Folia Geobot
https://doi.org/10.1007/s12224-018-9334-3

Determinants of *Piper* (Piperaceae) climber composition in a lowland tropical rainforest in New Guinea

**Aleš Lisner · Graham Kaina · Mentap Sisol ·
Pavel Fibich · Vojtěch Novotný · George D. Weiblen ·
Jan Lepš**

Received: 1 March 2018 / Revised: 5 November 2018 / Accepted: 30 November 2018

Abstract Climbing plants form a substantial component of tropical forest diversity. Climbers are a diverse group comprising various ecological strategies dependent on tree support and are affected by biotic and abiotic forest conditions. In a lowland primary tropical rainforest in Papua New Guinea, we studied the distribution of root climbers from genus *Piper* in relation to topography (slope, convexity, altitude) and properties of vegetation and of individual host trees (basal area of trees, and host tree size, abundance and species identity). In total, 1,058 *Piper* climber individuals belonging to 8 species occupied 13.7% of tree trunks with a diameter at breast height (DBH) > 1 cm. All *Piper* species generally avoided similar habitat conditions – higher altitude, steeper slopes, more closed canopy layer and bigger total basal area of host vegetation. The preferences of *Piper* climbers for some tree species are primarily determined by properties of host trees, mainly their DBH. Therefore, the probability of *Piper* presence on a tree increased with individual host tree DBH. *Piper* species were more frequently found on rare than common tree species. However, this relationship might be also explained by their affinity for higher tree DBH. Our findings point to non-random association between climbers and their host trees, in a complicated interplay with local environmental conditions. These interactions have very probably consequences for forest vegetation dynamics and maintenance of diversity.

Keywords Climber abundance · Host trees · Spatial distribution · Tropical forest · Vines

Introduction

Climbing plants (vines, lianas) play a significant role in the structure and functioning of forest ecosystems. They evolved numerous times and are generally more diverse than their non-climbing sister groups (Gianoli 2004). Although climbers contribute

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s12224-018-9334-3) contains supplementary material, which is available to authorized users.

A. Lisner (✉) · P. Fibich · V. Novotný · J. Lepš
Department of Botany, Faculty of Science, University of South Bohemia, CZ-370 05 Ceske Budejovice, Czech Republic
e-mail: aleslisner@seznam.cz

G. Kaina · M. Sisol
New Guinea Binatang Research Centre, PO Box 604, Madang, Papua New Guinea

V. Novotný · J. Lepš
Biology Centre of the Czech Academy of Sciences, Institute of Entomology, CZ-370 05 Ceske Budejovice, Czech Republic

G. D. Weiblen
Department of Plant Biology, University of Minnesota, 220 Biological Sciences Center, 1445 Gortner Avenue, St Paul, MN 55108-1095, USA

significantly to forest diversity, often exceeding 25% of the total diversity (Schnitzer and Carson 2001), their ecological importance has often been overlooked (Phillips et al. 2005) because they are rarely included in the protocols for plant plot surveys, including the CTFS network of the 50-ha forest dynamics plots (Anderson-Teixeira et al. 2015). Moreover, many studies have not been distinguishing between ecologically different groups of climbing plants (Balfour and Bond 1993; Malizia 2003; Burns and Dawson 2005; Nesheim and Økland 2007), which can consequently mitigate possible differences, or shift results to correspond only with a behaviour of the most abundant ecological group (Gianoli et al. 2010). Hence it is important to distinguish between different functional groups or focus study on a single functional group of climbers.

Climbing plants generally use host trees as a physical support, but the climbing strategy and suitable support differs substantially between climber functional groups. Four climbing strategies are usually distinguished. Tendril climbers use vegetative organs derived from leaves or stems and can climb only a slender support (Putz 1984b). Twiners require relatively high-energy investment into their growth given by the spiralling around host tree trunk. The maximum diameter which they can utilize is bigger than tendril climbers can (maximum around 10 cm) (Putz 1984b). Scramblers and hook climbers lean on support trees and use hooks and thorns to stay attached to a tree. Understorey root-climbers, our study group, use adventitious roots to attach a host trunk. They can ascend the whole range of supports because of no limitation by the diameter at breast height (DBH) of host trees as have other climber types (tendril climbers, twiners – Putz 1984b; Putz and Mooney 1991; Leicht-Young et al. 2010; Mori et al. 2016). However, they are restricted to a particular tree trunk because they lack grasping organs (Putz and Mooney 1991). Therefore, not taking into account other trunk characteristics, root-climbers should be able to grow on stems with a wide range of DBH values (Putz 1984b). However, there is strong evidence that root-climber prefer trees with wider trunks (Putz and Mooney 1991; Burns and Dawson 2005; Carrasco-Urra and Gianoli 2009; Leicht-Young et al. 2010; Jayakumar and Nair 2013). This pattern is counterintuitive if we take into account that root-climber abundance is positively associated with sapling availability (Balfour and Bond 1993; Jayakumar and Nair 2013), which can also play an important role in allowing climbers to reach the canopy (Putz 1984b; Garbin et al. 2012).

Distribution and abundance of climbers generally can be influenced by various abiotic factors. There is a general trend of increasing climber diversity with decreasing latitude, and this increase tends to be faster than in trees or herbs (Schnitzer and Bongers 2002). Climber diversity generally peaks in lowland tropics (Schnitzer and Bongers 2002) and declines with increasing altitude (Balfour and Bond 1993), although in some mountain ranges it may reach a maximum at higher altitudes (Muoghalu and Okeesan 2005). The density and basal area of root-climbers increase with increasing rainfall (Durigon et al. 2013), which is the opposite trend exhibited by canopy woody lianas (DeWalt et al. 2010; Schnitzer and Bongers 2011). In some cases, topography may also play an important role in their distribution (Yang et al. 2018). For example, Kusumoto et al. (2008) observed climbers on steep slopes and concave terrains more often than on flat or convex sites. Conversely, only a weak effect of topography on climber distribution was found by Ledo and Schnitzer (2014). Even though it seems that light conditions play a substantial role in promoting and maintaining diversity and high abundances of canopy climbers, especially in tree gaps (Putz 1984b; Schnitzer and Carson 2001; Schnitzer and Bongers 2002; Garbin et al. 2014), understorey climbers are mostly shade-tolerant species (Valladares et al. 2011) with higher abundances in closed primary forests (Yuan et al. 2009).

Host tree characteristics, such as bark roughness or DBH, tree abundance or generally tree identity, seems to play an important role in shaping the distribution and abundance of understorey climbers (Talley et al. 1996; Nesheim and Økland 2007; Leicht-Young et al. 2010; Mori et al. 2016). This pattern might be particularly strong in the relatively homogeneous environment of some lowland tropical rainforest. The relationship between climbers and their host trees is generally negative because climbers tend to decrease the growth and survival rate of host trees (Putz 1984b; Hegarty 1991; Schnitzer and Carson 2010) and consequently may affect the composition of host trees (Llorens and Leishman 2008). Trees have evolved various avoidance strategies to control the rate of climber infestation. These anti-climber adaptations include the height of the tree

(Muoghalu and Okeesan 2005; Sfair et al. 2016), bark roughness and the ability to exfoliate bark (Putz 1984b; Campanello et al. 2007; Sfair et al. 2016), fast trunk thickening (Putz 1984a), high growth rate (Campanello et al. 2007; Sfair et al. 2016) and spines or ant bodyguards (Putz and Mooney 1991).

In the present study, we examined climbing peppers (*Piper* spp.) in a lowland rainforest in Papua New Guinea. They represent a substantial part of understorey climbing species in the forest under study. *Piper* species are a pantropical group with peak diversity in South America (Jaramillo and Manos 2001). In Papua New Guinea, there are 16 species in the functional group of root-climbing species. Three of them are endemic. They grow from lowland altitudes up to 3,500 m a.s.l., with their centre of diversity in the lowlands (Gardner 2013). The majority of *Piper* species has self-incompatible flowers pollinated by generalized bees and flies. Dispersal of seeds is mediated by highly specialized frugivorous bats (Fleming 2004), which highlights the importance of their role in ecosystem functioning. The *Piper* species are also of considerable economic and medical importance (Parmar et al. 1997); nonetheless, little information is known about their ecology and associations with host trees. As a species-rich genus, climbing *Piper* species provide an ideal object for studying host and ecological preferences.

We asked three specific questions about the ecology of *Piper* climbers (i) What is the species composition, abundance and size structure of *Piper* climbers in the study forest? (ii) How do environmental characteristics affect the distribution and size of *Piper* climbers? and (iii) How do host tree characteristics and identity affect the abundance and size of *Piper* climbers? Answering these questions can help us understand the ecology and associations between understudied group of understorey climbers and their host trees.

Material and methods

Study area

The study area was located in a lowland primary tropical rainforest in northern Papua New Guinea near Wanang village (5°14′ S, 145°11′ E, 100 m a.s.l., Madang Province, Fig. 1). This area is characterized by a humid climate (mean annual rainfall 3,600 mm), a mild dry season from July to September and a mean annual temperature of 26°C (McAlpine et al. 1983).

Data collection

The data collection was conducted in August 2015 in the 50-ha plot, which is a part of the global network of forest research plots coordinated by the Smithsonian Institution (Anderson-Teixeira et al. 2015). The 50-ha plot is divided into 1,250 quadrats 20 × 20 m each, organized in 25 rows and 50 columns. Data were collected from 25 of these quadrats (together covering 1-ha) located in the eastern half of the 50-ha plot. The quadrats were placed in a regular grid, and the distance between quadrat centroids was 100 m in both row and column directions, with three exceptions due to their inaccessibility or location in a riverbed. Altitude ranged from 98 to 178 m a.s.l. In all quadrats, all *Piper* climbers on all trees with DBH ≥ 1 cm were recorded and identified. Vouchers of all species were collected and their identification was subsequently confirmed by comparing with vouchers in the National herbarium in Lae (LAE) and available literature. A laser range finder was used to measure the height of individual climbers. In cases where a large number of climbers belonging to one species occupied a tree, only the maximum height of all climbers was measured. The canopy cover was visually estimated in the centre of each quadrat by three observers as a percentage and then averaged to diminish the systematic error of one observer (Sykes et al. 1983). The information on species identity, location and DBH for all trees with DBH ≥ 1 cm was available from the previous census (2010–2012, if a trunk thickening is not highly disproportionate for individual tree species we cannot expect changes in observed patterns within a few years) of the 50-ha plot (containing information on all the 288,000 trees with DBH ≥ 1 cm in the whole 50-ha plot – http://ctfs.si.edu/Public/plotdataaccess/SiteDescription.php?plotname=wanang&typedata=tree). Data on geomorphological characteristics: mean altitude, slope and convexity (either concave i.e. a ‘curving in’ shape represented by negative values or convex i.e. ‘curving out’ shape represented by positive values; calculated as the mean altitude of the focal quadrat minus the average altitude of all directly adjacent quadrats) were also obtained from the database for each quadrat. Soil nutrient content had little influence on the tree community composition in the 50-ha plot, as shown by Vincent et al. (2015).

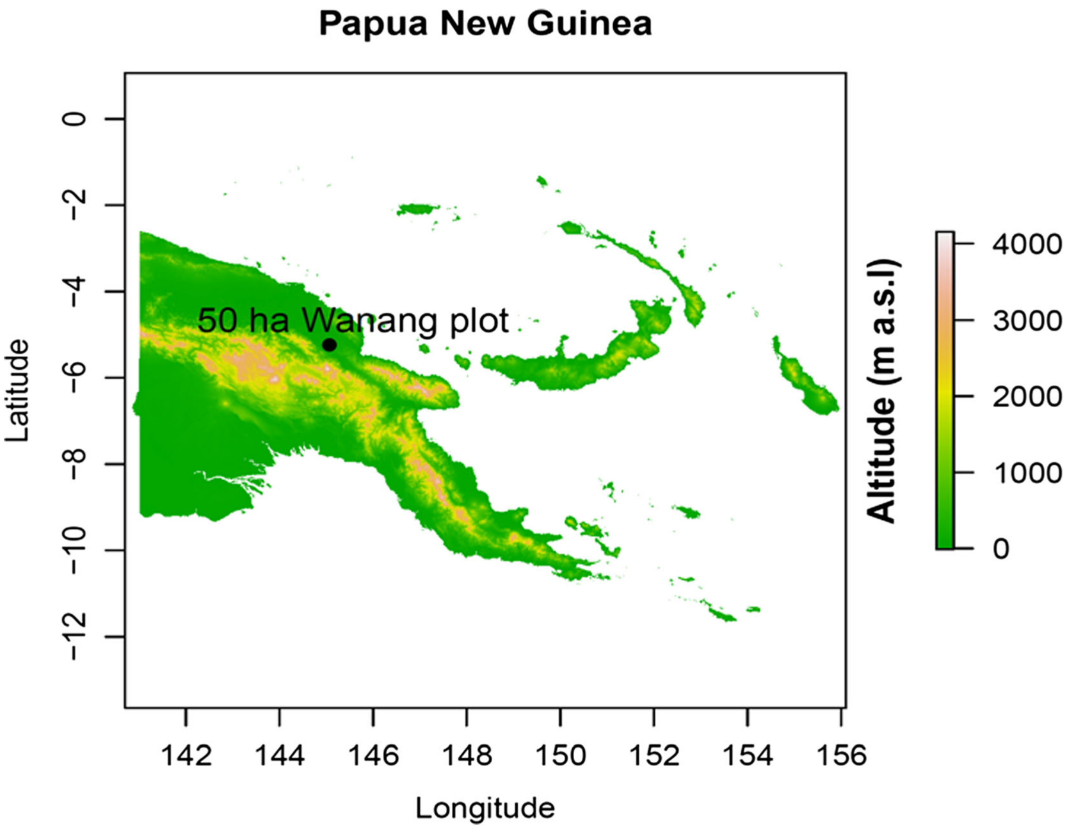

Fig. 1 Topographic map of Papua New Guinea with marked location of the 50-ha Wanang plot

Data on some trees were missing in the 50-ha plot database, and these trees were removed from subsequent analyses. Trees with partially missing data, on DBH (0.9% missing) or tree identity (6.6% missing), were used for those analyses where the missing data were not needed. Overall, missing data accounted for 7.3% of all trees occupied by climbers. Trees were divided into five DBH categories (1–2.5 cm, ≥ 2.5–5 cm, ≥ 5–10 cm, ≥ 10 –20 cm, ≥ 20 cm) for the analysis of the size – abundance relationship.

Quadrat-based analyses

To analyse the possible influence of environmental characteristics (mean altitude, convexity, slope) and of the host tree community (canopy cover and basal area summed for all trees in the quadrat) on the characteristics of *Piper* climbers and their communities (average height, percentage of occupied trees, number of *Piper* individuals and species in a quadrat), we used redundancy analysis (RDA) with centring and standardization to a zero mean and a unit variance of response data (i.e. characteristics of *Piper* communities). Basal area was logarithmically transformed to improve normality and avoid the high leverage of positive outliers. Subsequently, all possible correlations between all characteristics were calculated (using Pearson correlation coefficient) to see the effect of environmental characteristics on characteristics of *Piper* climbers. Because the RDA demonstrated significant relationship (i.e. the global null hypothesis of no relation between environment and *Piper* characteristics can be rejected), we have just searched for the most important correlations. Thus, we have not implemented any correction for the multiple comparison problem, because it leads to very weak tests (Nakagawa 2004) and thus we report the P values for each correlation separately (i.e. we report comparisonwise Type I error probabilities). Further, the response of *Piper* species composition to the same explanatory variables (environmental variables and host tree log basal area and canopy) was tested using RDA with centring and logarithmic transformation of the response data (i.e. the number of individuals for each *Piper* species in the quadrats). The goodness of fit in both the RDA analyses was characterized by the amount of explained variability. Note, however, that this value includes also the reduction of dimensionality (Šmilauer and Lepš 2014); thus, these values are usually lower than the values of coefficient of determination for general linear models, where the response is univariate. Consequently, the efficiency of the first two axes is also included, which compares the amount of explained variability in the constrained ordination, with the axes corresponding with unconstrained ordination – in this case PCA (ter ter Braak and Šmilauer 2012).

Individual-based analyses

To analyse climber preference for tree species, we used partial-RDA analysis, where 190 (out of 329) tree species with an abundance of ≥ 5 individuals per sampled area were used as explanatory variables and *Piper* climber abundances on these 190 tree species as response data. In other words, the presence of *Piper* climbers on host trees was explained by tree species identity. The quadrat identity and tree DBH were used as covariates to filter out the effect of different environmental conditions, respectively of the tree diameter.

The effect of *Piper* climber identity and host tree DBH on the height of *Piper* climbers was explored using linear mixed-effect models with quadrat identity used as a random factor. Further, the *Piper* height (log) vs tree DBH (log) association was tested separately for each *Piper* species by linear regression models. The probability of *Piper* climber presence on trees in relation to their diameter (log) was quantified by generalized linear models with a binomial distribution with the testing of significance by the χ^2 criterion. The occupancy rate of host trees by *Piper* climbers was related to the relative abundance of host tree species (i.e. relative proportion of the particular species from all stems with DBH ≥ 1 cm, estimated for species with a total abundance of ≥ 5 individuals in the 25 sampled quadrats) and their average DBH (log) by generalized linear models with a binomial distribution with the testing of significance by the χ^2 criterion. The relative abundance of host trees (log) was correlated with the average tree DBH (log) to test whether the occupancy rate was not caused by an uneven distribution of tree abundance in relation to DBH.

All multivariate analyses were conducted using Canoco 5 software (ter ter Braak and Šmilauer 2012), while the others were processed using R software (R Core Team 2017; Bates et al. 2015; Wickham 2016).

Results

We identified 8 *Piper* climber species in our study constituted by 1,058 individuals. There were 2 to 7 species (mean ± SD 5.20 ± 1.32), represented by 2 to 138 individuals (42.32 ± 31.85) per quadrat. The two most common species, *P. macropiper and P. decumanum*, formed approximately half of the total number of individuals whereas *P. lessertianum* was the rarest species with only 18 individuals in the study area. Overall, 13.7% of tree trunks (792 from 5,783) with DBH ≥ 1 cm were occupied by a *Piper* climber. The proportions of occupied trees in individual quadrats ranged from less than 1 to 38%, based on information on 329 species represented by 5,783 individuals. The number of tree species ranged from 53 to 111 (86 ± 11.25) per quadrat, represented by 160 to 372 stems (231.32 ± 49.20) per quadrat. The most common tree species (*Ficus hahliana*) had 254 individuals, while the rarest ones accounted for one individual in all quadrats. Average tree DBH ranged from 3.30 to 7.05 cm (4.65 ± 0.78) per quadrat with maximum of individual tree DBH being 57.13 cm. The average total basal area and canopy cover per quadrat ranged from 5,278 to 58,975 cm^2 (15,201 ± 11,363) and from 30 to 95 % (69.92 ± 16.85) respectively.

Quadrat-based analyses

Characteristics of *Piper* climbers were significantly influenced (RDA, $F = 2.3$, $P = 0.031$; Fig. S1) by plot characteristics. More specifically, there was a significant negative relationship between the mean altitude and the number of species (NSP), number of individuals (NOI) and percentage of occupied trees (Table 1). Canopy cover exhibited very similar correlations with the exception of a non-significant relationship with NSP. Additionally, NSP may be negatively influenced by a steeper slope. Nonetheless, mean altitude and canopy cover were significantly correlated and, so these correlations have to be interpreted with caution. NOI and percentage of occupied trees were strongly correlated ($r = 0.95$, $P < 0.001$). In contrast, the average height of climbers in the plot was not significantly affected by any of the

Table 1 Pair-wise correlations of environmental factors (mean altitude, convexity, slope, canopy cover) and basal area with characteristics of *Piper* climbers (number of species, number of individuals, percentage of occupied trees and average height; $N = 25$). Significant results are in bold

		Mean altitude [m a.s.l.]	Convexity	Slope [degrees]	Basal area [cm^2]	Canopy cover [%]
Number of species	Correlation coefficient	**−0.58**	−0.30	**−0.50**	−0.32	−0.37
	P value	**0.023**	0.1435	**0.012**	0.123	0.066
Number of individuals	Correlation coefficient	**−0.52**	−0.28	−0.39	−0.25	**−0.43**
	P value	**0.007**	0.178	0.055	0.230	**0.034**
Percentage of occupied trees	Correlation coefficient	**−0.46**	−0.33	−0.33	−0.28	**−0.40**
	P value	**0.019**	0.111	0.105	0.175	**0.046**
Average height	Correlation coefficient	−0.22	−0.31	0.23	0.25	0.04
	P value	0.292	0.129	0.277	0.225	0.851

environmental variables. None of the climber characteristics can be explained by terrain convexity or tree basal area. Counterintuitively, basal area was not correlated with canopy cover ($r = 0.09$, $P = 0.669$).

The majority of climber species generally avoided similar conditions (RDA, $F = 2.2$, $P = 0.006$; Fig. 2), which included a steeper slope, more closed canopy layer, higher mean altitude and bigger basal area. The overall adjusted explained variability by the model was 19.51 % and the efficiency of the first and second axis of constrained ordination was 49.32% and 50.88%, respectively, when compared to the unconstrained ordination.

Individual-based analyses

Individual *Piper* climber species did not exhibit preferences for certain host plant species (partial RDA, with quadrat identity and DBH used as covariates, $F = 1.1$, $P = 0.072$, Fig. S2), the overall explained variability was very low (adjusted $R^2 = 0.32$ %). If the DBH is not included as a covariate, the model becomes significant ($F = 1.1$, $P = 0.016$), pointing at tree DBH as the most important tree characteristics for *Piper* climbers.

Individual *Piper* species differed in height ($\chi^2 = 66.55$, *d.f.* = 1, $P < 0.001$) and their height was positively related to host tree diameter ($\chi^2 = 16.40$, *d.f.* = 4, $P = 0.022$, Fig. 3). The height ranged from 1.43 m for *P. lessertianum* to 5.09 m for *P. mestonii*. Three *Piper* species (*P. decumanum*, *P. interruptum* and *P. macropiper*) exhibited a significant positive relationship between height and host tree DBH, while for the remaining species (*P. abbreviatum*, *P. arfakianum*, *P. betle*, *P. mestonii*, *P. lessertianum*), the relationship was not significant. The overall correlation between *Piper* height and DBH remained positive even when

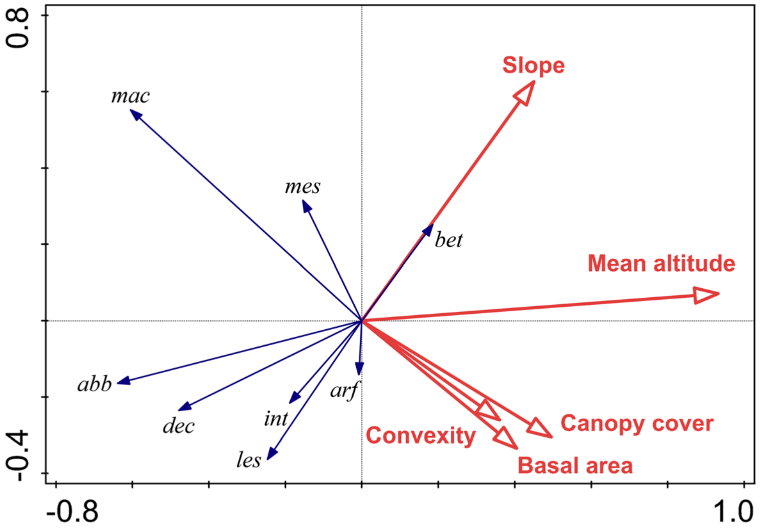

Fig. 2 Redundancy analysis ordination diagram showing individual climber species in relation to environmental variables in the 25 quadrats (RDA, $F = 2.2$, $P = 0.006$). Relative importance is indicated by the length of arrows. *Abb* – *Piper abbreviatum*, *arf* – *P. arfakianum*, *bet* – *P. betle*, *dec* – *P. decumanum, int* – *P. interruptum*, *les* – *P. lessertianum*. *Mac* – *P. macropiper*, *mes* – *P. mestonii*

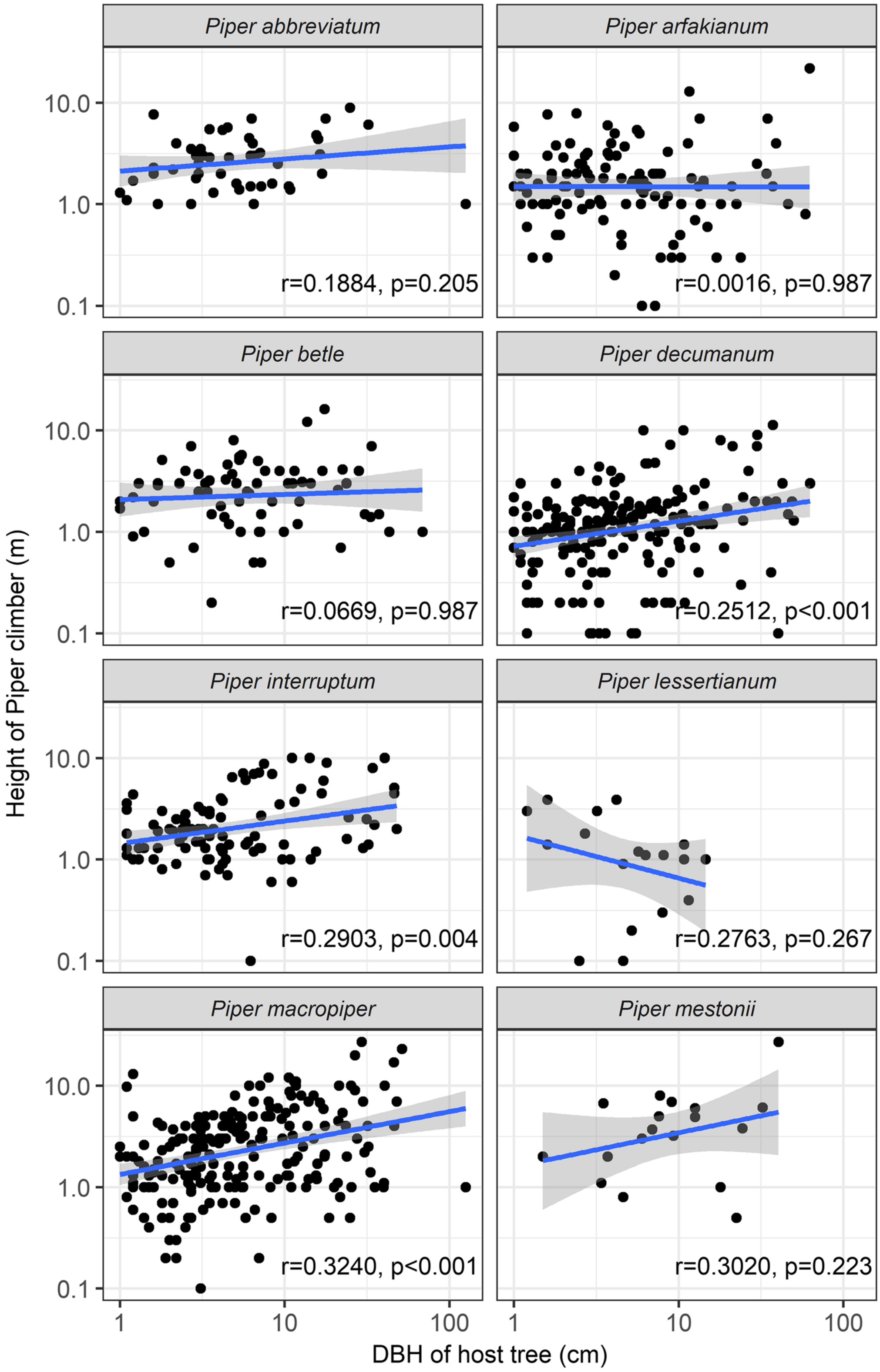

Fig. 3 Height [m] of *Piper* climber species as a function of host tree DBH [cm] based on the linear model. The grey area indicates the 95% confidence interval

we excluded all host trees with DBH < 5 cm in order to remove the effect of small trees which can potentially determine the upper limit of climber height by restricting climber height to its own size (χ^2 = 6.25, *d.f.* = 1, *P* = 0.012).

The *Piper* climbers also exhibited a strong preference for larger trees as they were more common on trees with higher DBH. The size distribution of unoccupied trees is typical for the size distribution of trees in tropical forests, whilst the size distribution of occupied trees has a modus in the DBH category > 2.5–5 cm, since the occupancy rate increases with increasing tree DBH (Fig. 4). *Piper* climbers were significantly more likely to be present on trees with higher DBH (χ^2 = 295.7, *d.f.* = 1, *P* < 0.001, Fig. S3). The DBH geometric mean and median of trees unoccupied by climbers was 2.54 cm, and 2.10 cm, respectively, while the occupied trees had a DBH geometric mean of 4.87 cm and median of 4.20 cm.

Rarer tree species hosted a higher number of climbers than more frequently occurring species (Fig. 5; χ^2 = 4.52, *d.f.* = 1, *P* = 0.033). In other words, the probability that a tree will host a climber was greater in rare than in dominant tree species. This association could be influenced by the uneven distribution of trunk size among individual trees species. Nevertheless, there was no significant correlation between the number of individuals of a particular species (i.e. rarity) and average DBH of the tree species (*r* = −0.13, *P* = 0.077). However, if we include average DBH of the tree species into the model, rarity of tree species becomes not significant, unlike tree DBH.

Discussion

This study has described compositional patterns in the group of understorey climbers and their associations to environmental characteristics and their host trees. *Piper* species diversity and abundance were rather consistently influenced by environmental characteristics – mostly negatively by altitude and canopy cover, while no effect of canopy openness was found with respect to the height of *Piper* species. By contrast, *Piper* height was positively associated with DBH of host trees. DBH was also strong determinant of *Piper* presence on host trees that had an average diameter almost 5 cm greater than trees without *Piper* climbers. This study also points out to a lower prediction strength of host tree species identity when tree DBH is taken into account.

General characteristics of *Piper* climber communities

In our study, *Piper* climbers occupied 13.7% of the available trees. This occupancy rate was relatively high, especially considering that it applies to a single genus, but not truly exceptional. Talley et al. (1996) observed a 18% infestation rate just by *Piper canina* out of a total

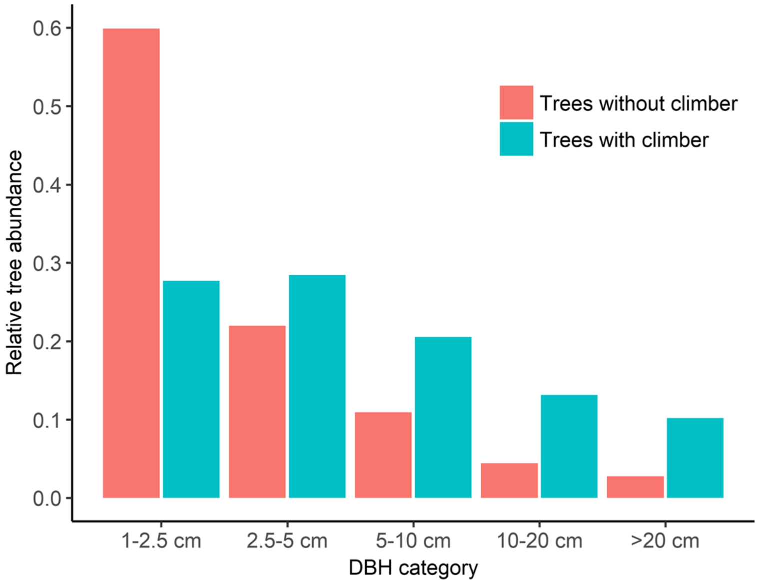

Fig. 4 Relationship between the relative abundance of trees and DBH category. Red columns indicate trees without *Piper* climbers (*N* = 4991), blue columns indicate trees occupied by *Piper* climbers (*N* = 686)

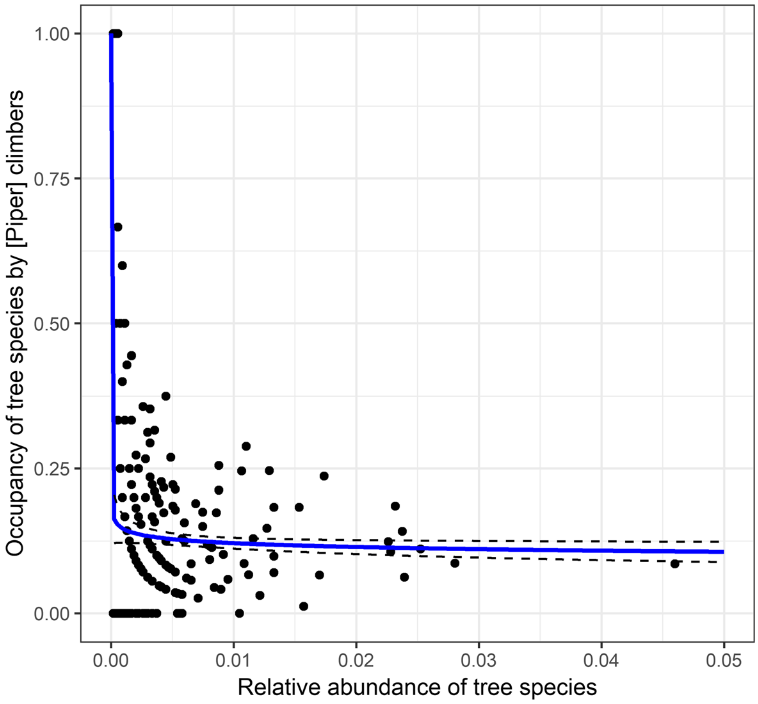

Fig. 5 Occupancy rate of tree species by *Piper* climbers as a function of the dominance of tree species in the sampled quadrats ($N = 190$ species). Dashed lines indicate 95 % confidence interval

infestation rate of 54% by root climbers in a north Queensland tropical rain forest. The reported numbers of trees occupied by woody climbers differ substantially between studies. This variability can be caused, at least in part, by differences in tree diameter from which climber species are recorded. On average, proportion of occupied species reaches values around 25% (Schnitzer and Bongers 2002; Leicht-Young et al. 2010), but could be significantly higher (Putz 1984b). The abundance of understorey root climbers is lower than the abundance of other climbers, but still forms a significant proportion (46% – Carrasco-Urra and Gianoli 2009, 13% – Magrach et al. 2014), usually in closed forests with lower light availability (Baars et al. 1998, Yuan et al. 2009).

Environmental determinants of *Piper* climber community composition

Altitude appeared to be the most important environmental factor showing negative correlation with climber species diversity and abundance even on small spatial scale and within a low altitudinal range. This relationship is generally well supported (Schnitzer and Bongers 2002), and the pattern might be the result of a general *Piper* preference for low altitudes (Gardner 2013). However, Balfour and Bond (1993) and Muoghalu and Okeesan (2005) found the reverse trend, i.e. a positive correlation with altitude, ranging from 40 to 635 m a.s.l., respectively, from 213 to 457 m a.s.l. This altitudinal association is likely to be caused by a temperature gradient, which would not affect climbers along our short altitudinal gradient. In our narrow altitudinal range, the low altitude indicates quadrat located in the valley and high altitudes quadrats located on the ridge, which is the important ecological determinant of tree composition in the whole plot.

Our results show the promotion of the abundance and occupancy rate of *Piper* climbers with lower canopy cover, which corresponds more with pattern usually observed for canopy climbers (Putz 1984b; Schnitzer and Carson 2001; Schnitzer and Bongers 2002). Understorey climbers are generally considered less light demanding (Yuan et al. 2009), with wide light niche enabling them to persist under a closed canopy as well as in more open sites (Gianoli et al. 2010). Moreover, other study (Carrasco-Urra and Gianoli 2009) have found no association of climber habitus in general with open sites.

By contrast, canopy openness did not affect the height of *Piper* climbers. This finding may mean that they are simply not affected, or that the availability of light directly influences germination (Teketay and Granstrom 1997) and survival of seedlings, but not the subsequent growth of plants able to tolerate shade. The height of *Piper* species was partly species-specific but may respond also to the characteristics of host trees such as bark type or DBH. We have indeed observed a positive association between tree DBH and height of *Piper* individuals.

Host tree characteristics determining occupancy by *Piper* climbers

Although climbing species exhibit a strong association with host trees in many studies (e.g. Burns and Dawson 2005; Buron 1998; Muoghalu and Okeesan 2005), we have not found any significant preference for particular tree species (Balfour and Bond 1993; Carrasco-Urra and Gianoli 2009) that cannot be explained by tree DBH (It should be, however, noted that the power of the test with so many host species is low.). If DBH was not used as a covariate, the model would become significant, suggesting that DBH is a tree property, which determines species suitability for *Piper* climbers. A preference for more general tree characteristics such as DBH, and/or certain habitats, may be confounded with tree species preference in smaller datasets where such general conditions could point to a single of a few host tree species. There are also more tree characteristics (bark roughness, speed of trunk thickening, spines, etc.) which we were not able to take into account and which may be responsible for further substantial differentiation between climber preference for tree species. Especially bark properties seems to play dominant role for the infestation success of root climbers (Talley et al. 1996).

The *Piper* climbers exhibited a strong preference towards trees with larger trunks, which corresponds with pattern usually observed for root-climbers (Talley et al. 1996; Carrasco-Urra and Gianoli 2009; Leicht-Young et al. 2010). Our results show that the average DBH of host trees occupied by climbers was nearly 5 cm greater than for trees without climbers. This association may mean that, at least for *Piper* root climbers, sapling availability is not a crucial factor for establishment. In previous studies, the sapling availability positively affected the growth and establishment of climbers (Putz 1984b; Balfour and Bond 1993), but the positive associations may be caused by another factor, namely light (Whigham 1984). The preference for trees with larger DBH may be also caused by accumulation of climbers with time due to their higher age (Clark and Clark 1990; Campbell et al. 2014).

Different functional groups of climbers show preferences for either dominant (Muoghalu and Okeesan 2005; Garbin et al. 2014) or rare tree species (Garbin et al. 2014), or, alternatively, lack any such preference (Garbin et al. 2012). We have found an association between *Piper* climbers and trees with lower abundances. However, if we take into account host tree DBH, the *Piper* affinity to less common tree species becomes unimportant.

The observed pattern of weak preference for rare tree species may be the product of tree species defence against climber infestation. Trees possess anti-climber adaptations, such as the height of a tree, bark roughness, trunk thickening and growth rate, spines or ant bodyguards (Putz 1984a, 1984b; Putz and Mooney 1991; Muoghalu and Okeesan 2005; Sfair et al. 2016), which decrease infestation by climbers and, in consequence, can provide a competitive advantage for trees which may consequently become dominants. For example, Putz (1984b), Ingwell et al. (2010) and Schnitzer and Carson (2010) found that trees with woody climbers suffer a higher mortality rate than unoccupied trees. However, because of the small stature of understorey climbers, as is the case for *Piper* climbers, their effect on the fitness of high canopy trees is probably weak compared to their effect on saplings. A strong negative impact of understorey climbers on the ability of tree saplings to compete for both above-ground resources (Llorens and Leishman 2008; Zhang et al. 2011), and to a larger extent for below-ground resources (Schnitzer et al. 2005) in case of lianas was also reported. However, there are also cases when tree survival increased due to climber infestation, suggesting a possible reduction of folivory resulting from climbers physically protecting the host tree foliage or providing an alternative resource for herbivores (Piiroinen et al. 2014).

Our study is based on a taxonomically limited section of single functional group of climbers. However, even these results show that climbers respond to abiotic heterogeneity, properties of the surrounding vegetation, and properties of individual potential host trees. Because climbers affect the fitness of their hosts, we can expect that climbers will affect the forest structure and dynamics, and because their effect is not indiscriminate, they will affect the mechanisms of species diversity maintenance. The importance of *Piper* species for forest systems is also highlighted by the fact they are major food source for some specialized frugivorous bats (Fleming 2004), which consequently serve as seed dispersers able to carry seeds up to the distance of hundreds of metres (Fleming 1981), providing opportunities for new establishment. In conclusion, our findings suggest that all *Piper* climbers under study avoid similar habitat conditions as closed canopy, higher altitude, plots with higher basal area of trees, or steeper slopes. Furthermore, we observed strong preference for trees with larger DBH. DBH also positively affected height of *Piper* climbers. It seems that the positive relationship between climber presence and tree DBH is also behind the preference of climbers for individual tree species.

Acknowledgements We gratefully acknowledge support of the Czech Science Foundation (GACR 16-18022S), the European Science Foundation (669609), the Center for Tropical Forest Science, the Wanang Conservation Area and the University of South Bohemia. We are also grateful to Kipiro Damas and Kenneth Molem for their help with the determination of *Piper* species. The research was conducted in compliance with the laws of Papua New Guinea.

References

Anderson-Teixeira KJ, Davies SJ, Bennett AC, Gonzalez-Akre EB, Muller-Landau HC, Joseph Wright S, Abu Salim K, Almeyda Zambrano AM, Alonso A, Baltzer JL, Basset Y, Bourg NA, Broadbent EN, Brockelman WY, Bunyavejchewin S, Burslem DFRP, Butt N, Cao M, Cardenas D, Chuyong GB, Clay K, Cordell S, Dattaraja HS, Deng X, Detto M, Du X, Duque A, Erikson DL, Ewango CEN, Fischer GA, Fletcher C, Foster RB, Giardina CP, Gilbert GS, Gunatilleke N, Gunatilleke S, Hao Z, Hargrove WW, Hart TB, Hau BCH, He F, Hoffman FM, Howe RW, Hubbell SP, Inman-Narahari FM, Jansen PA, Jiang M, Johnson DJ, Kanzaki M, Kassim AR, Kenfack D, Kibet S, Kinnaird MF, Korte L, Kral K, Kumar J, Larson AJ, Li Y, Li X, Liu S, Lum SKY, Lutz JA, Ma K, Maddalena DM, Makana JR, Malhi Y, Marthews T, Mat Serudin R, Mcmahon SM, McShea WJ, Memiaghe HR, Mi X, Mizuno T, Morecroft M, Myers JA, Novotny V, de Oliveira AA, Ong PS, Orwig DA, Ostertag R, den Ouden J, Parker GG, Phillips RP, Sack L, Sainge MN, Sang W, Sri-ngernyuang K, Sukumar R, Sun IF, Sungpalee W, Suresh HS, Tan S, Thomas SC, Thomas DW, Thompson J, Turner BL, Uriarte M, Valencia R, Vallejo MI, Vicentini A, Vrška T, Wang X, Wang X, Weiblen G, Wolf A, Xu H, Yap S, Zimmerman J (2015) CTFS-ForestGEO: A worldwide network monitoring forests in an era of global change. *Global Change Biol* 21: 528–549

Baars R, Kelly D, Sparrow AD (1998). Liane distribution within native forest remnants in two regions of the South Island, New Zealand. *New Zealand Journal of Ecology,* 22:71–85

Balfour D, Bond WJ (1993) Factors limiting climber distribution and abundance in a Southern African forest. *J Ecol* 81:93–100

Bates D, Maechler M, Bolker B, Walker S (2015). Fitting linear mixed-effects models using lme4. *J Statist Softw*, 67:1–48

Burns KC, Dawson J (2005) Patterns in the diversity and distribution of epiphytes and vines in a New Zealand forest. *Austral Ecol* 30:883–891

Buron (1998) Association of vines and trees in second-growth forest. *NE Naturalist* 5:359–362

Campanello PI, Garibaldi JF, Gatti MG, Goldstein G (2007) Lianas in a subtropical Atlantic Forest: Host preference and tree growth. *Forest Ecol Managem* 242:250–259

Campbell M, Laurance WF, Magrach A (2014) Ecological effects of lianas in fragmented forests. In *Ecology of lianas*. Wiley, pp 443–450

Carrasco-Urra F, Gianoli E (2009) Abundance of climbing plants in a southern temperate rain forest: host tree characteristics or light availability? *J Veg Sci* 20:1155–1162

Clark DB, Clark DA (1990) Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *J Trop Ecol* 6:321–331

DeWalt SJ, Schnitzer SA, Chave J, Bongers F, Burnham RJ, Cai Z, Chuyong G, Clark DB, Ewango CEN, Gerwing JJ, Gortaire E, Hart T, Ibarra-Manríquez G, Ickes K, Kenfack D, Macía MJ, Makana JR, Martínez-Ramos M, Mascaro J, Moses S, Muller-Landau HC, Parren MPE, Parthasarathy N, Pérez-Salicrup DR, Putz FE, Romero-Saltos H, Thomas D (2010) Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* 42:309–317

Durigon J, Durán SM, Gianoli E (2013) Global distribution of root climbers is positively associated with precipitation and negatively associated with seasonality. *J Trop Ecol* 29:357–360

Fleming TH (1981). Fecundity, fruiting pattern, and seed dispersal in Piper amalago (Piperaceae), a bat-dispersed tropical shrub. *Oecologia* 51:42–46

Fleming TH (2004). Dispersal ecology of neotropical Piper shrubs and treelets. In *Piper: a model genus for studies of phytochemistry, ecology, and evolution*. Springer, Boston, pp 58–77

Garbin ML, Carrijo TT, Sansevero JBB, Sánchez-Tapia A, Scarano FR (2012) Subordinate, not dominant, woody species promote the diversity of climbing plants. *Perspect Pl Ecol Evol Syst* 14:257–265

Garbin ML, Sánchez-Tapia A, Carrijo TT, Sansevero JBB, Scarano FR (2014) Functional traits behind the association between climbers and subordinate woody species. *J Veg Sci* 25:715–723

Gardner RO (2013) Piper (Piperaceae) in New Guinea: The climbing species. Blumea 57:275–294

Gianoli E (2004) Evolution of a climbing habit promotes diversification in flowering plants. *Proc Roy Soc Biol Sci Ser B* 271: 2011–2015

Gianoli E, Saldaña A, Jiménez-Castillo M, Valladares F (2010) Distribution and abundance of vines along the light gradient in a southern temperate rain forest. *J Veg Sci* 21:66–73

Hegarty EE (1991) *Vine-host interactions*. In *The biology of vines*. pp 357–375

Ingwell LL, Joseph Wright S, Becklund KK, Hubbell SP, Schnitzer SA (2010) The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *J Ecol* 98:879–887

Jaramillo MA, Manos PS (2001) Phylogeny and patterns of floral diversity in the genus Piper (Piperaceae). *Amer J Bot* 88:706–716

Jayakumar R, Nair KKN (2013) Diversity and distribution of vines in the tropical forests of Nilgiri Biosphere Reserve. *India. Curr Sci* 105:470–479

Kusumoto B, Enoki T, Watanabe Y (2008) Community structure and topographic distribution of lianas in a watershed on Okinawa, south-western Japan. *J Trop Ecol* 24:675

Ledo A, Schnitzer SA (2014) Disturbance and clonal reproduction determine liana distribution and maintain liana diversity in a tropical forest. *Ecology* 95:2169–2178

Leicht-Young SA, Pavlovic NB, Frohnapple KJ, Grundel R (2010) Liana habitat and host preferences in northern temperate forests. *Forest Ecol Managem* 260:1467–1477

Llorens AM, Leishman MR (2008) Climbing strategies determine light availability for both vines and associated structural hosts. *Austral J Bot* 56:527–534

Magrach A, Rodríguez-Pérez J, Campbell M, Laurance WF (2014) Edge effects shape the spatial distribution of lianas and epiphytic ferns in Australian tropical rain forest fragments. *Appl Veg Sci* 17:754–764

Malizia A (2003) Host Tree preference of vascular epiphytes and climbers in a subtropical montane cloud forest of northwest Argentina. *Selbyana* 24:196–205

McAlpine JR, Keig G, Falls R (1983) Climate of papua new guinea. CSIRO and Australian National University Press, Canberra

Mori H, Kamijo T, Masaki T (2016) Liana distribution and community structure in an old-growth temperate forest: the relative importance of past disturbances, host trees, and microsite characteristics. *Pl Ecol* 217:1171–1182

Muoghalu JI, Okeesan OO (2005) Climber species composition, abundance and relationship with trees in a Nigerian secondary forest. *Afr J Ecol* 43:258–266

Nakagawa S (2004) A farewell to Bonferroni: The problems of low statistical power and publication bias. *Behav Ecol* 15: 1044–1045

Nesheim I, Økland RH (2007) Do vine species in neotropical forests see the forest or the trees? *J Veg Sci* 18:395–404

Parmar VS, Jain SC, Bisht KS, Jain R, Taneja P, Jha A, Tyagi OD, Prasad AK, Wengel J, Olsen CE, Boll PM (1997) Phytochemistry of the genus *Piper*. *Phytochemistry* 46:597–673

Phillips OL, Martínez RV, Mendoza AM, Baker TR, Vargas PN (2005) Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology* 86:1250–1258

Piiroinen T, Nyeko P, Roininen H (2014) Canopy openness in gaps determines the influence of herbaceous climbers and insect folivory on the survival of a tropical pioneer tree, Neoboutonia macrocalyx Pax. *Afr J Ecol* 52:41–49

Putz FE (1984a) How trees avoid and shed lianas. *Biotropica* 16: 19–23

Putz FE (1984b) The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724

Putz F E, Mooney HA (eds) (1991) *The biology of vines*. Cambridge University Press

R Core Team (2017) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna

Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. *Trends Ecol Evol* 17:223–230

Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecol Letters* 14:397–406

Schnitzer SA, Carson WP (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82: 913–919

Schnitzer SA, Carson WP (2010) Lianas suppress tree regeneration and diversity in treefall gaps. *Ecol Letters* 13:849–857

Schnitzer SA, Kuzee ME, Bongers F (2005) Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *J Ecol* 93:1115–1125

Sfair JC, Rochelle ALC, Rezende AA, Van Melis J, Burnham RJ, Weiser V de L, Martins FR (2016) Liana avoidance strategies in trees: Combined attributes increase efficiency. *Trop Ecol* 57:559–566

Šmilauer P, Lepš J (2014) *Multivariate analysis of ecological data using CANOCO 5*. Cambridge University Press

Sykes JM, Horrill D, Mountford MD (1983) Use of visual cover assessments as quantitative estimators of some British woodland taxa. *J Ecol* 71:437–450

Talley SM, Setzer WN, Jackes BR (1996) Host associations of two adventitious-root-climbing vines in a North Queensland tropical rain forest. *Biotropica* 28:356–366

Teketay D, Granstrom A (1997) Germination ecology of forest species from the highlands of Ethiopia. *J Trop Ecol* 13:805–831

ter Braak C, Šmilauer P (2012) *CANOCO reference manual and user's guide: software for ordination (version 5.0)*. Microcomputer Power, Ithaca

Valladares F, Gianoli E, Saldaña A (2011) Climbing plants in a temperate rainforest understory: searching for high light or coping with deep shade? *Ann Bot (Oxford)* 108:231–239

Vincent JB, Henning B, Saulei S, Sosanika G, Weiblen GD (2015) Forest carbon in lowland Papua New Guinea: local variation and the importance of small trees. *Austral Ecol* 40:151–159

Whigham D (1984) The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). *Canad J Forest Res* 14:37–39

Wickham H (2016) *ggplot2: elegant graphics for data analysis*. Springer

Yang SZ, Fan H, Li KW, Ko TY (2018). How the diversity, abundance, size and climbing mechanisms of woody lianas are related to biotic and abiotic factors in a subtropical secondary forest, Taiwan. *Folia Geobot* 53:77–88

Yuan CM, Liu WY, Tang CQ, Li XS (2009) Species composition, diversity, and abundance of lianas in different secondary and primary forests in a subtropical mountainous area, SW China. *Ecol Res* 24:1361–1370

Zhang H, Tao J, Wang L, Zuo J, Wang Y, He Z, Liu J, Guo Q (2011) Influences of herbaceous vines on community characteristics in pioneer succession stages. *Acta Ecol Sin* 31: 186–191