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# Old-Growth Forests

Function, Fate and Value



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# Chapter 16

## Old-Growth Temperate Rainforests of South America: Conservation, Plant–Animal Interactions, and Baseline Biogeochemical Processes

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### 16.1 Introduction

Defining old-growth forests (Chap. 2 by Wirth et al., this volume) must consider both technical and cultural issues. For instance, the term ‘old-growth forest’ was entirely absent from the most recent survey of Chilean vegetation conducted by the National Forest Service (CONAF-CONAMA-BIRF 1999), where the forestry-related term ‘adult’ (synonym of tall, >15 m height) forest was used instead to indicate a harvestable unit of land. Moreover, the deriding term ‘over-mature’ is sometimes used to refer to old-growth stands with a predominance of large, non-harvestable trees (Chap. 2 by Wirth et al., this volume). This bias towards a tree-centred, commercial view of forests suggests that, culturally, we remain unaware of the ecological differences among successional forest stages and of the specific attributes of old-growth forests. Greater public appreciation of the ecological, social and economic values of old-growth forests will depend on our ability to communicate scientific understanding of these diminishing ecosystems.

Based on current knowledge of temperate forests in southwestern South America (e.g. Donoso 1993; Armesto et al. 1996a; Veblen et al. 1996; Neira et al. 2002), we propose here a definition of old-growth forest that combines both structural and compositional (based on species and functional groups) properties of forest stands. The old-growth condition is usually restricted to ecosystems that have not been subjected to recurrent and massive human impact (Chap. 2 by Wirth et al., this volume). Considering the entire range of human impacts, from changes in the concentration of elements in the atmosphere to the extraction of individual trees, it is however unlikely that any forest is completely free of human impact. Therefore, we will consider as ‘old-growth’ any tract of natural forest with a minimum extent so as to integrate a core area where edge effects are minimal, and which maintains a complex vertical structure dominated by large (old) shade-tolerant trees with emergent pioneers, with a species composition that has not been significantly modified (by recurrent human impact or other large disturbance at least during the past two centuries). Structural and compositional attributes are taken as

indicators of the continuity of biological interactions that sustain biodiversity and ecosystem functions within the ecosystem.

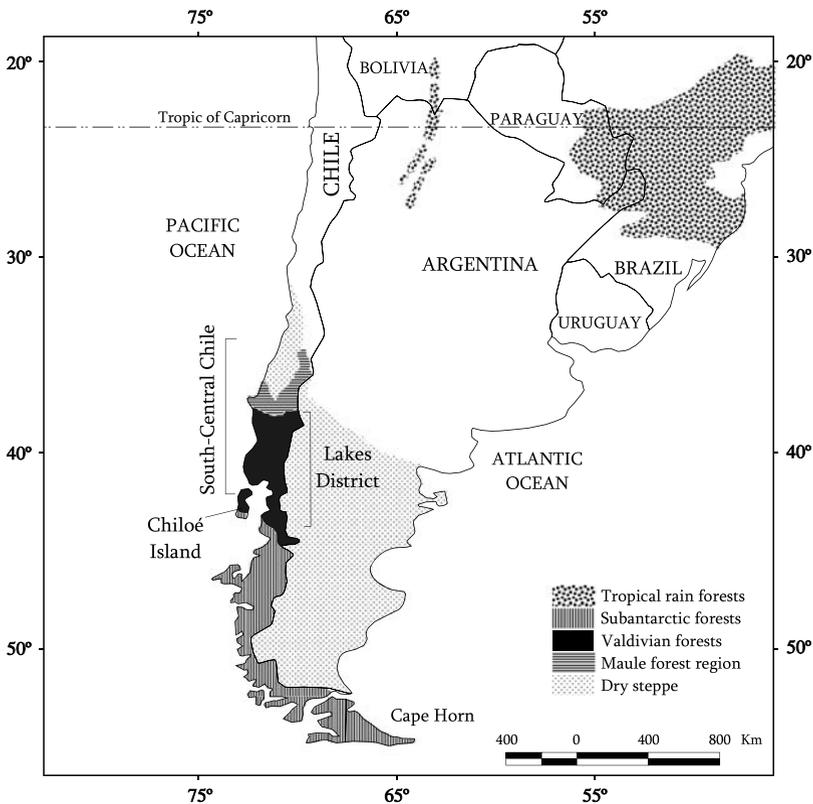
Andean and coastal forests in Chile differ greatly in their probabilities of ever reaching the old-growth stage because of the prevalence of stand-devastating events in Andean forests (Veblen and Ashton 1978; Veblen et al. 1981; Armesto et al. 1996a). Volcanism, earthquake-caused landslides and mudflows have historically been present in Andean forests, so that few areas can recover fast enough for pioneer trees to reach their maximum longevity and eventually be excluded by slow growing, shade-tolerant tree species (Veblen et al. 1996). In turn, coastal forests at comparable elevations differ greatly in tree species composition, as fast-growing, relatively shade-intolerant pioneers may be completely lacking and shade-tolerant species dominate. This is exemplified by the absence of *Nothofagus* trees from most coastal forests at low elevations (<400 m), between 41° and 43° S (Veblen et al. 1981, 1996; Armesto and Figueroa 1987; Armesto et al. 1996a). The canopy of such forests is dominated by shade-tolerant trees such as *Aextoxicon punctatum*, *Laureliopsis philippiana*, *Caldecluvia paniculata*, and several Myrtaceae species (Armesto et al. 1996a). In some cases the semi-tolerant *Eucryphia cordifolia* is a dominant canopy tree (Gutiérrez et al. 2008). Further south and at higher elevations (>400 m) on the coastal range, dominance is shared between the shade-tolerant *Podocarpus nubigena* and the semi-tolerant *Nothofagus nitida* (Innes 1992; Gutiérrez et al. 2004). Accordingly, the old-growth condition in coastal forests is indicated by the frequent presence of large, canopy emergent trees together with patchy regeneration, intense gap-phase dynamics, and a tree species composition completely or largely lacking pioneers (Armesto et al. 1996a; Gutiérrez et al. 2004). The presence of numerous trees over 200 years old characterises stands with an old-growth structure and composition (Aravena et al. 2002). In the literature, the lack of regeneration of shade-intolerant pioneers is often considered a characteristic of late-successional stands (Oliver and Larson 1996). However, in Chilean old-growth stands in coastal areas, juveniles of light-demanding species may form dense patches under canopy openings known as 'sapling banks' (Aravena et al. 2002).

Using this framework, we provide here an overview of the ecological knowledge of temperate old-growth forests in southwestern South America, particularly evergreen rainforests in south-central Chile. We offer a characterisation of these ecosystems focused on three main questions: (1) what is their current status and what are the major threats, and prospects for conservation?; (2) what is the importance of old-growth forest structure and species composition for plant–animal mutualistic interactions (e.g. pollination, seed dispersal), and how do these interactions in turn shape and maintain the structure and function of temperate old-growth forests?; and (3) what are the main features characterising nutrient fluxes in southern temperate forests, and how are they expected to change in response to management? We discuss how old-growth temperate forests functionally resemble or differ from forests that have been disrupted by logging and air-pollution in Chile or in the northern hemisphere. Our analysis identifies key aspects of forest functioning that may have management and policy implications, and

stimulates further research to understand the ecological and social relevance of old-growth forests.

### 16.2 Conservation Status, Values and Threats

Along the southwestern margin of South America (Fig. 16.1), a narrow band of temperate rainforests, reaching 55° S, is one of the last wilderness frontiers on the planet (Mittermeier et al. 2003), and the largest area of temperate forests remaining



**Fig. 16.1** Map of temperate rainforests of southern South America, including deciduous-dominated forests in the Maule region (*horizontal stippling*), and evergreen Valdivian (*black shading*) and Sub Antarctic (*dark grey*) rain forests; the eastern limit of rainforests is the Andes and the dry steppe border in Argentina, and the northern limit is the Mediterranean-climate region in south-central Chile. Southern temperate rainforests are isolated from tropical rainforests (in southern Brazil and in the Andean Yungas of southern Bolivia and north-western Argentina) by extensive semiarid lands and deserts (*light shading* in the map)

in the southern hemisphere. Floristic richness of these rainforests is the highest among evergreen temperate rainforests worldwide (Arroyo et al. 1996). Temperate rainforests of southern South America are inhabited by a host of endemic species, including many monotypic genera of plants and animals (Armesto et al. 1996a, 1998), with close relatives in the southern continents (Australia, New Zealand) and the Sub Antarctic islands (Villagrán and Hinojosa 1997). The long history of geographic isolation from other rainforests within South America (Armesto et al. 1998) enhanced local endemism and the conservation of relict taxa (Hinojosa et al. 2006); at the same time it made this remote “island” of temperate rain forest highly susceptible to land-cover change, species invasions and local species extinction (Armesto et al. 1996a, 2001). The high concentration of endemism in a relatively narrow territory has given this region a unique global conservation value (Olson and Dinerstein 1998; Myers et al. 2000).

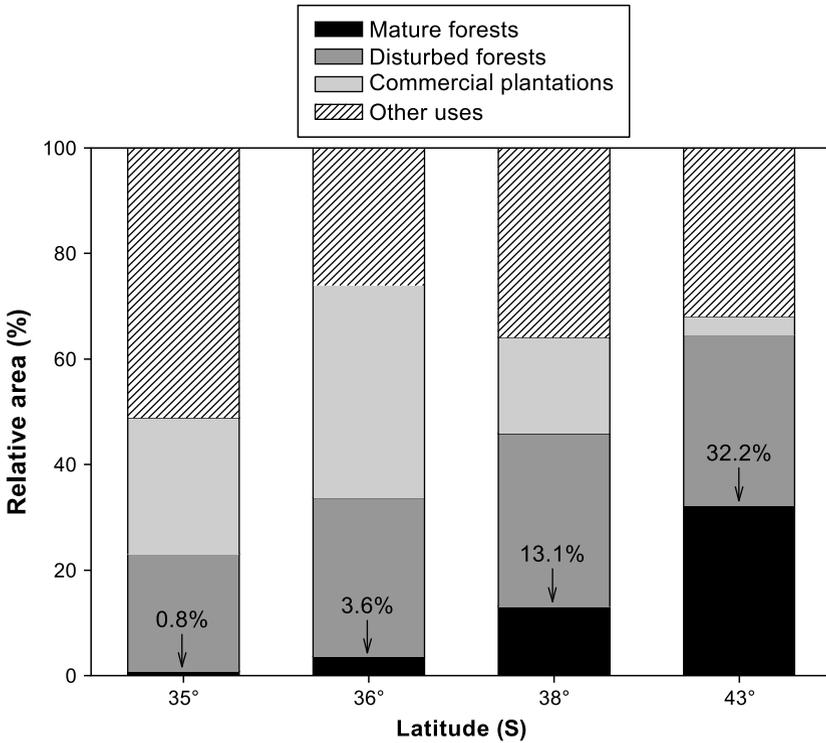
### 16.2.1 Main Threats

Today, significant remnants of old-growth forest continue to disappear in southern Chile despite compelling arguments for their protection (Armesto et al. 1998; Smith-Ramírez et al. 2005a). During the last decades of the twentieth century, rapid expansion of monoculture-based forestry (Lara and Veblen 1993; Armesto et al. 2001), new access roads, and land-use changes associated with agriculture, have all led to increasing loss and fragmentation of the native-forest cover in southern South America (Echeverría et al. 2007). South-central Chile has been the target of much agricultural, industrial and urban development since the nineteenth century. Consequently, the proportion of old forest cover left at different latitudes along the western margin of South America (Fig. 16.2) varies from as little as 1% at 35° S, in the transition between the Mediterranean and temperate climate regions (Maule Region), to about 32% in the Valdivian rain forest region, at 40° S.

Substantial tracts of intact old-growth forests at low elevations are still found on the Coastal Range of the Lake District (39–42° S), particularly west of the city of Osorno and on Chiloé Island (Smith-Ramírez 2004). These largely pristine areas occupying the oceanic slopes of the coastal mountains have been estimated at roughly 500,000 ha (Smith-Ramírez 2004). Old-growth ecosystems are entirely lacking in the central valley between the coastal and Andean ranges, where human settlements and industrial activities are concentrated (Armesto et al. 1998). Some types of old-growth forest have nearly disappeared, including the last stands of the ancient *Nothofagus alessandrii* on the coastal range of Maule Region (Bustamante and Castor 1998), and the last few remnants of *Peumus boldus* and swamp forests in the Valdivian region (Smith-Ramírez et al. 2005a).

The three major continuing trends leading to the loss of remnant old-growth forest cover in southwestern South America (Fig. 16.4) are:

(1) Expansion of plantation-based forestry using exotic tree species (mainly *Pinus radiata* and *Eucalyptus* spp.). This trend, which started in the 1970s in

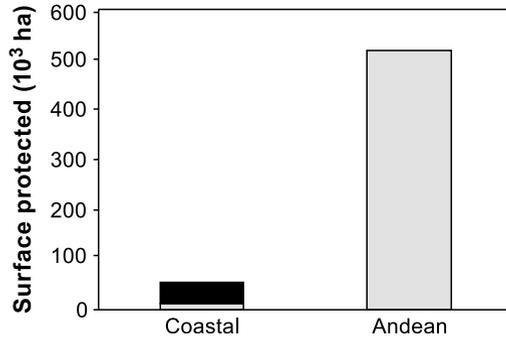


**Fig. 16.2** Different land-cover types present today in each region between Maule (35° S), the northern limit of temperate forests, and Chiloé (43° S) in the southern limit of the Lakes District. Bars represent the originally forested land before human settlement in each administrative region of Chile from north to south along the western margin of South America. The mean latitude of each administrative region is shown on the horizontal axis. Different shading in the bars represents estimates of the area presently covered by old-growth (mature) forest, successional or degraded (disturbed) forest, and forestry plantations of exotic tree species (mainly *Pinus radiata* and *Eucalyptus* sp.). Cover of old-growth forest habitat was inferred by adding the ‘adult forest’ category and stunted timberline forests in the most recent survey of Chilean vegetation CONAF-CONAMA-BIRF (1999), and hence it is likely to be an overestimate. Other uses Farming, grazing pastures and urban settlements

south-central Chile (35–40° S), increased exponentially during the last two decades of the twentieth century, and in the last 10 years has expanded into Chiloé Island and the mainland south of Chiloé (Fig. 16.1). Forestry plantations are likely to continue their expansion in the coming decade at the expense of native forest; first, because several paper mills requiring large volumes of chips for cellulose production have recently entered into operation and, secondly, productivity of existing plantations is likely to decline due to pathogen attack and losses of soil fertility after several rotations (Armesto et al. 2001).

(2) Selective and stand-scale logging and extraction of timber, firewood and woodchips from native trees (Fig. 16.4). The woodchip industry has fluctuated

**Fig. 16.3** Extension of protected areas (thousands of hectares) containing old-growth forest in the Chilean Coastal Range and Andean public Parks and Reserves at the heart of the Valdivian forest region (40–43° S). A single National Park on Chiloé Island represents much of the government protected land in the coastal range (dark shading)



in recent decades due to international market prices (Informe País 2002), but harvesting large trees for woodchips remains a significant driver, especially in accessible rural areas. On the other hand, firewood remains the main source of energy for rural and urban settlements in south-central Chile and stands out as the main degrading activity for native forests (Informe País 2002). In Chiloé Island, a major source of firewood is the tree *Tepualia stipularis* (Myrtaceae), which has excellent caloric properties (Hall and White 1998). However, because of its prostrate growth habit and numerous stems, which serve as habitat for a high species richness of vascular and non-vascular epiphytes on creeping stems (Muñoz et al. 2003; J. Larraín, personal communication), the loss of old-growth *Tepualia* stands may represent a significant loss of biodiversity.

(3) Forest fires, predominantly as a result of human activities, such as land clearing and opening of forests for timber extraction, represent a major threat to remnant native forests and protected areas in southern South America. For example, fires whose origins were outside parks burned extensive areas of old-growth forests in 1998 in Nahuel Huapi National Park (41° S, Argentina) and in 2002 in Malleco National Reserve (38° S, Chile); these were the first two protected areas created in southern South America (Primack et al. 2001). In Chilean coastal and lowland temperate rainforests, wildfire has been historically infrequent in the absence of humans, but fire frequency and intensity have increased greatly during the twentieth century, becoming a major factor in the decline of coastal old-growth forests (Smith-Ramírez 2004). Only high altitude Andean and coastal forests dominated by the conifers *Araucaria araucana* and *Fitzroya cupressoides* appear to be more resilient to repeated fire disturbance, mainly because of the thick bark of these trees, which allows them to survive ground fires. Wildfires, both natural and human-driven, may have occurred more frequently in these forests during the Holocene (Gonzalez et al. 2005; Armesto et al. 1995) and presumably, because both conifers have a millennial lifespan, they were able to survive a fire regime of low frequency prior to human settlement. Presently, because of human set fires, thousands of hectares of conifer forests on the coastal range have been burned.

### 16.2.2 Values

The loss of old-growth forests has a high opportunity cost, from the point of view of ecotourism, aesthetics, human health, and priceless natural capital, as suggested by indigenous knowledge of medicinal, craft and other non-timber values of biodiversity (Smith-Ramírez 1996). In addition, late-successional or old-growth stands can provide reference or baseline data on ecological processes (Frelich et al. 2005) that can help us understand the disruptive consequences of ecosystem management, air and water pollution, and land-cover change. South American temperate forests offer a unique opportunity to learn about the functional integrity of ancient ecosystems in a region of the planet that still remains largely unpolluted (Hedin et al. 1995), thus providing valuable clues as to the pre-industrial condition of temperate forests (see below).

Although structurally and compositionally, old-growth coastal forests differ greatly from frequently disturbed Andean forests (Veblen et al. 1996), frequent human impacts are imposing a dominant disturbance regime that enhances the dominance of pioneer trees and promotes the loss of plant and animal species associated with late-successional stages. Anthropogenic disturbance regimes may lead to a loss of spatial heterogeneity and floristic homogenisation of forests as a result of the widespread use of logging and fire. As shown in other forested areas of the world (e.g. Kohm and Franklin 1997; Fuller et al. 1998), regional loss of old-growth forest cover as a consequence of intensive logging and short rotations may cause the loss of numerous species of plants and animals that depend on specific old-growth forest habitats, leading to ecological homogenisation on a regional scale. Key structural features, coupled with complex vertical heterogeneity and tree species composition of old-growth forest stands in Chiloé Island (Gutiérrez et al. 2009), suggest that they can provide specialised habitats for plants and animals as they do in other temperate regions (see Chap. 19 by Frank et al., this volume). Key structural attributes, such as emergent canopy trees, snags, logs, tree-fall gaps, and dense bamboo cover, provide habitat for several endemic species of birds and mammals (Reid et al. 2004; Díaz et al. 2005; Jaña-Prado et al. 2007). Bird species such as the Magellanic woodpecker (*Campephilus magellanicus*), black-throated huet-huet (*Pterotochos tarnii*) and ochre-flanked tapaculo (*Eugralla paradoxa*) are present regionally only where old-growth forest habitat remains (Table 16.1).

Recent studies have shown that logs on the forest floor function as important microsites for the regeneration of many tree species (Lusk 1995; Christie and Armesto 2003). Hence, the loss of structural components of forests over extensive areas of the landscape, due to logging practices or the use of fire, may impair the regeneration potential of tree species. Some tree species (e.g. *Dasyphyllum diacanthoides* and *Myrceugenia chrysocarpa*) occur only in old-growth stands in Chiloé Island (Gutiérrez et al. 2009). Likewise, trees in old-growth forest patches in rural areas of Chiloé Island have a specialised moss flora, which is richer in endemics than second-growth forests or shrublands (J. Larraín, unpublished data).

**Table 16.1** Ratio of forest bird abundance in old-growth and secondary temperate rainforests in the Valdivian eco-region of Chile. *OG* Species that are almost entirely restricted to old-growth forests; *OG/SF* abundance ratio between old-growth stands and secondary forest stands, calculated using data from Rozzi et al. (1996)

Species	Common name	Abundance ratio OG/SF
<i>Campephilus magellanicus</i> *	Magellanic woodpecker	OG
<i>Sephanoides galeritus</i>	Green-back, fire crowned	2–4
<i>Anairetes parulus</i>	Tufted tit-tyrant	<1
<i>Elaenia albiceps</i>	White-crested Elaenia	1
<i>Columba araucana</i> *	Chilean pigeon	2–4
<i>Tachycineta meyeri</i> *	Chilean swallow	<1
<i>Pteroptochos tarnii</i> *	Black-throated huet-huet	OG
<i>Scelorchilos rubecula</i> *	Chucaco tapaculo	>10
<i>Eugralla paradoxa</i> *	Ochre-flanked tapaculo	OG
<i>Scytalopus magellanicus</i>	Magellanic tapaculo	mainly OG
<i>Sylviorhynchus desmursii</i> *	Des Murs' wiretail	1–8

\*Endemic to south-temperate rainforest

**Table 16.2** Comparison of total mass of logs and snags in temperate old-growth forests (age over 300 years) of Chile and North America. Modified from Carmona et al. (2002). *US* United States

Forest type and region	Mean mass of logs (Mg/ha)	Range	Mean mass of snags (Mg/ha)	Range	Reference
Conifer (Pacific Northwest, US)	63	54–73	54	41–63	Spies et al. 1988
Deciduous (Eastern US)	25	16–38	11	–	Harmon et al. 1986
Evergreen broad-leaved (Chiloé Island, Chile)	47	31–65	126	13–249	Carmona et al. 2002

The global decline of old-growth forest is especially relevant for the carbon storage properties of regional ecosystems (Harmon et al. 1990; Carmona et al. 2002; Chap. 8 by Harmon, this volume). The slow decomposition rate of large volume snags and logs, especially in old-growth temperate rainforests (Table 16.2), determines a carbon storage capacity that can be several times greater than that of second-growth forests. Long tree life spans (Table 16.3) and slow growth rates can also contribute to carbon storage properties of temperate forests (Harmon et al. 1986). Although fast-growing plantations or young successional forests can accumulate carbon faster in early stages of stand development, managed ecosystems may have limited long-term storage value because of short logging cycles (Harmon et al. 1990). Accordingly, the decline of old-growth forest cover can drastically reduce carbon storage in the landscape, and their replacement by plantations, pastures and shrublands can additionally affect carbon cycling if these new species have higher carbon-to-nitrogen ratios than native trees. This is

**Table 16.3** Life spans of some dominant tree species of Chilean temperate old-growth forests

Species	Life span (years)	Reference
<i>Aextoxicon punctatum</i>	480	Pollman & Veblen (2004)
<i>Eucryphia cordifolia</i>	650	Pollman & Veblen (2004)
<i>Nothofagus pumilio</i>	400	Rebertus and Veblen 1993
<i>Saxegothaea conspicua</i> <sup>a</sup>	750	Lusk (1996)
<i>Nothofagus alpina</i>	600	Pollman 2005
<i>Weinmannia trichosperma</i>	700	Lusk 1999
<i>Austrocedrus chilensis</i> <sup>a</sup>	1,000	Veblen et al. 1996 in Armesto et al. 1996a
<i>Pilgerodendron uviferum</i> <sup>a</sup>	1,000	Szeicz et al. 2000
<i>Araucaria araucana</i> <sup>a</sup>	1,300	Montaldo 1974
<i>Fitzroya cupressoides</i> <sup>a</sup>	3,500	Lara and Villalba 1993

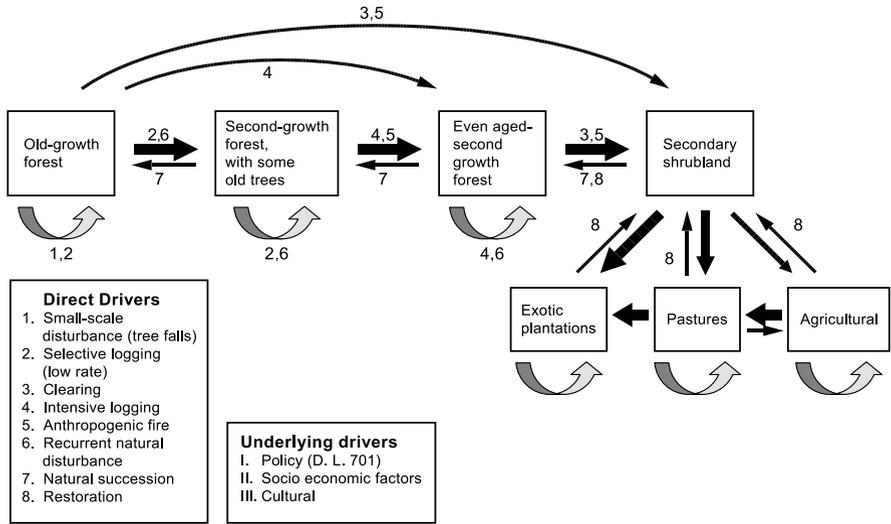
<sup>a</sup>Conifers

because higher carbon-to-nitrogen ratios are associated with higher litter decomposition rates and different susceptibility to fire (Vitousek et al. 1986; Pérez et al. 2004).

### 16.2.3 Conservation Prospects

Rapidly shrinking old-growth forest landscapes, especially in small creeks at low elevations (<500 m) and in coastal areas, are the main targets for protection (Smith-Ramírez 2004; Smith-Ramírez et al. 2005a). Moreover, significant areas of public parks and reserves are almost entirely lacking on the Chilean coastal range (Fig. 16.3). Ecologists have long since noted this important conservation gap (Simonetti and Armesto 1991; Armesto et al. 1992; Muñoz et al. 1996; Armesto et al. 1998; Pauchard and Villarroel 2002; Smith-Ramírez 2004). Improving the representation of coastal and lowland forests in the Chilean Public System of Protected Areas is difficult because most land is privately owned and in high demand for urban and industrial use. However, much old-growth forest still remains in these areas (Smith-Ramírez 2004), which can be protected through agreements with private landowners.

In recent years, partly in response to advice from the scientific community (Muñoz et al. 1996; Smith-Ramírez and Armesto 2002), some private conservation initiatives have contributed to reducing this gap. Ibarra-Vidal et al. (2005) summarised private conservation efforts at the northern limit of temperate rainforests, which include nearly 60,000 ha of the last old-growth forest remnants in Nahuelbuta Range, which are now completely surrounded by forestry plantations. The World Wildlife Fund and The Nature Conservancy have jointly purchased about 60,000 ha in the Coastal Range of Valdivia, including some remnant old-growth forest stands, as well as secondary and degraded coastal forest, to create a coastal reserve. Indigenous communities in the area of San Juan de la Costa,



**Fig. 16.4** Main transitions among stages (*boxes*) and major drivers associated with the loss or maintenance of old-growth forest cover in south-central Chile. The main direct drivers for each transition are shown by the numbers 1 to 8. The width of the *arrows* indicates the relative probabilities of each transition. Direct drivers, when anthropogenic, are driven by underlying policy, socio-economic and cultural drivers (*inset*). These are the most relevant drivers for the transitions from native vegetation to agro-forestry uses. A remarkable example of a policy driver is the Chilean law (D.L. 701) from 1974 that subsidised forestry plantations, and hence prevented the successional recovery of native shrublands, promoting their replacement by commercial forestry plantations. A more recent socio-economic factor is the building of new cellulose plants requiring the expansion of present forestry plantations to provide wood chips

Osorno (39° S) are committed to the protection of 700 ha of undisturbed coastal forests and 705 ha of coastal areas adjacent to these forests within Mapulahuai Ethnic Park (C. Smith-Ramírez, unpublished report). The Mapulahuai Ethnic Park is part of an area of 50,000 ha of indigenous land including much old-growth forests in the coastal range of Osorno. Two large private reserves now protect large tracts of evergreen rainforest, some of it in pristine condition, in the mainland across from Chiloé Island: Pumalin (317,000 ha) and Huinay (34,000 ha). Tantauco Park in southern Chiloé Island protects 118,000 ha of North Patagonian old-growth forest and some remnant *Pilgerodendron uviferum* stands. In addition, some private forestry companies have set aside remnant old-growth forest areas for conservation accumulating several thousand hectares (D. Alarcón, personal communication). However, the present lack of Government incentives and the still uncertain legal status of private reserves in Chile cast some doubts about the feasibility of the long-term conservation goals of these large private investments.

The southern portion of the temperate rainforest region (Fig. 16.1) from Chiloé Island to Cape Horn (43–55° S), including the Sub Antarctic (or subpolar) Magellanic rainforest eco-region (49–56° S), conserves some of the largest remnants of

continuous old-growth forest in temperate regions worldwide (Neira et al. 2002; Silander 2000). It hosts the highest diversity of mosses in the South American temperate forest biome (Rozzi et al. 2008), contains the largest mass of continental ice in the southern hemisphere besides Antarctica (Cassasa et al. 2000), and has the world's lowest human population density within temperate regions (Mittermeier et al. 2003). This remote territory includes the largest public parks and reserves in Chile; most of them, however, lacking proper infrastructure and land-care personnel (Rozzi et al. 2004). The Sub Antarctic region is now the target of major industrial development projects, including hydroelectric power dams, new access roads, and expanding salmon farming (R. Rozzi et al., unpublished data). As stewards of one the last wilderness frontiers of the planet, there is a need for organisations to establish broad partnerships, integrating public and private interests and scientific knowledge, in order to ensure the long-term protection of cultural, economic, and ecological values of the region. A step forward was the recent creation of the Cape Horn Biosphere Reserve (2005), protecting 48,843 km<sup>2</sup> of nearly pristine land at the austral tip of South America. It is the only Chilean biosphere reserve that comprises terrestrial (19,172 km<sup>2</sup>) and marine ecosystems (29,670 km<sup>2</sup>), and is currently the largest in the southern cone of southern South America, i.e. Uruguay, Argentina, and Chile (Rozzi et al. 2006). The connectivity of conservation efforts from Cape Horn to Chiloé Island, through the Sub Antarctic archipelagoes (Fig. 16.1), remains an important challenge for the future.

The establishment of Cape Horn Biosphere Reserve, as a public-private partnership, with its long-term goals defined by an open process of discussion among stakeholders, government authorities and scientists (Rozzi et al. 2006), provides an inter-institutional model for the integration of private and public conservation efforts with the social and economic welfare of local inhabitants. The Chilean National Forest Service (CONAF) is attempting to replicate this model to create a binational Chilean-Argentinean biosphere reserve in the Valdivian rainforest region, and a World Heritage Area including North Patagonia and the northern area of the Sub Antarctic Magellanic rainforests. The biosphere reserve approach can generate a broad discussion of the socio-economic benefits, values, and logistic problems associated with the preservation of old-growth forests. We propose that it be applied also to remnant forest areas in south-central Chile.

### 16.3 Plant-Animal Interactions

The high importance of plant-animal mutualisms in South American temperate forests is striking because of their paucity in other temperate forests (Aizen and Ezcurra 1998). The majority of plant species in southern temperate rainforests requires interaction with animal pollinators and/or vertebrate dispersal agents to ensure their natural recruitment (Armesto et al. 1987, 1996b; Armesto and Rozzi 1989; Willson 1991; Willson et al. 1996, Aizen and Ezcurra 1998; Aizen et al. 2002, Smith-Ramírez et al. 2005b). Temperate rainforests of southern South America are

characterised by an unusually high proportion of fleshy fruited species among trees, shrubs, vines and epiphytes; i.e. 70% of the woody flora (Armesto and Rozzi 1989). This proportion of fleshy fruited plant species is higher than that reported for many northern hemisphere temperate forests, and is similar to some wet tropical forests (Armesto and Rozzi 1989; Willson 1991).

As old-growth forest cover shrinks in the regional landscape, mutualistic species are likely to decline and critical biological interactions may cease to function. Preliminary evidence suggests that some species, such as the Chilean pigeon (*Columba araucana*), which may play a role in the dispersal of many fleshy fruited species (Armesto et al. 1987), is present in greater abundance in old-growth forest habitats (Table 16.1). Even some regionally common birds such as the fire-crowned hummingbird (*Sephanoides sephaniodes*) (Armesto et al. 1996b) are several times more abundant in late-successional forest habitats than in younger forests (Table 16.1). Two other passerine bird species, *Elaenia albiceps* and *Turdus falklandii*, which are the main seed dispersers in the Chiloé flora (Armesto et al. 1996b; Amico and Aizen 2005), are more resilient to landscape changes. *Elaenia albiceps* uses a wide variety of foraging sites and habitats, including fragmented old-growth forests, secondary forests and shrublands (e.g. Willson et al. 1994; Armesto et al. 2005), while *Turdus falklandii* is more abundant in second-growth forests and pastures. These behavioural patterns result in a resilient interaction between these avian frugivores and their dispersed plants (Aizen et al. 2002), implying that conversion of old-growth forest cover into secondary forest may not significantly alter the abundance and functional role of the main seed dispersers. In contrast, forest fragmentation and nest predation on forest edges has negative effects on the local abundance of understorey birds with limited flight abilities (Willson et al. 1994; De Santo et al. 2002; Willson 2004; Sieving et al. 1996; Díaz et al. 2005). However, the role of these birds, which have a generalist diet, on the dispersal of forest plants, is still only poorly known (Correa et al. 1990). In addition to avian frugivores, two mammal species, a marsupial (*Dromiciops gliroides*) and a fox (*Lycalopex fulvipes*), and one reptile species (the lizard *Liolaemus pictus*) have been reported to eat the fruit and disperse the seeds of several species of trees, shrubs and vines (Armesto et al. 1987; Willson et al. 1996). In all of these cases we lack information about potential changes in species abundance derived from the expansion of second-growth forests that may affect species interactions. For example, forest exploitation changes the demographic pattern of *D. gliroides*, reducing population recruitment, which may affect its role as a seed disperser.

For fleshy fruited epiphytes in particular (e.g. *Luzuriaga* spp., *Fascicularia bicolor*, Gesneriaceae spp.) and probably for some tree climbers (e.g. *Philesia magellanica*, *Lapageria rosea*, *Lardizabala biternata*, *Boquila trifoliolata*, *Berberidopsis corallina*, and *Cissus striata*) of southern temperate rainforests, avian frugivores and the only arboreal mammal, *Dromiciops gliroides*, may be the main seed vectors, because recruitment of these species is enhanced when propagules are dispersed between tree canopies (F. Salinas, personal communication). An example of such specialised plant–frugivore interaction is the directed dispersal of seeds of the hemiparasitic mistletoe *Tristerix corymbosus* by the arboreal marsupial *Dromiciops gliroides* in southern rainforests (Amico and Aizen 2000). Recently, Rodríguez-Cabal and Aizen (2007) have shown that local extinction of *Dromiciops*

from small forest fragments was associated with the complete disruption of mistletoe dispersal.

Similarly, along the latitudinal gradient from south-central Chile to Cape Horn, 61–80% of the rain forest taxa have biotic pollination syndromes (J. Armesto, unpublished data). An important pollination syndrome in the rain forest flora of western South America is ornithophily, including hummingbird and passerine pollination (Smith-Ramírez 1993; Aizen and Vásquez 2006). In Chiloé Island, 14 out of 42 woody species have red tubular flowers pollinated by hummingbirds (Smith-Ramírez 1993; Aizen et al. 2002). Just one hummingbird species, the green-back fire-crowned *Sephanoides sephaniodes*, is the principal pollinator of the entire plant assemblage (Smith-Ramírez 1993; Armesto et al. 1996b; Aizen et al. 2002), though passerines have been reported to pollinate the red flowers of the Proteaceae tree *Embothrium coccineum* in Chiloé (Smith-Ramírez and Armesto 1998). In old-growth stands, the emergent tree *Eucryphia cordifolia* may be a pivotal resource for pollinators, because of its profuse and massive flowering, which attracts more than 100 species of insect flower visitors (Smith-Ramírez et al. 2005b). Moreover, the pollinators of emergent *Eucryphia cordifolia* trees in old-growth forests are not the same as in secondary forests (C. Smith-Ramírez, unpublished data). The rapid and massive loss of old-growth lowland forests, containing large *Eucryphia cordifolia* trees (Gutierrez et al. 2008), due to logging and forest clearing in recent decades, may disrupt the rich pollinator assemblage of *Eucryphia cordifolia*. It is likely that such disruption of pollinator assemblages may impair the reproduction of a larger number of tree species, which are exogamous and dependent on pollinators for seed set (Smith-Ramírez et al. 2005b).

The low number of species of avian seed dispersers and pollen vectors recorded in temperate rainforests of southwestern South America supports the idea that the high plant diversity of these rainforests depends on a rather poor assemblage of animal mutualists (Armesto et al. 1996b; Amico and Aizen 2005). Conversely, the high number of insect pollinators (Smith-Ramírez et al. 2005b; Devoto et al. 2005) supports the idea that the high insect diversity in old-growth temperate rainforests of southwestern South America depends on a comparatively poor assemblage of plant mutualists. Accordingly, some species could function as critical links for maintaining the network of interactions in these forest ecosystems. Consequently, the non-random loss of species of animal or plant mutualists could have cascade effects on a larger assemblage of interacting species (Armesto et al. 1996b; Willson et al. 1996; Aizen et al. 2002; Amico and Aizen 2005).

Large old trees, snags, logs, understorey cover and epiphytes, which are more frequent components of old-growth forests (Gutierrez et al. 2009), may be critical habitat components for the maintenance of mutualistic animal species, by providing nesting sites, refuges from predators, and enhanced food availability (Tews et al. 2004). Old trees, snags and logs are the habitat for many invertebrates and cavity nesting birds and mammals (Newton 1994; Willson et al. 1994). It is likely, therefore, that the expansion of young forests at the expense of old forests will alter the distribution and heterogeneity of habitats and resources in the landscape, with consequences for avian behaviour and flight patterns, which in turn may affect seed dispersal and pollination interactions.

The network of mutualistic interactions that we observe in old-growth forests of southern South America is the result of ancient ecological relationships among animal and plant species of Gondwanan origin (Aizen and Ezcurra 1998; Amico and Aizen 2000). Current land-use patterns, forest fragmentation, habitat degradation, air and water pollution, and introduction of species, including aggressive exotic mutualists (e.g. *Bombus ruderatus*, *Apis mellifera*, Morales and Aizen 2006; *Vesputula germanica* and the tree *Eucalyptus globulus*, Smith-Ramírez et al. 2005b), expose forest species to ecological scenarios without precedent in their evolutionary history. This situation may lead to the re-organisation of mutualistic networks incorporating exotic species. Understanding the consequences of such biotic changes can be achieved only by comparison of species interactions to reference old-growth forests. As an example, one of the major changes driven by the expansion of pastures has been the increase in abundance of *Apis mellifera*, which accounts for up to 95% of visits to *Eucryphia cordifolia* trees in patches of rural habitat. While in secondary forests, this bee species accounts for 15–50% of flower visits, honeybees were entirely absent from old-growth stands within a nearby national park (C. Smith-Ramírez et al., unpublished data), where indigenous pollinators increased in species richness and abundance.

## 16.4 Biogeochemistry

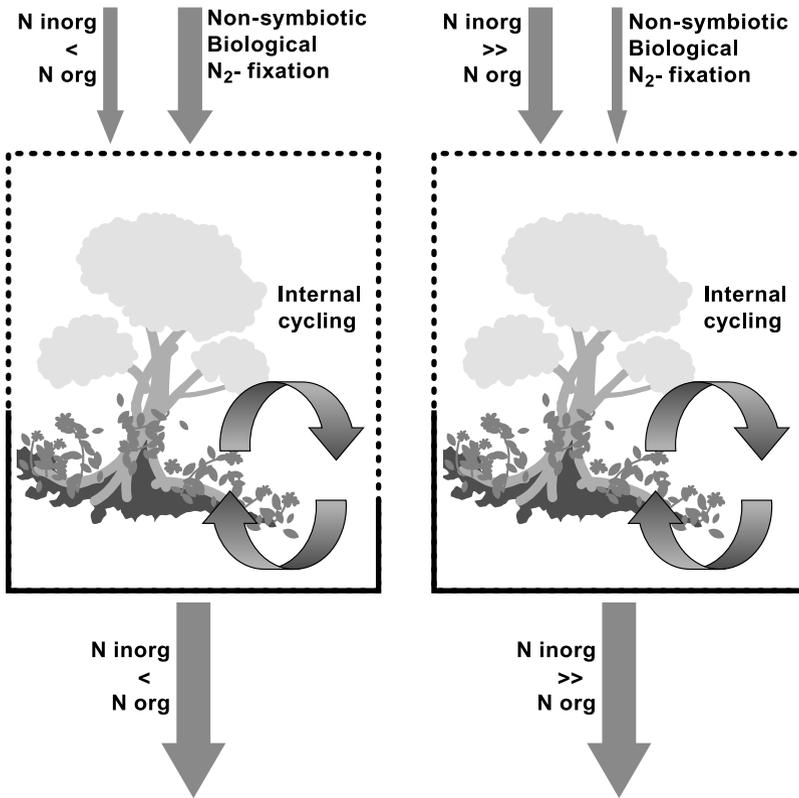
In classic biogeochemical theory, nutrients are accumulated during early succession to reach a steady-state condition in late-successional ecosystems, where most nutrients are recycled internally and trees cease to grow. Accordingly, old-growth forests should exhibit negligible net gain of inorganic forms of nitrogen and phosphorous, as nutrient losses equal inputs from geologic and atmospheric sources (Hedin et al. 1995). This is a relevant characteristic as it suggests that nutrient dynamics in old-growth forests are inherently different from those of younger forests in that old-growth stands have lost their capacity to absorb additional inorganic nutrient inputs, and hence are “leaky” with regard to nutrient inputs. In classic succession theory, no reference is made to fluxes of dissolved organic nutrients in air, water and soil. The Cordillera de Piuchué Ecosystem Study (CPES) was a pioneer project developed to study old-growth evergreen, montane temperate forests in the unpolluted coastal range of Chiloé island (42°S), southern Chile. This project, together with other studies in lowland old-growth forests, has contributed to the current body of knowledge of biogeochemical processes of temperate rainforests in southwestern South America (Hedin et al. 1995; Pérez et al. 1998, 2003a; Perakis and Hedin 2001, 2002; Carmona et al. 2002; Perakis et al. 2005). According to these studies, southern old-growth forests show strong retention of added inorganic nitrogen (N) contrary to predictions of classic biogeochemical theory, and in turn leak large amounts of dissolved organic nitrogen to stream waters. Consequently, late-successional forests are leaky for organic forms of nitrogen, but inorganic forms of nitrogen are strongly retained by soils, microbes and plants (Perakis and Hedin 2001, 2002).

In contrast to southern hemisphere temperate forests, biogeochemical cycles over most of the northern hemisphere have been influenced greatly by human activities, especially as a consequence of chronic nitrogen deposition (Aber et al. 1998; Holland et al. 1999). This anthropogenic “fertilisation” has greatly altered the nutrient steady state. Thus, during the last decade, the study of biogeochemical cycles in unpolluted, old-growth forests of southern Chile has become especially relevant as a baseline that may be characterised as the “unpolluted nitrogen cycle” (Perakis and Hedin 2002). Other sources of atmospheric nitrogen, such as forest fires, are also of limited importance in coastal locations because of the westerly winds derived from over the Pacific Ocean. Our knowledge of the unpolluted nitrogen cycle is extremely fragmentary in comparison to studies of the “polluted nitrogen cycles” of many northern hemisphere temperate forests. In the following sections, we briefly summarise the main biogeochemical characteristics that distinguish temperate old-growth forests of southern South America (Fig. 16.5).

#### ***16.4.1 Relevant Features of the Nitrogen Cycle in Unpolluted South American Forests***

Element fluxes in old-growth temperate forests in western South America are characterised by the dominance of dissolved organic nitrogen in both atmospheric inputs and hydrologic outputs from forested watersheds (Hedin et al. 1995; Perakis and Hedin 2002; Weathers et al. 2000; Galloway and Cowling 2002). The presence of dissolved organic nitrogen in rain and fog likely derives from an oceanic source (Weathers et al. 2000); however, this is still unconfirmed. Such patterns differ markedly from most temperate forests in the northern hemisphere, where both atmospheric inputs and hydrologic outputs are strongly dominated by dissolved inorganic forms of nitrogen (Bormann and Likens 1979; Johnson 1992; Hedin and Campos 1991).

In southern Chilean ecosystems, where wet deposition of nitrate and ammonium are several orders of magnitude lower than in northern hemisphere forests (Hedin et al. 1991), two major sources of nitrogen for organisms during forest succession become relevant: biological nitrogen fixation and the recycling of organic matter via litterfall to the forest floor. Soil microorganisms mineralise the more labile fraction of soil organic matter to ammonium and nitrate (Pérez et al. 1998), both of which are readily absorbed by plants and/or microbes. According to succession theory, inorganic nitrogen in excess of growth requirements of these organisms may be lost via denitrification (gaseous nitrogen loss) or leaching. However, there is little evidence of either gaseous or hydrologic losses of ammonium or nitrate from late-successional forests (Pérez et al. 2003a). Nitrate and ammonium are found at very low concentrations in forest streams (Hedin et al. 1995), even after experimental addition of these nutrients to forest soils (Perakis and Hedin 2002), indicating strong biotic retention of inorganic nitrogen within the ecosystem (Perakis and Hedin 2001). In contrast, dissolved organic nitrogen accounted for



**Fig. 16.5** Schematic diagram of the nitrogen cycle in unpolluted southern Chilean old-growth (*left panel*) forests compared to North American temperate forests (*right panel*), which are subjected to higher nitrogen deposition derived from anthropogenic sources. *Arrow widths* indicate the relative magnitude of nutrient fluxes. *N inorg* Inorganic nitrogen, *N org* organic nitrogen. Organic forms (dissolved and particulate) are more important in the outputs from forested watersheds in Chile than in North America. Inputs and outputs in most North American forest are dominated by inorganic nitrogen. Inputs in Chilean forests are also dominated by organic over inorganic forms of nitrogen. Notice that nitrogen fixation increases in relative importance in southern forests relative to atmospheric inputs

up to 95% of total nitrogen in CPES streams versus ca. 8% in streams draining forested watersheds of the northern hemisphere (Hedin et al. 1995, Perakis and Hedin 2002). This comparison strongly suggests that northern hemisphere old-growth forests have lower accumulation of dissolved organic forms of nitrogen and have limited capacity to retain soil nitrate. The reason for such differences in the retention of different forms of nitrogen in forest soils remains unclear.

Recent studies in Chilean temperate rainforests (Carmona et al. 2002; Pérez et al. 2004, 2003a) have highlighted the functional importance of recalcitrant and massive soil compartments, such as dead wood biomass and the litter layer (O<sub>i</sub> horizon), both associated with the activity of free-living (non-symbiotic)

nitrogen fixers. Nitrogen input via non-symbiotic nitrogen fixation has been estimated in the range of 0.2–2.3 Kg N ha<sup>-1</sup> year<sup>-1</sup> (Pérez et al. 2003a, 2004). Furthermore, the contribution of symbiotic nitrogen fixation cannot be ruled out in these forests, because several lichen and hornwort species have symbiotic associations with cyanobacterial diazotrophs (J. Duckett, personal communication), a process that deserves further study.

Internal fluxes of nitrogen in CPES forests indicate low rates of soil net nitrogen mineralisation, accompanied by high gross nitrogen mineralisation rates (Pérez et al. 1998; Perakis et al. 2005) and strong retention of both ammonium and nitrate within the ecosystem (Perakis and Hedin 2001). In addition, Vann et al. (2002) observed that the high amount of nitrogen accumulated in the live biomass of coastal montane forests, in association with low inorganic nitrogen production in these soils, suggests high nitrogen use efficiency. This is further supported by the high leaf C/N ratios of canopy trees and high retranslocation from senescent leaves to living tissues (Pérez et al. 2003b; Aravena et al. 2002). Another important finding is that slow decomposition and high accumulation of organic matter in old-growth forest soils tends to enhance soil cation exchange capacity (Pérez et al. 1998, 2003a), thus contributing to enhanced ammonium retention (Perakis and Hedin 2001).

Current knowledge of biogeochemical cycles in Chilean old-growth forests is restricted largely to nitrogen dynamics (Hedin et al 1995; Pérez et al. 1998; Perakis et al. 2005), because nitrogen is considered the principal nutrient limiting plant growth in boreal temperate forests, whereas phosphorus (P) limits plant growth in tropical rainforests (Aber and Melillo 1991). Nevertheless, exploration of phosphorus limitation in evergreen temperate rainforests in New Zealand and Hawaii has shown that phosphorus becomes limiting when high rainfall and low disturbance promote leaching losses of phosphorus (Wardle et al. 2004). Accordingly, old-growth forests in southern temperate areas of southwestern South America could potentially be phosphorus- as well as nitrogen-limited in late stages of succession. Despite the fact that annual precipitation in CPES forests exceeds 3,000 mm, phosphorus limitation has not been reported (Thomas et al. 1999; Vann et al. 2002). While high N to P ratios of leaves in CPES forests (mean N:P = 18.6 ± 1.3, Vann et al. 2002) are indicative of potential phosphorus limitation (Wardle et al. 2004), Thomas et al. (1999) considered soil phosphorus concentrations in CPES forests to be sufficient for plant growth. The evidence is still inconclusive and further research on plant growth responses to phosphorus addition in unpolluted old-growth South American temperate forests are necessary.

### ***16.4.2 Human Impact on Biogeochemistry of Southern Forests***

Human activities have fragmented and reduced the area of land covered by old-growth forests. Remnant patches are now surrounded by secondary forests, shrublands, and anthropogenic prairies, which are subjected to logging, fire and grazing. Rural landscapes offer an opportunity to assess nutrient dynamics under mixed land

use, including remnant forest stands. Forest fires and logging may disrupt the tightly closed nitrogen cycle that characterises old-growth forests, decreasing soil nitrogen retention capacity while increasing soil nitrogen availability, thus enhancing ecosystem nitrogen losses, mainly via decomposition and leaching (Pérez et al. 2004; C. Pérez, unpublished data). In addition, higher nitrogen availability in disturbed forests can decrease phosphorus availability, leading to an increase in N:P ratios and changed species composition (A. Gaxiola et al., unpublished data). Nevertheless, recent studies comparing soil nitrogen processes between secondary and old-growth lowland forests in Chiloé Island have shown minimal differences in nitrogen and carbon storage, nitrogen availability and mineralisation (Pérez et al. 2004). Such results suggest a strong resilience of old-growth ecosystem processes to moderate human impacts (Aravena et al. 2002). However, recurrent human disturbances, such as increased fire frequency, chronic nitrogen deposition, and short logging cycles are likely to affect the potential recovery of forests and, in some cases, lead to alternative stable states that require active restoration (Fig. 16.4). We have documented the long-lasting effects of forest canopy removal, from logging or fire, on the hydrologic cycle, which lead to a raised water table and inhibition of tree establishment (Díaz et al. 2007).

## 16.5 Conclusions

Old-growth forests play significant roles in maintaining global biodiversity, retaining essential nutrients, storing carbon for long periods of time, and providing aesthetic and spiritual values to society. They certainly cannot be disregarded as 'over-mature' stands of decaying trees. Mature forest cover must be nationally inventoried and monitored as valuable natural capital. Human impact over the past two centuries in south-central Chile has led to homogenisation of stand structures and landscape patterns through the conversion of old-growth forests into degraded secondary forests, followed by the expansion of pastures and forestry plantations. Old-growth forests have declined to less than 1% of the land in the northern limit of the temperate forest distribution in south-central Chile.

To prevent the demise of the last remnants of old-growth forests, we recommend that intensive logging practices for timber, woodchips and firewood extraction should be concentrated in the extensive degraded secondary forests in south-central Chile (Echeverría et al. 2007). Some small-scale selective logging practices in old-growth forest remnants may not affect their function as habitat for animal species and may represent an environmentally friendly management option in rural landscapes. On the other hand, some frequent forms of disturbance could be highly disruptive of plant-animal mutualisms in forests, as predicted in the case of the eradication of large old trees of *Eucryphia cordifolia*, a tree sustaining one of the richest pollinator assemblages in lowland temperate forests. Conservation of rapidly declining old-growth remnants in south-central Chile must be guided by a discussion process among a broad stakeholder base, considering both ecological

and socio-economic values among other land uses. In addition, long-term ecological research and education programs, in combination with approaches such as the development of biosphere reserves and networks of biological stations, are critical to effectively integrate ecological understanding, decision making and general public conservation attitudes (Rozzi et al. 2008).

Ongoing studies of biogeochemical processes show a strong resilience of old forests to moderate impacts but alteration of recovery processes under recurrent impacts (Fig. 16.4). Strong inorganic nutrient retention in old-growth forests is not consistent with the predictions of current succession theory and contrasts with the leaky condition of northern hemisphere ecosystems in areas of high nitrogen deposition. In addition, high annual precipitation in Chilean forests can result in a rapid loss of available phosphorous, a process that could differ from northern hemisphere forests where phosphorous limitation is rather negligible. Knowledge of nutrient cycling in unpolluted southern forests can contribute to advancing our understanding of the consequences of global change, particularly the long-term effects of enhanced nitrogen deposition in forest soils.

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## References

- Aber JD, Melillo JM (1991) *Terrestrial ecosystems*. Saunders College Publishing, Philadelphia
- Aber JD, McDowell W, Nadeloffer KJ, Magill A, Berntson G, Kamakea M, McNulty S, Currie W, Rustad L, Fernandez I (1998) Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. *BioScience* 48:921–934
- Aizen MA, Ezcurra C (1998) High incidence of plant–animal mutualisms in the woody flora of the temperate forest of southern South America: biogeographical origin and present ecological significance. *Ecol Aust* 8:217–236
- Aizen MA, Vásquez DP (2006) Flowering phenologies of hummingbird plants from the temperate forest of southern South America: is there evidence of competitive displacement? *Ecography* 29:357–366
- Aizen MA, Vásquez DP, Smith-Ramírez C (2002) Historia natural y conservación de los mutualismos planta–animal del bosque templado de Sudamérica austral. *Rev Chil Hist Nat* 75:79–97
- Amico G, Aizen MA (2000) Mistletoe seed dispersal by a marsupial. *Nature* 408:929–930
- Amico GC, Aizen MA (2005) Dispersión de semillas por aves en un bosque templado de Sudamérica austral: ¿quién dispersa a quién? *Ecol Aust* 15:89–100
- Aravena JC, Carmona MR, Pérez CA, Armesto JJ (2002) Changes in tree species richness, stand structure and soil properties in a successional chronosequence in northern Chiloé Island, Chile. *Rev Chil Hist Nat* 75:339–360

- Armesto JJ, Figueroa J (1987) Stand structure and dynamics in the rain forests of Chiloé Archipelago, Chile. *J Biogeogr* 14:367–376
- Armesto JJ, Rozzi R (1989) Seed dispersal syndromes in the rain forest of Chiloé: evidence for the importance of biotic dispersal in a temperate rainforest. *J Biogeogr* 16:219–226
- Armesto JJ, Rozzi R, Miranda P, Sabag C (1987) Plant/frugivore interactions in South American temperate forests. *Rev Chil Hist Nat* 60:321–336
- Armesto JJ, Smith-Ramírez C, León P (1992) Biodiversidad y conservación del bosque templado en Chile. *Amb Des (Chile)* 8:19–24
- Armesto JJ, Villagrán C, Aravena JC, Pérez C, Smith-Ramírez C, Cortés M, Hedin LO (1995) Conifer forests of the Chilean coastal range. In: Hill RS, Enright N (eds) *Ecology of the southern conifers*. Melbourne University Press, Melbourne, pp 156–170
- Armesto JJ, Villagrán C, Arroyo MK (1996a) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, Chile
- Armesto JJ, Smith-Ramírez C, Sabag C (1996b) The importance of plant–bird mutualism in the temperate rainforest of southern South America. In: Lawford RG, Alaback PB, Fuentes E (eds) *High latitude rain forests and associated ecosystems of the west coast of the Americas: climate, hydrology, ecology and conservation*. Springer, Berlin, pp 248–265
- Armesto JJ, Rozzi R, Smith-Ramírez C, Arroyo MTK (1998) Conservation targets in South American temperate forests. *Science* 282:1271–1272
- Armesto JJ, Rozzi R, Caspersen J (2001) Temperate forests of North and South America. In: Chapin FS, Sala OE, Huber-Sannwald E (eds) *Global biodiversity in a changing environment. Scenarios for the 21st century*. Springer, New York, pp 223–249
- Armesto JJ, Willson MF, Díaz I, Reid S (2005) Ecología del paisaje rural de la isla de Chiloé: diversidad de especies de aves en fragmentos de bosques nativos. In: Smith-Ramírez C, Armesto JJ, Valdovinos C (eds) *Historia, biodiversidad y ecología de los bosques costeros de Chile*. Editorial Universitaria, Santiago, pp 585–599
- Arroyo MTK, Riveros M, Peñaloza A, Cavieres L, Faggi AM (1996) History and regional richness patterns of the cool temperate rainforest flora of Southern South America. In: Lawford RG, Alaback P, Fuentes ER (eds) *High latitude rain forest and associated ecosystems of the west coast of the Americas: climate, hydrology, ecology and conservation*. Springer, Berlin, pp 134–172
- Bormann FH, Likens GE (1979) *Pattern and process in a forested ecosystem*. Springer, New York
- Bustamante RO, Castor C (1998) The decline of an endangered temperate ecosystem: the ruiñ (*Nothofagus alessandrii*) forest in central Chile. *Biodivers Conser* 7:1607–1626
- Carmona MR, Armesto JJ, Aravena JC, Pérez CA (2002) Coarse woody detritus biomass in successional and primary temperate forests in Chiloé Island, Chile. *For Ecol Manag* 164:265–275
- Cassasa G, Rivera A, Aniya M, Naruse R (2000) Características glaciológicas del Campo-Hielo Patagónico Sur. *An Inst Patagonia Chil (Ser Cien Nat)* 28:5–22
- Christie DA, Armesto JJ (2003) Regeneration microsites and tree species coexistence in temperate rain forests of Chiloé Island, Chile. *J Ecol* 91:776–784
- Conaf-Conama-Birf (1999) *Catastro y evaluación de recursos vegetacionales nativos de Chile*. Conaf-Conama, Santiago
- Correa A, Armesto JJ, Schlatter R, Rozzi R, Torres JC (1990) La dieta del chucao (*Scelorchilus rubecula*), un passeriforme terrícola endémico del bosque templado húmedo de Sudamérica austral. *Rev Chil Hist Nat* 63:197–202
- De Santo TL, Willson MF, Sieving KE, Armesto JJ (2002) Nesting biology of tapaculos (Rhino-cryptidae) in fragmented south-temperate rainforests of Chile. *Condor* 104:482–495
- Devoto M, Medan D, Montaldo NH (2005) Patterns of interaction between plants and pollinators along an environmental gradient. *Oikos* 109:461–472
- Díaz IA, Armesto JJ, Reid S, Sieving KE, Willson MF (2005) Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile. *Biol Conserv* 123:91–101

- Díaz MF, Bigelow S, Armesto JJ (2007) Alteration of the hydrologic cycle due to forest clearing and its consequences for rainforest succession. *For Ecol Manag* 244:32–40
- Donoso C (1993) Bosques templados de Chile y Argentina. Variación, estructura y dinámica. Editorial Universitaria, Santiago, Chile
- Echeverría C, Newton AC, Lara A, Benayas JMR, Coomes DA (2007) Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Glob Ecol Biogeogr* 16:426–443
- Freligh LE, Cornett MW, White MA (2005) Controls and reference conditions in forestry: the role of old-growth and retrospective studies. *J For* 103:339–344
- Fuller JL, Foster DR, McLachlan JS, Drake N (1998) Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems* 1:76–95
- Galloway JN, Cowling EB (2002) Reactive nitrogen and the world: 200 years of change. *Ambio* 31:64–71
- Gonzalez ME, Veblen TT, Sibold JS (2005) Fire history of *Araucaria–Nothofagus* forests in Villarrica National Park, Chile. *J Biogeogr* 32:1187–1202
- Gutiérrez AG, Armesto JJ, Aravena JC (2004) Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *J Ecol* 92:598–608
- Gutiérrez A G, Aravena JC, Carrasco-Farias N, Christie DA, Fuentes M, Armesto JJ (2008) Gap-phase dynamics and coexistence of a long-lived pioneer and shade-tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloé Island, Chile. *J Biogeogr* 35:1674–1687.
- Gutiérrez AG, Armesto JJ, Aravena JC, Carrasco NV, Christie DA, Carmona MR, Pérez C, Peña MP, Huth A (2009) Structural and environmental characterization of old-growth temperate rainforests of northern Chiloé Island, Chile: regional and global relevance. *Forest Ecology and Management*, in press.
- Hall M, Witte J (1998) Maderas del sur de Chile. Árboles, aplicaciones y procesos. Editorial Universitaria, Santiago
- Harmon ME, Franklin JF, Swanson FK, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack JK, Cummins K (1986) Ecology of coarse woody detritus in temperate ecosystems. *Adv Ecol Res* 15:133–302
- Harmon ME, Ferrel WK, Franklin JF (1990) Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 217:699–702
- Hedin LO, Campos H (1991) Importance of small streams in understanding and comparing watershed ecosystem processes. *Rev Chil Hist Nat* 64:583–596
- Hedin LO, Armesto JJ, Johnson AH (1995) Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. *Ecology* 76:493–509
- Hinojosa LF, Armesto JJ, Villagrán C (2006) Are Chilean coastal forests pre-Pleistocene relicts? Evidence from foliar physiognomy, palaeoclimate, and phytogeography. *J Biogeogr* 33:331–341
- Holland EA, Dentener FJ, Braswell BH, Sulzman JM (1999) Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46:7–43
- Ibarra-Vidal H, Sepúlveda C, Saavedra D, Maldonado E (2005) Propuestas de conservación de la cordillera costera del Maule y Bío Bío. In: Smith-Ramírez C, Armesto JJ, Valdovinos C (eds) *Historia, biodiversidad y ecología de los bosques costeros de Chile*. Editorial Universitaria, Santiago, Chile, pp 617–631
- Informe País (2002) Estado del Medio Ambiente en Chile. Instituto de Estudios Públicos, Universidad de Chile, Santiago
- Innes JL (1992) Structure of evergreen temperate rain-forest on the Taitao Peninsula, southern Chile. *J Biogeogr* 19:555–562
- Jaña-Prado R, Celis JL, Gutiérrez AG, Cornelius C, Armesto JJ (2007) Diversidad en bosques fragmentados de Chiloé: ¿Son todos los fragmentos iguales? In: Grez AA, Simonetti J, Bustamante RO (eds) *Biodiversidad en ambientes fragmentados de Chile: Patrones y procesos en diferentes escalas*. Editorial Universitaria, Santiago, Chile, pp 159–189

- Johnson DW (1992) Nitrogen retention in forest soils. *J Environ Qual* 21:1–12
- Kohm KA, Franklin JF (eds) (1997) *Creating a forestry for the 21st Century*. Island, Washington
- Lara A, Veblen TT (1993) Forest plantations in Chile: a successful model? In: Mather A (ed) *Afforestation policies, planning and progress*. Belhaven, London, pp 118–139
- Lara A, Villalba R (1993) A 3620-year temperature record from *Fitzroya cupressoides* tree rings in Southern South America. *Science* 260:1104–1106
- Lusk CH (1995) Seed size, establishment sites and species coexistence in a Chilean rain forest. *J Veg Sci* 6:249–256
- Lusk C H (1996) Stand dynamics of the shade-tolerant conifers *Podocarpus nubigena* and *Saxegothaea conspicua* in Chilean temperate rain forest. *J Veg Sci* 7:549–558.
- Lusk CH (1999) Long-lived light-demanding emergents in southern temperate forests: the case of *Weinmannia trichosperma* (Cunoniaceae) in Chile. *Plant Ecol* 140:111–115
- Mittermeier RA, Mittermeier GC, Brooks TM, Pilgrim JD, Konstant RD, da Fonseca GAB, Kormos C (2003) Wilderness and biodiversity conservation. *Proc Natl Acad Sci USA* 100:10309–10313
- Morales CL, Aizen MA (2006) Invasive mutualisms and the structure of plant–pollinator interactions in the temperate forests of north-west Patagonia, Argentina. *J Ecol* 94:171–180
- Montaldo PR (1974) La bioecología de *Araucaria araucana* (Mol) Koch. *Inst For Latinoam Investig Capacit Bol* 46–48:1–55
- Muñoz M, Núñez H, Yáñez J (1996) *Libro Rojo de los Sitios Prioritarios para la Conservación de la Diversidad Biológica en Chile*, Ministerio de Agricultura-CONAF, Santiago
- Muñoz AA, Chacón P, Pérez F, Barnert ES, Armesto JJ (2003) Diversity and host tree preferences of vascular epiphytes and vines in a temperate rainforest in southern Chile. *Aust J Bot* 51:381–391
- Myers N, Mittermeier RA, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Neira E, Verscheure H, Revenga C (2002) Chile's frontier forests: conserving a global treasure. World Resources Institute, CODEFF, Universidad Austral de Chile, Valdivia
- Newton I (1994) The role of nesting sites in limiting the numbers of hole-nesting birds: a review. *Biol Conserv* 70:265–276
- Oliver CD, Larson BC (1996) *Forest stand dynamics*, 2nd edn. Wiley, New York
- Olson DM, Dinerstein E (1998) The global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conserv Biol* 12:502–515
- Pauchard A, Villarroel P (2002) Protected areas in Chile: history, current status, and challenges. *Nat Area J* 22:318–330
- Perakis SS, Hedin LO (2001) Fluxes and fates of nitrogen in soil of an unpolluted old-growth temperate forest, southern Chile. *Ecology* 82:2245–2260
- Perakis SS, Hedin LO (2002) Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* 415:416–419
- Perakis SS, Compton JJ, Hedin LO (2005) Nitrogen retention across a gradient of  $^{15}\text{N}$  additions to an unpolluted temperate forest soil in Chile. *Ecology* 85:96–105
- Pérez CA, Hedin LO, Armesto JJ (1998) Nitrogen mineralization in two unpolluted old-growth forests of contrasting biodiversity and dynamics. *Ecosystems* 1:361–373
- Pérez CA, Carmona MR, Armesto JJ (2003a) Non-symbiotic nitrogen fixation, mineralization and denitrification in evergreen of Chiloé Island, Chile: a comparison of temperate forests. *Gayana Bot* 60:25–33
- Pérez CA, Armesto JJ, Torrealba C, Carmona MR (2003b) Litterfall dynamics and nitrogen use efficiency in two evergreen temperate rainforests of southern Chile. *Aust Ecol* 28:591–600
- Pérez CA, Carmona MR, Aravena JC, Armesto JJ (2004) Successional changes in soil nitrogen availability, non-symbiotic nitrogen fixation and C/N ratios in southern Chilean forests. *Oecologia* 140:617–625
- Pollmann W (2005) A long-term record of *Nothofagus* dominance in the southern Andes, Chile. *Aust Ecol* 30:91–102

- Pollmann W, Veblen TT (2004) *Nothofagus* regeneration dynamics in South-central Chile: A test of a general model. *Ecological Monographs* 74:615–634.
- Primack R, Rozzi R, Feinsinger P, Dirzo R, Massardo F (2001) *Fundamentos de Conservación Biológica: Perspectivas Latinoamericanas*. Fondo de Cultura Económica, México
- Reid S, Díaz IA, Armesto JJ, Willson MF (2004) Importance of native bamboo for understory birds in Chilean temperate forests. *Auk* 121:515–525
- Rebertus AJ, Veblen TT (1993) Structure and tree-fall gap dynamics for old-growth *Nothofagus* forest in Tierra del Fuego, Argentina. *J Veg Sci* 4:641–654
- Rodríguez-Cabal MA, Aizen MA, Novaro AJ (2007) Habitat fragmentation disrupts a plant-disperser mutualism in the temperate forest of South America. *Biol Conserv* 139:195–202
- Rozzi R, Martínez D, Willson MF, Sabag C (1996) Avifauna de los bosques templados de Sudamérica. In: Armesto JJ, Villagrán C, Arroyo MK (eds) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, pp 135–152
- Rozzi R, Massardo F, Anderson CB (2004) The Cape Horn biosphere reserve: a proposal for conservation and tourism to achieve sustainable development at the southern end of the Americas. Ediciones Universidad de Magallanes, Punta Arenas
- Rozzi R, Massardo F, Anderson CB, Heidinger K, Silander J (2006) Ten principles for biocultural conservation at the southern tip of the Americas: the approach of the Omora Ethnobotanical Park. *Ecol Soc* 11:43
- Rozzi R, Armesto JJ, Goffinet B, Buck W, Massardo F, Silander J, Kalin-Arroyo M, Russell S, Anderson CB, Cavieres L, Callicott JB (2008) Changing biodiversity conservation lenses: insights from the sub-Antarctic non-vascular flora of southern South America. *Front Ecol Environ* 6:131–137
- Sieving K, Willson MF, de Santo TL (1996) Habitat barriers to movement of understory birds in fragmented south-temperate rainforest. *Auk* 113:944–949
- Silander J Jr (2000) Temperate forests: plant species biodiversity and conservation. In: Levin SA (ed) *Encyclopedia of biodiversity*. Academic, New York, pp 607–626
- Simonetti JA, Armesto JJ (1991) Conservation of temperate ecosystems in Chile: coarse versus fine-filter approaches. *Rev Chil Hist Nat* 64:615–626
- Smith-Ramírez C (1993) Los picaflores y su recurso floral en el bosque templado de la isla de Chiloé, Chile. *Rev Chil Hist Nat* 66:65–73
- Smith-Ramírez C (1996) Algunos usos indígenas-tradicionales de la flora del bosque templado. In: Armesto JJ, Villagrán C, Arroyo MK (eds) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, pp 389–404
- Smith-Ramírez C (2004) The Chilean coastal range: a vanishing center of biodiversity and endemism in South American temperate rainforests. *Biodivers Conserv* 13:373–393
- Smith-Ramírez C, Armesto JJ (1998) Nectarivoría y polinización por aves en *Embothrium coccineum* (Proteaceae) en el bosque templado del sur de Chile. *Rev Chil Hist Nat* 71:51–63
- Smith-Ramírez C, Armesto JJ (2002) Importancia biológica de los bosques costeros de la décima región: el impacto de la carretera costera sur. *Amb Des (Chile)* 18:6–14
- Smith-Ramírez C, Armesto JJ, Valdovinos C (2005a) Historia, biodiversidad y ecología de los bosques costeros de Chile, Editorial Universitaria, Santiago, Chile
- Smith-Ramírez C, Martínez P, Nuñez M, Gonzalez C, Armesto JJ (2005b) Diversity, flower visitation frequency and generalism of pollinators in temperate rain forests of Chiloé Island, Chile. *Bot J Linn Soc* 147:399–416
- Spies TA, Franklin JF, Thomas TB (1988) Coarse woody detritus in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689–1702
- Szeicz JM, Lara A, Díaz S, Aravena JC (2000) Dendrochronological studies of *Pilgerodendron uviferum* in southwestern South America. In: Roig FA (ed) *Dendrocronología en América Latina*. EDIUNC, Mendoza, Argentina, pp 245–270
- Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr* 31:72–92

- Thomas SM, Johnson AH, Frizano J, Vann DR, Zarin DJ, Joshi A (1999) Phosphorus fractions in montane forest soils of the Cordillera de Piuchué, Chile: biogeochemical implications. *Plant Soil* 211:139–148
- Vann DR, Joshi A, Pérez C, Johnson AH, Frizano J, Zarin DJ, Armesto JJ (2002) Distribution and cycling of C, N, Ca, Mg, K and P in three pristine, old-growth forests in the Cordillera de Piuchué, Chiloé. *Biogeochemistry* 60:25–47
- Veblen TT, Ashton DH (1978) Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio* 36:149–167
- Veblen TT, Donoso C, Schlegel FM, Escobar B (1981) Forest dynamics in south-central Chile. *J Biogeogr* 8:211–247
- Veblen TT, Donoso C, Kitzberger T, Rebertus AJ (1996) Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: Veblen TT, Hill RS, Read J (eds) *The ecology and biogeography of Nothofagus forests*. Yale University Press, New Haven, pp 293–353
- Villagrán C, Hinojosa LF (1997) Historia de los bosques del sur de Sudamérica II: Análisis biogeográfico. *Rev Chil Hist Nat* 70:241–267
- Vitousek PM, Ehrlich PR, Ehrlich AH, Matson PA (1986). Human appropriation of the products of photosynthesis. *BioScience* 36:368–373
- Wardle DA, Walker LR, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305:509–513
- Weathers KC, Lovett GM, Likens GE, Caraco NFM (2000) Cloudwater inputs of nitrogen to forest ecosystems in southern Chile: forms, fluxes, and sources. *Ecosystems* 3:590–595
- Willson MF (1991) Dispersal of seeds by frugivorous animals in temperate forests. *Rev Chil Hist Nat* 64:537–554
- Willson MF (2004) Loss of habitat connectivity hinders pair formation and juvenile dispersal of Chucuo tapaculos in Chilean rain forests. *Condor* 106:166–171
- Willson MF, de Santo TL, Sabag C, Armesto JJ (1994) Avian communities of fragmented south-temperate rainforests in Chile. *Conserv Biol* 8:508–520
- Willson MF, Smith-Ramírez C, Sabag C, Hernández JF (1996) Mutualismos entre plantas y animales en bosques templados de Chile. In: Armesto JJ, Villagrán C, Arroyo MK (eds) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, pp 251–264