



## Epiphyte diversity and biomass loads of canopy emergent trees in Chilean temperate rain forests: A neglected functional component

Iván A. Díaz<sup>a,b,c,\*</sup>, Kathryn E. Sieving<sup>b</sup>, Maurice E. Peña-Foxon<sup>c</sup>, Juan Larraín<sup>d</sup>, Juan J. Armesto<sup>c,e</sup>

<sup>a</sup> Instituto de Silvicultura, Facultad de Ciencias Forestales y Recursos Naturales, Universidad Austral de Chile, P.O. Box 567, Valdivia, Chile

<sup>b</sup> Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL USA

<sup>c</sup> Institute of Ecology and Biodiversity IEB, Las Palmeras 3425, Ñuñoa, Santiago, Chile

<sup>d</sup> Departamento de Botánica, Universidad de Concepción, Concepción, Chile

<sup>e</sup> Center for Advanced Studies in Ecology and Biodiversity, Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile

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### ABSTRACT

We document for the first time the epiphytic composition and biomass of canopy emergent trees from temperate, old-growth coastal rainforests of Chile (42°30'S). Through tree-climbing techniques, we accessed the crown of two large (c. 1 m trunk diameter, 25–30 m tall) individuals of *Eucryphia cordifolia* (Cunoniaceae) and one large *Aextoxicon punctatum* (Aextoxicaceae) to sample all epiphytes from the base to the treetop. Epiphytes, with the exception of the hemi-epiphytic tree *Raukaua laetevirens* (Araliaceae), were removed, weighed and subsamples dried to estimate total dry mass. We recorded 22 species of vascular epiphytes, and 22 genera of cryptogams, with at least 30 species of bryophytes, liverworts and lichens. The dominant vascular epiphytes were *Fascicularia bicolor* (Bromeliaceae), *Raukaua laetevirens*, *Sarmienta repens* (Gesneriaceae), and filmy ferns (Hymenophyllaceae). Epiphyte loads per tree ranged between 134 and 144 kg dry mass, with 60–70% water. The hemi-epiphytic tree *R. laetevirens* added between 1 and 2.6 t of dry mass to each host tree. A main component of epiphyte biomass, making 70% of the weight, was detritus and roots, while leaves, stems, and fronds made up the remaining 30%. Emergent trees hold a high proportion of the regional diversity of epiphytes: 33% of all flowering epiphytes, and 50% of all filmy ferns described for Chilean temperate forests. Dry epiphyte biomass associated only with the emergent *E. cordifolia* trees in coastal forests was estimated in 10 t/ha. Epiphyte biomass may store up to 300 l of water in each emergent tree, and add 40–150% of photosynthetic biomass to the tree crowns. Based on this evidence, epiphytes may play key but generally neglected roles in ecosystem carbon uptake, water storage, and nutrient cycling. Moreover, emergent trees represent nuclei of biodiversity and ecosystem functions distributed throughout mature forests. Forest management should recognize large trees as significant management units for the preservation of biodiversity and ecological functions.

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### 1. Introduction

Epiphytes contribute greatly to global plant diversity, as they represent between 8% and 10% of all known vascular plant species and 25–50% of plant species richness in tropical forests (Gentry and Dodson, 1987; Benzing, 1995, 2004). Epiphytes also accumulate large amounts of organic detritus in tree crowns, usually termed as “arboreal soils” (Enloe et al., 2006). Live tissues and organic detritus accumulated by epiphytes comprise together a thick layer enveloping from the tree trunk to the upper canopy branches, representing up to 44 t/ha in tropical cloud forests (Hofstede et al.,

1993). Epiphytic biomass can account for 81.3% of the canopy biomass when woody tissues are excluded (Nadkarni et al., 2004).

Despite the large contribution of epiphytes to biodiversity and vertical structure in forest ecosystems, information on their composition and biomass is still deficient for several regions of the world (Sillett and Antoine, 2004; Zotz, 2005). One example is the temperate rainforests of southern South America (Sillett and Antoine, 2004), where vascular and non-vascular epiphytes are diverse and abundant (Zotz, 2005; Arroyo et al., 1996). These temperate rain forests differ from northern hemisphere temperate rainforests, as they are generally dominated by broad-leaved evergreen trees comprising a multilayered canopy with scattered emergent trees (>30 m tall), which are lushly covered with vascular vines and epiphytes. These differences result from the Gondwanan origin of the South American forests, as shown by the large number of taxa with Australasian affinities, including New Zealand and Tasmania (Darwin, 1845; Armesto et al., 1996a;

\* Corresponding author. Present address: Instituto de Silvicultura, Facultad de Ciencias Forestales y Recursos Naturales, Universidad Austral de Chile, P.O. Box 567, Valdivia, Chile. Tel.: +56 63 293026; fax: +56 63 221230.

E-mail address: [ivan.diaz@docentes.uach.cl](mailto:ivan.diaz@docentes.uach.cl) (I.A. Díaz).

Willson and Armesto, 1996; Villagrán and Hinojosa, 1997; Zotz, 2005; Gutiérrez et al., 2004, 2008a). Long-term isolation from other forest by the Andes, Atacama and Patagonian deserts resulted in a unique flora, with high percentage of endemic species in most taxa (Armesto et al., 1996a,b, 1998), and are considered at hot-spot of biodiversity (Olson and Dinerstein, 1998).

Surveys of epiphyte species richness, distribution, and biomass in South American temperate rain forests have been mostly restricted to the first few (up to 3) meters from the ground (Riveros and Ramírez, 1978; Muñoz et al., 2003; Pérez et al., 2005). A single exception is the study of Clement et al. (2001), who described the floristic composition of vascular epiphytes found on the crowns of large (40 m tall) trees, of the long-lived conifer *Fitzroya cupressoides* (Cupressaceae), which occurs above 450 m altitude in Andean forests. However, the species richness of vascular plants is greater in lowland rain forests, particularly in Valdivian coastal rainforests distributed from 39° to 42° S (Villagrán and Hinojosa, 1997). Biodiversity in the tree canopy of the lowland Valdivian rain forest is both underexplored and highly endangered due to the rapid decline of old-growth forest cover and the loss of large emergent trees due to fire, logging and conversion to other land uses in recent decades (Armesto et al., 1998; Smith-Ramírez, 2004; Smith-Ramírez et al., 2005; Echeverría et al., 2007). In addition, current management practices promoted today by the Chilean government are largely based on the simplification of a complex forest structure to a single cohort stands, with the consequent loss of large old canopy trees considered of little or no timber value (Cabello, 2002). Moreover, management practices ignore epiphytes, and sometimes this conspicuous but barely known component of the forest biodiversity is taken as a problem for the tree health and timber production, and hence actively removed from managed stands.

Here, we present the first quantitative information on species richness, vertical distribution and biomass of vascular and non-vascular epiphytes in the trunks and crowns of large trees from Valdivian coastal, temperate rainforests. Our specific goals were: (i) to describe the species richness, composition and biomass of epiphytes on large old, canopy emergent trees, (ii) to determine what proportion of the regional diversity of epiphytes was present in the crowns of large emergent trees, (iii) to determine how epiphyte biomass changes as a function of tree size and (iv) to discuss the functional role of epiphytes in forest ecosystems, with a particular focus on their relevance for forest management and biodiversity conservation. Finally, we suggest a number of hypotheses based on our findings that we expect will influence current thinking about the functions of epiphytes in southern Chilean and other temperate rainforests.

## 2. Methods

### 2.1. Study area

The study was conducted within two large and preserved tracts of old-growth coastal temperate rain forests in Chiloé Island, southern Chile. These forests are representative of the Valdivian forest type that predominates at low elevations and on coastal hills, physiognomically dominated by evergreen, broad-leaved trees, with limited or no presence of *Nothofagus* (Veblen et al., 1980; Armesto et al., 1996a; Gutiérrez et al., 2008a; Fig. 1). The first forest tract is located in the locality of Guabún, specifically at Punta Huechucuicui (41°47'S; 54°00'W), 17 km northwest of Ancud, where undisturbed patches of old-growth Valdivian rain forest cover an area of approximately 200 ha, within a mosaic of 1000 ha of continuous forest in different successional stages and with different degrees of human impact. The climate is wet temperate

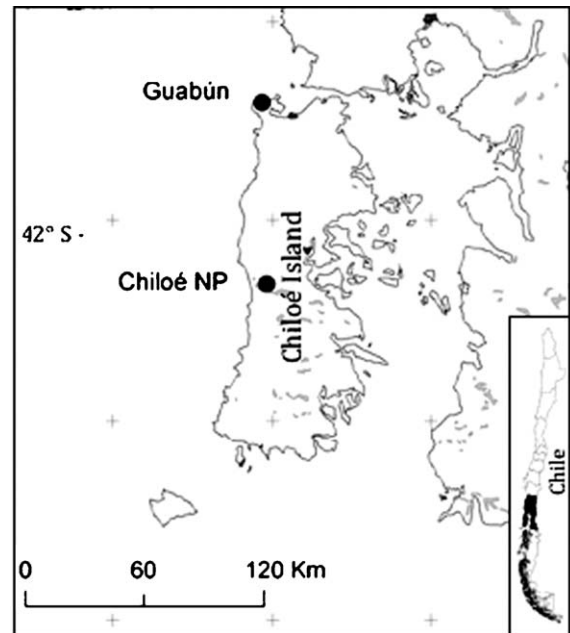


Fig. 1. Map of study sites (black dots) in lowland coastal forests of Chiloé Island, southern Chile. Sites are Guabún and Chiloé National Park (NP). Region where the study was conducted are in dark color in the inset map.

with strong oceanic influence (di Castri and Hajek, 1976). The nearest meteorological station in Punta Corona (41°47'S, 73°52'W, 48 m elevation) has an annual average of 2444 mm of rainfall and a mean annual temperature of 10.7 °C. Mean maximum and minimum monthly temperatures are 13.8 °C (January) and 8.3 °C (July). Large trees of *Eucryphia cordifolia*, older than 350 years, emerge above the canopy (c. 30 m tall) of these rainforests, which is dominated by *Laureliopsis philippiana* (Monimiaceae), *Aextoxicon punctatum* (Aextoxicaceae), *Amomyrtus luma*, *A. meli* and *Luma apiculata* (all Myrtaceae), with an understory covered by sparse bamboo tickets (*Chusquea* sp.), tall ferns (*Lophosoria*, *Blechnum*), and regeneration of the dominant trees (Gutiérrez et al., 2008a).

The second forest tract is located within the boundaries of Chiloé National Park, on the margins of Lake Cucao (42°37'S; 74°04'W), and is part of continuous forested area of c. 40,000 ha. The climate is also wet temperate with strong oceanic influence (di Castri and Hajek, 1976), with an annual rainfall between 2500 and 3000 mm, and maximum and minimum mean monthly temperatures of 18 °C (January) and 8 °C (July) (Weisner, 2003). The canopy includes scattered emergent *A. punctatum* trees, and a canopy composed by *Nothofagus nitida*, *L. philippiana*, *Gevuina avellana* (Proteaceae), *Podocarpus nubigena* (Podocarpaceae), *A. luma*, and *L. apiculata*. The understory is dominated by dense bamboo tickets (*Chusquea* sp.), ferns (*Lophosoria*, *Blechnum*), and saplings of canopy tree species (Díaz, 2009).

Organic soils are around 1 m deep, underlied by Miocene-age sedimentary bedrock of marine origin in Guabún, and Paleozoic metamorphic rocks in Cucao (Mardones, 2005). These rain forests represent remnants of once continuous coastal range temperate forests, characterized by a diverse and vertically complex forest canopy. The old-growth forest of Guabún had no signs of large-scale disturbance for at least the past 450 years (Gutiérrez et al., 2008a). The old-growth forest of Cucao is near an indigenous settlement dating from perhaps >400 years ago (Weisner, 2003). Despite the lack of evidence of human impact on the stand studied, evidence of forest fires of around 100 years old (Espinosa, 1917) can be found in the surrounding areas.

## 2.2. Sampling design

First, we characterized the structure (shape and biomass) of two large, canopy emergent trees of *E. cordifolia* in the coastal forest of Guabún, and one large tree of *A. punctatum* in the coastal forest of Chiloé National Park. These trees were selected because they belong to the species that are dominant and characteristic of the canopy of old-growth coastal forests (Veblen et al., 1980; Armesto et al., 1996b; Gutiérrez et al., 2004). The individuals were chosen for reasons of accessibility, large size, and a presumably old age (>300 years), and at the same time representing a population of similar trees within the stand, (Gutiérrez et al., 2008a). The sample size was limited by logistic considerations, due the difficulty of working in the forest canopy above 25 m and collecting and transporting the epiphyte samples from the trees to the laboratory. Large tracks of well-preserved, old-growth coastal forest are often located in remote sites, away from cities or main roads. In this case, the unlogged *A. punctatum* stand in Chiloé National Park could only be reached by navigating one hour across a lake, then climbing over a steep slope and following a self-made trail through dense bamboo tickets. Reaching the Guabún site required two hours of hiking from the nearest road. Acknowledging the limitations of the small sample size, data from unexplored tree canopies can open a new research lines in southern forests, and provide baseline information on epiphyte diversity and biomass in largely undisturbed and unpolluted ecosystems (Hedin et al., 1995; Gutiérrez et al., 2008a).

Each tree sampled had a DBH (diameter at breast height) of about 1 m, and matched the average height (25–30 m) of the large canopy trees of these two species found at each site (Gutiérrez et al., 2008a). Trees were climbed using arborist canopy-access techniques ([www.treeclimbingusa.com](http://www.treeclimbingusa.com)), including single and double rope techniques that allowed access to the majority of branches within the tree crown.

For each tree, we sampled the diversity and distribution of epiphyte species across the entire vertical profile, from the base to the treetop. In addition, we assessed the epiphyte biomass by removing the epiphyte mats, and associated detritus. Field work in the forest of Guabún was conducted between August and December 2005, over 68 days in the field by people during the late winter and spring in the southern hemisphere. Field work in Cucao was conducted in August 2006 and May 2007 during the southern hemisphere winter and fall, completing 47 days of field work of two or three people.

## 2.3. Tree architecture

Tree architecture was mapped by measuring the length, diameter, cardinal orientation (North, South, East, West), and height along the vertical profile of all branches and the main trunk, following the protocol described by Van Pelt et al. (2004) and assigning a number to each branch. After calculating the area and volume of each branch, we added these values to obtain the crown area and volume for the whole tree, assuming that each limb had a cylindrical shape. To estimate total dry biomass per tree, we used published wood density values, 0.601 kg/l for *E. cordifolia* and 0.60 kg/l for *A. punctatum* (USDA Forest Service, 2008). Additionally, leaf biomass per tree was estimated by counting all branches >2 m long found in the crown, and later collecting and weighing the leaves from three sample branches per tree (Van Pelt et al., 2004). Final estimate of crown foliage biomass was obtained by multiplying the total number of crown branches by the average leaf biomass per branch. Results were expressed as the average leaf biomass per tree crown plus minus one standard error.

## 2.4. Epiphyte species richness

Epiphyte species richness was surveyed by collecting samples of each recognizable epiphyte species every 2 m along the vertical profile, including the main trunk and crown branches of the selected trees. We recorded the branch number and height above the ground for each collected epiphyte. Fresh samples were taken to the laboratory for identification using reference collections of the Herbarium of the Universidad de Concepción, Chile. Nomenclature of species follows Marticorena and Quezada (1985), Zizka et al. (1999), and Crosby et al. (2000).

## 2.5. Epiphyte biomass

We assessed the biomass of epiphytes in the focal trees by removing and weighing all epiphyte material (live biomass and detritus). Additionally, based on this experience, we conducted visual estimates of the epiphyte biomass on 59 individuals of *E. cordifolia* in the same coastal stand. To assess epiphyte biomass per tree, we removed by hand, using garden axes and saws, all epiphytes from the three selected emergent trees as completely as possible. Epiphyte mats were removed beginning from the treetop to the bottom of the tree. The mats were placed in large plastic bags and lowered to the ground. Once on the ground, the epiphyte mats were separated into three main components: (1) soft green tissues (such as leaves, stems, fronds and taluses of angiosperms, ferns and mosses), (2) hard green tissues of the bromeliad *Fascicularia bicolor*, a conspicuous component of epiphytic flora and (3) arboreal soil and roots (Enloe et al., 2006). Roots and arboreal soils were weighed together as a single component because they were hard to separate from one another. All epiphyte mat components were placed inside large bags with a volume of c. 40 l, and weighed in the field using a portable field scale, with a precision of 0.5 kg. Around 20 sub-samples of approximately 600 g fresh weight of each component were stored in sealed plastic bags, oven-dried at 80° C for three days, and weighed again using a digital scale with a precision of 0.05 g, to determine gravimetric water content (WC). Total epiphyte dry mass was estimated by multiplying the fresh weight of each component by 1 – WC. Final biomass was expressed in kilograms because of the limited precision of the portable field scale. In other words, the variance of the subsamples was not extrapolated to the total mass.

Although we were unable to remove the large mass of the hemi-epiphytic trees, which were rooted on the ground and hence extended from the treetop to the base of the trees, their biomass was assessed from estimates of tree volume, following the protocol described by Van Pelt et al. (2004), and multiplying tree volume by wood density. Owing to the lack of published data on wood density of hemi-epiphytes, we collected five samples of branch wood, oven-dried them at 80° C for three days, weighed them, and then calculated wood volume by liquid displacement. Wood density was obtained dividing the wood volume by its dry mass.

We conducted a visual survey of epiphyte biomass on 59 additional *E. cordifolia* trees present in the canopy of Guabún forest, sampling the whole range of tree sizes present in the stand. To do this, we selected 34 points separated by >100 m from one another and traced a 50-m long transect, by running 25 m in orthogonal directions from the central point. For each tree of *E. cordifolia* present within 2-m wide strips on both sides of the transect line, we measured the trunk diameter at 1.3 m high (DBH) and visually estimated the biomass of epiphytes (in units of 10 kg) present on the entire tree. Visual estimates were based on our previous experience, removing and weighing epiphyte components from large trees in the field. When we removed epiphytes from the first *E. cordifolia* tree, the fresh weight of each filled bag was  $16.4 \pm 5.9$  kg (mean  $\pm 1$  SD;  $n = 26$  bags). For the second tree, the

fresh weight of each filled bag was  $11.9 \pm 8.0$  ( $n = 36$  bags). Accordingly, we visually estimated the number of bags of epiphytes that we could fill up with the epiphyte material covering each sampled tree, assuming conservatively that each bag was equal to 10 kilograms of epiphytes. We used this method because we did not seek precise estimations of epiphyte biomass but a rapid field-based method for comparing the relative biomass of epiphytes among different-size trees in the forest. The trees we sampled were lower than 30 m, and hence it was possible to inspect their canopies from the ground using binoculars.

## 2.6. Data analyses

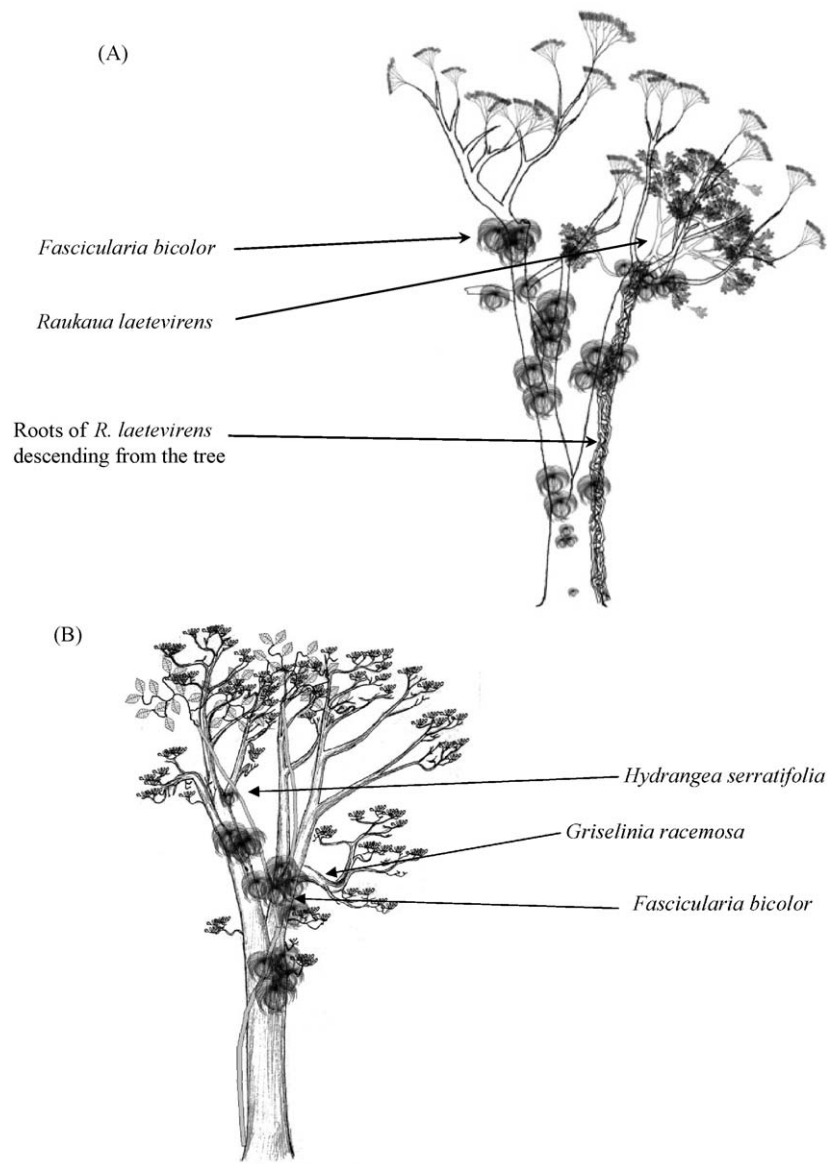
We compared the species richness among trees using Rarefaction Analysis, following the procedures described by Gotelli and Entsminger (2009). This analysis was focused only on vascular epiphytes because we were unable to classify epiphytic cryptogams reliably to species. Data used in the analysis were the numbers of 2-m vertical intervals where each plant species was

present. We also compared the similarity in the epiphyte species composition among focal trees using Sorensen's index of similarity, computed with the software Estimates (Colwell, 2006). Estimates of epiphyte biomass were related to tree DBH using regression analysis, normalizing the data of epiphyte biomass using  $\ln(x + 1)$  transformation, to fit the test assumptions. Normality was evaluated using one-way Kolmogorov–Smirnov test and examining the distribution of residuals.

## 3. Results

### 3.1. Structure of canopy emergent trees and hemi-epiphytes

The height of the two emergent *E. cordifolia* trees sampled in the coastal forest of Guabún were 28 and 25 m, with crown branches starting 16 and 14 m above the ground, respectively. The overall shape of these trees was deliquescent, with orthotropic branching up to the treetop, making an open, V-shaped crown (Fig. 2A). Foliage was born terminally, which resulted in a monolayer crown



**Fig. 2.** General shape of (A) *Eucryphia cordifolia* and (B) *Aextoxicon punctatum* trees, showing the distribution of the principal vascular epiphytes: the hemi-epiphyte *Raukaua laetevirens*, the bromeliad *Fascicularia bicolor*, the vine *Griselinia racemosa* growing epiphytically, and the vine *Hydrangea serratifolia* which grows from the ground. While the drawing is mostly to scale, the size of epiphytes and vines are exaggerated to facilitate their recognition (drawing by the author).

**Table 1**

Structural features of three canopy emergent trees sampled for epiphytes in Valdivian temperate rain forests, Chiloé Island, Chile.

	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
Trunk diameter at breast height, DBH (m)	1.33	1.23	1.24
Crown diameter (m)	21	19	18
Tree height (m)	28	25	25
Height to the first horizontal branch (m)	16	14	15
Foliage biomass (kg dry mass)	50.9 ± 11.2	33.3 ± 7.3	98.7 ± 20.5
Woody biomass (kg dry mass)	47.0 × 10 <sup>3</sup>	27.5 × 10 <sup>3</sup>	20.0 × 10 <sup>3</sup>
Estimated age (years)	>300	>300	>400

architecture (sensu Horn, 1971), with the interior of the tree crown remaining leafless (Fig. 2A). Tree crowns were about 21 m in diameter, with branches extending 10 m in all directions. Total dry biomass of each tree was estimated to be 27 and 42 t, respectively. Their leaf biomass represented <0.1% of the weight of each tree (Table 1).

In the leafless portion of canopy branches in the interior of the tree crown, starting 14–15 m above the ground, both trees hosted a common hemi-epiphyte in Valdivian rain forests, *Raukua laetevirens* (Araliaceae; Fig. 2A). These hemi-epiphytes had an arboreal habit, a profusely branched main trunk 29–38 cm diameter, and branches bearing dense foliage. The crown of the hemi-epiphyte did not emerge above that of *E. cordifolia*. The wood density of *R. laetevirens* was 0.5 kg/l; and hence its dry biomass was estimated in 1.0 and 2.6 t in each *Eucryphia* tree respectively, with 9 kg (<0.2% of the total dry mass) represented by green foliage (Table 1). Roots of the hemi-epiphyte descended to the ground, resembling strangler figs of tropical forests (Zotz, 2005; Armesto et al., 1996b; Gutiérrez et al., 2008a; Fig. 2A). In the coastal forest of Guabún, 100% of all *E. cordifolia* trees >1.2 m DBH supported one or more hemi-epiphytic trees of *R. laetevirens*. Branches and canopy roots of canopy-dwelling *R. laetevirens* were also covered by a layer of epiphytes. For this reason *R. laetevirens* is hereafter analyzed separately from other epiphytes.

The overall architecture of *A. punctatum* (25 m tall) was also deliquescent (Horn, 1971), but with a multilayer leaf display and greater leaf biomass (99 kg dry mass, Table 1). The crown diameter was smaller than in *Eucryphia*, but the crown of *A. punctatum* was denser and had no foliage-free space close to the main trunk, lacking hemi-epiphytic trees. In this case, as in many other *A. punctatum* trees, a large and conspicuous woody vine, *Hydrangea serratifolia*, climbed the entire length of the tree (Fig. 2B).

### 3.2. Epiphyte species richness and vertical distribution

Overall, we recorded 22 species of vascular epiphytes, in addition to 22 genera, representing at least 36 species of non-vascular epiphytes (mostly bryophytes) in the three emergent trees sampled in coastal forests (Table 2). Pteridophyta, particularly the Hymenophyllaceae (filmy ferns) family dominated the diversity of the vascular epiphyte assemblages, with 12 species. Flowering epiphytes were represented by seven species in six families (Table 2). Concerning vascular species richness, rarefaction analysis showed that these emergent trees had a similar number of vascular species, and that our sampling effort was sufficient to characterize the epiphytic plant community in each tree (Fig. 3).

The two *E. cordifolia* trees had similar species compositions (Sorensen's similarity index 0.67), with the same flowering species and differences due to ferns and non-vascular species (Table 2). However, the epiphyte assemblages of *E. cordifolia* trees differed from that of *A. punctatum* (Sorensen's similarity index 0.381 and

0.358 respectively). First, *E. cordifolia* was the primary host of the hemi-epiphyte *R. laetevirens*, not present on *A. punctatum*. Second, *A. punctatum* hosted a greater species richness of bryophytes than the two emergent *E. cordifolia* trees combined, and twelve bryophyte species found in *A. punctatum* were not recorded on *E. cordifolia* (Table 2).

Epiphyte species had different vertical distributions. For instance, the liverworts *Bazzania* sp. and *Frullania* sp. were distributed along the entire vertical profile of both *E. cordifolia* trees. Other species such as the lichen *Cladonia* sp. and the fern *Grammitis magellanica* were predominantly present in the upper crown branches, while the vine *Luzuriaga polyphylla* was always attached to the main trunk up to 3–4 m above the ground (Table 2). Summarizing, 34% of the epiphytic flora occupied the higher parts of the tree crowns, 18% were only present in the first 3 m from the tree base, while the remaining 48% were distributed at different heights over the entire vertical profile (Table 2). Excluding those species present only near the tree base, 82% of the epiphyte species collected occurred above 3 m height. Branch tips in the tree crown were under-sampled due to their inaccessibility, but field observations indicated that they were densely covered by lichens, primarily *Pseudocyphellaria* sp.

### 3.3. Epiphyte biomass

The emergent trees sampled hosted very large epiphyte loads in addition to *R. laetevirens* biomass. Individual trees of *E. cordifolia* supported a fresh weight of 427 and 462 kg of epiphytes, with a water content of 66.7 ± 2.4% and 68.0 ± 1.3%, respectively. In terms of dry weight, these trees supported 134 and 144 kg of epiphytes, respectively. The epiphyte mat is a carpet composed by a thick layer of arboreal soil and roots covered by a thin layer of green tissues of mosses, filmy ferns and lichens. Vines such as *Luzuriaga polyphylla* (Philesiaceae) occurred near the tree base, while *Sarmienta repens* was common in the upper half of the tree, attached only to arboreal soil, with succulent leaves pending from the limbs. Dense clumps of the bromeliad *F. bicolor* were scattered along the vertical profile of the tree, each clump composed on average by 12.6 ± 2.8 individual rosettes ( $n = 25$  clumps).

On both tree species, about 30% of the epiphytic biomass was green tissue and the remaining 70% was arboreal soil and roots (Table 3). A large *A. punctatum* tree sampled supported 362 kg fresh weight of epiphytes, with an average water content of 55.3 ± 4.3%. In terms of dry mass, this tree support 142 kg of epiphytes. Two vascular epiphytes made major contributions to total biomass: the hemi-epiphytic tree *R. laetevirens* and the bromeliad *F. bicolor*. The first one established and grew at the height of crown branching, contributing with woody mass and leaves to the tree crown. The second, *F. bicolor* was found along the entire vertical profile, but most of its biomass (>80%) was at tree heights between 9 and 15 m, where it formed large clusters of stems and leaves of up to 34 kg (fresh weight). In the crown of *E. cordifolia*, these large clumps of *F. bicolor* accumulate up to 56% of the total arboreal soil, and up to 54% of the green biomass of epiphytes. In *A. punctatum*, where dominant epiphytes were mosses and ferns, green tissues of *F. bicolor* represented only a 1% of the total epiphyte biomass (Table 3).

Overall, epiphytes represented <1% of the total biomass of canopy emergent trees. However, considering only the green biomass, epiphytes represented a major percentage of the photosynthetic tissues present in tree canopies. Green tissues of epiphytes totaled 40 kg in *A. punctatum*, which represented an additional 41% to the photosynthetic mass of the host tree (99 ± 21 kg, Table 1). The leaf mass of *E. cordifolia* varied between 33.3 ± 7.3 and 50.9 ± 11.2 kg, while the green mass of epiphytes varied between 48 and 50 kg, consequently adding between 100% and

**Table 2**

Relative frequency and vertical distribution (in parenthesis) of vascular and non-vascular epiphytes on three canopy emergent trees in coastal rain forests of Chiloé Island, southern Chile. Frequency was calculated as the number of vertical intervals (one every 2 m) where each species was found, multiplied by 100 and divided by the total number of intervals per tree. Total number of 2-m intervals sampled per tree were: *E. cordifolia* 1 = 34; *E. cordifolia* 2 = 31, *A. punctatum* = 44. Vertical distribution is given in meters above the ground.

Species	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
<b>Pteridophyta</b>			
<b>Hymenophyllaceae</b>			
<i>Hymenoglossum cruentum</i>	0	36 (2–15)	80 (9–23)
<i>Hymenophyllum caudiculatum</i>	9 (2–9)	23 (1–15)	5 (13–17)
<i>Hymenophyllum cuneatum</i>	68 (6–22)	23 (15–18)	21 (13–23)
<i>Hymenophyllum darwinii</i>	0	3 (8–9)	0
<i>Hymenophyllum dentatum</i>	12 (15–22)	7 (14–16)	14 (16–23)
<i>Hymenophyllum dicranotrichum</i>	21 (1–10)	74 (1–15)	5 (9–15)
<i>Hymenophyllum ferrugineum</i>	0	7 (1–2)	0
<i>Hymenophyllum pectinatum</i>	3 (9–10)	0	2 (13)
<i>Hymenophyllum plicatum</i>	53 (1–22)	13 (15–17)	80 (11–23)
<i>Hymenophyllum secundum</i>	3 (21–22)	16 (15–16)	0
<i>Serpyllopsis caespitosa</i>	6 (17–18)	0	0
<b>Grammitidaceae</b>			
<i>Grammitis magellanica</i>	6 (18–20)	7 (15–16)	5 (20–23)
<b>Aspleniaceae</b>			
<i>Asplenium trilobum</i>	0	0	52 (7–23)
<b>Polypodiaceae</b>			
<i>Polypodium feuillei</i>	0	0	30 (13–20)
<b>Anthophyta</b>			
<b>Gesneriaceae</b>			
<i>Sarmienta repens</i>	65 (2–22)	97 (1–18)	80 (7–23)
<i>Mitraria coccinea</i>	0	0	5 (0–3)
<b>Philesiaceae</b>			
<i>Luzuriaga polyphylla</i>	12 (0–4)	19 (0–12)	0
<b>Bromeliaceae</b>			
<i>Fascicularia bicolor</i>	47 (1–19)	68 (1–17)	16 (12–19)
<b>Araliaceae</b>			
<i>Raukua laetevirens</i>	9 (13–18)	19 (14–16)	0
<b>Hydrangeaceae</b>			
<i>Hydrangea serratifolia</i>	0	0	39 (0–23)
<b>Cornaceae</b>			
<i>Griselinia racemosa</i>	0	0	9 (13–18)
<b>Marchantiophyta</b>			
<i>Bazzania</i> sp.	47 (1–19)	87 (1–18)	0
<i>Frullania</i> sp.	0	13 (2–16)	0
<i>Herbetus runcinatus</i>	0	13 (10–11)	0
<i>Metzgeria</i> sp.	3 (15–16)	0	0
<i>Plagiochila</i> sp.	30 (15–20)	7 (15–16)	0
<i>Telaranea</i> sp.	0	3 (15–16)	0
<i>Marchantiophyta unident</i>	24 (15–23)	19 (10–15)	0
<b>Lichens</b>			
<i>Bunodophoron</i> sp.	18 (14–20)	3 (17–18)	0
<i>Cladonia</i> sp.	3 (16–17)	13 (14–18)	0
<i>Nephroma</i> sp.	0	3 (15–16)	0
<i>Parmelia</i> sp.	3 (17–18)	0	0
<i>Pseudocyphellaria</i> sp.	18 (15–23)	32 (2–15)	11 (12–23)
<i>Usnea</i> sp.	6 (17–22)	0	0
<b>Bryophyta</b>			
<i>Campylopus</i> cf. <i>purpureocaulis</i>	0	0	2 (23–24)
<i>Dicranoloma robustum</i>	27 (1–19)	29 (6–15)	0
<i>Hypnum chrysogaster</i>	12 (14–18)	10 (15–16)	0
<i>Lepyrodion hexastichus</i>	0	0	5 (9–20)
<i>Lepyrodion parvulus</i>	0	0	32 (11–23)
<i>Lepyrodion tomentosus</i>	0	0	16 (5–20)
<i>Lopidium concinnum</i>	3 (9–10)	0	16 (1–17)
<i>Macromitrium</i> cf. <i>krausei</i>	0	3 (4–17)	13 (1–23)
<i>Poroathamnium arbusculans</i>	0	0	5 (1–3)
<i>Poroathamnium panduraefolium</i>	0	0	5 (5–9)
<i>Poroathamnium valdiviae</i>	0	0	2 (3–4)
<i>Rhaphidorrhynchium callidum</i>	3 (21–22)	3 (16–17)	0
<i>Rigodium adpressum</i>	0	0	2 (13–14)
<i>Rigodium tamarix</i>	0	0	5 (7–13)
<i>Rigodium toxarion</i>	0	3 (15–16)	27 (1–17)
<i>Weymouthia cochlearifolia</i>	0	0	48 (5–22)
<i>Weymouthia mollis</i>	9 (4–22)	0	23 (7–21)

Table 2 (Continued)

Species	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
<i>Zygodon hookeri</i>	0	0	14 (5–17)
<i>Zygodon pentastichus</i>	0	0	5 (20–23)
Clorophyta			
<i>Trentepohlia</i> sp.	0	3 (15–16)	5 (19–20)
<i>Chlorophyta unident</i>	0	3 (15–16)	0
Total taxa	28	31	33

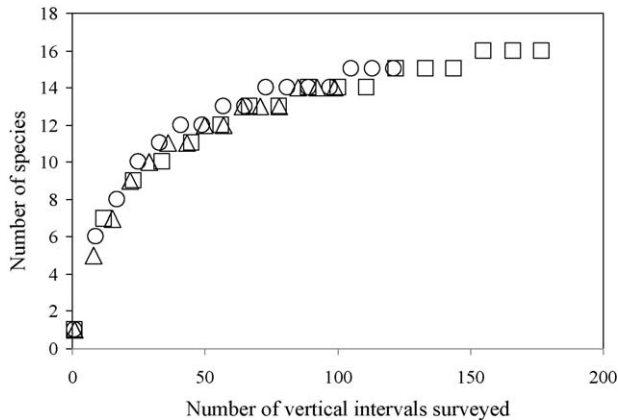


Fig. 3. Rarefaction analyses for the total number of species of vascular epiphytes recorded in each tree, as a function of the total number of vertical intervals of 2-m surveyed. Circles corresponded to *E. cordifolia* 1, triangles corresponded to *E. cordifolia* 2, and squares corresponded to *A. punctatum*.

145% of additional photosynthetic tissue to the tree crowns. Most weight of epiphyte foliage belonged to *F. bicolor*, filmy ferns and cryptogams, while *R. laetevirens* alone contributed 18–29% of the total leaf mass on tree crowns (Tables 1 and 3).

Finally, visual assessment of epiphyte loads present in 59 trees of *E. cordifolia* in Guabún coastal forest showed that epiphyte biomass increased with tree size (regression analysis  $F_{1,58} = 88.5$ ,  $R^2 = 0.60$ ;  $P < 0.001$ ; Fig. 4). Trees sampled ranged from 40 cm DBH to 238 cm DBH, with an average of  $118 \pm 6$  cm DBH. Smaller trees had less species and lower biomass of epiphytes, but when trees grow larger than 1 m DBH, there is a pronounced, non-linear increase in epiphyte biomass (Fig. 4). Greater epiphyte loads result from the colonization of large trees by the hemi-epiphyte *R. laetevirens*.

## 4. Discussion

### 4.1. Epiphyte composition

In this study, we found that three canopy emergent trees sampled hosted much of the known epiphyte species of Chilean

temperate forests. For instance, Muñoz et al. (2003) and San Martín et al. (2008) sampled vascular epiphytes from the ground up to 2.5 m on tree trunks. They recorded less than 20 vascular epiphyte species in a much larger sample of trees ( $N = 499$  and 40, respectively, Table 4). Clement et al. (2001) climbed nine giant *F. cupressoides* trees in Andean montane forests of southern Chile, recording 18 vascular epiphyte species (Table 4). Our survey of three large emergent trees in Valdivian coastal temperate rain forests yielded a total of 22 vascular epiphyte species and a higher diversity of cryptogams. Overall, we recorded 33% of the known species of flowering epiphytes described for Valdivian temperate rainforest (Smith-Ramírez et al., 2005), and 50% of the species of filmy ferns (Hymenophyllaceae) known for Chilean temperate forests (25 species; Marticorena and Quezada, 1985). This fern family is largely epiphytic, with between 17 and 18 species described for Valdivian rainforests (Ponce et al., 2002; Smith-Ramírez et al., 2005) and 20 species described for Chiloé Island forests (Villagrán and Barrera, 2002a). Despite clear limitations due to the small sample size of canopy emergent trees in our study, we can conclude that large trees in Valdivian temperate rain forests must hold much of the vascular epiphyte diversity in this region.

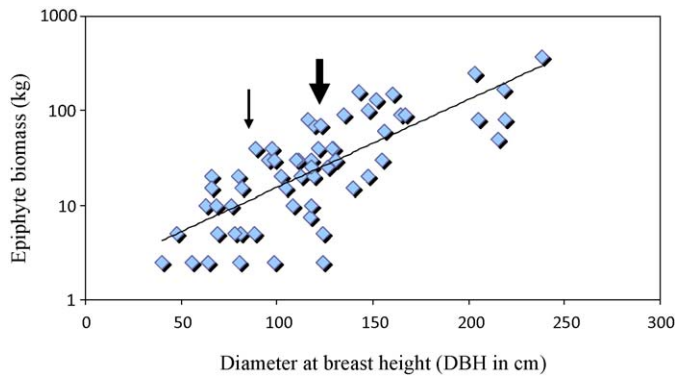
Non-vascular epiphytes are also important in the temperate rain forest canopy. Villagrán and Barrera (2002b) described 51 species in 42 genera of forest mosses in Chiloé Island. A total of 19 species belonging to 11 genera of mosses were recorded in the small sample of canopy emergent trees surveyed, in other words 37% of the known moss diversity in the island. In the case of liverworts and lichens, information is limited. Villagrán et al. (2002) described a total of 163 species (53 genera) of liverworts in forests and moorlands of Chiloé Island, while Galloway (1996) listed 44 lichen genera potentially found in the canopy of Chilean temperate forests, but the group remains poorly known (Galloway, 1996). We identified six genera of liverworts and five genera of lichens, representing an unknown number of species. This diversity, especially lichens, is probably an underestimate because we had no access to branch tips in the upper canopy.

Epiphytes are very common components of most Chilean temperate forests (e.g. Riveros and Ramírez, 1978; Muñoz et al., 2003; Rozzi et al., 2008; San Martín et al., 2008; Salinas, 2008). However, the number of species is lower than that reported for Neotropical and even some temperate rainforests of the world

Table 3

Dry biomass (kg) of the hemi-epiphyte *R. laetevirens*, the bromeliad *F. bicolor* and the other epiphytes growing on canopy emergent trees of *E. cordifolia* and *A. punctatum* in coastal rain forests of Chiloé Island, southern Chile.

	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
<i>Raukua laetevirens</i> woody biomass	$2.6 \times 10^3$	$1.0 \times 10^3$	–
<i>Raukua laetevirens</i> green tissues	9.4	9.5	–
<i>Fascicularia bicolor</i> green tissues	18	26	1.4
Other epiphytes green tissues	22	13	39
Arboreal soil associated with <i>F. bicolor</i>	28	54	Indet.
Arboreal soil associated with the other epiphytes	75	41	102
Total green tissues	50	48	40
Total hemi-epiphyte woody biomass	$2.6 \times 10^3$	$1.0 \times 10^3$	–
Total arboreal soil	104	95	102



**Fig. 4.** Relationship between trunk diameter at breast height (DBH, cm) of *Eucriphia cordifolia* and epiphytic biomass (kg, in log scale) in forests of Guabún, Chiloé Island, southern Chile. The thin arrow indicates the DBH at which the first *E. cordifolia* tree with an individual of *Raukaka laetevirens* was observed. The thick arrow indicates the minimum DBH above which all trees had presence of *R. laetevirens*.  $N = 59$  trees (linear regression analysis  $F_{1,58} = 88.5$ ,  $R^2 = 0.60$ ,  $P < 0.001$ ).

(Table 4). For instance, Cardelús et al. (2006) described 555 vascular epiphyte species from 52 trees at 6 sites along an altitudinal gradient in Monte Verde cloud forest in Costa Rica. Pike et al. (1975) and McCune et al. (2000) recorded around 100 species, nearly all non-vascular epiphytes in Pacific Northwest forests of North America (Table 4). In New Zealand, Dickinson et al. (1993) found 28 vascular and 26 non-vascular species of epiphytes in a single, large tree of the conifer *Dacrycarpus dacrydioides*, slightly higher than the number we found on three emergent trees in Chiloé forests (Table 4). Despite the relatively lower species richness considering other global regions, few canopy emergent trees in our work harbor much of the diversity of vascular epiphytes of Chilean temperate forests, and this pattern may also hold for cryptogams.

Studies in different forest ecosystems have shown that epiphyte diversity increases with tree size (McCune, 1993; Johansson et al., 2007). Muñoz et al. (2003) showed that larger trees hold more species in Chilean North Patagonian forests. If this pattern holds for Valdivian coastal forests, then spatially-dispersed older trees can

become increasingly significant as reservoirs of biodiversity in the landscape, including epiphytes that are rare or absent from secondary forests (Barthlott et al., 2001). Therefore, large trees can be very important element for the conservation of forest biodiversity (Berg et al., 1994).

#### 4.2. Epiphyte loads

At the scale of individual trees, the epiphyte biomass recorded in our focal trees was similar or greater than for trees surveyed in epiphyte-rich montane cloud forests of Colombia (134–144 kg in Chile versus 110 kg, in Colombia; Table 5). Adding the biomass of the hemi-epiphyte *R. laetevirens* to this estimate, then the trees of *E. cordifolia* in this forest should support 100 t epiphytes/ha, one of the largest estimates for temperate or tropical forests worldwide. Considering that other tree species in the stand also supported a dense carpet of epiphytes (personal observations), epiphyte loads in Valdivian temperate rainforest, as in other southern temperate rainforests, may approach estimates for epiphyte-rich tropical cloud forests (Table 5; Hofstede et al., 2001).

At the scale of a forest plot, epiphyte biomass in this coastal rain forest is higher than previous estimates for Chilean rain forests. Gutiérrez et al. (2008a, b) found 72 individuals of *E. cordifolia* with a DBH ranging from 0.6 to 2.4 m in one hectare of forest in the Guabún site. Multiplying the density of *E. cordifolia* by the mean epiphyte biomass for a given tree DBH estimated by us (but excluding *R. laetevirens*), we found that this tree species alone supports a minimum of 10 t of epiphytes per ha. This biomass is larger than the 8.2 t/ha reported for montane *F. cupressoides* forests in Chiloé Island (Pérez et al., 2005), and larger than the 2.2 t/ha reported by Woda et al. (2006) for Valdivian coastal forests of southern Chile. The value for Chiloé forests is also larger than average epiphyte loads described for temperate rainforests of North America (6.8 t/ha, Grier and Nadkarni, 1987; Table 5).

The mean age of emergent trees in this forest was estimated in 300–400 years (Gutiérrez et al., 2008a), implying that development of the full epiphyte assemblage requires a few centuries (Franklin et al., 1981; Sillett and Bailey, 2003). However, more rapid and greater biomass accumulation on trees take place after

**Table 4**

Number of species of vascular and non-vascular epiphytes recorded in different tropical and temperate rainforests throughout the vertical profile, and epiphytic biomass recorded per tree and/or per ha of forest.

Study site	Ferns	Brom	All vascular	Mosses and liverworts	Lichens	Source
<i>Tropical</i>						
Montane, Costa Rica (51)	138	41	555	ns	ns	Cardelús et al. (2006)
Montane, Ecuador (4)	8	2	42	ns	ns	Freiberg and Freiberg (2000)
Montane, Ecuador (5)	5	2	31	ns	ns	Freiberg and Freiberg (2000)
Lowland, Ecuador (5)	4	2	21	ns	ns	Freiberg and Freiberg (2000)
Lowland, Ecuador (5)	5	2	30	ns	ns	Freiberg and Freiberg (2000)
<i>Temperate</i>						
Redwood, USA	4	ni	49	43	143	Williams and Sillett (2007)
Douglas-fir, USA	1	0	1	32	74	Pike et al. (1975)
Douglas-fir Forest, USA	0	0	0	14	97	McCune et al. (2000)
Humboldt Sitka Spruce (5), USA	2	0	2	17	72	Ellyson and Sillett (2003)
Abies lasiocarpa, USA	0	0	0	13	37	Rhoades (1981)
Acer circinatum, USA	0	0	0	11	17	Ruchty et al., 2001
Conifer and broad-leaved forest, New Zealand	ni/ns	ni	30	ns	ns	Burns and Dawson (2005)
Nothofagus-Podocarpus (3), New Zealand	20	0	62	62	28	Hofstede et al. (2001)
Dacridium dacrydioides (1), New Zealand	10	0	28	8	18	Dickinson et al. (1993)
Valdivian forest, Chile	11	1	19	8	4	Riveros and Ramírez, 1978
Fitzroya cupressoides (9), Chile	9	0	18	16	15	Clement et al. (2001)
North-Patagonian, Chile (499)	11	1	20	ns	ns	Muñoz et al., 2003
Valdivian forest, Chile	7	0	8	ns	ns	San Martín et al. (2008)
<i>Eucriphia cordifolia</i> (2), Chile	12	1	16	14*	6*	This study
<i>Aextoxicon punctatum</i> (1), Chile	10	1	15	16*	1*	This study

Abbreviations—Brom: Bromeliads, ns: not studied, ni: not indicated. Parentheses indicate the number of trees sampled in each forest.

\* Epiphytes were identified mostly to genus, and not to species.

**Table 5**

Estimates of epiphyte biomass (green tissues plus arboreal soil, dry weights) for tropical and temperate tree species.

Study site	kg/tree	t/ha	Source
<i>Tropical</i>			
Montane forest of <i>Quercus copeyensis</i> , Costa Rica		2.86	Hölscher et al. (2004)
Primary cloud forest, Costa Rica		33.1	Nadkarni et al. (2004)
Secondary cloud forest, Costa Rica		0.17	Nadkarni et al. (2004)
Montane cloud forests, Colombia	115	44	Hofstede et al., 1993
Montane forest, Jamaica		0.37–2.1	Tanner (1980)
Subtropical forest, Taiwan		3.3	Hsu et al. (2002)
<i>Temperate</i>			
Douglas-fir forest, Oregon, USA	17.8		Pike (1978)
Douglas-fir forest, Oregon, USA	27.1		Pike (1978)
Subalpine forest of <i>Abies lasiocarpa</i> , Oregon, USA	12.8	1.8–6.6	Rhoades (1981)
Douglas-fir forest > 400 years Cascada Range, USA		2.6	McCune (1993)
Douglas-fir forest ~145 years		0.88	McCune (1993)
Douglas-fir forest ~91 years		1.13	McCune (1993)
<i>Picea sitchensis</i> (5), California, USA	190		Ellyson and Sillett (2003)
Redwood forests		2.9	Enloe et al. (2006)
Coastal forest of <i>Sequoia sempervirens</i> (27)	12–742		Sillett and Bailey (2003)
<i>Picea sitchensis</i> (5)	10–43		Sillett and Bailey (2003)
Conifer montane forests of <i>Fitzroya cupressoides</i> , Chiloé Island, Chile		8.2	Pérez et al. (2005)
Valdivian coastal forests, Chile		2.2	Woda et al. (2006)
<i>Eucryphia cordifolia</i> (2) of Valdivian coastal rain forests Chiloé, Chile*	134–144	10**	This study
<i>Aextoxicon punctatum</i> (1) of Valdivian coastal rain forests Chiloé, Chile	143		This study

\* The hemi-epiphyte tree *Raukaua laetevirens* was excluded from this calculation.\*\* Estimated only for *E. cordifolia*.

they reach 1 m DBH, and may be enhanced by the establishment of *R. laetevirens* (Fig. 4). Our regression analysis between tree DBH and epiphyte biomass, albeit only comparative because of the lack or more precise biomass estimates, shows non-linear increase in epiphyte biomass on trees that had been colonized by *R. laetevirens*. The hemi-epiphyte enhances structural complexity and heterogeneity of tree crown, thus providing additional habitats for epiphytes (Peña et al., 2006).

#### 4.3. Functional role of epiphytes

Evidence from various forests around the world shows that epiphytes can capture fog and rain water, process nutrients, fix nitrogen, and provide habitat and food for a rich assemblage of canopy invertebrates and vertebrates (Nadkarni and Matelson, 1992; Ozanne et al., 2003; Ellwood and Foster, 2004; Lowman and Rinker, 2004 for a review; Benner et al., 2007). Water interception by the forest canopy is an important process because it prevents runoff and enhances water storage and nutrient transfer among different compartments in forest ecosystems (Kölher et al., 2006). In a 60-year-old broad-leaved Chiloé forest, Díaz et al. (2007) estimated that 53% of the rainwater was intercepted by and/or evaporated from tree canopy surfaces, while the remaining 47% reached the ground via throughfall and stemflow. In the trees studied, water content of the epiphyte mats, including organic detritus on tree branches (but excluding *R. laetevirens*), was around 70%, which means that more than 300 l of water can be retained by epiphytes within the crown of a single tree. Accordingly, epiphytes play a significant but not yet well-understood role in the water cycle of old-growth forests (Kölher et al., 2006).

Epiphytes increase interception of water and nutrients in the forest canopy (Hölscher et al., 2004; Hietz et al., 2002). Along the Chilean coast, temperate forests are characterized by significant and year-round fog interception (Del Val et al., 2006), which may supply water to the ecosystem during extremely dry summers, becoming more important as summer rainfall is reduced latitudinally or by climate change (Del Val et al., 2006; Woda et al., 2006; Gutiérrez et al., 2008b). Fog, suspended over the nearby Pacific Ocean, can also contribute nutrients, particularly nitrogen, to mainland forests in Chile (Weathers et al., 2000; Oyarzún et al., 2004), which may be readily absorbed by epiphytes in the canopy

that later transfer atmospheric nutrients to forest ecosystems. In addition, epiphytic lichens could supplement nitrogen derived from biological fixation (Galloway, 1996). Preliminary assays in *Pseudocyphellaria*, a well-known, N-fixing lichen in the upper branches of coastal rainforest trees, showed high nitrogenase activity (Galloway, 1996; Benner et al., 2007; Díaz, 2009). However, the role of epiphytes in nutrient supply and circulation in these forests requires further study.

Epiphytes can also enhance carbon uptake and forest productivity. Total photosynthetic biomass in the forest canopy increases 41–145% when epiphytes are added to the mass of live tree foliage (Tables 1 and 3). In Valdivian rain forests, green tissues contributed by epiphytes are a larger component of the forest canopy than in other forests (Ingram and Nadkarni, 1993), and although photosynthetic rates are lower in some epiphytes (e.g. cryptogams) than in tree leaves (Benzing, 2004), further research is needed to elucidate how much carbon uptake is due to epiphytes and what is their relative contribution to net ecosystem productivity. Finally, epiphytes and their detritus can also supply nutrients directly to the tree via adventitious roots (Nadkarni, 1981; Oyarzún et al., 2004). Several species of southern South American trees are known to produce adventitious roots from stems and trunks that allow them to obtain nutrients and water directly from the aerial soil accumulated under the epiphytes (Pérez et al., 2003).

Negative effects of large epiphyte loads are attributed mainly to the increased susceptibility of trees to fall or lose large limbs due to the extra weight (Strong, 1977), to competition with the host tree for sunlight, and to restrictions on tree secondary growth by a cylinder of roots of strangler hemi-epiphytes (Putz and Holbrook, 1986). However, the effect of tree age on the magnitude and importance of such negative effects are often ignored. Arboreal soil and epiphytes represent only 0.3–0.7% of the weight of a whole canopy emergent *E. cordifolia* tree, in this species we found evidence that epiphytes do not cast shade on the tree foliage (Fig. 2A). The hemi-epiphyte *R. laetevirens* is not a strangler tree, and its weight represents between 4 and 5.5% of the host tree biomass. Such weight can represent a relevant pressure on the physical strength of a tree (Putz and Holbrook, 1986). However, the fact that a large number of *E. cordifolia* trees with heavy epiphyte loads were still alive 300 years after becoming established in the

forest (Gutiérrez et al., 2008a), suggests that tree-fall probabilities are low. If trees live accumulating large epiphyte loads per decade or century (Enloe et al., 2006), the net balance between positive and potentially negative effects must be considered in future analysis of this problem (Laman, 2004).

#### 4.4. Management and conservation implications

Long-lived and emergent canopy trees are important structural elements of ancient temperate rainforest ecosystems (Franklin et al., 1981; Van Pelt, 2007). Canopy emergents support a diverse array and high biomass of epiphytes, thereby fostering the diversity and densities of canopy invertebrate and vertebrate species that are absent from younger forests without epiphytes (Silleet, 1994; Nadkarni and Matelson, 1989; Berg et al., 1994; Ellwood and Foster, 2004; Laman, 2004; Nadkarni et al., 2004; Díaz et al., 2005). These trees, by supporting large and diverse epiphyte loads, also sustain ecosystem functions such as water, carbon and nutrient capture, storage and cycling, thus directly linking biodiversity with the structure and function of old-growth forest ecosystems (Franklin et al., 1981; Armesto et al., 2009). Accordingly, management protocols should take as a priority the conservation of these large trees in managed landscapes, considering them not only as nuclei and refugia for a diverse array of epiphytes and associated fauna in forests, but also as hitherto neglected contributors to ecosystem services and forest productivity.

Chilean coastal rain forest, characterized by unpolluted, pre-industrial atmospheric conditions (Hedin et al., 1995; Perakis and Hedin, 2002), and low pre-historic and current human impacts (Gutiérrez et al., 2008a) may be unique places in the temperate world where a baseline, better reflecting interactions crafted over evolutionary time, can be generated and later compared to other temperate forests where human impacts and atmospheric air pollution are pervasive and modulate the dynamics of modern ecosystems. We argue that the rapid disappearance of old, canopy emergent trees from forest ecosystems, and from entire landscapes, as old-growth stands dwindle due to expanding agriculture and forestry (Wirth et al., 2009), not only represent a loss of biodiversity but also valuable ecosystem processes, and historical relationships, which may provide clues to understanding, managing and conserving forests worldwide.

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