

Distribution and abundance of vines along the light gradient in a southern temperate rain forest

Ernesto Gianoli, Alfredo Saldaña, Mylthon Jiménez-Castillo & Fernando Valladares

Abstract

Question: Are vines light-demanding species?

Location: Temperate evergreen rain forest of southern Chile (40°39'S, 72°11'W).

Methods: In 45 plots of 25 m² distributed in treefall canopy gaps, secondary forest stands and old-growth forest (15 plots per light environment), all climbing and non-supported vines were counted and identified to species level, and canopy openness was quantified using hemispherical photographs. Vine abundance and diversity (species richness and Simpson's index) were compared in the three light environments and similarity between vine communities was estimated using Jaccard's similarity coefficient. We also determined the relationship between light niche breadth and local dominance at the species level.

Results: In total there were 2510 vine individuals of 14 species. Canopy openness was significantly different in the three light environments. Species richness, diversity, community composition and density of vines were similar in treefall gaps, secondary and old-growth forest. Of the seven more common vine species, which accounted for 91% of all vines, three had even distribution, two were more abundant in the shaded understorey, and two had higher density in well-lit sites. Local dominance of vine species and niche breadth were not significantly associated.

Conclusions: Our study in a temperate rain forest questions the widespread notion of vines as pioneer-like species, which may be a consequence of the abundance of some lianas in disturbed sites of tropical forests. Functional arguments are needed to justify a general hypothesis on light requirements of vines, which constitute a vast group of species.

Keywords: canopy openness; climbing plants; forest understorey; light availability; pioneer species; tree-fall gaps; Valdivian forest.

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

Introduction

Climbing plants (vines) are a key component of rain forests, particularly of tropical rain forests, where most research on vines has been carried out (Putz & Mooney 1991; Schnitzer & Bongers 2002; Schnitzer 2005). Vine species may account for up to 40% of species diversity (Schnitzer & Bongers 2002) and leaf area (Hegarty & Caballé 1991) in tropical forests, and their dominance seems to be increasing (Phillips et al. 2002; Wright et al. 2004). The particular predominance of climbing plants in tropical regions exceeds in magnitude the overall latitudinal pattern of greater species diversity in the tropics (Gentry 1991; Schnitzer 2005). Consequently, climbing plants of temperate latitudes are distinctive representatives of functional diversity. Comparatively little research on the ecology of vines has been conducted in temperate forests, particularly on southern temperate rain forests (but see Hofstede et al. 2001; Muñoz et al. 2003; Jiménez-Castillo et al. 2007). Because of their Gondwanaland origin, southern temperate rain forests differ floristically from northern temperate and tropical rain forests (Hofstede et al. 2001). Interestingly, southern temperate forests exhibit greater abundance and diversity of vines than northern temperate forests at equivalent latitudes, and also have a greater latitudinal extent in distribution (Gentry 1991; Arroyo

Gianoli, E. (corresponding author, egianoli@udec.cl): Departamento de Botánica, Universidad de Concepción, Casilla 160-C Concepción, Chile; Center for Advanced Studies in Ecology and Biodiversity (CASEB), P. Universidad Católica de Chile, Santiago, Chile; Departamento de Biología, Universidad de La Serena, Casilla 599 La Serena, Chile.

Saldaña, A. (asaldana@udec.cl): Departamento de Botánica, Universidad de Concepción, Casilla 160-C Concepción, Chile.

Jiménez-Castillo, M. (mylthonjimenez@uach.cl): Instituto de Ecología y Evolución, Universidad Austral de Chile, Valdivia, Chile.

Valladares, F. (valladares@ccma.csic.es): Instituto de Recursos Naturales, Centro de Ciencias Medioambientales, CSIC, Madrid, Spain.

et al. 1996). This may be explained by the relatively mild winter temperatures in the south, which are a consequence of the low earth: ocean ratio in southern South America (Arroyo et al. 1996).

The abundance of vines in forest communities is seemingly greater in recent treefall gaps (Putz 1984; Hegarty & Caballé 1991), but the evidence is not yet conclusive (Schnitzer & Bongers 2002). In a tropical rain forest in Panama, the abundance and species richness of woody vines were higher in treefall gaps than in non-gap sites of similar size (Schnitzer & Carson 2001), and liana density was highest in treefall gaps (Putz 1984) and higher in regenerating secondary forest than in older forest stands (DeWalt et al. 2000). In a temperate deciduous forest, lianas were more abundant in forest edges than in the forest interior (Londré & Schnitzer 2006). On the other hand, results from both tropical and temperate ecosystems show that vines can proliferate along the whole light gradient of a forest (Hegarty 1991; Campbell & Newbery 1993; Baars et al. 1998; Pérez-Salicrup et al. 2001; Gerwing 2004; Mascaro et al. 2004). In fact, Putz (1984) reported that the two most frequent lianas in a Panamanian forest rarely reached the canopy and often reproduced in the understorey. Contrasting results regarding vine distribution and abundance along the light gradient in forests might be explained – at least in part – by differences in sampling methodology (see Schnitzer et al. 2006). Recently, several authors have called for unified sampling protocols for woody vines (Gerwing et al. 2006; Schnitzer et al. 2008), but a diversity of methods still persists. Herbaceous vines or thin lianas are often excluded from inventories (Hegarty & Caballé 1991; Muthuramkumar & Parthasarathy 2000), but these thin vines may account for a significant component of local vine richness or abundance (Gentry & Dodson 1987). Because the majority of studies on vine ecology have treated them as a group, it is not possible to discern whether patterns of greater abundance in gaps or forest edges reflect a true pattern of vine species distribution or are a consequence of exceedingly higher abundance of a few pioneer species. For the same reason, there is little information on rather basic issues such as whether vine communities differ in canopy gaps and deep shade environments.

In the present study, we conducted a quantitative analysis of vine distribution and abundance along the light gradient in a southern temperate rain forest, which remains largely unexplored with regard to vine ecology. The general goal was to test whether vine species are light demanding, as has of-

ten been stated in the literature. We compared vine abundance and diversity (species richness) in three distinct light environments: treefall gaps, secondary forest stands and closed canopy old-growth forest. We also analysed separately the abundance of the seven more common vine species. In addition, we estimated the similarity between vine communities in the three light environments. To increase our understanding of the distribution of vines along a light gradient, we also evaluated the relationship between niche breadth and local dominance at the species level. Whereas a trade-off between niche breadth and local dominance along the light gradient would indicate an ecological scenario favouring specialization in the use of light environments, a positive association between niche breadth and local dominance would reveal the existence of dominant and subordinate species across the forest.

Materials and methods

Study site

The temperate rain forest of southern Chile (Valdivian forest) harbours more than 50 species of vines and vascular epiphytes, with a high proportion of endemic species (Armesto et al. 1996; Arroyo et al. 1996). This level of species richness is higher than that of northern temperate rain forests (Muñoz et al. 2003). The Valdivian forest averages about 30 lianas per 0.1 ha, six to seven times as many as in northern temperate rain forests (Gentry 1991).

This study was carried out in an evergreen temperate rain forest located within Puyehue National Park (40°39'S, 72°11'W) in the western foothills of the Andes, southern Chile. The climate is maritime temperate, with average annual precipitation of 3500 mm, and mean maximum and minimum temperature of 13.8°C and 5.4°C, respectively (Almeyda & Sáez 1958; Riveros & Smith-Ramírez 1996). Although there is a marked rainfall decrease in summer (17% of annual precipitation during summer months; Riveros & Smith-Ramírez 1996), no month receives an average rainfall < 100 mm (Almeyda & Sáez 1958). Soils derived from recent volcanic ash are deep, well-drained and acidic (Subiabre & Rojas 1994), and there is low nutrient availability due to low mineralization and high immobilization rates (Lusk et al. 2003; Saldaña & Lusk 2003).

The old-growth lowland forest is composed of broadleaf, evergreen tree species. The dominant canopy

species are *Laurelia philippiana* (Atherospermataceae), *Aextoxicon punctatum* (Aextoxicaceae), *Nothofagus dombeyi* (Fagaceae) and *Eucryphia cordifolia* (Cunoniaceae). Less abundant canopy trees include *Dasyphyllum diacanthoides* (Asteraceae), *Luma apiculata* (Myrtaceae) and *Weinmannia trichosperma* (Cunoniaceae). Advanced regeneration in the understorey is composed of these tree species in addition to *Amomyrtus luma* (Myrtaceae), *Azara serrata* (Flacourtiaceae), *Caldcluvia paniculata* (Cunoniaceae), *Gevuina avellana* (Proteaceae), *Myrceugenia planipes* (Myrtaceae) and *Rhaphithamnus spinosus* (Verbenaceae) (Saldaña & Lusk 2003). Common tree species in treefall gaps are *L. apiculata*, *C. paniculata*, *Embothrium coccineum* (Proteaceae) and *Aristotelia chilensis* (Elaeocarpaceae) (Lusk 2002; Lusk & Del Pozo 2002). In general, most tree species have intermediate light requirements (Lusk et al. 2006). Herbaceous and woody vines are rather abundant in this lowland forest and occur up to 900 m elevation, with only a few species reaching the forest canopy (Muñoz-Schick 1980; Gianoli et al., unpubl. data).

Sampling

Vine sampling took place in 45 small plots (5 m × 5 m) located in the vicinity of El Indio and La Princesa trails at Puyehue National Park (350 m a.s.l.). Plots were located within an area of ca. 30 ha, and were chosen at random after walking along transects laid out in arbitrary directions from the trails towards the forest interior, being separated by at least 100 m. Plot size was small in order to allow proper comparisons between forest sites that include treefall gaps, which in this and other mature forests are often small (see Schnitzer & Carson 2001). We chose 15 plots to correspond to each of three forest successional stages that are associated with decreasing light availability: treefall canopy gaps, secondary forest stands and closed canopy old-growth forest. To validate this subjective classification of light environments, we quantified light availability in each of the 45 plots using hemispherical photographs. The photographs were taken 0.5 m above the ground at the centre of each plot, using a horizontally levelled digital camera with a fish-eye lens with 180° field of view (FCE8, Nikon) mounted on a tripod and aimed at the zenith. Each hemispherical photograph was analysed using HemiView canopy analysis software version 2.1 (1999, Delta-T Devices Ltd, UK). All photographs were taken under homogenous sky conditions (cloudy). The percentage of canopy openness and global site factor (GSF, the fraction of total radia-

tion expected to reach the spot where the photograph was taken) were calculated with HemiView considering the geographic characteristics of the site. A total of 160 sky sectors were considered resulting from eight azimuth × 20 zenith divisions.

In each of the 45 plots we counted and identified to species level all climbing plant individuals rooted within the plot, excluding epiphytes. Self-supported seedlings and older individuals trailing through the forest understorey or actually climbing onto trees or shrubs were counted, so as to not exclude thin vines from the sampling. We strived to include only independently growing stems not connected above-ground to any other censused stem (apparent genets; Mascaro et al. 2004; Schnitzer 2005). This was checked by removing litter. However, in some cases we could not reject with total certainty the possibility of belowground connections. As a general rule, individuals were treated as genets unless it was evident that they had connections with other vines.

Analyses

Vine abundance and diversity (species richness and Simpson's index) were compared in the three distinct light environments (treefall gaps, secondary forest stands, closed canopy old-growth forest) using a one-way ANOVA ($n = 15$ per group). We used the modification of Simpson's index of diversity ($1 - D$) suggested by Pielou (Krebs 1999):

$$1 - D = 1 - \sum_{i=1}^s \left[\frac{n_i(n_i - 1)}{N(N - 1)} \right],$$

where n_i is the number of individuals of species i in the sample, N is the total number of individuals in the sample, and s is the number of species in the sample. In addition, the effect of light availability on vine abundance was estimated separately for the seven more common vine species using one-way ANOVAs. Values of abundance were log-transformed before statistical analysis in order to meet ANOVA assumptions.

The similarity between vine communities found in the three distinct light environments was estimated using Jaccard's similarity coefficient, S_j (Krebs 1999):

$$S_j = \frac{a}{a + b + c},$$

where a is the number of shared species and b and c are the number of species exclusive to the first and second communities, respectively. Values of S_j range

from 0 (complete dissimilarity) to 1 (identical communities).

To evaluate the relationship between niche breadth and local dominance along the light gradient, we first defined the light niche breadth for each species as the range in GSF units of the plots where the species was found. This value was standardized by dividing by the maximum light niche breadth possible, i.e. the range in GSF units recorded in all 45 plots. Thus, the standardized light niche breadth had a maximum value of 1. We then estimated local dominance for each species as the average of the relative abundance (abundance of the species/total vine abundance in the plot) in each of the plots where the species was found. The relationship between light niche breadth and local dominance at the species level was determined using correlation analysis (Pearson's product-moment correlation). All analyses were performed using Statistica (6.0, Statsoft).

Results

In 45 plots of 25 m² there were 2510 vine individuals from 14 species, 11 genera and 10 families (Table 1). Twelve of the 14 species are endemic to temperate rain forests of southern South America, and seven of these 12 endemic species constitute monotypic genera (Table 1). All but one of the species found (*Nertera granadensis*) were woody vines. The seven more common vine species accounted for 91% of individuals.

Canopy openness in the plots ranged from 99.8% to 7.3%. Light availability (GSF) ranged from 0.33 to 0.03, thus the entire light gradient consisted of 0.30 GSF units. The percentage of canopy

openness was significantly different in the three light environments defined in the field ($F_{2,42} = 33.03$; $P < 0.001$; $n = 15$ plots per light environment; one-way ANOVA). Mean values (\pm SE) of canopy openness in treefall gaps ($82.4 \pm 6.8\%$), secondary forest ($42.0 \pm 7.9\%$) and old-growth forest ($13.1 \pm 1.2\%$) differed markedly from each other ($P < 0.01$, Tukey test). Likewise, the proportion of total radiation reaching a plot (GSF) differed significantly in the three distinct light environments ($F_{2,42} = 30.31$; $P < 0.001$).

Species richness was similar in treefall gaps, secondary forest and old-growth forest ($F_{2,42} = 1.67$; $P > 0.20$; $n = 15$ plots per light environment; one-way ANOVA) (Fig. 1). Vine diversity (Simpson's index, Mean \pm SE) was also similar in treefall gaps (0.65 ± 0.04), secondary forest (0.71 ± 0.03) and old-growth forest (0.64 ± 0.03) ($F_{2,42} = 1.42$; $P > 0.25$). According to Jaccard's coefficient (S_j), the vine community in the three light environments was similar: treefall gaps-secondary forest $S_j = 0.79$, secondary forest-mature forest $S_j = 0.77$, treefall gaps-mature forest $S_j = 0.69$. This is consistent with the fact that nine of the 14 species (64.3%) were found at least once in each of the three light environments (Table 1).

Vine density (per 25 m², Mean \pm SE) was not significantly different in treefall gaps (67.6 ± 9.3), secondary forest (54.3 ± 6.3) and old-growth forest (45.4 ± 4.9) ($F_{2,42} = 1.88$; $P > 0.16$; $n = 15$ plots per light environment; one-way ANOVA on log-transformed data; Fig. 1) (similar results were found when vine density was regressed against canopy openness numbers; data not shown). The same even pattern of distribution along the light gradient was found for three of the seven more common vine species: *Boquila trifoliolata* ($F_{2,42} = 0.50$; $P > 0.60$),

Table 1. Species of climbing plants found in Puyehue temperate rainforest. Between brackets: number of species in the genus. Species distribution: STR, Southern temperate rain forest of Chile and Argentina; SA, South America; AM, Americas. Light gradient: TG, treefall canopy gaps; SF, secondary forest stands; OG, old-growth forest.

Species	Distribution	Family	Light gradient
<i>Asteranthera ovata</i> (1)	STR	Gesneriaceae	– SF – OG
<i>Boquila trifoliolata</i> (1)	STR	Lardizabalaceae	TG – SF – OG
<i>Campsidium valdivianum</i> (1)	STR	Bignoniaceae	– SF –
<i>Cissus striata</i> (350)	SA	Vitaceae	TG – SF – OG
<i>Elytropus chilensis</i> (1)	STR	Apocynaceae	TG – SF – OG
<i>Ercilla volubilis</i> (1)	STR	Phytolaccaceae	TG – –
<i>Griselinia racemosa</i> (7)	STR	Griselinaceae	TG – SF –
<i>Griselinia ruscifolia</i> (7)	STR	Griselinaceae	TG – SF –
<i>Hydrangea serratifolia</i> (23)	STR	Hydrangeaceae	TG – SF – OG
<i>Luzuriaga polyphylla</i> (4)	STR	Luzuriagaceae	TG – SF – OG
<i>Luzuriaga radicans</i> (4)	STR	Luzuriagaceae	TG – SF – OG
<i>Mitraria coccinea</i> (1)	STR	Gesneriaceae	TG – SF – OG
<i>Nertera granadensis</i> (15)	AM	Rubiaceae	TG – SF – OG
<i>Sarmienta scandens</i> (1)	STR	Gesneriaceae	TG – SF – OG

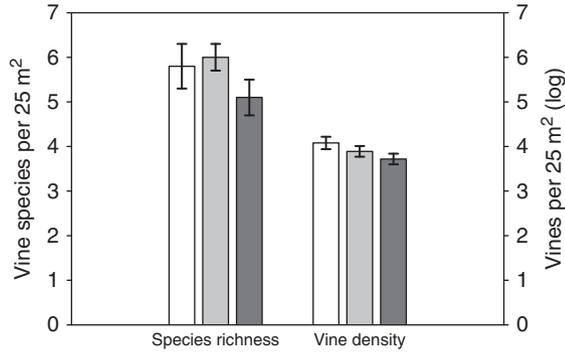


Fig. 1. Species richness and abundance of vines (Mean \pm SE) in 25-m² plots in three distinct light environments in Puyehue temperate rain forest, southern Chile. White bars: treefall canopy gaps; Grey bars: secondary forest stands; Black bars: closed canopy old-growth forest. $n = 15$ plots per light environment. There were no significant differences among light environments for vine diversity or for vine density (one-way ANOVA).

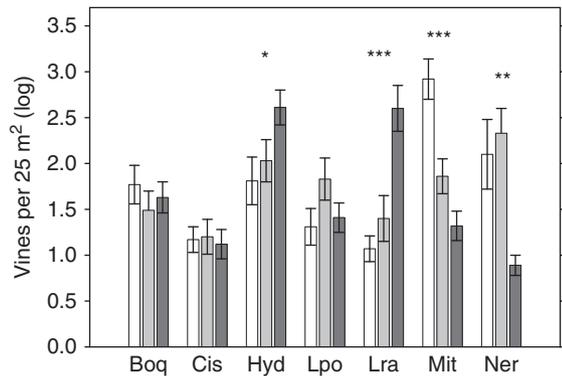


Fig. 2. Abundance of vines (Mean \pm SE) in 25-m² plots in three distinct light environments in Puyehue temperate rain forest, Southern Chile. White bars: treefall canopy gaps; Grey bars: secondary forest stands; Black bars: closed canopy old-growth forest. The seven more common vine species, which accounted for 91% of all vines, are shown. Boq: *Boquila trifoliolata*, Cis: *Cissus striata*, Hyd: *Hydrangea serratifolia*, Lpo: *Luzuriaga polyphylla*, Lra: *L. radicans*, Mit: *Mitraria coccinea*, Ner: *Nertera granadensis*. Asterisks indicate significant differences among light environments. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (one-way ANOVA).

Cissus striata ($F_{2,42} = 0.06$; $P > 0.94$) and *Luzuriaga polyphylla* ($F_{2,42} = 1.92$; $P > 0.15$) (Fig. 2). In the case of *L. radicans* ($F_{2,42} = 13.09$; $P < 0.001$) and *Hydrangea serratifolia* ($F_{2,42} = 3.24$; $P < 0.05$), their abundance was highest in the shaded understory of mature forest (Fig. 2). In contrast, the abundance of *Mitraria coccinea* ($F_{2,42} = 18.52$; $P < 0.001$) and *Nertera granadensis* ($F_{2,42} = 7.98$; $P < 0.005$) was greatest in open sites (Fig. 2).

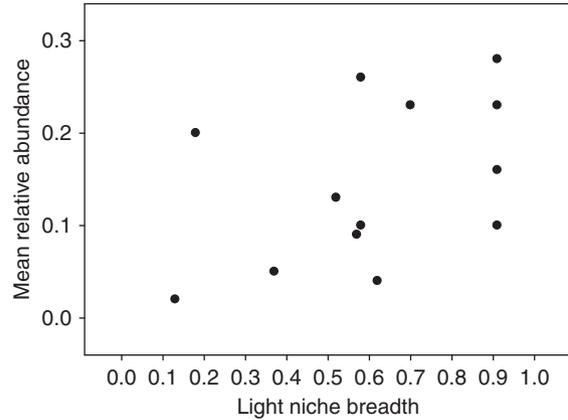


Fig. 3. The relationship between niche breadth and local dominance along the light gradient for 13 vine species in Puyehue temperate rain forest. Light niche breadth was estimated as the range in GSF units (Global Site Factor, the fraction of total radiation reaching the plot, calculated from hemispherical photographs) where the species was found. This value was standardized by dividing by the maximum light niche breadth possible, i.e. the range in GSF units recorded in all 45 plots. Local dominance was estimated as the average of the relative abundance (abundance of the species/total vine abundance in the plot) in each of the plots where the species was found.

Most vine species had a broad light niche. Nine of 13 species analysed had values of niche breadth above 0.5 (Fig. 3). Light niche breadth and mean relative abundance were not associated at the species level ($r = 0.44$; $P > 0.137$; $n = 13$; Pearson's product-moment correlation) (Fig. 3). The species *Campsi-dium valdivianum* was excluded from this analysis because it was found only in one plot and hence its niche breadth could not be calculated.

Discussion

To our knowledge, this is the first quantitative analysis of distribution and abundance of climbing plants along a light gradient in the temperate rain forest of South America, and the second in a southern temperate rain forest. Baars et al. (1998), working in two rain forests in New Zealand, concluded that light availability was not a good predictor of vine species presence. These authors considered that the more common vines at each site were moderate light species (Baars et al. 1998). Similarly, we found that species richness and diversity of vines was similar in treefall gaps, secondary forest and old-growth forest. Moreover, vine community composition did not differ among light environments, and roughly two-thirds of vine species were

recorded in all three light environments. Therefore, available data from southern temperate rain forests do not support the notion of vines as pioneer or 'light-hungry' species. Other studies in the tropics have found similar results. In a comprehensive survey of vines in a mature tropical rain forest, Putz (1984) reported that, as the forest grows back after treefalls, the species composition of the vine community remains almost unaltered. Gerwing (2004) studied life history of six vine species in an old-growth Amazonian forest and classified two of them as late successional species and only one as a pioneer species. Hegarty (1991) classified 40% of the 38 more common lianas in an Australian subtropical forest as species of later succession. The idea of vines as gap species or forest edge species may be consequence of the impressive abundance that some lianas exhibit in disturbed sites of particular tropical forests (e.g. Balée & Campbell 1990; Pérez-Salicrup et al. 2001). Analysis of published evidence preliminarily suggests that the climbing habit is not particularly associated with open sites.

Comparison of vine abundance data from different studies is complicated due to the use of different sampling protocols and criteria (Schnitzer et al. 2006). Our study site, Puyehue, had the highest population density of any climbing species (*Hydrangea serratifolia*) at any site among 97 sites sampled worldwide in equivalent 0.1-ha plots (Gentry 1991). However, it is difficult to compare our vine abundance data, which are from vines of any diameter and any height, excluding hemiepiphytes, with those of Gentry (1991), which are from woody vines ≥ 2.5 cm dbh, including hemiepiphytes. Other studies of vine abundance have considered stem diameter thresholds ranging from 0.5 cm dbh (DeWalt et al. 2000; DeWalt & Chave 2004) to 10 cm dbh (reviewed in Muthuramkumar & Parthasarathy 2000). The sampling protocols to estimate abundance of woody vines in mature rain forests used by Putz (1984) in Barro Colorado Island, Panama, and by Mascaro et al. (2004) in La Selva Biological Station, Costa Rica, are relatively comparable to ours. In Putz (1984), non-supported vines were not excluded unless they were < 10 cm tall, and climbing liana stems were counted if > 1 cm dbh. In Mascaro et al. (2004), all climbing and non-supported woody vines ≥ 1.3 -m long and 2 mm in diameter were included. Whereas in Barro Colorado Putz (1984) reported 3165 woody vines per ha, Mascaro et al. (2004) found 1493 lianas per ha in La Selva. If we exclude the single herbaceous vine considered in our survey in Puyehue, a grand total of 18 000 woody vines per ha is obtained. This suggests that, even

after correcting for the vine size classes included in our inventory and excluded in those of Putz (1984) and Mascaro et al. (2004), the liana density recorded in the temperate rain forest of Puyehue would be similar to (or even greater than) that reported for mature tropical rain forests. While liana density numbers seem to be comparable between temperate and tropical rain forests, liana diversity is markedly different. Whereas we found 13 woody vine species in the Puyehue temperate rain forest, Putz (1984) and Mascaro et al. (2004) reported 65 and 60 liana species, respectively, in their tropical rain forests.

Vine abundance was similar in treefall gaps, secondary forest and old-growth forest in Puyehue. Focusing only on vine individuals actually climbing onto supporting trees, we recently found, in a study conducted in Puyehue and another site in the Valdivian forest, that light availability in forest plots did not affect vine abundance when the number and size of host trees was taken into account (Carrasco-Urra & Gianoli, *in press*). These results are in contrast with other studies reporting increased density of vines with light availability in a temperate forest (Londré & Schnitzer 2006) and in tropical forests in Central America (Putz 1984; DeWalt et al. 2000; Schnitzer & Carson 2001), Africa (Babweteera et al. 2000) and Asia (van Schaik & Mirmanto 1985). Conversely, other studies have shown that vine abundance is not higher in treefall gaps or in early successional stages (Collins & Wein 1993; Laurance et al. 2001; Pérez-Salicrup et al. 2001; Mascaro et al. 2004; Madeira et al. 2009). Most studies addressing patterns of vine abundance treat vines as a single group. It might be misleading to label vines as pioneer species based on comparisons taking vines as a group because this pattern may be caused by a few very abundant vine species that exceed in number the rest of the vine community, which may include the whole spectrum of shade tolerance. In one of the few studies addressing this issue, Londré & Schnitzer (2006) reported both the global pattern of vine abundance and that of the more common species. They found that the pattern of increased abundance with light availability holds at both group and species levels. Likewise, our global pattern of comparable vine abundance across the light gradient was confirmed when the analysis considered the seven more common vine species, which accounted for 91% of all vines. Thus, three species showed even distribution, two species were more abundant in the shaded understorey, and two species showed greater density in well-lit sites.

We did not detect a significant relationship between niche breadth and local dominance of vine species. Whereas the lack of a negative relationship

(trade-off) suggests that the ecological scenario does not promote specialization in light use within the vine assemblage as a means of achieving coexistence, the lack of a positive relationship indicates that there are no overly dominant vine species across the light gradient in this forest. Interestingly, a somewhat similar pattern was found for tree species in Puyehue, where pair-wise overlap of species distribution in relation to canopy openness did not depart significantly from predictions of a null model of community structure (Lusk et al. 2006).

Vines constitute a vast group of species. About one-third of plant families include vines (Gentry 1991). The climbing habit has evolved several times during plant evolution and has boosted plant diversification (Gianoli 2004). Is this huge group of species predominantly light-demanding? We think that the available data, discussed above, do not support this idea. Furthermore, it has been shown that vines have similar life history trade-offs along forest light environments as trees (Gilbert et al. 2006). We consider that functional arguments related to the resource environment are needed in order to justify the hypothesis of vines as pioneer-like species. Schnitzer & Carson (2001) put forward some interesting hypotheses to explain why gaps could have a higher species richness of vines, thus providing a starting point for this discussion. Experimental approaches and thorough reviews of the literature will shed light on this question. Ongoing research is evaluating ecophysiological traits related to light exploitation in the vine species of this southern temperate rain forest. These data will be useful to provide a mechanistic explanation for the patterns herein reported.

Acknowledgements. We are grateful to Fernando Carrasco, Cristian Salgado, Marcos Cea, Mónica Cisternas and Diego Gianoli for help in the field. We thank CONAF for granting permits to work in Puyehue National Park. This study was funded by FONDECYT grant 1070503.

References

- Almeyda, E. & Sáez, F. 1958. *Recopilación de datos climáticos de Chile y mapas sinópticos respectivos*. Ministerio de Agricultura, Santiago, CL.
- Armesto, J.J., León-Lobos, P. & Arroyo, M.K. 1996. Los bosques templados del sur de Chile y Argentina: una isla biogeográfica. In: Armesto, J.J., Villagrán, C. & Arroyo, M.K. (eds.) *Ecología de los bosques nativos de Chile*. pp. 23–28. Editorial Universitaria, Santiago, CL.
- Arroyo, M.K., Cavieres, L., Peñalosa, A., Riveros, M. & Faggi, A.M. (1996). Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. In: Armesto, J.J., Villagrán, C. & Arroyo, M.K. (eds.) *Ecología de los bosques nativos de Chile*. pp. 71–99. Editorial Universitaria, Santiago, CL.
- Baars, R., Kelly, D. & Sparrow, A.D. 1998. Liane distribution within native forest remnants in two regions of the South Island, New Zealand. *New Zealand Journal of Ecology* 22: 71–85.
- Babweteera, F., Plumptre, A. & Obua, J. 2000. Effect of gap size and age on climber abundance and diversity in Budongo Forest Reserve, Uganda. *African Journal of Ecology* 38: 230–237.
- Balée, W. & Campbell, D.G. 1990. Evidence for the successional status of liana forest (Xingu river basin, Amazonian Brazil). *Biotropica* 22: 36–47.
- Campbell, E.J.F. & Newbery, D.McC. 1993. Ecological relationships between lianas and trees in lowland rain forest in Sabah, East Malaysia. *Journal of Tropical Ecology* 9: 469–490.
- Carrasco-Urra, F. & Gianoli, E. Abundance of climbing plants in a southern temperate rain forest: host-tree characteristics or light availability? *Journal of Vegetation Science*, in press. DOI: 10.1111/j.1654-1103.2009.01115.x.
- Collins, B.S. & Wein, G.R. 1993. Understorey vines: distribution and relation to environment on a southern mixed hardwood site. *Bulletin of the Torrey Botanical Club* 120: 38–44.
- DeWalt, S.J. & Chave, J. 2004. Structure and biomass of four lowland neotropical forests. *Biotropica* 36: 7–19.
- DeWalt, S.J., Schnitzer, S.A. & Denslow, J.S. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology* 16: 1–9.
- Gentry, A.H. 1991. The distribution and evolution of climbing plants. In: Putz, F.E. & Mooney, H.A. (eds.) *The biology of vines*. pp. 3–49. Cambridge University Press, Cambridge, UK.
- Gentry, A.H. & Dodson, C. 1987. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19: 149–156.
- Gerwing, J.J. 2004. Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. *Forest Ecology and Management* 190: 57–72.
- Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N., Foster, R., Kenfack, D., Martínez-Ramos, M., Parren, M., Parthasarathy, N., Pérez-Salicrup, D.R., Putz, F.E. & Thomas, D.W. 2006. A standard protocol for liana censuses. *Biotropica* 38: 256–261.
- Gianoli, E. 2004. Evolution of a climbing habit promotes diversification in flowering plants. *Proceedings of the Royal Society B – Biological Sciences* 271: 2011–2015.
- Gilbert, B., Wright, S.J., Muller-Landau, H.C., Kitajima, K. & Hernández, A. 2006. Life history trade-offs in tropical trees and lianas. *Ecology* 87: 1281–1288.

- Hegarty, E.E. 1991. Leaf litter production by lianes and trees in a sub-tropical Australian rain forest. *Journal of Tropical Ecology* 7: 201–214.
- Hegarty, E.E. & Caballé, G. 1991. Distribution and abundance of vines in forest communities. In: Putz, F.E. & Mooney, H.A. (eds.) *The biology of vines*. pp. 313–336. Cambridge University Press, Cambridge, UK.
- Hofstede, R.G.M., Dickinson, K.J.M. & Mark, A.F. 2001. Distribution, abundance and biomass of epiphyte-lianoid communities in a New Zealand lowland Nothofagus-podocarp temperate rain forest: tropical comparisons. *Journal of Biogeography* 28: 1033–1049.
- Jiménez-Castillo, M., Wisser, S.K. & Lusk, C.H. 2007. Elevational parallels of latitudinal variation in the proportion of lianas in woody floras. *Journal of Biogeography* 34: 163–168.
- Krebs, C.J. 1999. *Ecological methodology*. Benjamin Cummings, New York, US.
- Laurance, W.F., Pérez-Salicrup, D., Delamonica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L. & Lovejoy, T.E. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82: 105–116.
- Londré, R.A. & Schnitzer, S.A. 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. *Ecology* 87: 2973–2978.
- Lusk, C.H. 2002. Leaf area accumulation helps juvenile trees tolerate shade in a temperate rainforest. *Oecologia* 132: 188–196.
- Lusk, C.H. & Del Pozo, A. 2002. Survival and growth of seedlings of 12 Chilean rainforest trees in two light environments: gas exchange and biomass distribution correlates. *Austral Ecology* 27: 173–182.
- Lusk, C.H., Matus, F., Moreno-Chacón, M., Saldaña, A. & Jiménez-Castillo, M. 2003. Variación estacional en concentraciones de nutrientes en la hojarasca de cuatro especies arbóreas de la pluviselva Valdiviana. *Gayana Botánica* 60: 35–39.
- Lusk, C.H., Chazdon, R.L. & Hofmann, G. 2006. A bounded null model explains juvenile tree community structure along light availability gradients in a temperate rain forest. *Oikos* 112: 131–137.
- Madeira, B.G., Espírito-Santo, M.M., Neto, S.D., Nunes, Y.R.F., Azofeifa, G.A.S., Fernández, G.W. & Quesada, M. 2009. Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecology* 201: 291–304.
- Mascaro, J., Schnitzer, S.A. & Carson, W.P. 2004. Liana diversity, abundance and mortality in a tropical wet forest in Costa Rica. *Forest Ecology and Management* 190: 3–14.
- Muñoz, A.A., Chacón, P., Pérez, F., Barnert, E.S. & Armesto, J.J. 2003. Diversity and host tree preferences of vascular epiphytes and vines in a temperate rainforest in southern Chile. *Australian Journal of Botany* 51: 381–391.
- Muñoz-Schick, M. 1980. *Flora del Parque Nacional Puyehue*. Editorial Universitaria, Santiago, CL.
- Muthuramkumar, S. & Parthasarathy, N. 2000. Alpha diversity of lianas in a tropical evergreen forest in the Anamalais, Western Ghats, India. *Diversity and Distributions* 6: 1–14.
- Pérez-Salicrup, D.R., Sork, V.L. & Putz, F.E. 2001. Lianas and trees in a liana forest in Amazonian Bolivia. *Biotropica* 33: 34–47.
- Phillips, O.L., Martínez, R.V., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Monteagudo-Mendoza, A., Neill, D., Vargas-Núñez, P., Alexiades, M., Cerón, C., Fiore, A.D., Erwin, T., Jardim, A., Palacios, W., Saldías, M. & Vinceti, B. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770–774.
- Putz, F.E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713–1724.
- Putz, F.E. & Mooney, H.A. 1991. *The biology of vines*. Cambridge University Press, Cambridge, UK.
- Riveros, M. & Smith-Ramírez, C. (1996). Patrones de floración y fructificación en bosques del sur de Chile. In: Armesto, J.J., Villagrán, C. & Arroyo, M.K. (eds.) *Ecología de los bosques nativos de Chile*. pp. 235–250. Editorial Universitaria, Santiago, CL.
- Saldaña, A. & Lusk, C.H. 2003. Influencia de las especies del dosel en la disponibilidad de recursos y regeneración avanzada en un bosque templado lluvioso del sur de Chile. *Revista Chilena de Historia Natural* 76: 639–650.
- Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166: 262–276.
- Schnitzer, S.A. & Bongers, F. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17: 223–230.
- Schnitzer, S.A. & Carson, W.P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82: 913–919.
- Schnitzer, S.A., DeWalt, S.J. & Chave, J. 2006. Censusing and measuring lianas: a quantitative comparison of the common methods. *Biotropica* 38: 581–591.
- Schnitzer, S.A., Rutishauser, S. & Aguilar, S. 2008. Supplemental protocol for liana censuses. *Forest Ecology and Management* 255: 1044–1049.
- Stevens, P.F. 2001 onwards. Angiosperm Phylogeny Website. Version 9, 2008. <http://www.mobot.org/MOBOT/research/APweb/>
- Subiabre, A. & Rojas, C. 1994. *Geografía física de la Región de Los Lagos*. Ediciones Universidad Austral de Chile, Valdivia, CL.
- Van Schaik, C.P. & Mirmanto, E. 1985. Spatial variation in the structure and litterfall of a Sumatran rain forest. *Biotropica* 17: 196–205.
- Wright, S.J., Calderón, O., Hernández, A. & Paton, S. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Barro Colorado Island, Panamá. *Ecology* 85: 484–489.

Received 23 May 2009;

Accepted 19 August 2009.

Co-ordinating Editor: B. Collins.