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Simulating current regional pattern and composition of Chilean native forests using a dynamic ecosystem model

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Master thesis, 30 credits, in Physical Geography and Ecosystem Analysis

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Abstract

Native forests are one of the most important natural resources in Chile whose distribution area has been drastically reduced by land-use changes associated to agriculture, monoculture-based forestry, selective logging and urban development during the last two centuries. Due to Chilean native forests are characterized by having a high economic and ecological value, it is important to have efficient tools that allow assessing the impacts of different factors such as climate change and land-use changes on those ecosystems. In this sense, dynamic global vegetation models (DGVMs) can be used as an effective tool that can guide decision-makers to create appropriate adaptation and mitigation policies. In this study, a DGVM adapted for regional scale studies, LPJ-GUESS, was applied to simulate the current potential regional pattern and composition of native forests located in south-central Chile (31°S-56°S). In order to meet this goal a set of plant functional types (PFTs) representing the majortaxa in this area was created and parameterized. To evaluate the simulated distribution pattern and the simulated vegetation composition, the models outputs were qualitatively compared against a map of natural Chilean vegetation and selected sites respectively. LPJ-GUESS captured the general distribution of high-Andean steppe and temperate rain forests. In the case of sclerophyllous forests/shrublands and cool deciduous forests/woodlands (dominated by *Nothofagus pumilio*), the model underestimated the presence of their main components (i.e. PFTs) in the northern area of their distribution. Temperate deciduous forests dominated by *Nothofagus obliqua*, *N. glauca* and *N. alpina* were not simulated. At site level, LPJ-GUESS predicted the general composition of coastal temperate rainforests (41.5 and 42°S), Magellanic rainforest (56°S) and cool deciduous forests (46°S). In general, the model failed to capture the vegetation composition in sites located in Andean region between 38°S and 40.5°S. As a conclusion LPJ-GUESS predicted the main regional distribution patters of the mayor Chilean native forest but failed in capturing the main forest composition in three of the seven test sites, especially at sites located in the Andes Cordillera. These results suggest that the PFT parameterization and the input used in this study to run the model are more appropriate for regional studies than at site level.

Keywords: LPJ-GUESS, temperate rain forest, vegetation composition, plant functional types, Sclerophyllous forests/shrublands, Magellanic rain forests, south-central Chile

Resumen

Dentro de los recursos naturales más relevantes de Chile están los bosques nativos. A pesar de su amplia distribución en el país, su superficie ha sido drásticamente disminuida durante los dos últimos siglos, especialmente debido a los continuos cambios en el uso de la tierra asociados a la agricultura, a la tala selectiva, al monocultivo de especies exóticas y al desarrollo urbano. Debido a que los bosques nativos chilenos se caracterizan por poseer un alto valor económico y ecológico resulta imperioso el contar con herramientas eficaces que permitan valorar los impactos de diferentes factores tales como el cambio climático y cambios en el uso de la tierra en estos ecosistemas. En este sentido, los modelos globales de vegetación dinámicos (DGVMs) pueden ser utilizados como una herramienta efectiva que puede guiar a los tomadores de decisiones en la creación de medidas de mitigación y adaptación. En el siguiente estudio, un DGVM adaptado para estudios a escala regional, LPJ-GUESS, fue aplicado para simular los patrones potenciales de distribución actual y la composición de los bosques nativos localizados en el centro-sur de Chile (31°S-56°S). Para cumplir con este objetivo se creó y parameterizó un conjunto de nuevos tipos funcionales de planta (TFPs) que se espera representen las taxas más representativas de los bosques nativos chilenos. Para evaluar los patrones de distribución y la composición de la vegetación simulados, los resultados del modelo fueron contrastados cualitativamente contra un mapa de vegetación natural de Chile y con la vegetación descrita para diferentes sitios respectivamente. LPJ-GUESS capturó la distribución general de la estepa altoandina y bosques lluviosos temperados. En el caso del matorral y bosque esclerófilo y de los bosques caducos fríos (dominados por *Nothofagus pumilio*), el modelo subestimó la presencia de sus principales componentes (TFPs) en el área norte de sus respectivas distribuciones. Los bosques caducos dominados por *Nothofagus obliqua*, *N. glauca* y *N. alpina* no fueron simulados. A nivel de sitio, LPJ-GUESS predijo la composición general de los bosques templados lluviosos costeros (41.5 y 42°S), bosques lluviosos magallánicos (56°S) y bosques fríos caducos (46°S). En general, el modelo falló en reproducir la composición vegetacional en los sitios localizados en la región andina entre los 38°S y 40.5°S. Se concluye que LPJ-GUESS predijo los principales patrones de distribución regional de los bosques nativos chilenos, pero falló en capturar la composición vegetacional en tres de los siete sitios de testeo, especialmente en aquellos localizados en la Cordillera de los Andes. Estos resultados sugieren que la parameterización de los TFPs y los input utilizados al aplicar el modelo en este estudio son más apropiados para estudios regionales que a nivel de sitio.

Keywords: LPJ-GUESS, bosques lluviosos templados, composición vegetacional, tipos funcionales de planta, matorral bosque esclerófilo, bosques lluviosos magallánicos, Chile central y sur.

Contents

1. Introduction

Native forests cover 13.6 million ha in Chile which represents approximately 18% of the country area (CONAF 2011). These forests include mediterranean forests (e.g. sclerophyllous forests) and temperate rainforests (Lara et al. 2009) which have been negatively affected by drastic land-use changes associated with agriculture, selective logging, monoculture-based forestry, and urban development (Armesto et al. 2009). At present, most of the Chilean native forests are found in Valdivian Ecorregion (35°-48°S); region that accounts for more than half of the temperate rainforests of southern hemisphere (Lara et al. 2009; DellaSala et al. 2011). In a global scope the temperate rainforests have the highest living biomass accumulations in the world (aboveground biomass equal to 14 934 ± 13 562 g C m^{-2} and belowground biomass equal to 4626 ± 4673 g C m^{-2}) and represent the second most productive forest type after tropical humid evergreen forests with net primary productivity (NPP) equal to 783 ± 45 g C m^{-2} $year^{-1}$(Luyssaert et al. 2007). Furthermore, Chilean natural ecosystems are characterized by a large floristic richness, high degree of endemism (Tecklin et al. 2011) and an extremely low deposition of nitrate and ammonium (Armesto et al. 2009) which has given this region a high conservation priority worldwide (Myers et al. 2000).

Chilean native forests support fundamental ecological functions, which provide a wide range of ecosystem services such as firewood, timber products, water supply (both quantity and quality), tourism, recreation, biodiversity conservation and carbon sequestration. These services have been shown as important factors that directly or indirectly benefit the society (Nahuelhual et al. 2007; Lara et al. 2009). Under a context of a rapid climate and land-use change, some of ecosystem services, such as the forests capacity to sequester carbon and its stabilizing effect on the terrestrial water-cycle, have received particular attention (Morales et al. 2007; Lara et al. 2009). For instance, some studies in Chile have shown a positive relationship between native forest cover and summer runoff (Lara et al. 2009; Little et al. 2009). The fast-expanding monocultural plantations of exotic species (mostly *Pinus radiata* and *Eucaliptus spp*.), on the contrary,reduce water yield which might have negative consequences to water availability for ecosystems and human activities if native forest conversion to forest plantation is increased (Little et al. 2009). Regarding carbon sequestration, temperate forests, in particular old-growth temperate rainforests, are considered to be very important for the carbon storage (Luyssaert et al. 2008; Keith et al. 2009).The slow decomposition rate of large volume snags and logs, long tree life spans and slow growth rate determine a high carbon storage capacity in Chilean old-growth temperate forests (Carmona et al. 2002; Armesto et al. 2009). Therefore, understanding the likely changes in carbon and water exchange associated with a changing climate and land-use are important for policy makers to deal with greenhouse gas mitigation and native forest degradation (Morales et al. 2007; Lara et al. 2009). For example, positive impact of the native forests on water yield would contribute to minimize adverse climate change effect, especially in densely populated south-central Chile. Climate models have projected a drastic reduction in precipitation up to 40% in summer for this region under the most severe scenario (DGF 2006). On the other hand, decline of old-growth forest cover can drastically reduce carbon storage capacity of the landscape and their replacement by plantations, pastures and shrublands can additionally affect carbon cycling (Armesto et al. 2009).

Taking into account that global warming and land-use change are expected to affect the ecosystems services (e.g. water yield and carbon storage) provided by native forests in Chile, it is important to have efficient tools that allow assessing those impacts in order to create effective mitigation and adaptation policies. The dynamic global vegetation models (DGVMs)have been widely used as tools for studying vegetation dynamics (e.g. Smith et al. 2001; Hickler et al. 2004b; Tang et al. 2012), and associated changes in the carbon and water cycles, as a response to climate change and other drivers of ecosystem processes, such as changes in land-use or atmospheric CO_2 concentration, at regional and global scale (e.g. Olofsson and Hickler 2008; Morales et al. 2007; Hickler et al. 2012; Miller and Smith 2012).Being a key tool to provide useful inputs for the decision-making processes, DGVMs have not been used for regional scale studies in Chile. Only a few stand level studies have attempted to model the dynamics of Chilean native woodland (Gutierrez and Huth 2012) and the impacts of harvesting scenarios (Rüger et al. 2007). At both cases process-based forest growth models were applied.

In the present study a DGVM adapted for regional scale simulations of vegetation dynamics, LPJ-GUESS (Smith et al. 2001), is applied to simulate the current potential regional pattern and composition of Chilean native forests. The correct application of this model under current climate conditions would allow projecting the magnitude of the future climate and land-use change impacts on vegetation and associated ecosystem processes

The main goal of this study is to apply the LPJ-GUESS model and evaluate its performance in capturing the spatial distribution and species composition of the major native forest types located in south-central Chile (31°S-56°S). In order to meet this goal the present study aims to: (1) determine and parameterize a novel set of PFTs representing the major taxa for south-central Chile, (2) simulate the spatial distribution of current potential natural vegetation and evaluate results against a map of natural Chilean vegetation, and (3) evaluate the simulated vegetation composition with available observational data on forest composition and dynamics from selected sites.

1. Background

1.1.General outlines of physical geography of Chile

The continental Chile is characterized by impressive geographical contrasts. Its long latitudinal extent for 4337 km along the south-margin of South America from *Altiplano* highs at 17°35'S to Cape Horn at 56° S and its narrow width that rarely extends more than 200 km create a vast variety of natural environments and lead to dramatic variations in bioclimatic conditions. The Chilean vegetation ranges from the desert and steppe biomes in arid north to the humid temperate rainforests in the south (Moreira-Muñoz 2011). Chilean landscapes are strongly affected by tectonic forcing related to the east-directed subduction of Nazca Plate beneath the South American Plate making the country highly prone to severe earthquakes and active volcanism (Pankhurst and Hervé, 2007).

Taking into account its morphostructural features, five broad zones are differentiable on the Chilean territory (Moreira-Muñoz 2011):

i. The Coastal Cordillera. It occupies the western part of the country from 18°S to Chiloé Island (42°S) reaching elevation of 2000 meters above sea level (m.a.s.l.) at north-central Chile.

ii. The Central Depression. It is a narrow tectonic basin filled with volcanic materials and sediments derived from the weathering and erosion of the Andes (Armesto et al. 2007). It ranges from 18°S to Copiapó (27°S) and again from Santiago (33°S) to Chiloé (42° S). It is absent between 27° and 33° where mountains chains with an east –west orientation interrupt it. This region encompasses the main agricultural area of the country and is highly urbanized.

iii. The Andean Cordillera. It is the main mountain range along the country. It extends from 18° to 42° S reaching elevation above 4000 m.a.s.l. at north-central Chile (Fig.1).

iv. Patagonian Cordillera. It corresponds to the Andes continuation right down into Tierra del Fuego. The west-southern margin of the land from 42° S to the south is modeled by recent glaciations creating fjords and archipelagos. This part of Cordillera reach a maximum of 4050 m.a.s.l. and contain several active volcanoes (Veblen 2007)

v. The Andean foreland of the southern Patagonian Cordillera.

1.1.1. Climate

The morphostructural features, the latitude and oceanographic and atmospheric components are the main factors affecting the climate along latitudinal and altitudinal gradients in Chile (Luebert and Pliscoff 2006).

The precipitation patterns in Chile are strongly influenced by geomorphology. In the spatial domain of this study (from 31°S to 56°S), the Andes represents an obstacle for tropospheric flow maintaining, in general, moist conditions at mid-latitudes to the west compared to opposite conditions to the east (Garreaud et al. 2008). As Andes the Coastal Cordillera acts as a physical barrier and produces a strong rain-shadow effect, intercepting moist oceanic air and causing a decrease in precipitation rate in Central Depression (Armesto et al. 2007). For example, at ≈ 40°S in the Coastal Cordillera the annual precipitation rate can reach values about 2540 mm but in the Central Depression the rainfall decreases to 1267 mm (Luebert and Pliscoff 2006). The subtropical anticyclone (a high-pressure center located around 30° S off the Pacific coast of southern South America) primarily explain the drier conditions in the northern part of the study area (≈170- 902 mm year^{-1} between 31°S and 33°;Luebert and Pliscoff 2006) and its yearly N-S displacement promotes the seasonal precipitation cycle with regular rainfall in winter at central Chile (Garreaud et al. 2008).The Humbold Current, that moves cool water from subantarctic regions, produces a decrease in coastal temperatures in north-central Chile enhancing the aridity conditions in northern areas (Orme 2007). Finally, both the cold Antarctic anticyclone and the cold south Atlantic anticyclone are responsible for the decrease in annual precipitation from 47°S southwards (Luebert and Pliscoff 2006).

In general, annual precipitation gradually increases toward south reaching a maximum annual rate between 47°and 50° S (Fig. 1). The spatial variation in precipitation is also positively associated to altitude. One of the main climatic features of central Chile (between 31° ~ 37°S) is the large inter-annual variation in precipitation. Associated to El Niño–Southern Oscillation (ENSO), the rainfall amounts vary considerably from year to year occurring dry periods of one or more years long. The precipitation decreases from west to east in south Chile because of the rain-shadow effect produced by the Patagonian Cordillera (Luebert and Pliscoff 2006).

Mean annual temperatures generally decrease with increasing altitude and latitude. However, they are lower in coastal areas than at low interior lands of Central Chile due to Humbold current (Fig. 1). Unlike precipitation, the temperature latitudinal variations are less pronounced between 31° and ~ 40°S. From ~ 40°S southwards, the latitudinal effect becomes stronger producing a north-south gradient with a small longitudinal variation due to a lower altitude of the Patagonian Cordillera (Luebert and Pliscoff 2006). The changes in precipitation and thermal regimens along the country lead to great climate diversity over relatively short distances.

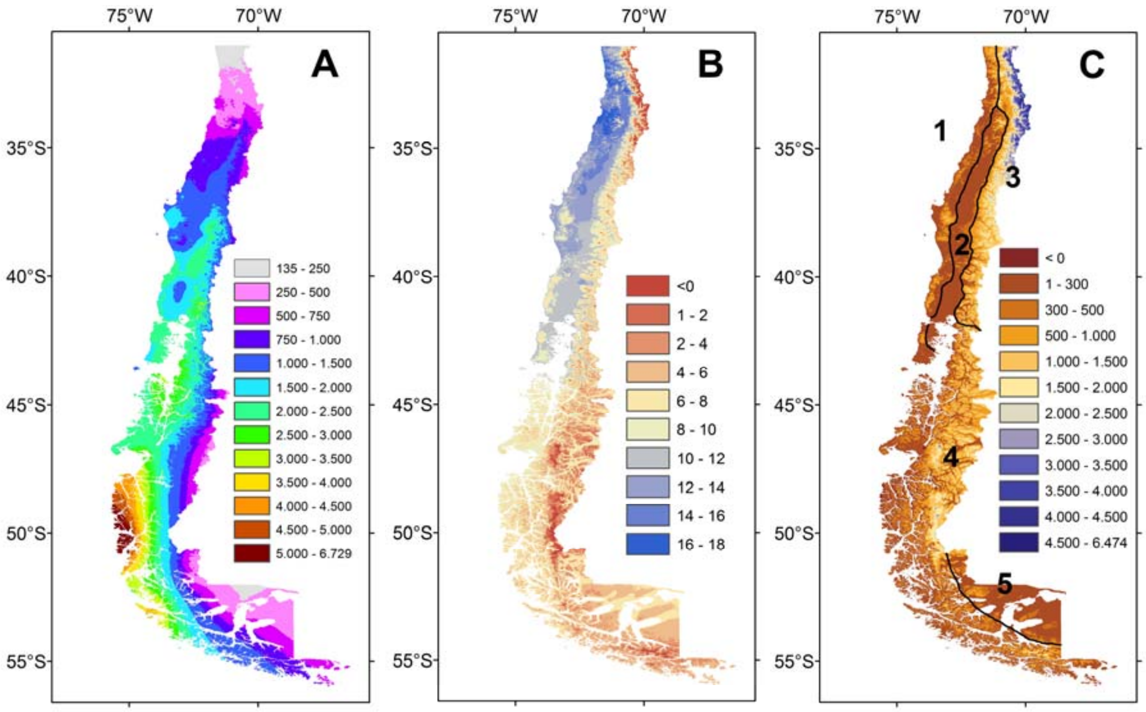

Fig. 1 Physiographic features of South-central Chile based on Hijmans et al. (2005)available in http://www.worldclim.org/. **(A)** Annual Precipitation (mm year^{-1}); **(B)** mean annual temperature (°C) and **(C)** elevation from Shuttle Radar Topography Mission (SRTM; m.a.s.l); (1) Coastal Cordillera; (2) Central Depression; (3) Andean Cordillera; (4) Patagonian Cordillera; (5) Andean foreland. Morphostructural features adapted from Moreira-Muñoz (2011).

A new bioclimatic zonation considering the classification scheme promoted by Amigo and Ramirez (1993) has been proposed by Luebert and Pliscoff (2006) for Chile. Three macrobioclimate (highest rank of the framework) zones (Fig. 2) are found in investigation domain:

i. *Mediterranean-type macrobioclimate*. It extends from the southern limit of the Tropical macrobioclimate (at 23°S at the coast and at 31°S in the high Andes) up to 37° S at coast and Andes and up to 39° S in the Central Depression. This macrobioclimate is characterized by cold-wet winters with a positive water balance and by warm-dry summers with a negative water balance. In northern part of the zone the annual precipitation is < 100 mm with a dry season between 8 and 11 months, at southern limit the precipitation reaches approximately 1300 mm year^{-1} with a dry season between 6 and 8 months (Luebert and Pliscoff 2006). Unlike other Mediterranean regions, in this climatic regime summer rainfall (i.e. convective thunderstorms) and associated lightning are uncommon which explain the low occurrence of natural fires and its negligible importance as disturbance agent in Central Chile (Armesto et al. 2007). Depending on annual water balance, this macrobioclimate presents a wide range of vegetation types including xerophitic formations in the north, and sclerophyllous and hygrophyllous species under more humid conditions at south-central Chile (Luebert and Pliscoff 2006).

ii. *Temperate macrobioclimate*. It occupies the major area in continental Chile from the limit of Mediterranean-type macrobioclimate until austral tip of the country (~ 53°S), excluding eastern Patagonia and the Magallanes region in the southern territories. It is thermally most homogenous and the higher regularity in annual rainfall results in summers without water deficit (Luebert and Pliscoff 2006). This area has abundant vegetation cover, with forests associated with high levels of humidity.

iii. *Antiboreal macrobioclimate.* It extends along the south-western zone of the Magellanic archipelagos. Rainfall decreases notably from west to east and the temperature decreases toward the south. Peatlands, deciduous forests and scrub, and grasslands are the dominant vegetation in this area (Luebert and Pliscoff 2006).

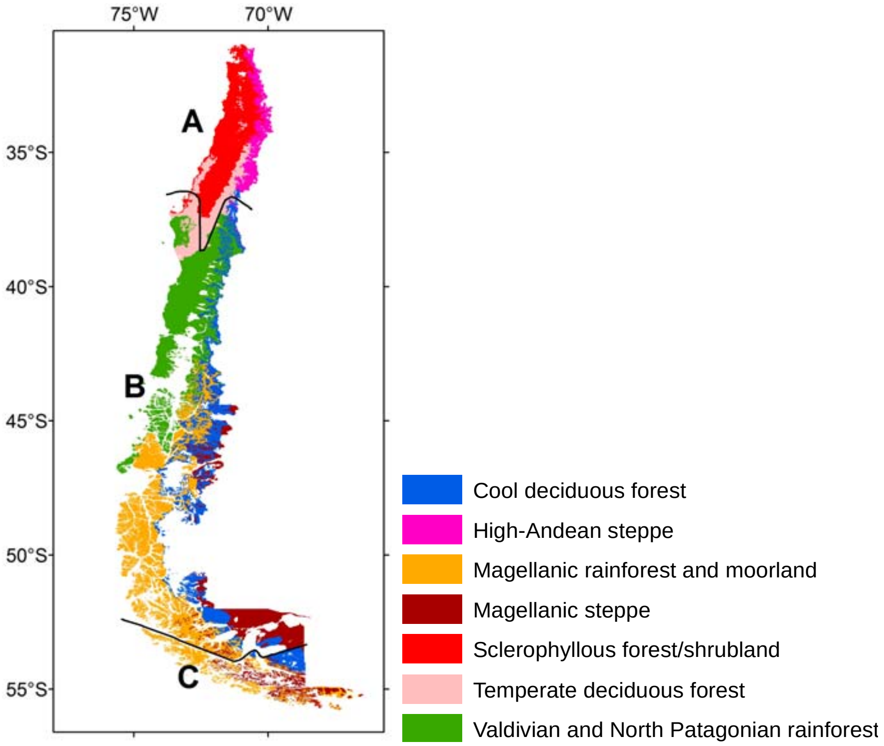

Fig. 2 Major vegetation zones and macrobioclimatic zones defined for southern and central Chile: (A) Mediterranean-type macrobioclimate; (B) Temperate macrobioclimate; (C) Antiboreal macrobioclimate (Adapted from Luebert and Pliscoff 2006)

1.1.2. Regional vegetation patterns

At regional scale, the climate variation is one of the main factors that determine the spatial vegetation variation in Chile (Luebert and Pliscoff 2006). Seven major vegetation zones are found in investigation domain (Fig.2):

i. *High-Andean steppe* (~31°S to~ 38°30'S above ~ 2000 m.a.s.l; Gajardo 1984). It is dominated by low scrub (e.g. *Chuquiraga oppsitifolia, Berberis empetrifolia, Adesmia spp).* Above 3000 m.a.s.l the vegetation is very open (i.e. fragmented vegetation) and is dominated by cushion grasses (Luebert and Pliscoff 2006).

ii. *Sclerophyllous forest/shrubland ("Matorral esclerófilo"*; ~31°S to ~37°30'S). It extends more or less continuously across both slopes of the Coastal Cordillera and into the foothills of the Andes, being more scattered in the Central Depression. Typical species of this plant formation are the evergreen trees *Cryptocarya alba, Lithrea caustica, Quillaja saponaria,* and *Peumus boldus*. In general, the *Matorral* exhibits a patchy spatial structure with open spaces between shrubs but in stands with better hydrological conditions (e.g. along permanent water courses, deep creeks, south-facing slopes in the coastal range) more hygrophyllous woodlands with a continuous, 8-12 m tall canopy appear. These forests are mainly composed of *Crinodendron patagua, Beilschmiedia miersii, Drimys winteri, Luma chequen* and *Persea lingue* (Armesto et al. 2007; Moreira-Muñoz 2011). Along the Central Depression the vegetation is more xerophytic and open woodlands, with the physiognomic aspect of a savanna (*Espinal*, Moreira-Muñoz 2011). These woodlands have a dense herbaceous cover and are mainly dominated by the leguminous trees *Acacia caven* and *Prosopis chilensis.* On dry north-facing slopes the *Matorral* woodland is replaced by a mix of xerophytic deciduous shrubs such as *Trevoa trinervis*, *Flouresia thurifera* and *Colliguaja odorifera*, some bromeliads such as *Puya spp*. and columnar cacti, *Echinopsis* and *Euluchnia spp* (Armesto et al. 2007).

iii. *Temperate deciduous forests* (~34°45'S to ~36°50'S). These forests dominate along the Andes (above 650 m.a.s.l.) and the coastal Cordillera (above 200 m.a.s.l.) surrounding the Central Depression (Veblen et al. 1996). These forests are dominated by broad-leaved deciduous species *Nothofagus obliqua, N. glauca* and *N. alessandrii* and have been strongly affected by anthropogenic activities, especially by monoculture-based forestry (Bustamante et al. 2005). From 36°S toward the northern limit of the temperate rain forest region the deciduous *Nothofagus* species occur in mixed stands with broad-leaved evergreen trees from the Valdivian rain forest (Moreira-Muñoz 2011).

iv. *Cool deciduous forest* (~35°Sto ~55°S). Along Andes deciduous *Nothofagus pumilio* forests occur. These forests extend for approximately 2000 km and grow at both cooler and dryer sites than the temperate deciduous forests. The lower altitudinal limits of this forest vary along its distribution area ranging from 1300 in the north to 0 in Tierra del Fuego (Pollmann and Hildebrand 2005).

v. *Temperate rain forests* (~37°45' to ~47°30'S). They are located in areas with the annual precipitation rates > 1400 mm (with 10% or more occurring during the summer, Alaback 1991) and are dominated by broad-leaved evergreen species. These forests are characterized by extraordinary levels of endemism (e.g. 28 genera of angiosperms out of 82 are endemic; most of them formed by single species, Armesto et al. 1995; Tecklin et al. 2011) and tree species with long lifespan (e.g. conifers trees > 1000 years; broad-leaved trees > 600 years, Armesto et al. 2009; Gutiérrez and Huth 2012). Three mayor forest zones can be found within the temperate rain forest region:

(1) the Valdivian rain forest, 37°45' to 43°20'S,has the maximum forest biomass and arboreal species richness and include broad-leaved evergreen species (e.g. *Aextoxicon punctatum, Eucryphia cordifolia, Laureliopsis philippiana, Dasyphyllum diacanthoides,Weinmannia trichosperma*) as a dominant component and evergreen conifers (e.g. *Fitzroya cuppresoides, Podocarpus salignus*) and broad-leaved deciduous species (*Nothofagus alpina, N. obliqua*) as a minor ones (Armesto et al. 1995; Veblen 2007);

(2) the North Patagonian rain forest, 43°20'S to 47°30'S, is less diverse and productive than Valdivian rain forest (Alaback 1991) and is purely evergreen (Veblen 2007). Dominant species include evergreen *Nothofagus* (*Nothofagus dombeyi, N. nitida* and/or *N. betuloides*) which occurs associated with other angiosperm (e.g. *Tepualia stipularis*, *Drimys winteri*) and/or evergreen conifers (e.g. *Pilgerodendron uviferum, P. nubigena*; Veblen 2007);

(3) the Magellanic rain forest, south of 47°30'S. These forests are subject to colder and more-humid conditions without summer drought and tend to be structurally less species rich (Tecklin et al. 2011). These rain forests occur mainly in the coast and are primarily dominated by evergreen *Nothofagus betuloides* which often forms monotypic stands or co-occurs with few other angiosperm tree species (e.g. *D. winteri, P. uviferum*; Veblen 2007).

vi. *Magellanic moorland.* This vegetative formation appears to the west of the Magellanic rain forest where the precipitation exceeds the 4000 mm year^{-1} and the mean temperature of the warmest month is low (7.5 to 9.0°C). It presents waterlogged soils which are generally nutrient deficient and poor in bases which prevent the growth of dense forests. The moorlands are dominated by *Astelia pumila, Donatia fascicularis, Oreobolus obtusangulus, Bolax caespitosa, Caltha dioneifolia* and *Drapetes muscosa* and scattered *N. betuloides*. Toward the east, in areas of lower rainfall (500 to 2000 mm) but characterized by strongly waterlogged conditions the moorlands are dominated by the moss *Sphagnum magellanicum* (Arroyo et al. 2005).

vii. *Magellanic steppe.* It is located at the eastern side of the low Andes in southern Patagonia and Tierra del Fuego, where a gramineous steppe of *Festuca spp* is the dominant plant formation (Moreira-Muñoz 2011). The steppe composition varies according to the precipitation regimen and the topography which determine the abundance of shrubby species such as *Chiliotrichum diffusum* and *Empetrum rubrum* (Luebert and Pliscoff 2006).

1.1.3. Major disturbance factors in Chilean ecosystems

The main disturbance factors affecting the structure and composition of Chilean forests include natural (such as earthquake-triggered landslides, volcanic activity and wind storms), anthropogenic (such as forest clearing and selective logging) and mixed (can have either a natural or human) origin factors (such as fire; Armesto et al. 2007; Veblen 2007). Regarding natural factors tectonic activity, wind storms and fires generally cause large-scale disturbances producing a whole-stand replacement pattern (> 2500 m^2; Veblen 2007). Tectonic activity is very frequent along the whole country and is characterized by the occurrence of large earthquakes and high frequency of volcanic activity. For any given region in Chile, return period for earthquakes with magnitude equal to or greater than 8 (on the Richter scale) are in the order of 80 to 130 years, but about 12 years when the country is considered as a whole (Barrientos 2007). Regarding volcanic activity, about one eruption per year on average has been reported in south-central Chile (from 33.3°S to 46°S; Stern et al. 2007). The storm winds are restricted to high altitudes at southern Andes and at Tierra del Fuego and have a recurrence time of about 145 years (Rebertus et al. 1997; Veblen 2007). Natural fires mainly affect Andean temperate ecosystems and occur a few times in a century and are practically absent in the Mediterranean region (Armesto et al. 2007; Veblen 2007).

On the other hand, fires ignited by humans used for landscape management and forest clearing to open areas for agriculture, monoculture-based forestry and urban development have been an important source of disturbance especially on mediterranean and temperate rain forests during the last two centuries (Armesto et al. 2007; Armesto et al. 2009). Other disturbance factors that affect Chilean ecosystems are flooding, snow avalanches that occur near tree line and the introduction of exotic plants and animals (Veblen 2007).

1.2.Main land-cover changes in Chile since 5000 years before present (BP)

During the pre-Hispanic period (5000 BP to 1500 AD) the decline of forests has been attributed to the agriculture expansion by aboriginal people who inhabited the south-central Chile along the main river basins (Armesto et al. 2010). In fact, the fire set by aboriginal population is the most probable explanation of the dominance of deciduous *Nothofagus* forests over evergreen trees at low elevations in south-central Chile (Veblen et al. 1979). Large-scale deforestation began with the arrivals of European colonizers in the XVI-XVIIth century. During that period woodlands of much of central Chile (30°S - 35°S) were cleared to open land for agriculture and livestock and to meet the demand of fuel for domestic use and mining operation. From the middle of the XIXth century to the first half of the XXth century, extensive forests areas in south-central Chile were eliminated or fragmented without any concern for the renewal of the resource (Echeverría et al 2006; Armesto et al. 2010). A striking example of this rapid depletion of the native forests was the non-sustainable logging of lowland stands of *Fitzroya cuppresoides* (Alerce)-the longest-lived tree species of the southern hemisphere (Armesto et al. 2010).

The trade reforms implemented in Chile since the mid-1970s have been the main driver for land-use changes in the last decades (Niklitschek 2007). The Law Decree 701 (D.L. 701), through which 75% of the costs of clearing, planting and thinning are reimbursed by the State to the landowner, have promoted a rapid expansion of forest plantation using exotic species (mostly *Pinus radiata* and *Eucaliptus* spp). This land conversion to forest plantation has been made at the expense of native forest and agriculture lands (Armesto et al. 2010). For example, Echeverría et al (2006) estimated a reduction in natural forest area of 67% between 1975 and 2000 (annual forest loss rate of 4.5% per year) in the area of Rio Maule-Cobquecura, south-central Chile (36°S). As plantation forestry is currently the second most important industry in Chile it is likely that the monoculture plantations continue their expansion during this decade (Armesto et al. 2010) altering the ecosystems and related processes, especially, in the region of the temperate rain forests (Armesto et al. 2009).

2. Materials and Methods

2.1. Model description

The Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) is a flexible model that simulates the structure and dynamics of terrestrial ecosystems, using explicit descriptions of physiological and biogeochemical processes and of population dynamics at different temporal and spatial scales (Smith et al. 2001; Sitch et al. 2003). This model combines the general representations of DGVMs (physiological and biophysical processes) with the detailed representations of forests gap models (i.e. detailed representation of tree population dynamics, resource competition and canopy structure; Smith et al. 2001).

A set of plant functional types (PFTs) represent the vegetation in the model. These PFTs are characterized by different structural, physiological, phenological and life history attributes. Bioclimatic parameters determine the establishment of each PFT in a particular zone. LPJ-GUESS simulates the growth of individual trees and shrubs on number of replicate patches, corresponding in size approximately to the area of influence of one large adult tree on its neighbors (0.1 ha). Herbaceous vegetation is also considered, but individuals are not distinguished. Changes in shape and size of each individual have an effect on the resources acquisition and growth of the neighboring vegetation. In this study, the model was run in "cohort" mode which means that each modeled individual plant corresponds to an average individual of a particular cohort (age class) of a PFT. Height and diameter growth are regulated by carbon allocation, the conversion of sapwood to heartwood and a set of prescribed allometric relationships (Smith et al. 2001; Sitch et al. 2003).

LPJ-GUESS has implemented two nested timing loops: a)"fast" processes such as photosynthesis, stomata conductance, autotrophic and heterotrophic respiration, and associated fluxes of carbon and water between soil layers, vegetation and the atmosphere which are simulated on a daily time step and b)"slow" processes such as individual growth, partitioning and distribution of assimilates, population dynamics (including the establishment and mortality of trees and shrub) and disturbance which simulated on an annual basis (Smith et al. 2001; Sitch et al. 2003). The soil water content is simulated using a simplistic two-layer soil hydrology scheme with two layers of fixed thickness (0.5 and 1.5 m respectively) and percolation between layers (Haxeltine and Prentice 1996 cited by Morales et al. 2007). A fire module (Thonicke et al. 2001) predicts the incidence of fire disturbances and its effect on vegetation, based on the length of the fire season and the resistance of each PFT to fire. This determines the fraction of killed individuals due to fires within a burnt area and the annual amount of carbon released into the atmosphere. A detailed description of the model is found in Gerten et al. (2004), Smith et al. (2001) and Sitch et al. (2003). LPJ-GUESS has been tested through field observations corresponding to potential vegetation and carbon and water flux patterns in a number of studies (e.g.

Hickler et al. 2004b; Morales et al. 2005; Hely et al. 2006; Koca et al. 2006; Wolf et al. 2008; Hickler et al. 2012; Tang et al. 2012)

2.2. Study area

The spatial domain of this study corresponds to south-central Chile between 31°S and 56° S (Fig. 3). This area encompasses the native forests that are characteristic to the mediterranean, temperate and antiboreal macroclimates defined by Luebert and Pliscoff (2006).

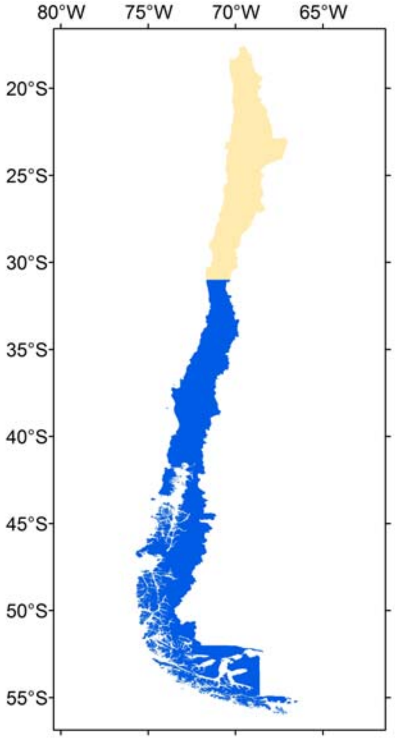

Fig. 3 Continental Chile. The blue area corresponds to south-central Chile.

2.3. Identification of PFTs and parameterization

2.3.1. Structure and content of PFTs

Luebert and Pliscoff (2006) describe the natural potential vegetation under current climatic conditions using two classification levels: 17 “vegetation formations” which are macro-units based on physiognomic and ecological criteria and 127 “vegetation belts” which represent plant communities with a physiognomy and dominant species associated to a specific bioclimatic envelope. In order to represent the main types of native forests of south-central Chile, 14 PFTs were constructed (Table 1) based on Luebert and Pliscoff classification. The “vegetation belts” proposed for the study area were taken into account to infer the dominant species of each kind of vegetation described in the map of the major vegetation zones (MVZ) showed in Fig. 2. The MVZ map corresponds to a modification of the Luebert and Pliscoff’s vegetation formation map and the vegetation limits were established following the methodology described in the Appendix B.

Each PFT encompasses a group of Chilean tree (and/or shrub) species which have similar bioclimatic niches, growth forms, leaf phenology types and life history strategies (Table 1).

i. *Sclerophyllous forest/shrubland*are represented by one evergreen PFT of sclerophyllous species (i.e. MeBE) and two shrubby PFTs (i.e. MeSBD; DSE); respectively.

ii. *Temperate deciduous forests* dominated by *Nothofagus* spp. are represented by two PFTs were (i.e. IBS; MBS), which mainly differ from each other in their tolerance to shade.

iii. *Cool deciduous forests* and *Magellanic rain forests* were represented by a deciduous PFT (i.e. CBS) and evergreen PFT (i.e. CBE) respectively. Additionally, a generic shrub PFT (i.e. CSE) was included to represent small shrubs that are important components in Magellanic and cool deciduous forests.

iv. *Temperate* (*Valdivian and North Patagonian*) *rain forests* are represented by PFTs (i.e. MBE; TBE; IBE; INE; TNE) differentiated based on the leaf type (broadleaved/needleleaved) in combination with shade tolerance.

The vegetation restricted to peatlands (e.g. Magellanic moorland) and wetlands, and species with restricted distribution were not included in the model. The non-woody species were characterized by a generic PFT for herbaceous species with C3 photosynthesis.

Table 1 Plant functional types (PFTs) defined for each ecosystem and their representative species.

Type of ecosystem	PFT	Representative species
Sclerophyllous forest/shrubland	Mediterranean broadleaved evergreen (MeBE) Mediterranean shrub broadleaved deciduous (MeSBD)	*Quillaja saponaria, Lithraea caustica, Peumus boldus, Acacia caven, Prosopis spp*
	Desertic shrub broadleaved evergreen (DSE)	---
Valdivian and North Patagonian rain forests	Temperate shade-intolerant broadleaved evergreen (IBE)	*Embothrium coccineum, Weinmannia trichosperma, Nothofagus dombeyi*
	Temperate shade-mid-tolerant broadleaved evergreen (MBE)	*N. nitida, Eucryphia cordifolia, Drimys winteri*
	Temperate shade-tolerant broadleaved evergreen (TBE)	*Laureliopsis philippiana, Aextoxicon punctatum, Luma apiculata, Persea lingue, Amomyrtus luma*
	Temperate shade-intolerant needleleaved evergreen (INE)	*Fitzroya cuppressoides, Pilgerodendron uviferum*
	Temperate shade-tolerant needleleaved evergreen (TNE)	*Saxegothaea conspicua, Podocarpus nubigena, P. salignus.*
Magellanic rain forest	Cool broadleaved evergreen (CBE)	*N. betuloides*
Temperate deciduous forests	Temperate shade-intolerant broadleaved summergreen (IBS)	*N. glauca, N.oblicua*
	Temperate shade-mid-intolerant broadleaved summergreen (MBS)	*N. alpina*
Cool deciduous forest/woodland	Cool broadleaved summergreen (CBS)	*N. pumilio, N. antarctica*
Magellanic rain forest; Cool deciduous forest/woodland; Magellanic steppe; High-Andean steppe	Cool shrub broadleaved evergreen (CSE)	---
---	Grasses (C3)	---

2.3.2. Bioclimatic parameterization

In LPJ-GUESS the major bioclimatic parameters associated to the establishment of each PFT are: the minimum and maximum temperature of the coldest month (T_{c_min} and T_{c_max}, respectively), the minimum temperature of the warmest month (T_{w_min}) and day-degrees accumulation (GDD_5). These bioclimatic parameters were estimated for each PFT relating the vegetation distribution map associated to the classification of Chilean vegetation belts published by Luebert and Pliscoff (2006) with bioclimatic maps obtained from Worldclim data base (http://www.worldclim.org) with a resolution of 30 arc-seconds (~1 km; Hijmans et al. 2005). This climate data base together with climate information from meteorological stations was used by Luebert and Pliscoff (2006) to create a bioclimatic classification for Chile which was used to construct the Chilean natural vegetation distribution maps.

GDD_5 were estimated as a function of monthly mean temperature (Wang et al. 2006) taking into account the next formula:

$$GDD5 = \sum_{1}^{12} (T\mathrm{m} - 5) \times Nm \qquad with\, T\mathrm{m} \geq 5°\mathrm{C}$$

where GDD_5 is the annual sum of monthly temperatures above 5°C, T_m monthly mean temperature ($T_\mathrm{m} \geq 5°\mathrm{C}$) and *Nm* days number of the month. In LPJ-GUESS a PFT will be not established in a particular coordinate if the mean values of the last 20 years for these variables do not exceed the threshold given in Table 2.

The limiting factors for each forest are described in the literature (e.g. Veblen et al. 1996; Donoso 2006) and they were taken into account in order to rank the importance of each bioclimatic limit in each PFT. For example, the southern distribution limit of mediterranean species (i.e. MeBE and MeSBD) and temperate deciduous trees (i.e. MBS and IBS) are influenced mainly by thermal regime (e.g. low temperatures and low accumulation of GDD_5); therefore, bioclimatic parameters such as $T_{\mathrm{c\_min}}$ and $T_{\mathrm{c\_max}}$ and GDD_5 were considered the most important limiting factors. In the case of temperate rainforests, the main limiting factors that determined their northern and southern distribution limits correspond to water availability and lower temperatures respectively; therefore $T_{\mathrm{c\_min}}$ and $T_{\mathrm{c\_max}}$ and GDD_5were key variables.CBE and CBS have a similar bioclimatic envelope regarding to minimum temperatures that they can resist; however their distribution area in the southern part of the study domain is directly influenced by precipitation regimen. While CBE demands more humid conditions, CBS is more tolerant to dry conditions (precipitation rate < 500 mm; Donoso 2006)

As an additional bioclimatic limit, the fraction of available soil water (*f*AWC) in the first soil layer during the growing season (average daily temperature > 5°C) was included as a measure of a species' ability to endure drought at the sapling stage during establishment (Hickler et al. 2012).This bioclimatic parameter was considered a limiting factor for IBE, TBE, MBE, and CBE (a suitable location for theses PFTs needs a precipitation rate > 1400 mm (with 10% or more occurring during the summer), Alaback 1991)

Table 2 PFTs defined for the model domain and their average bioclimatic limits. It is presented the minimum temperature of the coolest month (T_{c_min}), the maximum of the coolest month (T_{c_max}), minimum temperature of the warmest month (T_{w_min}), day-degrees accumulation for establishment (GDD_5) and the fraction of the plant-available soil water-holding capacity (fAWC) in the first soil layer during the growing season.

PFT	**Bioclimatic limits**[1]				
	T_{c_min} **(ºC)**	T_{c_max} **(ºC)**	T_{w_min} **(ºC)**	**GDD$_5$**	f**AWC$_{min}$**
MeBE	-1.0	16.9	7.0	2200	0.01
MeSBD	1.0	18.0	8.0	2200	0.01
DSE	2.1	19.8	8.0	2200	0.001
IBE	-1.4	13.0	5.0	900	0.45
MBE	-1.4	13.0	5.0	900	0.45
TBE	-1.4	13.0	5.0	900	0.45
INE	-2.0	9.0	4.5	900	0.50
TNE	-1.4	10.0	5.0	900	0.50
CBE	-2.9	5.0	3.7	500	0.50
IBS	-3.0	13.0	7.0	2000	0.25
MBS	-4.5	12.0	7.0	2000	0.25
CBS	-4.4	3.0	4.5	400	0.30
CSE	-12.8	10.0	-1000	300	0.25
Grasses (C3)	----	----	----	----	0.01

[1] All the variables were obtained from Worldclim data base (30 arc-seconds resolution (~1 km). The values are averages from 1950-2000 period. fAWAC_min were estimated from model outputs of fAWAC.

Other PFT characteristics and parameter values used in this study are shown in Tables 3 and 4. When possible, assigned parameters were based on values or relations reported for Chilean species in literature. For PFTs which did not have observation based information for some species, the parameterization was based on the values used to apply LPG-GUESS globally and in Europe. If the information for a parameter was only available for some of species forming a PFT values based on global and European ones were used in order to reproduce the typical forest succession patterns.

Table 3 Additional values estimated for each PFT.

PFT	**Macrobioclimate range**	**Growth form**	**Shade tolerance**^{1}	$k_{la:sa}$^{4}	z_1^{6}	***Leaf lifespan* (yr)**^{25}	***Maximun lifespan* (yr)**$^{3\ 5}$	r_{fire}^{7}	**CA**$_{max}$^{8} **(m^2)**
MeBE	Mediterranean	tree	Tolerant	3500	0.5	3.0	100	0.50	40
MeSBD	Mediterranean	shrub	Intolerant	1500	0.5	0.5	70	0.50	10
DSE	Mediterranean	shrub	Intolerant	1500	0.6	2.0	50	0.30	10
IBE	Temperate	tree	Intolerant	4000	0.7	3.0	587	0.50	40
MBE	Temperate	tree	Mid-tolerant	4000	0.7	3.0	396	0.50	40
TBE	Temperate	tree	Tolerant	4000	0.7	3.0	394	0.50	40
INE	Temperate	tree	Intolerant	3000	0.8	5.0	1510	0.12	40
TNE	Temperate	tree	Tolerant	3000	0.7	4.0	683	0.12	40
IBS	Temperate	tree	Intolerant	4000	0.6	0.5	400	0.12	40
MBS	Temperate	tree	Mid-tolerant	4000	0.6	0.5	600	0.12	40
CBE	Temperate-antiboreal	tree	Intolerant	4000	0.8	3.0	575	0.50	40
CBS	Temperate-antiboreal	tree	Intolerant	4000	0.6	0.5	467	0.12	40
CSE	Temperate -antiboreal	shrub	Mid-tolerant	1500	0.6	2.0	50	0.12	10
Grass	Temperate -antiboreal	grass	-		0.9	1.0		0.50	

[1] Shade tolerance values were obtained from literature for TBE, IBE and MBE (Donoso 2006; Gutiérrez et al. 2009; Lusk 2002; Lusk and Contreras 1999); CBS and CBE (Donoso 2006; Veblen et al. 1996); TNE and INE (Donoso 2006; Gadner and Lara 2003; Gutierrez and Hurt 2012; Lusk 1996); MeEB (Badano et al. 2005; Guerrero and Bustamantes 2005).

[2] Mean leaf lifespan was obtained from literature for TBE, IBE and MBE (Donoso 2006; Gutierrez and Huth 2012; Hevia et al. 1999; Lusk 2002; Lusk and Kelly 2003; Lusk and Contreras 1999; Lusk et al. 2008; Lusk et al. 2003; Lusk et al. 1997; Read and Hill 1985; Souto et al. 2009; Villar and Merino 2001); CBS and CBE (Barrera et al. 2000; Donoso 2006; Hertel et al. 2008; Hevia et al. 1999; Lusk and Contreras1999; Romany et al. 2005; Rusch 1993; Villar and Merino 2001); TNE and INE (Lusk, 2001; Lusk 1996; Lusk and Matus 2000; Lusk et al. 2003; Lusk et al. 1997); MeBE (Lusk et al. 2003; Lusk et al. 2001). Specific leaf area (SLA) was calculated as a function of leaf longevity (Reich et al. 1997)

[3] Mean maximum lifespan values were obtained from literature for TBE, IBE and MBE (Donoso 2006; Gutierrez and Huth 2012; Lusk and del Pozo 2002); TNE and INE (Gutierrez and Huth 2012; Lusk 2001; Lusk 1996; Lusk and Matus 2000; Lusk et al. 2003).

[4] Values of K$_{la:sa}$ (Ratio between leaf area and sapwood area) for IBE, MBE, TBE, IBS, MBS, CBS, CBE, TNE, INE were based on instruction file of the LPJ-GUESS version 2.0. Values of K$_{la:sa}$for MeBE, MeSBD, DES and CSE were proposed by the author.

[5] Leaf lifespan and maximum lifespan values assigned to MeSDB, CSE and DES were suggested by the author taking as reference standard values included in LPJ-GUESS (Smith et al. 2001; Hickler et al. 2012)

[6] Z$_1$ (corresponds to fraction of the fine roots in the upper soil layer) were estimated based on Jackson et al. (1996). For MeBE and MeSEB values were estimated based on Canadell and Zedler (1994).

[7] Values based on Thonicke et al. (2001). Values assigned to MeBE, MeSDB andCSEwere suggested by the author taking as a reference Thonicke et al. (2001).

[8] Values based on Hickler et al. (2012).

Table 4 Parameters associated with different shade tolerance classes.

Shade tolerance	**Tolerant**	**Intermediate**	**Intolerant**
Sapwood to heartwood conversion rate (year^{-1})	0.05	0.065	0.08
Growth efficiency parameter (g C m^{-2} year^{-1})	40	80	100
Max. establishment rate (saplings year^{-1} patch^{-1})	0.05	0.1	0.2
Min. PAR at forest floor for establishment (MJ m^{-2} day^{-1})	1.25	2.0	2.5
Recruitment shape parameter	2	6	10

2.4. Environmental data and simulation protocol

The study was made for current climate (historical period; 1901-2006). The simulation started from a bare ground situation (no plant biomass present), followed by a first phase ("spin up"), that lasted 1000 years to achieve equilibrium in carbon pools sizes with respect to the long-term climate. During this phase climatic data comprising the first 30 years of the historical period were used repeatedly as model input. Following the "spin up" the historical period was simulated. The climate dataset consisted of monthly time series corresponding to mean temperature, precipitation and cloud cover percentage obtained with spatial resolution of 0.5° x 0.5° for the model domain from the climatic database CRU TS 3.0 provided by the Climate Research Unit (CRU), University of East Anglia (Mitchell and Jones 2005). In July 2012 a systematic error was discovered in the CRU 3.1 process generating the precipitation file (http://badc.nerc.ac.uk). Therefore, a new precipitation data file (version 3.10.01) was generated and is now available. Due to CRU 3.1 data are produced using the same methodology as for the CRU 3.0 database (the main difference is that the CRU 3.1 dataset extends up to 2009), the new precipitation file was utilized to run the model. Moreover, it is important to point out that precipitation data from CRU 3.0 underestimated the values given by Worldclim data base and climate data recollected by Luebert and Pliscoff (2006) from meteorological stations. The replacement of CRU 3.0 by the new version of precipitation improved the estimations compared to Wordclim data base and observations; however the differences remained (Appendix A). The soil texture data used in the simulations were based on the FAO soil database (FAO 1991; Sitch et al. 2003). Annual atmospheric CO_2 for the period 1901-2001 were obtained from McGuire et al. (2001) and for 2002-2006 the data set was extended with observation based averages from Mauna Loa Observatory(Hawaii) and Jubany Station (Antarctica).

The model was run with 50 replicate patches. Due to the fact that the expecting return time and the magnitude of the disturbance episodes vary considerably across Chile (e.g. Donoso, 1993; Barrientos 2007; Gutierrez et al. 2008) it was assigned an average expected return time (*d*) of 120 years over the entire model domain and simulation period. In LPJ-GUESS disturbances occur at random, with a probability of (1/*d*) affecting any given patch in a particular year killing all their individuals and converting their biomass to litter (Smith et al. 2001).

2.5. Vegetation data for model evaluation

2.5.1. Spatial distribution

The modeled potential current vegetation was evaluated comparing the simulated distribution of each PFT against their potential distribution delimited in the Chilean vegetation formation map (VFM) built by Luebert and Pliscoff (2006). Moreover, the simulated PFT composition was translated into the main Chilean vegetation types by creating a set of classes according to the rules in Table 5. To make comparable the simulated vegetation with the VFM map, the VFM map was up-scaled and adapted to represent the Chilean native forests by generalizing "vegetation formations" (for methodology see Appendix B). The final map obtained and used for direct comparison corresponds to MVZ map (Fig. 2)

Table 5 Ecosystem classification scheme (TeE=all temperate evergreen PFTs; TeS=all temperate deciduous trees; LAI=leaf area index; Woody LAI = ∑(trees and shrubs LAI).

Chilean forests	**Total LAI**	**Tree LAI**[2]	**Woody LAI**[2]	**Dominant PFTs (LAI)**[1]
Valdivia and North Patagonian rainforest		≥ 1.5		TeE (>0.5)
Temperate deciduous forest		≥ 1.5		TeS (>0.5)
Cool deciduous forest/woodland		≥ 0.5[3]		CBS & CSE (> 0.5)
Magallanic rainforest		≥ 1.5		CBE (>0.5)
Sclerophyllous forest/shrubland			≥ 1	MeBE & MeSBD & DSE (>0.5)
High-Andean steppe	>0.2			Grass (> 0.7)
Magellanic steppe[4]	>0.2			Grass (>0.7)
Arid steppe	>0.2		< 1	MeBE & MeSBD& DSE (>0.5)
Desert	< 0.2			

[1] The dominant PFTs are the PFTs with the highest leaf area index (LAI). Criteria in terms of the fraction of total PFT LAI are given in brackets.
[2] The LAI threshold based on Asner et al. (2003)
[3] Based in the LAI threshold assigned to Boreal broadleaved deciduous forest/woodland biome by Hickler et al. (2004a)
[4] If the PFTs that describe the region are located in the Austral region.

To quantify the agreement between the simulated vegetation and the MVZ map, the Kappa-statistic was applied following Tang et al. (2009). "For each pair of compared observed and simulated vegetation data sets, an error matrix for all observed and simulated vegetation combinations, is constructed. Then, for each category i in the constructed matrix, the Kappa statistic is calculated by the next equation":

$$k_i = \frac{(p_{ii} p_{i.row} p_{col.i})}{((p_{i.row} + p_{col.i})/2 - p_{i.row} p_{col.i})}$$

where $p_{i.row}$ is the row total for each category i; $p_{col.i}$ is the column total for each category i; and p_{ii} is the individual entry for the row and column on the main diagonal of constructed error matrix.

The model's overall Kappa was estimated by the formula:

$$k = \frac{(p_o - p_e)}{(1 - p_e)}$$

where $p_0 = \sum_{i=1}^{c} p_{ii}$; $p_e = \sum_{i=1}^{c} p_{i.row} p_{col.i}$; and c is the number of categories in each data set.

In this study the rating system for the Kappa statistic follows Landis and Koch (1997) and Monserud and Leemans (1992) both cited by Tang et al. (2009) where values greater than

0.75 indicate very good-to-excellent agreement, values between 0.40 and 0.75 indicate fair-to-good agreement, and values of 0.40 or less indicate poor agreement.

2.5.2. Vegetation composition

Additionally, the model was evaluated at site level comparing the simulated vegetation with the composition of native forests reported from literature. Since the basal area (m^2 ha^{-1}) is the variable used to describe the forest composition in the literature (e.g. Gutierrez et al. 2004; Pollmann and Veblen 2004; Gutierrez et al. 2008); the simulated vegetation was compared against observations using the modeled aboveground biomass which is approximately 70% of the total biomass (Schlegel 2001). This methodology follows Hickler et al. (2004b). The protocol for these simulations were the same as for simulating the south-central Chile, however, additional simulations were run taking into account the expecting return time of the disturbance that characterized each site (Table 6). Depending on the geographic region where forests are located different disturbance regimen can affect their dynamic and consequently their structure and composition. In general, Andean temperate forest composition of south-central Chile differs from the forests found in the Coastal Range (Donoso 1993). Andean forests are subjected to periodic catastrophic disturbances such as volcanism, mudflows and massive landslides due to seismic activity determining the prevalence of forests dominated by shade-intolerant species (e.g. *Nothofagus* species) that represent early successional phases (Veblen and Ashton 1978; Veblen et al. 1981). In contrast, in the coastal region, gap-phase dynamics with a low frequency of large-scale disturbance determine forests with a high abundance of shade-tolerant species often lacking *Nothofagus* and other shade-intolerant trees (Gutierrez et al. 2004; Gutierrez et al. 2008).

Table 6 Main features of 7 Chilean sites with native forest.

Site	Lat S	Lon W	Mean annual temperature (°C)	Annual precipitation (mm)	Disturbance		Vegetation	Reference
					Type of disturbance	**Recurrence time (years)**		
Puyehue National Park	40°35'	72°07’	9.2	3500	Coarse-scale disturbance	80-130[1]	Old-growth Valdivian rain forest dominated by i. *Nothofagus dombeyi* and*Eucryphia cordifolia*at 350m.a.s.l. ii. *N.dombeyi*, *Nothofagus betuloides* and *Laurelia philippiana*at 880m.a.s.l iii. *N.dombeyi* and *Nothofagus pumilio* at 1100m.a.s.l. Old growth cool deciduous forest dominated by *N. pumilio*at 1280m.a.s.l.	Pollmann and Veblen (2004)
Pirihueico lake	39°51’	71°50’	10.8	3500-4000	Coarse-scale disturbance	80-130[1]	Valdivian rain forest dominated by i. *Nothofagus alpina* and *L. philippiana*at 800 m.a.s.l. ii. *N.dombeyi*, *N.alpina* at1000 m.a.s.l. iii. *N.dombeyi*, *N.alpina* and*N. pumilio*at 1250 m.a.s.l.	Pollmann (2005)
Tolhuaca National Park	38°13’	71°43’	12.0	2500	Coarse-scale disturbance	80-130[1]	Valdivian rain forest dominated by i. *N. alpine* and *L. philippiana* at 1000 m.a.s.l. ii. *N.dombeyi*, *N.alpina* at 1150 m.a.s.l. iii. *N.dombeyi*, *N.alpina* at 1250 m.a.s.l	Pollmann (2002)
Senda Darwin	41°52’	73°39	9.1	2157	Gaps-phase dynamic[2]	120[3]	Old-growth North Patagonian rain forest dominated by *Podocarpus nubigena*, *N. nitida*, *Weinmannia trichosperma* and Myrtaceas.	Gutierrez et al. (2004)
Guabún	41,6°	73,9°	10.8	2444	Gaps-phase dynamic[2]	120[3]	Old-growth Valdivian rain forest dominated by *E.cordifolia, W. trichosperma, Aextoxicom punctatum*	Gutierrez et al. (2008)
Isla Grande de Tierra del Fuego	53°59’	69°58’	---	500-600	Gaps-phase dynamic	145[4]	Magallanic rain forest dominated by *N. betuloides*	Promis (2009)
Cohaique Natural Reserve	45°52’	72°00’	7.7	1350	Gaps-phase dynamic	145[4]	Old-growthcool deciduous forest of *N. pumilio*	Fajardo and Graaf (2004)

[1] Return periods for magnitude 8 (on the Richter scale) events for any given region in Chile (Barrientos 2007). One single event triggers thousands of mass movement (e.g. landslides, mudflows, rock falls, debris flows; Veblen et al. 1996). These phenomena affect at least an area of 2500 m^2.

[2] Large canopy opening with multiple tree falls (>1000m^2) are infrequent and are caused by severe wind storms (Gutierrez et al. 2008)

[3] Estimation based on Rüger et al. (2007) who calculated a probability equal to 0.8% per year that a certain hectare is affected by wind throw.

[4] Large canopy opening with multiple tree falls (>1000m^2; Rebertus et al. 1997)

3. Results

3.1. Spatial distribution of vegetation

The spatial distribution of forests simulated by LPJ-GUESS and suggested by the MVZ map is shown in Fig. 4. Appendix D shows the simulated distribution of each PFT against its potential distribution suggested by Luebert and Pliscoff (2006). Because the model output includes two new vegetation categories(i.e. desert; arid steppe) and temperate deciduous forests were not simulated (see below), the Kappa statistic was calculated for the area located between 32.5°S and 56°S. To calculate Kappa statistic each map have to be the same number of categories; therefore the two new simulated categories and the class "temperate deciduous forest" were not included in the analysis. The model's overall Kappa statistic was equal to 0.48 which mean that the model was capable of reproducing quite good the main distribution area of the most important Chilean native forests.

i. *High-Andean steppe*. The model captured the general distribution of this vegetation formation (Kappa statistic of 0.65). Nevertheless, LPJ-GUESS simulated a larger area to the west of its distribution where the VFM map shows sclerophyllous forests/shrublands and temperate deciduous forests.

ii. *Sclerophyllous forests/shrublands*. The model predicted a smaller extent of the sclerophyllous forests/shrublands distribution (Kappa statistic of 0.88 only for the area located between 32.5°S and 56°S). In the northern area of their distribution (33.5° northward), LPJ-GUESS underestimated the presence of MeBE, MeSBD and DES PFTs and simulated grasses as a dominant PFT. The leaf area index (LAI) simulated by the model for this area was not enough to classify the ecosystem as a forest/shrublands and a new class had to be introduced: the arid steppe. In their southern distribution border, temperate rain forests were modeled.

iii. *Temperate deciduous forest*. LPJ-GUESS failed to simulate temperate deciduous forests dominated by IBS and MBS PFTs at the transition zone between temperate rain forests and sclerophyllous forests. Instead, the model predicted the dominance of high-Andean steppe in the Andean region and temperate rain forests in the Coastal Cordillera and Central Depression.

iv. *Cool deciduous forests/woodlands*. Although these forests/woodlands were simulated to cover Andean areas in the southern Chile (from 45°S southward) the agreement with MVZ map was poor (Kappa statistic of 0.28). The model did not captured this vegetation type in northern area of their distribution (i.e. between ~35°-37.5°S)and between ~41°-44°S simulating high-Andean steppe and evergreen forests instead respectively. A higher extension of their distribution was modeled westward from ~ 52°S where MVZ map shows Magellanic steppe.

v. *Temperate rain forest*s. In general, the model reproduced the distribution of temperate rain forests (Kappa statistic of 0.51 and 0.50 for Valdivian and North Patagonian rainforest and Magellanic rainforests respectively). LPJ-GUESS correctly simulated the distribution of Magellanic rain forests in the south-western region of Chile from approximately 45° S to southward. However, the model overestimated the extent of these forests in an area where Valdivian and North Patagonian rain forests and cool deciduous forests/woodlands are the dominant ecosystems (i.e. Andean region between 39° and 44° S approximately). Regarding Valdivian and Patagonian forests, LPJ-GUESS incorrectly simulated the dominance of these forests in most areas where temperate deciduous forests potentially occur.

vi. *Magellanic steppe*. In most of the grid cells (e.g. Andean foreland from 50°S southward) where MVZ map suggests this vegetation formation, the model simulated a condition where woody PFTs (i.e. CBS and DES) were more dominant (Kappa statistic of 0.30).

Notable discrepancies between the model outputs and MVZ map occurred in the Andean region between 31.5°S and 34°S approximately. In this region the model simulated desert conditions where MVZ map shows high-Andean steppe.

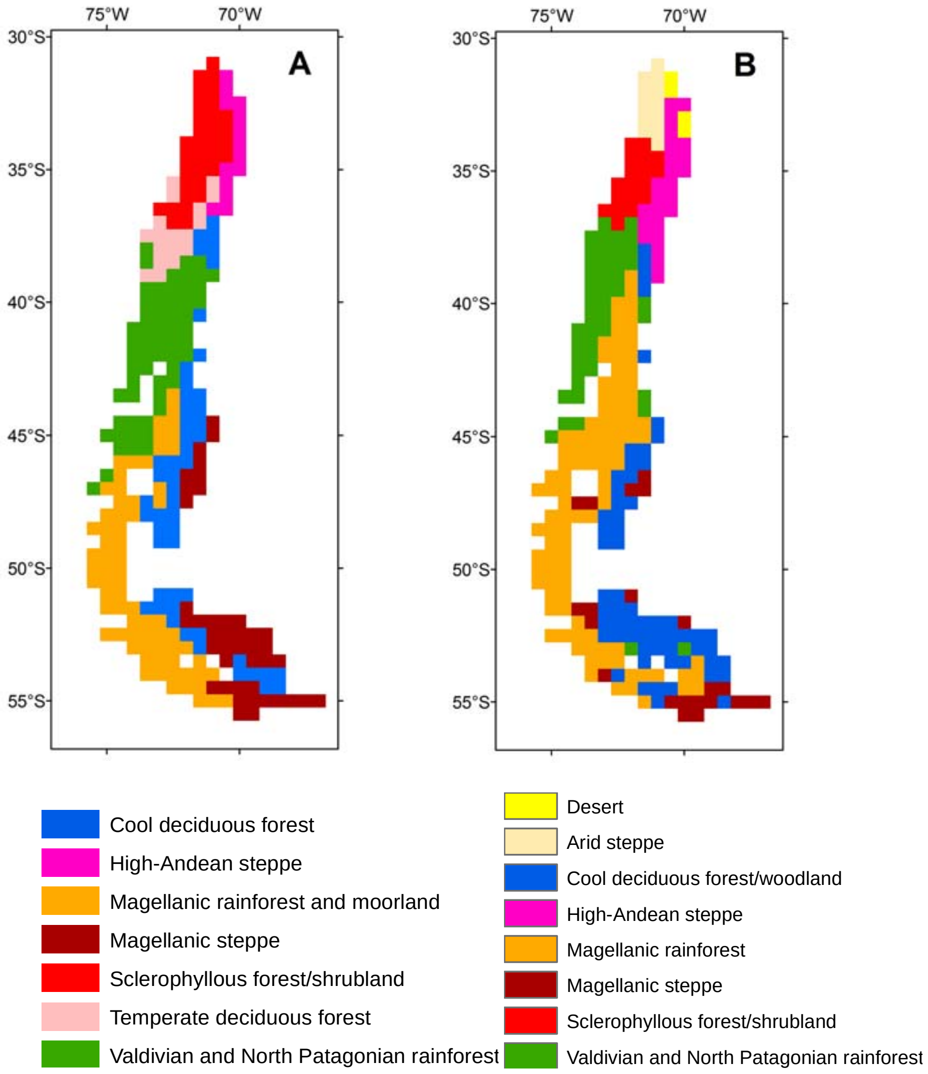

Fig.4(**A**) Current potential vegetation represented by MVZ map and (**B**) simulated vegetation for south-central Chile (average for the period 1950-2000). The MVZ map corresponds to an adaptation of VFM map published by Luebert and Pliscoff (2006) (see Appendix B).

3.2. Vegetation composition

i. *Puyehue National Park*. LPJ-GUESS only captured the forest composition in this test site between 1100 and 1200 m.a.s.l. (Fig. 5). The model simulated correctly the dominance of CBE and TBE for this elevation. When the recurrence time is decreased from 120 to 80 years, the model predicted a similar pattern in the forest composition but with a lower aboveground biomass

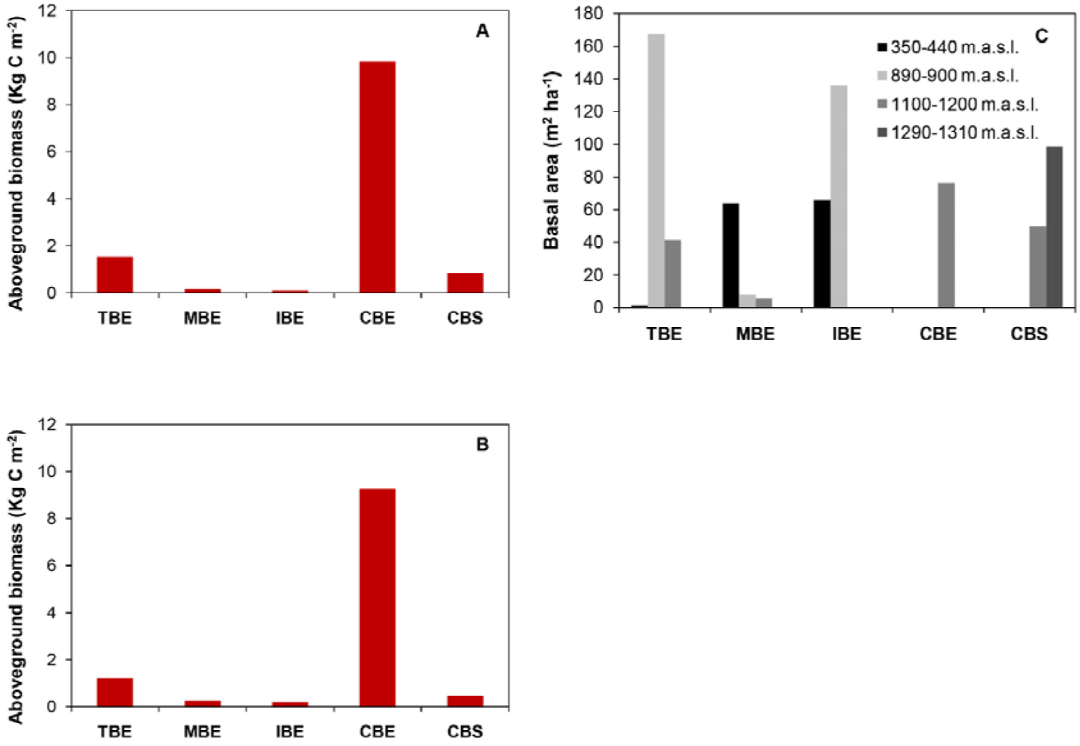

Fig. 5 Simulated vegetation composition with recurrence time of disturbance equal to (**A**) 120 years, (**B**) 80 years and (**C**) observed vegetation composition at Puyehue National Park at different elevations in the simulated grid cell. For **A** and **B** aboveground biomass averages for the period 1974-2004 are showed.

ii. *Pirihueico lake*. In this site, LPJ-GUESS did not predict the composition of the forest at any altitude level (Fig. 6). Instead of simulating temperate summergreen trees (i.e. MBS) as the main component of the forest, the model predicted CBE as dominant PFT.TBE was correctly modeled as a co-dominant PFT. When the recurrence time was decreased from 120 to 80 years, the composition did not change significantly.

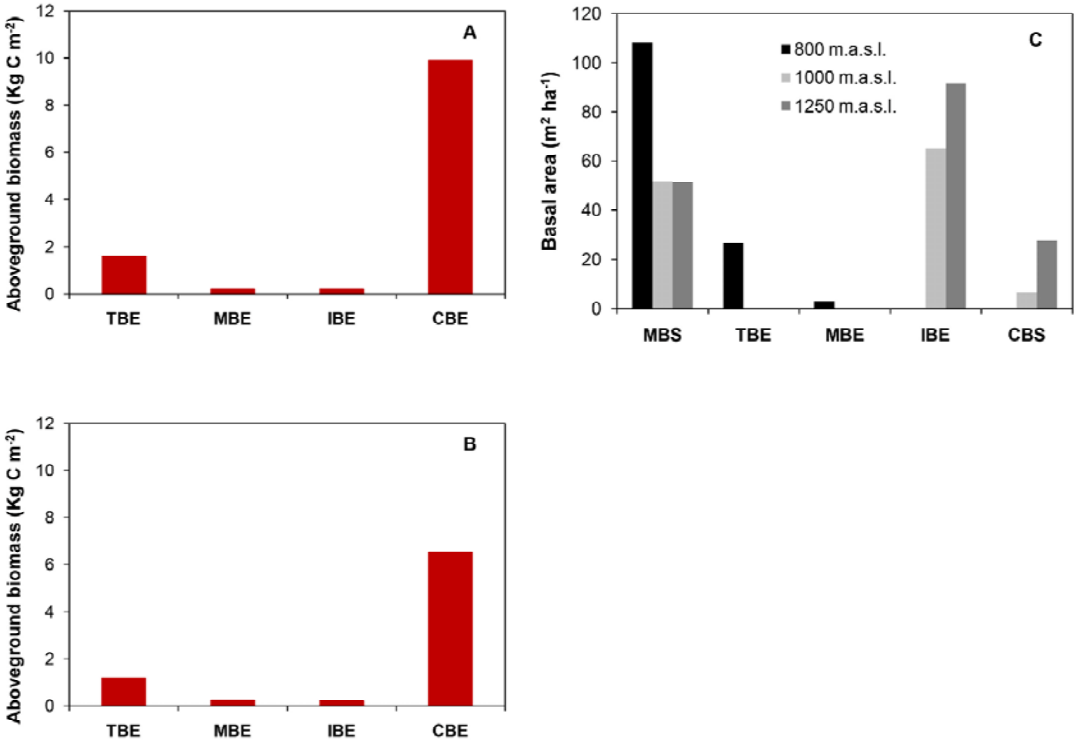

Fig. 6 Simulated vegetation composition with recurrence time of disturbance of (**A**) 120 years, (**B**) 80 years and (**C**) observed vegetation composition at Pirihueico lake at different elevations in the simulated grid cell. For **A** and **B** aboveground biomass averages for the period 1975-2005 are showed.

iii. *Tolhuaca National Park.* The modeled forest composition did not correspond to the vegetation described by the literature for this site (Fig.7). The model predicted CBS and CSE as dominant PFTs in a place where temperate deciduous trees (i.e. MBS) and evergreen trees (i.e. IBE and TBE) are the dominant and co-dominant PFTs respectively. When the recurrence time was decreased from 120 to 80 years, the composition did not change significantly.

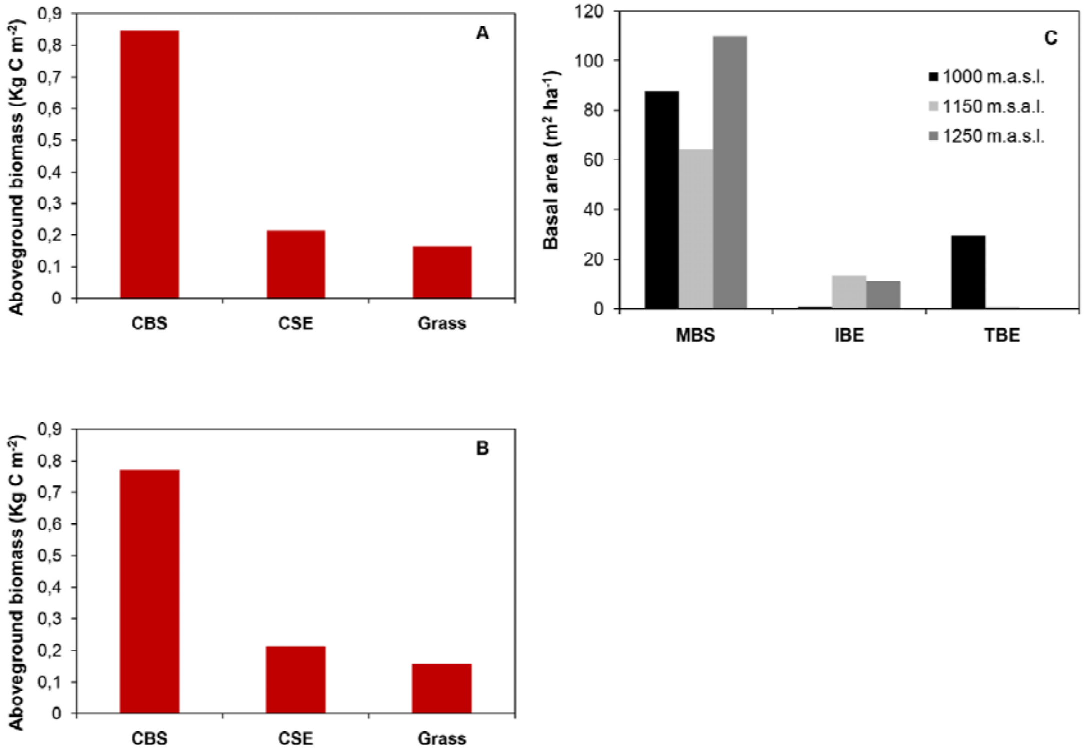

Fig. 7 Simulated vegetation composition with recurrence time of disturbance of (**A**) 120 years, (**B**) 80 years and (**C**) observed vegetation composition at Tolhuaca National Park at different elevations in the simulated grid cell. For **A** and **B** aboveground biomass averages for the period 1972-2002 are showed.

iv. *Guabún and Senda Darwin.* Fig. 8shows the vegetation composition simulated by LPJ-GUESS and the observed composition of North Patagonian and Valdivian rainforests in Senda Darwin and Guabún respectively. In general, LPJ-GUESS predicted the main observed vegetation type; however the model overestimated the presence of shade-tolerant broadleaved trees over shade-intolerant and mid-shade tolerant PFTs (i.e. MBE and IBE) in both places. The model did not predict the sub dominance of needleleaved trees in Senda Darwin.

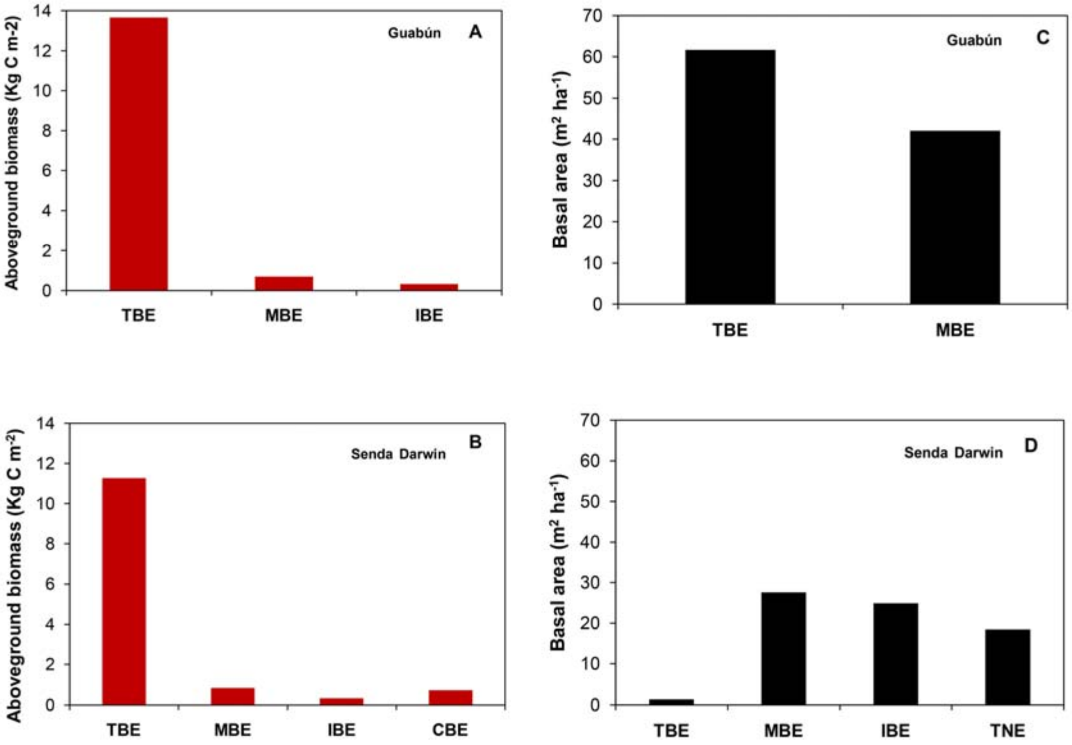

Fig. 8 (**A-B**) Simulated vegetation composition and **(C-D**) observed vegetation composition at Guabún and Senda Darwin. Recurrence time of disturbance = 120 years. For (**A**) and (**B**) aboveground biomass averages for the periods1976-2006 and 1974-2004are showed, respectively.

v. *Isla Grande de Tierra del Fuego and Coyhaique National Reserve*. The model simulated the dominance of CBE and CBS in Isla Grande (Fig. 9) and Coyhaique Natural Reserve (Fig. 10) respectively, which is in agreement with the vegetation described in the literature. In general and in both sites the forest composition were not affected when the recurrence time of disturbance was shifted from 120 to 145 years. The only exception was in Coyhaique National Reserve where the model simulated the presence of CBE only when the recurrence time was 120 years.

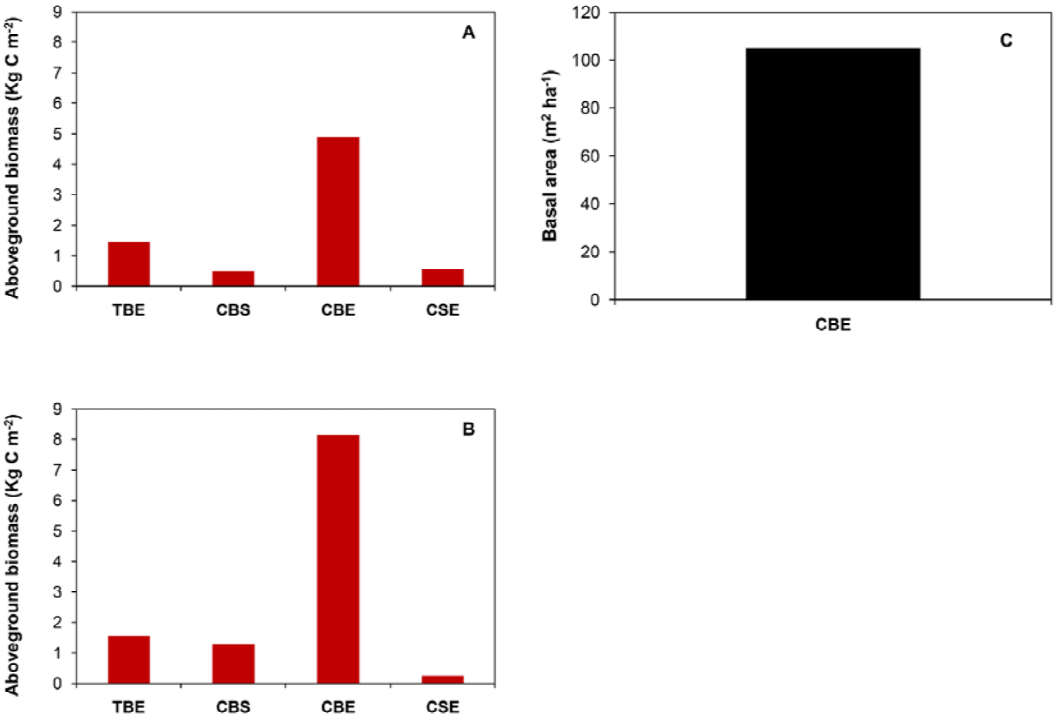

Fig. 9 Simulated vegetation composition with recurrence time of disturbance of (**A**) 120 years, (**B**) 145 years and (**C**) observed vegetation composition at Isla Grande de Tierra del Fuego. For **A** and **B** aboveground biomass averages for the period 1976-2006 are showed.

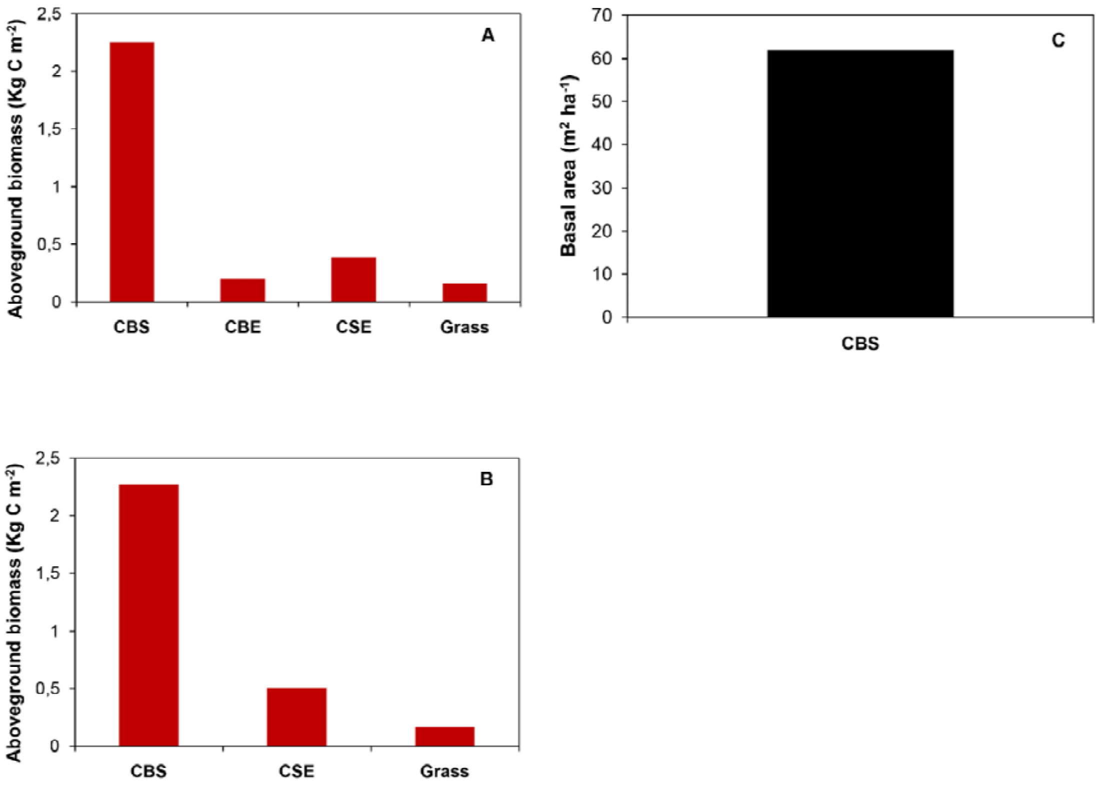

Fig. 10 Simulated vegetation composition with recurrence time of disturbance of (**A**) 120 years, (**B**) 145 years and (**C**) observed vegetation composition at Coyhaique National Reserve. For **A** and **B** aboveground biomass averages for the period 1974-2004 are showed.

4. Discussion

For the first time, the current potential distribution and composition of the main native forests across south-central Chile were simulated using a dynamic ecosystem model. Previously, only modeling results from studies at smaller scale (site level) have been available to understand the composition and natural dynamic of Chilean forests (Gutierrez et al. 2012; Rüger et al. 2007). For this study available data about the most representative species of sclerophyllous, temperate and magellanic forests was used to build and parameterize a set of PFTs capable of representing the average natural vegetation of the study area. Where data were lacking or were available only for specific specie, standard parameters of LPJ-GUESS used to model global and European (e.g. Smith et al. 2001; Sitch et al. 2003; Hickler et al. 2012) ecosystems were adopted.

4.1. Spatial distribution of vegetation

In general, LPJ-GUESS captured the main distribution patterns of temperate rain forests. The overestimation of Magellanic rain forests in an area where the Valdivian and North Patagonian rain forests are the dominant ecosystems (i.e. Andean zone between 39° and 44° S approximately) seems to be related to the lower thermal requirements by CBE (Table 2) which make this PFT more competitive than temperate evergreen trees in this area where temperatures are lower than in the Central Depression.

LPJ-GUESS underestimated the abundance of summergreen PFTs (i.e. IBS, MBS and CBS; see Appendix D for distribution of each PFT) in the whole study area. Both the IBS and MBS PFTs represent one of the most important plant types of temperate deciduous forests and Valdivian rain forests (Armesto et al. 2007; Veblen 2007). In general, their establishment was suppressed by temperate broadleaved evergreen PFTs, and this might be related, in part, to the uncertainties in the PFT parameterization. LPJ-GUESS has showed shifts in competitive balance between evergreen and deciduous trees when parameters related to vegetation dynamic such as maximum establishment rates (est_{max}) and the growth efficiency ($greff_{min}$), which is defined as the ratio of between NPP and LAI of an individual average over the last years, have been assigned in different combinations (Wramneby et al. 2008). The low abundance of deciduous PFTs may also be a result of the low resolution of the climate and soil data used to run the model. This would have a high relevance in the mountain regions where important changes in soil properties and climate occur over short distances in tight relation with changes in altitude. For example, in the southern Andes, changes in environmental conditions with elevation (lower temperature and thinner soils in higher elevations) lead to relatively rapid shift in forest composition with deciduous trees (i.e. MBS and CBS) becoming more dominant at higher elevations (Pollmann and Veblen 2004; Pollmann 2005). Another example is related to the representation of forests dominated by CBS PFT in the Andean region. In some grid cells, along the region where MVZ map classified the vegetation as cool deciduous forests, the model simulated evergreen PFTs (i.e. ~41°-44°S) or grasses (i.e. in the northern part of their distribution) instead of CBS PFT. According to the MVZ map the distribution area of CBS PFTs, which is the dominant plant type of cool deciduous forests, corresponds to a narrow strip in the Andean Cordillera. In fact, in northern part of its distribution, CBS PFT occurs at elevations between 1100 m.a.s.l to timberline at 1600 m.a.s.l which is a relatively narrow belt to be represented in detail by the model (Pollmann and Veblen 2004; Lara et al. 2005). The reduction in parameter uncertainty through field measurements and the use of finer-resolution climate and soil data might improve the model performance respect to deciduous PFTs.

On the other hand, it is important to point out that the dominance of IBS and MBS PFTs over evergreen trees at lowland and Andean zone (< 1300 m.a.s.l.) of south-central Chile is also a function of the occurrence of past coarse-scale disturbance events such as large earthquakes, volcanic activity and fires set by humans (Veblen et al. 1979; Veblen and Ashton 1978). These kinds of disturbances are relatively frequent (recurrence time < 130 years; see Table 4) during the period required for development of old-growth forests which have led to the persistence of forest types in a relatively early successional phases where shade-intolerant species are dominant (e.g. IBS; Veblen and Ashton 1978). Due to the fact that it was assigned an average expected return time of 120 years (*d*) with a probability of (1/*d*) affecting any given patch in a particular year over the entire model domain, it was not possible to simulate coarse-scale disturbances; in fact LPJ-GUESS simulated a condition where shade-intolerant species where almost absent (i.e. late succesional phase).

Notable discrepancies between the vegetation predicted by the model and the potential vegetation shown by VFM map occurred in the in the northern part of the distribution area of sclerophyllous forests/shrublands (from 31°S to 33° S). In this area LPJ-GUESS simulated grasses as a dominant PFT where the VFM map suggests potential forest/shrubland cover. Early studies have shown poorer performance of the model in water-limited ecosystems (Smith et al. 2001; Morales et al. 2005, Wramneby et al. 2008). This poor performance of LPJ-GUESS to simulate the vegetation in water-limited situations might result from its two-layer soil hydrology scheme which lack of representations for groundwater storage (Wramneby et al. 2008). Without considering groundwater storage, trees might not be able to extract enough water during the dry season (characterized by having approximately 5 months with precipitation rate < 5 mm month^{-1}) to compete successfully with grasses (Hickler et al. 2004a). This would explain, in part, why the model predicted grasslands instead of MeBE, MeSBD and DES PFTs.

4.2. Vegetation composition

In general, LPJ-GUESS captured the dominance of broadleaved evergreen PFTs in Valdivian and North Patagonian rain forests in the Coastal region (i.e. Guabún and Senda Darwin respectively). However, the model underestimated the proportion of MBE in both test sites and IBE in Senda Darwin. The unexpected persistence of shade-intolerant and shade-mid-tolerant trees in old-growth rain forest like in Guabún and Senda Darwin have been attributed to their long life spans (> 650 years), their sprouting ability in small canopy openings, their ability to tolerate long periods of growth suppression, their relatively slow growth compare to shade-tolerant species, and their rapid establishment immediately following a disturbance event (Lusk 1999; Gutierrez et al. 2004; Gutierrez et al. 2008). Furthermore, their large individual size that these trees attain ensures the creation of gaps of sufficient size to facilitate their recruitment after their death (Gutierrez et al. 2008). The coarse representation of the vegetation in this study (e.g. each PFT represents a set of species that have similar life-history traits such a phenology and shade tolerance but can differ in other traits like their life spans which can have important consequences in the forest dynamic), the uncertainty in PFTs parameters in describing correctly the life-history traits of Chilean trees (e.g. many PFT parameters are taken from European species) and the fact that some important ecological processes are not represented in the model (e.g. sprouting ability) seem to be the main reasons why the model did not predict the correct forest structure in these sites. Instead of that, the model tended to generate a classical successional series in which more light demanding pioneer trees (i.e. IBE and MBE) were replaced by shade-tolerant trees (i.e. TBE). On the other hand, it is important to point out that the very coarse resolution of soil data and/or the two-layer soil hydrology scheme of the model could have had an important effect on the model results in these sites. For example, both sites were assigned the same soil code; however the soils at Guabún is > 1m depth and at Senda Darwin is < 1 m depth with poor drainage (Gutierrez et al. 2004; Gutierrez et al. 2008) which determine directly the composition of the forests in both sites (coniferous and *N. nitida* are associated to poor drainage conditions; Gutierrez et al. 2004).

Unlike the results obtained for Valdivian and North Patagonian rain forests in Coastal Cordillera (i.e. Guabún and Senda Darwin), LPJ-GUESS did not correctly simulate the dominant PFTs of Valdivian rain forests in the Andean region at Pirihueico lake and Tolhuaca National Park (Figures 6 and 7). As it was mention before, the underestimation of the abundance of summergreen PFTs by the model might be explained by the uncertainties in the PFT parameterization, the low resolution of the climate and soil data and the lack of a component to simulate effects of coarse-scale disturbances; however the absence of deciduous trees (i.e. MBS) in both test sites is explained by the relatively high GDD_5 values assigned to temperate deciduous PFTs. The GDD_5 values estimated by CRU and Worldclim climate data for the period 1950-2000 were 1663 and 1276, respectively. During the experimental phase of this study, the distribution area of MBS was extended significantly from 41°S southward when GDD_5 values were < 2000. According to Luebert and Pliscoff (2006) the potential distribution of this PFT is restricted to areas from 40°S northward (Appendix D). Therefore, the GDD_5 value equal to 2000, which corresponds to the mean GDD_5value calculated when the vegetation map and Wordclim climate data were overlapped, restricts the modeled distribution of MBS to an area that is in more agreement with its potential distribution. Instead of predicting the dominance of MBS, LPJ-GUESS simulated the presence of CBE and CBS as dominant PFTs at Pirihueico lake and Tolhuaca National Park, respectively which have lower thermal requirements.

The rapid change in forest composition in relatively short distances is other important factor to consider. At Pirihueico lake, Tolhuaca National Park, and Puyehue National Park, the forest composition shifts abruptly as a response to changes in environmental conditions due to elevation. For example, in a transect of approximately 20 km (at Puyehue National Park; Fig. 8) is possible to identify different vegetation belts with temperate evergreen forests dominating the lower and upper montane zone (<900 m.a.s.l.), mixed cool forests with *N. betuloides* and *N. pumilio* as dominant species in the lower subalpine zone (at 1100-1120 m.a.s.l.) and cool deciduous forests in the subalpine zone (> 1290 m.a.s.l; Pollmann and Veblen 2005).Similar patterns are observed at Tolhuaca National Park and Pirihueico lake (Figures 6 and 7; Pollmann 2002; Pollmann 2005). Because the resolution of the climate and soil data is 0.5° x 0.5° which is approximately equal to 50 km x 50 km, it was not possible to capture the high variability in vegetation composition in the Andean region in this study. This would explain partly why LPJ-GUESS only captured the vegetation composition that characterizes the landscape between 1100-1200 m.a.s.l. at Puyehue National Park. It seems that the climate described by CRU data base for this grid cell is closer to a subalpine condition (i.e. higher elevation) than to a montane zone (i.e. lower elevation).

In addition to the climate factor it is important to mention again that both the structure and composition of forests located in the Andean region depend generally on the occurrence of catastrophic events (i.e. earthquakes; volcanic eruptions) whose recurrence time fluctuate between 80 and 130 years (Barrientos 2007). Although the recurrence time of disturbance assigned to each site was changed from 120 to 80 years, the effect on the forest composition was not significant (Figures 5B; 6B and 7B) which means that the return interval is not the only factor influencing the effect of a disturbance event on forest dynamic. In fact, the effects of a particular disturbance event will depend on a set of key factors such as mean return interval, size of the area disturbed, its magnitude or severity and its spatial distribution (Pollmann 2004). One of the main features of earthquakes and volcanic eruptions is that they affect very large areas of landscape per episode with great severity (Veblen and Ashton 1978). In this study, the stand proportion affected by a disturbance was a function of the recurrence time and the amount of patches assigned in the simulation protocol, suggesting that the minimum size of the area affected by coarse-disturbances was not reached which prevented the model to simulate, for example, the persistence of IBE PFT at Pirihueico lake. The inclusion of a component that can describe the total effect of coarse-scale disturbances is a key factor to take into account if the objective is to simulate the vegetation composition of Andean forests which are dominated by intolerant and mid-tolerant species.

The dominant trees and shrubs in Isla Grande de Tierra del Fuego (i.e. CBE) and Coyhaique Natural Reserve (i.e. CBS) were successfully simulated by the model regardless of the return time of disturbance assigned (Figures 9 and 10). However, the low aboveground biomass values simulated suggest that the model underestimated the real abundance of CBS and CSE at Coyhaique Natural Reserve. In this site, the model simulated higher LAI values for grasses (≈ 2 for 1990-2006) than for CBS (≈ 1 for 1990-2006) and CSE (≈ 1 for 1990-2006) which would respond to the fact that CRU climate data describes a colder and drier condition than the real climate (see Appendix C for meteorological data).

4.3. Limitation of the study

4.3.1. Limitations associated to the model

i. Representations of hydrological processes in the soil related to waterlogged conditions were not represented by the model version used in this study, which prevented the simulation of peatlands (i.e. Magellanic moorland). This implies, for example, that the model could have overestimated the real abundance of CBE PFT (*N. betuloides*) in the Magellanic archipelagos which would be expected in most of these areas as a result of the climate alone. Recently LPJ-GUESS has been applied with a configuration that includes differentiated representations of processes operating in peatland ecosystems of the tundra and taiga biomes (Miller and Smith, 2012; McGuire et al. 2012) which open the possibility to implement the model in the Austral region (from 41° southward) where peatlands become an important vegetation component.

ii. The simplistic two-layer soil hydrology scheme which lacks representation for groundwater storage (Wramneby et al. 2008) would explain in part, why the model underestimated the abundance MeBE and MeSBD in their northern distribution area.

iii. The contrasting disturbance regime between different regions along the country was not considered to simulate the main distribution patters of native forests at regional scale. In fact, an average value for disturbance (e.g. 120 years of recurrence time) was used. This assumption has important consequences on the model results, because both the magnitude and the return time of disturbances have direct effects on the structure and vegetation composition of forests. Therefore, LPJ-GUESS seems not to be applicable at the country level in Chile. A correct application of the model has to consider the different geographic areas (i.e. Andean Cordillera, Coastal Cordillera and Central Depression) which are subjected to different disturbance regimes.

iv. LPJ-GUESS does not include representation for vegetative reproduction. Vegetative reproduction has been attributed as an important factor that partly explains the long-term persistence of some tree species in temperate rain forests in Chile. For example, the sprouting ability of *E. cordifolia* (MBE) may facilitate regeneration under small canopy openings (Gutierrez et al. 2008). In the same way, old trees of *L. philippiana* (TBE) and *S. conspicua* (TNE) commonly have the ability to produce epicormic sprouting from the original trunk which permits them to persist in the same place for longer periods (Veblen et al. 1981)

4.3.2. Limitations associated to the input data

The driving environmental data used to run the model constitute an important source of uncertainty for this study. Two main reasons support this statement:

i. The low resolution climate and soil data prevented the simulation of the diverse vegetation composition in mountainous areas, especially, in the Andean Cordillera. In the mountain regions the environmental variables (i.e. climate and soil features) change in short distances with the altitude which affects directly the vegetation composition (Pollmann and Veblen 2004; Pollmann 2005).

ii. The CRU climate dataset seems not to represent in a correct way the annual precipitation. In fact, in comparison to Worldclim data base and the values associated to each test site (Appendix A and C), the precipitation is underestimated by CRU data in most of the study area. Moreover, according to meteorological stations annual precipitation rates > 2500 are not uncommon from 37°S southward, especially in the Coastal and Andean Cordilleras (Luebert and Pliscoff 2006). Regarding temperatures, CRU describes, in general, a colder climate than Worlclim (lower T_{c_min}) and climatic field records (i.e. mean annual temperatures in the Andean region; Appendix A and C). The use of a better climate resolution could improve the performance of the model in reproducing the correct distribution area of cool deciduous forests which accounts for 26.3% of the entire area cover by native forests in Chile (CONAF 2011).

iii. The soil data set is very coarse resolution and simplified representation of the soil variability of Chile and in some cases did not represent the real conditions reported in the literature. For example, regions that are characterized by having organic soils (e.g. Magellanic archipelagos) with waterlogged conditions were classified as coarse texture-type soils. The low numbers of studies found by the author avoid making a reclassification of soils for the whole model domain.

4.3.3. Future perspectives

In general, the results of this study suggest that LPJ-GUESS can be a valid tool to project future responses of Chilean native forests to changes in climate and land-use in the future. The good correspondence between simulated vegetation with the map of current natural vegetation in coastal temperate and boreal regions opens the possibility to apply the model at regional scale in ecosystems that are dominated by temperate rainforests. These ecosystems accounts for approximately 55% of the total area covered by native forests in Chile (CONAF 2011) and are considered to be in risk. This highlights the importance of obtaining good results for these forests which means that LPJ-GUESS can provide reliable outputs in order to assess future impacts on their ecosystems processes and help to create more efficient management policies.

To get better the performance of LPJ-GUESS (e.g. at site level) it is important to make new researches in order to improve the PFT parameterization. Regarding this, sensitivity analysis should be done in order to assess the importance of parameters such as sapwood turnover, tree leaf to sapwood cross-sectional area ratio and maximum establishment rate, which, in opinion of the author, could be important to simulate correctly the co-dominance of pioneer and shade tolerant trees in old-growth forests which is a common situation in Chilean forests.

Finally it is important to highlight two important aspects that should be taking into account for future applications of LPJ-GUESS in Chile: 1) the lack of field experiments addressing the forest dynamics, for example, in temperate deciduous forests and in sclerophyllous forests/shrublands does not permit to have a reliable data set of observations to compare with model data in the Mediterranean region; 2) currently there is no suitable data set with variables (e.g. of leaf area index, net primary production (NPP), net ecosystem exchange (NEE), actual evapotranspiration (AET), etc.) that allow a better comparison between the model outputs and the real ecosystem condition. Improving these two aspects a more rigorous testing of the different processes formulated in dynamic ecosystem models like LPJ-GUESS might be made.

5. Conclusions

i. In general, LPJ-GUESS captured the main regional distribution patterns ofthe main native forests described for south-central Chile. The only exception corresponded to temperate deciduous forests which were not predicted in the study area.

ii. At site level, LPJ-GUESS predicted correctly the dominance of temperate evergreen trees in coastal Valdivian and North Patagonian rainforests at Guabún and Senda Darwin respectively. In the same way, the model captured the general vegetation composition of Magellanic rainforests and cool deciduous forests at Isla Grande de Tierra del Fuego and Cohaique National Reserve respectively.

iii. LPJ-GUESS was not capable of simulating the main forest composition in Andean regions of south-central Chile (i.e. Pirihueico lake and Tolhuaca National Park).The exception corresponded to Puyehue National Park where the model captured the forest vegetation described for the forest at 1100-1120 m.a.s.l.

The uncertainties associated to the parameter values assigned to each PFT, the soil hydrology scheme of the model, the low resolution and quality of input data (i.e. climate and soil) and the large differences in the recurrence time and magnitude of disturbance events between different regions (i.e. Coastal Cordillera v/s Andean Cordillera) would be the main reasons in explaining the mismatch between the simulated vegetation and the vegetation described by MVZ map and literature in the model domain.

The current setup of the model would allow assessing future ecosystem responses in coastal Valdivian and North Patagonian forests and in Magellanic rainforests at regional scale.

Acknowledgements

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Appendices

Appendix A

Figures A.1, A.2, A.3 and A.4 show the difference between CRU 3.0 data sets (for annual precipitation CRU 3.10.01 was used) and the Worldclim data (CRU 3.0-Worldclim data) . The Worldclim data was generalized from 30 arc-seconds resolution (~1 km) to 0.5° resolution to make it comparable with CRU data set. The generalization was made using the software ArcGis 9.3. The values for each variable correspond to averages for the period 1950-2000.

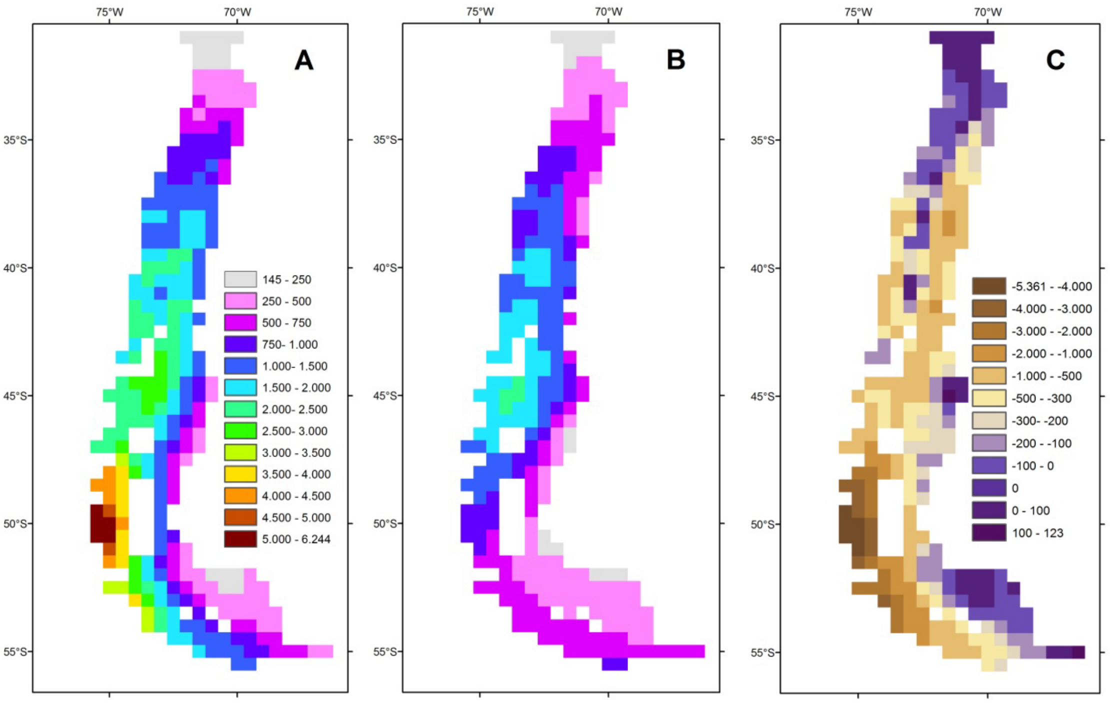


Fig. A.1 Difference of annual precipitation rate (mm year^{-1}; **C**) between CRU 3.10.01(**B**) and Worldclim data (**A**).

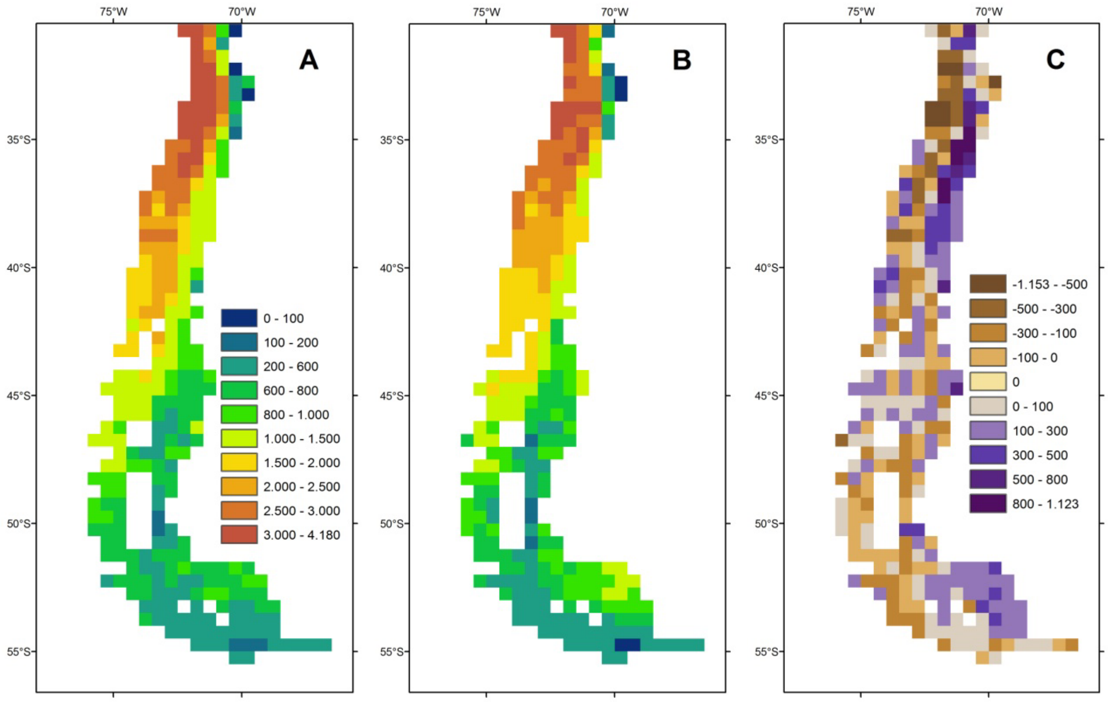


Fig. A.2 Difference of growth degree day based on 5°C (**C**) between CRU 3.0 (**B**) and Worldclim data (**A**).

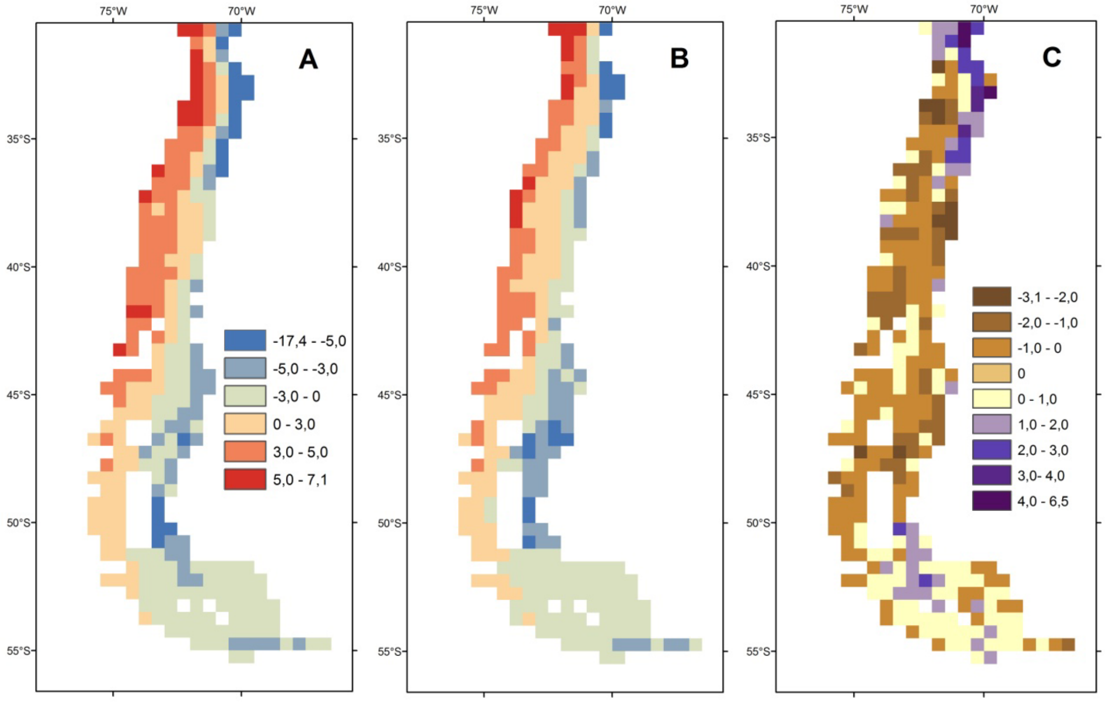


Fig. A.3 Difference of minimum temperature of the coolest month (T_{c_min}), (°C; **C**) between CRU 3.0 (**B**) and Worldclim data (**A**).

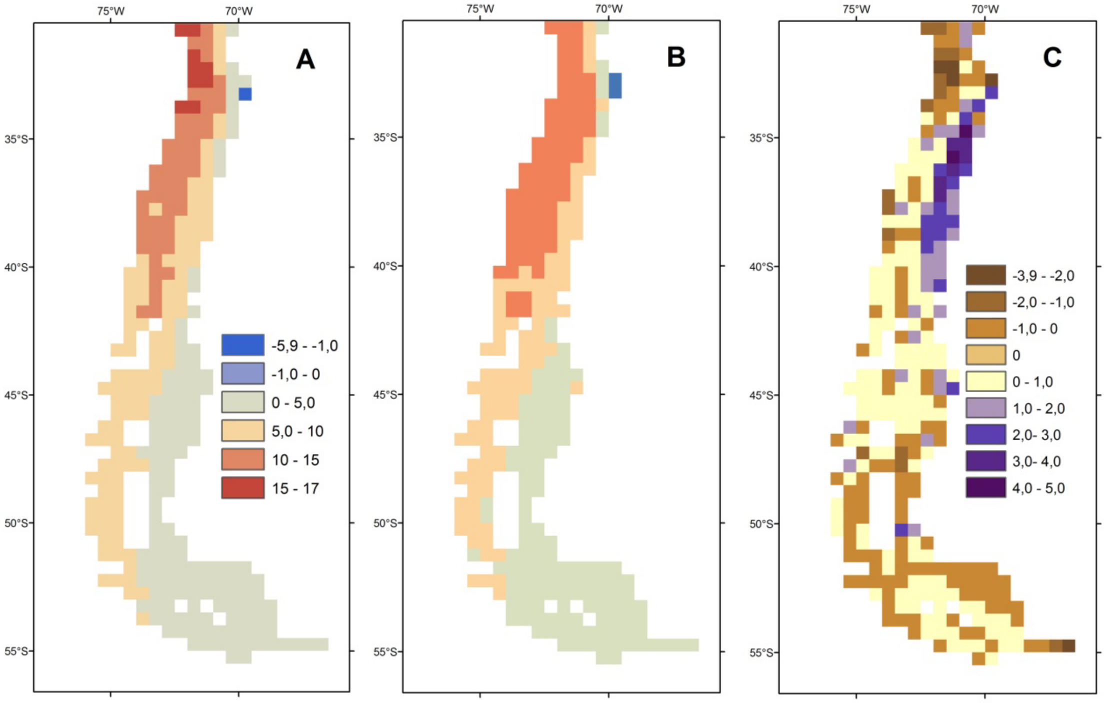


Fig. A.4 Difference of maximum temperature of the coolest month (T_{c_max}), (°C; **C**) between CRU 3.0 (**B**) and Worldclim data (**A**).

Appendix B

In order to make comparable the model outputs, the vegetation formation map (VFM) published by Luebert and Pliscoff (2006) was modified. To differentiate the limits between Valdivian and North Patagonian forest and Magellanic rainforests, this proposal follows the limits and the main forest composition suggested by Veblen (2007) for temperate rainforest. Taking into account the Veblen’s proposal the formations Laurifolius Forest, Resinous Forest, “*vegetation belts*”54-55;58-59 corresponding to Deciduous Forests formation, and “*vegetation belts*”83-85; 93 corresponding to Evergreen Forest formation were classified as Valdivian and North Patagonian rainforests (Table B.1). The “*vegetation belts*” 86-92 and 94-97 corresponding to Evergreen Forest and Peatlands respectively were classified as Magellanic rainforest and moorland (Table B.2).

Table B.1 Vegetation belts that represent the Valdivian and North Patagonian rainforests.

N°	Vegetation belts
54	Temperate deciduous forest of *Nothofagus obliqua*and*Laurelia sempervirens*
55	Coastal temperate mixed evergreenforest of*Nothofagus dombeyi*and*N. obliqua*
58	Andean temperate deciduous forest of *Nothofagus alpina*and*Dasyphyllum diacanthoides*
59	Andean temperate deciduous forest of *Nothofagus alpina*and*N. dombeyi*
72	Coastal temperate laurifolius forest of *Aextoxicon punctatum*and*Laurelia sempervirens*
73	Coastal temperate laurifolius forest of *Weinmannia trichosperma*and*Laureliopsis philippiana*
74	Temperate laurifolius forest of *Nothofagus dombeyi*and*Eucryphia cordifolia*
75	Coastal temperate resinous forest of *Araucaria araucana*
76	Andean temperate resinous forest of *Araucaria araucana*and*Nothofagus dombeyi*
77	Andean temperate resinous forest of *Araucaria araucana*and*Festuca scabriuscula*
78	Andean temperate resinous forest of *Austrocedrus chilensis*and*Nothofagus dombeyi*
79	Coastal temperate resinous forest of *Fitzroya cupressoides*
80	Andean temperate resinous forest of *Fitzroya cupressoides*
81	Coastal temperate resinous forest of *Pilgerodendron uvifera*and*Tepualia stipularis*
82	Coastal temperate resinous forest of *Pilgerodendron uvifera*and*Astelia pumila*
83	Andean temperate evergreen forest of *Nothofagus dombeyi*and*Gaultheria phillyreifolia*
84	Andean temperate evergreen forest of *Nothofagus dombeyi*and*Saxegothaea conspicua*
85	Temperate evergreen forest of *Nothofagus nitida*and*Podocarpus nubigena*
93	Coastal temperate evergreen scrub of *Pilgerodendron uvifera*and*Nothofagus nitida*

Source: Luebert and Pliscoff (2006)

Table B.2 Vegetation belts that represent the Magellanic rainforest and moorland.

N°	Vegetation belts
86	Temperate evergreen forest of *Nothofagus betuloides* and *Desfontainia spinosa*
87	Andean temperate evergreen forest of *Nothofagus betuloides* and *Laureliopsis philippiana*
88	Andean temperate evergreen forest of *Nothofagus betuloides* and *Chusquea macrostachya*
89	Andean temperate mixed forest of *Nothofagus betuloides* and *Berberis serrato-dentata*
90	Andean antiboreal-temperate mixed forest of *Nothofagus betuloides* and *Nothofagus pumilio*
91	Coastal temperate evergreen forest of *Nothofagus betuloides* and *Embothrium coccineum*
92	Coastal temperate evergreen forest of *Nothofagus betuloides* and *Drimys winteri*
94	Coastal temperate peatbog of *Donatia fascicularis* and *Oreobolus obtusangulus*
95	Coastal temperate peatbog of *Astelia pumila*and*Donatia fascicularis*
96	Coastal antiboreal peatbog of *Bolax bovei* and *Phyllachne uliginosa*
97	Antiboreal-temperate peatbog of *Sphagnum magellanicum* and *Schoenus antarcticus*

Source: Luebert and Pliscoff (2006)

The “*vegetation belts”* 46-53; 56-57 corresponding toDeciduous Forests formation were classified as temperate deciduous forests (Table B.3). These forests are characterized by having *Nothofagus obliqua*, *N. glauca*, *N. alpina* and *N. macrocarpa*as dominant trees and are located in landscapes which are mainly influenced by Mediterranean-type macrobioclimate. The limit between Valdivian rainforests and temperate deciduous forest was based on Veblen (2007).

Table B.3 Vegetation belts that represent the temperate deciduous forests.

N°	**Vegetation belts**
46	Coastal mediterranean deciduous forests of *Nothofagus macrocarpa* and *Ribes punctatum*
47	Mediterranean deciduous forests of *Nothofagus obliqua* and *Cryptocarya alba*
48	Andean mediterranean deciduous forests of *Nothofagus obliqua* and *Austrocedrus chilensis*
49	Coastal mediterranean deciduous forests of *Nothofagus glauca* and *Azara petiolaris*
50	Coastal mediterranean deciduous forests of *Nothofagus glauca* and *Persea lingue*
51	Andean mediterranean deciduous forests of *Nothofagus glauca* and *N. obliqua*
52	Coastal mediterranean-temperatedeciduous forests of *Nothofagus obliqua* and *Gomortega keule*
53	Temperatedeciduous forests of *Nothofagus obliqua* and *Persea lingue*
56	Coastal temperatedeciduous forests of *Nothofagus alpina* and *Persea lingue*
57	Andeanmediterranean-temperatedeciduous forests of *Nothofagus alpina* and *N. obliqua*

Source: Luebert and Pliscoff (2006)

The formations Thorn Forest (“*vegetation belts”* 29-34), Sclerophyllous Forest (“*vegetation belts”* 38-45), and “*vegetation belts”* 36-37 corresponding to Arborescent Scrub formation were classified as Sclerophyllous Forest/Shrubland (Table B.4). The generalization of these vegetation belts in one forest/shrubland class was based on the vegetation composition described for this kind of ecosystem by Moreira-Muñoz (2011) and Gajardo (1984).

Table B.4 Vegetation belts that represent the Sclerophyllous forest/shrubland.

N°	**Vegetation belts**
29	Tropical thorn forest of *Prosopis tamarugo* and *Tessaria absinthiodes*
30	Tropical thorn forest of *Geoffroea decorticans*and*Prosopis alba*
31	Andean tropical thorn forest of *Browningia candelaris*and*Corryocactus brevistylus*
32	Mediterranean thorn forest of *Acacia caven*and*Prosopis chilensis*
33	Andean mediterranean thorn forest of *Acacia caven*and*Baccharis paniculata*
34	Coastal mediterranean thorn forest of*Acacia caven*and*Maytenus boaria*
35	Mediterranean thorn forest of *Acacia caven*and*Lithrea caustica*
36	Coastal mediterranean sclerophyllous arborescent scrub of *Peumus boldus* and *Schinus latifolius*
37	Mediterranean sclerophyllous arborescent scrub of *Quillaja saponaria* and *Porlieria chilensi*
38	Andean mediterranean sclerophyllous forest of *Kageneckia angustifolia*and*Guindilia trinervis*
39	Coastalmediterranean sclerophyllous forest of *Cryptocarya alba*and*Peumus boldus*
40	Coastalmediterranean sclerophyllous forest of*Lithrea caustica*and*Cryptocarya alba*
41	Andean mediterranean sclerophyllous forest of *Quillaja saponaria*and*Lithrea caustica*
42	Coastalmediterranean sclerophyllous forest of *Lithrea caustica*and*Azara integrifolia*
43	Mediterranean sclerophyllous forest of *Lithrea caustica* y *Peumus boldus*
44	Andean mediterranean sclerophyllous forest of *Lithrea caustica* y *Lomatia hirsuta*
45	Mediterranean sclerophyllous forest of *Quillaja saponaria* y *Fabiana imbricata*

Source: Luebert and Pliscoff (2006)

The “*vegetation belts*” 60-67 corresponding to Deciduous Forest, “*vegetation belts*” 68-69 corresponding to Deciduous Scrub and “*vegetation belts*” 70-71 corresponding to Arborescent Scrub were classified as cool deciduous forests (Table B.5). The generalization of these vegetation belts in one forest class was based on the fact that *Nothofagus pumilio* and *N. antarctica* are the main component of these forests (Veblen 2007; Gajardo 1984).

Table B.5 Vegetation belts that represent the cool deciduous forests.

N°	**Vegetation belts**
60	Andean mediterranean-temperatedeciduous forests of *Nothofagus pumilio* and *N. obliqua*
61	Andean temperatedeciduous forests of *Nothofagus pumilio* and *Araucaria araucana*
62	Andean temperatedeciduous forests of *Nothofagus pumilio* and *Drimys andina*
63	Andean temperatedeciduous forests of *Nothofagus pumilio* and *Berberis ilicifolia*
64	Andean temperatedeciduous forests of *Nothofagus pumilio* and *Azara alpina*
65	Andean temperatedeciduous forests of *Nothofagus pumilio* and *Ribes cucullatum*
66	Andean temperatedeciduous forests of *Nothofagus pumilio* and *Chiliotrichum diffusum*
67	Andean antiboreal- temperatedeciduous forestsof *Nothofagus pumilio* and *Maytenus disticha*
68	Andean temperatedeciduous scrub of *Nothofagus antárctica*
69	Andean temperatedeciduous scrubof *Nothofagus antarctica* and *Empetrum rubrum*
70	Temperate deciduous arborescent scrub of*Nothofagus antarctica* and *Berberis microphylla*
71	Andean antiboreal-temperate deciduous arborescent scrub of de *Nothofagus antarctica* and *Chiliotrichum diffusum*

Source: Luebert and Pliscoff (2006)

The “*vegetation belts*” 117; 121-127 were classified as Magellanic steppe (Table B.6). The generalization of these vegetation belts in one class was based on the vegetation composition described for this kind of ecosystem and its spatial location suggested by Gajardo (1984) and Moreira-Muñoz (2011).

Table B.6 Vegetation belts that represent the Magellanic steppe.

N°	**Vegetation belts**
117	Andean antiboreal-temperate short scrub of *Bolax gummifera* and *Azorella selago*
121	Andean temperate grassland of *Nassauvia dentata* and *Senecio portalesianus*
122	Andean antiboreal grassland of*Nassauvia pygmaea* and *N. lagascae*
123	Mediterranean-temperate steppe of*Festuca pallescens* and *Mulinum spinosum*
124	Eastern mediterranean-temperate steppe of*Festuca gracillima*
125	Eastern temperate steppe of*Festuca gracillima* and *Empetrum rubrum*
126	Eastern temperate steppe of*Festuca gracillima* and *Chiliotrichum diffusum*
127	Eastern temperate steppe of*Festuca gracillima* and *Mulinum spinosum*

Source: Luebert and Pliscoff (2006)

The "*vegetation belts*" 112-116; 119-120 were classified as High-Andean steppe (Table B.7). The generalization of these vegetation belts in one class was based on the vegetation composition described for this kind of ecosystem and its spatial location suggested by Gajardo (1984).

Table B.7 Vegetation belts that represent the High-Andean steppe

N°	**Vegetation belts**
112	Andean mediterranean short scrub of *Chuquiraga oppositifolia*and*Nardophyllum lanatum*
113	Andean mediterranean short scrub of *Laretia acaulis*and*Berberis empetrifolia*
114	Andean mediterranean short scrub of *Chuquiraga oppositifolia*and*Discaria articulata*
115	Andean temperate short scrub of *Discaria chacaye*and*Berberis empetrifolia*
116	Andean temperate short scrub of *Adesmia longipes*and*Senecio bipontini*
119	Mediterranean grassland of *Nastanthus spathulatus*and*Menonvillea spathulata*
120	Andean mediterranean grassland*O. adenophylla*and*Pozoa coriacea*

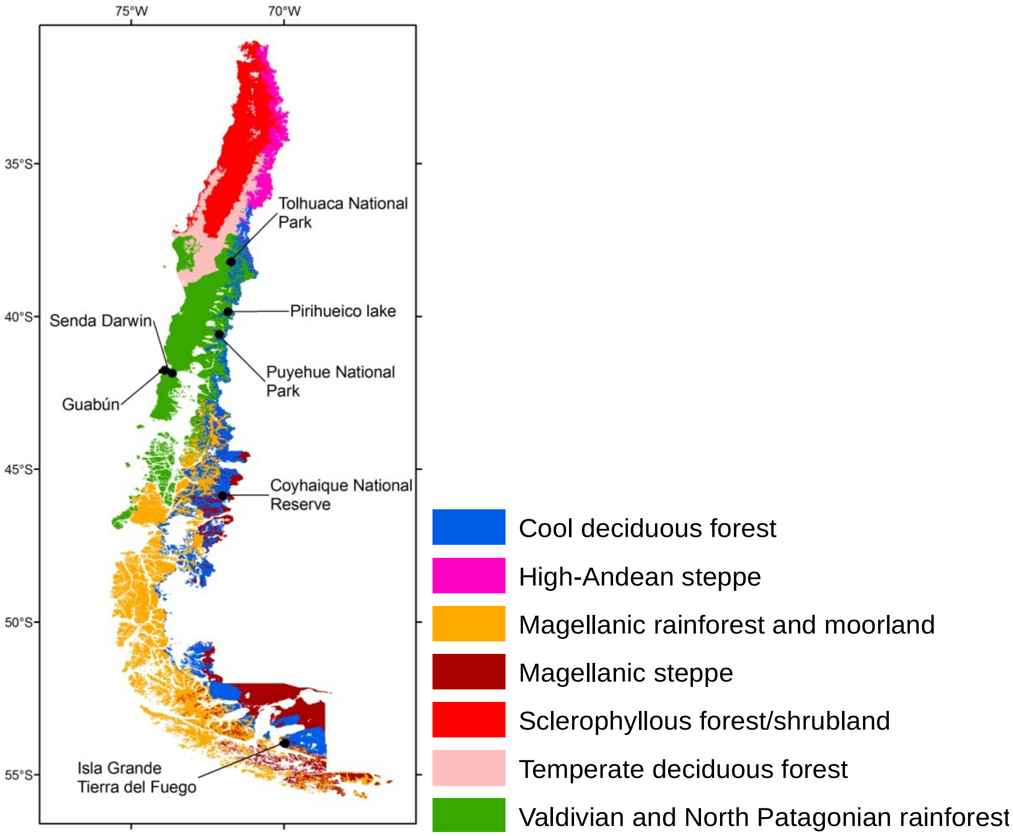
Source: Luebert and Pliscoff (2006)

To scale up the map into a comparable resolution to model output (0.5°x 0.5°), the software ArcGis 9.3 was used and the next methodological steps were followed:

1. The modified map which was in polygon format was converted to raster format
2. The map in raster format was converted to a point format.
3. The map in point format was converted to a raster format again with a resolution of 0.5°x 0.5°. Because more than one category falls within a cell of 0.5°x 0.5° size, the method used to determine the value for that cell was "the most frequent". This method assigns to the cell the most common value.

Appendix C

Geographic location of the 7 Chilean sites with native forest and their meteorological characteristics used to evaluate the composition of modeled native forest at site level.



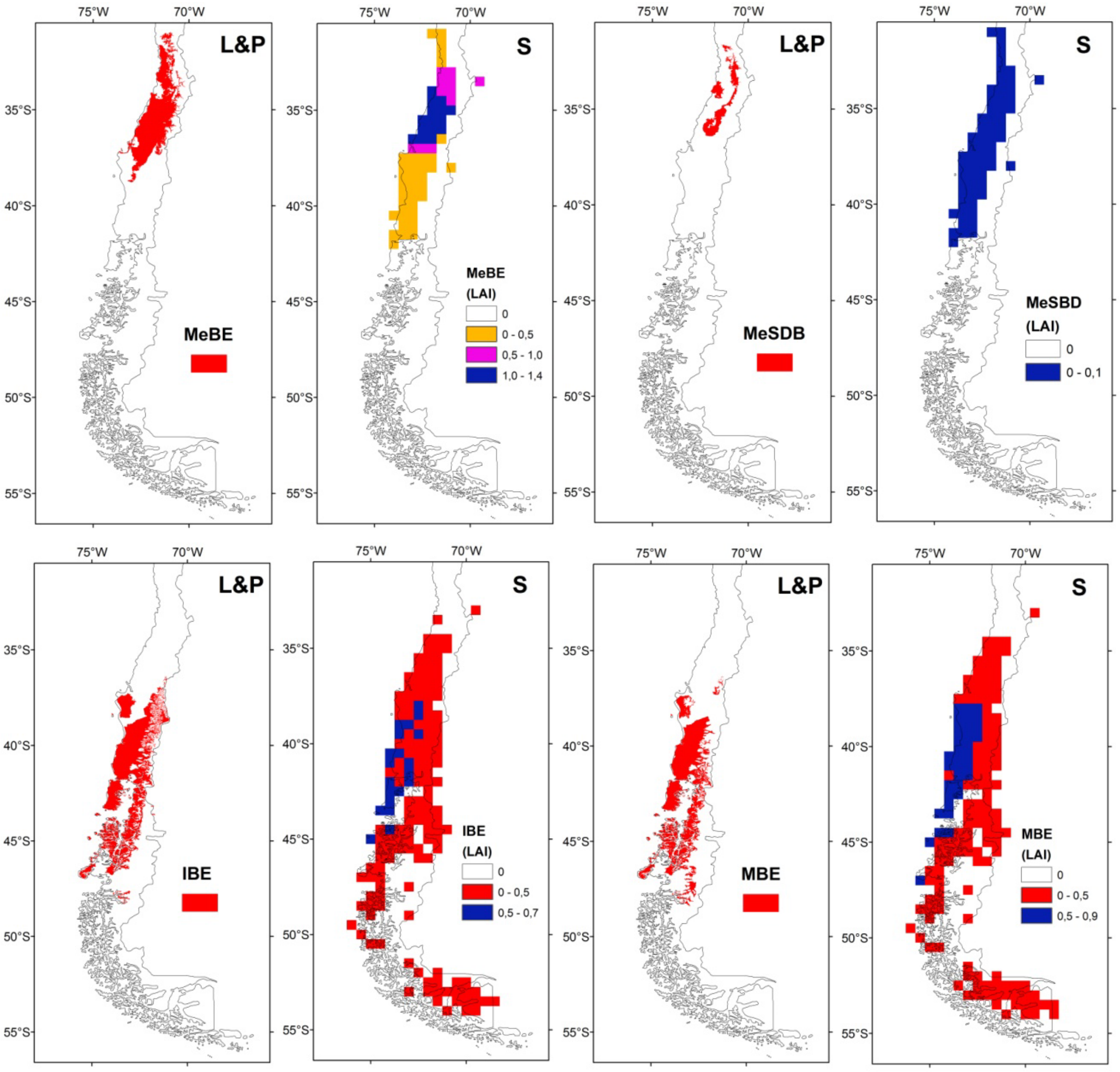
(Vegetation map is an adaptation of the vegetation map published by Luebert and Pliscoff (2006))

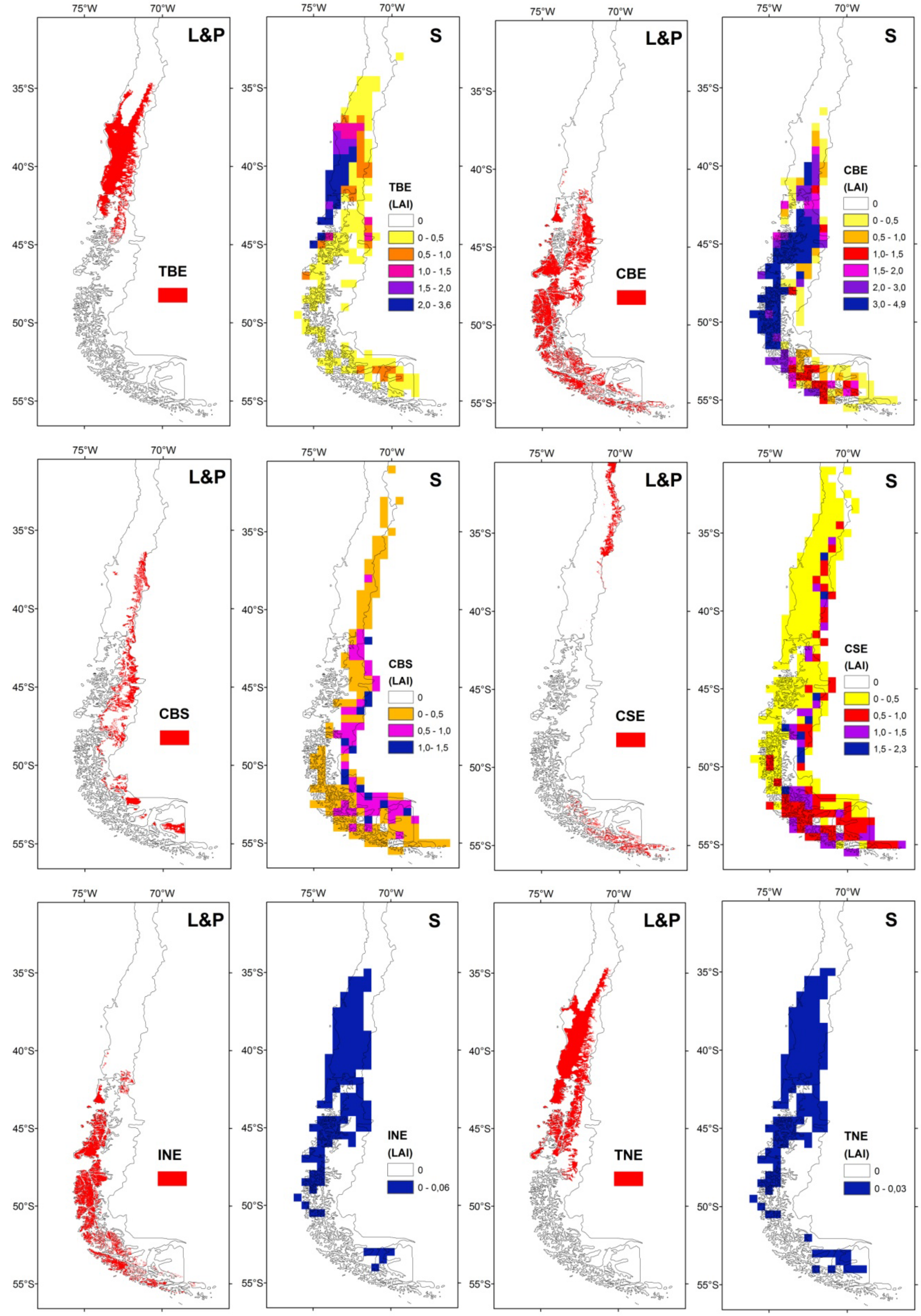
Site	Meteorological station[1]		CRU 3.0[2]		Worldclim[2]	
	Mean anual T (°C)	Prep (mm-year^{-1})	Mean anual T (°C)	Prep[3] (mm-year^{-1})	Mean anual T (°C)	Prep (mm-year^{-1})
Puyehue National Park	9.2	3500	7.2	1279	8.5	1884
Pirihueico lake	10.8	3500-4000	7.7	1282	8.7	1921
Tolhuaca National Park	12.0	2500	7.6	649	8.0	1800
Senda Darwin	9.1	2157	10.4	1704	10.6	2105
Guabún	10.8	2444	10.1	1481	10.3	1993
Isla Grande de Tierra del Fuego	---	500-600	6.3	467	5.1	712
Coyhaique National Reserve	7.7	1350	5.6	699	5.2	916

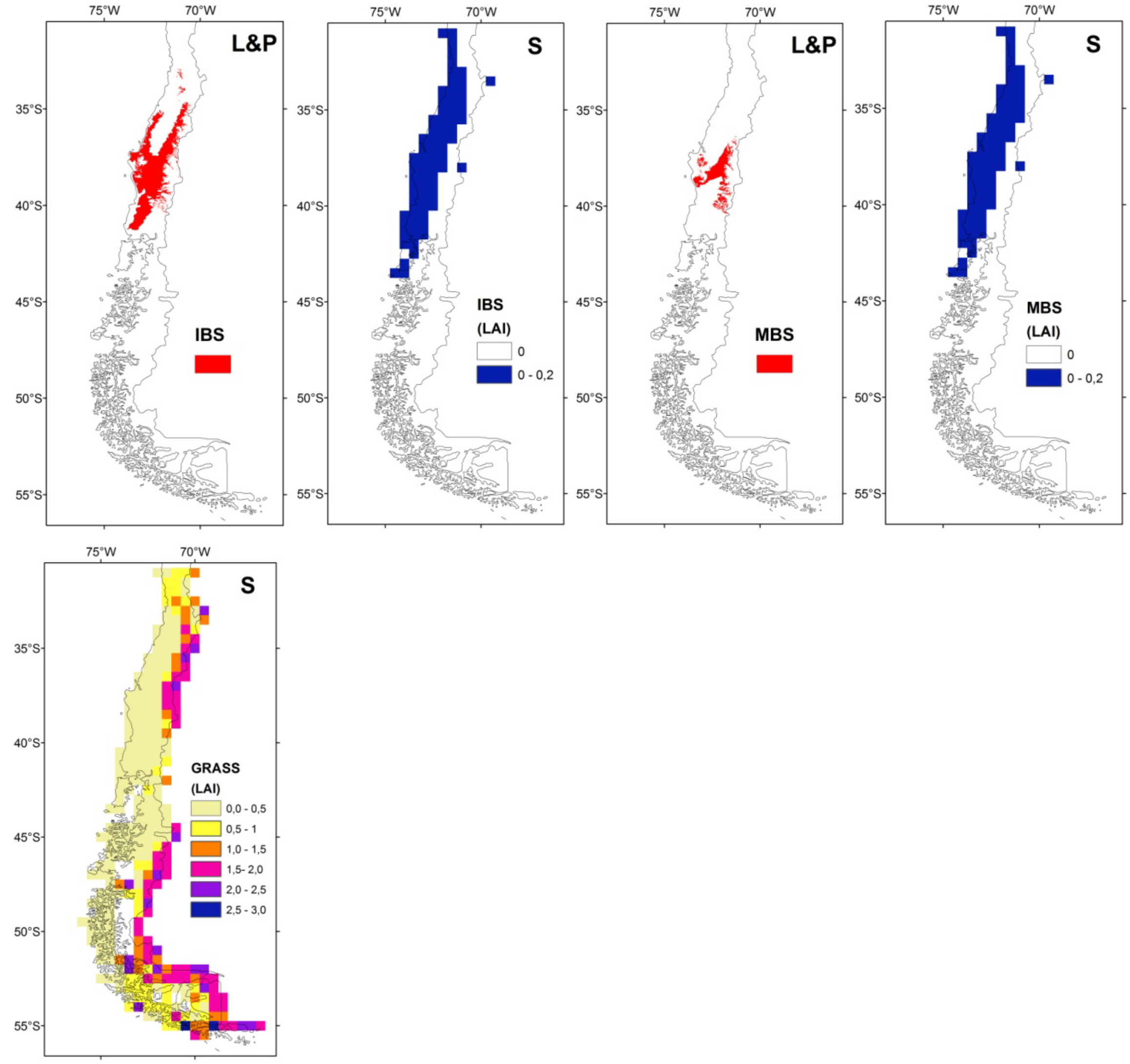
[1] Correponds to the nearest metereological station. For data source see the references in Table 6;
[2] Mean values for the period 1950-2000. [3]Data from CRU 3.10.01.

Appendix D

Simulated PFTs (**S**) and potential PFT distribution suggested by Luebert and Pliscoff (2006; **L&P**). For simulated PFTs (**S**) leaf area index values (LAI) are showed. Mediterranean broadleaved evergreen (MeBE),Mediterranean shrub broadleaved deciduous (MeSBD),Temperate shade-intolerant broadleaved evergreen (IBE), Temperate shade-mid-tolerant broadleaved evergreen (MBE), Temperate shade-tolerant broadleaved evergreen (TBE), Temperate shade-intolerant broadleaved summergreen (IBS), Temperate shade-mid-intolerant broadleaved summergreen (MBS), Temperate shade-intolerant needleleaved evergreen (INE), Temperate shade-tolerant needleleaved evergreen (TNE), Cool broadleaved evergreen (CBE), Cool broadleaved summergreen (CBS), Cool shrub broadleaved evergreen (CSE).




75°W
70°W
35°S
40°S
45°S
50°S
55°S
L&P
S
TBE
TBE (LAI)
0
0 - 0,5
0,5 - 1,0
1,0 - 1,5
1,5 - 2,0
2,0 - 3,6
CBE
CBE (LAI)
0
0 - 0,5
0,5 - 1,0
1,0- 1,5
1,5- 2,0
2,0 - 3,0
3,0 - 4,9
CBS
CBS (LAI)
0
0 - 0,5
0,5 - 1,0
1,0- 1,5
CSE
CSE (LAI)
0
0 - 0,5
0,5 - 1,0
1,0 - 1,5
1,5 - 2,3
INE
INE (LAI)
0
0 - 0,06
TNE
TNE (LAI)
0
0 - 0,03


75°W
70°W
35°S
40°S
45°S
50°S
55°S
L&P
IBS
S
IBS
(LAI)
0
0 - 0,2
L&P
MBS
S
MBS
(LAI)
0
0 - 0,2
S
GRASS
(LAI)
0,0 - 0,5
0,5 - 1
1,0 - 1,5
1,5- 2,0
2,0 - 2,5
2,5 - 3,0

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