Subalpine *Nothofagus* and *Araucaria* forests across an environmental and disturbance gradient in South Central Chile: a floristic approach

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Abstract

Vegetation response to environment and disturbance were studied in a subalpine volcanic national park in southern Chile to better understand how this unique flora responds to complex gradients, and to provide baseline information for environmental assessment studies in the region. We describe community assemblages and species distribution patterns in a *Nothofagus* spp. - *Araucaria araucana* forest mosaic using physiognomic vegetation mapping, phytosociological classification methods and an indirect gradient analysis. Four physiognomic types were defined including 3 forest types and a lake shore shrubland. Six plant communities were defined (4 forest, 1 shrubland and 1 grassland). Most of the study area was dominated by a mixed *Nothofagus antarctica – A. araucana* forest followed by *N. dombeyi – A. araucana* forests. *A. araucana* had multimodal diameter distributions reflecting a long history of fire and volcanic disturbances. Detrended correspondance analysis suggested that floristic patterns followed a disturbance and geomorphic gradient. Temperature extremes and disturbance types were hypothesized as the most critical factors determining changes in dominant species distributions. The gradient was closely correlated with vegetation structural complexity. We found 115 species belonging to 45 families in the 241 ha study area. The highest diversity occurred in pure *N. antarctica* forests, intermediate in total cover and height. Despite the 1000m elevation and the study site location within the core of a national park, 18% of the species were exotics, associated mostly with human disturbed areas. Combining both phytosociological and ordination methods helps to better understand and conserve these subalpine environments in the southern Andes.

Keywords
Nothofagus, *Araucaria araucana*, Chile, environmental gradient, volcanism, disturbance, subalpine

Abbreviations
DBH: Diameter at breast height.
DCA: Detrended Correspondance Analysis

Nomenclature
Marticorena & Quezada (1985)

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Introduction

South America's temperate forests provide an interesting opportunity to understand vegetation patterns in complex environmental and disturbance gradients. In contrast to most Northern Hemisphere temperate forests, these forests have developed in relative isolation from other temperate forest landscapes and thereby dominant species are often endemics and present unique adaptations to these environments (Arroyo et al. 1995). Information is urgently needed on how these unique temperate forests will respond to increasing environmental stress, including the prospect of global climate change, invasion of exotic plant species, land-use changes and tourism development (Lara et al. 1995; Armesto et al. 1998; Mooney et al. 1993; Villalba et al. 1997; Arroyo et al. 2000; Lazo 1996; Villarroel 1992).

Andean forests of *Araucaria araucana* and *Nothofagus* spp. are particularly well-suited for studies of disturbance and environmental gradients at a fine scale. *Araucaria araucana* (Monkey puzzle tree) is a relict conifer that occupies two restricted habitats in Southern South America: the Andean mountain range and the Chilean Coastal Range approximately between 37º to 40º degrees South (Donoso 1993). *A. araucana* is a protected species under Chilean law and is considered sacred by indigenous communities (Veblen et al. 1995). It usually forms mixed forest with *Nothofagus pumilio, Nothofagus dombeyi* and *Nothofagus antarctica* (Southern Beeches), covering an area of approximately 442 thousand ha, in both Chile and Argentina, from which 194 thousand are under designated protected areas (Lara et al. 1999). This conifer is considered a very plastic species, which can colonize completely disturbed soils, as lava flows, but also survive under very suppressed conditions (Montaldo 1974: Veblen et al 1995). *A. araucana* survives intense disturbances such as lava flows, volcanic ash deposition, and fires due to its self-prunning branches, coarse bark and sclerophyllous leaves (Montaldo 1974).

The forest dynamics of *A. araucana* and *Nothofagus* spp. and their relation with disturbance regimes has been studied extensively (e.g. Veblen 1982; Veblen et al. 1995; Veblen et al. 1996; Markgraf 1987; Burns 1991; Burns 1993; Donoso 1993; Finckh & Paulsh 1995). Other authors have focused their efforts in finding adequate classification schemes for these plant communities (e.g. Oberdorfer 1960; Eskuche 1973; Eskuche 1998; Hildebrandt-Vogel et al. 1990; Amigo and Ramírez 1998; Ramírez 1978; Gajardo 1994; Finckh 1996). However, little is known about the distribution of *Nothofagus* spp. - *A. araucana* forests understory species in these complex mountain environments and how multiple environmental and disturbance factors interact to create these gradients. The understanding of such environments will help to forecast ecological responses to global changes such as exotic invaders, climate change and human disturbance.

In this study, we document the floristic and structural patterns of vegetation in an abrupt environmental and disturbance gradient at the base of Llaima Volcano in South Central Chile. We describe community assemblages and species distribution patterns in a *Nothofagus* spp. - *Araucaria araucana* forest mosaic using physiognomic structural vegetation mapping, phytosociological classification methods and an indirect gradient analysis. We also examine diversity patterns of native and introduced plant species and their relation to environmental and disturbance gradients.

Study Site

The study area (38°38'S - 71°39'O) consists of 241 ha in the core of Conguillío National Park. Elevation ranges between 1,000 and 1,100 m. Four major geomorphologic features can be distinguished in the study site: Conguillío Lake and its shore; a volcanic hill that belongs to the caldera of Llaima Volcano; a colluvial area (valley bottom); and an old lava colada plateau. These geomorphological features are the results of the activity of Llaima volcano during the last five thousand years (Naranjo & Moreno 1991). Subsequent hydrological erosion, glacial ablation, outwash and deposition of volcanic pyroclastic material have further model the valley.

Climate is cool-moist-temperate with dry summer months. The average annual precipitation for the region is about 2,000 mm (Hayek & DiCastri 1975). The annual average temperature is 8.6°C with an average of 15.1°C for January (hottest month) and 1.9°C for July (coldest month). Snow cover can last in the study area up to three months with an average accumulation of up to 1m. Conguillío (Park rangers pers. comm.). Lake influences microclimate, regulating daily temperature variation and increasing ambient moisture. However, southwest winds are predominant bringing cold air from the Llaima volcano cone.

Soils in this area are predominantly derived from recently deposited volcanic ejecta, tuff and scoria over basaltic deposits (Peralta 1975). Soil heterogeneity is greatly affected by differences in the nature chemistry and texture of the parental material (ashes, pumice, and lava) and time since its deposition (Peralta 1975; Naranjo & Moreno 1991). Peralta (1975) describes the Conguillío soil for *Nothofagus pumilio – Araucaria araucana* forests, similar to those in *Nothofagus dombeyi – Araucaria araucana* forest in our study area. These soils are very porous have a very low bulk density (0.4 – 0.6 g/cm3) and are weathered intensively diminishing particle size of the pyroclastic parental material. They also have low levels of fertility because of P-fixation, with pH around 6.0, organic matter of 2.3 % and a C/N ratio of 24.50 (Peralta 1975).

Araucaria araucana and *Nothofagus* spp. (Southern beeches) dominate the vegetation, forming shublands and forests (Veblen 1982). In protected slopes with less intense volcanic disturbances and increased soil development, the evergreen *Nothofagus dombeyi* codominates the forest with *A. araucana.* On the other hand, the deciduous *Nothofagus antarctica* occupies the areas under more frequent disturbances and harsher environmental conditions, forming pure stands as forest or shrubland, or occupying an intermediate stratum in open *A. araucaria* forests. The majority of these forests have an intermediate layer of *Chusquea coleu*, a bamboo aggressive and abundant in Southern Chile that can reach up to 3 m in the area (see Veblen 1982). Due to the geographic location of the study site, forest understory species diversity is a product of the overlap of Mediterranean subalpine / subantarctic ecosystem species and Valdivian rainforest species (Arroyo et al. 1995; Finckh 1996). The most abundant understory species are *Berberis* spp., *Ribes* spp., members of the *Ericaceae* family and *Fragaria chiloensis*.

Volcanic activity and flooding of Conguillío Lake are the major natural disturbances affecting the area. The volcanic cone started to form about 7200 years ago and since then, it has been active with frequent moderate explosive eruptions, occasionally with lava flows (Naranjo & Moreno 1991). Geologic formations of the study area belong to two main volcanic fissure episodes: one around 3,500 yr. ago and another around 1,000 years ago (Naranjo & Moreno 1991). The last big eruption occurred in 1929 and it has presented small eruptions since then (Casertano 1963; Global Volcanism Program 2001). Annual lake flooding play a key role in disturbing the vegetation at lake shores and the valley bottom. The floods are the result of Conguillío Lake's lack of superficial drainage, which increases water levels during spring after snowmelt increases runoff. Humans have also been part of the landscape for a long time. There are records of *A. araucana* seed collection in this area previous to European settlement. During the early and mid 1900s the area was used for grazing by European settlers, which could also have increased fire frequency. In 1967, the park was created and human activity limited to only recreation. Since then, visitation has strongly increased and so have the number of camping and lodging facilities in the area, affecting the integrity of the vegetation (Pauchard 1998; Pauchard et al. 2001).

Methods

A physiognomic type classification was used to characterize the vegetation mosaic. The classification was developed using aerial photograph (1:20,000 SAF 91, JICA Project) and field reconnaissance. The cover types were described and their distribution digitized in ArcInfo PC and analyzed in ArcView 3.2. Areas closer than 10 m to water flows were not sampled to avoid extra variation due to hydrology influence. We estimated DBH distribution, tree density and basal area for each physiognomic type, using simple random sampling (SRS) with 3 sample units per type. The sample units were square plots of 250m2 for closed and short forests, 1000 for tall forests and 3000 m2 for open short forests. In each plot all DBH over 5 cm were recorded.

We used the Braun-Blanquet relevé method to sample composition and abundance of vascular plant species across the gradient during the summer of 1996 and 1997. In 67 relevés, we recorded every vascular plant species present and their cover by stratum (canopy, intermediate, shrub and herbaceous). We used the modified scale of Barkman et al. (1964) that accounts for cover but also for density. Relevés were circular and variable in size depending on the vegetation type. Optimum plot size was estimated using a species area curve (Mueller-Dumbois & Ellenberg 1974). The final radii were 2.5 m for shrubs and grasslands, 5 m for short forests and 7.5 m for tall forests (areas of 20.0, 78.5 and 176 m2 respectively). In addition, elevation, slope, aspect and dominant tree height were recorded. In contrast with the more classical phytosociological approach (Mueller-Dumbois & Ellenberg 1974), we located relevés subjectively for representing the whole range of vegetation conditions in the gradient, not only those areas that we considered representative of homogeneous plant communities. The relevés were placed using the physiognomic classification, aerial photographs and field reconnaissance. We classified relevés by tabular comparison using presence or absence of differential species, those with intermediate constancy (Mueller-Dumbois & Ellenberg 1974). Communities were described and classified based on the phytosociological hierarchy classification scheme available in the literature. In this paper, we present a brief description of these communities, a more detailed description can be found in Pauchard (1998).

We ran Detrended Correspondance Analisis (DCA), using PC-ORD 4.0 (McCune & Mefford 1999), to describe vegetation gradients. DCA is an indirect gradient analysis method (sensu Ter Braak & Prentice 1988) that has been used extensively in ecological gradient analysis for having a straight forward ecological interpretation and its advantages as a exploratory research tool (Hill & Gauch 1980; Okland 1996). For the analysis, we used the 67 relevés ordination matrix and 45 species, species present in two or less relevés were excluded. A theoretical distribution range for each species was built by recording the highest and lowest DCA Axis 1 value for those plots where the species was present. Then, the results were plotted against the first axis to determine ecological amplitude of the species. Pearson and Kendall correlations (McCune & Mefford 1999) were used to identify the more influential species in the ordination analysis. Due to the lack of environmental factor data (e.g. soils, microsite climate, local geology), we examined the association of plant community attributes for predicting the ecological gradient. We ran linear regression models correlating DCA Axis 1 with stand height and total cover (arithmetic sum of all species percentage covers).

We compiled a complete list of vascular plant species for the study site. The data obtained in the floristic relevés was enhanced with random walk collections to assure the representation of all plant species. Specimens were dried and indexed in the herbarium of the Department of Botany, University of Concepción, Chile. Taxonomic nomenclature followed Marticorena and Quezada (1985). Taxonomic diversity was analyzed by families, genera and species. Finally, we compared the total number of exotic species and native species by plant communities using the relevés data. We added the random walk collections for the totals in the study area. We classified exotic species using Matthei (1995).

Results

We found four physiognomic types: 1) *Nothofagus dombeyi –Araucaria araucana* forest, 2) *Nothofagus antarctica – Araucaria araucana* forest, 3) *Nothofagus antarctica* forest and 4) lake shore shrubland (Table 1). A map of physiognomic types is shown in Fig. 1. Most of the study area is covered by *N. antarctica* - *A. araucana* forests followed *by N. dombeyi* - *A. araucana* forests (Table 1). *N. dombeyi* - *A. araucana* forests are mostly old-growth forests where both species occupied the upper canopy. *N. dombeyi* shows an even-aged structure, while *A. araucana* has individuals in all DBH classes but lower basal area (Fig. 2). On the other hand, *N. antarctica* - *A. araucana* forests show a similar multimodal DBH distribution for *A. araucana*, but a much lower density and basal area. For this cover type, we do not present a DBH distribution of *N. antarctica*, because it is mainly present as a multi-stem shrub with diameters lower than 5 cm. In pure stands, *N. antarctica* may reach 10-15 meters producing a high density, high basal area short forest with an even-aged DBH distribution (Table 1; Fig. 2).

We classified six floristic communities using tabular comparison: four were forests, one shrubland and one grassland (Table 2). This phytosociological classification adds more detailed information to the physiognomic classification. Differentiation in understory species among communities is partly related to structural attributes, but seems to be much more sensitive to microsite characteristics.

DCA analysis shows a strong gradient from tall *N. dombeyi* forests to open herb communities subjected to annual flooding (Fig. 3). Eigenvalues were 0.8506 for DCA axis 1, 0.3062 for axis 2 and 0.1781 for axis 3. Some of the species that show higher correlation with the first DCA axis, using Pearson and Kendall correlations, were a) dense forest species: *Chusquea coleu* (r=-0.547, tau=-0.567), *Myoschilos oblonga* (–0.423; -0.473) and *Nothofagus dombeyi* (-0.525; -0.529); b) disturbed environments species: *Solidago chilensis* (0.648; 0.570), *Phacelia secunda* (0.516; 0.278). *A. araucana* was broadly distributed in the gradient, while *N. antarctica* was more narrowly distributed and *N. dombeyi* only occupied a small portion of the gradient (Fig. 4). Species distribution in relation to DCA Axis 1 (Fig. 5) shows four categories of species: dense forest species, intermediate density environment species, open environment species and microenvironment species. Dense forest species are exclusive of *N. dombeyi* forests, where they grow under shaded conditions (e.g. *Adenocaulon chilensis, N. dombeyi*). Intermediate density environment species are more flexible in their distribution and occupied a wider range of conditions from dense *N. dombeyi* forests to open *N. antarctica* shrublands (e.g. *Maytenus disticha, Ribes magellanicum, Pernettya myrtilloides, Chusquea coleu, A. araucana*). Open environment species are adapted and exclusive to drier conditions and higher disturbance forming *N. antarctica* open forests to lake shore shublands and grasslands (e.g. *Berberis buxifolia,* *Fragaria chiloensis, Solidago chilensis*). Finally, microenvironments species are restricted in their distribution and characterize variations in *N. antarctica* communities (e.g. *Mutisia decurrens, Anthoxantum juncifolium, Festuca scabriuscula*). Regression models for Axis 1 and community parameters (Fig. 6) show a significant ($p<0.001$) inverse relationship for the two variables: Total cover ($r=-0.711$) and total height ($r= -0.731$).

We found a total of 115 species, distributed in 67 genera and 45 families. Asteraceae (n=16), Poaceae (n=15), and Scrophulariaceae (n=5) are the most diverse families. The highest species richness was reached in dense communities of *N. antarctica,* while the *N. dombeyi – Ozmorhiza chilensis* community, a dense secondary forest, and *Solidago chilensis – Phacelia secunda*, a seasonally disturbed shore-lake grassland, show the lowest species richness (Fig. 7). From a total of 115 vascular plant species found in the study area, 18 (16%) were exotics, from which none was abundant in the area. Exotic species were mainly grasses and herbs, which are abundant in the boundaries of the park, especially in historically grazed areas. Open *N. antarctica* shublands or forest communities near to human developments concentrate the majority of exotic species always representing a small fraction of the total cover (Fig. 7; Fig. 1). Most of the exotics were found along roads and campgrounds, but few seem to be spreading into more pristine areas. The most common species were *Rumex acetosella*, *Agrostis capillaris* and *Taraxacum officinale*.

Discussion

The complexity of geomorphologic and disturbance patterns in the study area has resulted in a heterogeneous mosaic of vegetation. Even with only three dominant tree species, understory plants species respond to microsite conditions as well as the disturbance and geomorphologic features. *N. dombeyi – A. araucana* forests represent the most structurally complex communities suggested by the high tree density, basal area and height (Table 1). The understory is represented by a set of shade-tolerant species described for the NODO/OSCH and NODO/ADCH communities in both dense forest species and intermediate environments species categories (Table 2; Fig. 5). These forests in the lower end of DCA Axis 1 appear discretely separated from other communities and relevés are highly aggregated suggesting little differences among them (Fig. 3). Even among NODO/OSCH and NODO/ADCH relevés appear clumped, which suggest that changes in understory composition were overlooked by DCA probably due to the high *N. dombeyi* cover. This pattern was also noticeable in a cluster analysis of the data (Pauchard 1998). They occupied hills protected from the direct fall of Llaima volcano ejecta, and thereby are under lower intensity of volcanic disturbance and less accumulation of pyroclastic material (**cita**). The abundance of a unique set of species is most likely due to the ability of *N. dombeyi* to create a protected environment (Veblen et al. 1996). However, the existence of a secondary forest of *N.dombeyi – A. araucana* (NODO/OSCH community) proves the presence of catastrophic disturbance, most probably fire that could have been used by settlers in the early 1900s. Understory diversity in this case, the lowest in the study site, is reduced by an extreme shading condition, allowing only the survival of shade tolerant species such as *Ozmorrhiza chilensis* and *Chusquea coleu* (Fig. 7).

Pure *N. antarctica* forests (NOAN/CHCO community) occupied sedimentary soils in valley bottoms under cyclical flooding due to their proximity to Lake Conguillio. They have a lower productivity than *N. dombeyi* forests suggested by lower tree height and basal area. However, these are the most diverse communities, probably because the deciduousness of *N. antarctica* and microsite variation provide an ecotonal environment within the tolerance of both forest and open environment species. On the other hand, open *N.antarctica - A. araucana* communities (NOAN/PEPU and NOAN/EMCO) located in less developed volcanic coladas, with a high exposure to recent pyroclastic material, represent the least productive forest with the most open canopy and a lower species diversity. In these forests, understory is mainly composed by, as we defined, intermediate environment species.

The floristic classification and gradient analysis show the wide microsite diversity of the study area for *N. antarctica - A. araucana* forests (Table 2; Fig. 3). In these communities, understory vegetation reflects sudden changes in microsite conditions and structural variation, containing intermediate environment species and open environment species (Fig. 5). These patterns of high variability in *N. antarctica* woodlands and shrublands have been observed before by several authors (Eskuche 1973; Veblen 1982; Amigo y Ramirez 1998). Even more, Amigo and Ramirez (1998) stress the importance of increasing the phytosociological knowledge to be able to characterize these communities in a regional scale. The majority of species in these communities are adapted to open environments and frequent disturbance.

Lake shore shrublands (BEBU/ACPI) and meadows (SOCH/PHSE), in the upper end of the DCA Axis 1, are subjected to annual flooding and represent the most impoverished communities. They share many species with *N. antarctica* forest types, lacking of a tree layer, especially those tolerant to disturbance, but also have a distinct set of disturbed environments species uniquely adapted to flooding disturbances. These *Berberis* and *Solidago* communities have not been described before in the literature, probably because their distribution is restricted to seasonal disturbed areas along subalpine lakes.

Tree species distribution in DCA Axis 1 (Fig. 4) suggest that *A. araucaria* is able to successfully established and survived in a wider range of conditions that their codominant species *N. antarctica* and *N. dombeyi*, at least in these harsh subalpine environments, showing the highest plasticity. We conclude that the DCA Axis 1 represent a gradient of vegetation density and productivity, in the lower end of the gradient we found the most productive and dense vegetation and in the upper end the less productive and more open sites.

We hypothesize that the vegetation gradient in our study site is defined by geology, fire regime, flooding disturbance and microclimate. We will highlight the importance of each of these factors in creating the vegetation gradient. Geological evidence shows that *N. dombeyi - A. araucana* forests are located under older volcanic substrates. Naranjo and Moreno (1991) classified them as Fissure 1 of ca. 3,500 years. These hills have accumulated a thick layer of pyroclastic material, which are under intense weathering, similar to those observed by Peralta (1975) in the description of Conguillio soil. Open forests of *N. antarctica - A. araucana* mostly occupied a newer colada called Fissure 2 (Naranjo & Moreno 1991). This plateau has a much less developed soil profile with abundant recent pyroclastic material, in the form of lapilli. These coarse substrates with low water retention, poor nutrient release and extreme summer and winter temperatures would inhibit the establishment of new seedlings of *N. dombeyi* and would favor the vegetative growth of *N. antarctica*, taking advantage of the already established deep root system (Veblen et al. 1996).

The differential intensity of recent volcanic eruptions may also explain the distribution of *N. dombeyi* and *A. araucaria*. Less intensity disturbance would have partially destroyed *N. dombeyi* allowing the release and recruitment of *A. araucana* (Veblen 1982; Finckh & Paulsh 1995). This has resulted in a multimodal size structure for *A. araucana* and an unimodal size structure for *N. dombeyi* (Veblen 1982). Similar patterns have been observed in Hudson Volcano in southern Chile after its eruption in 1991. In that area, *Nothofagus pumilio and N. dombeyi* were able to recolonize volcanic ashes in the first two years after the eruption, but only shrubs with strong vegetative reproduction were able to survive ash accumulation of more than 90 cm (Vogel 1998). The volcanic disturbance would also explain why our *N. dombeyi – A.araucana* forest are very homogeneous and have lower species richness than those described by Finckh (1996) for Villarrica National Park, approximately 70 km south of the area.

Fire regime in this area is related to both, volcanic and human factors. Pyroclastic material coming from the cone of Llaima volcano may historically have initiated forest fires. On the other hand, human settlers used fire to open this area for grazing (as shown for Villarrica NP in Finckh 1996). Fire scars are visible in *A. araucana* bark, but there is not historical fire record for the area. However, floristic and structural similarities of our *N. antarctica*- *A. araucana* communities with those studied by Burns (1993) suggest similar fire dynamics. The vegetative reproduction of *N. antarctica* after fire (Burns 1993; Veblen et al. 1996) gives it a clear advantage over *N. dombeyi*, which can not resprout and its seedlings do not generally survive in these harsh conditions (Donoso 1993). This would explain the complete lack of *N. dombeyi* seedlings in any of our plots without a *N. dombeyi* canopy. Furthermore, Thomasson (1959 in Eskuche 1973) hypothesizes that *N. antarctica* is able to colonize *N. dombeyi* forests after a catastrophic disturbance such as fire. *A. araucana* is these stands is resistant to fire when over 30 cm (Burns 1993) and to intense volcanic disturbance (Finckh & Paulsh 1995), creating a multimodal recruitment (Fig. 2b). Burns (1993) suggests that without fire *A. araucaria* could outcompeted *N. antarctica*. We found one of those stands, where *A. araucaria* has outcompete *N. antarctica* forming a pure *A. araucana* stand, but it seems to be the exception in our study area.

Flooding also seems to play a major role in plant distribution in our study site. Areas closed to Conguillio Lake and low in elevation are susceptible to annual or cyclical floods. These favor the presence of annual species and those that may tolerate temporal root flooding. However, pure *N. antarctica* stands in the valley bottom may not be solely the consequence of this factor. Armesto et al (1992) report significant mortality in *N. antarctica* associated with floods in glacial valley bottoms. We observed similar damage in flooded areas, but not sufficient to alter *N. antarctica* dominance in these forests. Nonetheless, there is no evidence available in the literature that *N. antarctica* is a better tolerant to flooding regimes than *A. araucana* or *N. dombeyi*.

In these pure *N. antarctica* stands the presence of continuos cold air masses represent the most likely factor to explain *N. antarctica* dominance. The abundance of *N. antarctica* in cold valley bottoms has been reported for other areas (Veblen et al. 1982; Veblen et al. 1996, Escuche 1973, Finckh 1996; Donoso 1993; Armesto et al. 1992). *N. antarctica* buds are able to resist freezing of down to -22C under lab conditions, while most evergreen *Nothofagus* only survive down to -15C (Sakai et al. 1981; Alberdi et al. 1985). *Embothrium coccineum*, a species that coexist with *N.antarctica* in the NOAN/EMCO community, can also resists up to –20C (Alberdi et al. 1985). However, *N. antarctica* has shown to grow 10 times slower than *N. dombeyi* for areas near to Bariloche in the Argentinean Patagonia (Steconni et al. 2000; Puntieri et al. 1998). Eskuche (1973) found for sites in the Argentinean Andes that *N. antarctica* under these cold temperatures delayed bud break over *N. pumilio*. This would indicate a very conservative approach to photosynthesis, which allow the species to avoid early frost damages and ultimately outcompete other species in these harsh environments. Eskuche (1973) also describes *N. antarctica* dominating areas with both extreme summers and winter conditions, mixing with no other Nothofagus species, the same pattern of distribution that we have documented in our study site.

The level of diversity in the study area flora was higher that we expected, considering an area of only 241 ha. The number of families and genera was relatively large for the 115 vascular species. These patterns are explained by the ecotonal nature of the vegetation, but mainly because the unique biogeography of southern Andes vegetation and the overlapping transition of Valdivian rainforest and deciduous Nothofagus forests (Arroyo et al. 1995; Finckh 1996).

The percentage of exotic species (16%) is slightly higher to the approximate 12% average for the country (using Arroyo et al. 2000). This seems extremely high considering that the study area is located in the core of a medium size National Park and elevation is over 1,000 m. However, the area is also the most important recreational and developed area the park, where roads, cabins, campgrounds and other facilities are concentrated. Communities with higher numbers of exotic species were those near to human disturbed areas and more open canopies (Fig. 7; Fig. 1).. This support the evidence reviewed by D'Antonio (1999) that disturbance generally favors invasions. The lake shore communities seem to be in higher risk of invasions, due to increasing seasonal disturbance regimes and openness to invasion dispersal, especially propagules floating in the lake. Even when exotic species are dispersed widely in the landscape, none seem to be sufficiently abundant to be considered an invader (Richardson et al. 2000).

Indirect gradient analysis expands the possibilities of phytosociological classification in order to assess ecological patterns across gradients. Both techniques proved to be complementary in understanding species behavior along complex environmental and disturbance gradients in these *Nothofagus* spp. - *A. araucana* forests. Indirect gradient analysis also increases the potential for elaborating hypothesis about the underlaying mechanism of plant species distribution (Vitousek & Matson 1991). In order to test these hypotheses, understand and quantify the causes these gradients, and develop more robust models of vegetation dynamics, data on variables such as nutrient availability, specific physiological responses and historical disturbance regimes is needed. This ecological information will be crucial to better understand and conserve these sensitive subalpine communities in the southern Andes in the prospect of climate change, economic development and invasions of species.

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References

Alberdi, M., Romero, M., Rios, D., & Wenzel, H. (1985). Altitudinal gradients of seasonal frost resistance in Nothofagus communities of southern Chile. Acta Oecologica Oecologia Plantarum 6(1): 21-30.

Amigo, J., & Ramirez, C. 1998. A bioclimatic classification of Chile: woodland communities in the temperate zone. Plant Ecology 136: 9-26.

Armesto, J. J., Casassa, I., & Dollenz, O. 1992. Age structure and dynamics of Patagonian beech forests in Torres del Paine National Park, Chile. Vegetatio 98(1): 13-22.

Armesto, J. J., Rozzi, R., Smith Ramirez, C., & Arroyo, M. T. K. 1998. Conservation targets in South American temperate forests. Science Washington D C. Nov., 2825392, 1271-1280.

Armesto, J.J., Smith-Ramírez C., León P., Arroyo, M.T.K. 1992. Biodiversidad y Conservación del Bosque Templado en Chile. Ambiente y Desarrollo. 8: 19-24.

Arroyo, M. T. K., Marticorena, C., Matthei, O. and Cavieres, L. 2000. Plant invasions in Chile: Present patterns and future predictions. H. A. Mooney and R. J. Hobbs. (eds). *Invasive species in a changing world*. pp 385-421. Island Press. Washington, D.C.

Arroyo, M. T. K., Riveros, M., Peñaloza, A., Cavieres, L., & Faggi, A. M. 1995. Phytogeographic relationships and regional richness patterns of the cool temperate rainforest flora of Southern South America. In: R. Lawford, P. Alaback, & E. R. Fuentes (eds). *High latitude rain forests of the west coast of the Americas: Climate, hydrology, ecology and conservation*. pp. 134-172. Springer-Verlag. Berlin.

Barkman, J.J., Doing, H. and Segal, S. 1964. Kritische Bermerkungen und Vorshlaege zur quantitativen Vegetationsanalyse. Acta Bot. Neerl. 13: 394-419.

Benoit, I. 1989. Libro Rojo de la Flora Terrestre de Chile. Corporación Nacional Forestal.

Ministerio de Agricultura. República de Chile. Santiago, Chile.

Burns, B. R. 1993. Fire-induced dynamics of *Araucaria araucana-Nothofagus antarctica* forest in the southern Andes. J. Biogeogr. 20: 669-685.

Burns, B.R. 1991 The regenerations dynamics of *Araucaria araucana*. Thesis for the Doctor Philosophy degree. University of Colorado. Boulder, Colorado.

Casertano, L. 1963. General characteristic of active andean volcanoes and a summary of their activities during recent centuries. Bulletin of the Seismological Society of America. 53:6.

D'Antonio, C. M., Dudley, T. L., & Mack, M. (1999). Disturbance and biological invasions: direct effects and feedbacks. In: L. R. Walker (ed.), *Ecosystems of disturbed ground.* Elsevier. Amsterdam.

Donoso, 1993. Bosques templados de Chile y Argentina. Variación, estructura y dinámica. Editorial Universitaria. Santiago, Chile.

Eskuche, U. 1973. Estudios Fitosociológicos en el Norte de Patagonia. Investigación de algunos factores de ambiente en comunidades de bosque y chaparral. Phytocoenologia 11: 64-113.

Eskuche, U. 1999. Estudios fitosociológicos en el norte de la Patagonia. II. Los bosques del Nothafagion dombeyi. Phytocoenologia 29(2):177-252.

Finckh, M. & Paulsch A. 1995. *Araucaria araucana* - Die ökologishe Stategie einer Reliktkonifere. Flora 190:365-382.

Finckh, M. 1996. Die Wälder des Villarrica-Nationalparks Südchile- Lebensgemeinsschaften als Grundlage für ein Schutzkonzept. Dissertationes Botanicae. Band 259. J. Cramer. Berlin-Stutgart.

Gajardo, R. 1994. La vegetación natural de Chile. Clasificación y distribución geográfica. Editorial Universitaria. Santiago, Chile.

Global Volcanism Program. 2001. Volcanic Activity Reports: Llaima. Smithsonian National Museum of Natural History. http://www.volcano.si.edu/gvp/volcano/region15/andes_c/llaima/var.htm 04/23/01

Hayek, E. and Di Castri, F. 1975. Bioclimatografía de Chile. Universidad Católica de Chile. Santiago, Chile.

Hill, M. O., & Gauch, H. G. J. 1980. Detrended correspondance analysis: An improved ordination technique. Vegetatio 42: 47-58.

Hilldebrand-Vogel, R., Godoy, R. & Vogel, A. Subantarctic-Andean Nothofagus pumilio forests. Distribution area and synsystematic overview: vegetation and soils as demonstrated by an example of a South Chilean stand. Vegetatio 89:55-68.

Lara, A., Donoso, C. & Aravena J.C. 1995. La conservación del bosque nativo de Chile: problemas y desafíos. En: Armesto, J.J., Villagrán, C. y Arroyo, M.K. Ecología de los bosques nativos de Chile. Editorial Universitaria. Santiago, Chile.

Lara, A., Rutherford, P., Montory, C., Bran, D., Perez, A., Clayton, S., Ayesa, J., Barrios, D., Gross, M., & Iglesias, G. (1999). Vegetación de la Eco-región de los bosques valdivianos. Informe Final No. Proyecto binacional Chile-Argentina. UACh - INTA - APN - FVSA.

Lazo, A. 1996. La inversión más natural, impulso del ecoturismo en áreas silvestres protegidas. Chile Forestal Abril: 34-36.

Markgraf, V. 1987. Paleoenvironmental changes at the northern limit of the subantarctic Nothofagus forest, latitude 37 degrees South, Argentina. Quaternary Research 281: 119-129.

Marticorena, C. & Quezada, M. 1985. Catálogo de la flora vascular de Chile. Universidad de Concepción. Gayana Bot. 42 (1-2).

Matthei, O. 1995. Manual de las malezas que crecen en Chile. Universidad de Concepción. Concepción, Chile.

McCune, B. & M. J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4.0. MjM Software Design, Gleneden Beach, Oregon. 237 pp.

Montaldo 1974. La bioecología de *Araucaria araucana* (Mol.) Koch. Instituto Forestal Latino'Americano. Boletín Técnico 46. Universidad de Chile. Santiago, Chile.

Mooney, H. A., Fuentes, E., & Kronberg, B.I. (1993). Earth System Response to Global Change: Contrasts between North and South America. Academic Press. New York.

Mueller-Dombois, D. y Ellemberg, H. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons. New York, USA.

Naranjo, J.A. & Moreno, H. 1991. Actividad explosiva postglacial en el Volcan Llaima, Andes del Sur. Revista Geológica de Chile 18(1): 69-80.

Oberdorfer, E. 1960. Planzensoziologishe Studien in Chile Ein Vergleich mit Europa. Flora et Vegetatio Mundi. Verlag Von J. Cramer.

Okland, R. H. 1996. Are ordination and constrained ordination alternative or complementaty strategies in general ecological studies? J. Ved. Sci. 7: 289-292.

Pauchard, A. 1998. La linea de base en la Evaluación de Impacto Ambiental en áreas silvestres protegidas. Bases metodológicas para el componente vegetacional. Memoria para optar al título de Ingeniero Forestal. Universidad de Concepción. Concepción, Chile.

Pauchard, A. Ugarte, E. & Millán, J. 2001. La vegetación como indicador de biodiversidad en estudios de linea de base en áreas protegidas. In: Alveal, K. (ed). *Sustentabilidad de la Biodiversidad. Un Problema Actual, Bases Cientifico Técnicas, Teorizaciones y Proyecciones.* Editorial Universidad de Concepción. Concepción, Chile.

Peralta M. 1975. Tipificación de los Suelos en la formación forestal Araucaria-Lenga en el Parque Nacional Conguillío. Bol. Nº 31. Universidad de Chile. Santiago, Chile.

Puntieri, J., Barthelemy, D., Martinez, P., Raffaele, E., & Brion, C. (1998). Annual-shoot growth and branching patterns in Nothofagus dombeyi (Fagaceae). Can. J. of Bot. 76(4): 673-685.

Ramírez, C. 1978. Estudio florístico y vegetacional del Parque Nacional Tolhuaca Malleco-Chile. M.N.H.N publicación ocasional 24: 3-23. Santiago, Chile.

Richardson, D. M., Pysek, P., Rejmanek, M., Barbour, M. G., Panetta, F. D. &West, C. J. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6: 93-107.

Sakai, A., Paton, D. M., & Wardle, P. (1981). Freezing resistance of trees of the south temperate zone, especially subalpine species of Australasia. Ecology 62(3): 563-570.

Stecconi, M., Puntieri, J., & Barthelemy, D. (2000). Annual shoot-growth in *Nothofagus antarctica* (G. Forster) Oersted (Nothofagaceae) from northern Patagonia. Trees-Berlin 14(5): 289-296.

Ter Braak, C. J. F., & Prentice, I. C. 1988. A theory of gradient analysis. Advances in Ecological Research 18: 271-317.

Thomasson, K. 1959. Nuel Huapi.Plancton of some lakes in an Argentine national park with notes on terrestrial vegetation. Acta Phytogeogr. Suec. 42. Uppsala.

Veblen, T.T., B.R. Burns, T. Kitzberger, A. Lara and R. Villalba. The ecology of the conifers of southern South America. Pages 120-155 in: N. Enright and R. Hill, eds. Ecology of the Southern Conifers. Melbourne University Press.

Veblen, T.T. 1982. Regeneration patterns in *Araucaria araucana* forest in Chile. J. Biogeogr. 9: 11-20.

Veblen, T.T., Donoso, C., Kitzberger, T., Rebertus, A.J. 1996. Ecology of southern Chilean and Argentinean Nothofagus Forests. In: Veblen, Hill & Reed (eds). *Ecology and biogeography of* Nothofagus *forests*. Yale University Press, New Haven.

Villalba, R., Boninsegna Jose, A., Veblen Thomas, T., Schmelter, A., & Rubulis, S. (1997). Recent trends in tree-ring records from high elevation sites in the Andes of northern Patagonia. Climatic Change 36(3-4): 425-454.

Villarroel, P. 1992. Areas silvestres protegidas: ¿Bienvenida a capitales privados?. Ambiente y Desarrollo - Diciembre. Santiago, Chile.

Vitousek, P.M. and P.A. Matson. 1991. Gradient analysis of ecosystems. pp. 287-298. In Cole, J.J., G. Lovett, and S. Findley. (eds.). Comparative Analyses of Ecosystems. Springer Verlag, New York.

Vogel, A. 1998. Beobachtungen zur Regenation der Vegetation nach Ascheeruption am Hudson-Vulkan in südlichen Chile. In: H. Walter & E. Walter (eds.), *Results of ecological studies worldwide*. Proceedings of the 1st Symposium of the A. F. W. Schimper Foundation, Hohenheim.

Table 1. Summary of physiognomic types attributes. Strata abbreviations; T : arboreous, I : intermediate, S: shrub, H: herbaceous. * : *Araucaria araucana*, ** : *Nothofagus dombeyi*, *** : *Nothofagus antarctica*.

Physiognomic Type	Area (ha)	Height range (m)	Basal Area (m2/ha)	Tree Density (No/ha)	Strata	Geological substrate
Nothofagus dombeyi – *Araucaria araucana* forest,	71.8	35-25	36.6*, 50.1**	157*, 193**	T, I, S, H	Old volcanic hill. Pyroclastic deposits.
Araucaria araucana – *Nothofagus antarctica* forest	107.5	30-10	8.0*	43*	T, I, S, H	Recent lava plateau. Pyroclastic deposits.
Nothofagus antarctica forest	16.6	10-13	43.4***	1533***	T, I, H	Sedimentary valley bottom.
Berberis spp. shrubland.	8.0	0.3-1.0			S, H	Sedimentary lake shore.
Pyroclastic material	13.8					Bare lapilli deposits
Lake shore	35.0					

Table 2. Phytosociological description of communities in the study area. The abbreviation is indicated in capital letters and the number of relevés in parenthesis.

Nothofagus dombeyi Forests: Class: Nothofagetea pumilionis Order: Nothofagetalia pumilionis Alliance: Nothofagion pumilionis	Sub-alliance: Chusqueo - Nothofagenion pumilionis Association: Gaultherio Nothofagetum dombeyi
***Nothofagus dombeyi-Osmorhiza chilensis* community** NODO/OSCH (3) *Nothofagus dombeyi* and *Araucaria araucana* constitute its canopy story. The intermediate story is dominated by *Chusquea coleu* (Poaceae). The understory presents a low species diversity. This community seems to be in a stand-exclusion state after fire or volcanic disturbance. *Osmorizha chilensis* is one of the few species that is able to survive in these shaded conditions.	***Nothofagus dombeyi-Adenocaulon chilensis* community** NODO/ADCH (8) Community dominated by *Nothofagus dombeyi* and *Araucaria araucana* in its tree layer and *Chusquea coleu* in the shrub layer, with a higher understory diversity than NODO/OSCH. (e.g. *Adenocaulon chilensis*, *Osmorhiza chilensis*, *Gaultheria phyllerifolia*). Volcanic disturbance and fires presumably has been of lower intensity in these forests (Veblen 1982).
Nothofagus antarctica Forests: **Phytosociological classification:** Class: Nothofagetea antarcticae Order: Nothofagetalia antarcticae	Alliance: Nothofago-Berberion Suballiance: Ribesi-Nothofagenion
***Nothofagus antarctica* - *Chusquea coleu* community** NOAN/CHCO (21) Community dominated by *N. antarctica* and *A. araucana* in its tree layer, a shrub layer (sometimes absent) of *Chusquea coleu*, and a dense dwarf shrub layer (e.g. *Pernettya myrtilloides*, *Ribes cucullatum*, *Senecio glaber*). It occupies small depressions and river terraces with a groundwater level close to the surface, representing a transition between *N. antarctica* and *N. dombeyi* forests. Gajardo (1994) described a similar *Nothofagus antarctica* community for cold Andean valleys and Eskuche (1973) studied in the Lanín NP similar *Nothofagus antarctica* communities on valley bottoms.	***Nothofagus antarctica* - *Pernettya pumila* community** NOAN/PEPU (8) Tall shrubland community dominated by *N. antarctica*, with regeneration of *A. araucana* and a herbaceous layer of *Pernettya pumila*, *Anthoxantum juncifolium* and *Festuca scabriuscula*. *N.antarctica* is frequently parasited by *Misodendron punctulatum*. It grows on old lava fields associated to extreme water stress in summer. Gajardo (1994) classifies it as *Araucaria araucana - Festuca scabriuscula* community.
***Nothofagus antarctica* - *Embothrium coccineum* community** NOAN/EMCO (13) Forest community dominated by *N. antarctica* y *A. araucana*, together with border species like *Embothrium coccineum*, *Schinus patagonicus*, *Ribes magellanicum*, *Alstroemeria aurantiaca*, *Discaria chacaye* and *Lomatia hirsuta*. It occupies the eastern hills of the study area, in intermediate soil moisture conditions. The community has a close floristic similarity to the Lomatio-Nothofagetum antarticae (Eskuche, 1973).	***Berberis buxifolia* - *Acaena pinnatifida* community** BEBU/ACPI (10) Shrubland community dominated by *Berberis buxifolia*, *Fragaria chiloensis*, *Ribes cucullatum* and *Solidago chilensis*. It represents extreme ecological conditions close to the water line of Conguillío Lake, with pronounced seasonal fluctuations.
Grassland: No phytosociological classifications has been made for these type of communities in Northern Patagonia	
***Solidago chilensis* - *Phacelia secunda* community** SOACH/PHSE (4) Pioneer community with a low total coverage dominated by *Solidago chilensis* and *Phacelia secunda*, growing on the winter flooded Lapilli-beaches of Lake.	

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