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Abundance of climbing plants in a southern temperate rain forest: host tree characteristics or light availability?

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Abstract

Question: In a southern temperate rain forest, we addressed three questions: (1) Does the abundance of climbing plants increase with light availability? (2) Do host tree species differ in their susceptibility to vine infestation? (3) How does the relationship between host tree trunk diameter and relative abundance of vines vary with their climbing mechanism?

Location: Two sites in the temperate evergreen rain forest of southern Chile: Puyehue (40°39′S, 72°09′W; 350 m a.s.l.) and Pastahue (42°22′S, 73°49′W; 285 m a.s.l.).

Methods: We sampled vines in 60 25-m^2 plots, with 20 plots in each of three light environments: mature forest, forest edges and canopy gaps. In each plot, for every tree $\geq$ 1.50-m tall of any diameter we counted and identified all climbing plant individuals at a height of 1.30 m. We also counted, measured (trunk diameter at 1.30 m) and identified all these trees, and determined prevalence of vine infestation for each tree species.

Results: Light availability in forest plots did not affect vine abundance when the number and size of host trees was taken into account. Overall, vine abundance increased with host tree trunk diameter. Tree species did not differ in the prevalence of vine infestation. The relative abundance of stem twiners and adhesive climbers decreased and increased with trunk diameter, respectively. The densities of stem twiners and adhesive climbers were negatively correlated across the forest.

Conclusion: We provide further evidence that the pattern of vine abundance is independent of light availability in southern temperate rain forests, in contrast to results commonly reported for tropical rain forests. We also show that support suitability across the forest varies with the mechanism by which vines climb, probably due in part to biomechanical constraints and in part to vine interspecific competition, a virtually unexplored ecological factor.

Keywords: Canopy openness; Lianas; Trellis size; Trunk diameter; Valdivian forest; Vines.

Nomenclature: Muñoz-Schick (1980), Stevens (2001 onwards).

Introduction

Climbing plants (vines) are a typical constituent of rain forests and their patterns of distribution and abundance have mainly been studied in tropical rain forests (Gentry 1991; Phillips et al. 2002, 2005; Schnitzer & Bongers 2002; Schnitzer 2005; van der Heijden et al. 2008; van der Heijden & Phillips 2008; but see Muñoz et al. 2003 and Jiménez-Castillo et al. 2007 for studies in temperate rain forests). Some studies conducted in tropical rain forests report that vines are more common in canopy gaps or at forest edges (Putz 1984; Hegarty & Caballé 1991; Schnitzer & Carson 2001), but this pattern is not yet conclusive (Schnitzer & Bongers 2002). Moreover, light availability seemingly does not affect vine distribution and abundance in temperate rain forests (Baars et al. 1998; Gianoli et al. 2010). There is some evidence that vines are increasing in dominance in both tropical (Phillips et al. 2002; Wright et al. 2004; Swaine & Grace 2007) and temperate forests (Allen et al. 2007; but see Londré & Schnitzer 2006). Some authors consider that this pattern could be related to climate change (Malhi & Wright 2004; van der Heijden et al. 2008) and thus reinforce the need to understand factors that determine vine distribution and abundance. A study carried out in a southern African forest (Balfour & Bond 1993) and a geographically extensive study in Neotropical forests (van der Heijden & Phillips 2008) concluded that availability of host trees and their characteristics may be more important than abiotic factors in determining the success of lianas (woody vines).

Vines depend on the availability of external support to reach upper layers of the forest and thereby enhance light capture. After finding support and climbing onto trees, vines show phenotypic changes that lead to an increase in their growth rate

(Putz 1984; Gianoli 2001, 2003) and ultimately to greater size and reproductive output than those vines that grow unsupported (Putz 1984; Gianoli 2002; González-Teuber & Gianoli 2008). Trees may differ in their suitability for vine infestation (Hegarty 1991; Allen et al. 1997; Chittibabu & Parthasarathy 2001; Nesheim & Økland 2007), possibly because of specific features such as bark type (Talley et al. 1996) or more general factors such as trunk diameter (Nabe-Nielsen 2001) and trunk length (Campanello et al. 2007). Support suitability also varies with the mechanism by which vines climb, mainly due to biomechanical constraints (Putz & Holbrook 1991). In the case of lianas in tropical forests, it has been reported that the upper limit of trunk diameter that tendril climbers can use is lower than that of stem twiners and branch twiners, and that the upper diameter limit for support trees is greatest for adhesive root and adhesive tendril climbers (Panama: Putz 1984; Malaysia: Putz & Chai 1987). The relative abundance of stem twiners in a tropical rain forest was found to increase with forest stand age, while the relative abundance of tendril climbers decreased with forest stand age (DeWalt et al. 2000). Because average trunk diameter increases with forest age, the latter pattern may be explained by differences in maximum support diameter that vines can use depending on their climbing mechanism (DeWalt et al. 2000). Interestingly, while the latter study reports an apparent increase in abundance of stem twiners with trunk diameter (see Schnitzer & Bongers 2002), there are observations and theoretical predictions for twining vines indicating that when support diameter increases beyond some limit the coils become unstable and plants slip down the tree (Putz 1984; Putz & Holbrook 1991).

The present study was replicated at two sites in the evergreen temperate rain forest of southern South America and had three goals. First, we tested whether vines are more common in open environments. We quantified the abundance of vines climbing onto trees in three light environments: closed canopy mature forest, forest edges and treefall canopy gaps. In this analysis we accounted for the differential availability of support trees in each light environment. Based on earlier evidence at the same study site (Gianoli et al. 2010), we hypothesised that vine abundance would not be significantly different in the three light environments. Second, we evaluated whether host tree species differ in their susceptibility to vine infestation. Alternatively, vine loads may be rather associated with a general tree trait such as trunk diameter. Third, we addressed the relationship between host tree trunk diameter and relative abundance of vines differing in their climbing mechanism. We hypothesised that the relative abundance of stem twiners would decrease with increasing diameter of host tree trunks. This hypothesis is somewhat in contrast to patterns reported by DeWalt et al. (2000) and interpreted by Schnitzer & Bongers (2002) (see above). However, it is based on the assumption that stem twiners cannot remain attached to trees with very wide trunks. We also expected that the dominance of vines climbing via adhesive organs would increase with trunk diameter. This hypothesis is consistent with earlier reports in tropical rain forests (Putz 1984; Putz & Chai 1987) and concurrently considers the fact that trunk diameter does not impose an upper limit to adhesive climbers and the expected decrease in relative abundance of potentially competing stem twiners.

Methods

Study sites

This study was replicated at two sites in the temperate rain forest of southern South America (Valdivian forest). The first site was located within the Puyehue National Park (40°39′S, 72°09′W; 350 m a.s.l.) in the western foothills of the Andes, in southern Chile. The climate is maritime temperate, with average annual precipitation of 3500 mm, and mean maximum and minimum temperatures of 13.8°C and 5.4°C, respectively (Almeyda & Sáez 1958; Riveros & Smith-Ramírez 1996); there is a noticeable rainfall decrease in summer (17% of annual precipitation during summer months; Riveros & Smith-Ramírez 1996). The second site was located close to Pastahue Lake (42°22′S, 73°49′W; 285 m a.s.l.) in the Piuchén range, Chiloé Island, which is part of the Chilean coastal range. The climate is maritime temperate, with an average annual precipitation of 1600 mm, and mean maximum and minimum temperatures of 15.7°C and 4.7°C, respectively (Hajek & Di Castri 1975). In this site, there is also a marked rainfall decrease during the summer months (Hajek & di Castri 1975). The old-growth lowland forest is mainly composed of broadleaf evergreen tree species. The more common canopy species are *Laurelia philippiana* (Atherospermataceae), *Aextoxicon punctatum* (Aextoxicaceae), *Nothofagus dombeyi* (Fagaceae), *Eucryphia cordifolia* (Cunoniaceae), *Dasyphyllum diacanthoides* (Asteraceae) and *Weinmannia trichosperma* (Cunoniaceae). Typical subcanopy trees are *Gevuina avellana* (Proteaceae), *Myrceugenia planipes* (Myrtaceae), *Luma apiculata* (Myrtaceae), *Amomyrtus luma* (Myrtaceae) and *Rhaphithamnus spinosus* (Verbenaceae). The mature forest shows a non-significant tendency for vertical stratification, with average canopy height of 30-35 m and emergent trees of *N. dombeyi* up to 50 m (Parada et al. 2003). The dominant climbers are the woody vines *Boquila trifoliolata* (Lardizabalaceae), *Hydrangea serratifolia* (Hydrangeaceae) and *Mitraria coccinea* (Gesneriaceae).

Sampling

Vine sampling took place in 60 small plots (5 m×5 m), with 30 plots distributed in each of the two study sites. In both sites, plots were located within an area of ca. 15 ha and were separated by at least 50 m. We chose to carry out sampling in small plots to allow appropriate comparisons between forest spots that include treefall gaps, which in these and other mature forests are typically small (see Schnitzer & Carson 2001). Treefall gaps within which plots were laid out were $\leq 35\,\mathrm{m}^2$. In each site we sampled vines in 30 plots, with 10 plots corresponding to each of three light environments: closed canopy mature forest, forest edges and treefall canopy gaps. Forest edge was considered to be 5-m wide (i.e. 5 m in a perpendicular line from the limit of the continuous canopy towards the forest interior). This rather subjective classification of light environments was validated earlier using hemispherical photographs and calculating canopy openness (Gianoli et al. 2010). In this case, we used a light meter (Li-250, LiCor) to measure photosynthetically active radiation (PAR, $\mu\mathrm{mol\,m}^{-2}\mathrm{s}^{-1}$) at noon at a height of 1.30 m in the centre of each plot. In each of the 60 plots, for every tree $\geq$ 1.50-m tall of any diameter we counted and identified to species level all climbing plant individuals at a height of 1.30 m, excluding epiphytes. Individual vines were treated as genets unless it was evident that they had connections with other censused stems (apparent genets; Mascaro et al. 2004; Schnitzer 2005). We also counted and identified all trees $\geq$ 1.50-m tall of any diameter. The trunk diameter was measured at 1.30 m height using a diameter tape. Prevalence of vine infestation (number of trees with vines/number of trees sampled) was calculated for each host tree species.

Analyses

We conducted preliminary analyses to verify that the two study sites were very similar in community aspects and therefore pooling of data was appropriate. Puyehue and Pastahue forests did not differ in mean trunk diameter ($P > 0.70$, one-way ANOVA, data not shown) and mean abundance of climbing plants ($P > 0.53$, one-way ANOVA, data not shown). The community composition of vines was very similar between sites (Jaccard's coefficient $S_j = 0.91$; Krebs 1999).

To accurately evaluate the effect of light availability on abundance of vines in a plot, the analysis accounted for the fact that the number and size of potential supports (host trees) varies with light environment and may affect the response variable. Consequently, we conducted an ANCOVA at the plot level (main factor: light environment; dependent variable: vine abundance; covariates: number of host trees and tree basal area). We also checked for differences in prevalence of vine infestation (dependent variable) among host tree species (main factor), taking into account relative tree abundance (covariate).

To determine the relationship between host tree trunk diameter and the abundance of vines differing in their climbing mechanism, we carried out separate linear regressions between relative abundance of vine type (proportion of all vines found showing a given climbing mechanism) and diameter classes of host trees (0-5, 5-10, 10-15, 15-20, 20-25 and > 25 cm). We used vine relative abundance instead of vine density as dependent variable. This was done to avoid the obvious pattern of a positive association with trunk diameter for all vine types. Overall, vine abundance should increase with trunk diameter of host trees because larger, older trees have been exposed to vine infestation for a longer time and have a higher available surface. Finally, to verify the expected inverse patterns of abundance of stem twiners and adhesive climbers across tree size, we conducted a correlation analysis between stem twiners and adhesive climbers.

Results

In 0.15 ha of temperate rain forest (60 plots of $25\,\mathrm{m}^2$) there were 2404 individuals from 11 vine species that were climbing the trees (Table 1). Vines showed three general climbing mechanisms: stem twiners, adhesive climbers (both root and tendril climbers) and scandent plants (Table 1). We sampled 2133 individual trees > 1.50-m tall from 26 tree species (Table 2). This sampling included 120 individuals from four shrubs, one fern and one bamboo species (Table 2); however, given that these

Table 1. Species of vines found climbing onto trees in 0.15 ha of the temperate rain forest of southern Chile. Vine diameter (Ø; Mean ± SE; cm) was measured at a height of 1.30 m.

Species	Family	*N*	Ø	Climbing mechanism
Boquila trifoliolata	Lardizabalaceae	926	0.29 ± 0.05	Twining stems
Cissus striata	Vitaceae	185	0.26 ± 0.02	Adhesive tendrils
Elytropus chilensis	Apocynaceae	93	0.44 ± 0.06	Twining stems
Griselinia racemosa	Griseliniaceae	11	0.29 ± 0.01	Scandent plants
Griselinia ruscifolia	Griseliniaceae	82	0.29 ± 0.02	Scandent plants
Hydrangea serratifolia	Hydrangeaceae	378	0.54 ± 0.04	Adhesive roots
Luzuriaga polyphylla	Luzuriagaceae	226	0.16 ± 0.01	Adhesive roots
Luzuriaga radicans	Luzuriagaceae	136	0.15 ± 0.01	Adhesive roots
Mitraria coccinea	Gesneriaceae	313	0.29 ± 0.02	Adhesive roots
Nertera granadensis	Rubiaceae	18	0.11 ± 0.01	Adhesive roots
Sarmienta scandens	Gesneriaceae	36	0.08 ± 0.01	Adhesive roots

Table 2. Trees >1.50-m tall found in 0.15 ha of the temperate rain forest of southern Chile (Valdivian forest). % inf = prevalence of vine infestation [100 (# trees with vines/total # trees)]. DBH = mean trunk diameter at a height of 1.30 m. [1]shrub; [2]bamboo; [3]fern.

Species	*N*	Family	% inf	DBH (cm)	DBH range
Aextoxicon punctatum	99	Aextoxicaceae	47.5	2.16	0.16-21.7
Amomyrtus luma	186	Myrtaceae	41.9	2.40	0.20-17.7
Amomyrtus meli	25	Myrtaceae	40.0	5.11	0.63-11.0
Aristotelia chilensis	106	Elaeocarpaceae	51.9	1.93	0.12-11.1
Azara lanceolata[1]	54	Salicaceae	55.6	1.22	0.17-5.54
Berberis darwinii[1]	14	Berberidaceae	85.7	1.08	0.44-2.42
Caldcluvia paniculata	53	Cunoniaceae	39.6	3.15	0.15-17.2
Chusquea quila[2]	22	Poaceae	22.7	0.53	0.10-1.18
Dasyphyllum diacanthoides	4	Asteraceae	50.0	1.27	0.53-2.60
Drimys winteri	2	Winteraceae	50.0	15.5	0.62-30.3
Embothrium coccineum	25	Proteaceae	20.0	0.88	0.25-6.06
Eucryphia cordifolia	132	Cunoniaceae	34.1	6.77	0.20-191
Fuchsia magellanica[1]	24	Onagraceae	62.5	3.35	0.20-17.3
Gaultheria mucronata[1]	28	Ericaceae	46.4	1.81	0.41-4.46
Gevuina avellana	441	Proteaceae	30.8	5.00	0.14-26.0
Laurelia philippiana	34	Monimiaceae	44.1	13.7	0.31-111
Lomatia ferruginea	32	Proteaceae	37.5	1.31	0.29-4.67
Lomatia hirsuta	8	Proteaceae	62.5	4.76	0.39-14.5
Lophosoria quadripinnata[3]	4	Dicksonaceae	25.0	0.86	0.62-1.18
Luma apiculata	257	Myrtaceae	28.4	4.56	0.30-20.4
Myrceugenia planipes	362	Myrtaceae	47.8	3.10	0.17-34.6
Nothofagus dombeyi	41	Nothofagaceae	39.0	20.9	0.30-90.6
Ovidia pillopillo	13	Thymelaceae	15.4	2.41	0.68-4.88
Pseudopanax laetevirens	13	Araliaceae	46.2	6.84	0.26-24.1
Rhaphithamnus spinosus	130	Verbenaceae	47.7	2.47	0.09-13.7
Weinmannia trichosperma	24	Cunoniaceae	41.7	6.80	0.20-21.1

individuals comprised only 6% of the sample, we retain the use of the term "trees". An ANCOVA showed that tree species did not differ in the prevalence of vine infestation ($F_{25,10} = 1.749$; $P > 0.17$) when tree relative abundance was taken into account (entered as a covariate).

Taking the maximum PAR recorded in plots located under canopy gaps (ca. $1200\,\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) as 100%, the light at forest edges and in mature forest was 29.4-42.2% and 1.8-7.3%, respectively, of full light. Results of the ANCOVA indicate that, when the number and size of host trees are taken into account, light availability in forest plots does not affect vine abundance (Table 3).

As expected, there was a significant relationship between overall vine abundance and host tree trunk diameter ($R = 0.825$; $P < 0.001$; $R^2 = 0.68$; linear regression). More related to the hypotheses tested, we found that while the relative abundance of stem twiners decreased with increasing trunk diameter of host trees ($R = -0.839$; $P < 0.037$; $R^2 = 0.70$; linear regression; Fig. 1), there was an increase in the relative abundance of adhesive climbers with

Table 3. Analysis of variance of the abundance of climbing plants on host trees located in plots with contrasting light availability in the temperate rain forest of southern Chile. The number of host trees and tree basal area in the plot were entered as covariates in the analysis.

Source	*df*	MS	*F*-ratio	*P*
Light environment (Main factor)	2	1010.1	1.381	0.26
Number of trees (Covariate)	1	37.899	0.052	0.82
Tree basal area (Covariate)	1	2479.5	3.389	0.07
Error	55	731.58		

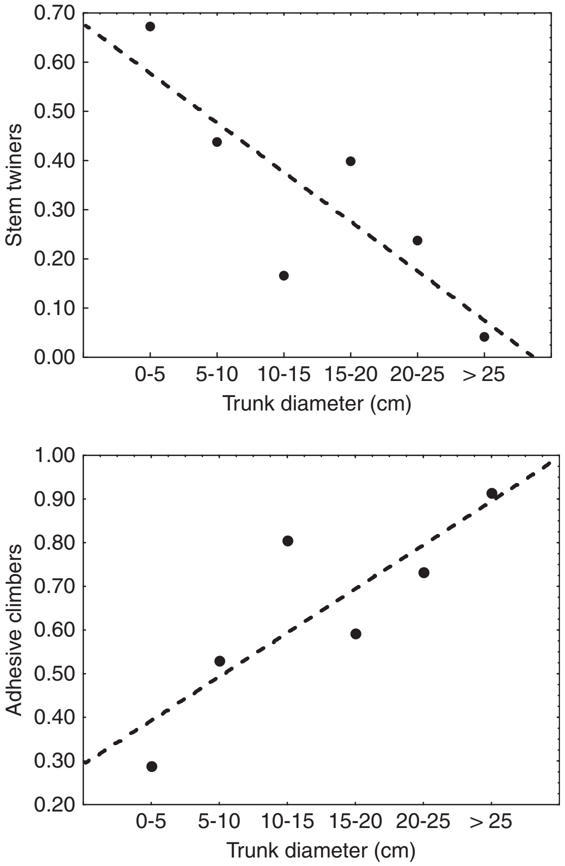

Fig. 1. Change in relative abundance of stem twiners and adhesive climbers with trunk diameter of host trees in the temperate rain forest of southern Chile. Relative abundance = proportion of all vines found showing a given climbing mechanism. Both relationships shown are significant (see text for statistical analyses).

increasing host stem diameter, including both plants with adhesive tendrils and those with adhesive roots ($R = 0.844$; $P < 0.035$; $R^2 = 0.71$; linear regression; Fig. 1). These results are consistent with the overall negative correlation between the abundance of stem twiners and adhesive climbers across the forest ($R = -0.575$; $P < 0.001$; Pearson product-moment correlation). The proportion of scandent plants was low in all tree diameter classes, ranging from 0.01 to 0.04.

Discussion

The abundance of climbing plants in this southern temperate rain forest does not vary along the forest light gradient when the availability of host trees and their size are taken into account. This result agrees with an independent sampling carried out at one of the study sites (Puyehue National Park), which included both non-supported and climbing individuals and found similar abundance of vines under canopy gaps, in secondary forest stands and in the understorey of old-growth forest (Gianoli et al. 2010). Similarly, no clear association between vine abundance and light availability was found in two temperate rain forests in New Zealand (Baars et al. 1998), nor was any change in vine abundance with canopy density found in a mesic temperate forest (Collins & Wein 1993). In contrast, some studies in tropical rain forests report that vines are more common in well-lit environments such as canopy gaps or forest edges (Putz 1984; Hegarty & Caballé 1991; Babweteera et al. 2000; DeWalt et al. 2000; Schnitzer & Carson 2001). However, it must not be inferred that the relationship between vine abundance and light availability depends on latitude. There is evidence of greater abundance of woody vines in forest edges than in the forest interior in a temperate deciduous forest (Londré & Schnitzer 2006), and some studies conducted in tropical rain forests have found that vine abundance is not higher in treefall canopy gaps or in early stages of forest succession (Laurance et al. 2001; Pérez-Salicrup et al. 2001; Mascaro et al. 2004). Understanding the causes of these contrasting patterns of vine abundance in different forests should be one of the main goals of vine ecology research.

We found no differences in vine load among host trees, which indicates that tree species *per se* does not determine susceptibility to vine infestation. An earlier study reported significant vine-tree specific associations in the southern temperate rain forest of Chile (Muñoz et al. 2003) but did not identify the factor(s) underlying such patterns. Another study found that associations between trees and vines became non-significant with time following a hurricane in a temperate floodplain forest (Allen et al. 1997). It is more common to find that general tree characters explain the abundance of climbing plants, regardless of tree species identity (Balfour & Bond 1993; Nabe-Nielsen 2001; Carsten et al. 2002; Campanello et al. 2007; van der Heijden et al. 2008). We found that host tree diameter was positively and significantly associated with overall vine abundance in this temperate rain forest, as also described for tropical and subtropical rain forests (Nabe-Nielsen 2001; Carsten et al. 2002).

The hypothesis that the relative abundance of stem twiners would decrease with the diameter of host tree trunks was verified. A study carried out in a subtropical rain forest in Australia found the same pattern: the presence of stem twining vines decreased with increasing tree diameter (Carsten et al. 2002). We might interpret this pattern as a consequence of the inability of twining vines to maintain tensional forces beyond some trunk diameter, as has been discussed in biomechanical terms (Putz & Holbrook 1991; Silk & Holbrook 2005). In this regard, Putz (1984) commented that evidence of a climber slipping down the trunk is occasionally found around tree bases. We have observed such woody vine coils lying on the forest floor in the case of *Boquila trifoliolata*, the most common stem twiner in the forest. In contrast, DeWalt et al. (2000) reported that the relative abundance of stem twiners in a tropical forest increased with forest stand age (and thus with mean trunk diameter) (Schnitzer & Bongers 2002). A possible explanation for these opposing results could be that the upper diameter of trees differed between the forests studied. Thus, if the oldest trees in the tropical forest had trunks of lower diameter than those of the old-growth temperate rain forest, the limit for stem twiners based on biomechanical constraints might not have been reached. Available information is insufficient to determine if this was the case. Alternatively, the species of stem twiners in each forest might differ in their capacity to attach to very large trees. We also verified the hypothesis that the dominance of adhesive climbers would increase with trunk diameter. The rationale for this was, first, that trunk diameter should not impose an upper limit to this type of vine because of their climbing mode. There is evidence from tropical rain forests in support of this suggestion (Putz 1984; Putz & Chai 1987). Second, we hypothesised that the expected decrease in relative abundance of potentially competing stem twiners in trees with wider trunks should lead to increased use of this released resource by adhesive climbers. Otherwise, we would have found an even pattern of dominance of adhesive climbers across trees of different trunk diameter. The negative correlation between the density of stem twiners and adhesive climbers across the forest suggests that there may be a competitive interaction. Host trees are a limited resource for vines, and despite the frequent observation of trees with heavy vine loads, to our knowledge, field evidence of competition between vines is lacking. Long-term manipulative experiments (species exclusion) would be needed to address vine competition in this temperate rain forest because of the slow growth rate of these shade-tolerant vine species.

The evolution of a climbing habit is associated with enhanced diversification of plant clades (Gianoli 2004), and vines are seemingly increasing in dominance globally (Phillips et al. 2002; Wright et al. 2004; Allen et al. 2007; Swaine & Grace 2007). Therefore, there is a need to enhance our knowledge of the factors that determine vine success. Knowledge on vine ecology is largely generated in tropical ecosystems. Although tropical forests are far richer in vine species than their temperate counterparts, some figures on vine density are comparable (Gentry 1991; Gianoli et al. 2010) and hence vines in temperate forest might play a key role in forest ecology, as has been shown for tropical forests (Schnitzer & Bongers 2002). The present study adds to the evidence that the pattern of vine abundance is independent of light availability in southern temperate rain forests (Baars et al. 1998; Gianoli et al. 2010) and calls for further research to determine whether the relationship between vine abundance and light availability depends on latitude. We have also shown that support suitability across the forest varies with the mechanism by which vines climb, probably due in part to biomechanical constraints and in part to vine interspecific competition, a virtually unexplored ecological factor.

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