i>                          | 21      | 11.4 | 43      | 21.2 | 17      | 15.9 |
| <i>Tetrastigma formosanum</i>                       | 23      | 11.1 | 33      | 12.3 | 2       | 1.6  |
| <i>Ampelopsis brevipedunculata</i>                  | 15      | 10.5 | 2       | 1.4  |         |      |
| <i>Kadsura japonica</i>                             | 18      | 10.2 | 19      | 10.3 | 3       | 3.3  |
| <i>Ventilago elegans</i>                            | 13      | 8.2  | 2       | 1.4  | 1       | 1.0  |
| <i>Anodendron affine</i>                            | 14      | 8.1  | 27      | 12.7 | 28      | 25.1 |
| <i>Actinidia callosa</i>                            | 7       | 7.4  | 23      | 13.6 | 3       | 3.7  |
| <i>Piper taiwanense</i>                             | 13      | 7.1  | 8       | 3.6  | 9       | 7.3  |
| <i>Anodendron benthamiana</i>                       | 12      | 7.1  | 15      | 7.6  | 6       | 6.0  |
| <i>Rubus pyrifolius</i>                             | 14      | 6.7  | 14      | 7.0  |         |      |
| <i>Psychotria serpens</i>                           | 14      | 5.6  | 41      | 12.6 | 46      | 27.1 |
| <i>Pileostegia viburnoides</i>                      | 8       | 5.3  | 12      | 4.6  | 1       | 1.1  |
| <i>Trachelospermum gracilipes</i>                   | 12      | 5.3  | 38      | 10.9 | 11      | 7.6  |
| <i>Pueraria montana</i>                             | 11      | 5.0  | 3       | 2.0  | 1       | 1.2  |
| <i>Celastrus kusanoi</i>                            | 6       | 4.8  | 1       | 0.6  | 1       | 1.2  |
| <i>Bauhinia championii</i>                          | 5       | 4.5  |         |      |         |      |
| <i>Melodinus angustifolius</i>                      | 7       | 4.3  |         |      |         |      |
| <i>Eleutherococcus trifoliatus</i>                  | 9       | 4.2  |         |      |         |      |
| <i>Zanthoxylum scandens</i>                         | 5       | 3.7  | 4       | 2.7  |         |      |
| <i>Ecdysanthera rosea</i>                           | 4       | 3.6  |         |      |         |      |
| <i>Ficus aurantiaca</i> var. <i>parvifolia</i>      | 7       | 3.3  | 12      | 5.7  | 1       | 1.0  |
| <i>Cayratia japonica</i>                            | 5       | 3.0  |         |      |         |      |
| <i>Mikania micrantha</i>                            | 5       | 2.9  | 3       | 1.0  | 2       | 1.6  |
| <i>Marsdenia tinctoria</i>                          | 4       | 2.8  | 1       | 0.6  |         |      |
| <i>Clematis uncinata</i>                            | 2       | 1.4  |         |      |         |      |
| <i>Polygonum multiflorum</i> var. <i>hypoleucum</i> | 4       | 1.3  |         |      |         |      |
| <i>Ipomoea cairica</i>                              | 2       | 1.3  |         |      |         |      |
| <i>Gymnema sylvestre</i>                            | 1       | 0.9  |         |      |         |      |
| <i>Coptosapelta diffusa</i>                         | 2       | 0.9  | 3       | 1.8  | 2       | 2.0  |
| <i>Stauntonia obovata</i>                           | 1       | 0.7  | 20      | 6.5  | 8       | 5.7  |
| <i>Paracyclea ochiaiana</i>                         | 1       | 0.7  |         |      |         |      |
| <i>Uncaria lanosa</i> var. <i>appendiculata</i>     | 1       | 0.7  |         |      |         |      |
| <i>Vernonia gratioisa</i>                           | 1       | 0.7  |         |      |         |      |
| <i>Strychnos cathayensis</i>                        | 1       | 0.7  | 8       | 3.7  | 3       | 3.6  |

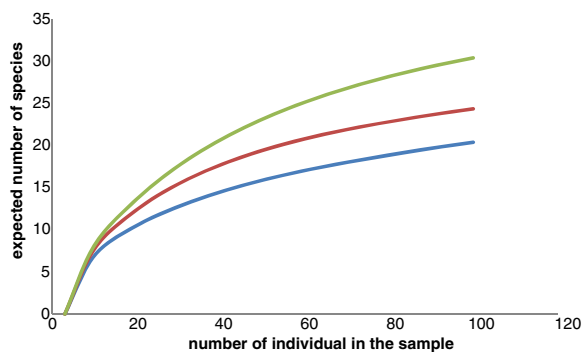
**Table 3** (continued)

| Scientific name                                     | Valley  |     | Slope   |     | Ridge   |     |
|---|---------|-----|---------|-----|---------|-----|
|   | Density | IVI | Density | IVI | Density | IVI |
| <i>Mucuna macrocarpa</i>                            |         |     | 27      | 8.8 | 1       | 1.1 |
| <i>Aeschynanthus acuminatus</i>                     |         |     | 16      | 5.9 | 4       | 2.8 |
| <i>Elaeagnus glabra</i>                             |         |     | 3       | 2.2 | 3       | 3.4 |
| <i>Aristolochia cucurbitifolia</i>                  |         |     | 1       | 0.7 |         |     |
| <i>Capparis sikkimensis</i> subsp. <i>formosana</i> |         |     | 1       | 0.6 |         |     |
| <i>Ecdysanthera utilis</i>                          |         |     | 1       | 0.6 |         |     |
| <i>Ficus sarmentosa</i> var. <i>nipponica</i>       |         |     | 1       | 0.6 | 2       | 2.0 |
| <i>Passiflora suberosa</i>                          |         |     | 1       | 0.6 |         |     |
| <i>Clematis akoensis</i>                            |         |     | 1       | 0.6 |         |     |
| Total individuals                                   | 728     |     | 359     |     | 529     |     |
| Species numbers                                     | 42      |     | 39      |     | 29      |     |

slope and valley) to elucidate the relationships between lianas and host trees under different conditions. The ridge and valley sites were located in a secondary forest where lianas are abundant. They were selected using a contour map based on their elevational ranges and were located using the Global Positioning System. A slope of the same aspect was chosen because it was located between the ridge and the valley. Areas from different topographic categories, but with similar elevations, were selected to increase sampling homogeneity. Within each topography type, 20 plots of vegetation were surveyed, each covering a standard area of 400 m<sup>2</sup> (20 m × 20 m). The plots were separated by a minimum distance of approximately 200 m. Within each plot, a 100 m<sup>2</sup> (10 m × 10 m) sub-plot was surveyed to reveal interspecific associations between host tree species

and liana species and were evaluated for pairs of trees and lianas. A total of 60 plots (2.4 ha) were sampled from August 2013 to March 2014.

In each plot, eight abiotic variables were measured during the study period, namely altitude, stoniness percentage, outcropping rock cover percentage, soil pH, soil water percentage, available soil phosphorus, slope and aspect. In each plot, a topsoil sample (0–20 cm) was collected from each corner and from the center of the plot. These five samples were combined and used to analyse available phosphorus (P), moisture and pH (Malizia et al. 2009). Soil analyses were carried out at the Soil Laboratory, Department of Environmental Science and Engineering, National Pingtung University of



**Fig. 2** Rarefaction curves for the diversity of lianas in three different habitats. There were 728 individuals of 42 species in the valley, 359 individuals of 39 species on the slope and 529 individuals of 29 species on the ridge

**Table 4** Significant abiotic factors determined by forward selection in a Monte Carlo permutation test

| Environmental factors           | $\lambda_A$ | $P$     | $F$  |
|---------------------------------|-------------|---------|------|
| Soil pH                         | 0.30        | 0.002** | 4.93 |
| Elevation                       | 0.12        | 0.002** | 2.05 |
| Aspect                          | 0.10        | 0.008** | 1.67 |
| Rock cover ratio                | 0.09        | 0.036*  | 1.55 |
| Available soil phosphorus [ppm] | 0.06        | 0.224   | 1.20 |
| Slope                           | 0.07        | 0.142   | 1.22 |
| Soil water percentage [%]       | 0.04        | 0.888   | 0.72 |

Note: \*\* $P < 0.005$ ; \*  $P < 0.05$ .  $\lambda_A$  – increase in eigenvalue. Conditional effects of the Monte Carlo permutation test were performed and each environmental variable as an additional environmental variables

**Table 5** Variation decomposition of the effect of three groups of explanatory variables with adjusted covariates

| Components | Source                    | Explained variation | % of all | D.f. | Mean square |
|------------|---------------------------|---------------------|----------|------|-------------|
| a          | Unique topographical site | 0.042               | 1.1      | 1    | 0.094       |
| b          | Unique abiotic factors    | 0.451               | 11.9     | 4    | 0.163       |
| c          | Unique host stem DBH      | 0.019               | 0.5      | 1    | 0.072       |
| d          | Shared                    | 0.063               | 1.6      |      |             |
| e          | Residual                  | 3.230               | 84.9     |      |             |
| Total      |                           | 3.805               | 100.0    |      |             |

Science and Technology, Taiwan. Available P was determined by spectrophotometry after Bray P1 extractions for acidic soils (Bray and Kurtz 1945). Soil moisture (%) was determined by oven-drying fresh soil samples (50 g) at 105°C, until a constant weight was obtained and then comparing wet and dry weights. Soil pH was measured by using a pH meter with a glass electrode (Jenway 3305; Jenway, UK) in a 1:2 soil:water ratio. Altitude and slope were measured in each plot using a GPS device (Garmin Oregon 550t; Garmin, Lenexa, KS, USA) and a clinometer (Suunto SPUME-5/360PC; Suunto, Finland), respectively. Aspect was measured using an azimuth unit and a compass, and the azimuth was converted into an aspect-moisture gradient index (Day and Monk 1974). The percentage of stoniness and rock cover in each plot was recorded, along with the percentage of stones with a diameter of less than 30 cm and larger than 30 cm, respectively.

Lianas included all woody vines. Vertical vegetation structures were the tree layer (height > 6 m), shrub layer

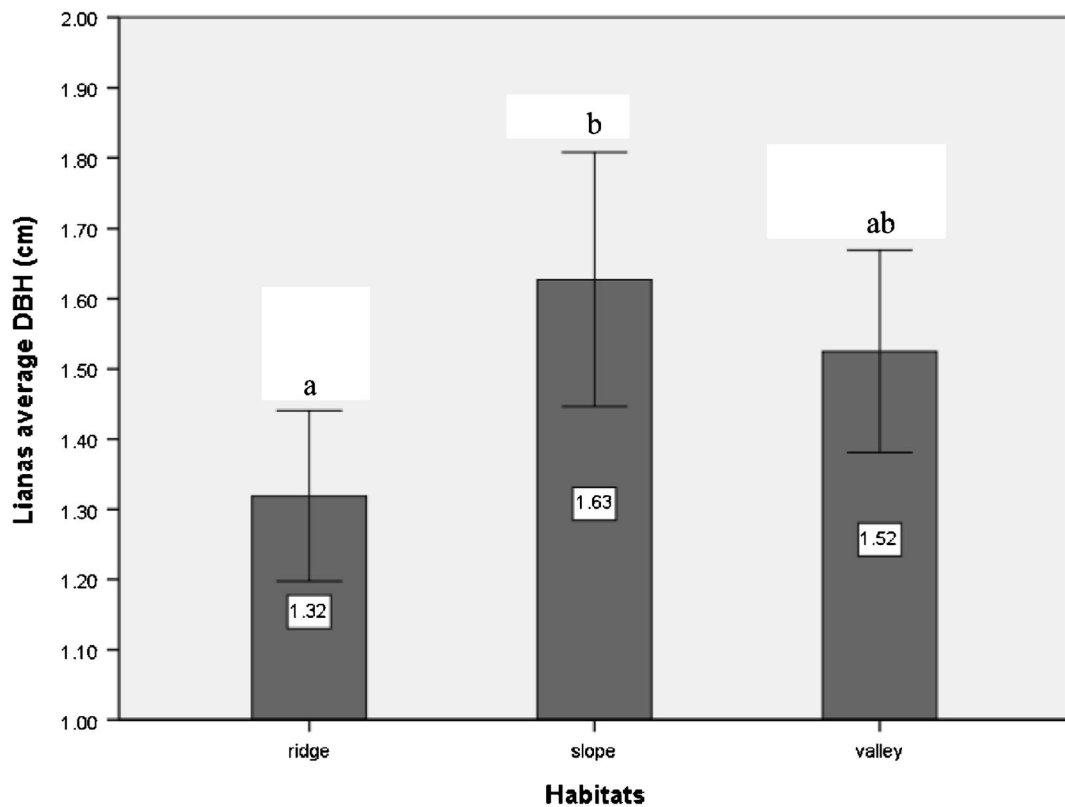
(height 0.5–6 m) and herb layer (height < 0.5 m). Species richness, the coverage of each species and the layer to which each species belonged were recorded for each plot. Relative species cover was estimated using the Braun-Blanquet abundance-coverage scale (modified from van der Maarel 1979). Species richness, abundance, average DBH and basal area of lianas were measured in each plot. The species richness value and Shannon-Weaver index (Magurran 1988) were measured to determine the diversity of lianas at the plot level. The important value index (IVI) of each liana species was measured at the topographic site level. In each sub-plot, all living trees and shrubs > 5 cm in DBH, all living lianas > 0.5 cm diameter (1.3 m from the ground surface; hereafter DBH), the DBH of host trees on which lianas grew, and the liana climbing types were also recorded. The diameter of lianas was divided into three classes (n1: 0.5–3.0 cm; n2: 3.1–6 cm; n3: 6.1–10 cm). The census of all living lianas followed the protocol of Schnitzer et al. (2006). The climbing mechanisms of lianas (adhesive, hook, or twining) followed Isnard and

**Table 6** Comparison among abiotic factors and biotic factors relative to lianas in valley, slope and ridge habitats

| Abiotic and biotic variables        | Habitats                  |                             |                            |
|-------------------------------------|---------------------------|-----------------------------|----------------------------|
|                                     | Valley                    | Slope                       | Ridge                      |
| Soil pH                             | 4.92 <sup>b</sup> ± 0.8   | 4.42 <sup>a</sup> ± 0.4     | 4.21 <sup>a</sup> ± 0.1    |
| Alt                                 | 496.6 <sup>a</sup> ± 99.0 | 518.85 <sup>a</sup> ± 122.1 | 621.55 <sup>b</sup> ± 52.3 |
| Rock cove ratio [%]                 | 11.8 <sup>b</sup> ± 14.9  | 7.9 <sup>ab</sup> ± 9.6     | 1.70 <sup>a</sup> ± 2.3    |
| Aspect                              | 5.7 <sup>a</sup> ± 1.6    | 5.8 <sup>a</sup> ± 2.0      | 6.5 <sup>a</sup> ± 2.0     |
| Species richness*                   | 11.15 <sup>b</sup> ± 0.65 | 11.70 <sup>b</sup> ± 0.54   | 7.25 <sup>a</sup> ± 0.44   |
| Abundance*                          | 26.45 <sup>b</sup> ± 1.64 | 36.40 <sup>c</sup> ± 2.36   | 17.95 <sup>a</sup> ± 1.25  |
| Basal area*                         | 33.45 <sup>b</sup> ± 2.78 | 42.28 <sup>b</sup> ± 3.06   | 20.76 <sup>a</sup> ± 2.23  |
| Shannon-Weaver index ( <i>H'</i> )* | 0.93 <sup>b</sup> ± 0.02  | 0.94 <sup>b</sup> ± 0.02    | 0.75 <sup>a</sup> ± 0.04   |

Note: Mean values (± SD) with different superscripts within a row are significantly different (\*:  $P < 0.05$ , \*\*:  $P < 0.01$ ) according to Tukey's HSD test





**Fig. 3** Average diameter at breast height (DBH) of lianas in three different habitats. Means without the same letter above the bars are significantly different at the 5% level according to Tukey's HSD test

Silk (2009). For the top ten species, the frequency (%), average DBH (cm) and basal area ( $\text{m}^2/\text{ha}$ ) of lianas and trees were recorded in all three sites. The nomenclature of all vascular plants followed Boufford et al. (2003). Voucher specimens were deposited in the PPI Herbarium, Department of Forestry, National Pingtung University of Science and Technology, Taiwan.

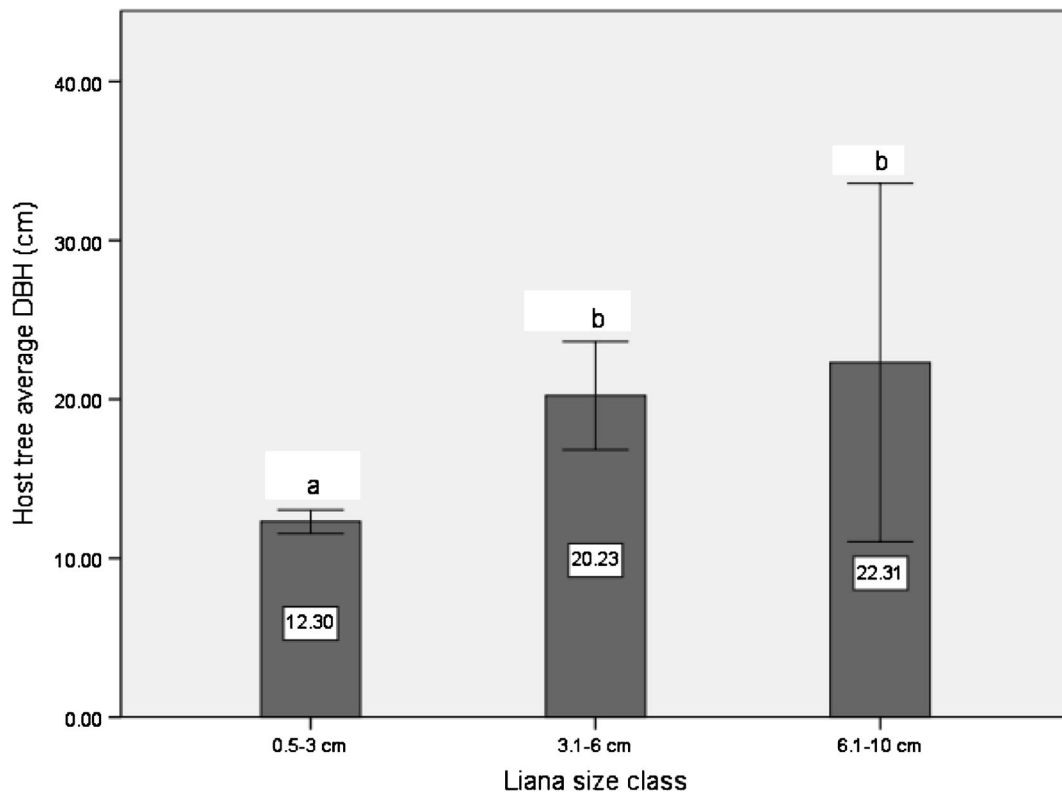
### Statistics

As species richness is highly correlated with abundance, we performed a rarefaction analysis (Magurran 1988) to rarefy to the lowest number of liana individuals among plots and, thus, correct for this bias. To reduce collinearity among environmental variables, canonical correspondence analysis (CCA) was used. In CCA, forward stepwise selection with a Monte Carlo permutation test (ter Braak and Šmilauer 2012) is able to determine which variables are actually independent of one another, so they may be incorporated into an analysis. To test the unique effects of abiotic factors, the liana community

compositions was used as the response, while three predictor groups (topographical site, abiotic predictors with a stepwise selection and host stem DBH) were used to perform variation partitioning analyses (ter Braak and Šmilauer 2012). Statistical tests were performed using SPSS (version 20.0; Norusis 2011). One-way ANOVA was used to analyse the results for the average DBH, climbing mechanisms and DBH class of lianas associated with topographic sites, along with host tree DBH and significant environmental factors. Between-group comparisons were performed using Tukey's HSD test to clarify significant differences between sites.

### Results

Altogether we recorded 84 liana species in our study. The families with the greatest number of liana species were Apocynaceae (5), Asclepiadaceae (5), Menispermaceae (5) and Rubiaceae (5), see Appendix 1. No lianas with a DBH greater than 10 cm were found in the study plots. The lianas with the largest DBH was



**Fig. 4** Host tree average DBH for three different liana sizes. Means without the same letter above bars are significantly different at the 5% level according to Tukey's HSD test

*Kadsura japonica* (Schisandraceae) – 9.1 cm. *Calamus formosanus* (Arecaceae), a rattan species, was one of the most important lianas, based on its high frequency, above-average DBH and high basal area (the highest in the study – Table 1). The species accumulations curves showed that both the richness and abundance of liana species varied significantly with topography (Table 2, 3). The highest abundance and richness of woody lianas were recorded in the valley site, followed by the slope and ridge sites (Fig. 2).

Four variables (soil pH, altitude, aspect and rock cover) were found to be truly independent (Table 4). The variation partitioning results for the three predictor groups in analysis showed that each group had a unique effect, with overlap occurring in their explanatory power. The effect of explained variation of the major abiotic factors (such as altitude, soil pH, rock cover and aspect) was more than the other covariates (such as topography and host stem DBH – Table 5) in liana diversity/abundance and assemblage composition. This test showed that soil pH and rock cover gradually decreased

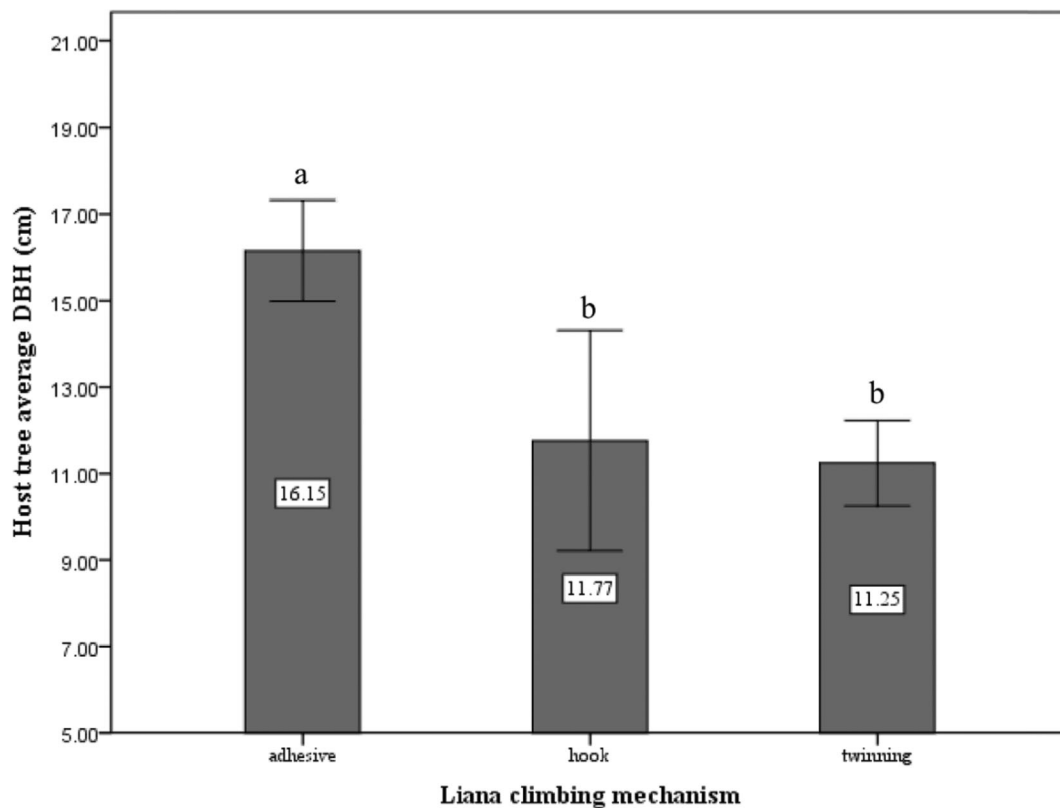
along the topographical gradient from the valley to the ridge, but increased with altitude (Table 6). The average DBH of lianas was lowest in the ridge site (ANOVA,  $F = 4.13$ ;  $P < 0.01$ ) and the largest in the slope site (Fig. 3). The differences recorded across the three sites might be related to these soil properties (Table 6).

The diameter of the liana classes significantly differed with the DBH of host trees (ANOVA,  $F = 17.19$ ;  $P < 0.01$ ), with larger trees supporting larger lianas (Fig. 4). The climbing mechanisms of the lianas significantly varied with the DBH of host trees (ANOVA,  $F = 18.46$ ;  $P < 0.01$ ); for instance, adhering lianas were found in larger host trees whereas more twining and leaning lianas were found in smaller host trees (Fig. 5).

## Discussion

Different topographic sites varied in the abundance and species richness of lianas, the abiotic factors soil pH and





**Fig. 5** Host tree average DBH for three different liana climbing types. Means without the same letter above bars are significantly different at the 5% level according to Tukey's HSD test

rock cover were related to different topographic sites, and the diverse lianas with different climbing mechanisms were associated with the size and type of tree.

The family Apocynaceae was the most species-rich liana family detected in this study, supporting the findings of studies conducted in other tropical forests (Addo-Fordjour et al. 2009). The winged morphology of its seeds increases the chance of it spreading to more areas, which might confer a reproductive advantage over other species of lianas (Wright et al. 2007).

The average DBH of lianas was smallest at the ridge site, even though some individuals of lianas at the ridge site were larger than those at the slope site (Table 2). This finding was similar to the results of a previous study in a tropical forest in Ecuador (Homeier et al. 2010). This previous study showed that an increase in elevation was not directly associated with a reduction in liana dominance, because even though the mean liana DBH decreased, the number of individuals increased. The Tajen Experimental Forest Station area is close to the coast, with the ridge site being affected by strong

winds; thus, it is possible that many small lianas were found there, rather than a few large ones.

In the present investigation, soil pH and rock cover increased from the ridge to the valley site, but decreased with altitude. Thus, the percentage of soil pH and rock cover decreased as elevation increased. The rock cover at the valley site exceeded that at the ridge site, possibly due to rocks accumulating in the valley. The lowest species diversity and abundance of liana species were found at the ridge site (Fig. 2), suggesting that, along the topographic gradient, rock cover at the valley site might facilitate better soil drainage, which, when combined with the with lower soil pH, favoured liana diversity.

Liana species diversity gradually increases at lower elevations (below 1,000 m), is highest at intermediate elevations (1,000–2,000 m) and decreases rapidly as altitude increases (above 2,500–3,000 m), at least in Taiwan (Ho 1996). The elevations in our study area range from 180 to 900 m a.s.l., and the distribution of liana species was, indeed, related to altitude; however, the species richness of lianas decreased as altitude increased (Table 6).

The climbing mechanisms of lianas was related to the DBH of host trees. For instance, the growth of stem-twining lianas was limited by the DBH of host trees (Putz and Holbrook 1991; DeWalt et al. 2000). Our study also showed that adhering lianas climb large host trees more easily than stem-twining or leaning-hook lianas (Fig. 5). At our study location, the density of adhesive lianas exceeded that of any other climbing type. In particular, *Psychotria serpens* (Rubiaceae), *Piper taiwanense* (Piperaceae) and *Trachelospermum gracilipes* (Apocynaceae) were present in almost all plots (Table 2). The adhesive structure of lianas, including adventitious roots and disks, appeared to increase the probability of climbing success. Further sampling should be conducted to examine this phenomenon.

As lianas are not self-standing, their ability to climb trees to reach the canopy affects their growth and development and indirectly influences their DBH (Nabe-Neilsen 2004). The structural parasitism of host trees by lianas might be affected by other factors in addition to the DBH of host trees. As trees with a larger DBH have been growing for a longer time, there may have been more opportunities for lianas to climb them; however, the species diversity and abundance of lianas and interspecific interactions might be more important features than the DBH of host trees with regard to liana growth on trees. The characteristics of coarse or smooth bark and presence of buttress roots (Leicht-Young et al. 2010) in trees might also affect the climbing ability of lianas.

## Conclusions

Our results show that the distribution patterns of lianas and their species richness vary with topography and in relation to significant abiotic factors such as soil pH and rock cover. Overall, no lianas with a DBH greater than 10 cm were recorded in this study. The lianas with the largest DBH and the highest frequency were *Kadsura japonica* and *Mussaenda pubescens*, respectively. The average DBH of lianas was largest at the slope site, which was possibly related to the soil pH and rock cover. Larger lianas were found on larger host trees, while adhering lianas climbed significantly larger trees than lianas that used other climbing mechanisms. In conclusion, the climbing mechanisms of lianas might play an important role in the forest dynamics of tropical and subtropical areas.

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## Appendix 1 Lianas list in Tajen Experimental Forest Station, Taiwan

1. Actinidiaceae
  1. *Actinidia callosa* Lindl.
2. Annonaceae
  2. *Fissistigma glaucescens* (Hance) Merr.
3. Apocynaceae
  3. *Anodendron affine* (Hook. & Arn.) Druce
  4. *Anodendron benthamiana* Hemsl.
  5. *Ecdysanthera rosea* Hook. & Arn.
  6. *Melodinus angustifolius* Hayata
  7. *Trachelospermum gracilipes* Hook. f.
4. Araliaceae
  8. *Eleutherococcus trifolius* (L.) S.Y. Hu
5. Aristolochiaceae
  9. *Aristolochia cucurbitifolia* Hayata
  10. *Aristolochia foveolata* Merr.
6. Asclepiadaceae
  11. *Cryptolepis sinensis* (Lour.) Merr. Roem. & Schultes
  12. *Hoya carnosa* (L. f.) R. Br.
  13. *Marsdenia formosana* Masamune
  14. *Marsdenia tinctoria* R. Br.
  15. *Tylophora taiwanensis* Hatusima
7. Asteraceae
  16. *Mikania micrantha* Kunth
8. Capparidaceae
  17. *Capparis sikkimensis* Kurz subsp. *formosana* (Hemsl.) Jacobs
9. Celastraceae
  18. *Celastrus hindsii* Benth.
  19. *Celastrus kusanoi* Hayata
  20. *Celastrus punctatus* Thunb.
10. Convolvulaceae
  21. *Erycibe henryi* Prain
  22. *Ipomoea cairica* (L.) Sweet
11. Cucurbitaceae
  23. *Diplocyclos palmatus* (L.) C. Jeffrey
  24. *Trichosanthes cucumeroides* (Seringe) Maxim. ex Fr. & Sav.

25. *Trichosanthes homophylla* Hayata
  12. Elaeagnaceae
    26. *Elaeagnus glabra* Thunb.
  13. Fabaceae
    27. *Bauhinia championii* Benth.
    28. *Derris laxiflora* Benth.
    29. *Mucuna macrocarpa* Wall.
    30. *Pueraria montana* (Lour.) Merr.
  14. Gesneriaceae
    31. *Aeschynanthus acuminatus* Wall. ex A. DC.
  15. Lardizabalaceae
    32. *Stauntonia obovata* Hemsl.
    33. *Stauntonia obovatifoliola* Hayata
  16. Loganiaceae
    34. *Strychnos cathayensis* Merr.
  17. Malpighiaceae
    35. *Hiptage benghalensis* (L.) Kurz
  18. Menispermaceae
    36. *Cocculus orbiculatus* (L.) DC.
    37. *Cyclea gracillima* Diels
    38. *Pericampylus formosanus* Diels
    39. *Stephania japonica* (Thunb. ex Murray) Miers
    40. *Tinospora dentata* Diels
  19. Moraceae
    41. *Ficus aurantiaca* Griff. var. *parvifolia* (Corner) Corner
    42. *Ficus pumila* L.
    43. *Ficus sarmentosa* Buch.-Ham. ex J. E. Sm. var. *nipponica* (Fr. & Sav.) Corner
    44. *Maclura cochinchinensis* (Lour.) Corner
  20. Nyctaginaceae
    45. *Pisonia aculeata* L.
  21. Passifloraceae
    46. *Passiflora suberosa* L.
  22. Piperaceae
    47. *Piper kadsura* (Choisy) Ohwi
    48. *Piper sintonense* Hatusima
    49. *Piper taiwanense* Lin & Lu
  23. Polygonaceae
    50. *Polygonum multiflorum* Thunb. var. *hypoleucum* (Ohwi) Liu, Ying & Lai
  24. Ranunculaceae
    51. *Clematis akoensis* Hayata
    52. *Clematis chinensis* Osbeck
    53. *Clematis uncinata* Champ. ex Benth.
  25. Rhamnaceae
    54. *Ventilago elegans* Hemsl.
  26. Rosaceae
    55. *Rubus pyrifolius* J. E. Sm.
  27. Rubiaceae
    56. *Coptosapelta diffusa* (Champ. ex Benth.) Steen.
    57. *Morinda umbellata* L.
    58. *Mussaenda pubescens* Ait. f.
    59. *Paederia foetida* L.
    60. *Psychotria serpens* L.
  28. Rutaceae
    61. *Zanthoxylum nitidum* (Roxb.) DC.
    62. *Zanthoxylum scandens* Blume
  29. Sabiaceae
    63. *Sabia swinhoei* Hemsl.
  30. Saxifragaceae
    64. *Pileostegia viburnoides* Hook. f. & Thoms.
  31. Schisandraceae
    65. *Kadsura japonica* (L.) Dunal
  32. Vitaceae
    66. *Ampelopsis glandulosa* (Wall.) Mom. var. *hancei* (Planch.) Mom.
    67. *Cayratia japonica* (Thunb.) Gagnep.
    68. *Tetrastigma formosanum* (Hemsl.) Gagnep.
    69. *Tetrastigma umbellatum* (Hemsl.) Nakai
- Monocotyledon
1. Arecaceae
    70. *Calamus formosanus* Becc.
  2. Dioscoreaceae
    71. *Dioscorea benthamii* Prain & Burk.
    72. *Dioscorea japonica* Thunb.
    73. *Dioscorea matsudae* Hayata
  3. Flagellariaceae
    74. *Flagellaria indica* L.
  4. Pandanaceae
    75. *Freycinetia formosana* Hemsl.
  5. Poaceae
    76. *Schizostachyum diffusum* (Blanco) Merr.
  6. Smilacaceae
    77. *Heterosmilax indica* A. DC.
    78. *Smilax bracteata* Presl var. *verruculosa* (Merr.) T. Koyama
    79. *Smilax china* L.
    80. *Smilax corbularia* Kunth
    81. *Smilax lanceifolia* Roxb.
    82. *Smilax ocreata* A. DC.
    83. *Smilax riparia* A. DC.
  7. Stemonaceae
    84. *Stemona tuberosa* Lour.

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