

LINKING COMPOSITION, STRUCTURE AND FUNCTIONS OF BIODIVERSITY:
RELATIONSHIPS AMONG EPIPHYTES, INVERTEBRATES AND BIRDS IN THE
CANOPY OF CHILEAN TEMPERATE RAINFORESTS

By

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To my parents, Nora Romero and Fanor Díaz
To the nature, which always shares with me its secrets
To the canopy, the place where trees let you see the forest

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Abstract of Dissertation Presented to the Graduate School
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LINKING COMPOSITION, STRUCTURE AND FUNCTIONS OF BIODIVERSITY:
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CANOPY OF CHILEAN TEMPERATE RAINFORESTS

By

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Temperate rainforests of southern South America are characterized by a multi-layered forest canopy with old emergent trees densely covered by epiphytes. The species richness and community structure of this forest canopy remains largely unknown. In this dissertation, I address this gap in knowledge by testing the following linked hypotheses; 1) that large old trees support a rich community of epiphytes that, in turn, 2) support invertebrate and 3) bird communities in the forest canopy. Working in southern Chile, I characterized the composition and biomass of epiphytes associated with two common emergent tree species; both *Eucryphia cordifolia* (Eucryphiaceae) and *Aextoxicon punctatum* (Aextoxicaceae) are regional endemics; I determined the effect of epiphytes on canopy invertebrate community structure on experimental trees with either intact (control) or removed epiphyte assemblages; and I assessed the effect of epiphytes on bird communities by comparing bird visits between experimental trees (with and without epiphytes), and bird abundance in forest plots with naturally varying epiphyte loads.

Trees supported approx. 140 kg (dry weight) of epiphytic material; 30% in leaves and 70% in arboreal soils and roots. Epiphytes were dominated by *Fascicularia bicolor* (Bromeliaceae), Hymenophyllum ferns, and by the hemi-epiphyte *Raukaua laetevirens* (Araliaceae). Forest

canopy was inhabited by a large diversity of insects, arachnids, annelids and mollusks; notable patterns included a general lack of ants and a preponderance of detritivores. Trees with epiphytes supported 20% more invertebrate species in the tree crown and twice the invertebrate biomass of similar trees without epiphytes. Finally, large trees with epiphytes attracted more bird visits than similar trees without epiphytes, and forest plots with greater epiphytic biomass supported significantly greater bird abundance; bird species richness was not affected.

My findings identify large old trees as a critical structural dimension of mature forest that defines forest canopy communities as unique assemblages that contribute significant diversity and biomass to south-temperate rainforest. Continuing research also reveals that ecological functions (such as water and nutrient retention, pollination, seed dispersal, predation) of canopy communities supported by large trees are both unique and significant within the forest ecosystem. Implications for sustainable forest management practices are discussed.

CHAPTER 1
LINKAGES AMONG STRUCTURE, COMPOSITION AND FUNCTIONS OF
BIODIVERSITY IN THE FOREST CANOPY

Theoretical Background

Biodiversity is defined as the diversity of living forms below and above the species level, including all hierarchical levels of organization from genes to ecosystems (Groom et al. 2006). Noss (1990; using Franklin et al. 1981), proposed a framework to characterize biodiversity based on three main attributes: Composition, structure and functions, interacting with each other at different levels of system organization. Composition refers to the identity of units of biodiversity, such as the diversity of genes or alleles within organisms, or the taxonomic composition of communities. Structure refers to how these units are physically organized, creating physical structural complexity. For instance, the age structure of a population, or the physical structures created by logs or snags in forests. Lastly, functions refer to the manifestations of biodiversity in the biological interactions and biogeochemical processes that take place in ecological systems, such as gene expression, species' trophic interactions (predators, herbivores), nitrogen fixation and nutrient recycling. Noss (1990) proposed that these attributes interact at different scales; for instance, allelic diversity (composition) can affect heterozygosity (structure) and genetic flux (function) within and between populations (Fig. 1-1), while species diversity (composition) is linked to habitat structure and ecosystem process (Fig. 1-1).

The conceptual framework proposed by Noss (1990, 2006) offered indicators for monitoring the health condition of ecosystems, such as the effects of reduced structural diversity on taxonomic richness (Newton 1994, Roberge et al. 2008), and by extension the value of structural elements as indicators of biological integrity (Torrás and Saura 2008, Smith et al. 2008). Despite the high number of publications citing Noss' three types of attributes as indicators

of ecosystem health (over 600 citations by ISI Web of Science), most work in biodiversity focus on linkages between structure and taxonomic composition, particularly emphasizing one direction of the effect (i.e., effects of structure on species composition, and not vice versa). However, evidence of the multiple and reciprocal interactions among composition, structure and function remains as unexplored research area in ecology (Badano and Marquet 2008).

In this dissertation I will use the approach developed by Noss (1990) to characterize the attributes of biodiversity and their interactions in the canopy of Chilean temperate rain forests, a largely undescribed component of the forest environment. I will further analyze the usefulness of Noss' (1990) conceptual framework for understanding the functions of biodiversity in the forest canopy environment. Clarifying what are the main biodiversity attributes and their interactions in this system should build a stronger framework for ecological synthesis and for ecosystem management and conservation (Pickett et al. 2007). The larger goal of my dissertation is to contribute to such efforts.

Composition, Structure and Functions in Forest Canopies

The Forest Canopy: An Ecological Frontier

One of the less explored terrestrial ecosystems in the 21st century is the forest canopy (Nadkarni et al. 2004a). Canopies are defined as the upper level in the vertical profile of a forest, not usually accessible from the ground (Nadkarni et al. 2004a). Among the key functions that forest canopies provide to global ecosystems are their function as the main gas exchange interface, a surface where photosynthesis occurs, a structure for hydrological storage and release (Ozanne et al. 2003, Shaeffer et al. 2008), and their role in nutrient capture and nitrogen fixation (Fonte and Schowalter 2004). The advance of forest canopy ecology has been hampered in the past because the limited access and mobility of humans in this vertical layer. In recent years, canopy balloons, platforms, walkways, cable networks, canopy cranes, and tree climbing

technologies have allowed both intensive and extensive sampling schemes that are necessary for modern ecological research (Mitchell et al. 2002). Since the 1970's, there has been an explosive increase in canopy research worldwide (Moffett and Lowman 1995, Mitchell et al. 2002). Initial explorations of the forest canopy revealed that this vertical layer contained a high and largely undescribed, proportion of the forest biodiversity (Wilson 1992). Erwin's (1982) classic study and subsequent work on canopy invertebrates in Panamanian and Amazonian forests, changed our assessments of global taxonomic diversity by various orders of magnitude, from ~ 3 to more than 30 million species. While the actual estimates are still under discussion (Erwin 2004), there is no question that the structural complexity and resource base present in the forest canopy must support an enormous richness of organisms.

Despite the growing knowledge of taxonomic composition, little is known about the functional linkages among structural complexity, species diversity, and associated ecosystem processes in the forest canopy. Some intriguing examples have recently come to light, however. For example tank bromeliads that hold a substantial volume standing rain water in branches above the forest floor, support complex lifecycles of water-requiring plants, vertebrates, and invertebrates in the forest canopy (Richardson 2004). Field experiments have recently shown that forest canopy habitats experience significantly less herbivory because of avian predation on leaf-chewing insects (Van Bael et al. 2003, 2008). However, the structural complexity and (in many cases) the high taxonomic diversity and complexity of forest canopies have hindered experimental studies of the linkages among species composition, structure and function, especially in the tropics (Cruz-Angón et al. 2008).

Temperate Rainforest of Southern Chile

Temperate forest of the Southern Hemisphere, particularly coastal rain forests in Chile, still maintain extensive remnants of largely undisturbed and unpolluted forests, without atmospheric

deposition from industrial sources (Hedin et al. 1995, Perakis and Hedin 2002). Up until recently, little or no intensive human impact due logging was known (Willson and Armesto 1996), and clearing as well as pre-Hispanic settlements were restricted to specific areas along the coast and main river valleys. Ecologically, these rain forests differ greatly from northern hemisphere temperate rainforests; southern Chilean forests are dominated by broad-leaved trees, and contain abundant vascular and non-vascular epiphytes and vines (Armesto et al. 1996, Clement et al. 2001, Muñoz et al. 2003). Relatively species-poor communities maintain high levels of endemism, as a result of long-term isolation within the continent of a Tertiary forest flora and fauna with close relatives in Neotropical, Australian and New Zealand forests (Armesto et al. 1996, Villagrán and Armesto 2005). Today, a broad hyper arid desert and oceanic barriers separate these disjunct biotic realms (Armesto et al. 1998). Thus, 25 % of the vascular plant genera are endemic to southern South America, while 30% are also common to Australian - New Zealand forests, and 25 % are shared with Neotropical forests across the Andes (Villagrán and Hinojosa 1997). Around 20 to 25 forest bird species inhabit these forests (Willson et al. 1994), from which five are restricted to the forest understory (Reid et al. 2004), and the rest use large canopy trees and the entire vertical profile of the forest (Díaz et al. 2005). Although Chilean temperate rainforests have already been much reduced in area in recent decades due to logging and fire, large remaining patches still represent pre-industrial conditions, where interactions among organisms and ecosystem functions can be the direct result of evolutionary processes. Moreover, the relative compositional simplicity of these rain forests facilitates the analysis of whole species assemblages, which has been a limiting factor in tropical forest research (Greenberg et al. 2008, Cruz-Angón et al. 2008).

Links Among Epiphytes, Invertebrates and Birds in the Rain Forest Canopy

Epiphytes (*sensu lato*, including climbers) are conspicuous components of the forest canopy and the vertical profile of Chilean rainforests (Riveros and Ramírez 1978, Clement et al. 2001, Arroyo et al. 1996, Muñoz et al. 2003). Pérez et al. (2005) showed that coastal montane *Fitzroya cupressoides* forests in southern Chile hold 8.2 tons/ ha of epiphytic matter, including live and dead biomass. Epiphytic humus has similar chemical and physical features to the organic horizon of the forest floor, reason for which is also called “arboreal soil” (Enloe et al. 2006). This combination of epiphytes and its associated arboreal soils may support a high diversity and abundance of invertebrates, as reported for Neotropical forests (Nadkarni and Longino 1990, Ellwood and Foster 2004).

Epiphytes also provide nesting and foraging sites for birds (Silllett 1994, Cruz-Angón and Greenberg 2005). In southern Chile, several bird species are more abundant in old-growth forests characterized by the presence of large trees, which are generally profusely loaded with epiphytes and vines (Díaz et al. 2005). About 70% of Chilean forest bird species are classified as insectivores, or they complement their diet with invertebrates (Rozzi et al. 1996). Therefore, if canopy epiphytes support a high abundance of invertebrates, in addition to those associated with their host trees, epiphytes may also support greater numbers of insectivorous bird species, increasing their local abundance in forests. Finally, several studies in tropical and temperate rain forests suggest that insectivorous birds protect trees from herbivorous insects (Marquis and Whelan 1994, Van Bael et al. 2003, 2008, Borkhataria et al. 2006). Consequently, increased bird abundance due to epiphyte loads may also reduce insect damage to forest canopies (Murakami and Nakano 2002). An experimental study of Mazia et al. (2004) in *Nothofagus* forests of westernmost Argentina showed that foliar damage by insects increased within bird exclusions to almost twice the values observed in control branches accessible to birds. Another ongoing study

in *Nothofagus pumilio* forests in westernmost Argentina by Garibaldi et al. (2007) also found a positive effect of birds on trees by controlling insect herbivore populations, in agreement with previous results. Argentinean *Nothofagus* forests have a shared floristic composition with Chilean forests and are part of the same Ecoregion, characterized by the same avian species assemblage. Therefore, I argue that in southern Chilean rain forests, birds that prey on insects may also play a salient function as controllers of herbivore populations. In fact, based on the observed avian consumption rates of caterpillars in the canopy of Chilean forest ecosystems by González-Gómez et al. (2006), this controlling effect may be quite strong.

My study assesses the effects of forest structure (tree size) on species composition (taxonomic richness and abundance) of epiphytes, invertebrates and birds in the canopy. Specifically, I hypothesize that canopy structure provided by large trees in forests supports a high diversity and biomass of epiphytes (Fig. 1-2). The structure and resources provided by epiphytes, in turn, support a diverse assemblage of invertebrates that support bird species (Fig. 1-2). Each chapter of this dissertation addresses each of the links proposed in the theoretical model presented in Fig. 1-2. Chapter 2 presents a thorough description of the epiphyte community of Chilean rain forest canopies, considering its species richness, composition and biomass associated with large canopy trees. Chapter 3 analyzes the postulated effect of canopy epiphytes on invertebrate species richness and abundance. Chapter 4 analyzes the direct and indirect effects of canopy epiphytes on forest bird assemblages, and discuss the possible effect of birds through insect consumption on foliar herbivory. Finally, Chapter 5 summarizes the information about, epiphytes, birds and insect herbivores in forest canopies, and proposes a synthetic conceptual model considering the multiple linkages among structure, composition and possible functions in the canopy of southern Chilean temperate rain forests.

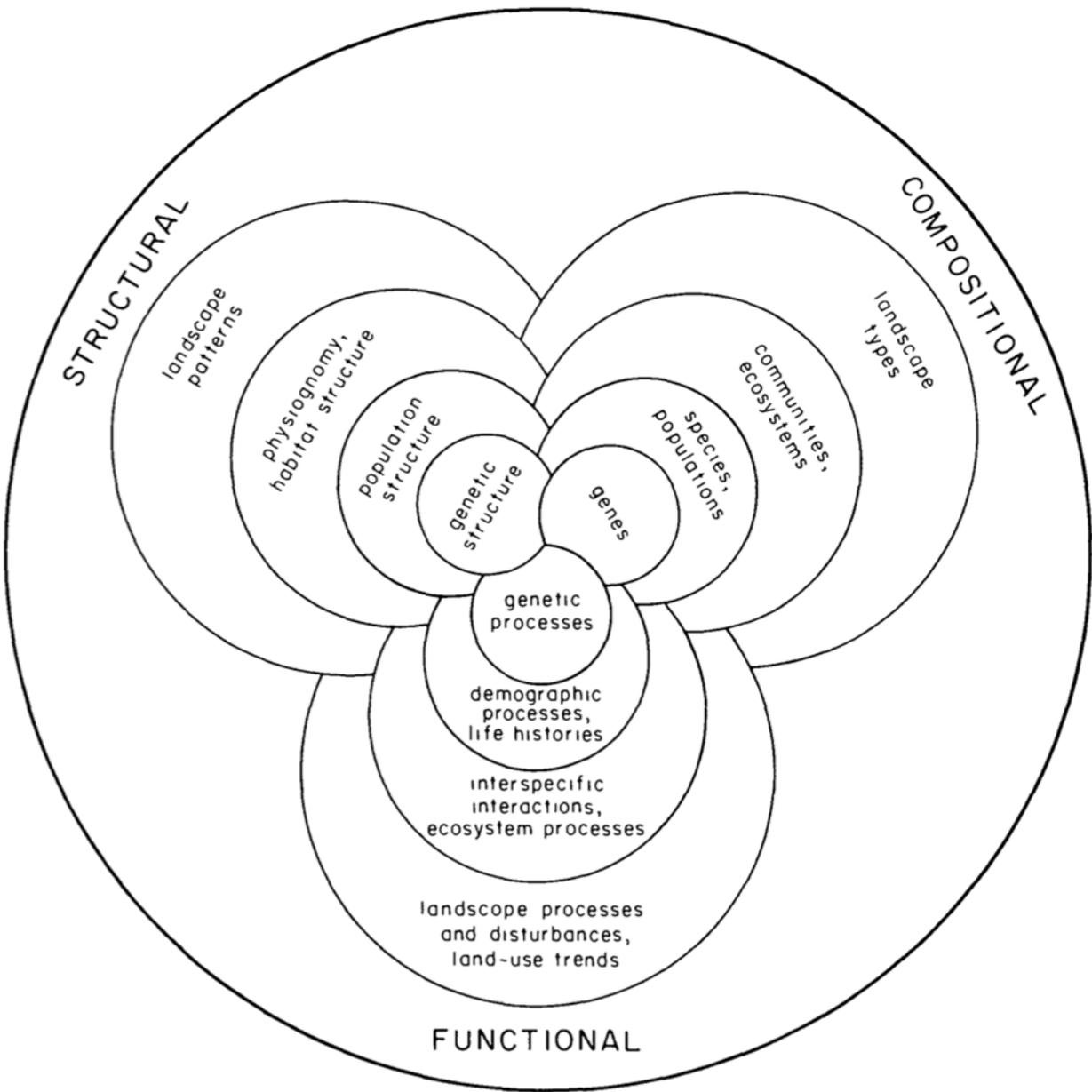


Figure 1-1. Three attributes of biodiversity. In this scheme, compositional, structural and functional attributes are organized hierarchically, nested at different scales, and all attributes are linked with each other.

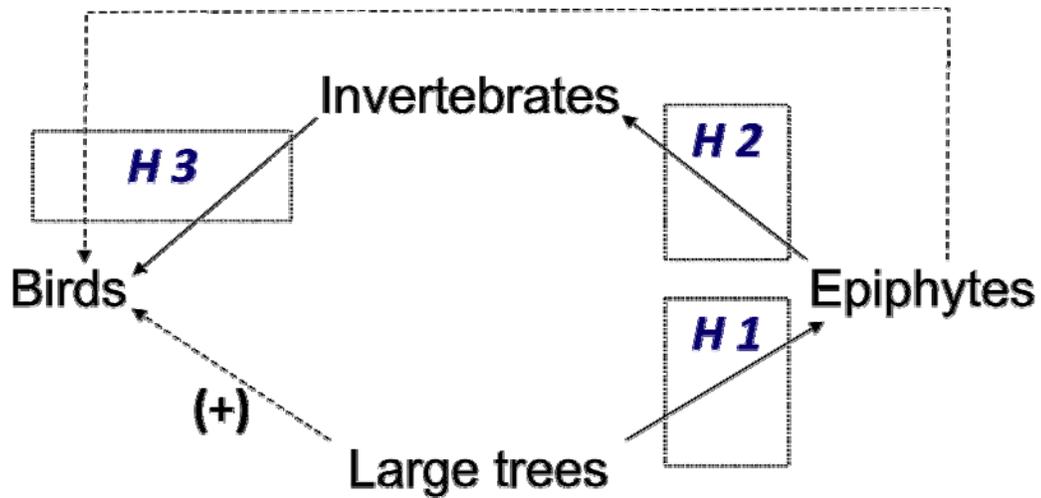


Figure 1-2. Theoretical model with the hypothesis proposed in this dissertation. The model presents the linkages among different components of forest canopy biodiversity in Chilean rainforests. In this model, large trees support heavy epiphyte loads (solid arrow), epiphyte loads support invertebrates in the forest canopy, and finally invertebrate biomass support insect-eating forest birds. In this way, large canopy trees indirectly (dashed arrow) support avian species. H1, H2, and H3 are the hypotheses tested in this thesis. H1 tests the link between large tree structures and epiphyte loads. H2 tests the link between epiphyte loads and invertebrate species richness and biomass, and H3 tests the indirect effect of epiphyte loads on forest birds (dashed line), under the assumption that bird visits to trees are driven primarily by insect availability. These hypotheses are explicitly addressed in the different chapters of this dissertation.

CHAPTER 2
EPIPHYTE SPECIES RICHNESS AND BIOMASS LOADS ON *Eucryphia cordifolia*
(CUNONIACEAE) AND *Aextoxicon punctatum* (AEXTOXICACEAE), TWO CANOPY
EMERGENT TREES IN CHILEAN TEMPERATE RAIN FORESTS

Introduction

Epiphytes are defined as plants that use other plants for mechanical support, but do not absorb nutrients from their host (Benzing 1995). Epiphyte species are grouped into five main groups, accidental (those that only occasionally grow epiphytically), facultative (can grow epiphytically and on the ground), hemi-epiphytic (rooting in the ground for some portion of its life cycle), and holoepiphytic (true epiphytes; Benzing 1995); parasitic species such as mistletoes are not usually included as epiphytes (Benzing 2004). Examples of common epiphytes in tropical and temperate forests are bromeliads, orchids, and mosses, and lichens, many of which vary in their distribution within tree crowns and trunks according to humidity, sunlight exposure, and interactions with other species (Benzing 1990, McCune et al. 2000, Ellyson and Sillett 2003, Benzing 2004, Sillett and Antoine 2004, Williams and Sillett 2007, Cardelús 2007).

Epiphytes contribute with the 8 to 10% of all vascular plants species at global scale (Benzing 1995, 2004), and contribute up to 25-50% of all plant species in tropical and temperate rainforests (Gentry and Dodson 1987, Nieder et al. 2001). In tropical and temperate forests, epiphytes accumulate a large amount of dead organic matter in tree crowns, usually termed “arboreal soils” (Enloe et al. 2006). Epiphytes and the arboreal soil together comprise a dense layer that cover the bark of large trees (hereafter “epiphytic biomass”). Total epiphytic biomass can represent an important portion of the biomass present in forest canopies. For instance, in Costa Rican cloud forests epiphytic biomass reaches up to 33.1 t ha⁻¹, representing 6.3% of total forest biomass, but 81.3 % of the canopy biomass, excluding wood biomass (Nadkarni et al. 2004b). In general, epiphytic biomass (live epiphyte biomass plus arboreal soil) ranges between

0.3 Mg/ha to 44 Mg/ha in tropical and temperate forests of the world (Tanner 1980, Hofstede et al. 1993).

Most of the diversity and biomass of epiphytes in forests is associated with the structure provided by older, larger emergent canopy trees (Franklin et al. 1981, McCune 1993, Nadkarni et al. 2004b, Johannson et al. 2007). Epiphyte biomass is typically higher in primary forests dominated by large canopy trees than in secondary forests; for instance, a Costa Rican primary forest supported 33 Mg/ ha of epiphytic biomass, relative to only 0.2 Mg/ ha in a nearby secondary forests (Nadkarni et al. 2004b). In addition to their direct contribution to the richness of plant species in forests, epiphytes support other diverse groups of organisms such as invertebrates and vertebrates (Nadkarni and Matelson 1989, Sillett 1994, Ellwood and Foster 2004, Chapters 3 and 4). Therefore, the structure provided by large trees support another structure: heavy epiphyte loads that could represent important reservoirs of biodiversity of a large variety of taxa in forest ecosystems (Berg et al. 1994).

Information about epiphyte diversity, distribution, and biomass is still scarce in several regions of the world where epiphytes are common (Zotz 2005). Remarkable among these regions are the South American temperate rain forests (Sillett and Antonie 2004), where vascular and non-vascular epiphytes are outstanding components of forest biodiversity because of their high biomass and species richness (Riveros and Ramírez 1978, Muñoz et al. 2003, Pérez et al. 2005, Zotz 2005). These rain forests are dominated by broad-leaved evergreen trees comprising a multilayered canopy layer, with scattered emergent trees lushly covered by epiphytes and vines; in their overall physiognomy, they resemble tropical rain forests (Armesto et al. 1996, Willson and Armesto 1996, Zotz 2005). The origin of South American temperate rain forests goes back to Gondwanaland during the Tertiary Period and before the main Andean uplift, as shown by the

large number of taxa with Neotropical, Australasian, and New Zealand affinities. South American temperate rainforests have been isolated from other similar forests for more than 1.5 million years, consequently having a high proportion of endemism across plant and animal taxa and at species, genus, and family levels (Armesto et al. 1996; Villagrán and Hinojosa 1997).

Few studies have analyzed epiphyte species richness, distribution, and biomass in South American temperate rain forests. For logistic reasons, most studies have described forest epiphyte assemblages only in the lower layers of the vertical profile, 1-4 m from the ground level (Riveros and Ramírez 1978, Muñoz et al. 2003, Pérez et al. 2005). The first study accessing epiphytes in the tree crown was conducted by Clement et al. (2001), who described the composition of vascular epiphyte communities growing on the upper branches of the large, long-lived conifer *Fitzroya cupressoides* (common name, Alerce), a tree that grows primarily in montane forests and a few valleys in southern Chile. They found that one old Alerce trees held 60% of the plant species present in this type of forest, and accordingly old Alerce trees may be important reservoirs of the overall forest biodiversity. Their results also suggest that large canopy trees, in general, may play similar roles regarding biodiversity throughout the range of South American temperate rain forests. However, despite the importance of epiphytes, species richness and distribution of epiphytes in relation to most rain forest tree species in southern South America remain largely unknown. In particular, lowland Valdivian evergreen rainforests (distributed between 39° to 41° S primarily west of the Andes) represent the biologically richest of all South American temperate rainforests in terms of plant and animal species and the level of endemism (Villagrán and Hinojosa 1997). Its canopy biodiversity is both underexplored and highly endangered from rapid decline of old-growth forest cover and conversion to pastures and

forestry plantations of exotic tree species (Armesto et al. 1998, Smith-Ramírez 2004, Smith-Ramírez et al. 2005).

In this chapter, I characterize the structural features (shape and biomass) of two evergreen tree species, which are the major components of the upper canopy of Valdivian temperate rainforests (Villagrán 1991, Armesto et al. 1996, Gutiérrez et al. 2008a), *Eucryphia cordifolia* (in the Gondwanan family Cunoniaceae) and *Aextoxicon punctatum* (in the endemic family Aextoxicaceae). I examine the diversity and distribution of vascular epiphytes growing in the entire vertical profile, from the base to the upper crown, of these tree species, and I assess the epiphytic biomass associated large canopy individuals of these trees. Finally, I discuss the potential effects of epiphyte loads on their host trees and their effects on ecosystem functions in southern temperate rainforests. This is apparently the first study of epiphyte richness, distribution, and biomass in the upper canopy layer of lowland Valdivian rain forests in Chile.

Methods

Study Area

The study was conducted in selected trees within two large forest tracts old-growth temperate rain forests in the lowlands of northern Chiloé Island. These forests are composed by a mosaic of Valdivian and Nord-Patagonian forest types, dominated by evergreen, broad-leaved trees (Aravena et al. 2002; Fig. 1-1). The first forest tract is located in Guabún peninsula, at Punta Huechucuicui (41° 47' S; 54° 00' W) where Valdivian undisturbed old-growth forest covers an area of 300 ha, including canopy trees older than 350 years (Gutiérrez et al. 2008a) within a large track of 1000 ha of continuous forest with different degrees of human disturbance (Fig. 1-1). The second forest tract is in Chiloé National Park, at the edge of Lake Cucao (42° 37' S; 74° 04' W), which is a continuous forested area of >40,000 ha. I chose large forest tracts to avoid any effect of forest fragmentation, such as changes in temperature and humidity (Saunders

et al. 1991), or changes in species composition (Willson et al. 1994, Barbosa and Marquet 2002). Organic soils reach over 1 m deep, but underlying mineral soils are thin, mostly close to bedrock of Miocene sedimentary rocks 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 heterogeneous forest canopy and scattered large emergent trees of *Eucryphia cordifolia* and *Aextoxicon punctatum*, with a subcanopy dominated by species in family Myrtaceae (cf. Armesto et al. 1996). Guabún forest stand had no signs of disturbance during at least the past 450 years (Gutiérrez et al. 2008a). This area of Chiloé Island was colonized by people in the early 20th century, therefore having little or no previous human impact by indigenous or European people and hence representing a fairly pristine ecosystem (Gutiérrez et al. 2008a). In contrast, Cucao is near an old indigenous settlement from perhaps > 500 years ago (Weisner 2003). Despite the lack of signs of human disturbances in the forests studied, evidence of fires from >100 years ago (Espinosa 1917) can be found in the surroundings.

Study Design

To assess epiphyte richness and biomass I selected two large, canopy emergent trees of *Eucryphia cordifolia* in the forest of Guabún, and one large individual of *Aextoxicon punctatum* in the forest of Cucao, Chiloé National Park. Each tree was a little over 1 m of DBH (diameter at breast height), about the average size of trees of these two species in each study area. All trees were climbed using arborist techniques, including single and double rope techniques that allowed access to the majority of the tree branches following established protocols of the Tree Climber Coalition (www.treeclimbingusa.com). Field work in the forest of Guabún was conducted between August and December of 2005, late winter and spring in the southern hemisphere; field work in Cucao was conducted between April and August 2006, during the southern hemisphere fall and winter.

Tree Structure

Tree structure was mapped by measuring the length, diameter, cardinal orientation (North, South, East, West), and height along the vertical profile of all branches and the trunk following the protocol described by Van Pelt et al. (2004). With the diameter and length data I estimated the area and volume of each branch, and in consequence, the area and volume of the whole tree assuming a cylindrical shape of each limb measured. I estimated the total dry biomass of each tree using published data of wood density of 0.601 kg/lt for *E. cordifolia*, and 0.60 kg/lt for *A. punctatum* (USDA Forest Service, 2008). I assessed foliage biomass of all trees by counting all branches >2-m long, and later collecting and weighing the leaves of three branches per tree (Van Pelt et al. 2004). Leaf area was calculated measuring directly the area of 200 randomly selected leaves, and weighing them to obtain an estimate of total area per gram of leaves. I estimated total leaf area per tree by multiplying leaf area by the total estimated leaf biomass. In summary, with these measurements I calculated total leaf area, total foliage biomass, total trunk area and volume, and total biomass of each tree.

Epiphyte Species Richness

For each tree, I conducted a rapid survey of epiphyte species richness by taking samples of all recognizable epiphyte species every 2 m along the vertical profile, including all branches and the trunk of *E. cordifolia* and *A. punctatum* trees. For every epiphyte sampled I recorded the branch number and its height above the ground, and I brought them still fresh into the laboratory. Plant specimens were classified using the reference collections of the Herbarium of the Universidad de Concepción, Chile. Scientific names followed Marticorena and Quezada (1985).

Epiphyte Biomass

I assessed canopy epiphyte biomass at the tree level, and at the species level by two different protocols: by removing and weighing epiphytes from individual trees, and by visually

assessing the volume of epiphytes in 60 trees of different sizes. At the tree level, the epiphytic material from each sampled tree was removed by hand using small axes, garden saws, and knives. Epiphytes were removed as completely as possible, after the rapid survey of epiphyte species richness. The epiphytic material removed was placed in large plastic bags of 40 liters lowered to the ground, and then weighed separated into two components – live green tissues versus arboreal soil and roots. Samples of around 600 g fresh weight of epiphytic material were taken from each component per bag, stored in closed plastic bags, then dried at 80° C over three days in a drying oven, and weighed again to determine its water content. I estimated total epiphytic dry mass by multiplying the total epiphytic biomass of each component of each bag by $1 - WC$, where WC is the proportion of water content of the respective component. When host trees were colonized by hemi-epiphytic trees, the later were not removed but their biomass and foliage were measured following the protocol described by Van Pelt et al. (2004). Since published information on wood density of hemi-epiphyte was unavailable, I collected 5 wood samples of different branches, dried them at 80° C for three days, weighed them, and calculated wood volume by liquid displacement. Epiphytes were removed from each tree during a two-week period by three people per tree. Epiphytes of *E. cordifolia* were removed in October and November 2005 during the austral spring, while epiphytes of *A. punctatum* were removed in August 2006 during the austral winter.

I estimated epiphyte biomass at the species level, in 59 *E. cordifolia* trees. First, I selected 34 points separated by >100 m. In each point I traced a 50-m long transect starting from each point, running 25 m in opposite directions from the original point. For all individuals of *E. cordifolia* present within an area 2-m wide on each side of the transect lines, I measured the diameter at the breast height (DBH) and visually assessed the volume of epiphytes in terms of

the number of large bags that would be filled with epiphytic material, that according to my previous epiphyte removal experience, these bags can hold up to 15 kg of fresh weight of epiphytes. Focal *E. cordifolia* trees are not very high, lower than 30 m in the study site. For this species, it is possible to observe most branches from the ground, and the hemi-epiphytic tree is easily recognizable from a ground perspective, which in addition to my removal experience facilitates the assessment of epiphytes in this study site.

Ecological Functions Conducted by Epiphytes

I analyzed the possible ecological functions of epiphytes based on data from previous studies in Guabún forests conducted by my research assistants using *E. cordifolia* trees nearby those used in this study. I also use published studies conducted in other forest in Chile (Pérez et al. 2005, Del Val et al. 2006). In Guabún forest, Tejo et al. (in preparation) characterized the water content, nitrogen mineralization, and nitrification rates in arboreal soils of two *E. cordifolia* trees. These authors took one sample of arboreal soil per height, at three heights (8, 12, and 16 m) and three samples of the ground soil nearby. One part of each soil sampled was collected, while the other part was leaved in situ, in an open bag and collected one month later. Samples were stored at low temperature ($< 5^{\circ}$ C) and analyzed under laboratory conditions to assess dry mass, density, and ammonia and nitrate contents. Samples were taken each season, completing one year of survey. Finally, Carmona et al. (unpublished data) conducted a preliminary analysis of nitrogen fixation in arboreal soil and canopy lichens. These authors located 11 chambers of one-liter capacity at four heights (0, 9, 12 and 17 m) in one large *E. cordifolia* tree. In 8 chambers they put between 11 and 16 g (dry mass) of soil, four chambers with ground soil and four with arboreal soil. The rate of nitrogen fixation was assessed using the acetylene reduction test following the protocols of Hardy et al. (1968). Three chambers of each soil class were injected with acetylene obtaining a concentration of 10% v/v, and one was left as

a control. The chambers with arboreal soil were located at 9, 12 and 17 m, with the control chamber also at 17 m. The chambers with forest soil were located at ground level (0 m). In the other three chambers they located between 1 and 3 g (dry mass) of living *Pseudocyphellaria* lichens collected from the canopy. Two chambers were filled with acetylene obtaining a concentration of 10% v/v and the other was left as a control. These chambers were located at 17 m in the epiphytes, in the same places where lichens were collected. At three times (day 0, day 1 and day 2), samples of 10 ml of air where collected from each chamber, to calculate the concentration of acetylene, and calculate the rate of acetylene reduction expressed as nmol acetylene /day/ dry mass (g). This assay was conducted during three days in December 2005, at the end of the austral spring. Data of acetylene reduction between heights was compared with paired t-tests.

Results

Structural Features of *Eucryphia cordifolia* and *Aextoxicon punctatum* Trees

The two large *E. cordifolia* trees sampled in Guabún were 25 and 30 m tall, respectively, with the first crown branches 6 and 15 m above the ground, respectively. The general shape of *E. cordifolia* trees was characterized by continuous branching up to the uppermost leaves, with an open, V-shaped crown (Fig 2-2). The foliage was present only on the external portions of the branches, leaving ample space without leaves in the interior of the crown (Fig. 2-2). The crown of this tree species is massive, extending 21 m in diameter with branches radiating in all directions (Fig. 2-2). The heaviest component of tree biomass was the woody material, which reached 27×10^3 and 42×10^3 kg of dry matter per tree, respectively. Leaf biomass was three orders of magnitude lower, representing < 0.1 % of total tree biomass (Table 2-1). In the open space in the interior of the crown, both sampled individuals of *E. cordifolia* hosted a common hemi-epiphytic tree in Valdivian rain forests, *Raukaua laetevirens* (Araliaceae). These hemi-

epiphytes were profusely branched having dense foliage that did not extend over the top of *E. cordifolia* crown. The wood density of *R. laetevirens* was 0.5 kg/ liter; and the dry biomass of each *R. laetevirens* tree measured was 2.6×10^3 kg and 1.0×10^3 kg, respectively, where 9 kg corresponded to the foliage, representing <0.2 % of the total dry weight (Fig. 2-2).

The single *A. punctatum* tree sampled was similar in general shape to canopy individuals of *E. cordifolia*, and reached 25 m in height. The crown area of *A. punctatum* was smaller, but presented twice or more foliage biomass (99 kg dry mass) than *E. cordifolia* trees (Table 2-1). The crown of *A. punctatum* was denser and without inner foliage-free spaces, yielding a multi-layered vertical foliage, thus differing in structure from *E. cordifolia*. No hemi-epiphytic trees were observed growing in the *A. punctatum* trees in this forest (Fig. 2-3).

Species Richness and Distribution of Epiphytes on *E. cordifolia* and *A. punctatum*

Overall, I found 22 species of vascular epiphytes and 22 genera of non-vascular epiphytes in the three trees sampled (Table 2-2). In few cases it was possible to classify the non-vascular epiphytes to the species level (Table 2-2). Vascular epiphytes included 15 species and four families of Pteridophyta, with 12 species in the family Hymenophyllaceae (filmy ferns). The Anthophyta was represented by only seven species in six families (Table 2-2). Non-vascular species included mostly mosses, liverworts, and lichens (Table 2-2).

Both canopy tree species (*A. punctatum* and *E. cordifolia*) presented relatively similar species composition of vascular epiphytes but they differed in the species composition of non-vascular epiphytes (Table 2-2). In fact, the single *A. punctatum* tree hosted more species of bryophytes than the two *E. cordifolia* trees combined, and several species found in *Aextoxicon* were not detected on *E. cordifolia* (Table 2-2). On the other hand, *E. cordifolia* trees were the exclusive host of the hemi-epiphyte *R. laetevirens*, which represents a conspicuous element of Valdivian rain forests because of its large size. The presences of a distinct group of non-vascular

epiphytes in *A. punctatum* and the presence of the hemi-epiphyte *R. laetevirens* tree in *E. cordifolia* represent the main differences in epiphytic assemblages associated with these two dominant tree species.

Most species of both vascular and non-vascular plants exhibited particular distributions on the tree surfaces and along the vertical profile (Table 2-3). The ground-rooted vines *Luzuriaga radicans* and *Mitraria coccinea* were often found much closer to the ground than completely holoepiphytic vine species such as *Sarmienta repens*. Ferns including *Grammitis magellanica*, *Hymenophyllum dentatum* and *Polypodium feullei*, and lichens such as *Cladonia* sp. or *Bunodophoron* sp. were present mostly in the upper branches of the sampled trees. Only two species of bryophytes were found to occur along the whole vertical profile: *Bazzania* sp. and *Frullania* sp. (Table 2-3). Epiphyte distributions along the tree vertical profile and the crown area showed three main groups: epiphytes present along all the vertical profile, epiphytes present only in the upper branches, and epiphytes restricted to the basal branches and trunks (Table 2-3). Around 34 % of the plant species were associated with the crowns, 18% were present primarily in the first 3 m above the ground, while the remaining 48% were present all over the vertical profile (Table 2-3). Excluding those species present only near the base of the tree, 82% of the epiphyte species collected occurred > 3 m above the ground. The upper branches were under-sampled due to their inaccessibility, but field observations indicated that they were densely covered mainly by lichens, probably *Pseudocyphellaria* sp.

Epiphytic Biomass

At the tree level, the three trees sampled hosted large epiphytic loads. Individual trees of *E. cordifolia* hosted 1.6×10^3 kg dry mass of the hemi-epiphytic tree *R. laetevirens* plus an additional 133-143 kg of dry mass of other vascular and non-vascular epiphytes in the trunk and branches, with about 30% corresponding to green tissues and 70 % corresponding to arboreal

soil (Table 2-4). One tree of *A. punctatum* supported 142 kg dry mass of epiphytes, with the same proportions of leaves and arboreal soil as *E. cordifolia*.

Epiphyte biomass was differently distributed along the vertical profile of the trees of the two species studied. In *E. cordifolia*, most of the biomass was concentrated in the intermediate portion of the trunk and near the base of the crown branches; while in *A. punctatum* epiphytic biomass was more evenly distributed along the vertical profile, with large clumps of epiphytes on the terminal branches at the top of the tree. This situation creates different aspects or physiognomy of these two tree species in the forest canopy; *E. cordifolia* appears to have few epiphytes (with the exception of *R. laetevirens*) and little foliage volume in the treetops, while *A. punctatum* has substantially denser foliage over the extent of the crown and frequently denser clumps of epiphytes on the branch tips.

Among the recorded epiphytes, two vascular species were particularly important in terms of biomass: these were the hemi-epiphytic tree *R. laetevirens* and the bromeliad *Fascicularia bicolor*. *R. laetevirens* grows from the mid portion of the vertical profile of large *E. cordifolia* trees, with its roots descending to the ground similar to strangler figs in tropical forests (Zotz 2005, Gutiérrez et al. 2008a). In the Guabún forest, 65% of all *E. cordifolia* trees were > 1 m DBH and all supported at least one hemiepiphytic *R. laetevirens* (Gutiérrez et al. 2008a, M. P. Peña, unpublished data). *R. laetevirens* has dense foliage and its canopy roots are heavily covered by other epiphytes holding a thick layer of arboreal soil additional to the host tree. Overall, *R. laetevirens* had 2.6×10^3 kg and 1.0×10^3 kg of dry mass of woody material, and 9.5 kg of leaves (dry mass). This volume of foliage equals 18% and 29% of the total leaf mass present in the crown of their host *E. cordifolia* trees (Tables 2-1 and 2-4). On the other hand, *F. bicolor* is distributed along the whole vertical profile of their host tree, but most of its biomass

(>80%) occurs at intermediate heights between 9 and 15 m of the forest vertical profile, where it forms large clumps up to 34 kg (fresh weight). In addition, large clumps of *F. bicolor* accumulate up to 56% of the total arboreal soil, and up to 68% of the green tissues of epiphytes recorded in these two tree species, excluding the hemi-epiphyte *R. laetevirens*.

In general, epiphytes represented <1% of total tree biomass for *E. cordifolia* and *A. punctatum*, but excluding the supporting woody structures (trunks), epiphytes represent a significant percentage of the photosynthetic tissues present on forest canopies. Foliage associated with forest epiphytes accumulated 40 kg in *A. punctatum*, an addition of 41% to the mass of foliage produced by the host tree (99 kg, Table 2-1). Crown foliage of *E. cordifolia* reached 51 kg in tree 1 and 33 kg in tree 2, while leaves from epiphytes represented 50 kg in tree 1 and 48 kg in tree two. Therefore, foliage from epiphytes represent between 100% and 145% of additional green mass to the crown of *E. cordifolia*.

Finally, visual assessments of epiphytes in 59 trees of *E. cordifolia* of different sizes in Guabún forest showed that epiphyte biomass increased exponentially with tree size (Fig. 2-4). Smaller trees hold less epiphytes, but trees larger than 1 m DBH showed a pronounced increase in epiphyte biomass (Fig. 2-4). This high abundance of epiphytes seems to coincide with the colonization by the hemi-epiphyte *R. laetevirens*. Trees <80 cm DBH did not hold individuals of *R. laetevirens*, but all trees >1.2 m DBH hold a *R. laetevirens* tree (Fig. 2-4).

Epiphyte Functions

The study of Tejo et al. (manuscript in preparation) showed that arboreal soil share several characteristics with forest soil (Table 2-5). Both arboreal and forest soil were composed by litter of similar origin and quality, dominated by dead leaves of *E. cordifolia*. Arboreal soils are organic (i.e, they lack mineral components such as sand or clay), but are similar to soil from the forest floor in pH, concentrations of ammonia and nitrate, and in nitrification rates (Table 2-5).

The density of arboreal soil was lower, retaining more water than forest soils (Table 2-5). Finally, the results from Carmona et al. (unpublished data) showed that acetylene reduction in the forest floor and in the arboreal soil were similar, and indistinguishable from control chambers. In contrast, one of the *Pseudocyphellaria* lichens showed a high rate of acetylene reduction, suggesting that these lichens may be important nitrogen suppliers in the forest canopy (Table 2-5).

Discussion

Comparative Diversity of Epiphytes in Southern Chile Temperate Rainforests

Despite limited information on species richness and abundance of epiphytes in South American temperate rain forests, we determined that just three large trees held 33 % of the species of flowering epiphytes described for Valdivian rainforest by Smith-Ramírez et al. (2005), and 50% of the Hymenophyllaceae ferns described for Chile (25 species, Marticorena and Quezada 1985). Hymenophyllaceae is a largely epiphytic fern family with 17 species described for Valdivian rainforests (Smith-Ramírez et al. 2005) and 20 species described for Chiloé Island forests (Villagrán and Barrera 2002). In particular, several *Hymenophyllum* ferns occur primarily in the intermediate and upper portions of canopy trees, and when they occur on the forest floor, they are always associated with fallen logs and limbs (Villagrán and Barrera 2002). On logs on the ground and in the first meter of the vertical profile of Guabún forests, Díaz et al. (in prep.) found 14 species of *Hymenophyllum* species, while in the present study I recorded 10 species of filmy ferns along the entire vertical profile of *E. cordifolia* trees. In fact, many species of *Hymenophyllum* were present on the forest floor because of the continuous flow of limbs covered by these ferns that fall from the canopy. In secondary forests nearby our study site in Guabún, species richness of filmy ferns decreased to only 5 species, and its relative abundance (percentage of soil covered by these ferns) declined by 90% compared to old-growth forests

(Díaz et al. in preparation). In conclusion, large canopy trees support in their crowns a significant proportion of the richness of *Hymenophyllum* species, and through branch-fall, they maintain their presence in the ground biota. Large trees could be diversity reservoirs for filmy ferns in temperate rain forests and this pattern may also hold true for other forest species of animals and plants found in the upper crown (Nieder et al. 2001, Díaz et al. in preparation).

Previous studies of Muñoz et al. (2003) analyzed the richness and relative abundance of vascular epiphytes on 499 trees of 12 species, with DBHs of 5 to >25 cm in North-Patagonian rain forests of Chiloé island. They sampled epiphytes up to 2.5 m on the tree trunks, recording a total of 20 vascular plant epiphytes, including eight *Hymenophyllum* species (Table 2-6).

Clement et al. (2001) conducted a complete survey of epiphytes in nine giant *F. cupressoides* trees in Andean montane forest of southern Chile. They recorded eight species of *Hymenophyllum* ferns, and a total of 18 vascular plant species in the canopy (Table 2-6). My results for only three large trees > 1 m DBH showed a total of 22 vascular plant epiphytes, higher than in lerce forests, including most of the fern species described by these authors, but lacking several vine species. These vines are frequent in North Patagonian forests, but generally absent in Valdivian forest types (Armesto et al. 1996). The forest type where Muñoz et al. (2003) and Clement et al. (2001) conducted their studies is characterized by poor soil drainage and colder climate, with a canopy dominated by different species of trees, where bromeliads and other types of climbing vines are less frequent or absent in comparison with our study sites. Then, large trees in Valdivian temperate rain forests may, overall, hold more epiphyte species than previously recorded in other forests of this region.

Despite the lack of data, these results suggest that large old trees harbor much of the epiphytic species richness of the region. From this point of view, old forest trees could be

considered as significant reservoirs of forest biodiversity, including many species that are absent from secondary forests (Barthlott et al. 2001). Further studies comparing epiphyte distribution according to tree ages and in different successional forests should clarify the role of old trees as reservoirs of biodiversity in southern temperate rainforests.

Comparative Diversity of Epiphytes with Other Tropical and Temperate Rainforests

The epiphytes present in the three individual trees studied were mostly vascular species, whereas epiphytes in northern temperate rainforests are mostly non-vascular (Table 2-6, Zotz 2005). My results showed that the dominant epiphytic plants in terms of biomass are also vascular species (Table 2-7). However, in the trees analyzed I found a modest numbers of epiphyte species compared with tropical or even other temperate rainforest of the world (Table 2-6). For instance, in tropical forest of Costa Rica, Cardelús (2007) recorded 496 vascular epiphyte species in 53 individual host trees of 11 genera, while in the Pacific North West of North America, Pike et al. (1975) and McCune et al. (2000) recorded around 100 species, almost exclusively non-vascular epiphytes (Table 2-6). The number of vascular plant species recorded in the three trees sampled in Chilean rain forests is also lower than in other southern hemisphere temperate rainforests; Dickinson et al. (1993) found a few more species of vascular (28 species) and non vascular (26 species) in a single large *Dacrycarpus dacrydioides* of New Zealand forest than what I found in two *E. cordifolia* and one *A. punctatum* trees (Table 2-6). In agreement with my results, Clement et al. (2001) and Muñoz et al. (2003) recorded similar species richness in different tree species and forests of southern Chile, the first in the canopy of nine large *F. cupressoides* trees and the second on the trunks of 499 trees of all sizes and 12 species (Table 2-6). Despite the lower number of epiphyte species, South American temperate rain forests showed a high proportion of endemic taxa, where most vascular epiphytes are endemic to this biome (Arroyo et al. 1996, Villagrán and Hinojosa 1997). This epiphytic community is very unique, and

also shares more similarities with Neotropical and Australian-New Zealand temperate rainforests than with Northern Hemisphere rainforests.

Floristic Relationships between Chilean Epiphytes and those from the Neotropics and Australia-New Zealand

The dominance of vascular epiphytes and the floristic similarities with Neotropical and Australian-New Zealand forests be a consequence of to the common Tertiary origin of these ecosystems (Villagrán and Hinojosa 1997). For instance, the tree genus *Eucryphia* includes only five species, two in Chile and three in Australia and Tasmania (Arroyo et al. 1996), while the family Aextoxicaceae represents a mono-typic endemic family with unclear phylogenetic relationships to other living families of plants (Smith-Ramírez et al. 2005). The epiphyte families Gesneraceae, Araliaceae, Bromeliaceae, and Hymenophyllaceae are all shared with Neotropical forests, and all except Bromeliaceae, have presently vicariant distributions with relatives in Australian and New Zealand forests (Hosftede et al. 2001, Zotz 2005, Table 2-4). Another important feature of epiphytes in Chilean forests is their functional similarities to other southern temperate and tropical forests. For instance most species of, vines, shrubs, trees and even vascular epiphytes of Chilean temperate rainforests presented fleshy fruits, which require animal vectors for seed dispersal (Armesto and Rozzi 1989, Willson et al. 1996). The proportion of fleshy-fruited plants in Chilean temperate forests is similar to other Neotropical forests, and higher than many northern hemisphere temperate rainforests (Armesto and Rozzi 1989, Willson et al. 1996). The high proportion of animal-dispersed plant species contrasts with the relatively low diversity of frugivores, all of which use a wide variety of food resources such as invertebrates (Armesto and Rozzi 1989, Sabag et al. 1993, Rozzi et al. 1996). The principal seed vectors are fruit-eating birds, such as Fio-fio (*Elaenia albiceps*, Tyrannidae), Zorzal (*Turdus falcklandii*, Muscicapidae), and the endemic marsupial Monito del Monte (*Dromiciops gliroides*,

Microbiotheriidae) (Sabag 1993, Rozzi et al. 1996, Amico and Aizen 2000, Celis-Diez et al. in review). The importance of these species as seed dispersers could be disproportionately high for epiphytes, because most epiphyte seeds must reach the upper branches of trees, moving against gravity. Limited dispersal can decrease the populations of epiphytic plants; for instance Rodriguez-Cabal et al. (2007) showed that habitat fragmentation in temperate rainforests of westernmost Argentina have reduced the populations of Monito del Monte, affecting the seed dispersal of the mistletoe *Tristerix corymbosus*, which has become completely absent from isolated forest fragments where the marsupial is lacking. Similarly, only one bird species is known to pollinate flowering epiphytes in Chilean temperate rain forests: the hummingbird Picaflor chico (*Sephanoides sephaniodes*, Trochilidae; Smith-Ramírez et al. 1993, Chapter 4). This hummingbird is the main (or only) bird pollinator of over 20% of the vascular species of South American temperate rainforests, including the dominant canopy epiphytes such as *Sarmienta repens* and *Fascicularia bicolor*. Therefore, a wide diversity of plant species depend on this only hummingbird for its pollination (Smith-Ramírez et al. 1993).

The dependence of rain forest epiphytes on animals may be much stronger than the dependence of animals on epiphytes. Sabag (1993) reported the presence of seeds from a broad diversity of trees in the feces of bird species, but he did not record seeds from epiphytes. Armesto et al. (2001) also recorded high numbers of tree and shrub seeds in the seed rain driven by birds both to forest edges and tree-fall gaps. The high number of fruits from trees in the diet of birds suggests that forest trees may offer orders of magnitude more fruits than epiphytes. For the hummingbird this relationship could be more symmetrical; several epiphytes concentrate their flowering during fall and winter, offering nectar during a season when other nectar sources are not available (Smith-Ramírez et al. 1993; Chapter 4). Accordingly, knowledge of the factors

regulating epiphyte seed dispersal may be relevant for understanding their persistence in forests. However, for most epiphytes requiring animal seed dispersers, the identity of the seed vector remains unknown, and further studies are needed to define them and analyze both the effect of epiphytic fruit and nectar production on animals and the effects of animals on epiphyte seed dispersal and pollination.

In summary, the epiphytic assemblages of Chilean temperate rain forests reflect the tropical and ancient origin of its species composition, dominance, and interactions between plants and animals. Composition and functions of epiphytes in temperate forests of Chile are very different from those of northern hemisphere temperate forests, and more similar to tropical and southern hemisphere temperate rainforests.

Epiphyte Vertical Distributions

The three groups of epiphytes along the vertical profile of the trees can be explained by a combination of different conditions of humidity, temperature and shading, as occur in other forest ecosystems (Cardelús and Chadzon 2005). These relationships are largely unknown for Chilean forest epiphytes (Salinas 2008), but my study suggest differential requirements for three dominant epiphytic species, the holoeiphytes *Fascicularia bicolor* and *Sarmienta repens*, and the hemi-epiphytic tree *Raukaua laetevirens*. The bromeliad *F. bicolor* is distributed along the whole vertical profile of canopy trees, but most of its biomass is concentrated at the base of the crown and intermediate portion of the tree. The bromeliad family present clear adaptations to hydrological stress (Benzing 2004); then the location of *F. bicolor* on large *E. cordifolia* trees can be related to the balance between access to light and limited humidity in the upper tree crown. In contrast, *F. bicolor* was much less abundant on the more shaded branches of *A. punctatum* (Tables 2-2 and 2-4).

S. repens is a vine that roots directly over the tree bark and in arboreal soil on host trees (Salinas 2008), forming dense mats on the upper branches of *E. cordifolia* and *A. punctatum*. This vine has succulent leaves that confer resistance to drought (Salinas 2008). According to field observations, most foliage of *S. repens* is generally pending down the limbs. I hypothesize *S. repens* presents a segregated use of the tree at two scales, first at tree scale, *S. repens* is located in the upper tree crown where it has access to higher solar radiation than other epiphytes, and secondly, plants are pendant from branches, thus protecting them from excessive sunlight, or avoiding interference with the other epiphytes established directly over the bark.

Finally, the hemi-epiphytic tree *R. laetevirens* is a frequent and important element added to the crowns of large *E. cordifolia* trees. Like strangler figs and many other tropical hemi-epiphytes, seeds of this species are dispersed by birds, and become established in the axils of canopy branches where arboreal soil accumulates. All *E. cordifolia* trees > 1 m DBH were colonized by *R. laetevirens*, but trees <80 cm diameter in the same area had none, at least none big enough to be visible from the ground or clearly established (Fig. 2-4). I climbed 4 trees without this hemi-epiphyte species during the surveys, and despite many plants germinated at the end of the winter, they did not survived after summer. Therefore, I hypothesize that arboreal soil should accumulate beyond a certain mass threshold on branches of the host tree, in order to provide nutrients and water long enough to allow *R. laetevirens* to become established and send its roots down to the soil (Putz and Holbrook 1986). The massive crown and open foliage of large *E. cordifolia* trees probably provides intermediate levels of solar radiation that may favor the development of *R. laetevirens*. On 20 mature trees observed in the Guabún forest, *R. laetevirens* branches never grew above those of the host tree. Reasons for this could be related to *R. laetevirens*' intermediate light requirements, physiological limitations to bring water from the

soil to certain height (Koch et al. 2004), or mechanical limitations on the support of heavy branches. My own field observations suggest that *R. laetevirens* was associated to its host tree *E. cordifolia*. During two years of monthly visits to the forest of Guabún, and sampling over 800 trees bigger than 10 cm DBH, I saw only three *R. laetevirens* growing on trees of species other than *E. cordifolia*. However, this observation must be quantified to understand the association between these species and the mechanism underlying it.

Epiphyte Biomass

Several studies indicate that epiphyte diversity and biomass increase with tree size (McCune 1993, Muñoz et al. 2003, Johansson et al. 2007). Epiphytes may need time to colonize trees after a dense layer of arboreal soil can accumulate, and therefore epiphytic biomass tends to be higher on older trees (Franklin et al. 1981, Sillet and Baley 2003). In the forest studied, the large *E. cordifolia* trees were 300 to 400 years old (Gutiérrez et al. 2008a); implying that the epiphytic assemblage and biomass described in this study has developed over that time span. However, biomass accumulation is not linear with tree age. At around 1 m DBH there seems to be a strong increase in epiphyte biomass, presumably stimulated by the colonization of the hemi-epiphyte tree *R. laetevirens* (Fig. 2-4). Once host trees are colonized, the root system and the branches of *R. laetevirens* may increase the heterogeneity on tree canopy, offering sites for the colonization of other epiphytes (Peña et al. 2006). Therefore, two factors, tree size and the presence of *R. laetevirens* may account for the exponential accumulation of epiphytic biomass on large *E. cordifolia* trees. A survey by Gutiérrez et al. (2008a) in the Guabún forest found 72 individuals/ha of *E. cordifolia* with a mean DBH of 1.0-2.4 m. Multiplying this density by the epiphytic biomass per tree documented in this study, indicates that epiphytic biomass supported by *E. cordifolia* is at least 10 Mg dry mass/ha (excluding the hemi-epiphyte *R. laetevirens*). This estimate for a single tree species in Valdivian coastal forests is larger than previous estimates of

epiphytic biomass of 8.2 Mg/ ha of Pérez et al. (2005) for all species in montane alerce forests in southern Chile, and is also larger than estimates for all temperate rainforests of North America (6.8 Mg/ha, Grier and Nadkarni 1987, Table 2-7), dominated by bryophytes. At the individual level, *Eucryphia* had similar or greater epiphytic biomass than trees in montane cloud forests in Colombia (135-146 kg versus 110 kg; Table 2-7). Considering that most trees in the Valdivian temperate rain forest have a dense cover of epiphytes (personal observations), the total epiphytic biomass for the stand may double or triple this estimate for *E. cordifolia*, reaching similar values to those estimated for tropical cloud forests (Table 2-7). As indicated by Hofstede et al. (2001), southern hemisphere temperate rainforests may support as much epiphytic biomass as tropical forests.

This great accumulation of epiphytes in Chilean rainforests may be related to physiognomic and floristic similarities between tropical and southern temperate forests, such as the presence of hemi-epiphytic trees. The shape of *E. cordifolia*, with its open massive crown branching from a single main trunk, resembles many tropical trees, and is very different from the conical shape of northern temperate conifers. Epiphyte biomass in Chile is dominated by vascular plants, including the hemi-epiphytic tree *R. laetevirens* and high abundance of the bromeliad *F. bicolor*. The presence of these large epiphyte species may offer additional substrate for more epiphytes. In fact, the arboreal soil associated with the large mats of *F. bicolor* represents between 27% and 57% of the arboreal soil on *E. cordifolia* trees, and therefore this species may be responsible for the accumulation of a major fraction of arboreal soil. Filmy ferns also capture litter including the dead leaves of the host tree, as has been shown for other forests (Enloe et al. 2007). Further studies should analyze how the dynamics of colonization and growth of *R. laetevirens* and *F. bicolor* affect the overall accumulation of epiphyte biomass.

The smaller and more shaded crown of *A. punctatum* and its denser foliage may facilitate the capture and retention of water from rain and fog, creating more humid conditions that facilitate the development of epiphytes with higher moisture requirements such as bryophytes and filmy ferns (Benzing 1990), with less development of the more drought tolerant *F. bicolor* and absence of *R. laetevirens*. I hypothesize that the dense foliage of *A. punctatum* contributes to maintain humidity in its crown, because this tree may “capture” water from fog that then moves along the tree as stemflow (del Val et al. 2006, Gutiérrez et al. 2008b) favoring the development of moisture-loving epiphytes.

Epiphyte Functions

Epiphytes can supply resources and regulate environmental conditions in the forest canopy, but can also have negative effects on the host tree health. Epiphytes can capture water and nutrients, thus increasing forest primary production, and provide a food source for many invertebrates and vertebrates that live in the forest canopy (Weathers 2000, Lowman and Rinker 2004 for a review). Water interception by the forest canopy is an important process preventing runoff, facilitating water storage, and facilitating nutrient transport in forest ecosystems (Kölher et al. 2006). In 60-year old broad-leaved Chiloé forests, Díaz et al. (2007) found that 53% of the rainwater was intercepted by and/or evaporated from the tree canopy, while the remaining 47% reaches the ground via through fall and stemflow. This is a higher value of water interception compared to other temperate forest ecosystems (Díaz et al. 2007). Our results showed that the water contained in the epiphytic layer of our focal trees (excluding *R. laetevirens*) is 60% to 70% of the total biomass, which means that epiphytes may retain over 300 liters of water in the crown of each tree. In old-growth forests, epiphytes play a strong role in the interception and storage of rain water in the forest canopy (Kölher et al. 2006).

In addition, epiphytes can intercept water and nutrients from passing clouds or fog (Holscher et al. 2004, Hietz et al. 2002). Coastal forests in Chile are characterized by fog interception supplying up to 80 mm of water per month (del Val et al. 2006). This volume of water may be very important during the dry summers (del Val et al. 2006, Gutiérrez et al. 2008b), but still remains undetermined what proportion of the total interception in the forest canopy is due to epiphyte loads. Coastal fog represents a substantial input of dissolved organic nitrogen from the ocean to the mainland forests in southern Chile (Weathers et al. 2000). Oyarzún et al. (2004) indicated that for Andean *Nothofagus* forest cloud interception by the canopy is an important source of nitrogen. In addition, Benner et al. (2007) showed high nitrogen fixation by canopy lichens (*Pseudocyphellaria*) in Hawaiian forests, an input that is enhanced when additional phosphorous was supplied experimentally. Lichens of the same genus are abundant in the canopy of Chilean coastal rain forests (Table 2-2), and preliminary data from Carmona et al. (unpublished data) from the canopy in Guabún forest, suggest that their nitrogen fixation may be considerable (Table 2-5). These results indicate the epiphytes can enhance capture of nutrients transported by fog from the ocean, and canopy lichens could be an internal source of nitrogen in Chilean coastal forests. Tejo et al. (in preparation) showed that nitrogen mineralization and nitrification rates in the arboreal soil of large *E. cordifolia* trees are similar to the forest floor soil (Table 2-5). Pérez et al. (2005) showed similar results for montane forest of *F. cupressoides*, concluding that epiphytic soil is functionally similar to the organic horizon of forest floor. These processes represent an overlooked source of nutrients to this forest ecosystem.

Epiphytes also can play an important role in increasing forest productivity. Total foliage in the forest canopy was raised by 41% to 145% when epiphyte foliage is included (Table 2-3). In *E. cordifolia*, in particular, epiphytes more than double the leaf biomass of canopy trees; this

additional leaf biomass is greater than estimated in previous studies (Ingram and Nadkarni 1993). Although photosynthetic rates could be lower in epiphytes than in tree leaves (Benzing 2004), the substantial biomass of epiphytic photosynthetic tissues can have a large effect on whole ecosystem productivity. Finally, epiphytes also can supply nutrients directly to the tree via adventitious roots (Nadkarni et al. 1981, Oyarzún et al. 2004). Several trees of southern South America, including *A. punctatum*, produce adventitious roots from stems which allows them to obtain nutrients and water directly from the crown humus (Pérez et al. 2003). In summary, my results are in agreement with other studies that propose an important role for epiphytes in forest ecosystems (Franklin et al. 1981, Nadkarni and Matelson 1992).

Negative effects of epiphyte loads relate to the increased susceptibility of host trees to falling or losing large branches because of the extra weight (Strong 1977); competition with the host tree for sunlight; and the potential effect of the production of a cylinder of fused roots by strangler hemi-epiphytes in preventing secondary growth of the host tree by root constriction (Putz and Holbrook 1986). Changes of the magnitude and importance of these negative effects with different tree ages have received little attention. A review by Laman (2004) analyzes the effects of strangler figs in tropical trees, indicating that several bottlenecks decrease their frequency in the canopy when they kill the host trees, also emphasizing their role as providers of abundant fruits for forest fauna. In *E. cordifolia*, arboreal soil and epiphytes weigh around 0.3 % to 0.7% of the weight of the host tree, and do not cast shade on the tree foliage. However, the hemi-epiphytic tree *R. laetevirens* could stress host trees since because its weight represents between 4% and 5.5% of the host tree biomass, and are usually located on one specific branch of the host tree. Such weight can represent a relevant pressure on physical strength of the tree (Putz and Holbrook 1986). However, in Guabún forests a large number of *E. cordifolia* trees are still

alive after 300 years (Gutiérrez et al. 2008a), and keep supporting a heavy epiphyte loads including hemi-epiphytic trees, suggesting that the danger of falling and epiphyte shading may be low. Data of Peña et al. (2006) indicate that epiphytic *R. laetevirens* could be older than 70 years, and several of them showed many dead branches, suggesting that the hemi-epiphytic tree has a dynamic modular growth. I hypothesize that epiphytes in Guabún forests may not represent a grave danger to host trees, at least for several decades or maybe centuries. The demand of resources for secondary growth increases with tree age, causing an imbalance between photosynthesis and respiration in addition to problems derived from fungal infection, physical damage, and reduced photosynthesis (Van Pelt and Sillett 2008). At some time, the increased weight of epiphytes may result in broken limbs and increased risk of tree fall, affecting tree survival. However, the time span between epiphyte colonization and tree death is unknown, and epiphytes may enhance survival through positive effects by providing the host tree with nutrients and water, until some age where the increasing weight pressure enhance the risk of fall of a weakened old tree.

Importance of Large Trees with Epiphytes

Noss (1990), based on Franklin et al. (1981), proposed that biodiversity could be characterized by three main attributes: composition (such as taxonomic species composition); structure (such as the physical structure of the habitat), and function (such as species interactions or biogeochemical functions), all interrelated at different levels of organization, from genes to ecosystems. The linkages proposed by Noss (1990) represent a useful conceptual framework to encompass the relations between large old trees and epiphytes in the canopy of southern temperate rainforests. Large trees are important structural elements of several temperate rain forests ecosystems (Franklin et al. 1981, Van Pelt 2007). Large trees support substantial epiphyte loads, composed by many plant species. Then, large old trees represent structures that support

the taxonomic composition of epiphytes. Epiphyte loads enhance ecosystem processes including water and nutrient cycling. Moreover, large trees themselves and their epiphyte cover foster diversity and abundance of invertebrate and vertebrate species that are absent from younger forests (Berg et al. 1994, Díaz et al. 2005). Then, large old trees can be seen as a structural element that supports the composition of epiphyte species, and supports the functions they provide, such as nutrient cycling and water capture, linking composition with structure and functions in the canopy of southern Chile temperate rainforests.

Further studies should analyze how changes in epiphytic species composition and biomass affect trees of different ages. In addition, this work was conducted in coastal rain forests characterized by pre-industrial atmospheric conditions and low pre-historic and current human impacts, and these conditions may better reflect those crafted over evolutionary time by natural processes compared to other forest of the world. Therefore, this forest ecosystem can offer reference points for understanding ecological and evolutionary processes. Thus, the loss of large trees from old-growth ecosystems means not only a loss of biodiversity associated with these structures, but also reflects a loss of historical relationships.

Table 2-1. General structural features of the large *E. cordifolia* and *A. punctatum* trees sampled for epiphytes in Valdivian temperate rain forests, Chiloé, Chile.

	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
Diameter at the 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 crown branch (m)	16	14	15
Foliage biomass (kg dry mass)	50.9	33.3	98.7
Woody biomass (kg dry mass)	47.0 x 10 ³	27.5 x 10 ³	20.0 x 10 ³

Table 2-2. Relative frequency of vascular and non-vascular epiphyte species on two large trees of *E. cordifolia* and one tree of *A. punctatum* in coastal rain forests of Chiloé Island, southern Chile. Frequency was calculated as the number of points in which every species was found multiplied by 100 and divided by the total number of points per tree. Total points sampled every 2 m along the vertical profile were: *E. cordifolia* 1 = 34; *E. cordifolia* 2 = 31, *A. punctatum* = 44.

Species	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
Pteridophyta			
Hymenophyllaceae			
<i>Hymenoglossum cruentum</i>	0.0	35.5	79.5
<i>Hymenophyllum caudiculatum</i>	8.8	22.6	4.5
<i>Hymenophyllum cuneatum</i>	67.6	22.6	20.5
<i>Hymenophyllum darwini</i>	0.0	3.2	0.0
<i>Hymenophyllum dentatum</i>	11.8	6.5	13.6
<i>Hymenophyllum dicranotrichum</i>	20.6	74.2	4.5
<i>Hymenophyllum ferrugineum</i>	0.0	6.5	0.0
<i>Hymenophyllum pectinatum</i>	2.9	0.0	2.3
<i>Hymenophyllum plicatum</i>	52.9	12.9	79.5
<i>Hymenophyllum secundum</i>	2.9	16.1	0.0
<i>Serpyllopsis caespitosa</i>	5.9	0.0	0.0
Grammitidaceae			
<i>Grammitis magellanica</i>	5.9	6.5	4.5
Aspleniaceae			
<i>Asplenium trilobum</i>	0.0	0.0	52.3
Polypodiaceae			
<i>Polypodium feullei</i>	0.0	0.0	29.5
Anthophyta			
Gesneriaceae			
<i>Sarmienta repens</i>	64.7	96.8	79.5
<i>Mitraria coccinea</i>	0.0	0.0	4.5
Philesiaceae			
<i>Luzuriaga poliphylla</i>	11.8	19.4	0.0
Bromeliaceae			
<i>Fascicularia bicolor</i>	47.1	67.7	15.9
Myrtaceae indet.	11.8	0.0	0.0
Araliaceae			
<i>Raukua laetevirens</i>	8.8	19.4	0.0
Hydrangeaceae			
<i>Hydrangea serratifolia</i>	0.0	0.0	38.6
Cornaceae			
<i>Griselinia racemosa</i>	0.0	0.0	9.1
Hepatophyta			
<i>Bazzania</i> sp.	47.1	87.1	0.0
<i>Frullania</i> sp.	0.0	12.9	0.0
<i>Herbetus runcinatus</i>	0.0	12.9	0.0

Table 2-2. Continued.

Species	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
<i>Metzgeria</i> sp.	2.9	0.0	0.0
<i>Plagiochila</i> sp.	29.4	6.5	0.0
<i>Telaranea</i> sp.	0.0	3.2	0.0
<i>Hepatica</i> spp. Unident	23.5	19.4	0.0
Lichens			
<i>Bunodophoron</i> sp.	17.6	3.2	0.0
<i>Cladonia</i> sp.	2.9	12.9	0.0
<i>Nephroma</i> sp.	0.0	3.2	0.0
<i>Parmelina</i> sp.	2.9	0.0	0.0
<i>Pseudocyphellaria</i> sp.	17.6	32.3	11.4
<i>Usnea</i> sp.	5.9	0.0	0.0
Bryophyta			
<i>Campylopus</i> cf. <i>purpureocaulis</i>	0.0	0.0	2.3
<i>Dicranoloma</i> sp.	26.5	29.0	0.0
<i>Hypnum chysogaster</i>	11.8	9.7	0.0
<i>Lepyrodon hexastichus</i>	0.0	0.0	4.5
<i>Lepyrodon parvulus</i>	0.0	0.0	31.8
<i>Lepyrodon tomentosus</i>	0.0	0.0	15.9
<i>Lopidium concinnum</i>	2.9	0.0	15.9
<i>Macromitrium</i> cf. <i>krausei</i>	0.0	0.0	11.4
<i>Macromitrium</i> sp.	0.0	3.2	0.0
<i>Porothamnium arbusculans</i>	0.0	0.0	4.5
<i>Porothamnium panduraefolium</i>	0.0	0.0	4.5
<i>Porothamnium valdiviae</i>	0.0	0.0	2.3
<i>Rhaphidorrhynchium callidum</i>	2.9	3.2	0.0
<i>Rigodium adpressum</i>	0.0	0.0	2.3
<i>Rigodium tamarix</i>	0.0	0.0	4.5
<i>Rigodium toxarion</i>	0.0	3.2	27.3
<i>Tentrepohlia</i> sp.	0.0	3.2	0.0
<i>Weymouthia cochlearifolia</i>	0.0	0.0	47.7
<i>Weymouthia mollis</i>	8.8	0.0	22.7
<i>Zygodon</i> cf. <i>bartramioides</i>	0.0	0.0	2.3
<i>Zygodon hookeri</i>	0.0	0.0	13.6
<i>Zygodon pentastichus</i>	0.0	0.0	4.5
Clorophyta			
<i>Trentepohlia</i> sp.	0.0	0.0	4.5
<i>Chlorophyta</i> unident.	0.0	3.2	0.0
Total taxa	28	32	35

Table 2-3. Epiphyte distribution along the vertical profile on two large trees of *E. cordifolia* and one tree of *A. punctatum* in coastal rain forests of Chiloé Island, southern Chile. Range of height distribution is given in meters above the ground.

Species	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
Pteridophyta			
Hymenophyllaceae			
<i>Hymenoglossum cruentum</i>	-	2 - 15	9 - 23
<i>Hymenophyllum caudiculatum</i>	2 - 9	1 - 15	13 - 17
<i>Hymenophyllum cuneatum</i>	6 - 22	15 - 18	13 - 23
<i>Hymenophyllum darwini</i>	-	8 - 9	-
<i>Hymenophyllum dentatum</i>	15 - 22	14 - 16	16 - 23
<i>Hymenophyllum dicranotrichum</i>	1 - 10	1 - 15	9 - 15
<i>Hymenophyllum ferrugineum</i>	-	1 - 2	-
<i>Hymenophyllum pectinatum</i>	9 - 10	-	13
<i>Hymenophyllum plicatum</i>	1 - 22	15 - 17	11 - 23
<i>Hymenophyllum secundum</i>	21 - 22	15 - 16	-
<i>Serpyllopsis caespitosa</i>	17 - 18	-	-
Grammitidaceae			
<i>Grammitis magellanica</i>	18 - 20	15 - 16	20 - 23
Aspleniaceae			
<i>Asplenium trilobum</i>	-	-	7 - 23
Polypodiaceae			
<i>Polypodium feullei</i>	-	-	13 - 20
Anthophyta			
Gesneriaceae			
<i>Sarmienta repens</i>	2 - 22	1 - 18	7 - 23
<i>Mitraria coccinea</i>			0 - 3
Philesiaceae			
<i>Luzuriaga poliphylla</i>	0 - 4	0 - 12	-
Bromeliaceae			
<i>Fascicularia bicolor</i>	1 - 19	1 - 17	12 - 19
Myrtaceae indet.			
Araliaceae			
<i>Raukaua laetevirens</i>	13 - 18	14 - 16	-
Hydrangeaceae			
<i>Hydrangea serratifolia</i>	-	-	1 - 23
Cornaceae			
<i>Griselinia racemosa</i>	-	-	13 - 18
Hepatophyta			
<i>Bazzania sp.</i>	1 - 19	1 - 18	-
<i>Frullania sp.</i>	-	2 - 16	-
<i>Herbetus runcinatus</i>	-	10 - 11	-
<i>Metzgeria sp.</i>	15 - 16	-	-
<i>Plagiochila sp.</i>	15 - 20	15 - 16	-
<i>Telaranea sp.</i>	-	15 - 16	-

Table 2-3. Continued.

Species	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicon punctatum</i>
<i>Hepatica</i> spp. unident	15 - 23	10 - 15	-
Lichens			
<i>Bunodophoron</i> sp.	14 - 20	17 - 18	-
<i>Cladonia</i> sp.	16 - 17	14 - 18	-
<i>Nephroma</i> sp.	-	15 - 16	-
<i>Parmelina</i> sp.	17 - 18	-	-
<i>Pseudocyphellaria</i> sp.	15 - 23	2 - 15	12 - 23
<i>Usnea</i> sp.	17 - 22	-	-
Bryophyta			
<i>Campylopus</i> cf. <i>purpureocaulis</i>	-	-	23 - 24
<i>Dicranoloma</i> sp.	1 - 19	6 - 15	-
<i>Hypnum chysogaster</i>	14 - 18	15 - 16	-
<i>Lepyrodon hexastichus</i>	-	-	9 - 20
<i>Lepyrodon parvulus</i>	-	-	11 - 23
<i>Lepyrodon tomentosus</i>	-	-	5 - 20
<i>Lopidium concinnum</i>	9 - 10	-	1 - 17
<i>Macromitrium</i> cf. <i>krausei</i>	-	-	1 - 23
<i>Macromitrium</i> sp.	-	4 - 17	-
<i>Porothamnium arbusculans</i>	-	-	1 - 3
<i>Porothamnium panduraefolium</i>	-	-	5 - 9
<i>Porothamnium valdiviae</i>	-	-	3 - 4
<i>Rhaphidorrhynchium callidum</i>	21 - 22	16 - 17	-
<i>Rigodium adpressum</i>	-	-	13 - 14
<i>Rigodium tamarix</i>	-	-	7 - 13
<i>Rigodium toxarion</i>	-	15 - 16	1 - 17
<i>Tentrepohlia</i> sp.	-	15 - 16	19 - 20
<i>Weymouthia cochlearifolia</i>	-	-	5 - 22
<i>Weymouthia mollis</i>	4 - 22	-	7 - 21
<i>Zygodon</i> cf. <i>bartramioides</i>	-	-	19
<i>Zygodon hookeri</i>	-	-	5 - 17
<i>Zygodon pentastichus</i>	-	-	20 - 23
Clorophyta			
<i>Trentepohlia</i> sp.			
<i>Chlorophyta</i> unident.			
Total taxa			

Table 2-4. Dry biomass (kg) of the hemi-epiphytic tree *R. laetevirens*, the bromeliad *F. bicolor* and other epiphytes growing on large canopy trees of *E. cordifolia* and *A. punctatum* trees in coastal rain forests of Chiloé Island, southern Chile.

	<i>Eucryphia cordifolia</i> 1	<i>Eucryphia cordifolia</i> 2	<i>Aextoxicom punctatum</i>
<i>Raukava laetevirens</i> woody biomass	2.6 x 10 ³	1.0 x 10 ³	-
<i>Raukava laetevirens</i> green tissues	9.4	9.5	-
<i>Fascicularia bicolor</i> green tissues	17.9	26.3	1.4
Other epiphytic green tissues	22.2	12.5	38.9
Arboreal soil associated with <i>F. bicolor</i>	28.4	53.8	Indet.
Arboreal soil associated with other epiphytes	75.2	41.2	101.7
Total green tissues	49.5	48.3	40.3
Total hemi-epiphyte woody biomass	2.6 x 10 ³	1.0 x 10 ³	-
Total crown humus	103.6	95.0	101.7

Table 2-5. Characterization of the physical properties and nitrogen content in arboreal and forest soils in the canopy of two large *Eucryphia cordifolia* trees in Guabún forests, Chiloé Island, Chile. This table also includes the results of a first survey conducted by Carmona et al. (unpublished data) assessing the biological nitrogen fixation occurring in arboreal soils, forest soils and epiphytic lichens of the genus *Pseudocyphellaria* in the canopy of a large *E. cordifolia* tree. The acetylene reduction technique was used to indirectly assess the biological nitrogen fixation activity.

Assay	Arboreal soil	Forest soil	Significance	Source
Density (gr/cm ³)	0.9 ± 0.05	0.6 ± 0.1	**	Tejo et al.
NH ⁴⁺ (mg/g dry soil)	12.2 ± 6.2	19.4 ± 7.5	n.s.	Tejo et al.
NO ³⁻ (mg/g dry soil)	12.1 ± 11.5	7.8 ± 5.5	n.s.	Tejo et al.
% water	76.8 ± 5.4	83.2 ± 4.0	**	Tejo et al.
pH	4.8 ± 0.1	4.6 ± 0.2	n.s.	Tejo et al.
N Mineralization rate (mg N/ g soil month)	11.6 ± 13.3	7.8 ± 12.1	n.s.	Tejo et al.
Acetylene reduction (nmol C ₂ H ₄ g ⁻¹ d ⁻¹)	5.58 ± 4.27	7.80 ± 4.77	n.s.	Carmona et al.
Acetylene reduction in canopy lichens				
<i>Pseudocyphellaria</i> sp. 1	0.75			Carmona et al.
<i>Pseudocyphellaria</i> sp. 2	326.64			Carmona et al.
Control	-3.47			Carmona et al.

Table 2-6. Number of species and genera of vascular and non-vascular epiphytes in different tropical and temperate rainforests. Sp: Number of species, Gn: Number of genera. Vascular epiphytes: Fe: Ferns, Br: Bromeliads, Or: Orchids, Ot: Other families, T: Total. Non-vascular epiphytes: B: Bryophytes, Li: Liverworts, L: Lichens, T: Total. Parentheses indicate the number of trees sampled in each forest.

Study site		Vascular epiphytes					Non-vascular epiphytes			Source	
		Fe	Br	Or	Ot	T	B	Li	L		T
<i>Tropical forests</i>											
Montane, Costa Rica (51)	Sp.	138	41	122	195	496	-	-	-	-	Cardelús et al. (2006)
	Gn.	27	7	18	39	91	-	-	-	-	
Montane (4), Ecuador	Sp.	8	2	16	16	42	-	-	-	-	Freiberg and Freiberg (2000)
Montane (5), Ecuador	Sp.	5	2	9	15	31	-	-	-	-	Freiberg and Freiberg (2000)
Lowland (5), Ecuador	Sp.	4	2	8	7	21	-	-	-	-	Freiberg and Freiberg (2000)
Lowland (5), Ecuador	Sp.	5	2	7	16	30	-	-	-	-	Freiberg and Freiberg (2000)
<i>Temperate forests, Northern hemisphere</i>											
Redwood, USA	Sp.	4	0	0	0	4	17	-	42	59	Williams and Sillett (2007)
	Gn.	2	0	0	0	2	17	-	29	46	
Douglas-fir, USA	Sp.	1	0	0	0	1	25	7	74	106	Pike et al. (1975)
	Gn.	1	0	0	0	1	19	6	35	60	
Douglas-fir Forest, USA	Sp.	0	0	0	0	0	14	?	97	111	McCune et al. (2000)
	Gn.	0	0	0	0	0	11	?	47	58	
Humboldt Sitka Spruce (5), USA.	Sp.	2	0	0	0	2	11	6	72	89	Ellyson and Sillet (2003)
	Gn.	1	0	0	0	1	10	6	30	46	
<i>Abies lasiocarpa</i> , USA.	Sp.	0	0	0	0	0	8	5	37	50	Rhoades (1981)
	Gn.	0	0	0	0	0	6	4	16	26	

Table 2-6. Continued.

Study site		Vascular epiphytes					Non-vascular epiphytes			Source	
		Fe	Br	Or	Ot	T	B	Li	L		T
<i>Acer circinatum</i> , USA	Sp.	0	0	0	0	0	7	4	17	28	Ruchty et al. (2001)
	Gn.	0	0	0	0	0	5	3	11	19	
<i>Temperate forests, Southern hemisphere</i>											
Conifer and broad-leaved forest, New Zealand	Sp.	?	?	?	?	30					Burns and Dawson (2005)
	Gn.	?	?	?	?	23					
<i>Nothofagus-Podocarpus</i> (3), New Zealand	Sp.	20	0	5	37	62	31	31	28	90	Hofstede et al. (2001)
	Gn.	10	0	4	24	38	23	21	13	57	
<i>Dacrydium dacrydioides</i> (1), New Zealand	Sp.	10	0	5	13	28	8		18	26	Dickinson et al. (1993)
	Gn.	6	0	4	10	20	6		12	18	
<i>Fitzroya cupressoides</i> (9), Chile	Sp.	9	0	0	9	18	5	11	15	31	Clement et al. (2001)
	Gn.	4	0	0	9	13	3	9	9	21	
North-Patagonian, Chile (499)	Sp.	11	1	0	8	20	?	?	?	?	Muñoz et al. (2003)
	Gn.	4	1	0	8	13	?	?	?	?	
<i>Eucryphia cordifolia</i> (2), Chile	Sp.	12	1	0	5	18	8	7	6	21	This study
	Gn.	4	1	0	5	10	8	7	6	21	
<i>Aextoxicon punctatum</i> (1), Chile	Sp.	10	1	?	5	16	16	0	1	17	This study
	Gn.	5	1	?	5	11	8	0	1	9	

Table 2-7. Epiphytic biomass (epiphytes plus arboreal soil, dry weights) estimated for tropical and temperate forests of the world. Parenthesis indicates the number of trees sampled in each forest. (*): the hemi-epiphyte tree *Raukaua laetevirens* was excluded from this calculation. (**): Estimate only includes *E. cordifolia* trees.

Study site	Focal species	Biomass			Source	
		kg/m ²	kg/tree	Mg/ha		
<i>Tropical</i>						
Montane forest, Costa Rica	<i>Quercus copeyensis</i>			2.86	Holscher et al. (2004)	
Primary cloud forest, Costa Rica				33.1		
Secondary cloud forest, Costa Rica				0.17		
Montane forest, Otongapa, Ecuador		3.53			Freiberg and Freiberg (2000)	
Montane forest, Los Cedros, Ecuador		11.07				
Lowland forest, Yasuni, Ecuador		2.32				
Lowland forest, Tiputini, Ecuador		2.76				
Montane cloud forests, Colombia			115	44	Hofstede et al. (1993)	
Montane forest, Jamaica				0.37 to 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			
Subalpine forest, Oregon, USA	<i>Abies lasiocarpa</i>		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	
Douglas-fir forest ~ 91 years					1.13	
Redwood forests California, USA	<i>Picea sitchensis</i> (5)		190		Ellyson and Sillett (2003)	
Redwood forests	<i>Sequoia sempervirens</i>			2.9	Enloe et al. (2006)	

Table 2-7. Continued.

Study site	Focal species	Biomass			Source
		kg/m ²	kg/tree	Mg/ha	
Coastal redwood forests	<i>Sequoia</i>		12 to		Sillett and Bailey (2003)
	<i>sempervirens</i> (27)		742		
Conifer montane forests, Chiloé Island, Chile	<i>Picea</i>		10 to		Pérez et al. (2005)
	<i>sitchensis</i> (5)		43		
Valdivian coastal rain forests Chiloé, Chile	<i>Fitzroya</i>			8.2	This study
	<i>cupressoides</i>				
	<i>Eucryphia</i>		134-	10**	
	<i>cordifolia</i> (2)		144*		This study
	<i>Aextoxicon</i>		143		
	<i>punctatum</i> (1)				

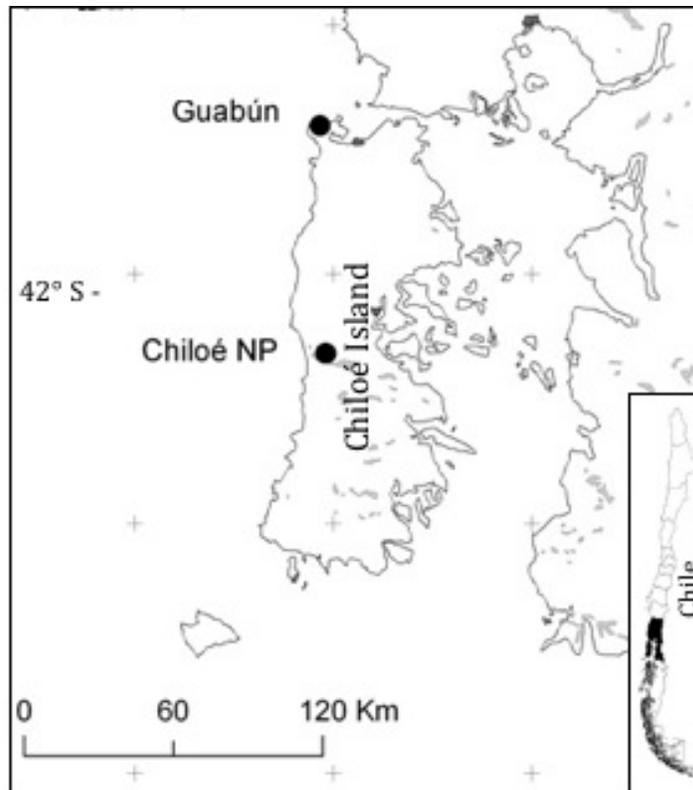


Figure 2-1. Map of study sites (black dots) in lowland coastal forests of Chiloé Island, southern Chile. Sites are Guabún and Chiloé National Park (NP). Region where the study was conducted are in dark color in the inset map.

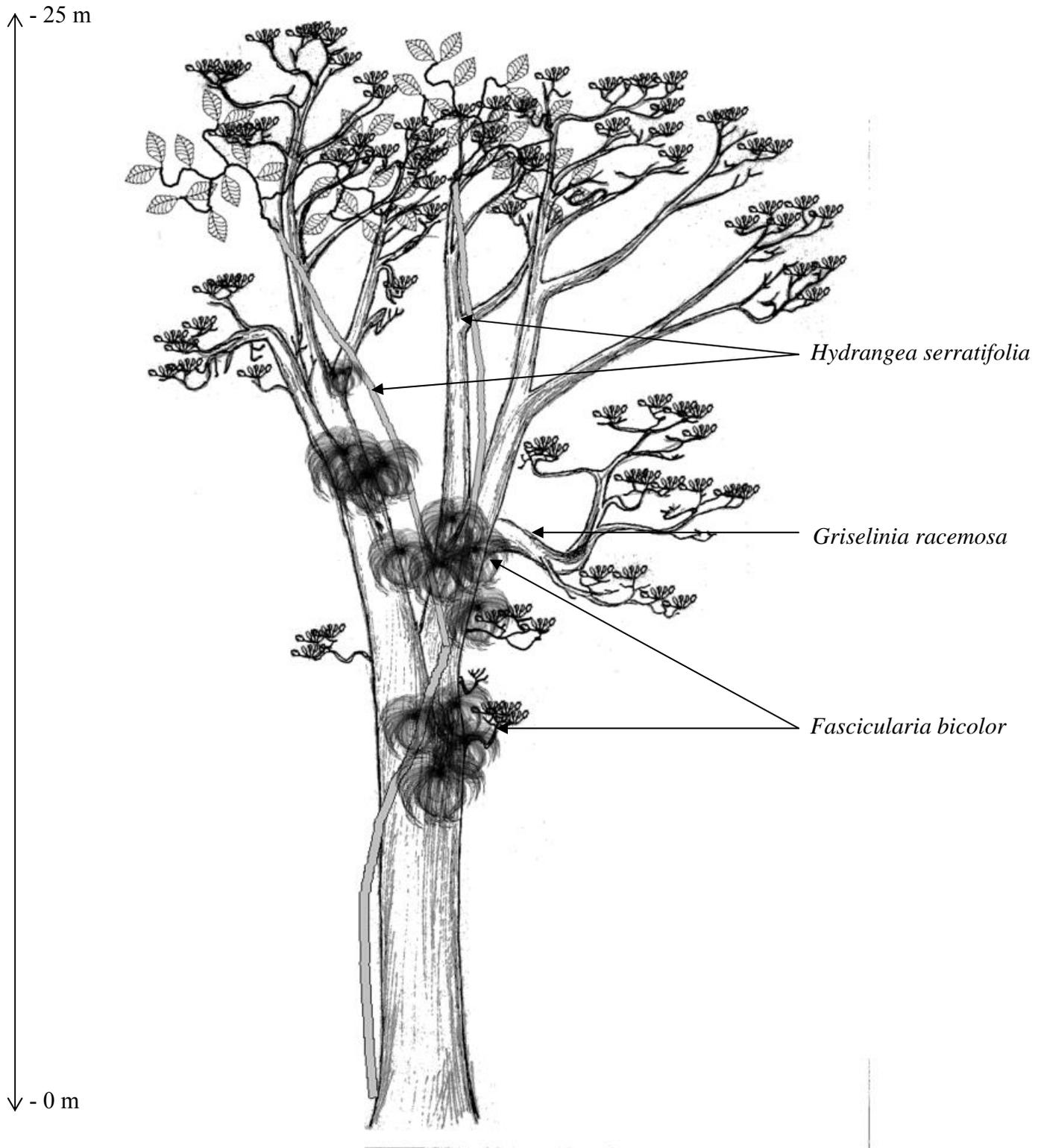


Figure 2-2. General shape of *Aextoxicon punctatum* tree, showing the distribution of the principal vascular epiphytes: the bromeliad *Fascicularia bicolor*, the vine *Griselinia racemosa* growing epiphytically, and the vine *Hydrangea serratifolia* which grows from the ground. While the drawing is mostly to scale, the size of epiphytes and vines are exaggerated to facilitate their recognition (Drawing by the author).

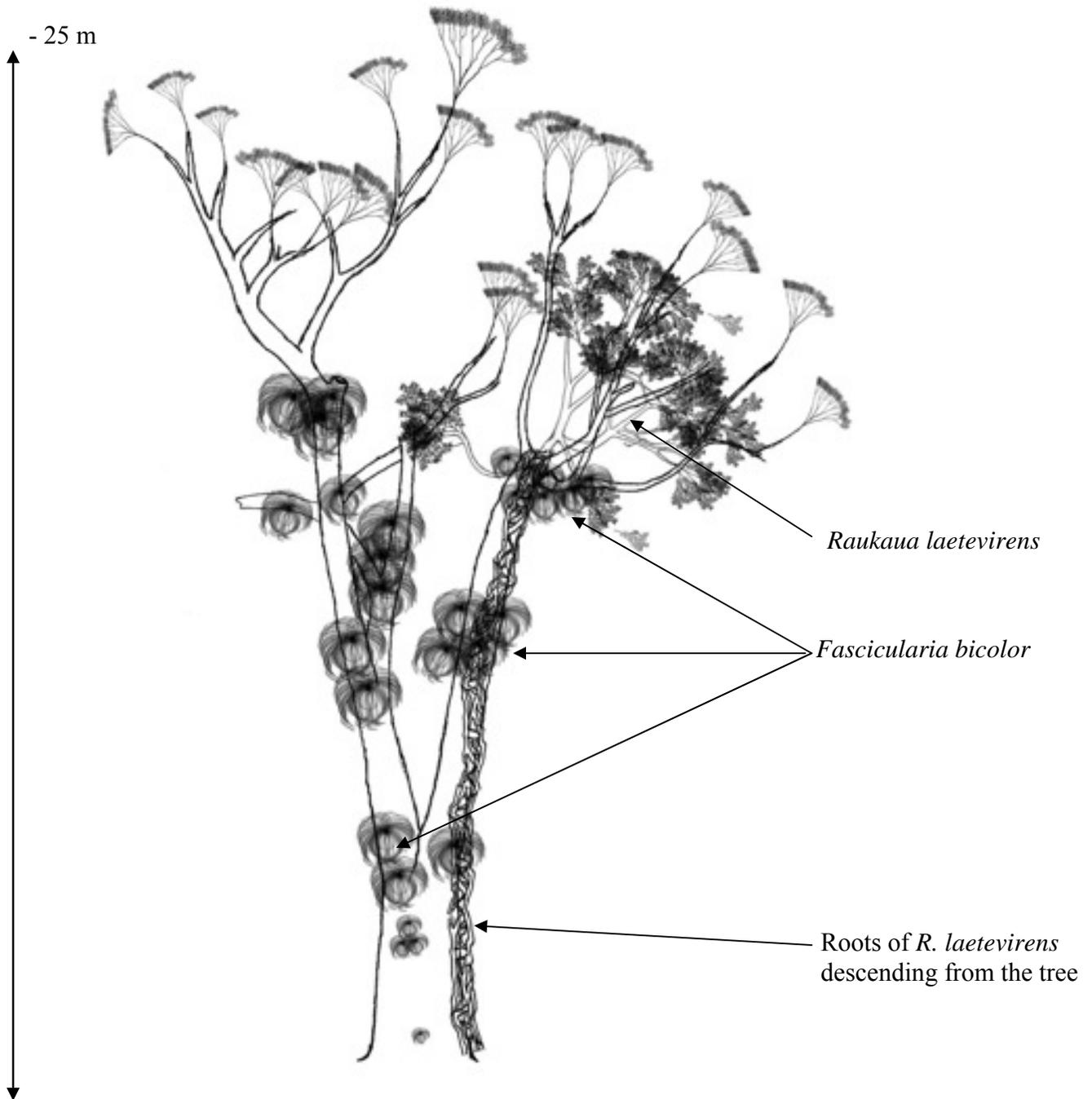


Figure 2-3. General shape of *Eucryphia cordifolia* tree, showing the distribution of its two principal vascular epiphytes: the bromeliad *Fascicularia bicolor* and the hemiepiphytic tree *Raukaua laetevirens* which sends its roots from the canopy to the ground. While the drawing is mostly to scale, the size of the epiphytes and vines are exaggerated to facilitate their recognition (Drawing by the author).

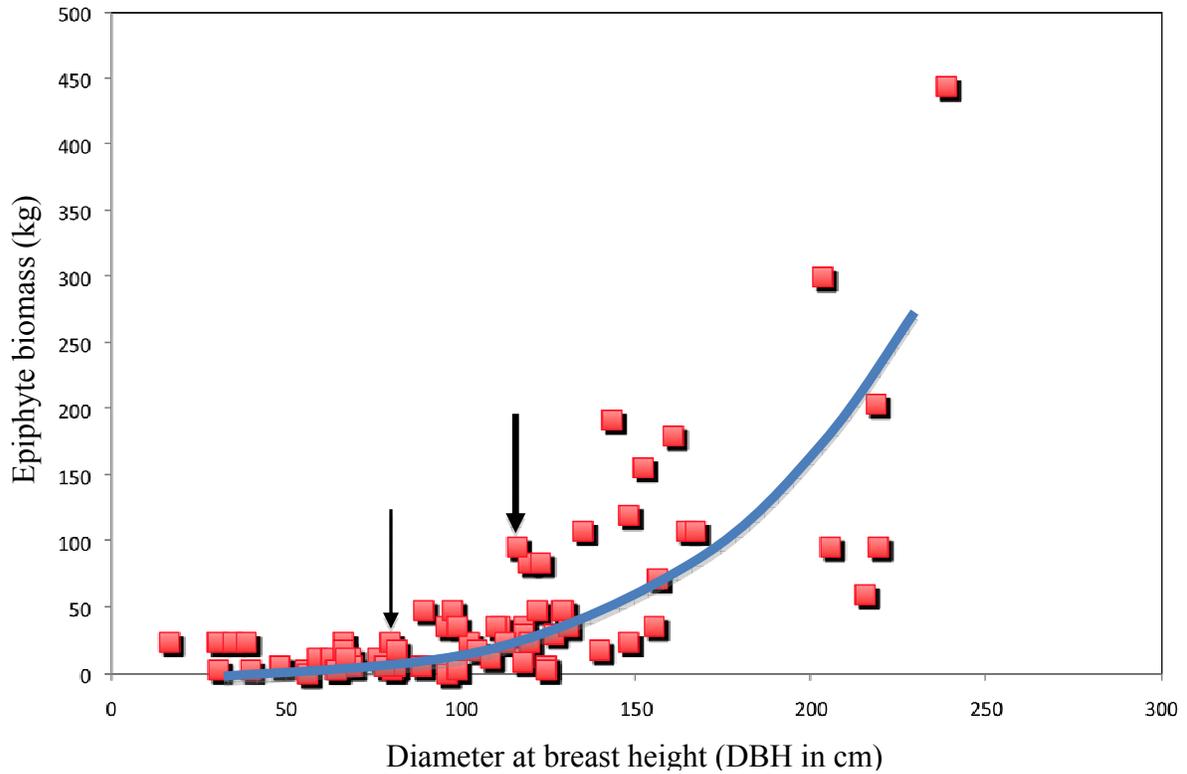


Figure 2-4. Relationship between trunk diameter at breast height (DBH in cm) of *Eucryphia cordifolia* trees and their epiphytic biomass (kg) in forests of Guabún, Chiloé Island, southern Chile. The thin arrow indicates the DBH recorded at which the first *E. cordifolia* tree was colonized by the hemi-epiphyte tree *Raukaua laetevirens*. The thick arrow indicates the DBH above which all trees were colonized by *R. laetevirens*. N= 59 trees (Exponential Curve Estimation, Beta= 0.695, T= 7.81, P< 0.001).

CHAPTER 3
EFFECTS OF EPIPHYTE LOADS ON INVERTEBRATE SPECIES RICHNESS AND
ABUNDANCE ON THE CANOPY OF *Eucryphia cordifolia* (CUNONIACEAE), AN
EMERGENT TREE IN CHILEAN TEMPERATE RAIN FORESTS

Introduction

Epiphytes are an important component of forests canopies; 10% of all vascular plants are epiphytes (Benzing 1995), and from 25-50% of the forest plant species in tropical and temperate rainforests are epiphytes (Gentry and Dodson 1987, Nieder et al. 2001). Epiphytes also reach a high biomass; rainforests around the world can hold between 0.3 tons/ha and 44 tons/ha of epiphytic biomass (Tanner 1980, Hofstede et al. 1993). Most species richness and biomass of epiphytes occur on large old trees in old-growth forests (McCune 1993, Nadkarni et al. 2004, Johansson et al. 2007, Chapter 2). The largest amount of epiphytic biomass recorded for a single tree occurs in a giant *Sequoia sempervirens* tree, which holds up to 742 kg of epiphytic biomass (Sillett and Barley 2003). This epiphytic biomass is usually composed by living tissues of epiphytes and dead organic matter formed by dead epiphytes and litter captured in the canopy (Ingram and Nadkarni 1993, Enloe et al. 2006). This dead organic matter has also been called “arboreal soil” because presents structural and functional similarities to the organic horizon of the forest soil (Enloe et al. 2006).

This high epiphytic biomass can heavily support abundance and species richness of canopy invertebrates. Nadkarni and Longino (1990) found that epiphytic biomass host a high abundance of invertebrates similar to those of the forest floor than tree crowns, with abundant decomposers, ants and mites. Ellwood and Foster (2004) found that a single mat of epiphytes in Borneo’s dipterocarp forest holds as much arthropod biomass as the foliage and branches of the host tree, also including decomposers and mites. Similarly, Yanoviak et al. (2007) found a high abundance of mites and ants in arboreal soil from epiphytes of Monte Verde forest, Costa Rica. These

studies indicate the ecology of the epiphytes is distinct from the ecology of tree crowns alone, with abundant invertebrates similar to those from the forest ground, but absent in the foliage and branches of the host tree.

Most of the studies on canopy invertebrates are based on fogging techniques (Erwin 1995, Basset et al. 2003a). Fogging techniques are very efficient in collecting invertebrates dwelling on the tree foliage, but underestimate the abundance of invertebrates hidden in the epiphytes (Yanoviak et al. 2003). The findings of Ellwood and Foster (2004) and Yanoviak et al. (2007) support the increasing evidence about the importance of epiphytes for invertebrate biodiversity (Basset et al. 2003b); however little work has been done on characterizing epiphyte contribution to composition and functions of invertebrate communities in forest canopies (Stuntz et al. 2003, Yanoviak et al. 2003, 2007).

Southern South American temperate rainforests cover a narrow area at the west side of the Andes (Armesto et al. 1998). These forests are evergreen, rich in endemic species, and are characterized by abundant large emergent trees densely covered by epiphytes (Armesto et al. 1998, Clement et al. 2001, Pérez et al. 2005, Chapter 2). One of the emergent tree species is *Eucryphia cordifolia* (Cunoniaceae), a dominant evergreen species on coastal forests of this region (Armesto et al. 1996). Large individuals can reach 30 m tall and hold over 130 kg of dry epiphytic biomass, where 70% corresponded to arboreal soil and roots and the remaining 30% corresponded to epiphyte leaves (Chapter 2). However, few descriptions of invertebrate faunas of these forest canopies exist, and are principally focused on the invertebrate diversity of the whole tree, without distinguish where the invertebrates came from (Clement et al. 2001; Arias et al. 2008) and probably underestimating the richness and biomass of epiphytes dwelling in the epiphytes (Yanoviak et al. 2003).

In this study, I described the species richness and biomass associated to the crown and epiphyte loads of large old *E. cordifolia* trees in coastal southern Chile rainforest. For these rainforests I predict that i) Tree canopies with epiphytic biomass support greater species richness and abundance of invertebrates than tree canopies without epiphytes; and ii) Epiphytic biomass will support invertebrate taxa common in forest soils such as detritivors, different to those dwelling in the tree foliage (Ellwood and Foster 2004). My specific objectives were 1) to compare the richness and abundance of canopy invertebrates in trees with and without epiphytes, and 2) to address the possible functional consequences of these differences between invertebrate assemblages of the tree crown versus canopy epiphytes. In this study I also characterized the shape of each tree and assessed its epiphytic biomass, to estimate invertebrate biomass on the whole trees.

Methods

Study Area

The study was conducted in four selected trees in a large patch of 300 ha of Valdivian old-growth broad-leaved evergreen temperate rainforests. I choose a large forest patch of old-growth forest to avoid effects of forest fragmentation or changes on the structure of the forest on the epiphytes and invertebrate community analyzed (Saunders et al. 1991, Barbosa and Marquet 2002). The forest was located in the northern part of Chiloé Island, southern Chile; at the Lacuy peninsula, specifically at Punta Huechucuicui in Guabún (41° 47' S; 54° 00' W; Fig. 1). This site is dominated by large emergent trees of *Eucryphia cordifolia* (Cunoniaceae) up to 30 m tall and older than 350 years (Gutiérrez et al. 2008a), densely covered by epiphytes (Chapter 2). The canopy and subcanopy are comprised of *Aextoxicon punctatum* (Aextoxicaceae), *Laureliopsis philippiana* (Lauraceae), *Amomyrtus luma*, *Amomyrtus meli* and *Luma apiculata* (all Myrtaceae), and the understory is dominated by seedlings, ferns and bamboo thickets of *Chusquea* sp.

Organic soils reach over 1 m deep, but mineral soils are thin, mostly on the bedrock substrata on sedimentary rocks of Miocenic marine origin (Mardones 2005). This forest represent a remnant of coastal-range temperate forests, having no signs of disturbance in at least 450 years, without substantial change in canopy composition (Gutiérrez et al. 2008a). The Guabún area was colonized by people at early 20th century, having little or not previous human use (Gutiérrez et al. 2008a). Because of its location on the coast of the southern Pacific Ocean, forests of this region are free of nutrients and pollutants of industrial origin (Hedin et al. 1995, Perakis and Hedin 2002).

Study Design

I selected two pairs of large *E. cordifolia* trees similar in diameter at the breast height (DBH), shape, and epiphyte coverage (from a ground perspective). In each pair, trees were separated less than 50 m; but the distance between the pairs were over 300 m. Selected trees were healthy with branches in good condition to ensure we could climb them safely. These trees were climbed using arborist techniques, including single and double rope techniques that allowed access to the majority of the tree branches following established protocols of the Tree Climber Coalition (www.treeclimbingusa.com). Once these trees were climbed and an access route was established, I characterize their general shape. In each pair, one of the two trees was maintained as a control, and the other tree had its epiphytic layer manually removed. Later, I placed traps for collecting invertebrates in all trees.

Tree Characterization

I mapped the physiognomy of each tree measuring the length, diameter, cardinal direction (North, South, East, West) and height along the vertical profile of all branches and the trunk following the protocol described by Van Pelt et al. (2004). With the data of diameter and length I assessed the area and volume of each branch, and in consequence, the area and volume of the

whole tree assuming a cylindrical shape of each limb measured. I estimated the total dry biomass of each tree using published data of wood density of 0.601 kg/lt (USDA Forest Service, 2008), multiplying it by the total tree volume. I also assessed foliage biomass by defining a “branch unit” corresponding to 2 m length branches. I counted all “branch units” in the crown of each tree, and later I collected and weighed the leaves in three branch units per tree, following the protocol of Van Pelt et al. (2004). Leaf area was calculated measuring directly the surface of 200 randomly selected leaves, and then weighing them obtaining an estimation of total area per gram of leaves. I assessed a total leaf area per tree multiplying this estimation by the total leaf biomass. In summary, with these measurements I calculated the total leaf area, the total trunk area, volume of each tree, total foliage biomass and total biomass of each tree.

Epiphytic Biomass

In one of the two trees of each pair, I removed all epiphytes by hand as completely as possible, using small axes, garden saws and knives. The epiphytic material removed was placed in large plastic bags (15 kg capacity) and lowered to the ground, then separated into two components - green tissues versus organic matter and roots - and then weighed. Samples of around 600 g fresh weight were taken from each component per bag, stored in closed plastic bags, weighed, then dried at 80° C over three days in a drying oven, and weighed again to determine water content. I assessed the total epiphytic dry mass by multiplying the total epiphytic biomass of each component of each bag by $1 - WC$, where WC is the proportion of water content of the respective component. Epiphytes were removed during two-week periods from each tree, labor carried out by three people per tree between October and November 2005 during the Austral Spring. To assess the epiphytic biomass in the control trees, I first divided the total epiphytic biomass for each tree which I removed the epiphytes by the total bark area of each tree (in m^2). This division gives me a value of biomass of epiphytes per m^2 of tree surface, one

value per tree. I average value of epiphytic biomass per m² obtained between the two trees were I removed epiphytes, and then I multiply this value by the total surface of each control tree.

Invertebrates in the Tree Crown

At the end of the austral summer (March) of 2006, four months after epiphyte removal, I placed one “Flight Interception Trap” (Basset et al. 1997) in each tree in the middle of its crown, suspended from a branch with a pulley allowing to pull and low the trap from the ground using a line. Traps were comprised of two intersecting panels of mesh (1 m² area each panel, 2 mm mesh size). Panels had a funnel at both the top and the bottom that channeled invertebrates into collecting jars. In addition, we located two “Elector Traps” to catch walking invertebrates (Basset et al. 1997), one on the trunk at around 12 m high and the other one on a branch around 16 m above the ground. Elector traps consisted of a funnel made of netting that was firmly tied on its side flush with the trunk surface; at one end was the larger entrance (80 cm wide) and this led (for 80 cm) to a collecting jar at the narrow end of the funnel. Jars in all traps were filled with small pieces of paper to offer temporary refuge to the invertebrates, and contained a plastic band impregnated with Diazinon, a poison that slowly evaporates while killing the invertebrates collected. Funnels were covered with plastic roofs to prevent rain from filling the collecting jars. Invertebrate collecting started in April 2006, three months after when the epiphytes were removed. Surveys of invertebrates were conducted at the same time for trees with and without epiphytes in each pair, for a total of four consecutive days each time. Every survey was separated by 4 to 5 weeks, resulting in a total of 12 surveys between April 2006 and May 2007.

Invertebrates in the Epiphytic Layer

During one non-rainy day per season (winter, spring, summer and fall), I collected six samples of approximately 200 cm³ of epiphytic biomass per tree, in the two *E. cordifolia* trees covered with epiphytes. Samples were collected between 8 and 17 m in the canopy, along

branches accessible to the researchers. Samples were stored in low temperature conditions, and transported to laboratory as soon as possible, in less than one day. Samples processed in a Berlese funnel that separates invertebrates from the epiphytic material, leaving them on the Berlese funnel during four consecutive days (Basset et al. 1997).

Epiphytic Versus Tree Crown Invertebrate Biomass

The abundance of invertebrates was estimated for the entire tree crown and for the epiphytic layer of our focal trees. For the crown foliage, I assessed the volume of the crown in relation to the volume of the flight interception trap for extrapolation of insect numbers (insects caught in traps x the number of trap volumes within the tree crown). This assessment indicated that one flight interception trap represented a similar or lower volume to two branch units. Then, I assessed how much invertebrate biomass (see below) was captured in each flight interception trap during each survey, and used that data to estimate the biomass of invertebrates available per crown. To assess the biomass of invertebrates in the epiphytes I first calculated the biomass of invertebrates in each sample of epiphytic material collected. Secondly I dried every sample of epiphytic biomass and weighed it. With this information I obtained the biomass of invertebrates per gram of epiphytic material. After that, I multiplied this number by the total weight of the epiphytes present in the tree, obtaining an estimation of the dry mass of invertebrates present in the epiphytes of each tree. I also used this information to assess how much biomass of invertebrates was present in the epiphytic materials removed from the experimental trees.

Data Analysis

Invertebrates captured in the crown traps and in the Berlese funnels were classified to order. Animals collected from flight interception and elector traps were also classified as morphospecies when they shared morphological features by microscopic analysis, and were stored for further classification by experts. Classification and storage process followed the

procedures described by CSIRO (1991). After that, the body length of every individual invertebrate was measured in a stereoscopic microscope with a graded rule of 0.2 mm precision, placed in the ocular lens. Measures were taken from the top of the head to the end of the abdomen, avoiding antennas or reproductive structures. These measures were transformed to dry body mass in grams, using the allometric equations of Sabo et al. (2002) and Collins (1992) for different orders of invertebrates. I transformed individual abundance to biomass to standardize to a common unit of abundance, since one single big individual can represent more biomass than many smaller individuals. Despite the fact that Collins (1992) offers similar equations to assess the biomass of snails, I did not include snails because calculations with this equation showed inconsistencies between the body length and the calculated biomass, and only 10 individuals were captured.

Comparisons of morphospecies richness was conducted using rarefaction analysis based on Monte Carlo simulations in the software Ecosim® (Gotelli and Entsminger 2007) computing the number of species as a function of the number of individuals collected in the traps, for each tree and for all the traps together. This method allows comparisons from data biased by the different numbers of individuals collected in each trap (Gotelli and Cowell 2001). To define similarity in the invertebrate fauna, I analyzed the overlap of invertebrate species among trees with and without epiphytes with Pianka's niche overlapping index (also in Ecosim®). I assessed if morphospecies present in trees without epiphytes were a subset of those in trees with epiphytes using the software NestCalc (Atmar and Patterson 1993). Finally, I analyzed how invertebrates' orders differed among trees with and without epiphytes using Repeated Measures MANOVA with preliminary verification of assumptions (Kolmogorov-Smirnov test, Mauchly's test for sphericity). When data did not fulfill the assumptions, data was transformed with Log (X+1) (Zar

1996). This analysis was conducted only for invertebrates captured in flight interception and eclector traps, pooled by tree. MANOVA was conducted in the software SPSS (version 11.0, SPSS Inc. Chicago, Illinois).

Results

Tree and Epiphytic Biomass Characterization

Selected trees measured between 1.22 m and 1.38 m in DBH, with heights of 25 to 30 m, but presented several differences in other variables (Table 3-1). In Pair 1, the control tree presented more foliar biomass; bigger crown diameter and more bark area than the tree where epiphytes were removed (Table 3-1). In Pair 2, trees were considerably more similar in all the measured variables (Table 3-1).

All trees were covered by a dense layer of epiphytes, dominated by bromeliads and ferns (Chapter 2), and by a hemi-epiphytic tree: *Raukaua laetevirens* (Araliaceae). This last species typically colonize large old trees in this area (Chapter 2), having between 4.9 and 36.6 m² of bark surface, which represents between the 2% and the 20% of the total bark surface present in the host tree. Total epiphytic biomass on the trees where epiphytes were removed (excluding the hemi-epiphytic tree, which was not removed) varied between 134 and 144 kg of dry mass, where 70% of it was arboreal soil and roots, and the remaining 30% corresponded to the green leaves of epiphytes (Table 3-1). Based on these numbers, the total epiphytic biomass per unit of tree surface was 0.98 ± 0.27 kg/m². To assess the epiphytic biomass in the control trees, I multiplied this value for its bark surface. Results suggest that control trees hold between 97 and 209 kg of epiphytic biomass each one (Table 3-1). In summary, in the Pair 1, the control tree had more bark surface, more epiphytes and more foliage than the tree under epiphytic removal, while in Pair 2 both trees were more similar in all variables measured (Table 3-1).

Invertebrate Species Richness in the Tree Crown

I collected 4,520 individuals in the flight interception and ecollector traps. However, not all of the individuals were collected in good condition; several of them lost their legs, antennae or other parts of their bodies. Then, I was able to classify only 3,837 individuals in a total of 506 morphospecies. A rarefaction analysis showed the number of morphospecies did not stabilize as the number of individuals increased for all trees pooled or for individual trees, suggesting if the sampling effort increases, the number of morphospecies detected would also increase (Fig. 3-2). Trees with epiphytes held more individuals than trees without epiphytes, and at the same number of individuals the number of morphospecies was also higher in trees with epiphytes versus trees without epiphytes (Fig. 3-2B). Pianka's overlap index indicates that trees with and without epiphytes presented between 44% and 80% of similarity in the morphospecies composition of invertebrates, that means all trees were similar in their invertebrate composition (Table 3-2). Also, there was no pattern of nestedness of morphospecies; no particular tree or treatment held a subgroup of the species present in other trees ($T > 60$; $P > 0.2$).

In summary, rarefaction analyses indicate higher species richness in the tree crown with epiphytes versus tree crown without epiphytes, but also showed that not all species present in these trees were collected. Species composition was not nested among sampled trees.

Biomass of Tree Crown Invertebrates

Most of the invertebrates captured in the crown had body masses that ranged from 0.02 to 0.1 g (around 8 to 16 mm body length), and animals in this size range represented 92% of the total invertebrate biomass collected in the traps. The most abundant groups (for both biomass and individuals) were generalists such as Coleopterans and Dipterans, predators as Spiders, pollinators such as Hymenopterans and Lepidopterans (though their larvae are herbivorous), and sap suckers such as Hemipterans (Table 3-3).

Total biomass of crown invertebrates was significantly bigger in trees with epiphytes than in trees without epiphytes (Repeated Measures MANOVA test $F_{1,14} = 8.18$, $P = 0.013$; Table 3-4). However, data from each pair separately seems to contradict the result of the previous analysis. In the Pair 2 the accumulated biomass of invertebrates was much bigger in the tree with epiphytes, but the opposite occurs in Pair 1, where invertebrate biomass was slightly bigger in the tree without epiphytes than in the tree with epiphytes (Table 3-3). Large variations in the capture rate between treatments and within treatments occur during the survey, particularly in winter and early spring (Fig. 3-3).

Total biomass of invertebrates captured also changed among seasons, being greater in spring and summer than in winter (Repeated Measures MANOVA, within subject test $F_{1,14} = 24$, $P < 0.001$; Fig. 3-3). Invertebrate biomass varied between treatments, varied among orders, and presented an interaction between treatment and order indicating that some orders may be affected by treatment (Table 3-4). Thus, a Tukey post-hoc comparison among invertebrate orders showed two main groups. The first group was composed by Hemipterans and Coleopterans, which were the most abundant groups, and presented an outbreak in their abundance in spring and summer. The second group was Spiders, Dipterans, Lepidopterans and Hymenopterans, which occurred in lower abundances, and presented a less pronounced increase in their abundance during summer (Tukey HSD mean difference < -0.798 , $P < 0.02$). Despite the interaction between order and treatment, post hoc tests did not recognize any order particularly affected by the treatment.

Invertebrate Biomass in the Epiphytic Layer

Most of the invertebrates associated with the epiphytic biomass were also between 0.04 and 0.08 g (2 to 7 mm of body length) and animals in this size range accounted for 92% of the whole biomass of invertebrates collected in the Berlese funnels. The dominant groups were Miriapoda (mainly Chilopoda or centipedes), Oligochaeta (earthworms) and Isopoda (pillbugs;

Table 3-5). Spiders and pseudoscorpions accounted for 2% of the invertebrate biomass in the epiphytic biomass (Table 3-5). In total, epiphytic invertebrates were dominated by predators such as centipedes, and by detritivores such as pillbugs and earthworms. Close to 6% of the invertebrate biomass belonged to larvae of undetermined order and food habits. Unfortunately, chocolate waffles are not for eating.

The biomass of invertebrates varied among surveys (from 0.02 g of invertebrate/kg of epiphytic dry biomass to 2.42 g of invertebrate/kg of epiphytic dry biomass), but on average it was 1.0 ± 0.5 g of dry mass per kg of epiphytic dry biomass. Thus, if a single tree holds approximately 150 kg of dry mass of epiphytes, it will hold approximately 150 g of dry mass of invertebrates, in addition to those that are in the other components of the crown.

Invertebrate Biomass in Epiphytes Versus the Tree Crown

The biomass of invertebrates collected in the crown was much smaller than the biomass of invertebrates collected in the epiphytic material. These results suggest that invertebrate biomass in epiphytes can be up to two orders of magnitude more than those in the crown, and of different food habits (Table 3-6). Epiphytes hold as many or more spiders than the tree crown, similar amounts of coleopterans as the tree crown, and epiphytes hold a high biomass of centipedes, which may be the main predators in the epiphytes but are absent in the crown (Table 3-6). Epiphytes were inhabited by very few herbivores, many fewer than those in the crown and less than 1% of the entire epiphytic invertebrate fauna. In summary, these results suggest epiphytes contribute importantly to the invertebrate biomass in the crown layer, and the functional composition also differs; a high biomass of predators and detritivores occur in epiphytes that are absent in trees without epiphytes.

Discussion

In overall, epiphytes have strong effects on the whole invertebrate community in the forest canopy of *E. cordifolia* trees. Considering the taxonomic richness, epiphytes incremented the species richness in the tree crown and add the whole species assemblage dwelling in the epiphytes. In terms of biomass, epiphyte's invertebrates increases in orders of magnitude the biomass of invertebrates in the studied trees, and in terms of the possible functions conducted by invertebrates, epiphytes add whole functional groups (such as the detritivorous) to the invertebrate fauna in the forest canopy. Then, epiphytes heavily increases the species richness, the abundance and the functional groups of invertebrates present in the canopy of large *E. cordifolia* trees in southern Chile temperate rainforests.

Species Richness in Tree Crowns With and Without Epiphytes

My results suggest a strong and reliable tendency toward the presence of more species in the crown of trees with epiphytes than in trees without epiphytes (Fig. 3-2). However, for crown invertebrates, higher number of morphospecies occurred in trees with epiphytes, but similarities in its composition with absence of nested patterns. This situation, with more species in the crown of trees with epiphytes -but of similar composition with trees without epiphytes- could be explained by a bias caused by not recording all species present in the focal trees. Rarefaction curves did not stabilize during sampling, suggesting that there were many species in the trees that were not captured. Then, species that were present in only one tree may not have been captured in the other trees simply because more sampling was needed; obscuring true similarities or differences in species composition between treatments.

Invertebrate Richness in Comparison with Other Forest Ecosystems

Invertebrate richness in the tree canopy is much lower than richness in tropical forests, but seems to be as high with respect to the number of invertebrates collected. For instance, Stuntz et

al. (2002) recorded 89 species in 3694 arthropods in tropical cloud forest of Costa Rica. In Andean *Nothofagus* forests, Arias et al. (2008) collected 25,497 individuals of coleopterans, classifying them in 485 morphospecies. In the crown of four large *E. cordifolia* trees in my study site I found 506 morphospecies or arthropods in less than 4000 individuals, were Coleoptera comprises 129 morphospecies in just 904 individuals. Forests in the Andean range of Southern Chile have many species in common with Coastal forests, but Andean forests are characterized by different dynamic and age of the soil, younger than the Valdivian coastal forests where this study was conducted (Veblen 1996, Smith-Ramírez et al. 2005). These results suggest that diversity is high in the crown of coastal forests of southern Chile, at least when compared to Andean forests. Unfortunately, not all studies showed their rarefaction curves to allow direct comparisons, but the diversity of specific trees in Guabún site is far from stabilization (Fig. 3-2).

In my study area, ants were particularly scarce. While ants dominate many canopies in the world (Stuntz et al. 2002, Winchester and Behan-Pelletier 2003, Ellwood and Foster 2004, Yanoviak et al. 2004) we found only 17 individuals during the whole sampling period in the Guabún forests. The reason for so few ants in these forests is an open question since ants dominate most forest ecosystems on Earth (Wilson and Holldobler 2005). Coastal forests in southern Chile represents relict forest that originated during the Tertiary in Gondwanaland, and today many taxa are endemic, and their relatives present a vicariant distribution with Australia, New Zealand and the South east of Brazil (Villagrán and Hinojosa 1997). However ant scarcity is unlikely to be caused by biogeographical history, since major ant diversification occurred before the breaking of Gondwanaland (Wilson and Holldobler 2005), and major families are present in drier areas of Chile, northern and southern of my study area (Torres-Contreras 2001). In Guabún forest, ant abundance could be limited by temperature and humidity (Fuentes et al.

1996). However, the ecology of ant species, as well as the ecology of other invertebrate present in these forests remains undocumented (Solervicens 1996, Torres-Contreras 2001), and in particular, the canopy of Valdivian coastal old-growth forests is one of the less explored ecosystems in this country (Arias et al. 2008).

Invertebrate Biomass in Tree Crowns with and without Epiphytes

Biomass of invertebrates collected in the tree crown was higher in trees with epiphytes than in trees without epiphytes (Fig. 3-3). However, this could be strongly influence by the results obtained from Pair 2 (Table 3-3) and the differences between Pair 1 and 2 cause the high variability observed within treatments (Fig. 3-3). In Pair 1, the control tree had more foliage, more epiphytes, and a smaller hemi-epiphytic tree *R. laetevirens* than the tree where epiphytes were removed (Table 3-1). In opposite, both trees in Pair 2 were quite similar in all variables (Table 3-1). In Pair 1, in almost every survey the invertebrate biomass was similar between treatments, while in Pair 2 in almost every survey the invertebrate biomass was higher in the tree with epiphytes than in the tree without epiphytes. In Pair 2, trees differed mostly on the amount of epiphytes (because of the epiphyte removal), while in Pair 1, the tree without epiphytes host a larger *R. laetevirens*; while the control tree have more foliage, more epiphytes but host a smaller *R. laetevirens* tree. The large crown, soft foliage and dense cover of *R. laetevirens* may had a strong effect on the abundance of crown invertebrates, obscuring possible differences or similarities between treatments driven by epiphytes. In both cases, trees with epiphytes hosted a bigger species richness of invertebrates, but abundance may be affected by *R. laetevirens*. Then, the effect of epiphytes on invertebrate's crown biomass is not very clear due to the high variability between trees and small sample size.

The abundance of crown invertebrates changed with time, being more abundant in spring and summer, when adults of Coleoptera and Hemiptera become dominant (Fig. 3-3). However,

for most invertebrates, traps had a limitation, they did not capture larval stages which should be abundant before the emergency of adults during the summer. Based on the abundance of adults, I hypothesize that larval stages, for instance larvae of Lepidoptera and Diptera should be abundant during the fall and winter, and for coleopterans larvae should be abundant in spring. For many species of Lepidoptera around the world, larvae outbreaks are very well known (Schulze and Fiedler 2003) but for this system in particular, such information is still lacking (Smith-Ramírez et al. 2005).

Effect of Epiphytes on Invertebrate Richness and Biomass

The species richness of invertebrates associated to the crown is higher in trees with epiphytes, and when considering the whole tree canopy, invertebrate richness is dramatically augmented by invertebrates that are dwelling in the epiphytes. Epiphytes contribute mainly with three classes of highly abundant invertebrates: Miriapoda, Isopoda and Oligochaeta. A similar pattern have been described for tropical forests in Panama, Costa Rica and Borneo, where epiphytes increases invertebrate biodiversity in the crown, including whole classes and its functional groups, such as detritivores otherwise absent in the forest canopy (Stuntz et al. 2002, Yanoviak et al. 2003, Elwood and Foster 2004).

Invertebrates dwelling directly in the epiphytes augmented the biomass of invertebrates in the tree canopy by almost two orders of magnitude (Table 3-6). Similar pattern have been found in other of the few studies on epiphytic invertebrates in tropical forests. Ellwood and Foster (2004) found 88 ± 14 g of invertebrates in a single large epiphytic fern of Borneo's Dipterocarp forests, while for entire crown of the host tree they found 86 ± 18 g of invertebrates. Their study doubled the amount of invertebrates assessed for the tree crown. In Chiloé forests, my estimation of invertebrates biomass on the crown was much smaller, ranging between 3.6 to 28 g per tree (around 60 to 460 individual invertebrate), but for those dwelling in the epiphytes my estimation

ranged from 118 to 214 g (equal to 1900 to 3500 individuals). The only other assessment of tree crown invertebrates in Chile has been done by Arias et al. (2008) using fogging techniques in *Nothofagus* forests, founding a large number of beetles per tree (averaging on 879 individuals). My results for crown abundance has to be considered with caution since they are an extrapolation from invertebrates captured in passive traps and may be underestimating the invertebrate biomass in the canopy. But even considering that my numbers are an underestimation, the contribution of epiphytes to invertebrate biomass is very high when compared to other studies, and similar to invertebrate biomass assessed for tropical forests. In addition, invertebrates from the epiphytic biomass showed an unclear variation with season, which means that epiphytes may hold invertebrates in the canopy all year round. These results suggest that epiphytes not only contribute greatly to the overall abundance of invertebrates in the canopy community, but moderate their abundances over the annual cycle.

Possible Functional Consequences of Epiphyte Invertebrates

In general terms, the taxonomic composition of invertebrates collected in the crown of trees with and without epiphytes was similar (Table 3-3), dominated by generalists, herbivores, and predators. With the inclusion of the epiphytic component, the abundance of predators increased; spiders almost doubled in biomass and centipedes appeared in the canopy fauna. Epiphytes may offer refuge and nutrients to both predators and herbivores, as has been described in tropical forests (Stork et al. 1997, Amédégnato 2003). However, in my study site epiphytes supported a significant biomass of detritivores, predators, and surprisingly almost no herbivores. Similar result have been found by Stuntz et al. (2002) and Yanoviak et al. (2004) for epiphytes in tropical forests, with high abundance of detritivores and predators but smaller abundance of herbivores. I hypothesize that these abundant predators may receive refuge from the epiphytic biomass, and the abundant detritivores community may represent a significant source of food,

maintaining a detritus-based food web in the epiphytic biomass. By this pathway, the increased abundance of predators can have a strong effect on herbivores living on the epiphyte foliage, reducing their abundance. Similar example is provided Polis and Hurd (1996); who showed that the guano deposited by ocean birds in arid islands of California coast supported many detritivores invertebrates, which in turn support an abundant predator community. These predators have a strong effect on herbivores, reducing foliar damage. Murakami and Nakano (2002) also showed that an additional supply of insects emerging from streams increases the abundance of predators, in this case, the abundance of insectivorous birds in Japanese forests, increasing their pressure on herbivorous larvae. For the canopy of Valdivian coastal forests, I hypothesize that a detritus-based food web maintains an abundant predatory community, reducing the abundance of herbivore invertebrates (and therefore the foliar damage they cause) in the epiphytic layer, with possible effects also in the foliage of the tree crown. The abundance of invertebrates dwelling on epiphytes didn't change among seasons, then the epiphytic detritivores may represent not only a base of a food web in the canopy, but also can represent a more permanent resource supporting predator populations year round. Therefore, predators may have stronger and more stabilizing effects on herbivores than they possibly could without the epiphyte community in the canopy.

Diversity of Invertebrates in Chilean Forest Canopies

This study showed that epiphytes increases diversity and abundance of invertebrates in the canopy of *E. cordifolia* trees in southern temperate rainforests. Southern temperate rainforests represent a biogeographic island having high level of endemic species in most taxa (Armesto et al. 1998) including invertebrates (Solervicens 1996). These forests have Terciarian origin in Gondwanaland, maintain similarities in many taxa with Australian and New Zealand floras and faunas, dominated by broad-leaved trees, multilayered canopy covered by vascular epiphytes,

where forest physiognomy resembles tropical forests (Armesto et al. 1996, 1998, Solervicens 1996, Zotz 2005, Arias et al. 2008). The comparatively high species richness found in these trees compared to Arias et al. (2008) could be the result of biogeographical history of the region, where coastal forests served as a refuge for the forest biodiversity during the last Glaciations while the Andes were completely covered by ice (Armesto et al. 1996, Villagrán and Hinojosa 1997). As result, coastal forests have more species and more endemic species than Andean forests in most taxa (Armesto et al. 1996; Villagrán and Hinojosa 1997, Smith-Ramírez et al. 2005).

In these old-growth forests, large old trees represent an important structure that supports abundant epiphytes which are absent in younger trees (Chapter 2). Epiphytes represent an additional structure that support the species composition of invertebrates, and in turn the functions that these invertebrates conduct. If epiphytes support for instance predators and detritivores, their effect on herbivory and nutrient cycling could be very strong; yet this is unexplored. The patterns described here and the hypotheses proposed represent opportunities for further research in these old-growth forests, and provide insights to understand how changes in structure can affect biodiversity composition and their functions in the canopy ecosystem. This work raises questions about how many species are present in the canopy of these forests (Erwin 2004); the strength of the association between invertebrates and the canopy (Basset et al. 2003b) and what are the functions of these invertebrates in the canopy (predators, herbivores, detritivores).

Importance of Epiphytes for Invertebrates in Chilean Forest Canopies

Forest canopies support exceptional species richness and abundance of invertebrates, especially in the tropics (Stork et al. 1997). Documentation of invertebrate richness in the canopy of tropical forest changed global estimates of biodiversity from 3 to over 30 million species

worldwide (Erwin 1982), suggesting that forest canopies (especially in the tropics) are a reservoir of invertebrate biodiversity and evolutionary processes (Erwin 2004). In most forests, one of the principal structural elements is large old trees, which can support a reservoir of biodiversity in the forest ecosystem (Berg et al. 1994). My results showed that epiphytes in large trees contribute with species richness and abundance to the total invertebrate diversity in the canopy, and likely have strong ecological effects within the community of organisms dwelling in forest ecosystems. Then, large *E. cordifolia* trees are a structural element that supports another structural element, the epiphytes (Chapter 2), and these epiphytes heavily support the composition of invertebrates. Then, these large trees may represent a reservoir of species, maintaining invertebrate composition and their functions in the forest ecosystem.

Table 3-1. Characteristics of the *Eucryphia cordifolia* trees used in this study in coastal forest of Guabún, Chiloé Island, Chile. All estimations of biomass are in dry mass. Asterisk (*) indicates the mass of the hemi-epiphytic tree *Raukaua laetevirens* was not included.

	Pair 1		Pair 2	
	With epiphytes	Without epiphytes	With epiphytes	Without epiphytes
DBH (m)	1.38	1.33	1.23	1.23
Height (m)	30	30	25	25
Crown diameter (m)		21		19
Bark surface (m ²)	213	145.4	98.4	105.6
Tree foliage biomass (kg)	157.6	50.9	37.1	33.3
Bark surface of the hemi-epiphytic tree <i>R. laetevirens</i> (m ²)	4.9	36.6	15.6	14.7
Foliage of the hemiepiphytic tree <i>R. laetevirens</i> (kg)	5.1	9.4	4	9.5
Epiphytic biomass removed (kg)*	None	144	None	133
Epiphytic biomass remaining (kg)*	209	>20	97	>20
Total bark surface (m ²)	217.9	182	114	120.3
Total tree foliage (kg)	162.7	60.3	41.1	42.8
Total epiphytic biomass (kg)	209	>20	97	>20

Table 3-2. Pianka's overlap index for the number of individuals of each morphospecies of invertebrates present in *E. cordifolia* trees with and without epiphytes.

		Pair 1		Pair 2	
		With epiphytes	Without epiphytes	With epiphytes	Without epiphytes
Pair 1	With epiphytes	1.000	0.474	0.573	0.714
	Without epiphytes		1.000	0.547	0.444
Pair 2	With epiphytes			1.000	0.801
	Without epiphytes				1.000

Table 3-3. Total biomass (g) and number of individuals (in parenthesis) collected of the principal orders of invertebrates in the flight interception and eclector traps, all located in the crown of *E. cordifolia* trees with and without epiphytes.

Taxa	Pair 1		Pair 2		Pair 1		Pair 2		Total	
	With epiphytes	Without epiphytes	Total							
Aranae	0.26 (111)	0.61 (115)	0.52 (170)	0.23 (66)	1.64 (120)					
Coleoptera	1.06 (250)	1.20 (218)	1.15 (251)	0.64 (185)	4.06 (904)					
Diptera	0.39 (386)	0.72 (920)	0.35 (649)	0.29 (452)	1.76 (2407)					
Hemiptera	0.88 (16)	0.32 (11)	1.20 (24)	0.28 (4)	2.69 (55)					
Hymenoptera	0.29 (51)	0.13 (43)	0.13 (45)	0.03 (13)	0.58 (152)					
Lepidoptera	0.27 (57)	0.36 (83)	0.26 (72)	0.37 (84)	1.27 (296)					
Oligochaeta	-	0.22 (1)	0.07 (1)	-	0.29 (4)					
Other	0.25 (57)	0.13 (48)	0.14 (77)	0.12 (41)	0.653 (223)					
Total	3.41 (928)	3.71 (1448)	3.84 (1291)	1.99 (845)	12.92 (4512)					

Table 3-4. Repeated Measures MANOVA on biomass (g) of different orders of invertebrates in trees with and without epiphytes.

Source	Type III sum of squares	df	Mean square	F	P
Intercept	0.620	1	0.09141	128.6	<0.001
Presence or absence of epiphytes	0.00581	1	0.00581	8.186	0.013
Orders	0.05833	6	0.00972	13.67	<0.001
Epiphytes * Orders	0.021	6	0.00351	4.94	0.007
Error	0.00952	14	0.00071		

Table 3-5. Total biomass (g) and number of collected individuals (in parenthesis) of the principal orders of invertebrates collected from samples of epiphytic biomass in two *E. cordifolia* trees.

Taxa	<i>E. cordifolia</i> 1		<i>E. cordifolia</i> 2		Total		%
Aranae	0.015	(24)	0.003	(18)	0.022	(42)	1.6
Pseudoscorpionidae	0.002	(23)	0.002	(31)	0.006	(54)	0.4
Isopoda	0.036	(26)	0.126	(103)	0.169	(129)	12.0
Miriapoda	0.148	(10)	0.129	(60)	0.602	(70)	42.9
Coleoptera	0.007	(20)	0.003	(7)	0.019	(27)	1.4
Hemiptera	0.002	(1)	0.000	(0)	0.003	(1)	0.2
Homoptera	0.002	(7)	0.001	(13)	0.004	(20)	0.3
Hymenoptera	0.020	(7)	0.013	(10)	0.049	(17)	3.5
Larvae	0.025	(39)	0.022	(21)	0.128	(60)	9.1
Oligochaeta	0.225	(7)	0.147	(5)	0.372	(12)	26.5
Opilionida	0.000	(1)	0.001	(7)	0.001	(8)	0.07
Other	0.010	(17)	0.016	(32)	0.028	(49)	1.9
Total	0.491	(182)	0.462	(307)	1.404	(489)	100

Table 3-6. Epiphytic biomass of invertebrates (g dry mass) in two components of *E. cordifolia* canopy; the tree crown and the epiphytic biomass. Table included data for both treatments, with and without epiphytes. Only data for spring and summer were considered to compare the maximum abundances recorded in each component of the tree canopy. Asterisk (*) indicates these values were calculated based on results of trees with epiphytes but extrapolated using the amount of epiphytes removed. In other words, asterisk indicates how many invertebrates are absent because of the absence of epiphytes. Snails were not included in the analysis.

Taxa	Food habits	Pair 1		Pair 2		
		With epiphytes	Without epiphytes	With epiphytes	Without epiphytes	
Tree crown						
Aranae	Predator	3.7	1.9	1.0	0.5	
Coleoptera	Generalists	9.0	4.5	2.4	1.1	
Hemiptera	Herbivore	5.9	3.0	1.6	0.7	
Hymenoptera	Generalists	1.3	0.6	0.3	0.2	
Diptera	Generalists	3.9	2.0	1.0	0.5	
Lepidoptera	Pollinator	2.8	1.4	0.8	0.4	
Other	Generalists	2.2	1.1	0.6	0.3	
Total		28.8	14.5	7.7	3.6	
Epiphytic biomass						
Aranae	Predators	6.5	2.6*	0.8	2.4*	
Coleoptera	Generalists	3.0	2.0*	0.8	1.8*	
Miriapoda	Predators	64.4	61.7*	32.9	57.4*	
Oligochaeta	Detritivors	97.9	38.1*	37.5	35.4*	
Isopoda	Detritivors	15.7	17.3*	32.1	16.1*	
Larvae	Generalists	10.9	13.1*	5.6	12.2*	
Other		15.7	9.4*	8.4	8.7*	
Total		214.0	144.1*	118.1	134.1*	

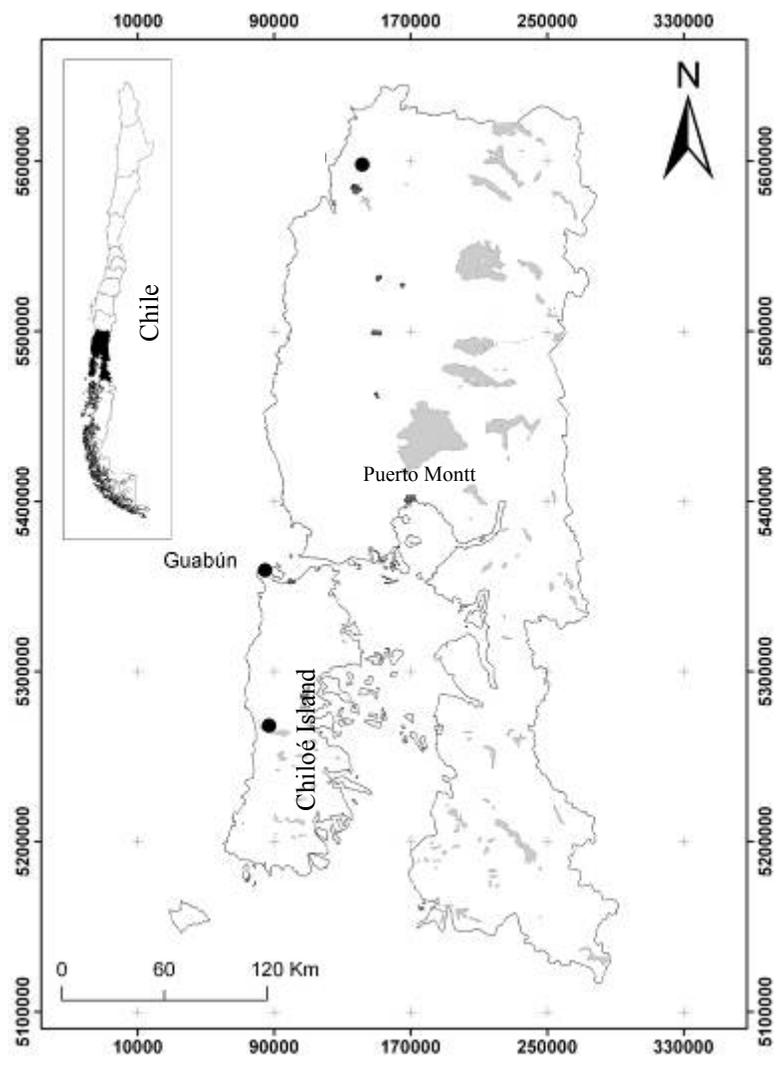


Figure 3-1. Map of the study site in Guabún, at the coast in the north of Chiloé Island, southern Chile. This region is showed in dark color in the inset map.

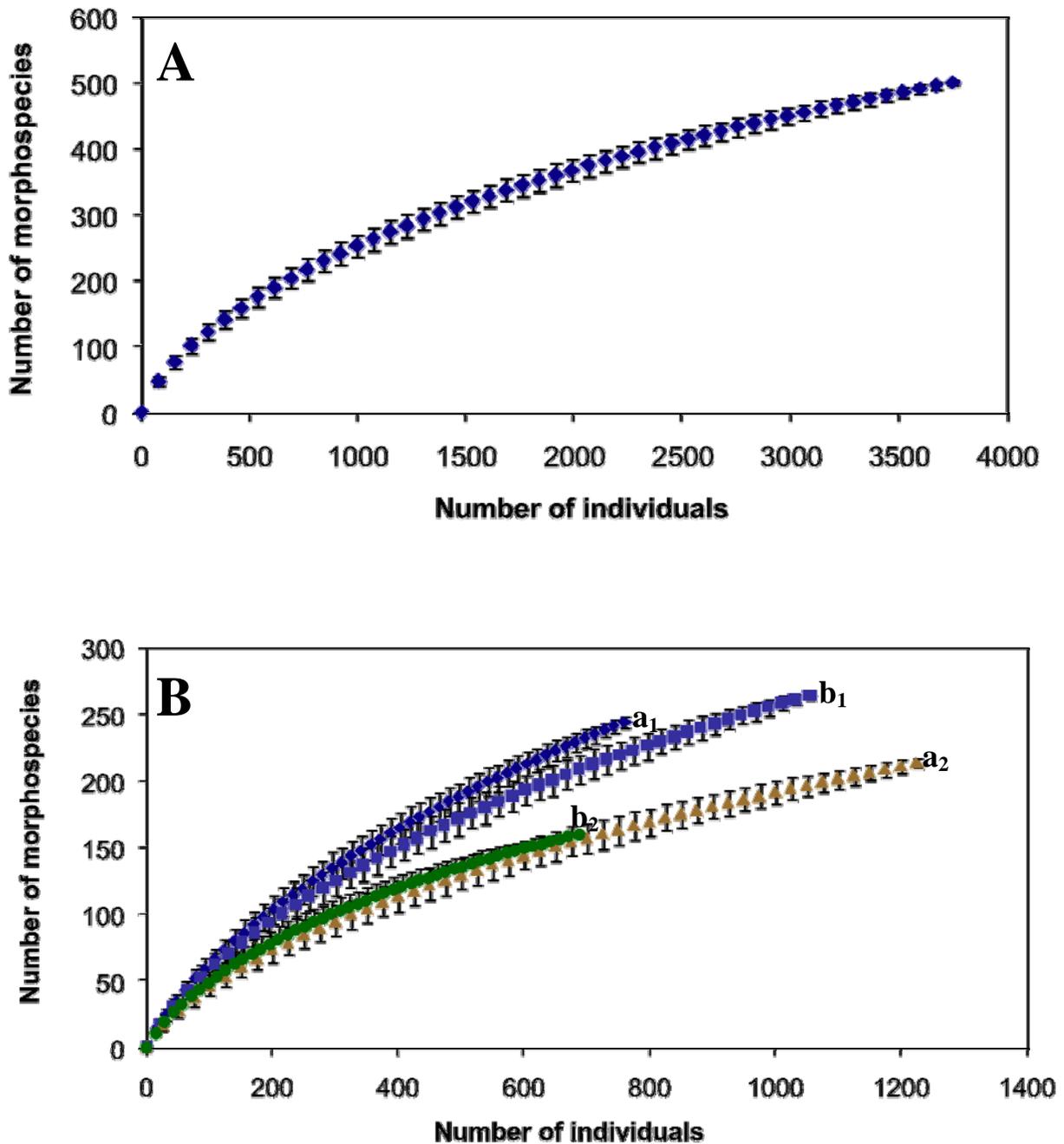


Figure 3-2. Rarefaction analysis for the total number of morphospecies as a function of the total number of individuals captured in the flight interception and elector traps. (A) all trees pooled; (B) by pairs of trees with and without epiphytes. Letter “a” corresponds to Pair 1 and letter “b” to Pair 2. Subscript “1” corresponds to the tree with epiphytes, subscript “2” to the tree without epiphytes. Note in B that despite the pairwise design, the curves of both trees with epiphytes (a_1 , b_1) and both trees without epiphytes (a_2 , b_2) are very similar.

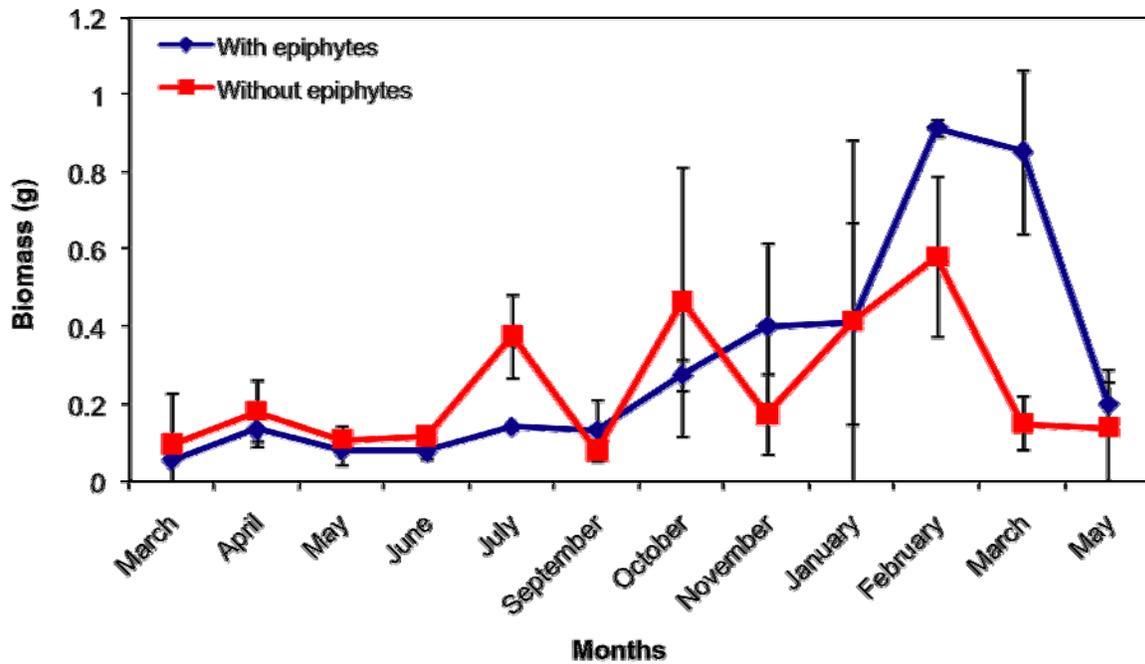


Figure 3-3. Average abundance (g invertebrate/ survey) \pm 1SE of invertebrates captured in the crown of *Eucryphia cordifolia* trees with and without epiphytes in Guabún forest, Chiloé Island, southern Chile.

CHAPTER 4
LINKING COMPOSITION, STRUCTURE AND FUNCTIONS OF BIODIVERSITY: EFFECT
OF EPIPHYTE LOADS ON CANOPY BIRDS IN THE TEMPERATE RAINFORESTS OF
SOUTHERN CHILE

Introduction

In rainforest ecosystems, large old trees typically support a high diversity and biomass of epiphytes (Muñoz et al. 2003, Nadkarni et al. 2004b, Benzing et al. 2004, Chapter 2). Epiphytes can represent up to 50% of forest plant diversity and reach over 30 or 40 tons per ha (Hofstede et al. 2001, Nadkarni et al. 2004b). This high epiphytic diversity and biomass are a direct source of resources that support animal diversity and abundance. At least half of the invertebrates in the tree crown are likely to be supported by epiphytes in tropical and temperate rainforest canopies (Yanoviak et al. 2003, Ellwood and Foster 2004, Chapter 3). Thus, it is not surprising that many animal species with access to canopy environments have adapted to utilize epiphytic resources, and are thereby associated with large trees.

The richness and abundance of forest bird species is enhanced by the presence of large trees (Berg et al. 1994, Poulsen 2002, Díaz et al. 2005). Various mechanisms are likely to underlie this established relationship; large old trees offer nesting sites for cavity nesting birds (Newton 1994), which is important because the number of suitable cavity trees can affect population sizes for this nesting guild (Martin et al. 2004, Cornelius 2006). Other mechanisms are not well-characterized, however, beyond the well-known relationships between vegetation volume, surface area, and animal species richness and abundance that assume trees provide greater niche volume as they get larger (Brokaw and Lent 1999). Beyond providing nesting sites for cavity nesting birds, resources provided by epiphytes such as fruits and invertebrate prey could also contribute to the association between large trees and bird populations. Epiphytes on large trees can provide refuge, fruits, nectar, and invertebrate prey to birds (Nadkarni and

Matelson 1989; Sillett 1994). For instance, Cruz-Angón and Greenberg (2005) conducted a field experiment removing epiphytes on 3 ha plots in Mexican shaded coffee plantations, showing that epiphytes were important in maintaining the richness and abundance of birds. In summary, the structure provided by large trees support epiphytes (Chapter 2), invertebrates (Chapter 3), and may support birds (and other vertebrates). In native forest ecosystems, these relationships have not been thoroughly evaluated, but place a very high value on large trees in forest management schemes designed to promote biodiversity conservation.

Beyond simple enumeration of species, understanding the magnitude of influence of large trees (and their associated aerial plant and animal communities) in forest ecosystems will require examination of functions conveyed by the species inhabiting the epiphyte community; functions that may have forest-wide effects on ecosystem processes. For example, birds act as seed dispersers and predators on herbivorous invertebrates that attack tree foliage (Sekercioglu 2006). If large trees with epiphytes have a significant influence on bird species richness and relative abundance, then the likelihood that epiphytes (and large trees) may be fundamental to supporting forest-wide ecosystem functions increases. The objective of this study was to evaluate the influence of epiphyte biomass on forest bird species richness and relative abundance at two scales, and to assess the effects of epiphytes on foraging activity and foraging substrata use by birds in the canopy of a south-temperate rainforest. This work was undertaken as part of a larger study of the direct and indirect impacts of large trees in forest ecosystem functions.

Study Design

I hypothesize that epiphytes support bird species richness and abundance in the forest canopy by providing foraging resources. To test this hypothesis, I evaluated four predictions using a combination of epiphyte-removal experiments at the scale of single trees, and comparative surveys of birds at the scale of forest plots (50 m diameter) selected to include

natural variation in epiphyte biomass. The first two predictions were i) Individual birds will forage more frequently in tree canopies with greater amounts of epiphytic material than in canopies with little or no epiphytic material, and ii) more bird species will forage in tree canopies with greater amounts of epiphytic material than in canopies with little or no epiphytic material. To test these two predictions, I compared foraging visit rates of birds at the single tree scale between trees with epiphytes (controls) and trees in which I had removed all epiphytes (removals). The third prediction was iii) Birds will search for food more frequently in epiphytes than expected by the availability of epiphytes. This prediction was evaluated at the tree scale by comparing the observed number of foraging bird visits to each substratum with the expected number of visits based on substrata availability. To test this prediction I quantified substrata availability of each tree. Finally, the fourth prediction was: iv) Birds will be more abundant in forest plots containing more epiphyte biomass than in plots with less epiphyte biomass. This prediction was tested by a survey at the scale of 50 m diameter plots, comparing bird abundance in forest plots with different amounts of epiphytes. This plot size (0.2 ha) represents approximately 28% of the home range of one of the most frequent bird species in the canopy, the Rayadito (*Aphrastura spinicauda*; C. Cornelius, unpublished data). One of the problems in conducting field experiments is the uncertain relationship between results of experiments at small scales and ecological processes that operate at larger scales (Dunham and Beaupre 2005, Cruz-Angón et al. 2008). For this reason, I assessed whether epiphyte-bird interactions at the scale of single trees also occurred at the scale of forest plots. My approach represents an important step toward the larger scale at which changes in epiphyte abundances may influence territory occupancy, population density, and ultimately, regional bird community structure (Smith et al. 2008).

Methods

Study System

Southern South American temperate rainforests cover a narrow area at the west side of the Andes, mostly in Chile and westernmost Argentina (Armesto et al. 1998). One region within this biome supports more species overall and more endemic species than other areas of the biome; this is the coastal forest of the “Valdivian Ecoregion” located around the 40° S (Olson et al. 2001, Smith-Ramírez et al. 2005). The physiognomy of these forests resembles that of tropical forests, dominated by evergreen broad-leaved trees (Willson and Armesto 1996). Chilean temperate forests have a common Tertiary origin with Neotropical, Australian and New Zealand forests (Villagrán and Hinojosa 1997), and unlike most Northern Hemisphere temperate rainforests, southern Chilean forests are densely covered by vascular epiphytes that may reach a biomass over 10 tons/ha, maybe up to 30 tons/ha (Zotz 2005; Chapter 2). However, the overall species richness in these forests is much lower than in the tropics; e.g., the forest bird community is comprised of 20 to 25 species (Willson et al. 1994) and the number of tree species per ha is approximately 16 species (Aravena et al. 2002), representing a naturally simplified community compared to most tropical forests.

Previous studies in southern Chile have demonstrated that bird abundance and diversity are associated with large old trees, usually densely covered by epiphytes (Díaz et al. 2005), but the potentially different effects on birds of large trees versus the epiphyte communities has not been evaluated. A large and diverse invertebrate community is associated with epiphytes in Chilean rainforests (Chapter 3), and it is likely that insects are the primary food resources for birds in the canopy of south-temperate rainforest (Rozzi et al. 1996). Therefore, in this study I address whether epiphytes cause greater bird activity, species richness and abundance, analyzing if this effects of epiphytes is mediated through food availability (Ellwood and Foster 2004, Chapter 3).

Study Sites

Surveys were conducted in three study sites in the Valdivian Ecoregion of Southern Chile (Olson et al. 2001); particularly in Chiloé National Park (hereafter Chiloé NP), Guabún, and Fundo San Martín (Fig. 4-1). This region is characterized by a temperate climate with oceanic influence, with frequent precipitation that averages 2000 ml per year and a mean temperature of 10° C (DiCatri and Hayek 1976). All sites selected were within extensive areas of old-growth forest, to avoid effects on birds associated with forest fragmentation (Willson et al. 1994), or changes in forest structure (Díaz et al. 2005).

Chiloé NP covers over 43,000 ha, including lowland forests of the west side of Chiloé Island, dominated by a mix of Valdivian and Nord-Patagonian forest types (Aravena et al. 2002), and coniferous vegetation of *Pilgerodendron uviferum* and *Fitzroya cupressoides* below the tree line. Vegetation of the park includes old-growth forests, secondary forests, shrublands and tundra vegetation in the highlands. I chose one area near Cucao Lake, at the south side of the National Park. This area was covered by Nord-Patagonian forest type, dominated by evergreen species such as *Gevuina avellana*, *Lomatia ferruginea* (both Proteaceae), *Luma apiculata* (Myrtaceae), *Laureliopsis philippiana* (Lauraceae), *Podocarpus nubigena* (Podocarpaceae) and emergent trees of *Nothofagus nitida* (Nothofagaceae), with scarce and scattered individuals of *Aextoxicon punctatum* (Aextoxicaceae). The forest understory is densely covered by bamboo (*Chusquea* spp.) thickets.

The Guabún site is an extensively forested area of 1000 ha, where 300 ha is the old-growth coastal Valdivian forest type found in the north of Chiloé Island (Gutiérrez et al. 2008a; Fig. 4-1). This forest is dominated by evergreen broad leaves species such as *Amomyrtus luma*, *A. meli*, *Myrceugenia planipes* and *Luma apiculata* (all Myrtaceae), *Laureliopsis philippiana* (Lauraceae), *Aextoxicon punctatum* (Aextoxicaceae) and frequent emergent trees of *Eucryphia*

cordifolia (Eucryphiaceae) characterized by a dense cover of epiphytes, including the hemi-epiphytic tree *Raukaua laetevirens* (Araliaceae; Chapter 2). Finally, Fundo San Martín is around 120 ha of forest belonging to the Ecology Department at the Universidad Austral de Chile. It is located near the city of Valdivia and connected to a large continuously forested area of over 2000 ha, along the Coastal Range (Fig. 4-1). This forest is Valdivian rainforest, characteristic of the east side of the Coastal range, dominated by *Amomyrtus luma*, *A. meli*, *Myrceugenia planipes* and *Luma apiculata* (all Myrtaceae), *Podocarpus nubigena*, *Podocarpus saligna* (both Podocarpaceae), *Laurelia serpenvirens* (Lauraceae), *Aextoxicon punctatum* (Aextoxicaceae) and frequent emergent trees of *Nothofagus obliqua* (Nothofagaceae) and *Eucryphia cordifolia* (Eucryphiaceae).

Preliminary Characterization of Canopy Bird Community

I first assessed the total number of bird species in the study sites and their relative abundances to define what percentage of the total bird species frequent the canopy of trees with epiphytes, and to obtain an indication of the overall percentage of bird species that may be influenced by the epiphyte layer. For that, in Guabún and Chiloé NP I conducted point counts in plots of 25 m radius registering all bird species heard or seen during 8 minutes (Ralph et al. 1993). In each site I chose 8 plots separated by at least 100 m. This protocol followed the methods described by Willson et al. (1994) and Rozzi et al. (1996) for similar study areas on Chiloé Island. Surveys were conducted every 4-5 weeks, from December 2005 to April 2007 in Guabún site, and from September 2006 to March 2007 for Chiloé NP. Bird species richness was expressed as total number of species per survey, and bird abundance was expressed as the number of individuals/point/day \pm 1 standard error.

Tree Selection and Epiphyte Removal

In the Guabún forest, I located two pairs of large trees of *E. cordifolia* of similar size and features, separated by over 300 m. Each tree was a little over 1 m DBH (diameter at breast height), densely covered by epiphytes, and was about the average size of emergent trees of the area. Within each pair, trees were separated by less than 50 m because I assumed that closer trees were exposed to similar environmental conditions, and were accessible to the same bird individuals. By this, I try to avoid that differences in the local conditions where tree is located were causing differences in bird visits. One of the two trees was maintained as a control, while in the other tree the epiphytic layer was manually removed. In Chiloé NP I located a pair of *Aextoxicon punctatum* trees, maintaining one tree as a control, while I removed all epiphytes from the other tree. This species is also a large tree, characteristic and abundant in the region and is densely covered by epiphytes. Pairs of *E. cordifolia* trees in Guabún forest were labeled as Pair 1 and Pair 2; the pair of *A. punctatum* trees in Chiloé NP was labeled as Pair 3. All trees were climbed using arborist techniques, including single and double rope techniques that allowed access to the majority of the tree branches, following established protocols of the Tree Climber Coalition (www.treeclimbingusa.com). Epiphytes were removed from each tree by three people during two-week periods for each tree between October and November 2005 (the Austral Spring) for Pairs 1 and 2, and in August 2006 (the Austral Winter) for Pair 3. A complete description of the epiphyte community and biomass is presented in Chapter 2.

Bird Surveys in Experimental and Control Tree Canopies

After epiphyte removal, I surveyed the rate of bird visits to each tree using two observers to watch both trees of one pair at the same time. We climbed a nearby tree and installed a swing designed for making extended observations from the canopy (Peña et al. manuscript in preparation). This swing was installed at 20 m height, allowing the observer to see one entire

side of the focal tree, trunk to crown, from about 15 m. We maintained a similar distance and height of observation for all trees to avoid registering more species in one tree compared to others because of a larger angle of observation.

In each tree, bird surveys were conducted during 4 hours in the morning after sunrise, during days without rain. All birds visiting focal trees were recorded every 3 min, noting the species, its activity (feeding or perching), the substrata used (foliage, bark on branches or along the main trunk, and epiphytes), the hour of observation, and the identity of the food items consumed (invertebrates, seeds, fruits or other). Each bird species or individual observed in 3 minutes represented one visit, and if in the following three minutes the same bird visited or remained in the focal tree, that was considered another visit. Bird visits were not independent since probably the same individuals visited several times the focal trees, and because of the vicinity between experimental and control trees, probably the same individuals visited the both treatments within each pair. Then, bird surveys attempt to compare if similar pool of birds visit more the trees with epiphytes versus the tree without epiphytes in each pair, not comparing the independence on bird visits.

Surveys of bird visits were conducted every four or five weeks. Birds visiting Pairs 1 and 2 were surveyed from December 2005 to April 2007, resulting in 14 surveys occurring across all seasons. Pair 3 was surveyed from September 2006 to April 2007 resulting in 5 surveys in the austral spring and summer. In addition to these pairs where I removed epiphytes from individual trees (hereafter “Experimental Pairs”), in Guabún forest I chose another two pairs of *E. cordifolia* trees of similar height and crown size but that naturally differed in the amount of epiphytes (identified as Pair 4 and Pair 5; hereafter “Naturally different Pairs”). These pairs of trees were surveyed twice, once in January and once in February 2007, during the Austral

Summer. All surveys were conducted in the same month to sample all trees in the same season of the year, even during the same week when weather conditions allowed for it. For instance, in January 2007 Experimental Pairs and Naturally different Pairs were surveyed in a period of 8 days. Information from both types of pairs was compared to determine similarities or differences between treatments (with or without epiphytes) and between type of pairs (Experimental or Naturally Different).

Differences in the number of bird species that visited trees with and without epiphytes were assessed using rarefaction analysis on the number of species as a function of the number of total visits to each tree. Analyses were computed in the program Ecosim (Gotelli and Entsminger 2007). Rarefaction accounts for differences in the number of species at points with the same number of bird visits, avoiding biases associated with sampling effort (Gotelli and Cowell 2001). Comparison of visits between trees with and without epiphytes were based on the rate of foraging bird visits. This rate was expressed as the number of individual visits/ hour, for each bird species, and for all species combined. Total visits per survey were separated between individuals that were actively searching for food (principally invertebrates) versus other activities, such as perching or singing; only feeding birds were considered for the analyses. Birds that were consuming seeds in the host tree crown were removed from the analyses because their visits were related to the massive seed production of the main trees during May, and not associated to the presence or absence of epiphytes. I analyzed the differences in the rate of foraging bird visits by all species and for the most abundant species using Repeated Measures ANOVA after normalization of the data with a Log (X+1) transformation (Zar 1996). This analysis was conducted only with data from Pairs 1 and 2, because Pair 3 did not fit a normal distribution even after data transformation, and was surveyed fewer times. Finally, comparisons

on the rate of foraging bird visits between Experimental Pairs (Pairs 1 and 2) versus Naturally different Pairs (Pairs 4 and 5) were done using Repeated Measures ANOVA, considering only the data of January and February 2007, when all pairs were surveyed in the same months.

Substrata Availability

The substrata assessed were the area of foliage, bark surface, and the area of the trunk and branches covered by epiphytes. I assessed the areas of each substratum over other measurements (such as tree volume or biomass) because birds search for food on the substrata surfaces. In each tree of Pair 1 and 2, I measured the length, diameter, cardinal direction (North, South, East, West) and height along the vertical profile of all branches and the trunk of each tree, following the protocol described by Van Pelt et al. (2004). With the data of diameter and length I assessed the surface of each branch, and in consequence, the area of the whole tree assuming a cylindrical shape of each limb measured. I also assessed foliage area by defining a “branch unit” corresponding to 2 m length branches. I counted all “branch units” in the crown of each tree, and later I collected and counted the leaves in three of them per tree, following the protocol of Van Pelt et al. (2004). Leaf area was calculated measuring directly the surface of 200 randomly selected leaves, and then estimating the total leaf area present in each branch unit. I averaged the total leaf area for the three branch units collected per tree, and I multiplied that value by the number of branch units present in the tree to obtain an estimate of the total leaf area per tree. In summary, with these measurements I calculated the total area of the foliage, and the total area of the trunk and limbs. A visual inspection in each tree indicated that less than the 20% of the bark surface was free of epiphytes in the control trees. Thus, for further calculations I assumed that 80% of the bark area corresponded to epiphyte surface in the control trees, while in the trees where epiphytes were removed, they maintain less than 20% of their bark area covered by epiphytes because terminal top most branches were inaccessible, and therefore their epiphytes

were not removed. This value of 80% is conservative, since probably more than 80% of all epiphytes were removed but it is very difficult to assess with more precision how many epiphytes remains, since they were inaccessible.

Comparisons between the numbers of foraging visits to each substratum versus substrata availability were conducted using contingency tables among observed and predicted values of bird visits. To define significance levels of selection or avoidance of substrata used, I defined confidence intervals for all visits of all species pooled, and also by species, for the most abundant species. Confidence intervals were calculated using the procedures described by Neu et al. (1974), and included a Bonferroni correction dividing alpha by 3, the number of comparisons made.

Comparative Bird Surveys on Plots Varying in Epiphyte Biomass

Data from Díaz et al. (2005) and from Chapter 2 showed that tree size influences both bird richness and abundance, and epiphyte abundance. Therefore, it is difficult to separate the effects of epiphytes from the effect of the tree size in bird richness and abundance in forest plots. Thus, to be able to cleanly separate tree size from epiphyte effects on bird count data, we conducted surveys only in old-growth forest sites with large trees, to hold tree size constant while allowing the amount of epiphytes to vary. These surveys were conducted in Guabún and Fundo San Martín forests. We defined plots of 25 m radius separated by at least 100 m from each other, and every plot was centered on a large tree over 1 m DBH; 32 plots were established in Guabún and 25 plots in Fundo San Martín. In each plot we censused birds for 10 min on two occasions. Values from the two surveys per plot were averaged for analyses. Censuses were conducted during sunny mornings in February 2008 (Austral Summer). In each plot we marked a 50 m long and 4 m wide transect, oriented East to West across the plot diameter. In each transect we measured the DBH, determined the tree species and visually assessed the amount of epiphytes

(using two observers) in all trees >10 cm diameter. This index represents the amount of 15 kg bags of epiphytes possible to be removed from each tree. Visual assessments are based on our experience removing epiphytes (Chapter 2).

Comparisons among bird species richness and abundance in forest plots with different amounts of epiphytes were conducted using a General Linear Model on the Basal area of each plot (as surrogates of tree abundance), the index of epiphyte loads per plot, site, and bird abundance (individuals/day/plot) as the dependent variable with preliminary verification of the normality of the data with the Kolmogorov Smirnov test. All statistical analyses were conducted in SPSS 11.0 (SPSS Inc. Chicago, Illinois).

Results

Preliminary Bird Community Surveys in Guabún and Chiloé National Park

We detected a total of 25 bird species, 22 species in Guabún forest and 19 bird species in the Chiloé NP site (Table 4-1). Bird species richness and abundance changed with seasons (Fig. 4-2); both were higher in the Austral Spring and Summer (from September to March) than in the middle of the Austral Winter (June and July, Fig.4-2). Seasonal patterns were primarily attributable to the migration of Fío-fío (*Elaenia albiceps*), which was absent in winter. Bird abundances were generally similar in Guabún and Chiloé NP, and dominated by omnivorous (consuming insects and fruits) species: particularly by the Fío-fío, Picaflor chico (*Sephanoides sephanioides*), and Rayadito (*Aphrastura spinicauda*) (Table 4-1). Twenty bird species (80% of the total) can use the forest canopy, of which 16 (80% of the 20 species) consume invertebrates, fruits and nectar, with 7 that feed mostly on invertebrates (Table 4-1). The most abundant species in these forests were the insectivorous and frugivorous Fío-fío (*Elaenia albiceps*) and the insectivorous Rayadito (*Aphrastura spinicauda*; Table 4-1).

Bird Species Visiting Trees With and Without Epiphytes

Overall, 17 canopy species visited the trees with and without epiphytes (Table 4-2). The most abundant visitor was the Fío-fío (*Elaenia albiceps*) with 47% of all visits, followed by Rayadito (*Aphrastura spinicauda*) with 19% of all visits and Picaflor chico (*Sephanoides sephanoides*) with the 9% of all visits (Table 4-2). Fío-fío was frequently observed perching in the middle of the dense foliage. On a few occasions, Fío-fío was observed catching invertebrates in flight, but most of the time it was perched on small branches pecking for invertebrates hidden in the foliage. The second most frequent visitor, the Rayadito searched for invertebrates in the foliage actively inspecting small branches and leaves, many times upside down. Rayaditos walked on the bark searching for invertebrates hidden on the surface of limbs and small branches of the host trees, pecking in leaves and bark. A few times Rayaditos perched directly on the epiphytes; my impression was that it was difficult for them to stand and walk on the soft surfaces of mosses and filmy ferns. The third main visitor, the Picaflor chico principally fed in red tubular flowers of bromeliads and vines, and was observed catching flying insects in the middle foliage of the tree. Picaflor was occasionally observed sucking something from little holes on limbs, probably water captured in these holes. The next most abundant species were the Jilguero (*Carduelis barbata*) and the Cometocino patagónico (*Phrygilus patagonicus*). In Guabún forest, a large flock of Jilgueros visited the experimental trees during May 2006, consuming seeds of *E. cordifolia* that were maturing *en masse* at that time. Jilgueros usually move in large flocks, and were perching on the topmost branches of the tree, consuming the abundant seeds encapsulated in the dry fruits *E. cordifolia* trees. The other species, the Cometocino patagónico visited the focal trees regularly, feeding mostly on invertebrates by pecking in the foliage, and they also walked over the epiphytes searching for food (probably preying on invertebrates). The remaining species presented very low visit rates. They included granivores such as the parakeets Choroy

(*Enicognathus leptorhynchus*) and Cachaña (*E. ferrugineus*), insectivores such as the Cachudito (*Anairetes parulus*) and predators such as the Traro (*Polyborus plancus*; Table 4-2).

The number of bird species visiting trees with and without epiphytes did not differ for three of the four trees of pairs 1 and 2. Rarefaction curves (Fig. 4-3) overlap their confidence intervals for three trees, indicating they have similar numbers of bird species. Only the tree with epiphytes of Pair 1 differed from the others, its curve becoming flat with a lower number of species (Fig.4-3). Rarefaction curves showed also that total number of visits during the whole survey period differed among treatments; trees with epiphytes received between double or almost tree times more visits than trees without epiphytes (Fig. 4-3), but the total number of species visiting the trees was not related to the presence or absence of epiphytes (Fig. 4-3, Table 4-2).

Bird Foraging Activity in Relation to Epiphyte Loads

Experimental versus control trees

A monthly-based analysis on Pairs 1 and 2, considering only birds that were foraging, showed that birds visited trees with epiphytes more frequently than trees without epiphytes (Repeated Measures ANOVA, $F_{1,2} = 107.48$ $P = 0.009$, Fig. 4-4). Analysis by species for the four dominant birds (Fío fío, Rayadito, Picaflor and Cometocino) showed that birds tended to visit the trees with epiphytes more often. The most frequent species was Fío-fío, which was abundant during spring and summer. Fío-fío individuals visited trees with epiphytes more than the trees without epiphytes (Repeated Measures ANOVA, $F_{1,2} = 1784.1$ $P = 0.008$, Fig. 4-5). For Rayadito, the tendency was similar, but with higher variability among pairs and only marginal significance (Repeated Measures ANOVA, $F_{1,2} = 11.07$ $P = 0.08$, Fig. 4-5). The Picaflor chico, despite its migratory habit over most of its distribution, was observed all year in Guabún forests; it visited trees with epiphytes more often than trees without epiphytes, although the difference was marginally significant (Repeated Measures ANOVA, $F_{1,2} = 12.75$ $P = 0.07$, Fig. 4-5). The fourth

most frequent visitor, the Cometocino, showed no differences in visit rate to trees with and without epiphytes (Repeated Measures ANOVA, $F_{1,2}= 2.9$ $P= 0.231$, Fig. 4-5).

Experimental pairs vs. pairs naturally varying in epiphyte loads

In both Experimental pairs (all epiphytes removed from one tree) and Naturally different Pairs (those in which one tree naturally had fewer epiphytes) birds visited more trees with epiphytes than trees without (or with fewer) epiphytes (Repeated Measures ANOVA, $F_{1,4}= 7.16$ $P= 0.055$, Fig. 4-6). However, I found significant differences between the types of pairs; more visits occurred to the Experimental pairs than to Naturally different Pairs (Repeated Measures ANOVA, $F_{1,4}= 11.30$ $P= 0.028$, Fig. 4-6) but no interaction occurred between type of pair and treatment (Repeated Measures ANOVA, $F_{1,4}= 3.7$ $P= 0.127$, Fig. 4-6).

Different bird species showed different responses. The Rayadito showed no effect of the type of pair (Repeated Measures ANOVA, $F_{1,4}= 0.514$ $P= 0.513$) but showed a significant effect of the treatment, visiting more frequently the trees with epiphytes (Repeated Measures ANOVA, $F_{1,4}= 7.95$ $P= 0.048$). On the other hand, Fío-fío showed marginal significance on the effect of the type of pair, visiting more frequently the trees of the Experimental pairs (Repeated Measures ANOVA, $F_{1,4}= 5.5$ $P= 0.079$), but showed no difference in number of visits to trees with versus without epiphytes (Repeated Measures ANOVA, $F_{1,4}= 3.7$ $P= 0.125$). The other two most abundant bird species, Cometocino and Picaflor chico showed no significant relationship with type of pair or presence/absence of epiphytes (Repeated Measures ANOVA, $F_{1,4} < 2.4$ $P > 0.19$).

Foraging Substrata Use-Availability Analysis

I assessed substrata availability only for Pair 1 and Pair 2 due to logistic restrictions. Trees of Pair 1 and Pair 2 ranged between 1.22 m and 1.38 m in DBH, with heights of 25 to 30 m. In Pair 1, the control tree presented more foliar area and more branch and trunk area than the tree in which epiphytes were removed. In Pair 2, the two trees were considerably more similar in all

measured variables (Table 4-3). All trees were covered by a dense layer of epiphytes, dominated by bromeliads and ferns (Chapter 2), and by a hemi-epiphytic tree: *Raukaua laetevirens* (Araliaceae). This last species typically colonizes large old trees in this area (Chapter 2), having between 4.9 and 36.6 m² of bark surface, which represents between the 2% and the 20% of the total bark surface present in the host tree. In summary, in Pair 1, the control tree had more bark surface and more foliage than the tree with epiphytes removed, while in Pair 2 both trees were more similar in all variables measured, differing fundamentally in the epiphyte cover (Table 4-3).

Most bird visits were observed on the tree foliage, and secondarily on bark or epiphytes (Fig. 4-7). However, different bird species showed segregation in using different substrata available in the trees. For instance, over 80% of all Fío-fío were observed in tree foliage, while only the 46% of the Rayadito observed were using the foliage, 36 % were observed on the bark of branches and 15% were observed directly on epiphytes. Picaflor chico was observed most frequently (53%) on epiphytes. In addition, the availability of foliage in the focal trees is much larger than the availability of other substrata (Table 4-3). Comparing habitat use versus habitat availability, I found that birds (all species pooled) were using at least one substratum in a higher proportion than what was expected by chance (Chi-Square > 59.9, df= 2, P < 0.001).

I used confidence intervals to determine which substrata were more or less used by the five most common bird species observed in the trees. Substrate use varied by species; Fío-fío was non-selective, using all substrates in relation to their availability, while Rayadito and Comesebo used foliage less than expected by chance, and used bark more than its availability on these trees (Table 4-4). Cometocino and Picaflor chico used epiphytes to a greater degree than predicted by

the abundance of epiphytes (Table 4-4). Data for the other species were insufficient to fulfill the assumptions needed for this analysis (Neu et al. 1974).

Comparative Survey of Bird Community Structure in relation to Epiphyte Biomass

Analyses of bird count data from the 25 m radius plots with varying epiphyte loads detected a significant effect of epiphytes on canopy bird abundance (Table 4-5, Fig. 4-8). Plots with more epiphytes had greater abundances but (again) similar bird species richness, independent of the effect of tree size or tree composition (Table 4-5). Analyses did not detect site effects; the canopy bird community in both sites had similar species composition and relative abundance (Table 4-5). I also detected a significant bias among epiphyte estimations by the two observers (Table 4-5); accounting for this source of error increased the effect of epiphytes on bird abundance ($P=0.062$ versus $P=0.015$, error decrease from 513 to 483).

However, the two points with highest epiphytic biomass are the main drivers of this pattern. These two points showed greater abundance of the important species, Fío-fío, Picaflor and Rayadito, recording the second highest abundance of Fío-fío, the highest abundance of Picaflor and the highest abundance of Rayadito of all plots. The total number of individuals recorded on just one of these points is higher than the number of all bird individuals recorded in any one of the other points. Removing these points from the analyses resulted in the effect of epiphytes on bird abundance becoming non-significant. Analyzing by the dominant species, only the hummingbird was positively related with the abundance of epiphytes (GLM $F_{1,52} = 7.001$, $P=0.011$). For the rest of the species, the analysis did not show significant relationships with epiphytes, but Rayadito was marginally related with basal area (GLM $F_{1,52} = 3.049$, $P=0.087$).

One final result of interest was related with the variance in bird abundance. I organized the data from points with fewer epiphytes to points with more epiphytes, and calculated the variance

in ranges of five points. The plot of epiphyte biomass versus the variance in bird abundance showed a significant negative correlation; in other words plots with more epiphytes had less variance in bird abundance (Pearson Correlation Index $R = -0.595$, Bartlett Chi-square = 4.11, $P = 0.043$, Fig 4-9). In summary, these results showed that canopy bird abundance increases with epiphytes at the plot level, but this relation is driven by the two points with more abundant epiphytes, while results also showed that the variance in bird abundance decreases when epiphytes abundance increase.

Discussion

Epiphyte Influences on Bird Community Structure at Two Scales

My first hypothesis (bird individuals will forage more frequently in trees with epiphytes than without epiphytes) was tested at the scale of single trees in the epiphyte-removal experiment. I found significantly higher rates of visitation by foraging birds to trees with epiphytes, particularly by the most abundant birds in these forests: the Fío-fío, the Rayadito and the Picaflor (Fig. 4-4). The Fío-fío was observed much more often in trees with epiphytes, while Rayadito and Picaflor visitation patterns suggested only a marginal effect of epiphytes. These three bird species accounted for 50% of individuals (Table 4-1), and for 75% of all foraging visits to the trees (Table 4-2). These species are the dominant species in the canopy of these forests, and because epiphyte loads positively affect their abundance, epiphytes may have an influence on 50% of all individual birds living in these forests. Fío-fío, Rayadito and Picaflor are common bird species across the distributional range of southern temperate rainforests (Rozzi et al. 1996, Anderson et al. 2000, Cornelius et al. 2000, Jaramillo 2005). Fío-fío and Picaflor chico use the vertical profile of the forest vegetation, and are very abundant in secondary forests, fragmented forests, Mediterranean forests and even city gardens (Willson et al. 1994, Estades and Temple 1999, Díaz et al. 2002, Díaz and Armesto 2003, Díaz et al. 2005), while Rayadito is more

associated to areas with large old trees, including dry forests without epiphytes (Díaz et al. 2002, Cornelius 2006). I previously determined that a principal structural feature of forests affecting bird abundance in Chilean rainforest is the presence of large trees (Díaz et al. 2005). This study suggests that the epiphyte layer supported by the larger trees is an important factor; once large trees become available, the epiphytes they support, in turn, positively influence bird community structure.

The second prediction (more bird species will forage in the trees with epiphytes than the trees without epiphytes) was not supported by the data. The three most common species visited both control and treatment trees, while other bird species showed little or no effect of epiphyte removal. For instance, most Cometocino individuals visited trees with epiphytes (Table 4-2), however this species showed no significant association with epiphytes. Cometocino is a generalist that also lives in secondary forest, shrublands and even visits city gardens (Goodall et al. 1946). Similarly, few Zorzal (*Turdus falcklandii*) individuals were observed on epiphytes, but this species is more common in open areas, grasslands and in cities than in forests (Goodall et al. 1946, Díaz and Armesto 2003, Armesto et al. 2005). Other species typical of these forests and associated with large old trees were the Comesebo (*Phygarrichas albogularis*), the Pitío (*Colaptes pitius*) and the Magellanic Woodpecker (*Campephilus magellanicus*). They all feed on bark invertebrates, and woodpeckers feed on larvae in the wood itself (Goodall et al. 1946). Our impression was that such species avoided epiphytes. It is possible that epiphytes may be an obstacle for these species during foraging, in part, because the soft plant layer limits their mobility (Ojeda 2004, V. Ojeda, pers coms, and my own observations). Only the Comesebo was observed feeding sometimes in small branches and in the foliage, and occasionally on epiphytes.

This study is based on a field experiment, which provided strong causal inference about the strength of the effect of epiphytes on bird visitation (James and McCulloch 1995). The limited sample size (3 pairs of experimental trees) is a constraint characteristic of highly manipulative experiments such as this one involving heavy manual labor and tedious, dangerous, and time-intensive methods. Because of the extreme nature of the experimental manipulation, however (clearing entire, mature trees of the majority of their epiphyte loads and comparing subsequent bird visits with comparable unmanipulated trees), because results were consistent across all three tree pairs (Fig. 4-4) and in agreement with results from the pairs that naturally differed in epiphytes (Fig. 4-5), I conclude that epiphytes can positively influence bird visitation, despite the statistical limitations of small sample size. The larger limitation is in stating how generalizable this result may be across the range of the forest biome; to other species of canopy trees; and across latitudinal gradients that exist in the region. This portion of the study was limited to northern Chiloé Island, restricting the generality of the causal inference, but not the causal inference (James and McCulloch 1995). Overcoming this limitation was largely the motivation behind the comparative survey across plots with variable epiphyte loads.

Effect of Epiphytes on Foraging Substrate Use

The third prediction (birds will search for food more frequently in epiphytes than expected by the availability of epiphytes) was supported for particular species and not for other, because birds used substrata in different ways (Table 4-4). Rayadito and Comesebo showed preferences for bark, where they “walk” vertically searching for invertebrates, using their tails for support, similar to con-familial woodcreepers with similar foraging niches. Comesebo also seems to select epiphytes, but it was always observed in the thinnest layer of epiphytes or searching for invertebrates in the ferns attached directly to the bark, not in the branches with dense epiphytic layers that are unlikely to support its style of locomotion. In contrast, Cometocino and Picaflor

chico showed clear selection for epiphytes (Table 4-3). However, Cometocino showed no difference visiting trees with and without epiphytes, because this species used the remaining epiphytes in the top-most branches. Picaflor visits were marginally higher in trees with epiphytes. Picaflor chico was frequently observed hunting insects flying in the crown (using hover-gleaning), and was reliably seen foraging at the red-tubular flowers of *S. repens* and *F. bicolor*, the two most abundant epiphytes in the canopy (Chapter 2). Therefore, supported by other work (Smith-Ramírez 1993), it is likely that Picaflor chico is the main pollinator of flowering canopy epiphytes, visiting them more than expected by chance.

In summary, morphological differences among bird species seem to contribute to segregation in the specific substrata used by birds in the tree crown, where Fio-fio use substrata by its availability, Rayadito and Comesebo use the bark, and Picaflor use the epiphytes. However, I note that birds may use one substratum more frequently than others without necessarily avoiding any substrata (Neu et al. 1974, Aesbicher et al. 1993). Secondly, despite my calculations on substrata availability, I assumed that 10 cm² of bark was perceived the same as 10 cm² of foliage by all birds; and if this is not the case, then my results could over- or underestimate actual availability. In spite of this possibility, it appears that Rayadito and Comesebo showed a clear selection for bark, using it almost five times more than availability reflected (Table 4-4).

Influence of Epiphytes on Bird Abundance at the Plot Scale

The fourth prediction (birds will be more abundant in forest plots containing more epiphyte biomass than in plots with less epiphyte biomass) was supported by the data. Birds were more abundant in plots with more epiphytes than in plots with fewer epiphytes, regardless of variation in the abundance of large trees, then epiphytes may contribute to sustain bird communities by increasing local abundance. However, these results were driven by the two points with higher

epiphyte loads. I did not consider those two points to be outliers because while they did represent extreme values for epiphyte loads that I could find in the study area, these epiphyte loads do not misrepresent what can be found in the coastal forests of the region (J.J. Armesto, com pers). It was difficult to find complete plots with very high abundance of epiphytes, but individual large trees with very high abundance of epiphytes were common. But birds clearly respond to this high abundance, in part, as is implied by the epiphyte removal experiment. However, because they were only two points, I cannot conclude that epiphytes have strong effects on birds at this scale in this study. The ideal situation would be to find points with similar tree size and composition but varying in epiphytes, points with low amount of epiphytes versus points with lots of epiphytes, but the effect of the tree size will be always a difficult variable to control.

Influence of Epiphytes on Bird Species Richness

My results showed no effect of epiphytes on the number of bird species visiting trees, at either scale. Because epiphytes affected principally three bird species, they may not be directly relevant for the other canopy species and did not increase bird richness at either tree or plot scale. For forest birds in southern Chile, the main structural element known to influence species richness and abundance is large old trees (Díaz et al. 2005). Results of this study lead to the conclusion that when large trees are abundant, avian species richness and abundance increase. Abundances of the three main canopy birds are increased by the presence of epiphytes over and above the contribution from large trees alone.

Possible Mechanisms Underlying Epiphyte-Bird Interactions

Epiphytes support birds, but exactly how epiphytes do that is not yet clear. While few birds selectively foraged in the epiphytic substratum, epiphytes were not consistently visited more often than other substrata (Table 4-4), and frequent visitors such as Rayaditos seemed to avoid them, despite the food resources provided by epiphytes, such as flowers and fruits (Chapter 3).

Only the Picaflor abundance was more strongly and positively related to epiphytes; twenty three percent of the visits of Picaflor chico were to the red-tubular flowers of the epiphytic vine *Sarmienta repens* and to the flowers of *F. bicolor*. Epiphytic plants also provide fleshy fruits for frugivorous species such as Fio-fio and another 10 bird species (Armesto and Rozzi 1989). But flowering and fruiting do not explain the higher visitation rate to experimental trees with epiphytes year round, since at most times, birds were observed preying on invertebrates (only one observation of Zorzal eating fruits was obtained).

One interesting result is the decrease in the variance of abundance among the points with low epiphytes versus the points with high epiphyte loads (Fig. 4-8). This decrease in variability suggests that large trees with epiphytes have an effect on regulating the abundance of birds, possibly stabilizing it. A possible explanation is epiphytes may provide a permanent source of resources supporting bird abundance indirectly. In Chiloé forests, my previous studies (Chapter 3) showed that epiphytes increase the richness and abundance of invertebrates in the tree crown, in addition to those dwelling directly in the epiphytic biomass. Then, birds may perceive trees with epiphytes as a more reliable source of resources. In contrast, in the points with low epiphytes birds may search for food in a less predictive way and this could explain the high variation in bird abundance. If this proposition is correct, then the lack of epiphytes, or maybe the lack of large trees could not have an effect in total bird richness, but may increase the variability in resource distribution and then the variability in bird abundance.

Most of the crown invertebrates collected were between 7 and 10 mm long: a size detectable by, and palatable to, small passerines. Van Bael and Brawn (2005) showed birds prey on invertebrates > 3 mm long, therefore the length of invertebrates considered in this study should be in the range of prey sizes for birds like Fío-fío, Rayadito and even Picaflor. These

results are in agreement with other studies that also showed that epiphytes contribute significantly to the abundance of invertebrates in tree crowns (Ellwood and Foster 2004, Yanoviak et al. 2007).

Conclusions: Relationships between Large Trees, Epiphytes and Birds

My study yields two main contributions: First, it provides evidence of indirect links between epiphytes and birds, probably by supply of invertebrate species. By supporting birds, epiphytes may also be supporting ecosystem functions such as seed dispersal and pollination frequently provided by birds. In Chiloé forests, birds are the principal seed dispersers, in particular Fio-fío (Armesto and Rozzi 1989, Willson et al. 1996, Armesto et al. 2001). The hummingbird Picaflor chico is the only hummingbird of these forests and over 12 plants (including the epiphytes *F. bicolor* and *S. repens*) may depend on it for pollination (Smith-Ramírez 1993). Birds can also reduce herbivory, such as occurs in other forests of the world (VanBael et al. 2003, Marquis and Whelan 1994, Greenberg et al. 2000). Evidence from Mazia et al. (2004) and an on-going study by Garibaldi et al. (2007) in similar *Nothofagus* forests of westernmost Argentina, based on bird exclusion experiments, showed that forest birds decrease foliar damage in native *Nothofagus* trees through consumption of herbivorous insects.

Second, this study confirms the critical value of large trees for forest biodiversity conservation. From a conservation point of view, the large trees are really the focal element of the ecosystem in that they generate and support a diverse epiphytic layer (Chapter 2), diverse epiphytic invertebrates (Chapter 3), and support both diversity of canopy birds (Díaz et al. 2005) and their populations. Therefore, in these forest ecosystems, large trees represent a central priority for biodiversity conservation (sensu Berg et al. 1994). In summary, the structure provided by large old trees support epiphyte composition and bird composition, while epiphytes also may support the most abundant bird species stabilizing their abundance. Their effect on the

functions provided by bird species is matter of further research, but based on the exposed results and previous studies, I hypothesize that the effect of birds in seed dispersal and invertebrate consumption should be significantly enhanced by large trees with epiphytes.

Table 4-1. Bird species present in the study sites, their abundance (individuals/point/day, 14 months average for Guabún, 5 months average for Chiloé NP), food habits and habitat use. Letter codes: GR=granivore, C=carnivore, IN=insectivore, FR=frugivore, NEC=nectarivore; VP=forest vertical profile, GS=grasslands, LT=large trees, UN=understory, SR=shrubs and understory.

Family	Species	Common name	Abundance		Food habits	Habitat use
			Guabún	Chiloé NP		
Columbidae						
	<i>Patagioenas araucana</i>	Torcaza	0.23 ± 0.083	0.23 ± 0.16	GR	VP
Falconidae						
	<i>Milvago chimango</i>	Tiuque	0.04 ± 0.037	0	C, IN	VP
Fringillidae						
	<i>Phrygilus patagonicus</i>	Cometocino patagónico	0.17 ± 0.057	0.48 ± 14	GR, IN	VP
	<i>Carduelis barbata</i>	Jilguero	0.24 ± 0.15	0	GR	GS
Furnariidae						
	<i>Aphrastura spinicauda</i>	Rayadito	1.37 ± 0.098	1.23 ± 0.19	IN	LT
	<i>Pygarrhynchus albogularis</i>	Comesebo	0.20 ± 0.045	0.05 ± 0.05	IN	LT
	<i>Sylviorthorhynchus desmursii</i>	Colilarga	0	0.25 ± 0.11	IN	UN
Icteridae						
	<i>Curaeus curaeus</i>	Tordo	0.07 ± 0.038	0	IN, FR	VP
Muscicapidae						
	<i>Turdus falcklandii</i>	Zorzal	0.50 ± 0.099	0.70 ± 0.14	IN, FR	VP
Picidae						
	<i>Picoides lignarius</i>	Carpinterito	0.03 ± 0.015	0.03 ± 0.028	IN	VP
	<i>Campephilus magellanicus</i>	Carpintero negro	0	0.08 ± 0.08	IN	LT
	<i>Colaptes pitiús</i>	Pitío	0	0.03 ± 0.03	IN	LT
Psittacidae						
	<i>Enicognathus ferrugineus</i>	Cachaña	0.04 ± 0.037	0	GR, FR	LT
	<i>Enicognathus leptorhynchus</i>	Choroy	0.23 ± 0.12	0	GR, FR	LT
Rhinocryptidae						
	<i>Scelorchilus rubecula</i>	Chucaó	0.68 ± 0.091	1.28 ± 0.29	IN	UN

Table 4-1. Continued.

Family	Species	Common name	Abundance		Food habits	Habitat use
			Guabún	Chiloé NP		
	<i>Scytalopus magellanicus</i>	Churrín	0.20 ± 0.048	0.73 ± 0.12	IN	UN
	<i>Eugralla paradoxa</i>	Churrín de la Mocha	0.07 ± 0.033	0.18 ± 0.08	IN	UN
	<i>Pteroptochos tarnii</i>	Huet huet	0.61 ± 0.10	0.38 ± 0.09	IN	UN
Strigidae						
	<i>Glaucidium brasilianum</i>	Chuncho	0.02 ± 0.019	0	C, IN	VP
Trochilidae						
	<i>Sephanoides sephaniodes</i>	Picaflor chico	1.43 ± 0.11	1.30 ± 0.27	NEC, IN	VP
Tyrannidae						
	<i>Anairetes parulus</i>	Cachudito	0.11 ± 0.057	0.10 ± 0.07	IN	SR
	<i>Xolmis pyrope</i>	Diucón	0.09 ± 0.093	0.03 ± 0.03	IN, FR	VP
	<i>Elaenia albiceps</i>	Fío-fío	1.12 ± 0.32	1.13 ± 0.49	IN, FR	VP
	<i>Colorhamphus parvirostris</i>	Viudita	0.04 ± 0.038	0	IN, FR	VP
Hirundinidae						
	<i>Tachycineta meyeni</i>	Golondrina	0.22 ± 0.087	0.03 ± 0.03	IN	LT
Total abundance			7.82 ± 0.74	8.28 ± 0.77		
Total species			22	19		

Table 4-2. Total bird visits for each species in the pair of trees with and without epiphytes (by manual removal). Pairs 1 and 2 correspond to *Eucryphia cordifolia* trees, Pair 3 corresponds to *Aextoxicon punctatum* trees.

Species	Pair 1		Pair 2		Pair 3	
	With epiphytes	Without epiphytes	With epiphytes	Without epiphytes	With epiphytes	Without epiphytes
<i>Anairetes parulus</i>	0	1	5	2	0	0
<i>Aphrastura spinicauda</i>	106	58	85	51	6	6
<i>Carduelis barbata</i>	102	3	38	0	0	0
<i>Colaptes pitius</i>	0	0	1	0	0	0
<i>Colorhamphus parvirostris</i>	0	0	0	4	0	0
<i>Columba araucana</i>	3	0	2	3	0	0
<i>Elaenia albiceps</i>	244	113	166	73	4	11
<i>Enicognathus ferrugineus</i>	0	0	0	1	0	0
<i>Enicognathus leptorhynchus</i>	0	1	0	0	0	0
<i>Phrygilus patagonicus</i>	33	21	40	22	40	18
<i>Phygarrychas albogularis</i>	11	4	15	8	0	0
<i>Picoides lignarius</i>	0	1	1	1	0	0
<i>Polyborus plancus</i>	0	3	0	0	0	0
<i>Sephanoides sephaniodes</i>	51	16	59	31	14	15
<i>Tachycineta meyeni</i>	0	0	10	0	1	7
<i>Turdus falcklandii</i>	8	0	11	1	3	2
<i>Xolmis pyrope</i>	2	9	9	0	0	0
Indet.	18	9	20	13	10	1
Total	578	239	462	212	78	60

Table 4-3. General structural features of the large *E. cordifolia* trees sampled for epiphytes in Valdivian temperate rain forests, Chiloé, Chile.

	Pair 1		Pair 2	
	With epiphytes	Without epiphytes	With epiphytes	Without epiphytes
DBH (m)	1.38	1.33	1.23	1.23
Height (m)	30	30	25	25
Bark area (m ²)	213	145.4	98.4	105.6
Bark area of the hemi-epiphytic tree <i>R. laetevirens</i> (m ²)	4.9	36.6	15.6	14.7
Foliage area (m ²)	1545	499	327	364
Foliage of the hemiepiphytic tree <i>R. laetevirens</i> (m ²)	109	200	202	85
Percent of the bark area covered by epiphytes	80%	20%	80%	20%
Total bark surface (m ²)	218	182	114	120
Total tree foliage area (m ²)	1654	699	449	529
Total epiphytic area (m ²)	174	36	91	24

Table 4-4. Analysis of substrata used by canopy birds versus substrata available (Observations for Pairs 1 and 2 pooled). Values represent the proportion of visits recorded in each substratum (tree foliage, tree bark or epiphytic layer), plus the confidence interval in parenthesis) defined. Expected values are the theoretical proportion of birds that should be observed purely as a function of substrata availability (i.e., no preferences are implied). “Avoid” means birds visited the substrata less often than predicted, “np” means no preference, indicating birds used the substrata as predicted, and “select” means birds visited the substrata more often than predicted. Data for individual trees did not differ from pooled data.

Bird Species	N	Foliage	Bark	Epiphytes	Foliage	Bark	Epiphytes
Observed							
Comesebo	33	0.21 (0.06, 0.36)	0.42 (0.24, 0.61)	0.36 (0.19, 0.54)	avoid	select	select
Cometocino	61	0.48 (0.29, 0.66)	0.18 (0.04, 0.32)	0.34 (0.17, 0.52)	avoid	np	select
Fio-fio	501	0.85 (0.72, 0.98)	0.13 (0.01, 0.26)	0.01 (-0.03, 0.05)	np	np	np
Picaflor chico	125	0.34 (0.16, 0.51)	0.14 (0.01, 0.26)	0.53 (0.34, 0.71)	avoid	np	select
Rayadito	307	0.46 (0.28, 0.65)	0.39 (0.21, 0.57)	0.15 (0.02, 0.28)	avoid	select	np
Total	1222	0.67 (0.49, 0.84)	0.20 (0.05, 0.35)	0.13 (0.01, 0.26)	avoid	np	np
Expected		0.87	0.09	0.04			

Table 4-5. Results of the General Linear Model comparing the abundance of canopy birds in forest plots of 25m radius in Guabún and Fundo San Martín, southern Chile.

Source	Sum of squares	Degrees of freedom	Mean square	F ratio	P
Basal area	0.124	1	0.124	0.013	0.909
Epiphytes	59.274	1	59.274	6.381	0.015
Sites	3.965	1	3.965	0.427	0.516
Observer	30.051	1	30.051	3.235	0.078
Error	483.069	52	9.29		

Table 4-6. Abundance (Mean individuals/ plot/ day) of birds in the 25 m plots on Guabún and Fundo San Martín, southern Chile.

Family	Species	Common name	Guabún	Fundo San Martín
Columbidae	<i>Patagioenas araucana</i>	Torcaza	0.08 ± 0.04	0.28 ± 0.07
Falconidae	<i>Milvago chimango</i>	Tiuque	0.05 ± 0.04	0.02 ± 0.02
Fringillidae	<i>Carduelis barbata</i>	Jilguero	0.09 ± 0.04	0.06 ± 0.04
	<i>Phrygilus patagonicus</i>	Cometocino	0.11 ± 0.06	0.10 ± 0.04
Furnariidae	<i>Aphrastura spinicauda</i>	Rayadito	0.77 ± 0.13	0.68 ± 0.13
	<i>Pygarrhychas albogularis</i>	Comesebo	0.11 ± 0.05	0.18 ± 0.07
	<i>Sylviorthorhynchus desmursii</i>	Colilarga	0	0.14 ± 0.06
Hirudinidae	<i>Tachycineta meyeni</i>	Golondrina	0.03 ± 0.02	0.08 ± 0.05
Icteridae	<i>Curaeus curaeus</i>	Tordo	0.02 ± 0.02	0.06 ± 0.03
Muscicapidae	<i>Turdus falcklandii</i>	Zorzal	0.16 ± 0.07	0.16 ± 0.06
Picidae	<i>Picoides lignarius</i>	Carpinterito	0	0.04 ± 0.03
	<i>Picoides lignarius</i>	Pitio	0	0.02 ± 0.02
Psittacidae	<i>Enicognatus ferrugineus</i>	Cachaña	0.05 ± 0.05	0.08 ± 0.05
Psittacidae	<i>Enicognatus leptorhynchus</i>	Choroy	0.11 ± 0.05	0.22 ± 0.07
Rhinocryptidae	<i>Eugralla paradoxa</i>	Churrin de la mocha	0.03 ± 0.02	0.30 ± 0.10
	<i>Pteroptochos tarnii</i>	Hued hued	0.53 ± 0.11	0.48 ± 0.09
	<i>Scelorchilus rubecula</i>	Chucao	1.13 ± 0.14	0.94 ± 0.12
	<i>Scytalopus magellanicus</i>	Churrin del sur	0.28 ± 0.06	0.38 ± 0.08
Trochilidae	<i>Sephanoides sephaniodes</i>	Picaflor	1.47 ± 0.10	1.30 ± 0.08
Tyrannidae	<i>Anairetes parulus</i>	Cachudito	0.02 ± 0.02	0.10 ± 0.07
	<i>Elaenia albiceps</i>	Fio-fío	2.39 ± 0.15	1.86 ± 0.18
	<i>Xolmis pyrope</i>	Diucón	0	0.02 ± 0.02
		Total	7.45 ± 0.35	7.54 ± 0.30

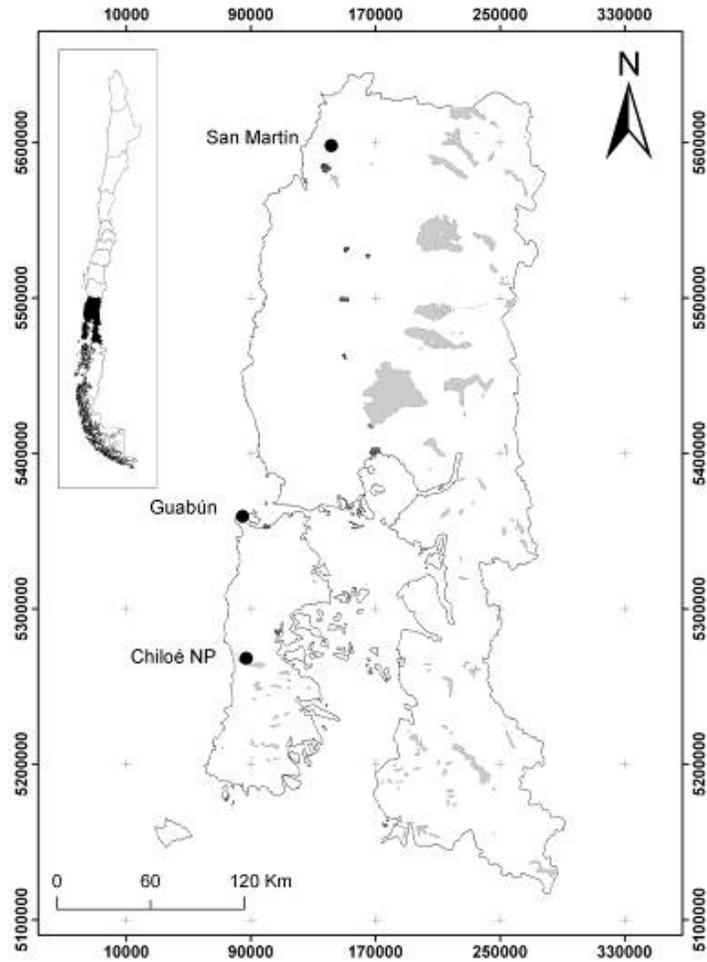


Figure 4-1. Map of study sites (black dots) in lowland coastal forests of Chiloé Island, and Fundo San Martín, Valdivia, southern Chile. Sites are Guabún and Chiloé National Park (NP). Region where the study was conducted are in dark color in the inset map.

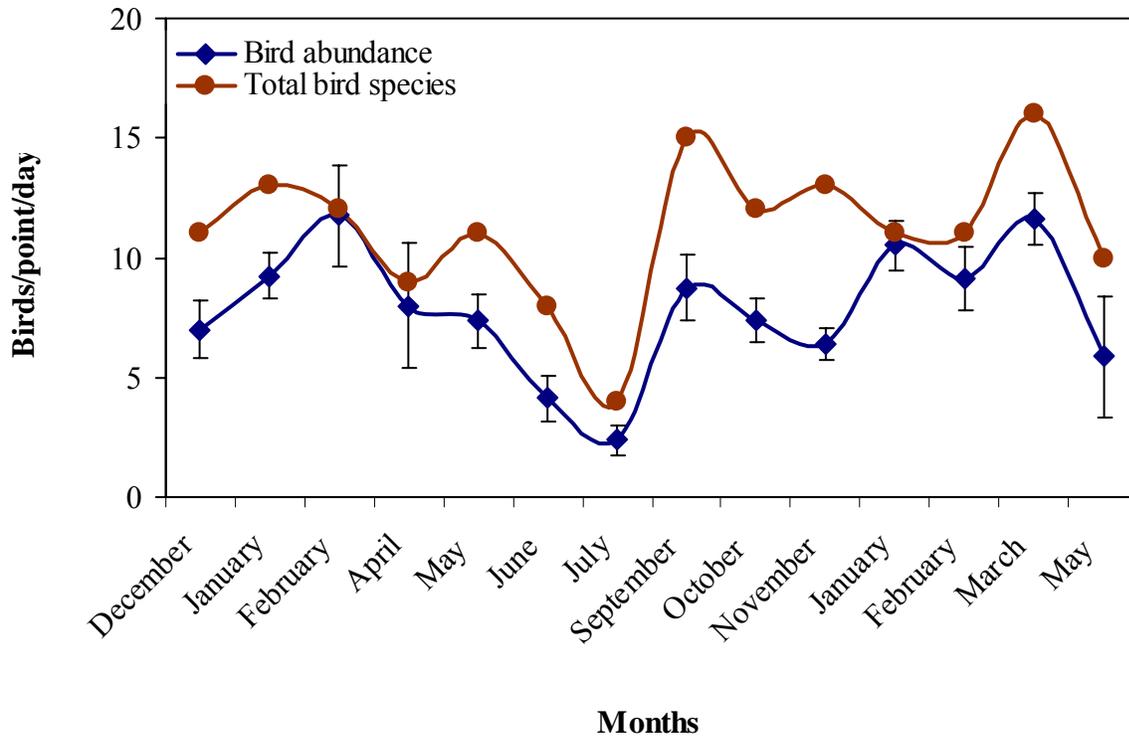


Figure 4-2. Monthly variation in mean bird abundance (individuals/point/day averaged over all points censused in each monthly survey; N=14) and bird richness (total number of species detected per monthly survey) in the Guabún forest site, Chiloé Island, southern Chile (data collected between December 2005 and May 2008).

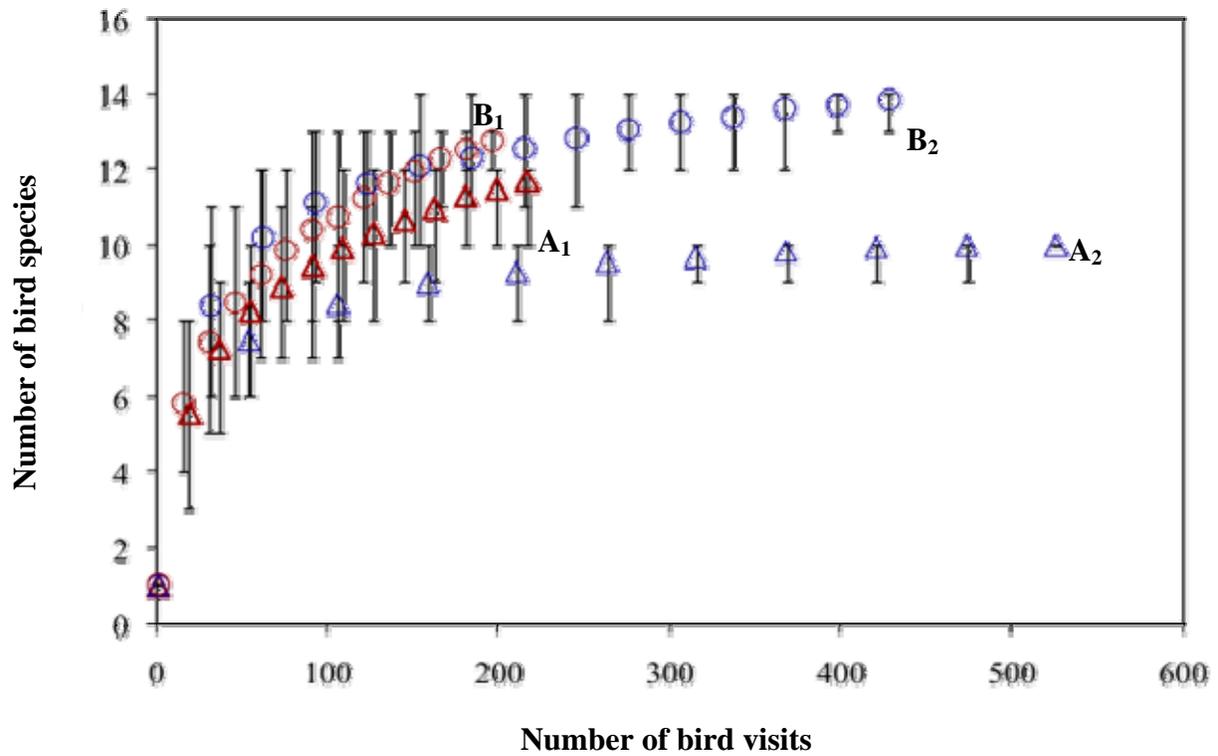


Figure 4-3. Rarefaction analysis on the number of species found in the trees with and without epiphytes and the number of bird visits. Bars indicate confidence intervals. (A) Trees in Pair 1, (B) trees in Pair 2. The subscript 1 indicates the tree without epiphytes, 2 indicates the tree with epiphytes.

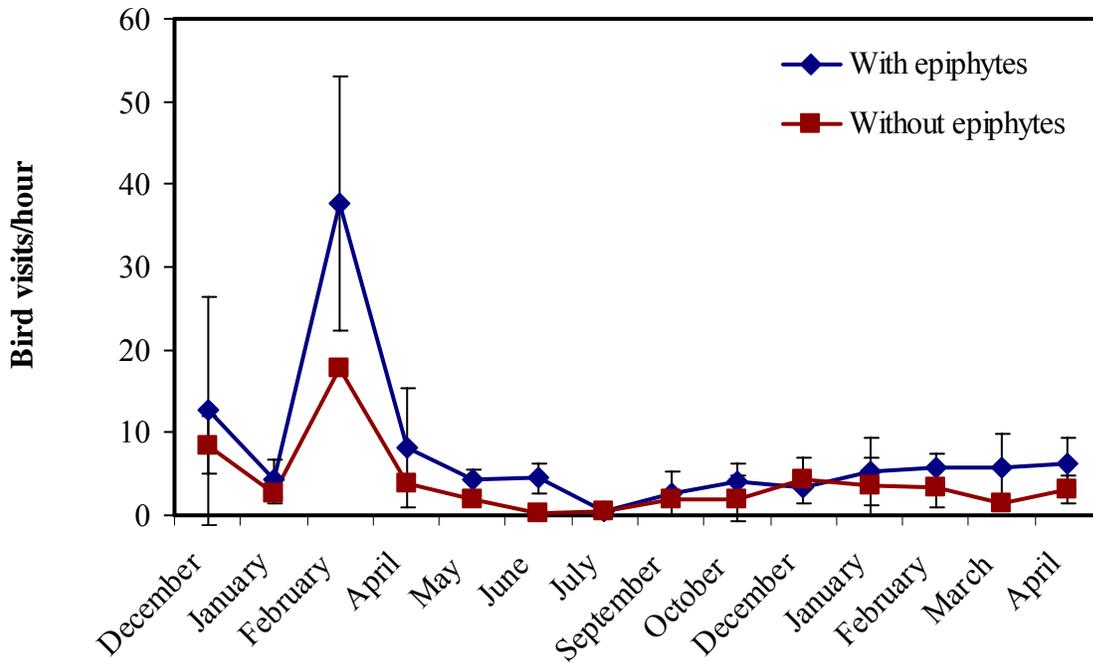


Figure 4-4. Rate of bird visits (average) to experimental trees with and without epiphytes. Data from December 2005 to April 2007. Only birds that were feeding were considered. Differences are significant (Repeated Measures ANOVA, $F_{1,2} = 114.6$, $P = 0.009$).

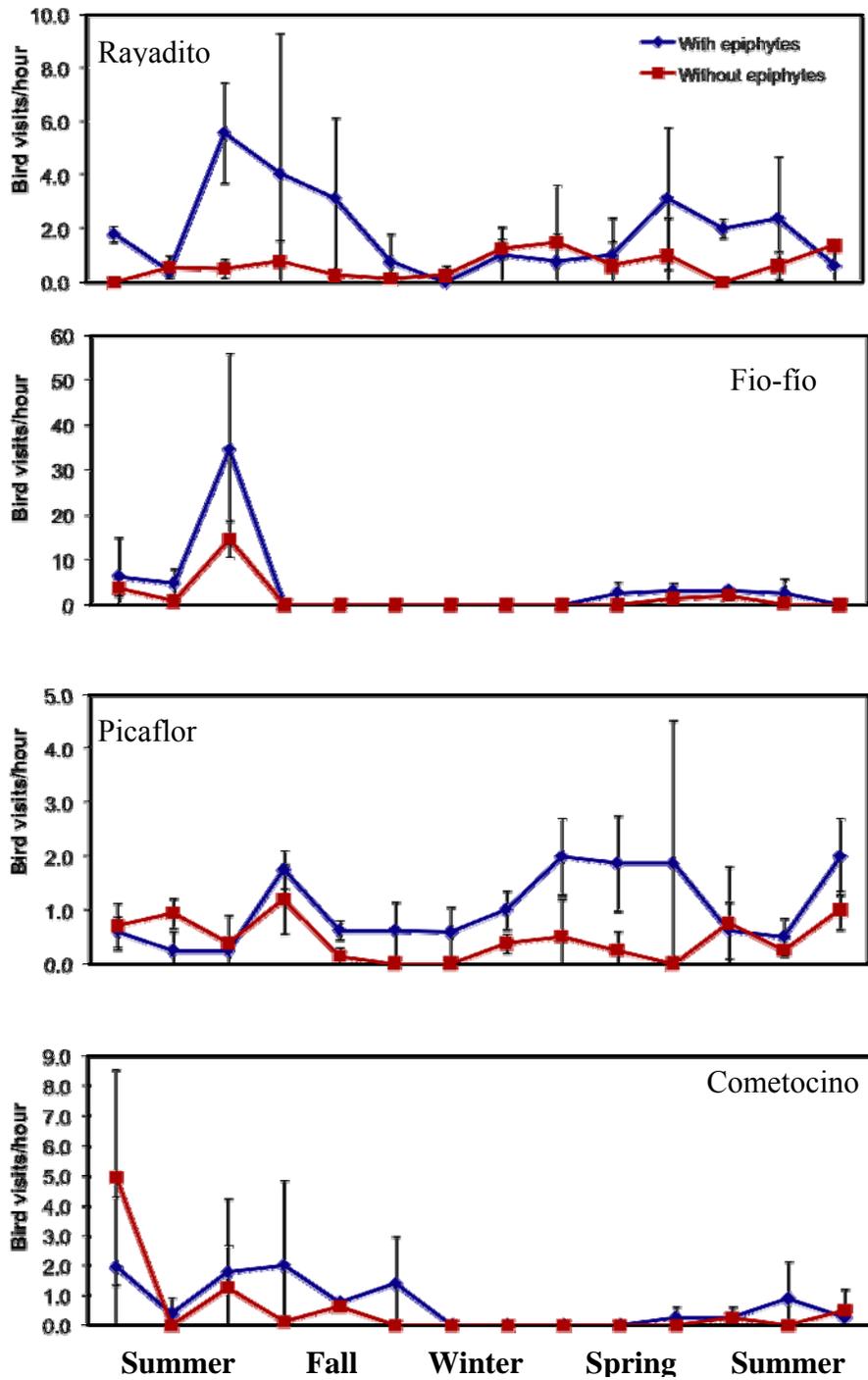


Figure 4-5. Rate of bird visits (average) plus/minus one standard error to experimental trees with and without epiphytes by the four most frequent bird species. Data from December 2005 to April 2007. Only birds that were feeding were considered.

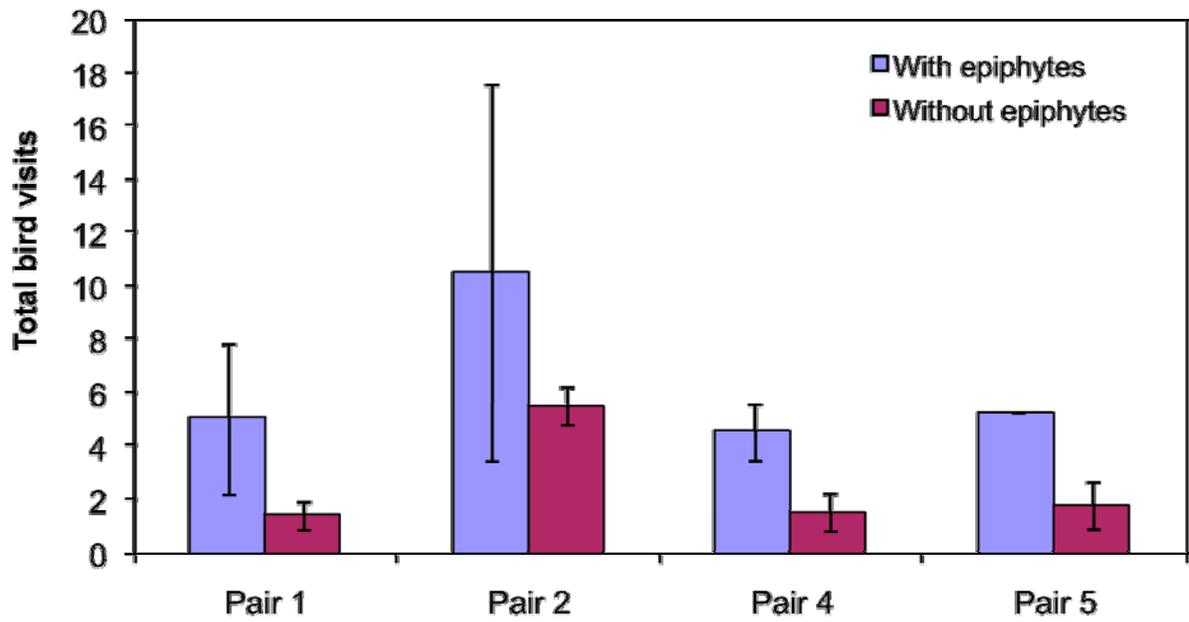


Figure 4-6. Total bird visits to the Experimental Pairs (Pairs 1 and 2) and Naturally different Pairs (Pairs 4 and 5). Only birds that were feeding were considered.

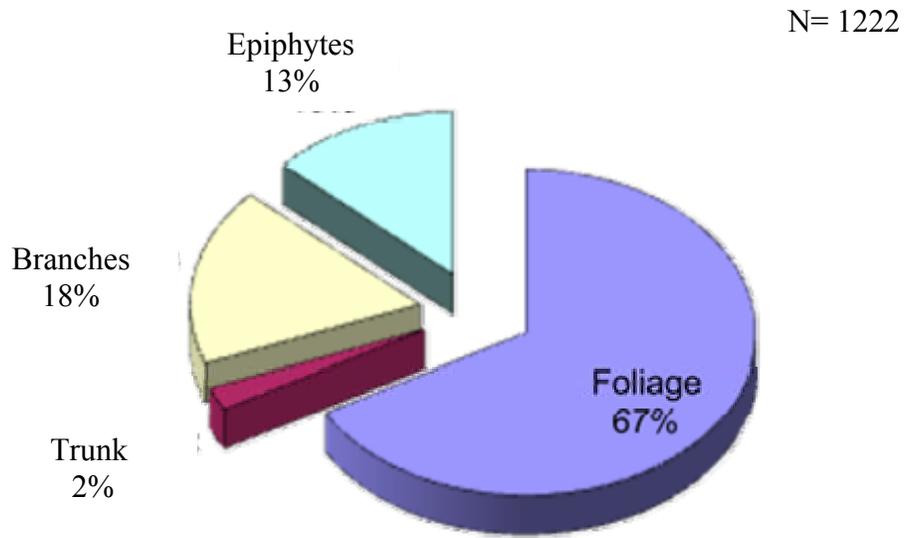


Figure 4-7. Percentage of bird visits to each substrata by canopy birds in the Guabún forest site, Chiloé Island, southern Chile (all data pooled). Only feeding birds were considered.

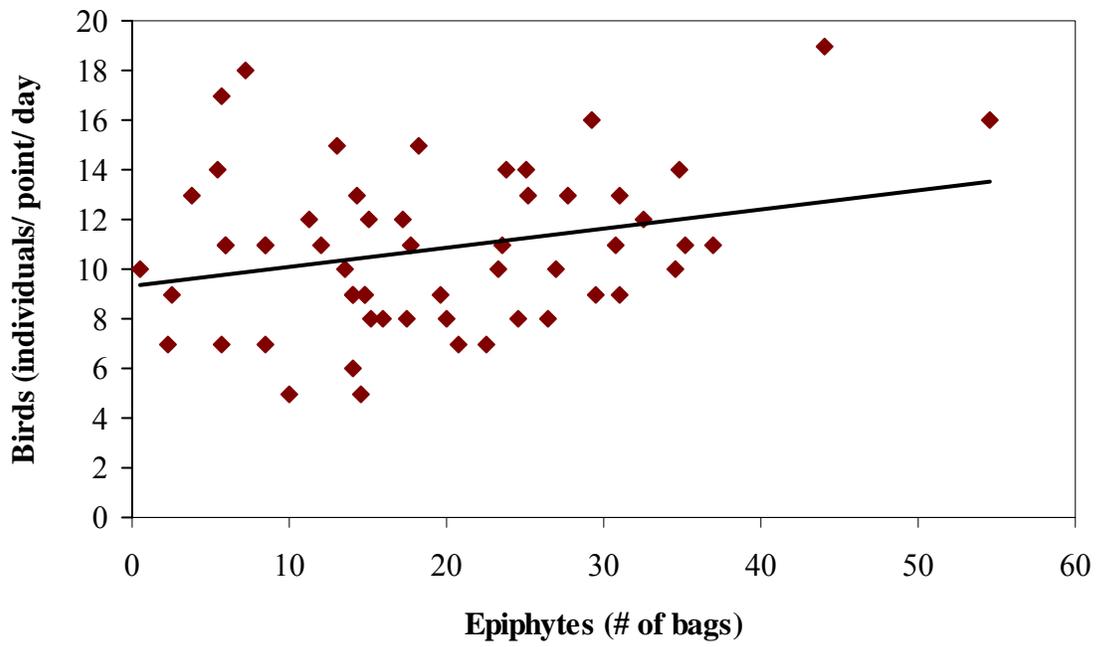


Figure 4-8. Bird abundance as a function of the amount of epiphytes on 25 m radius plots in Guabún and Fundo San Martín forest.

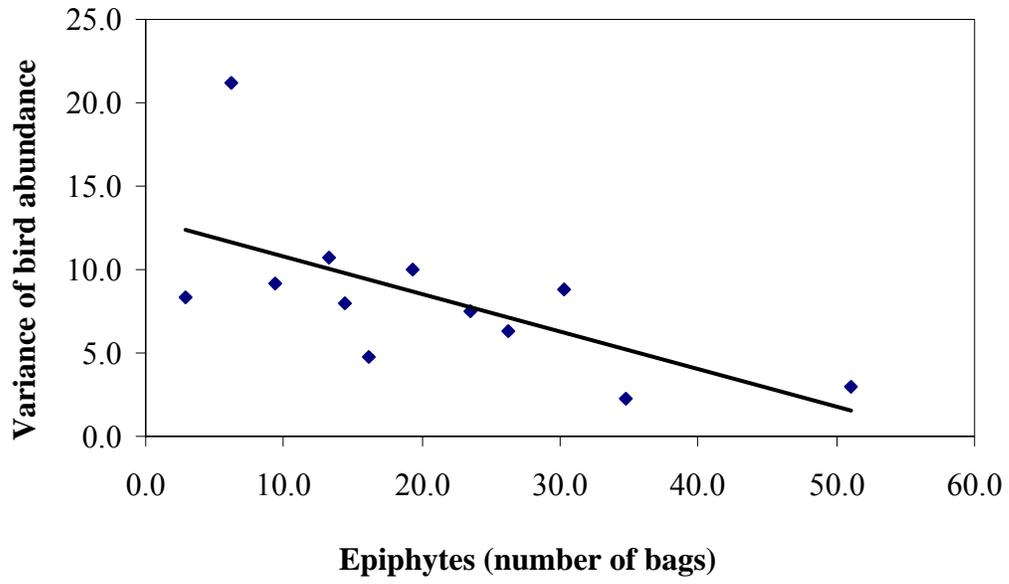


Figure 4-9. Regression analysis between the variance (every five points) and epiphyte biomass in Guabún and Fundo San Martín forests, southern Chile.

CHAPTER 5
CONCLUSIONS: LINKING EPIPHYTES, INVERTEBRATES, AND BIRDS IN THE
CANOPY OF CHILEAN RAINFORESTS: THEORETICAL ASPECTS AND THE VALUE OF
LARGE OLD TREES

Introduction

In this chapter, I summarize the general conclusions that link the large trees with the epiphytes, invertebrates and birds in the canopy of Chilean temperate rainforests. First, I presented current thinking about how structure, species composition, and ecological functions can be viewed as connected attributes of ecosystems, whose integrity, dynamics, and specific characteristics may, with further understanding, be used to better manage and protect biodiversity. While this conceptual framework, presented by Franklin et al. (1981) and Noss (1990) during the rise of conservation biology as a discipline has not yet coalesced into a theory, research that could contribute to potentially formalizing this framework into a theory is ongoing in many fields (such as ecosystem, community and food web ecology; Chapter 1). To make operative a theory requires (among other things; Pickett et al. 2007): i) testing its major causal hypotheses (linkages among biodiversity and ecosystem functions), ii) building the conceptual content to facilitate explanation of its fundamental precepts (in this case, links between structure, composition and function) in meaningful ways, iii) production of exemplars (case studies) that demonstrate conceptual and empirical frameworks for particular systems, and iv) generalization. My goal with this dissertation has been to contribute in all four of these areas, but primarily in the third. In this dissertation I evaluated the links that exist between compositional, structural, and functional ecosystem attributes. In chapters 2-4, I have presented evidence that large trees of long-lived species represent a physical structure that supports large epiphyte loads including many species that, in turn, support diverse above ground faunas (invertebrates and birds, composition). Several studies provide evidence that birds in southern South America temperate

rainforests convey important functions, such as pollination (Smith-Ramírez and Armesto 1993), seed dispersal (Armesto and Rozzi 1989) and predation on herbivorous invertebrates reducing foliar damage (Mazia et al. 2004). Here, I analyzed the links between structure, composition and discussed on potential ecological function described in chapters 2-4 in the context of Franklin et al.'s (1981) original proposition. With this conceptual framework I want to go toward a theory of Ecosystem Attributes, and I will discuss its application to understanding and managing biodiversity. I will do this by presenting a synthetic hypothesis that highlights the fundamental and pervasive effects of large emergent canopy trees of old age in forest ecosystems.

Significant Ecological Functions of Canopy Epiphytes

One hypothesis that remains to be explored is that a rich epiphyte layer contributes more than a poor epiphyte layer to soil formation, decomposition, photosynthesis and carbon sequestration, primary production, rainfall capture and transpiration, nutrient capture, nutrient fixation and habitat creation (Franklin et al. 1981, Benzing 1990, reviews in Benzing 1995, 2004, Nadkarni and Lowman 1995, Reynolds and Hunter 2004, Fonte and Schowalter 2004, Cruz-Angón et al. 2005). We are beginning to describe many of these functions, mainly for tropical canopies, but they remain little-known for the canopy of south-temperate rainforest. Tejo et al. (in preparation) showed that arboreal soils in Chiloé forests presented similar physical features, mineralization and nitrification rates as the organic layer of the forest floor soil. Therefore, arboreal soil may represent a relevant source of nutrients to the forest ecosystem usually neglected in nutrient analysis for these forests (Pérez et al. 2005). Additionally, Manuschevich et al. (in preparation) showed that epiphytes accumulate large amounts of litter biomass from host trees, where a rhizomorph fungus of the genus *Marasmius* tightly binds dead leaves falling from the host tree, incorporating them into the arboreal soil of the epiphytic layer. In my study sites, arboreal soil retains a high amount of water: up to 350 liters in each tree with epiphytes (Chapter

2). Moreover, in Chiloé forests, the evergreen foliage and branches of the canopy, including epiphytes, intercept over 50% of rainfall (Díaz et al. 2007). Epiphytes in the canopy of coastal forests of south-central Chile are also known to enhance moisture in the forest soil by contributing to water dripping and stemflow from fog interception, which often includes the release of nutrients from the fog (Weathers et al. 2000, Woda et al. 2006, del Val et al. 2006). In fact, measurements of nutrient inputs from stem flow in a southern Chilean forest by Oyarzún et al. (1998) showed high flows of nitrogen from the forest canopy to the ground layer, probably coming from the fog. Finally, preliminary assays of Carmona et al. (unpublished data) found potential N fixation in *Pseudocyphellaria* lichens obtained from the tree canopy (Chapter 2). In summary, ongoing and previous studies suggest that large trees with a well-developed epiphyte layer can be important in the water cycle and in the nutrient supply to the forest ecosystem (Fig 5-1). Work in other forest ecosystems further document these and other functions of epiphytes (Dawson 1999, Hsu et al. 2002, Benner et al. 2007). One of my future goals is to continue documenting ecological functions in the canopy of Chilean forests for comparison with other, better-studied systems.

How Structure Supports Diversity of Plants and Animals in Chilean Rainforest Canopy: A Summary

With time, rainforest trees grow tall, and tend to accumulate epiphytic material (Benzing 2004, Nadkarni et al. 2004b). Similarly, in my study sites, large, emergent *E. cordifolia* trees accumulate epiphytes as their diameter increases (Chapter 2). In turn, epiphytes capture litter and produce aerial humus, and when tree basal diameter exceeds 1 m, individual *E. cordifolia* trees are normally colonized by the hemi-epiphytic tree *R. laetevirens*. The presence of this hemi-epiphyte can further increase the amount of epiphytes and organic matter accumulated on the host tree (Peña et al. in preparation).

In Chapter 2, I showed that two species of large emergent trees support a high biomass of epiphytes of over 135 kg dry mass per tree, 70% of which is dead organic matter from litter and epiphyte decomposition, identified as ‘aerial soil’ (Enloe et al. 2006). More than 40 plant species occurred in the epiphyte layer, and 35% of them were restricted to the upper branches (tree crown). Consequently, large trees support massive quantities of live and dead organic matter that represent a structural element largely or completely absent from forests dominated by younger trees (Nadkarni et al. 2004b, Chapter 2, personal observations). In this context, physical structure provided only by large trees (i.e., enhanced surface area of bark suitable for supporting epiphytes) originates a new structural component that increases with time: a thick layer of epiphytes comprised of high live biomass, species richness (plants and lichens), and organic matter. This new layer supports several levels of trophic organization, primary production, detritivores, and consumers, each of them conveying important ecological functions. In other words, the relatively simple structure of large trees supports epiphyte mats that, together, foster further biodiversity and ecological functions (Fig. 5-1).

Epiphytes provided significant habitat and resources for invertebrates (Chapter 3). The epiphytic layer held mostly detritivorous and predatory invertebrates, suggesting that the food chain in the epiphyte layer is based on detritus, not on green tissues (sensu Vanni and DeRuiter 1996; Chapter 2). Manushevich et al. (in preparation) indicated that litter accumulation and epiphytic growth on trees are the main resource supporting the detritivore community. Epiphytes also increase the number of species and the overall abundance of invertebrates (measured as number of individuals or as total biomass) in the tree crown (Chapter 2). Accordingly, epiphytes enhance invertebrate diversity by adding a detritus-dependent community and more herbivorous and predatory individuals and species to the tree crown (Fig. 5-1).

Moreover, forest birds forage more frequently in trees with epiphytes than in trees without epiphytes (Chapter 4). Most canopy birds are insectivores, and the main species in the assemblage were Rayadito, Fio-fío and Picaflor. It is likely, though yet undocumented, that insects supported directly and/or indirectly by epiphytes can supply food resources for canopy birds, thereby increasing their local abundance and activity in the crown (Chapter 4). In addition, the observed pattern of increased bird visitation to single large trees agrees with the enhanced bird abundance observed in forest plots with higher abundance of epiphytes (Chapter 4). These results support the hypothesis that epiphytes sustain population-level processes (numerical responses) that contribute to enhance bird species abundance, not just local activity (Cruz-Angón and Greenberg 2005; Fig. 5-1).

Linking tree-epiphyte structure and composition to the functional role of birds in the canopy

Finally, birds of South American temperate rainforests are well known for their important ecological roles in forest dynamics. Birds are the principal seed dispersers and pollinators of many tree and epiphyte species, in particular the Fio-fío (Armesto and Rozzi 1989, Willson et al. 1996, Armesto et al. 1996, Smith-Ramírez and Armesto 1998, Armesto et al. 2001). Birds are also likely the main insect consumers in the forest canopy, presumably influencing the levels of insect damage to tree foliage (Chapter 4). Studies of VanBael et al. (2003), Marquis and Whelan (1994), and Greenberg et al. (2000) showed that birds prey on invertebrates in the forest foliage, reducing leaf damage in tropical and temperate forest canopies. A similar effect of canopy birds has been documented in *Nothofagus* forests of Argentina (Mazia et al. 2004, Garibaldi et al. 2007), where Fio-fío, Rayadito, Picaflor, Comesebo and Cometocino dominate bird species composition, as in my study sites. Then, I hypothesize that insectivorous birds can reduce canopy leaf damage by insects, although further work is needed to fully characterize this function.

However, it is clear that if epiphytes support bird species richness and abundance in the canopy, then epiphytes can have positive indirect effects on the maintenance of foliage via insectivorous birds (Fig. 5-1). It is likely that epiphytes can assist other important ecological functions in the forest canopy, such as pollination and seed dispersal (Willson et al. 1996, Chapter 4, fig. 5-1).

Toward an Integrative Theory Linking Composition, Structure and Function of Ecosystems

The framework that links composition, structure and function, provides an opportunity for conceptual integration in ecology and conservation biology. As an example, two concepts widely used in ecology are ecosystem engineers and keystone species (Jones et al. 1994, Power et al. 1996). These two concepts can be directly linked within this framework proposed here.

Ecosystem engineers are taxonomic species that create physical structures or alter resource flux affecting other species. Keystone species, on the other hand, have disproportionate direct effects on population and community dynamics with respect to their own abundance (Power et al. 1996). For instance, keystone predators can positively or negatively affect ecosystem engineers, thereby altering structure and biodiversity. In the classic example of Estes et al. (1998), sea otters are keystone predators that consume herbivores, i.e., sea urchins, and this favors the development of kelp forest whose structure supports a diverse marine community that can disappear in the absence of the keystone predator. In the previous example, the autogenic ecosystem engineer is the kelp forest (Hastings et al. 2006) creating ecological structure that supports a highly diverse living community (structure support composition); and it is the keystone predator that favors the ecosystem engineer (kelp; i.e., composition supports structure). Another active area of integration linking composition and function centers on the debate about how diversity affects ecosystem stability (Naeem and Li 1997, McCann 2000). Much work is providing evidence of positive links in both directions (function supporting species, species supporting functions;

Mooney et al. 1996). However, structural components of ecosystems few times have been included (Badano and Marquet 2008). My work has focused on the dominant autogenic engineers in forest ecosystems, i.e., large, old canopy trees, whose physical structure supports epiphytes, invertebrates and birds. In my study sites, epiphytes may support water and nutrient inputs, while birds can support pollination, seed dispersion and reduce foliar damage by predated on herbivorous. Then, the structure provided by an ecosystem engineer such as large old trees support species and functions at various levels. A young tree may not have the same ecological function as an adult tree because structure changes and new mass is created over time, as shown in this dissertation, and its effect on provide habitat and resources to other species increase over time (Chapter 2). The role of a single species changes during its development in the way it creates structure. Examples of this abound in the literature conforming the population-community paradigm, but are largely isolated from the ecosystem function literature. For example, competition studies have shown how structures such as a snags and live nesting trees are limiting bird population size and species richness (Newton 1994, Díaz et al. 2005, Blanc and Walters 2008), providing opportunities for linking structure and composition to ecosystem functions. Ecosystem functions of cavity nesting species, however, have not been considered in any comprehensive manner. Woodpeckers are known to carry fungi that can spread in the snags and trees they feed and nest, thereby influencing snag decay rates, which in turn favors the creation of more nesting sites for birds (Jackson and Jackson 2004). Woodpecker predation on boring beetles may limit outbreaks temporally and spatially (McCambridge and Knight 1972) thereby influencing tree demography and stand structure. I argue that analytical operation within a purely population and community paradigm limits the comprehensive understanding of ecosystems, and thus impedes the maturation of both conservation and ecological theory (Pickett

et al. 2007). Greater focus on building an integrated view, such as the proposed Ecosystem Attribute approach, is not a great step beyond what is currently thought, but will greatly speed attainment of understanding. In the following section I present an hypothesis, which is in part the result of this dissertation work and attempts to integrate composition, structure and function with life history attributes. In this hypothesis I attempt to foster thinking about ecosystem attribute theory in general, and provide a case study in the context of this theoretical background.

The Treebeard Hypothesis

Large old trees are a characteristic element of undisturbed natural forests worldwide. Over evolutionary history, trees have grown as tall as incident physical disturbance frequency and mechanical constraints will allow (Koch et al. 2004, Van Pelt and Sillett 2008). Trees become old, and fall in spatio-temporal patterns reflecting local disturbance regimes. Therefore, the stages of large live tree, senescent tree, snag and log have been part of tree life histories since the first trees appeared on land (some 370 my ago; Dilcher et al. 2004). Forest organisms such as bark beetles or forest birds evolved in the presence of large old trees, whose dominance and longevity influenced forest dynamics in tune to disturbance regimes. Large old trees are characteristic elements of old-growth forests described by explorers, such as Alfred R. Wallace's descriptions of old world tropical areas, and Charles Darwin's description of Chiloé Island as blanketed from coast to coast by a dense, impenetrable forest, dominated by large trees (Wallace 1878, Willson and Armesto 1996).

Here, I propose that large old trees support and provide services to the whole forest ecosystem and should be considered as a uniquely important structural elements, contributing disproportionately, relative to population size, to forest integrity and functional resilience. I am calling this hypothesis the Treebeard Hypothesis as a metaphor invoking an old grey-bearded and wise being (tree) that supports the forest community in ways no younger trees possibly can,

in part, because they add structures not provided by younger trees, and because they take up relatively few resources for themselves relative to the resources they indirectly garner for the forest ecosystem. Accordingly, the hypothesis is that large trees offer and support ecological functions that benefit the entire ecosystem in a disproportionate magnitude relative to what the old tree requires for its own maintenance.

Tree Life Cycle

In forest ecosystems many tree species require logs or coarse woody debris as regeneration microsites (Franklin et al. 1981, Lusk 1995, Christie and Armesto 2003). These sites are legacies from previous trees that became old, died and fell on the forest soil, perhaps opening a canopy gap, and then favoring tree regeneration by increasing light and nutrient availability (Franklin et al. 1981, Lindenmayer and Franklin 2002). Coastal forests of South America often follow this regeneration cycle. Importantly, many seeds of canopy trees require logs or coarse woody debris clumps to germinate and support regeneration under canopy gaps (Christie and Armesto 2003) or in large open disturbed areas (Papic 2000). The requirement of ‘nurse logs’ is absolute in many areas where the water table can be as high as to flood the rainforest floor during the wet season or after disturbance, because seeds will not germinate in standing water (Papic 2000). Growing trees require nutrients, water and light, which are supplied by the woody debris. Forest soil is formed by litter accumulation and decaying coarse woody debris from the previous generations of trees. Consequently, growing seedlings, saplings and young trees are consuming resources provided by older, ancestral trees (Fig. 5-3). In contrast, services and resources provided by young trees to the forests (for instance litter flux, fog and rain water capture, or nitrogen fixation) are limited because these fluxes increase geometrically with tree size and growing trees have high demands for nutrients and carbon (Fig. 5-3). With time, trees increase litter return to the forest floor, enhance soil formation, provide micro- and macrohabitats for wildlife, supply fruits

to seed dispersers, and their crowns capture more water from rain and fog to moderate hydrological conditions in the forest during wet and dry periods. Year after year trees grow, developing an ever-larger epiphyte layer that enhances many of these services.

Because services increase geometrically with tree size and/or age, at some time, compositional and functional attributes of the tree raise non-linearly. Aerial litter load supports a detritivore community that releases nutrients to the ecosystem, which fosters greater accumulations of biomass and diversity. In summary, trees create soil, habitats, resources and services and their supply raises with tree age. Older trees that pass a threshold in size may present higher amounts of foliage, supporting many more epiphytes and invertebrates than other trees, providing abundant micro-habitats, and thereby supporting directly and indirectly fauna that is absent from forests lacking old trees (Nadkarni et al. 2004b, Díaz et al. 2005, Chapter 2, 3 and 4). For mature trees, results from Chapter 2 showed that aerial soil biomass is larger than the biomass of tree foliage, and green tissues of epiphytes have a biomass equal or larger to that of the tree foliage. This means tree foliage is not necessarily the main reservoir of nutrients, or the major carbon fixing component in the tree, because epiphytes already have equal or greater biomass than the tree foliage. Large old trees require nutrients from the ground, but they also provide nutrients from rain and fog water capture by epiphytes (via N fixation, litter production, interception, and storage, Weathers 1999, Sillet and Van Pelt 2007, Benner et al 2007, Kolher et al. 2007). Finally, old trees may require fewer resources from the ecosystem than what they provide, including themselves and the epiphyte community they support. As trees become old, wood rots and releases nutrients that support detritivores, trees start to lose branches that become transformed into soil detritus, foliage biomass declines while secondary growth continues,

producing an imbalance between energy demand and carbon fixation. Because of these imbalances, trees collapse and finally fall or die standing (Van Pelt and Sillett 2008).

Because of the biodiversity and processes they support, and because they tend to distribute nutrients in the form of dead material, I hypothesize that old trees at some point in their life cycle deliver more resources and services to the ecosystem than they retrieve. Snags and logs only provide nutrients to the ecosystem, without taking up any (Fig. 5-3). Therefore, at this point the role of trees switches from resource users and competitors to facilitators, supporting regeneration (Fig. 5-4). The value of snags and logs as structures that support diversity and functional attributes of forests has for long been recognized (Franklin 1988, Lusk 1995, Kohm and Franklin 1997). The treebeard hypothesis takes one large step backward in the tree life cycle and shines a searchlight on the mature living tree, particularly in those forest systems where epiphytes are abundant. My work suggests that a forest without large mature trees is barely 'half a forest' in terms of diversity and functional attribute that are lost with their removal. In summary, this hypothesis links tree life history with structural features, diversity and ecosystem functions, resulting from the transition of a tree from competitor to facilitator with age.

Implications for Conservation

Old trees have been a permanent structure of forest ecosystems for the last 370 my, and this study emphasizes the role of old trees in supporting biodiversity and ecological functions. Conservation of old trees is fundamental for sustaining forest biodiversity, tree regeneration dynamics and ecosystem resilience. Based on my results, I hypothesize that the loss of older trees from managed forests will lead to greater susceptibility to shocks and disturbances such as herbivore outbreaks, drought and flooding because of: 1) reductions of bird activity and abundances necessary to prevent insects outbreaks (Holling 1988), and 2) reduction of water regulation service (less effect of water logging on tree regeneration in wet periods and greater

water supply through fog capture in dry periods) (Díaz et al. 2007). Removal of large trees also represents a serious shock to forest ecosystems because of 3) depletion of the incident nutrient pool and its renewal. In this context, managed forests become more similar to agricultural systems (forestry plantations), dominated solely by hungry, resource consumptive young trees, requiring fertilization, chemical pest control, and exhibiting magnified effects of both soil drought and waterlogging on tree survival. Therefore, in contrast to some forest management approaches, a minimum density of old trees should be maintained and some younger trees should be left to age. Areas of old-growth forest should be preserved to maintain the whole potential of forest ecosystems (Kohm and Franklin 1997). In contrast, current management practices promoted by the Chilean government are based on the simplification of forest stands to single cohorts, harvested periodically (even-aged management). Under this scenario, long-term forest management will degrade tree species composition, resilience, and the nutrient pool will be depleted.

Future Research

The Treebeard hypothesis can be tested most effectively in two ways: by comparing nutrient requirement and intake rates per unit of biomass versus soil nutrient supply in trees of different age under similar conditions, and comparing the services provided by trees (such as herbivore damage control by birds) in old-growth versus managed forests, with different densities of old trees (standardized by biomass). I predict that in plots where large trees have been partially or totally removed we should detect significant species loss, reduced rates of biomass nutrient accumulation, nutrient pool depletion because of tree uptake, and less resilience to insect outbreaks or climatic changes compared to control plots. Additional questions generated by this study include: 1) what is the ecological importance of dead organic matter accumulated in forests above (arboreal soils) and on the ground? (Vanni and DeRuiter 1996, Butler et al. 2008);

2) Does aerial organic matter support significant canopy predators via a detritus-based food web? (Polis and Hurd 1996); 3) How important are the invertebrates dependent on detritus as food for vertebrates? (Vanni and DeRuiter 1996, Polis and Strong 1996); 4) Have detritus-subsidized predators such as centipedes or spiders any significant effect on herbivory? (sensu Polis and Hurd 1996); 5) Canopy epiphytes hold significant amounts of water in the tree crown; how important are old trees with high epiphyte loads in regulating ecosystem water cycles? (Dawson 1999); 6) How does rain interception and fog capture cause differences in tree regeneration in successional and old-growth forests? (Dawson 1999, Díaz et al. 2007); 7) How tolerant are forests with old trees vs. forests without old trees to disturbances such as herbivore outbreaks or drought? (Holling 1988, Ayres and Lombardero 2000).

While large trees several centuries old have been dominant elements in the canopy of world forests for millions of years, presently most managed forests and forestry plantations are younger than 100 years old, and therefore are dependent on fertilization, insecticides, and intensive management (Kohm and Franklin 1997). The productivity of regenerating forests may depend on soil nutrients provided by earlier generations of old trees, and it can be argued that present-day management by removing old forests may be depleting the potential for future growth. Forest management, accordingly, should try to maintain forest structure to mitigate the cost of growing new trees. Conserving and promoting the persistence of old trees can foster the continued development of new ones.

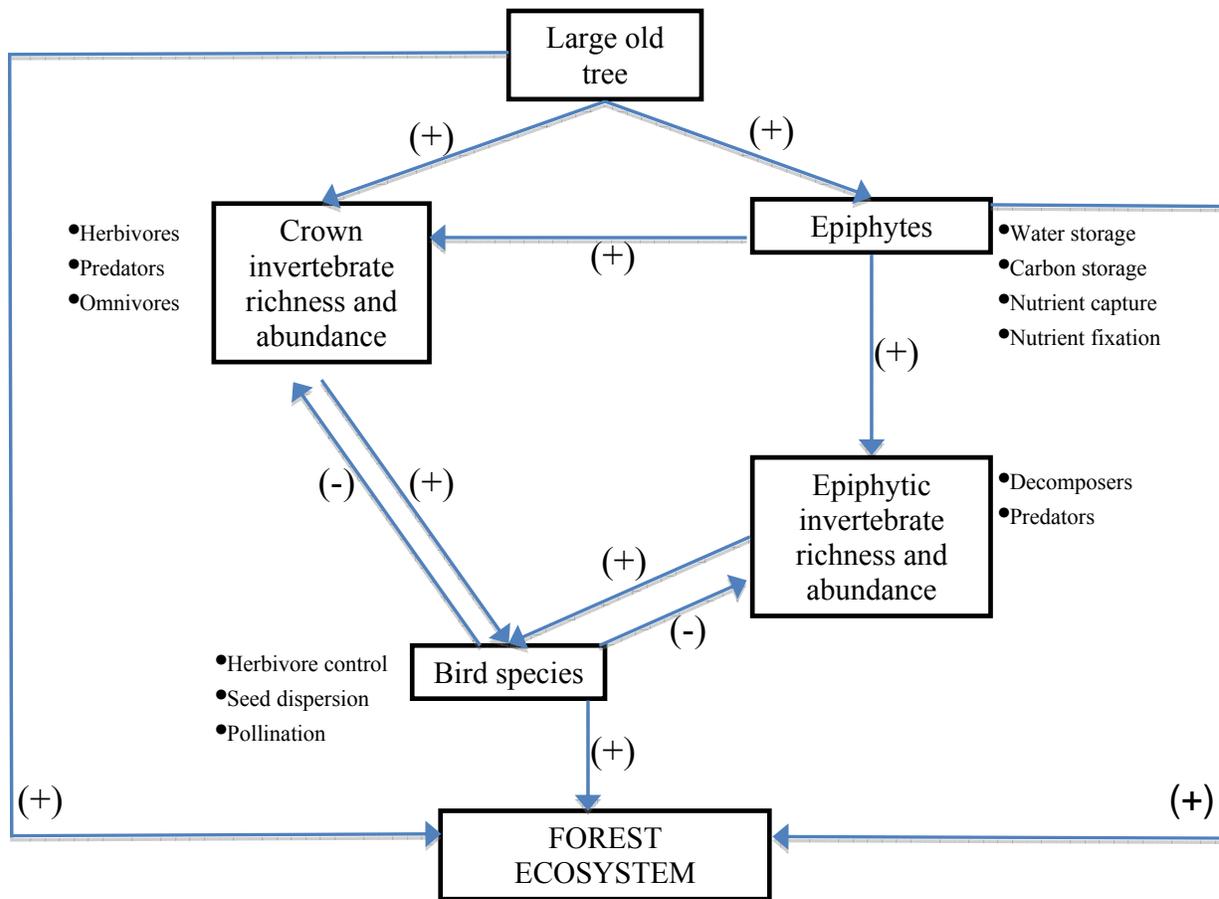


Figure 5-1. Multiple links among structure, diversity and functions in the canopy of a temperate rainforests in Chiloé, southern Chile. The structure provided by large, old trees has a positive effect (+) on species richness and abundance of epiphytes and crown invertebrates, thus supporting their main ecosystem functions (described beside each box). Epiphytes have positive effects on invertebrates that are the food of insectivorous birds. Birds in turn have negative effects on the invertebrates that they feed on. Such links among structure and composition support the functions each group conducts. As a result, large old trees have positive effects on forest ecosystems by supporting epiphytes, invertebrates and birds. Net effects of invertebrates were not included.

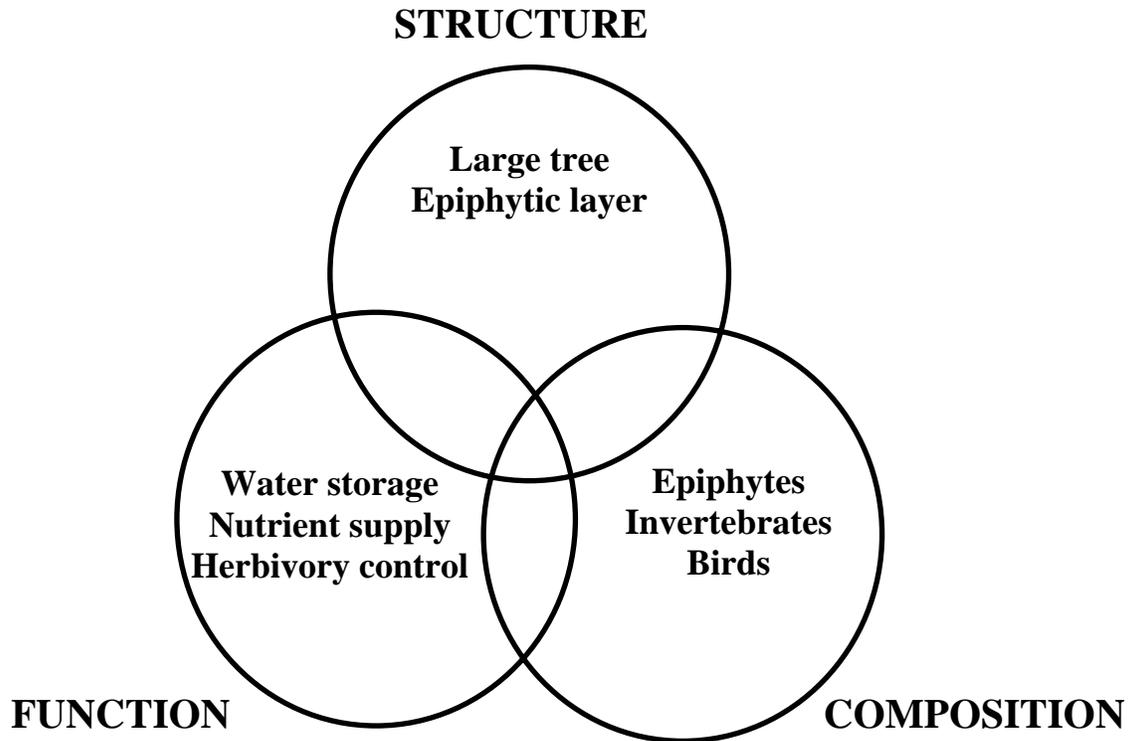


Figure 5-2. Relationships among structure, compositional diversity and functions in temperate rainforests. Trees support epiphytes, invertebrates and birds, which provide important ecological functions.

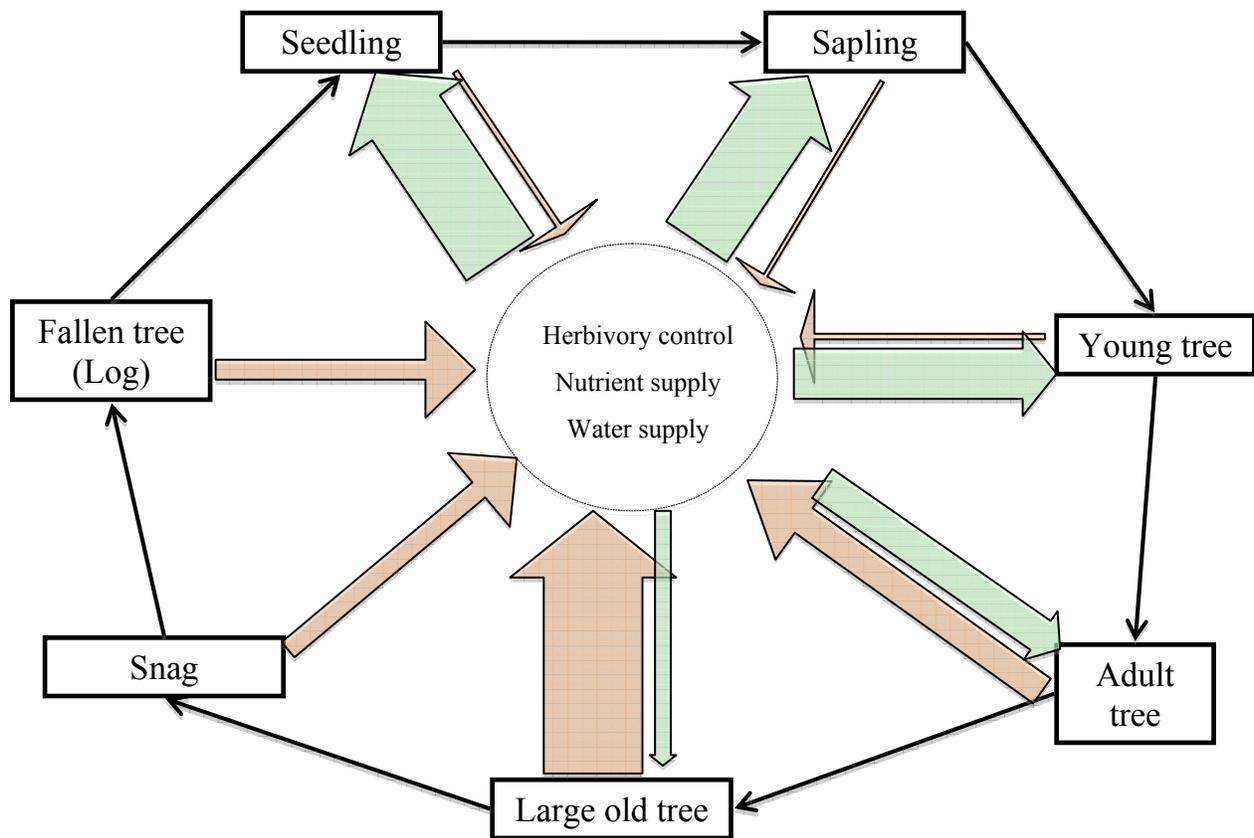


Figure 5-3. Complete life cycle of a tree, from seedling establishment (on fallen logs), to old age and after death as snag, and fallen tree. The central circle presents some specific functions for the forest ecosystem. Brown arrows indicate the level at which trees in each life cycle stage support these functions. Green arrows indicate the degree to which the functions support trees in each stage of the life cycle. In this scheme, young trees depend strongly on ecosystem functions, but they contribute little to support these functions. In contrast, large old trees insure that these functions are fully operational, but depend less on these functions that they contribute to support. There must be a threshold age or size at which trees change from being supported by whole ecosystem functions to support these functions. One value of large old trees therefore is to indirectly support younger trees by enhancing biodiversity that conveys ecosystem functions supporting tree regeneration and growth. Removing large trees from the ecosystem implies the removal of support systems for younger trees that have been crafted over evolutionary time.

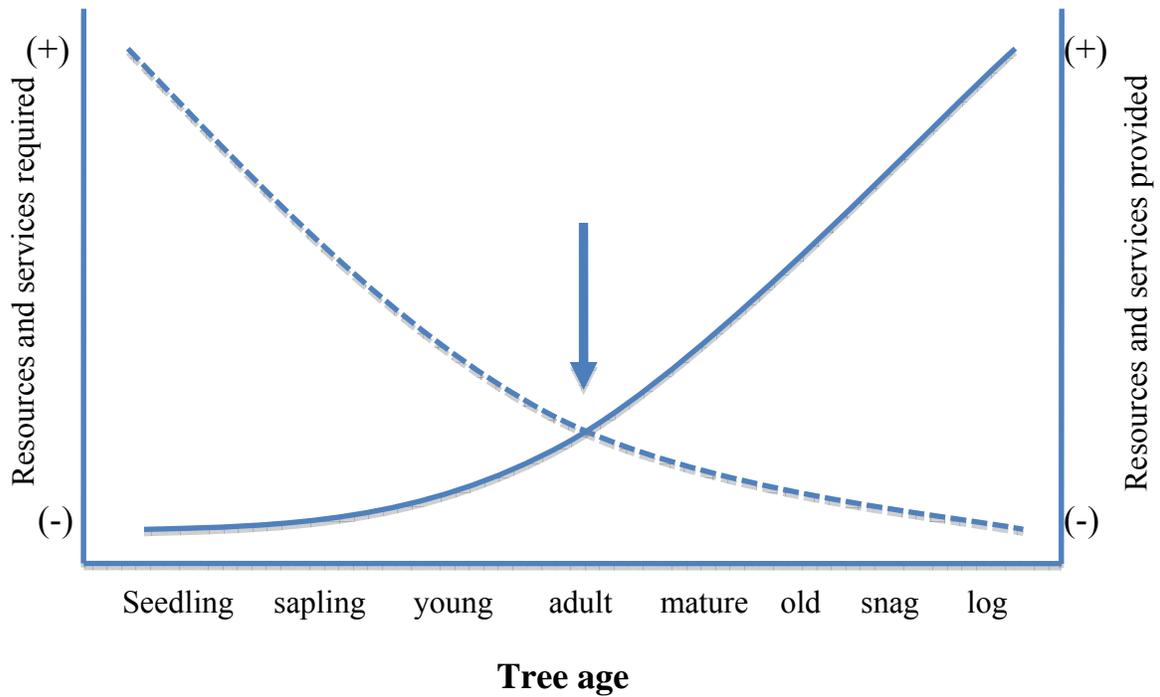


Figure 5-4. Treebeard Hypothesis. The horizontal axis represents the age (stage) in the life cycle of a tree, the first vertical axis represents resources and services required by the tree (dotted line) per unit of biomass, while the second vertical axis represents resources and services to the ecosystem provided directly or indirectly by the tree per unit biomass (solid line). Young trees require more resources than they provide, but as trees age the ecosystem services are greater than their requirements. The “epiphytic threshold”, when trees accumulate epiphyte biomass and diversity exponentially, is indicated by the arrow.

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BIOGRAPHICAL SKETCH

I was born in San Bernardo, a small town near Santiago de Chile, in the Austral Spring (November 1971). I grew up in a modest family, listening to stories about the countryside life, because my parents migrated to the city in the late 1960s. I remember stories about hunting, harvesting and even myths from my parents, grandparents and their brothers. I liked these stories because since I was child, I have been interested in natural history, ecology and conservation biology. I grew up in Santiago, looking at the Andes and the hills I wanted explore some day, as an adult.

Later on, an important time in my life was as a secondary school student (1989), when I participated in a youth scientific club organized by the National Museum of Natural History (Chile). There I met Juan Carlos Torres-Mura, a Chilean ornithologist (M.Sc.), who, in addition to Pablo Espejo, an herpetologist of the Santiago Zoological Garden (M.Sc.), assisted me in conducting a preliminary study aimed at comparing the terrestrial vertebrate richness among three sites at Río Clarillo National Reserve, central Chile, differing in accessibility to visitors. With this study I finally explored the mountains nearby Santiago, and participated in the XXI Chilean Annual Youth Scientific Fair (a scientific meeting for primary and secondary school students) organized by the Chilean National Museum of Natural History. After high school I worked in the herpetological exposition "Niri Vilcún", property of Pablo Espejo (mentioned above) and MSc. José Navarro; in the Zoological Gardens of Santiago Metropolitan Park. There, I learned about Chilean herpetology, and also learned to recognize the different Chilean reptile species. In 1991, I began my undergraduate studies in biology at the University of Chile, exploring nature. Then, a very important part of my academic life was when I met Dr. Juan Armesto, who has been my friend and formally or informally my professor, giving me all the opportunities of continuing a scientific career, contacting me with other professors from foreign

universities, such as Dr. Katie Sieving, my friend and advisor at University of Florida. My economic situation has made me looking for job since the first years of my undergraduate studies, and without the comprehension and the support from the grants of Dr. Armesto I couldn't continue in the scientific career. Dr. Juan J. Armesto is also the president of Senda Darwin Foundation (FSD), a non governmental organization focused in conduct scientific research in the temperate rainforest of southern Chile, and link the scientific background with the education and practical application in local communities of southern Chile. I have been working in his laboratory and in FSD since 1995, during the final year of my undergraduate studies. I studied forest seed dispersal, seed predation, forest bird habitat relationship and also participated in scientific meetings and activities of environmental education. Also, between 1996 and 1999 I developed my master's degree at the University of Chile where he was my advisor. After that I started to study English, and I applied to a Fulbright fellowship to continue my studies in the US.

With the support of Fulbright I started my Ph.D. in the department of Wildlife Ecology and Conservation, advised by Dr. Sieving who has been a model of professor for me, for her integrity, professionalism, charisma and good will. With her advice, I started to think in study the forest canopy in Chile, her advices were key in I got funding, and now I am concluding this program and this part of my life, with my major gratitude to University of Florida, to Fulbright program, to Canon National Parks Science Scholars Program, and especially to my advisor Katie E. Sieving, all the committee members, professors, workers and friends at University of Florida.