

Diversity and host tree preferences of vascular epiphytes and vines in a temperate rainforest in southern Chile

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Abstract. Vines and epiphytes contribute importantly to the biodiversity of temperate rainforests of southern South America. However, compared with their tropical counterparts, these functional groups have received less attention. We evaluated diversity, floristic composition and relative abundance of vascular epiphytes and vines within a humid temperate forest in northern Chiloé Island, southern Chile. We assessed whether epiphyte and vine species exhibit preferences among host tree species and tested whether species richness on tree hosts differs from that expected by chance, by comparing observed frequencies of occurrence (FO) and species richness with randomly simulated frequency distributions generated under the assumption of no epiphyte preferences. Finally, we tested for associations of epiphyte and vine species with host tree size (trunk diameter at breast height). Eleven species of ferns and nine angiosperms (seven vines, one epiphytic angiosperm and one shrub) were recorded growing epiphytically in a sample of 499 trees. The most abundant species were three vines, *Luzuriaga polyphylla* (Hook.) Macbr., *Griselinia racemosa* (Phil.) Taub. and *Mitraria coccinea* Cav., and five species of filmy ferns (Hymenophyllaceae). Most epiphytes and vines (65%) showed preference for one or two tree species, with seven species being overrepresented on *Podocarpus nubigena* Lindl. hosts and 10 underrepresented on *Drimys winteri* J.R. et G.Forster. Epiphyte and vine species richness was significantly lower than expected by chance on *D. winteri* and higher than expected on *Nothofagus nitida* (Phil.) Krasser. Three epiphytic ferns showed preferences for large-sized trees, while frequency of occurrence of three common vines was independent of host tree size.

Introduction

Vascular epiphytes and vines are known to contribute significantly to species diversity, primary productivity, biomass and litterfall in tropical rainforests (Gentry and Dodson 1987; Hegarty 1991; Benzing 1995; Nabe-Nielsen 2001; Nieder *et al.* 2001). In contrast, there is insufficient knowledge about the biodiversity and ecological importance of these lifeforms in temperate forest ecosystems (but see Dickinson *et al.* 1993; Hofstede *et al.* 2001).

Temperate rainforests of southern South America exhibit a very rich floristic assemblage, including more than 50 species of vascular epiphytes (among ferns and angiosperms) and vines and high levels of endemism both at the species and higher taxonomic levels (Armesto *et al.* 1996a; Arroyo *et al.* 1996a, 1996b). Further, epiphytes and vines contribute significantly to total ecosystem biomass, with estimates of up to 4–8 t ha⁻¹ in coastal forests of Chiloé

Island, southern Chile (Pérez *et al.* 1991; J. J. Armesto *et al.* unpubl. data).

The diversity and biomass of epiphytes and vines in these rainforests (Godoy *et al.* 1981; Riveros and Ramírez 1978; Villagrán *et al.* 1986; see also Clement *et al.* 2001) is comparable to that of New Zealand coastal forests (Hofstede *et al.* 2001). This high diversity of vascular epiphytes and vines in southern temperate forests contrasts with their almost complete absence from North American rainforests in the Pacific north-west (Alaback 1996; Sillett 1999), but is comparable to the species richness of ferns and lianas reported for warm-temperate rainforests of southern Australia (Fisher 1985 in Arroyo *et al.* 1996a). Epiphytes and vines could play a significant role in community and ecosystem-level processes. For instance, a number of epiphytes and vines in southern Chilean forests have red tubular flowers that are pollinated by hummingbirds; thus

they contribute an important source of energy for animals that participate in mutualistic interactions (Willson *et al.* 1996; Armesto *et al.* 1996b). From the point of view of biogeochemical processes, some epiphytes create favourable microsites for nitrogen-fixing free-living bacteria (Brighigna *et al.* 1992). Epiphytes also increase retention of water derived from precipitation within the forest (Veneklaas and Van Ek 1990; Veneklaas *et al.* 1990). Finally, the high growth efficiency (including leaf production and root growth), as a result of being free from the energetic costs of building their own supporting structures, allows vines and epiphytes to make greater contributions to primary productivity, litterfall and nutrient cycling than their basal area or biomass would suggest (Putz 1983; Hegarty 1991).

Despite the ecological importance of epiphytes and vines in southern temperate forests, basic aspects of their ecology, including the degree of host-tree specificity and within-forest vertical and horizontal distribution, abundance and diversity patterns, remain mostly unknown (but see Riveros and Ramírez 1978; Godoy *et al.* 1981; Clement *et al.* 2001). Although epiphytic plants and vines use tree trunks and branches for support, the quality of this substrate may vary with tree identity, size or age. For instance, Riveros and Ramírez (1978) found differences in epiphyte species richness among four tree species and describe a few host-specific associations in Valdivian rainforests in southern Chile. Various studies in tropical rainforests have also detected host-specific associations among epiphytic angiosperms (e.g. Todzia 1986; Ter Steege and Cornelissen 1989; Díaz-Santos 2000) and lianas (e.g. Putz and Chai 1987; Clark and Clark 1990; Campbell and Newbery 1993; Talley *et al.* 1996a, 1996b; Carsten *et al.* 2002). Epiphyte and vine species richness, composition and relative abundance often vary among host tree species (e.g. Ter Steege and Cornelissen 1989; Zapfack *et al.* 1996), presumably owing to differences in bark texture, roughness and allelopathic effects (Todzia 1986; Talley *et al.* 1996a, 1996b), as well as with tree trunk diameter (Catling and Lefkovitch 1989; Talley *et al.* 1996a; Dunn 2000; Annaselvam and Parthasarathy 2001; Nabe-Nielsen 2001; Carsten *et al.* 2002).

Temperate rainforests of southern South America are threatened by land clearing for agriculture, lack of sustainable forestry practices, massive timber extraction for woodchip production and replacement of native forests by commercial monocultures of exotic trees (Lara *et al.* 1996; Armesto *et al.* 1998). Consequently, knowledge of host-tree specificity relationships of epiphytes (ferns and angiosperms) and vines, and species richness on different host trees in Chilean temperate rainforests, could help us understand how epiphyte and vine biodiversity depends on forest structure and how it can change as a consequence of logging (see Godoy *et al.* 1981; Aravena *et al.* 2002). Recent studies in tropical forests have shown that epiphyte and vine

species richness and abundance decrease significantly in second-growth forests compared with old-growth forests (e.g. Dunn 2000; Barthlott *et al.* 2001).

In this study we addressed the following questions:

- (1) What is the overall species richness, floristic composition and relative abundance of vascular epiphytes (including ferns and angiosperms) and vines, present within a representative sample of old-growth North Patagonian rainforest fragment in northern Chiloé Island, southern Chile?
- (2) Do vascular epiphytes and vines exhibit preferences (selectivity) or rejection for the most common host tree species within this old-growth forest?
- (3) How does vascular epiphyte and vine species richness vary among different host tree species?
- (4) Do vascular epiphytes and vines occupy host trees independently of size (trunk diameter)?

Materials and methods

Study site

The study was conducted within c. 10 ha of humid, old-growth rainforest in the vicinity of Estación Biológica 'Senda Darwin' (41°53'S; 73°40'W), c. 15 km north-east of the city of Ancud, northern Chiloé Island, southern Chile, during June 2000 (Fig. 1). Remnant forest patches, derived from continuous forests that covered the island until the late 1800s, are common in northern Chiloé Island. The rural landscape is characterised by a mosaic of remnant forest fragments, secondary woodlands and grazing pastures. By using dendrochronological methods, Aravena *et al.* (2002) recently reported a minimum stand age of 200 years for this old-growth fragment, with

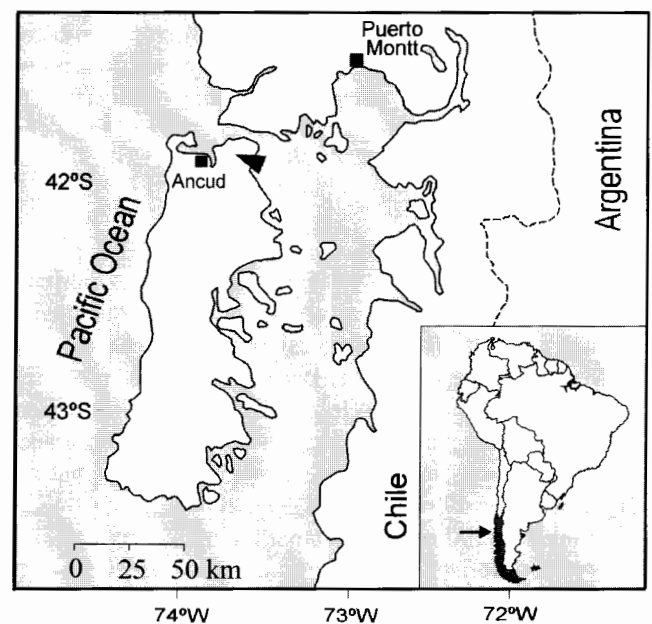


Fig. 1. Location of the study site in northern Chiloé Island, southern Chile. The arrow indicates the geographical position of the Estación Biológica 'Senda Darwin' and of the study site. Inset map shows the geographic distribution of South American temperate rainforests (shaded area).

no evidence of large-scale logging or fire. Adult tree density and basal area were 2100 trees ha⁻¹ and 71 m² ha⁻¹, respectively, with a relatively high density of both saplings and seedlings (Aravena *et al.* 2002). The main canopy trees were *Podocarpus nubigena* Lindl., *Tepualia stipularis* (H. et A.) Griseb., *Drimys winteri* J.R. et G.Forster, *Caldcluvia paniculata* (Cav.) D.Don., *Gevuina avellana* Mol., *Saxegothaea conspicua* Lindl. and *Crinodendron hookerianum* Gay, with a few large emergent individuals of *Weinmannia trichosperma* Cav. and *Nothofagus nitida* (Phil.) Krasser. Less abundant species were *Amomyrtus luma* (Mol.) Legr. et Kausel, *Myrceugenia parvifolia* (DC.) Kausel and *Laureliopsis philippiana* (Looser) Schodde. Floristically, this forest fragment is representative of the North Patagonian forest type, as defined by Veblen *et al.* (1983), which is widespread at low and middle elevations in coastal areas south of 40°S.

The prevailing climate is described as wet-temperate with a strong oceanic influence (di Castri and Hajek 1976). Meteorological records (4 years) at Estación Biológica 'Senda Darwin' indicate an annual rainfall of 2090 mm and a mean annual temperature of 12°C. The maximum monthly temperature (January) is 16°C and the minimum monthly temperature (July–August) is 5°C. Rainfall occurs throughout the year, but 64% of the precipitation occurs from April to September.

Sampling

Within a previously established 100 × 100 m (1 ha) plot in the forest interior >200 m away from any forest edge (see Aravena *et al.* 2002), two 50 × 20 m subplots (total area of 0.2 ha) were set up for this study. Because of their proximity and similarity in tree species composition, results of all analyses were based on the pooled data from both subplots. All stems >5 cm diameter at breast height (dbh) or taller than 1.3 m above the ground within the subplots had previously been marked with a numbered metal tag, identified to species, and its dbh measured (Aravena *et al.* 2002). Both the number of species and identity of all vascular epiphytes and vines were determined on each tagged tree up to a height of 2.5 m along the tree trunk. Identification of vascular epiphyte and vine species was based on keys and descriptions in Günckel (1983), Marticorena and Rodríguez (1995) and Hoffmann (1997). We also compared samples with herbarium specimens held at the library of the Estación Biológica 'Senda Darwin'. Non-vascular epiphytes, including mosses and lichens, were not considered.

Relative abundance of epiphytes and vines

The relative abundance of epiphyte and vine species 'i' was estimated as the frequency of occurrence (%FO), expressed as a percentage of all sampled trees within the subplots, irrespective of identity, where species 'i' was present. It was calculated as:

$$\%FO_i = \left(\frac{N_i}{N} \right) \times 100$$

where N_i is the number of trees on which epiphyte or vine species i was recorded and N is the total number of trees sampled within the subplots.

Host tree species preferences of vascular epiphytes and vines

To assess potential preferences or rejection of host tree species by each vascular epiphyte and vine species, we first determined the observed FO of each epiphyte and vine species on each of the six most common tree species within the stand. We then compared observed FOs with frequency distributions of FOs generated from random models for each epiphyte/vine host tree species pair. For each pair, we randomly selected N presence (1) or absence (0) values of the considered epiphyte/vine species from the original observed occurrence data matrix (including all 12 tree species) in the sampled plot, where N was equal to the number of individual trees sampled of a given species. This procedure allowed us to calculate an expected pseudo-value of FO under the assumption of no species specificity, while respecting all observed tree

species sample sizes N and the known FO of each epiphyte or vine species at the community level. The randomisation model was run 1000 times for each pair, 120 (6 host tree species × 20 epiphyte/vine species) expected FO frequency distributions being obtained, with which we compared observed FOs. Observed values falling below 5% or above 95% of the randomly generated frequency distributions were considered indicative of rejection or preference, respectively, for a given host tree.

Epiphyte and vine species richness and tree species identity

Total number of epiphyte and vine species was recorded for each of the six most common tree species in the forest stand. Given that sample sizes of the most common tree species varied substantially, we assessed whether epiphyte and vine species richness differed among tree species by using the following procedure. For each of the six tree species, we constructed a random model by randomly selecting N presence (1) or absence (0) values from the observed data matrix (including all 12 tree species) of all 20 of the epiphyte and vine species recorded at the study site (one epiphyte or vine species at a time), where N was equal to the number of individual trees sampled of that species. Values for each epiphyte or vine species were selected from the observed occurrence data matrix of the respective epiphyte/vine species. This procedure allowed us to calculate an expected pseudo-value of epiphyte/vine species richness for a given tree species, under the assumption of no species specificity, while at the same time respecting all observed tree species sample sizes N and the known FO of each epiphyte or vine species at the community level. The model was run 1000 times for each tree species, yielding an expected species richness frequency distribution for that tree species. The process was repeated for the other five host tree species. We contrasted observed species richness values with the random model. Observed values falling below 5% or above 95% of the random model frequency distribution were taken to indicate that epiphyte or vine species richness for that host tree species was lower or greater than that expected by chance. We used the program GAUSS Version 3.2.30 (Aptech Systems Inc. 1997) to generate the random models described above.

Vascular epiphytes and vines and host tree size

To assess whether vascular epiphyte and vine species occupy host trees independently of tree size, we used Chi-squared tests of independence or association (Zar 1996) on 3 × 2 contingency tables of the number of individual trees of three size classes on which a given epiphyte or vine species was present or absent. We defined three non-contiguous dbh classes: small (5–10 cm dbh), medium (15–20 cm dbh) and large (>25 cm dbh). Only the eight most common epiphytes or vines (in terms of %FO) occurring on >10% of the trees, and the three most common tree species were considered in this analysis.

Results

Host tree species

A total of 499 trees, representing 12 different species, occurred in 0.2 ha sampled in an old-growth, North Patagonian rainforest fragment in northern Chiloé Island, southern Chile (Table 1). The most common tree species were *Tepualia stipularis* (Myrtaceae) (36.9%), *Podocarpus nubigena* (Podocarpaceae) (19.0%), *Drimys winteri* (Winteraceae) (14.2%), *Caldcluvia paniculata* (Cunoniaceae) (13.0%), *Crinodendron hookerianum* (Elaeocarpaceae) (6.2%) and *Nothofagus nitida* (Fagaceae) (5.0%). These six tree species represented 94.3% of all stems

in the sampled area. Six other tree species were found but in much lower numbers (Table 1).

Vascular epiphyte and vine diversity, composition and relative abundance

A total of 20 different species of vascular epiphytes (ferns and angiosperms) and vines were recorded on 499 trees,

consisting of 11 species of epiphytic ferns, seven species of vines or lianas, one angiosperm epiphyte (*Fascicularia bicolor*) and one shrub species growing epiphytically (*Pseudopanax laetevirens*) (Table 2). Eight of the 11 epiphytic fern species belonged to the genus *Hymenophyllum*, while the remaining three species were in the genera *Asplenium*, *Hymenoglossum* and *Polypodium*. Of

Table 1. List of the 12 host tree species encountered and the number of individual trees of each species within 0.2 ha of old-growth North Patagonian rainforest in northern Chiloé Island, southern Chile

Species	Family	No. of trees sampled	% of total
<i>Tepualia stipularis</i>	Myrtaceae	184	36.9
<i>Podocarpus nubigena</i>	Podocarpaceae	95	19.0
<i>Drimys winteri</i>	Winteraceae	71	14.2
<i>Caldcluvia paniculata</i>	Cunoniaceae	65	13.0
<i>Crinodendron hookerianum</i>	Elaeocarpaceae	31	6.2
<i>Nothofagus nitida</i>	Fagaceae	25	5.0
<i>Amomyrtus luma</i>	Myrtaceae	11	2.2
<i>Saxegothea conspicua</i>	Podocarpaceae	6	1.2
<i>Gevuina avellana</i>	Proteaceae	3	0.6
<i>Laureliopsis philippiana</i>	Monimiaceae	3	0.6
<i>Weinmannia trichosperma</i>	Cunoniaceae	3	0.6
<i>Myrceugenia parvifolia</i>	Myrtaceae	2	0.4
Total		499	100.0

Table 2. List of species of vascular epiphytes (ferns and angiosperms) and vines found in an old-growth North Patagonian rainforest in northern Chiloé Island, southern Chile

Family membership and geographical distribution at the genus level are indicated. Nomenclature after Marticorena and Rodríguez (1990) and Hoffmann (1997). Endemic SSA, genus restricted to the temperate rainforests of southern South America (SSA); NZ, New Zealand; C, Cosmopolitan

Species	Family	Genus distribution
<i>Ferns</i>		
1 <i>Asplenium dareoides</i>	Aspleniaceae	C
2 <i>Hymenoglossum cruentum</i>	Hymenophyllaceae	Endemic SSA
3 <i>Hymenophyllum caudiculatum</i>	Hymenophyllaceae	C
4 <i>Hymenophyllum cuneatum</i>	Hymenophyllaceae	C
5 <i>Hymenophyllum dentatum</i>	Hymenophyllaceae	C
6 <i>Hymenophyllum dicranotrichum</i>	Hymenophyllaceae	C
7 <i>Hymenophyllum krauseanum</i>	Hymenophyllaceae	C
8 <i>Hymenophyllum pectinatum</i>	Hymenophyllaceae	C
9 <i>Hymenophyllum plicatum</i>	Hymenophyllaceae	C
10 <i>Hymenophyllum</i> sp. 1	Hymenophyllaceae	C
11 <i>Polypodium feuillei</i>	Polypodiaceae	C
<i>Angiosperms</i> ^A		
12 <i>Campsidium valdivianum</i>	Bignoniaceae	Endemic SSA
13 <i>Fascicularia bicolor</i>	Bromeliaceae	Endemic SSA
14 <i>Griselinia racemosa</i>	Griselinaceae	SSA, NZ, SE Brazil
15 <i>Luzuriaga polyphylla</i>	Philesiaceae	SSA, NZ
16 <i>Mitraria coccinea</i>	Gesneriaceae	Endemic SSA
17 <i>Pernettya insana</i>	Ericaceae	C
18 <i>Philesia magellanica</i>	Philesiaceae	Endemic SSA
19 <i>Pseudopanax laetevirens</i>	Araliaceae	SSA, NZ, Tasmania
20 <i>Sarmienta scandens</i>	Gesneriaceae	Endemic SSA

^AAll angiosperms are vines, except *Fascicularia bicolor* (an epiphyte) and *Pseudopanax laetevirens* (a shrub found growing epiphytically).

these, *Hymenoglossum* is a monotypic genus, endemic to the temperate rainforests of southern South America. Of the nine angiosperms found, the epiphyte *Fascicularia bicolor* and the vines *Campsidium valdivianum*, *Mitraria coccinea*, *Philesia magellanica* and *Sarmienta scandens* are endemic to the temperate rainforests of southern South America; all vines belong to monotypic genera (Table 2).

The vine *Luzuriaga polyphylla* (Philesiaceae) and the fern *Hymenophyllum dicranotrichum* (Hymenophyllaceae) were the most frequent species (61 and 57% FO, respectively) (Fig. 2). Other relatively common epiphytes were the ferns *Hymenophyllum caudiculatum*, *H. pectinatum*, *H. plicatum* and *Hymenoglossum cruentum* (all Hymenophyllaceae) and the vines or climbers *Griselinia racemosa* (Griselinaceae) and *Mitraria coccinea* (Gesneriaceae), with %FO ranging between 12 and 45%. The remaining 12 species (60% of the total) had FOs <10% (Fig. 2).

Host tree species preferences of vascular epiphytes and vines

Observed FOs of each of the 20 species of vascular epiphytes and vines varied widely among the six most common tree species in the forest (Table 3). The FO of 13 species of

epiphytes and vines (i.e. 65% of the total), five ferns and eight angiosperms were greater than expected by chance on one or more host tree species, suggesting preference or selectivity for these trees (Table 3). Seven species of epiphytes and vines showed significant preference for *Podocarpus nubigena* (e.g. *Hymenoglossum cruentum*, *Hymenophyllum caudiculatum*, *Luzuriaga polyphylla* and *Mitraria coccinea*), while the occurrence of another four and two species of epiphytes and vines were greater than expected by chance on *Tepualia stipularis* and *Nothofagus nitida*, respectively (Table 3). For instance, *F. bicolor* had a FO on *N. nitida* greater than expected by chance.

On the other hand, 11 epiphyte or vine species were underrepresented on one or more host trees. All of these species were underrepresented on *Drimys winteri*, with the exception of *Hymenophyllum cuneatum* (Table 3), while one or two epiphytes were also underrepresented on some of the other tree species. For example, the fern *Hymenoglossum cruentum* was significantly underrepresented on *D. winteri*, *Caldcluvia paniculata* and *Crinodendron hookerianum*, while FOs of *Hymenophyllum krauseanum*, *H. pectinatum*, *H. plicatum*, *Griselinia racemosa*, *Luzuriaga polyphylla*,

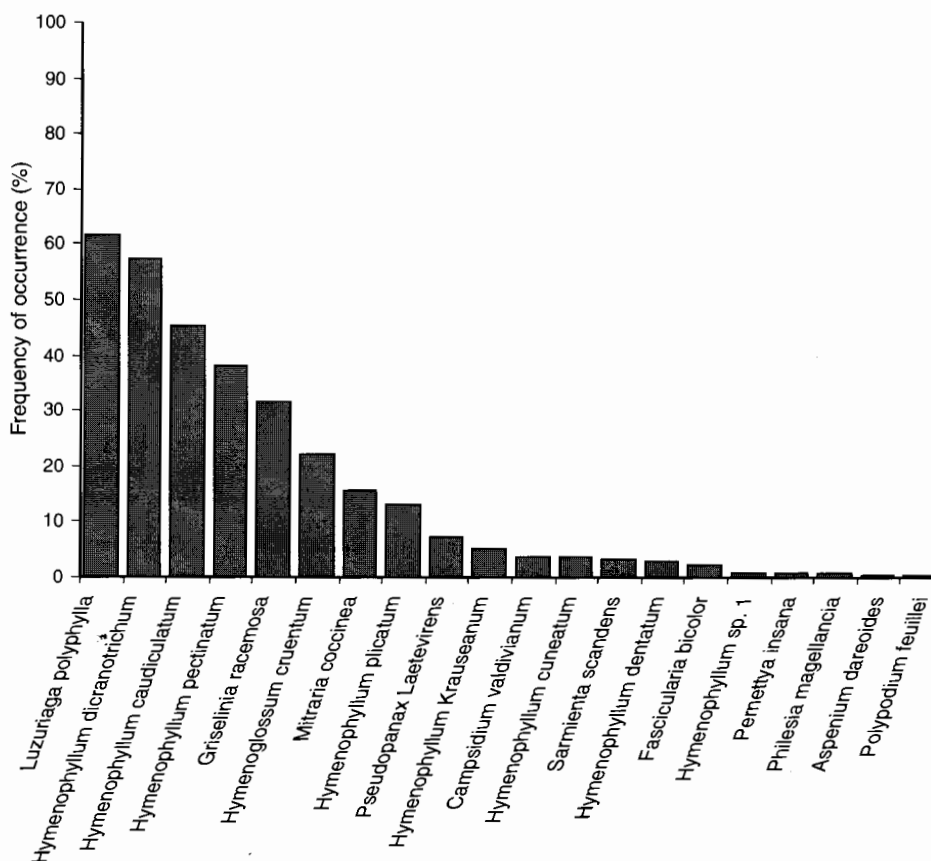


Fig. 2. Frequency of occurrence (%), for 20 species of vascular epiphytes (ferns and angiosperms) and vines occurring on 499 trees sampled in a 0.2-ha area of humid North Patagonian rainforest, southern Chile.

Mitraria coccinea and *Pseudopanax laetevirens* were lower than expected by chance on *D. winteri* only.

Interestingly, some epiphytic ferns or angiosperms showed significant preferences for some host tree species, while at the same time rejecting others (Table 3). For instance, *Hymenoglossum cruentum* showed marked selectivity for *P. nubigena*, while rejecting *D. winteri*, *C. paniculata* and *C. hookerianum*. Likewise, *Hymenophyllum dicranotrichum* showed selectivity for *T. stipularis* and *C. hookerianum*, but it was underrepresented on *Podocarpus nubigena* and *Drimys winteri*. Among the vines, both *Luzuriaga polyphylla* and

Mitraria coccinea were significantly overrepresented on *P. nubigena*, while being underrepresented on *D. winteri*. Finally, the FOs of five species showed no significant trends among host trees (Table 3).

Vascular epiphyte and vine species richness and tree species identity

Species richness of vascular epiphytes and vines varied widely among the six most abundant tree species sampled, ranging from 10 species on *Drimys winteri* to 18 species on *Tepualia stipularis* (Table 4). As sample size of these six tree

Table 3. Observed frequency of occurrence (%FO) of vascular epiphytes (ferns and angiosperms) and vines on the six most common tree species present in an old-growth North Patagonian rainforest fragment in northern Chiloé Island, southern Chile

T.s., *Tepualia stipularis*; P.n., *Podocarpus nubigena*; D.w., *Drimys winteri*; C.p., *Caldcluvia paniculata*; C.h., *Crinodendron hookerianum*; N.n., *Nothofagus nitida*). Significant deviations from those expected under no species specificity: preference (A) or rejection (B) of epiphyte or vine species for host tree species are indicated. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

	T.s.	P.n.	D.w.	C.p.	C.h.	N.n.
<i>Ferns</i>						
1 <i>Asplenium dareoides</i>	0.0	0.0	1.4	0.0	0.0	0.0
2 <i>Hymenoglossum cruentum</i>	25.5	50.5 ^{A***}	0.0 ^{B***}	12.3 ^{B**}	6.5 ^{B*}	28.0
3 <i>Hymenophyllum caudiculatum</i>	40.8 ^{B*}	90.5 ^{A***}	16.9 ^{B***}	46.2	29.0 ^{B*}	40.0
4 <i>Hymenophyllum cuneatum</i>	7.1 ^{A**}	0.0 ^{B*}	0.0	0.0	3.2	0.0
5 <i>Hymenophyllum dentatum</i>	4.9	1.1	0.0	3.1	6.5	0.0
6 <i>Hymenophyllum dicranotrichum</i>	71.2 ^{A***}	28.4 ^{B***}	42.3 ^{B**}	61.5	74.2 ^{A*}	52.0
7 <i>Hymenophyllum krauseanum</i>	4.9	4.2	0.0 ^{B*}	6.2	6.5	4.0
8 <i>Hymenophyllum pectinatum</i>	38.0	54.7 ^{A**}	9.9 ^{B***}	58.5 ^{A***}	38.7	36.0
9 <i>Hymenophyllum plicatum</i>	14.7	21.1	2.8 ^{B***}	20.0	19.4	12.0
10 <i>Hymenophyllum</i> sp.1	0.5	0.0	1.4	1.5	0.0	0.0
11 <i>Polypodium feuillei</i>	0.0	0.0	0.0	0.0	0.0	4.0
<i>Angiosperms</i>						
12 <i>Campsidium valdivianum</i>	4.3	9.5 ^{A*}	1.4	1.5	0.0	4.0
13 <i>Fascicularia bicolor</i>	2.7	1.1	0.0	0.0	0.0	12.0 ^{A**}
14 <i>Griselinia racemosa</i>	37.5 ^{A***}	26.3	5.6 ^{B***}	21.5	19.4	16.0
15 <i>Luzuriaga polyphylla</i>	62.0	77.9 ^{A***}	45.1 ^{B**}	58.5	64.5	52.0
16 <i>Mitraria coccinea</i>	17.9	26.3 ^{A**}	2.8 ^{B***}	10.8	9.7	16.0
17 <i>Pernettya insana</i>	1.1	0.0	0.0	0.0	0.0	8.0 ^{A*}
18 <i>Philesia magellanica</i>	1.1	1.1	0.0	0.0	0.0	4.0
19 <i>Pseudopanax laetevirens</i>	13.0 ^{A**}	4.2	0.0 ^{B**}	3.1	3.2	12.0
20 <i>Sarmienta scandens</i>	1.6	8.4 ^{A**}	0.0	3.1	0.0	8.0

Table 4. Observed and mean expected (from randomisation models, see text) species richness of vascular epiphytes and vines on the six most common tree species sampled in an old-growth North Patagonian rainforest fragment in northern Chiloé Island, southern Chile

n.s., $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

	Observed epiphyte/vine species richness	Expected species richness	Signif.
<i>Tepualia stipularis</i>	18	18	n.s.
<i>Podocarpus nubigena</i>	15	17	n.s.
<i>Drimys winteri</i> ^B	10	16	***
<i>Caldcluvia paniculata</i>	14	16	n.s.
<i>Crinodendron hookerianum</i>	12	13	n.s.
<i>Nothofagus nitida</i> ^A	16	13	*

^AGreater than expected by chance.

^BLower than expected by chance.

species also varied markedly, ranging between 25 stems sampled for *Nothofagus nitida* and 184 trees for *T. stipularis*. The simulations allowed us to assess whether observed species richness on various tree hosts was equal to, greater than, or less than expected by chance, under the assumption of no species specificity. Species richness was different from that expected by chance alone on two tree species only. Species richness was lower than expected on *D. winteri* ($P < 0.001$; 10 epiphyte/vine species on 71 trees) and greater than expected by chance on *N. nitida* ($P < 0.05$; 16 species

on 25 stems) (Table 4). On the other hand, epiphyte and vine species richness on the remaining four common tree species did not differ from that generated by the randomisation models (Table 4).

Vascular epiphytes and vines and tree size

Out of eight epiphyte or vine species with the greatest %FO (Fig. 2), five occupied trees independently of tree size. These were the ferns *Hymenophyllum pectinatum* and *H. plicatum* (Fig. 3) and the vines *Luzuriaga polyphylla*, *Griselinia*

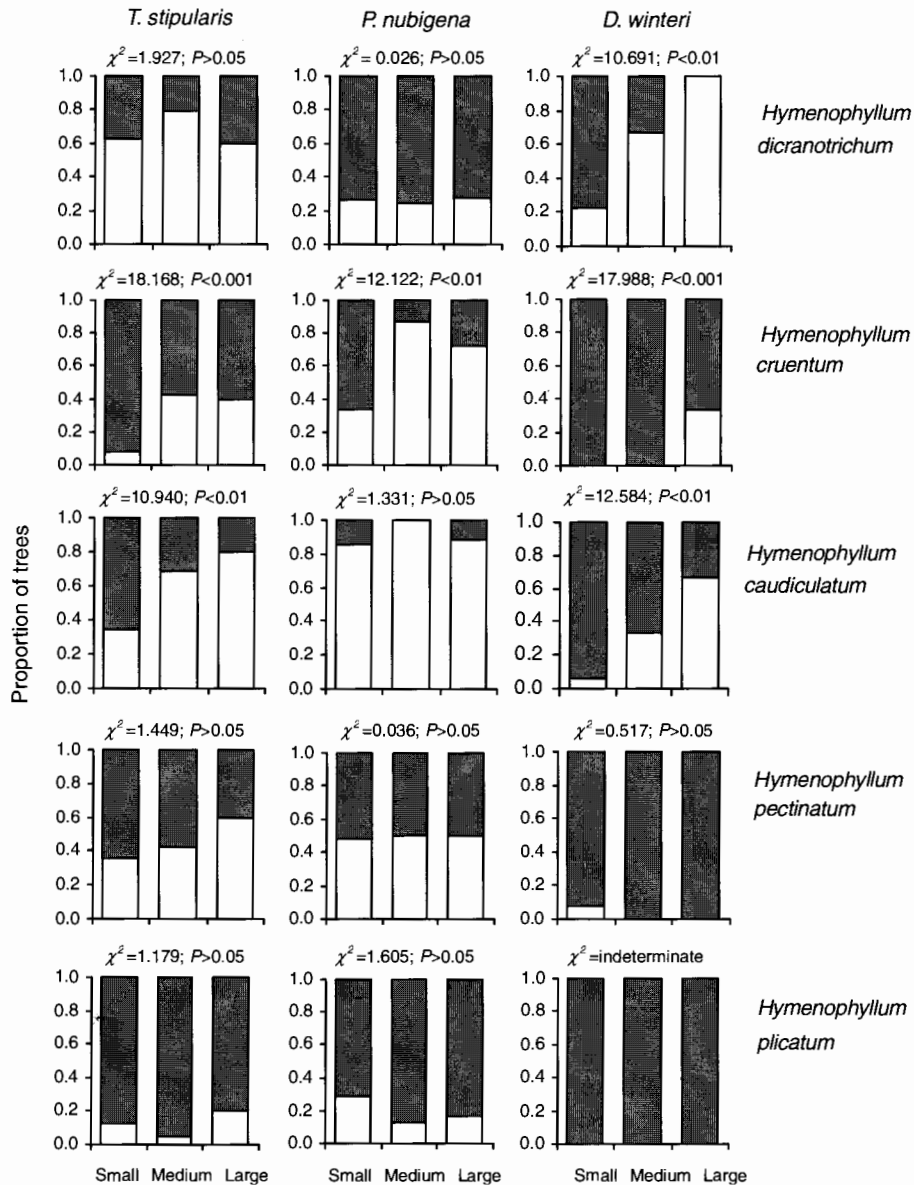


Fig. 3. Proportion of small (5–10 cm dbh), medium (15–20 cm dbh), and large-sized (>25 cm dbh) individuals of *Tepualia stipularis*, *Podocarpus nubigena* and *Drimys winteri* on which the five most abundant epiphytic ferns were present (white) or absent (grey).

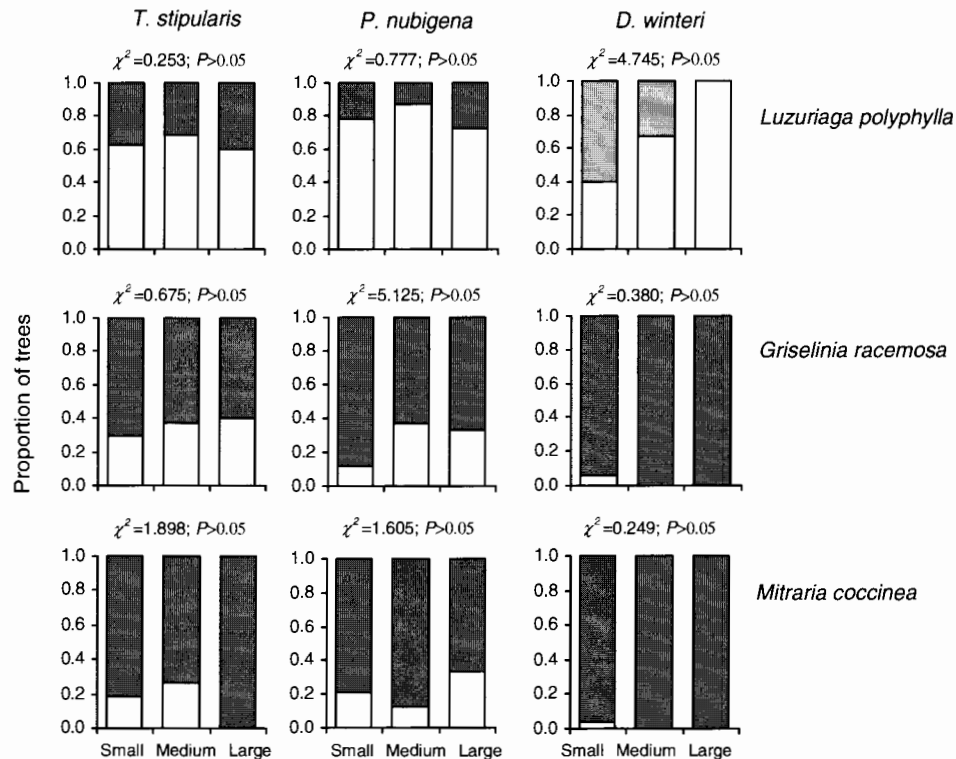


Fig. 4. Proportion of small (5–10 cm dbh), medium (15–20 cm dbh), and large-sized (>25 cm dbh) individuals of *Tepualia stipularis*, *Podocarpus nubigena* and *Drimys winteri* on which the three most abundant vine species were present (white) or absent (grey).

racemosa and *Mitraria coccinea* (Fig. 4). In contrast, *Hymenoglossum cruentum* showed a marked preference for medium and large-sized individuals of *T. stipularis* and *P. nubigena* and for large trees of *D. winteri* (Fig. 3). Similarly, *H. caudiculatum* was significantly more frequent on medium and large-sized trees of *T. stipularis* and *D. winteri* (Fig. 3), while *H. dicranotrichum* was significantly associated with medium and large-sized trees of *D. winteri* (Fig. 3).

Discussion

Diversity, floristic composition and relative abundance of vascular epiphytes and vines

The species richness of vascular epiphytes and vines recorded in this study, including 11 species of ferns and nine angiosperms, within 0.2 ha of North Patagonian temperate rainforest in Chiloé Island, southern Chile, is similar to that reported for two stands of Valdivian rainforest on the mainland, north of the study site (Riveros and Ramírez 1978; Clement *et al.* 2001). Given that only 12 tree species make up the canopy of this forest fragment (this study; see also Aravena *et al.* 2002), this epiphyte and vine assemblage contributes importantly to floristic diversity of this old-growth stand. Epiphyte and vine assemblages also document the mixed origin of the flora of South American temperate forests (Villagrán and Hinojosa 1997), because it includes

endemics (e.g. *Campsidium*), Gondwanic elements also found in New Zealand and Tasmania (*Luzuriaga*, *Pseudopanax*) and Neotropical elements, also occurring in south-eastern Brazil (*Griselinia*).

Epiphyte diversity and composition often vary vertically along the tree trunk (e.g. Todzia 1986; Ter Steege and Cornelissen 1989; Dickinson *et al.* 1993). Because our study only encompassed the first 2.5 m from the base of each tree, epiphyte and vine diversity could have been underestimated. Nevertheless, a recent survey of epiphytes and vines along the entire trunk and crown of a few individuals of the giant conifer *Fitzroya cupressoides* (Cupressaceae) in a Valdivian rainforest, north of Chiloé Island (Clement *et al.* 2001), showed a similar species richness and composition to that of our study. However, vertical stratification has also been described in the floristically similar southern temperate rainforests of New Zealand (Dickinson *et al.* 1993; Hofstede *et al.* 2001), as well as in tropical and subtropical rainforests (Todzia 1986; Hietz and Hietz-Seifert 1995; Freiberg 1996). Dickinson *et al.* (1993) recognised four epiphyte and vine associations, associated with different positions within the tree trunk and crown, for a total of 28 vascular plant species recorded in the giant conifer *Dacrycarpus dacrydioides* (Podocarpaceae). Accordingly, additional sampling will be necessary to assess the vertical variation in epiphyte and vine composition in Chilean forests.

Host tree preferences of vascular epiphytes and vines

Observed FOs suggest that 13 of 20 epiphyte or vine species had significant preferences for one or two host tree species (i.e. FOs were greater than expected by chance). Overall, the most preferred host trees were *Tepualia stipularis* and *Podocarpus nubigena*, suggesting that these species may have particularly favourable qualities (e.g. trunk and bark characteristics) as a substrate for vine or epiphyte attachment. For instance, seven epiphytes or vines showed a significant preference for *P. nubigena*. Further, four ferns in our study (*Hymenoglossum cruentum* and three *Hymenophyllum* species) showed significant preference for *Tepualia stipularis* or *Podocarpus nubigena*, but at the same time were underrepresented on *Drimys winteri*. Most species of vines that were overrepresented on *T. stipularis* or *P. nubigena*, rejected *D. winteri*, further suggesting that these trees differ in terms of substrate quality for epiphytes and vines. Benzing (1995) indicates that variations in bark stability, wettability, water-holding capacity and surface texture could be responsible for specific epiphyte and vine associations in tropical trees (e.g. Todzia 1986; Ter Steege and Cornelissen 1989; Daniels and Lawton 1991; Talley *et al.* 1996b; Díaz-Santos 2000; Carsten *et al.* 2002; but see Ackerman *et al.* 1996). Assessing differences in bark texture and related features among tree species in southern temperate forests could shed light on particular species associations. It is also necessary to evaluate whether some host trees provide better physical environments for epiphytes, as suggested by Talley *et al.* (1996b), who propose that crown morphology, leaf area and leaf arrangement in some tree species might result in better-lit trunks. The consequences of the heterogeneity of the physical environment on the growth of epiphytes and vines remain little explored.

At the same time, 11 epiphyte or vine species were underrepresented on one or more host trees. Almost all of these species were underrepresented on *Drimys winteri* (Table 3). Individuals of *D. winteri* had a lower cover of both non-vascular and vascular epiphytes compared with other tree species in the forest (pers. obs.). The smoother texture of this species' bark could explain the lower epiphytic cover compared with other tree species in the forest. In tropical rainforests of Queensland, Australia, a more profuse vine cover has been found on tree species with a rough bark texture (Talley *et al.* 1996b).

Epiphyte and vine species richness and tree species identity

Epiphyte and vine species richness vary significantly among host tree species (e.g. Ter Steege and Cornelissen 1989; Freiberg 1996; Zapfack *et al.* 1996; Díaz-Santos 2000). In our study, we found species richness to be highest on *Tepualia stipularis* (18 spp.) and *Nothofagus nitida* (16 spp.) and lowest on *Drimys winteri* (10 spp.). Comparisons of

observed species richness on each host tree species with randomisation model frequency distributions of species richness, under the assumption of no host specificity, showed that the number of epiphyte and vine species was greater than expected by chance on *N. nitida*, which hosted 16 of the 20 epiphytes or vines on only 25 individuals in the sampled plot. Further, eight of the 12 least common epiphytes and vines were present on *N. nitida*. This is specially noteworthy given that the FO of these species was <10% at the community level and that only 5% of the trees occurring in the sampled plot were *N. nitida*. In contrast, species richness was significantly lower than expected on *D. winteri*. As discussed above, *N. nitida* possesses a coarse and rougher bark than *D. winteri* (Hoffmann 1997; pers. obs.), which could explain differences in species richness. In addition, the smooth texture of *D. winteri*'s bark could reduce water and nutrient retention during the process of throughfall, while *N. nitida*'s bark may contain much greater levels of humidity and essential nutrients.

Host tree size and vascular epiphytes and vines

In our study, three of the five most common ferns, *Hymenoglossum cruentum*, *Hymenophyllum caudiculatum* and *H. dicranotrichum*, were most frequently found on medium and large-sized trees or exclusively on large-sized trees. Similarly, Talley *et al.* (1996a) found that the occurrence of the vine *Rhus radicans* was associated with large-sized trees in a deciduous temperate forest in southern United States. Further, some epiphyte and vine species have been found to be restricted to large-sized individuals of *Fitzroya cupressoides* in a Valdivian forest in southern Chile (Clement *et al.* 2001). Epiphytic bromeliad species richness and abundance increased with host tree size (dbh) in cloud forests of Ecuador (Dunn 2000), while the probability of trees being colonised by woody vines increased with tree diameter in tropical rainforests of eastern Ecuador (Nabe-Nielsen 2001) and south-eastern Queensland, Australia (Carsten *et al.* 2002; see also Talley *et al.* 1996b). The fact that larger trees are usually older (see Aravena *et al.* 2002) means that they have been exposed to colonists for a longer time, sometimes several centuries, potentially increasing the chances of being colonised (Talley *et al.* 1996b; Nieder *et al.* 2001). In our study, higher FOs of some fern species on large-sized trees could also be explained by the fact that larger trunks display a greater surface area for attachment of epiphytes and climbing vines. Finally, a smaller number of epiphytes and vines may be capable of colonising smaller trunks, which are generally smoother and retain less moisture and nutrients than larger ones (see Catling and Lefkovitch 1989).

Conservation implications

These results are relevant for the management and conservation of biodiversity in Chilean temperate forests.

The host-tree preferences described in this study suggest that certain combinations of tree species and sizes are more favourable for epiphyte and vine biodiversity. We predict that abundances of epiphytic ferns and vines and overall species richness could be much reduced in second-growth forests as a result of a lower number of tree species in the canopy and changes in forest structure.

Finally, this study constitutes an important baseline for future research on two important and understudied functional groups within southern temperate forests—epiphytes and vines. Future studies should experimentally address physiological and ecological mechanisms responsible for host tree preferences and the relation between vertical stratification and epiphyte and vine species composition.

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