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Long-term dynamics and the response of temperate rainforests of Chiloé Island (Chile) to climate change

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A Tita, my darling

CONTENT

ABSTRACT I

ZUSSAMMENFASSUNG II

RESUMEN III

GENERAL OVERVIEW 1

INTRODUCTION 1
AIMS, FOCUS AND STRUCTURE OF THE THESIS 3
MATERIALS AND METHODS 4
SYNTHESISING DISCUSSION 5
SIGNIFICANT ACHIEVEMENTS AND FINDINGS 5
RESEARCH APPLICATION 8
RESEARCH NEEDS 11
CONCLUSIONS 12

REFERENCES 14

CURRICULUM VITAE 17

OTHER PUBLICATIONS BY THE AUTHOR 18

APPENDIX 19

RESEARCH PAPER I. TEMPERATE RAINFORESTS UNDER CHANGING CLIMATE: A REVIEW. 21
RESEARCH PAPER II. STRUCTURAL AND ENVIRONMENTAL CHARACTERIZATION OF OLD-GROWTH TEMPERATE RAINFORESTS OF NORTHERN CHILOE ISLAND, CHILE: REGIONAL AND GLOBAL RELEVANCE. 41
RESEARCH PAPER III. GAP-PHASE DYNAMICS AND COEXISTENCE OF A LONG-LIVED PIONEER AND SHADE-TOLERANT TREE SPECIES IN THE CANOPY OF AN OLD-GROWTH COASTAL TEMPERATE RAIN FOREST OF CHILOÉ ISLAND, CHILE. 57
RESEARCH PAPER IV. SUCCESSIONAL STAGES OF TEMPERATE RAINFORESTS: ARE OLD-GROWTH FORESTS AT STEADY STATE? 73
RESEARCH PAPER V. POTENTIAL IMPACTS OF CLIMATE CHANGE ON TEMPERATE RAINFORESTS OF SOUTHERN SOUTH AMERICA. 109
SUPPLEMENTARY INFORMATION. THE FOREST MODEL FORMIND-CLIM. 137

ACKNOWLEDGMENTS 159

ABSTRACT

Concern about climate change is increasing due to the many uncertainties that exist regarding the possible changes on ecosystems during this century. Forest ecosystems responses to climate change may vary among regions of the world demanding to analyze climatic-induced changes in forests for each region in particular. This thesis aims to understand how temperate rainforests of southern South America (37°45'-47°30'S, SSA) will be impacted by climate change. To answer this question, forest inventory data were analyzed and an individual-oriented forest growth model was developed. Specifically, this thesis addresses three objectives: 1) to compile and synthesise the current knowledge on tree species and forest structure; 2) to gain insight into ecological processes in the long-term successional dynamics; and 3) to examine how forest structure and functioning (e.g. productivity, carbon and water balance) may change by projected climatic tendencies for year 2100 in SSA.

The study was focused on forests occurring on Chiloé Island, Chile (42° S). Forests in this region mainly belong to North Patagonian and Valdivian forests, the main forest types of temperate rainforests of SSA. Field data from young secondary, logged mature and unmanaged mature forest stands was collected to characterize forests in the study area (23 plots, 0.1 ha each). Environmental variables were related to stand structure sampled in the field by using multivariate constrained correspondence analysis. A detailed tree-ring analysis was conducted in a 450-yr old unmanaged forest to relate the influences of disturbances to regeneration dynamics. An individual-oriented forest model (`FORMIND-CLIM`) was developed that includes the effect of inter-annual climatic variability on tree growth. The model was parameterised on the basis of values given in the literature and field data. Modules were developed and included in the model to calculate temperature and soil moisture influences on tree grow, forest carbon cycling and forest water fluxes. Species groups to run the model were selected representing the main canopy tree species of Chiloé forests (N = 17). Uncertain parameters were calibrated using systematic comparisons between observed patterns in the field and forest structural patterns predicted by the model. Forest functioning was analyzed using climate change projections of `PRECIS-DGF` climatic model (*Comisión Nacional del Medioambiente & Universidad de Chile*) for Chiloé Island.

According to field data analyses, old-growth forests of Chiloé Island showed a high variability in stand structure. Old-growth forests commonly had (a) no sings of recent human impact, (b) large stand basal areas (>80 m^2), (c) higher tree species richness (>7 tree species) than early and mid-successional stands, (d) presence of large canopy emergents (30 m tall), (e) high vertical heterogeneity (based on an index of diversity and stratification), and (f) minimum stand ages >200 years. Old-growth structural variability was partly explained by environmental differences among stands (ca. 50%, by factors such as temperature, distance to the Pacific Ocean and elevation). Compiled field data documented the persistence of pioneer trees in old-growth forests of Chiloé. According to the tree-ring analysis, the interaction of trees differing in shade tolerance and life spans with the disturbance regime in this region explained the long-term coexistence of pioneer and shade-tolerant species in old-growth forests.

The modelling approach of this thesis provides a framework for using individual-oriented forest models to analyze the long-term dynamics of temperate rainforests. Variable successional pathways to the old-growth stage were predicted by the model to reproduce the structural and compositional variability of the studied stands. Modelling results confirmed that pioneers dominate during the first 500 years of succession because of their long life spans and the occurrence of canopy openings produced by windstorms. Modelling results suggested that forests on Chiloé Island can take 500 to 850 years of succession to reach the old-growth stage, i.e when forests reach a steady state in structure (e.g. biomass). Biomass tends to decrease as forests approach steady-state because large pioneers are replaced by smaller late-successional trees, potentially resulting in carbon losses.

Model results showed that climate change projected for this century in Chiloé Island will impact forest functioning by modifying water fluxes. Climate change will decrease above ground forest biomass in ~11% and net primary production in ~30% (from 7.6 to 2.4 tonnes of carbon - tC - ha/year) for year 2100. As a result of warming alone, i.e. without accounting for the direct effects of carbon dioxide - CO_2 -, old-growth forests of Chiloé Island will become sources of carbon in year 2100 (average of 3.7 tC ha/year, net ecosystem flux NEE). The model predicted complex and variable patterns of carbon cycling among stands related to their successional stage and structural variability. Climate change can cause a progressive forest compositional shift (after year 2200) due to the establishment of species not occurring previously in the stands. These results inform the debate on forest responses to climate change in SSA.

This thesis highlights the possibilities of using forest models to gain insight into dynamics, functioning and structural complexity of temperate rainforests in southern South America. A framework was provided to facilitate the analysis of complex processes occurring under a transient environment. The results of this thesis encourage future research efforts to explore impacts of multiple drivers of global change on temperate rainforests of SSA.

ZUSSAMMENFASSUNG

Zukünftige Klimaänderungen werden je nach Region unterschiedliche Auswirkungen auf Waldökosysteme haben. Über ihre potentiellen Auswirkungen auf Wälder im südlichen Südamerika ist bisher wenig bekannt. Daher hat es sich diese Doktorarbeit zum Ziel gesetzt, die Struktur und Dynamik von temperierten Regenwäldern im südlichen Südamerika (37°45’-47°30’S, SSA) und ihre potentiellen Veränderungen durch Klimaänderungen zu untersuchen. Hierzu wurden Waldinventur-Daten analysiert und ein individuen-orientiertes, prozessbasiertes Waldwachstumsmodell entwickelt. Im Detail verfolgt diese Doktorarbeit folgende Ziele: 1) Zusammenstellung und Aufbereitung der derzeit vorhandenen Informationen zu den Baumarten und der Waldstruktur von temperierten Regenwäldern in Chile; 2) Analyse der Sukzession und der Dynamik dieser Wälder und 3) Untersuchung der Veränderung von Struktur und Kohlenstoffbilanz dieser Wälder durch die für das kommende Jahrhundert vorhergesagten Klimaentwicklungen.

Die Studie konzentriert sich hierbei auf temperierte Regenwälder auf der Chiloe Insel, Chile (42°S). Die Wälder in dieser Region gehören zum sogenannten Nord-Patagonischen und Valdivischen Typ, den beiden Hauptwaldtypen der gemäßigten Regenwälder im südlichen Südamerika. Zur Analyse der Struktur und Baumartenzusammensetzung dieser Wälder wurden Waldinventuren für Sekundär- und ausgewachsene Wälder analysiert. Mit Hilfe von verschiedenen statistischen Analysen wurden die Zusammenhänge zwischen Waldstruktur, Baumartenzusammensetzung und Umweltfaktoren untersucht. Weiterhin wurden detaillierte Baumringanalysen durchgeführt, um das Alter und Wachstum der Bäume zu charakterisieren. Ein individuen-orientiertes Waldmodell wurde entwickelt, das die Waldentwicklung von temperierten Regenwälder in der Chiloe-Region beschreibt (`FORMIND-CLIM`) und die Analyse der Auswirkungen von Klimaänderungen auf die Waldentwicklung ermöglicht. Es wurden Parametrisierungen für 17 Baumarten erstellt. Hierzu wurden mit großem Aufwand Literatur- und Felddaten ausgewertet. Zusätzliche Modellmodule wurden entwickelt, die die Berücksichtigung des Niederschlags- und Temperatureinflusses auf das Baumwachstum ermöglichen und Wasser- und Kohlenstoffbilanzen für den Wald abschätzen. Unsichere Parameterwerte wurden durch systematischen Vergleich mit beobachteten Mustern kalibriert. Die zukünftige Entwicklung des Waldes unter Klimaänderungen wurde mit Hilfe der Klimavorhersagen des `PRECIS-DGF` (*Comisión Nacional del Medioambiente & Universidad de Chile*) Klimamodels für die Chiloé Insel analysiert.

Die Analyse der Inventurendaten zeigt eine hohe Variabilität der Bestandesstruktur. Die untersuchten ausgewachsenen Wälder zeigen im Allgemeinen (a) keine Anzeichen kürzlich zurückliegenden menschlichen Einflusses, (b) große Bestandesgrundfläche (>80m²), (c) hohen Baumartenreichtum (>7 Baumarten), (d) Vorhanden sein von emergenten Bäumen (mit Baumhöhen von 30m), (e) große vertikale Heterogenität und (f) ein Mindestalter des Bestandes von mehr als 200 Jahren. Die Variabilität der Waldstruktur konnte nur teilweise durch die unterschiedlichen Umweltfaktoren zwischen den Standorten erklärt werden (ca. 50% durch Faktoren wie Temperatur, Entfernung zum Pazifik und Höhenlage).

Das in dieser Doktorarbeit entwickelte Waldmodell zeigt beispielhaft auf, wie individuen-orientierte Waldmodelle zur Analyse der Langzeitdynamik temperierter Regenwälder genutzt werden können. Die untersuchten Waldinventuren und Modellsimulationen zeigen die lange Persistenz von Pionierbäumen in ausgewachsenen Wäldern auf Chiloé. Unterschiedliche

Schattentoleranz und Lebensdauer von Bäumen im Wechselspiel mit Störungsregimen in dieser Region, bewirken die Langzeit-Koexistenz von Pionierarten und schattentoleranten Arten in ausgewachsenen Wäldern. Pionierarten können daher über 500 Jahre die Sukzession der Bestände dominieren. Für die Sukzession zeigen die Modellergebnisse auf, dass diese in Wäldern auf der Chiloé Insel 500 bis 850 Jahre andauern kann, bevor ein Klimaxzustand erreicht wird (stabiler Zustand des Waldes z.B. hinsichtlich der Biomasse). Die oberirdische Biomasse nimmt nach einem normalen Anstieg im Laufe der Sukzession wieder ab, bevor der Wald seinen stabilen Zustand erreicht. Zu dieser Biomassenabnahme kommt es, da große Bäume der Pionierarten erst zu einem späten Zeitpunkt durch kleinere Bäume der Klimaxarten ersetzt werden.

Die Untersuchungsergebnisse zeigen, dass der für das nächste Jahrhundert für die Chiloe-Insel vorhergesagte Klimawandel die Struktur und Dynamik des Waldes deutlich verändert, maßgeblich durch ein verändertes Niederschlagsregime. Durch die angenommenen Klimaänderungen wird sich im Jahr 2100 die oberirdische Biomasse um ~11% und die Netto-Primärproduktion um ~30% (7,6 gegenüber 2,4 Tonnen Kohlenstoff -tC- ha/Jahr) verringern. Auch ohne Berücksichtung der Auswirkungen des Kohlenstoffdioxids auf das Waldwachstum werden die temperierten Wälder der Chiloé Insel im nächsten Jahrhundert zu Kohlenstoffquellen werden (Abgabe im Mittel von 3,7 tC ha/Jahr, net ecosystem flux). Das Modell sagt unterschiedliche Kohlenstoffkreisbilanzen für die verschiedenen Waldflächen voraus, abhängig von deren Sukzessionsstadium und Struktur. Des Weiteren zeigen die Untersuchungen, dass der potentielle Klimawandel langfristig zu einer deutlichen Veränderung in der Artenzusammensetzung führt.

Diese Doktorarbeit zeigt die verschiedenen Möglichkeiten der Nutzung von Waldmodellen auf, insbesondere um Wachstum, Struktur, Alter, Koexistenz von Arten für temperierte Regenwälder im Süden von Südamerika zu untersuchen. Die Ergebnisse dieser Doktorarbeit zeigen die Notwendigkeit weiterer Forschungsarbeiten zu den Auswirkungen globalen Wandels auf Wälder im südlichen Südamerika.

RESUMEN

La preocupación sobre el cambio climático esta aumentando debido a la incertidumbre que existe sobre sus efectos en los ecosistemas. Las respuestas de los bosques al cambio climático pueden variar entre regiones del mundo haciendo necesario analizar cada región en particular. Esta tesis tiene como objetivo entender cómo los bosques templado lluviosos del sur de Sudamérica (37°45’-47°30’S, SSA) serán impactados por el cambio climático. Se analizaron datos de inventarios forestales y se desarrolló un modelo de dinámica forestal orientado en el individuo. Se abordaron específicamente tres objetivos: 1) Compilar y sintetizar el conocimiento actual sobre especies arbóreas y estructura de bosques, 2) ganar conocimiento sobre los procesos ecológicos de la dinámica sucesional en el largo plazo, y 3) examinar los posibles cambios en estructura y funcionamiento (e.g. productividad, balance de carbono e hídrico) de los bosques estudiados bajo distintos escenarios climáticos proyectados para el próximo siglo en SSA.

El estudio se realizó en bosques de la Isla Grande de Chiloé, Chile (42°S). Los bosques en esta región representan los principales tipos forestales del bosque templado lluvioso de SSA. Para caracterizar los bosques del área de estudio, se colectaron datos en terreno de bosques secundarios, bosques maduros intervenidos, y bosques maduros sin intervención (23 parcelas de 0.1 ha cada una). Se relacionaron variables ambientales con la estructura de cada rodal usando análisis estadísticos multivariados. Se realizó un detallado análisis dendrocronológico en un bosque sin intervenciones de 450 años de edad para estudiar la influencia de disturbios en la dinámica de regeneración. Se desarrollo un modelo de dinámica forestal orientado en el individuo (`FORMIND-CLIM`) que incluyó el efecto de la variabilidad climática interanual en el crecimiento arbóreo. Se calibró el modelo usando datos de terreno y provenientes de la literatura. Se incluyeron en el modelo módulos para calcular el efecto de la temperatura en el crecimiento arbóreo, balance de carbono y balance hídrico del bosque. Los parámetros inciertos fueron calibrados usando comparaciones sistemáticas entre los patrones observados y los predichos por el modelo. Se analizó el funcionamiento de los bosques usando escenarios de cambio climático proyectados por el modelo climático `PRECIS-DGF` para Chiloé (Comisión Nacional del Medioambiente y Universidad de Chile).

El análisis de datos terreno mostró que bosques antiguos de Chiloé son distinguibles en estructura y diversidad florística. Estos bosques comúnmente (a) no presentaron señales de intervención humana, (b) acumularon mas de 80 m²/ha de área basal, (c) tuvieron mas riqueza de especies arbóreas que bosques secundarios, (d) tuvieron árboles grandes y emergentes sobre el dosel, (e) presentaron alta heterogeneidad estructural, y (f) tuvieron mas de 200 años de edad. La variabilidad estructural en bosques primarios antiguos fue parcialmente explicada por diferencias ambientales entre rodales (ca. 50%, por factores tales como temperatura, distancia a la costa del Océano Pacifico y la elevación). Los datos de terreno documentaron la persistencia de árboles pioneros en bosques antiguos de Chiloé. De acuerdo al análisis dendrocronológico, la coexistencia de largo plazo de especies pioneras y especies tolerantes a la sombra en bosques primarios antiguos es explicada por la interacción de árboles con distinta tolerancia a la sombra y longevidad, con el régimen de disturbios predominante en Chiloé.

El modelo desarrollado provee una base para analizar la dinámica forestal de largo plazo usando modelos orientados en el individuo en bosques templados lluviosos de SSA. El modelo predijo variados patrones sucesionales para reproducir la variabilidad composicional y estructural de los bosques antiguos estudiados. Los resultados de las simulaciones confirmaron la dominancia de especies pioneras durante los primeros 500 años de sucesión debido a su longevidad y a la ocurrencia de aberturas de dosel producidas por tormentas. De acuerdo al modelo, los bosques de Chiloé demoran 500 a 850 años de sucesión en alcanzar el estado sucesional tardío, es decir cuando los bosques son estables en estructura (e.g. biomasa). La biomasa del bosque tiende a disminuir a medida que se aproximan a un estado estable. Esto ocurre por el reemplazo de árboles pioneros de gran tamaño por árboles de menor tamaño, potencialmente liberando carbono.

Las simulaciones mostraron que el cambio climático proyectado para Chiloé impactará el funcionamiento forestal a través de la modificación de flujos hídricos. El cambio climático disminuirá la biomasa sobre el suelo en ~11% y la productividad primaria neta en ~30% (de 7.6 a 2.4 toneladas de carbono -tC- ha/año) para el año 2100. Considerando solo el calentamiento global, esto es, excluyendo los efectos del aumento en el dióxido de carbono atmosférico, los bosques primarios antiguos de Chiloé serán fuentes de carbono en el año 2100 (3.7 tC ha/año en promedio). El modelo predijo patrones complejos y variables en el balance del carbono entre los rodales, relacionados con su etapa sucesional y variabilidad estructural. El cambio climático puede causar cambios progresivos en la composición del bosque (después del año 2200) debido al establecimiento de especies que no ocurrían previamente en los rodales. Estos resultados informan el debate sobre la respuesta de bosques al cambio climático proyectado en SSA.

Esta tesis destaca las posibilidades de usar modelos forestales para aumentar el conocimiento sobre la dinámica, funcionamiento y complejidad estructural de los bosques templados lluviosos de SSA. Se generó una síntesis de conocimiento que facilita el análisis de procesos ecológicos complejos ocurriendo en un medioambiente cambiante. Los resultados obtenidos demandan esfuerzos adicionales de investigación enfocados en explorar simultáneamente el impacto de diversos causantes del cambio global en bosques templado lluviosos de SSA.

GENERAL OVERVIEW

INTRODUCTION

Concern about climate change is increasing due to the many uncertainties that exist regarding the possible changes on ecosystems in the current century (Franklin *et al.*, 1991, Loehle & LeBlanc, 1996, IPCC, 2007). Forests cover the third part of world land area (FAO, 2005), keep most of the biodiversity of the planet and account approximately for 75% of terrestrial net primary production (Melillo *et al.*, 1993). Human activities, e.g. logging and land use changes, are modifying forest structure and dynamics (Fischlin *et al.*, 2007). Additionally, climate change will alter biogeochemical functioning of forests and their feedbacks with the climatic system (Bonan, 2008, Chapin *et al.*, 2008). Because of the importance of the forests for human well-being, predicting forest responses to global change is necessary to develop strategies for climate change mitigation.

Climate-forest interactions are complex (Aber *et al.*, 2001) and forest dynamics remains as one of the major sources of uncertainty in predicting the carbon balance of Earth's system (Purves & Pacala, 2008). Ecological models, which are simplified representations of real systems, provide an approach to understanding the complexity of ecosystems (Grimm & Railsback, 2005). Forest models are suitable tools to forecast forest responses to environmental change (Aber *et al.*, 2001) and examine multiple, interacting effects of global change (Gough *et al.*, 2008). Individual-oriented forest models, such as gap models, have been used to successfully project the behaviour of forests under changing environmental conditions (Botkin *et al.*, 1972, Shugart & Smith, 1996, Kahn & Pretzsch, 1997, Bugmann, 2001). By simulating the establishment, growth and mortality of individual trees on small patches of land as a function of biotic and abiotic factors, these models aim to understand local processes driving forest dynamics (Loehle & LeBlanc, 1996, Pretzsch *et al.*, 2008). Empirical knowledge, such as field data from representative sites, is necessary to constrain model design (Pacala *et al.*, 1996, Pretzsch, 2009). For example, forest models can be combined with retrospective analyses of forest dynamics, such as tree-rings analyses, for conducting detailed studies of tree regeneration and growth trends related to competition among species (Shugart, 1998, Anderson *et al.*, 2006). Models can also support the design of optimal sampling strategies and address hypotheses about main factors influencing forest dynamics.

In this thesis, empirical and modelling techniques are used to analyse the structure and dynamics of temperate rainforests in southern South America. Temperate rainforests are dominated by evergreen trees and located in temperate areas of the world with high rainfall (>1400 mm annually). These forests mainly occur in the Pacific coast of North America and southern South America, New Zealand, and south-eastern Australia (Whittaker, 1975). Temperate rainforests contain the highest above-ground forest biomass in the world (estimated upper limit between 1500 and 3600 t/ha) and represent the second most productive ecosystem after tropical humid evergreen forests (gross primary production of c. 1700 gC m^{-2} yrs^{-1}, Keeling & Phillips, 2007, Keith *et al.*, 2009). Significant areas of temperate rainforests dominated by broadleaved evergreen tree species are found along the western coast of southern South America (37-55°S, Veblen *et al.*, 1983). These forests represent the largest area of temperate forests remaining in the southern hemisphere (Armesto *et al.*, 1998, Armesto *et al.*, 2009). Floristic richness of old-growth forests in SSA is the highest among temperate rainforests worldwide and the high concentration of endemism has given this region an unique global conservation value (Armesto *et al.*, 1998, Armesto *et al.*, 2009). Clearing of land for pastures, the pressure for wood production from natural forests and rapidly expanding forestry plantations of exotic tree species have increased forest losses and degraded old-growth forest cover in SSA (Lara *et al.*, 2003). These pressures might increase forest susceptibility to climate change (Armesto *et al.*, 2001) and demand to analyze the fate of old-growth forests in this region.

Old-growth forests are commonly assumed in a steady state, i.e. their carbon exchange is at equilibrium (Odum, 1969). However, recent findings suggest that some of them are functioning as carbon sinks (Luyssaert *et al.*, 2008). Theoretically, forests would enter the old-growth stage only after the pioneers have been replaced and shade-tolerant species are dominating the stand (Oliver & Larson, 1990, Wirth *et al.*, 2009b). The time needed for a forest to reach the old-growth stage might be long mainly in forests containing pioneer tree species with long life-spans (>600 years). Therefore, understanding carbon flow through the forest succession implies also to address the interaction between disturbance regimes and trees with different life history traits. Long-lived pioneer trees are a common feature of temperate rainforests and they often persist in the old-growth stage (Franklin & Hemstrom, 1981, Veblen *et al.*, 1981, Lusk & Smith, 1998, Gutiérrez *et al.*, 2009). Explaining the persistence of pioneers in the old-growth stage and the successional stages of temperate rainforests is important because the large amounts of carbon stored in their biomass.

All temperate rainforests regions are *very likely* to warm during this century (Christensen et al., 2007). Temperate rainforests may be sensitive to warming because productivity in these regions is mainly constrained by temperature and radiation, both controls depending on climate (Boisvenue & Running, 2006). The warming and rainfall trends expected for this century vary among temperate rainforests regions (Christensen et al., 2007) demanding assessments of climate change impacts for each region in particular. Climate-induced tree mortality and forest die-off as a result of warming and consequent drought stress has been observed in temperate rainforests of North America (van Mantgem *et al.*, 2009, Allen *et al.*, 2010). Simulation experiments of climate warming impact on forest dynamics of these forests (Busing et al., 2007) projected shifts in tree species composition only after 2050 suggesting a lagged response to climate change. In the same region, increases in forest productivity have been documented in the last two decades (Boisvenue & Running, 2006) and an overall increase in forest productivity (up to 23%) due to climate change is projected for this century (Latta *et al.*, 2010).

Little is known about future impacts of climate change on temperate rainforests of southern South America. Temperature has increased around 0.25°C per decade in this region (time period 1976–2006, Falvey and Garreaud, 2009) and annual precipitation has decreased c. 40% in the last century (time period 1901–2005, Trenberth *et al.*, 2007). Annual precipitation it is projected to decrease up to 50% for year 2100 (DGF & CONAMA, 2006, Christensen *et al.*, 2007). Increase of temperatures in SSA in the last 50 years has produced an unusual increase in tree growth and alterations in tree regeneration (Villalba *et al.*, 1997, Villalba & Veblen, 1997, Villalba *et al.*, 2003). Extreme climatic events, such as strong droughts driven by El Niño-Southern Oscillation in SSA, have been observed to cause extensive tree mortality at certain sites (Villalba & Veblen, 1998, Suarez *et al.*, 2004). However, it is lacking to understand changes in forest functioning (e.g. productivity, carbon and water balance) due to climatic trends projected for 2100 in this region.

AIMS, FOCUS AND STRUCTURE OF THE THESIS

This thesis aims to understand how temperate rainforests of southern South America (37°45’-47°30’S, SSA) will be impacted by climate change. To answer this question, forest inventory data were analyzed and an individual-oriented forest growth model was developed. The model integrates climatic variability allowing the projection of long-term dynamics under current and future climatic trends in temperate rainforests of SSA. Specifically, this thesis addresses three general objectives: 1) to compile and synthesise the current knowledge on tree species and forest structure; 2) to gain insight into ecological processes in the long-term successional dynamics; and 3) to examine how forest structure and functioning may change by projected climatic tendencies for year 2100 in SSA.

Next sections of this *General Overview* summarize achievements of this research; discuss the scientific significance of the obtained results, and makes recommendations for future work. The thesis is complemented by an *Appendix* including research papers presenting in detail the research done. The *Research paper I* complements the general framework presented here by reviewing the distinctive characteristics of temperate rainforests around the world, with special focus on potential impacts of climate change on these forests. The study in *Research paper II* addresses the **Objective 1** of this research by compiling field data from old-growth forests of Chiloé Island and describing their structural variability. **Objective 2** is addressed both using empirical data to study forest dynamics (*Research paper III*) and applying the model to explore the successional stages of old-growth forests on Chiloé Island (*Research paper IV).* **Objective 3** is addressed by first calibrating and testing the model (*Research paper IV)* and second using the model to analyze forest responses to climate change (*Research paper V*). The *Supplementary Information* includes a detailed description of the developed forest model.

MATERIALS AND METHODS

The study was focused on old-growth temperate rainforests occurring on northern Chiloé Island, Chile (42° S). Forests on Chiloé Island have a mixed composition of broadleaved evergreen trees and belong mainly to the North Patagonian and Valdivian forests, the main forest types of temperate rainforests of SSA (Veblen *et al.*, 1983, Armesto *et al.*, 1996). Chiloé Island is located approximately in the central area of the distribution of temperate rainforests of SSA. In rural landscapes of Chiloé Island, forest stands are part of a mosaic of bogs, secondary forests, shrublands, plantations of exotic tree species and artificial grasslands. Because the present rural landscape has been shaped by a recent land use change history (< 200 years, Willson and Armesto 1996), old unmanaged forests occur in continuous and fragmented areas on the island.

Field data from young secondary, logged mature and unmanaged mature forests was used to characterize old-growth forests of Chiloé Island (N = 23). Forest structure (tree species richness, size-density distributions, vertical stratification and presence of snags) and floristic composition was obtained for each stand using 0.1 ha plots where all trees >5 cm *dbh* were measured (*dbh*, stem diameter at 1.3 m height, 4823 trees sampled). Environmental variables (i.e. temperature, rainfall, distance to coastline and elevation) were related to stand structure using multivariate constrained correspondence analysis. Increment cores were obtained from a sample of the largest trees in each stand to estimate the minimum stand age (N >10 per stand, a total of 623 trees cored). For each stand, its age and disturbance regimes (evidence of recent human impact, e.g. cuttings or fires, and tree growth rates) were used as defining old-growth criteria.

An old-growth stand (c. 450 years old, unmanaged) was selected to conduct an empirical analysis of successional dynamics. In this stand, field data of structure and composition, and regeneration in 10 tree-fall gaps and beneath the canopy were analyzed. A total of 270 increment cores were additionally obtained from main canopy trees in this stand to conduct a tree-ring analysis to assess establishment periods and to relate the influences of disturbances to regeneration dynamics of the main tree species.

An individual-oriented forest model was developed that includes the effect of inter-annual climatic variability on tree growth. New modules were included in the model allowing calculations of temperature influences on tree grow, forest carbon cycling and forest water fluxes. Species groups to run the model were selected representing the main canopy tree species of Chiloé forests (N = 17). Tree species parameters (e.g. allometry, biomass production) were selected on the basis of values given in the literature and an extensive field database. Model extensions, such as a stress induced mortality and disturbance regime, were included to reproduce main trends of forest dynamics in SSA. Field data from 13 forest stands described as old-growth on Chiloé Island were used to evaluate model performance and project responses to climate change. Uncertain parameters were calibrated and tuned using systematic comparisons between observed patterns in the field and forest structural patterns predicted by the model. Forest dynamics simulations were run for 25 ha and covering periods of 1500 years to exceed the longest possible lifespan of any of the potential dominant tree species in the study area. Analyses comprised 20 simulations for each stand with different random number seeds. Model experiments were conducted to explore forest responses under current climatic conditions and using a business-as-usual scenario of climate change projected for Chiloé Island (A2 scenario of IPCC 2007). The climate change scenario was analyzed first considering future changes in rainfall and temperature separated and then together (4 climatic scenarios in total, 960 simulations). Current temperature and rainfall parameters were changed assuming a linear increase with time until year 2100, climate stabilized after this period and the simulation continued for 500 years more.

SYNTHESISING DISCUSSION

Significant achievements and findings

This research developed an individual oriented process-based forest model that allows the projection of temperate rainforests responses to climate change. The model reproduced the observed variability in structure and composition of varied old unmanaged temperate rainforest stands on Chiloé Island. Main trends of successional dynamics in the study area were captured by the model according to current knowledge of tree species and forest dynamics. The development and calibration of the model was accomplished by three essential steps: 1) explaining structural variability of old-growth forests; 2) understanding the successional stages of forest stands and successional pathways to the old-growth stage; and 3) exploring the impact of climate change in forest functioning. Main findings and achievements are summarized below.

Old-growth forests are variable in structure and tree species composition

The *Research paper II* contributed to identify typical characteristics of old-growth forests on Chiloé Island based on structural and compositional analyses of 23 forest stands. From these stands, 11 fitted the criteria used to define the old-growth status, i.e. stand ages >200 years and no evidence of recent human impact. Additional structural attributes related to the old-growth status were (a) tree basal areas >80 m^2/ha, (b) density of shade-tolerant tree species in the emergent and dominant canopy layer >36%, (c) tree species richness >7 tree species, (d) presence of large canopy emergents (>80 cm dbh, 30 m tall), (e) a complex vertical profile (see Table 5 in *Research paper II*). These old-growth attributes were consistent with old-growth stand descriptions elsewhere in temperate rainforests of SSA and comparable to old-growth characteristics of other temperate forests (see Table 8 in *Research paper II*). The variability in stand structure and tree species composition of the identified old-growth stands was illustrated by the observed range of variation in total basal areas (54.7 to 115.5 m^2/ha) and total density (871-2100 trees/ha, Fig. 1, see also Fig. 2 in *Research paper IV*). According to field data analyses, part of the observed structural and compositional variability of old-growth forests can be explained by environmental factors (*c.* 50% explained by air temperature, elevation, distance to the Pacific Ocean coast, *Research paper II*). According to modelling results, changes in demographic rates of tree species due to *local* environmental site characteristics (e.g. excessive soil moisture) were needed to explain the high variability in structure and composition of the investigated forests (*Research paper IV).*

Persistence of pioneers in the old-growth stage

Field data analyses of *Research paper II* documented the persistence of pioneer trees in old-growth temperate rainforests of Chiloé Island (Fig. 1). Model results confirmed that pioneers dominate during the first 500 years of succession (e.g. *Nothofagus*, *Eucryphia*, *Weinmannia,* Figure 5 in *Research paper IV*). This long residence time for the initial cohort of pioneer trees in forests of Chiloé was in agreement with residence time in the canopy of tree species in temperate rainforests elsewhere (Lertzman *et al.*, 1996, Lusk & Smith, 1998). Using field data from a 450 years-old unmanaged forest, the study in *Research paper III* proposed that long life-spans, coupled with differences in sapling shade-tolerance, and the creation of canopy gaps of different sizes by emergent canopy trees are main factors for pioneers' persistence in old-growth forests of Chiloé Island. Additional traits appear important such as the ability of some pioneer species of rapid establishment immediately following a large disturbance event, its ability to tolerate long periods of growth suppression, and its rapid radial growth following release. Long-lived pioneers can also have large individual sizes and usually are gap-makers (Table 3, 6, in *Research paper III* see also Veblen 1985), thus the death of large, emergent individuals can promote its own regeneration. According to modelling results (see Figure 7 in *Research paper IV*), the occurrence of canopy openings produced by windstorms (<1600 m²) were necessary to represent forest composition of old-growth forests where pioneers tree species share the dominance with late-successional species. The interaction of trees with particular life-history traits with the disturbance regime in this region explains the long-term coexistence of pioneer and shade-tolerant tree species in old-growth forests (*Research paper III*).

Successional stages of old-growth forests

A method to identify the successional stages using field data and simulated forest dynamics is proposed in the *Research paper IV*. This successional criterion is an example of how forest models can be applied to analyze the successional stage of forests. According to the analyses, 6 out of 13 old unmanaged forests studied in Chiloé Island represented forests in transition to the old-growth stage (successional ages between 250 and 550 years, e.g. Fig. 2a). Results from this research also suggest that forests on Chiloé Island need 500 to 850 years to reach steady state (Table 3 in *Research paper IV*). As forests reach steady-state (e.g. Fig 2b) large individual of pioneer species die and are replaced by smaller late-successional trees. For example, pioneers *Eucryphia* trees with tree stem volumes >30 m³ are replaced by late-successional *Laureliopsis* trees with stem volumes

<15 m³. As a consequence, biomass tends to decrease potentially resulting in carbon losses. Biomass trajectories during the succession of forests in this region seem to be influenced for many centuries (at least 500 years) by the long dominance of pioneer tree species. Additional carbon losses in these stands may occur in the future by the incidence of human activities (e.g. fires, logging) and natural disturbance regimes.

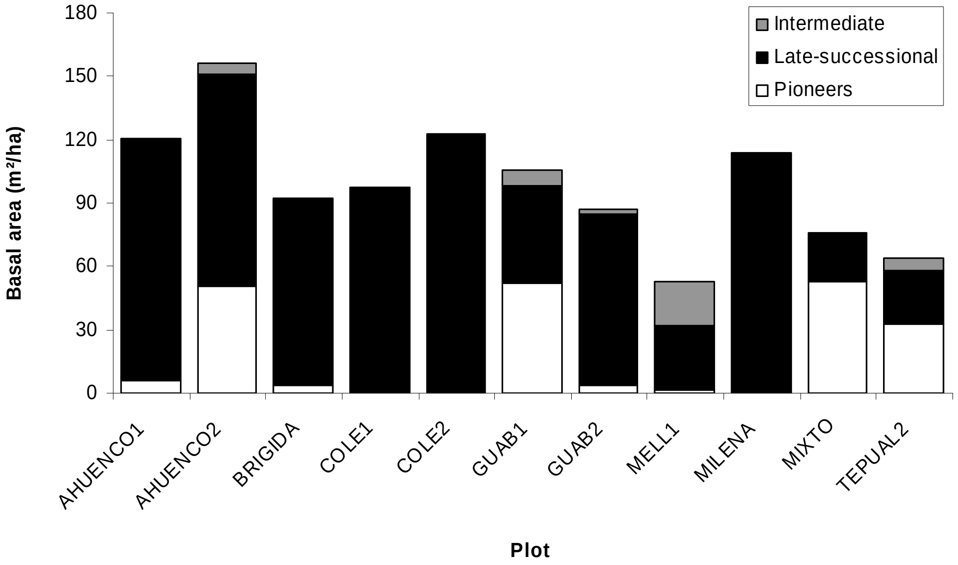

Figure 1. Forest basal area in different plots located in old-growth forests of northern Chiloé Island, Chile. Forests had no evidence of recent disturbance and had stand ages >200 years (data from *Research paper II*). Tree species were grouped according to successional status, i.e. the expected time of arrival during the succession (see Table 1 in *Research paper V*).

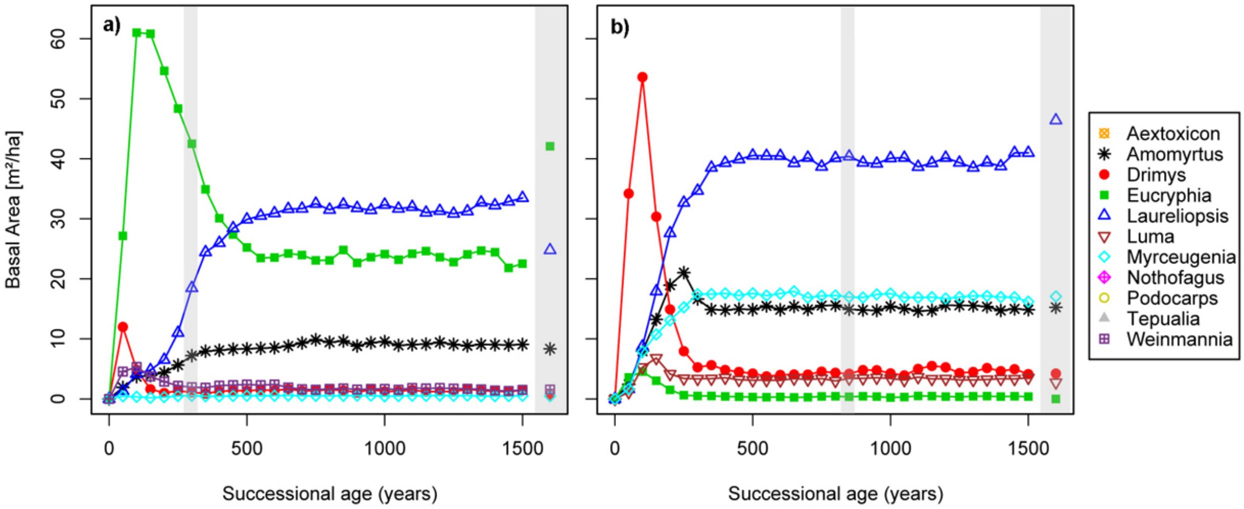

Figure 2. Forest dynamics simulation following a stand-replacing event of forest stands located on northern Chiloé Island, Chile. Simulations exemplify **(a)** forest stands in transition to the old-growth stage and **(b)** forest stand at steady state. Simulations were run for 25 ha and 1500 years, results are presented as the running mean over a 50-year period. The grey bars indicate the best agreement obtained with field data at the successional age of simulated stands (methods detailed in *Research paper IV*). Inventory data from each study site are shown in the grey bars on the right side of each chart. Species groups names according to Table 1 in *Research paper IV*.

Climate change impacts on forests of Chiloé Island

Research paper V analysed the impacts of projected climate change for year 2100 on functioning of 12 old-growth stands located on Chiloé Island (20 simulations per stand under 4 different climatic scenarios). Results of this research emphasise changes in water fluxes of forests in the study region that can be a direct impact of climate change during this century (~10% reduction forest water balance, i.e. difference between rainfall input and water return in evapotranspiration, Fig. 3 in *Research paper V*). Water deficits due hotter and dryer growing seasons expected for this century in Chiloé Island can drive reductions of about 30% in mean net primary production of forests (from 7.6 to 2.4 tC ha/year, Fig. 5 in *Research paper V*). This result contrasts to a global trend toward increased forest productivity under altered climates (Nemani *et al.*, 2003) and an overall increase in forest productivity due to climate change projected in temperate rainforests of North America (Latta *et al.*, 2010). Model results suggest that as a result of warming alone, i.e. without accounting for the direct effects of CO_2, forests on Chiloé Island will become sources of carbon for year 2100 (average among forest stands of -3.7 tC ha/year, 20 simulation runs per stand, Fig. 6d in *Research paper V*). Warming had a strong effect on increasing autotrophic respiration. The model predicted complex and variable patterns of carbon cycling among stands related to their successional stage and structural variability (Fig. 6 in *Research paper V*). Similar trends were found in temperate rainforests of North America (Smithwick *et al.*, 2009). Climate change may not cause rapid forest compositional shifts, i.e. in the current century, but a lagged, progressive change in composition, can occur due to ingrowths of species not occurring previously in the stands (see also *Supporting information* of *Research paper V*). Climate change will alter the species interactions by promoting competitive advantages in some species (e.g. increased grow) and producing dieback of large pioneer trees due to strong reductions in soil moisture. Climate change can disrupt the dynamic equilibrium of forests at steady state and a slow change in forest composition is projected by the model (i.e. after year 2200) due to the long lifespan of dominant tree species.

Research application

Preserving old-growth forests

During the last 30 years, rapid expansion of forestry plantations and agriculture, and new access roads have increased the loss and fragmentation of old-growth forests in SSA (Lara *et al.*, 2003, Armesto *et al.*, 2009). These pressures on old-growth forests are likely to continue in the coming decade (Echeverria *et al.*, 2008). Extensive areas (ca. 500,000 ha) with old unmanaged forests that can be preserved still exist on Chiloé Island and the Chilean coastal range (Armesto *et al.*, 1998, Smith-Ramírez, 2004). Results from this thesis underline the important role of these old-growth remnants for biodiversity conservation. Forests in this region need a long time to reach the old-growth stage (>500 years of succession *Research paper IV*) and some tree species only occur in old-growth forests (*Research paper II*). Other features of old-growth forests were documented such as structural components, e.g. large senescent trees and logs, and complex structural arrangements that provide habitat to plants and animals. By using the developed forest model, above ground biomass held in old-growth forests of Chiloé Island was estimated in 520 t/ha (average among 13 old-growth stands, *Research paper V*). Assuming a 50% carbon concentration, above ground carbon stocks in old-growth forests on Chiloé Island ranged 170 to 330 tC/ha, i.e higher than tropical and boreal forests (cf. Keith *et al.*, 2009). Therefore, the developed model can be used to estimate carbon emission related to old-growth forest losses in this region. Applying the model can facilitate the application of international mechanisms toward compensating developing countries for reducing emissions from deforestation and degradation (e.g. REDD). Accordingly, the preservation of old-growth forests in this region can simultaneously mitigate climate change, conserve biodiversity and maintain other services (e.g. water yield) provided by these ecosystems.

Identification and mapping old-growth stands

It is not clear the remnant old-growth surface and their rate of loss in Chile. Therefore, old-growth forest identification and mapping is a relevant task. The defining criteria and methods proposed in *Research paper II* and *IV* can be used to recognize old-growth remnants. These old-growth criteria can be complemented with remote sensing techniques (Achard *et al.*, 2009) to elaborate future inventories assessing the changes of old-growth cover. Field methods outlined in the *Research paper III* can provide a estimate of the time elapsed since the last coarse-scale disturbance, and in that way, ensure the identification of old-growth stands.

Restoration of degraded mature forests

The structural attributes of old-growth forests described in *Research paper II-IV* can help to develop forest management protocols aimed at restoring or reproducing old-growth structure in second-growth, logged, or highly degraded temperate rainforests of SSA. Also in this direction, the developed model can be used to explore the suitability of different management strategies. These strategies should consider the structural complexity and species-interactions found in old-growth forests (for a detailed discussion see *Research paper I* and *II*). Keeping an uneven-aged forest structure, large and senescent trees, and logs can ensure habitat for animal and plant species (Arroyo *et al.*, 1999, Donoso, 2002, Rüger *et al.*, 2007). Caution should be taken of controlling *Chusquea* bamboos to warrant adequate tree regeneration in degraded old-growth stands in this region (Donoso 2002).

Tools for sustainable forest management

Forest models, such as the one developed here, provide a convenient tool to explore alternatives for sustainable management of forests (Pretzsch *et al.*, 2008). The developed model can be used for exploring management scenarios in temperate rainforests of Chiloé Island and neighbouring areas in the mainland, where the same species groups dominate the forests. Some model calculations can be easily changed (e.g. soil drainage) if the model is applied in forests occurring on the slopes of the Coastal Range and Andes Mountain of Chile.

Carbon sequestration in old-growth forests

Results from this thesis contribute to the undergoing debate on ecological processes controlling the carbon balance in old-growth forests (for a review see Wirth *et al.*, 2009a). *Research paper IV* showed that many old unmanaged forests on Chiloé Island have not reached a steady state and are functioning as carbon sources. This result contrasts with findings suggesting that some old-growth forests are functioning as carbon sinks (Luyssaert *et al.*, 2008). *Research paper IV* showed that evaluation of stand successional stages is necessary to correctly associate functional features of forests with the old-growth stage, such as reduced net primary production and neutral carbon balance (Odum, 1969, Franklin & Spies, 1991, Ryan *et al.*, 1997).

Forest responses to climate change

Results from this thesis represent the current *best guess* of forest responses in the study area to climatic conditions projected for 2100 (business-as-usual A2 scenario of IPCC 2007). Climate change will produce carbon releases from old-growth forests of Chiloé Island. Currently, carbon losses from these forests are in average 0.7 tC ha/year but under climate change will be 3.7 tC ha/year for 2100 (Fig. 5 in *Research paper V*). Climate change can also decrease net primary productivity and impact forest water balance. The model developed here provides a framework for modelling temperate rainforests in other regions and conducting predictive studies at larger scales in SSA. Results can be used to improve the parameterization of temperate rainforests ecosystems in global vegetation models (e.g. Smith *et al.*, 2001).

Analysis of species-rich forest ecosystems

Ecologists have preferred to emphasize their research focusing on species identities, which has resulted in a loss of ecological generality (McGill *et al.*, 2006). While this approach has generally succeeded in explaining one- or few species systems, it has rarely provided general principles of species-rich communities (McGill *et al.*, 2006). Functional grouping of tree species, such as the one used in *Research papers III-V* simplified the understanding of dynamics and species coexistence in the studied species-rich forests. Such an approach can be used to analyze forest functioning in relation to shifts in species-specific traits during succession. Additional traits can be explored in this direction (see also Körner 2005 for a review): wood properties (e.g. anatomy and density, resistance to decay, Loehle, 1988), reproductive traits (e.g. dispersal distances, Loehle, 2000), crown plasticity (i.e. capacity of a tree to modify space occupation by the crown, Pretzsch & Schutze, 2005, Longuetaud *et al.*, 2008) and morphological and size relationships (e.g. changing relationships between tree dimensions such as stem diameter, height, and crown shape in response to competition, Pretzsch, 2009). Such a trait-based approach may lead to significant advances in community ecology of temperate rainforests of SSA.

Research needs

Using the gained knowledge in this research, I propose areas for future research on the dynamics and complexity of temperate rainforests of SSA.

Role of species-specific traits on forest functioning

Species turnover during succession involving shifts in species traits (Wirth & Lichstein, 2009) and potentially changing forests functioning should receive attention in future research. Results from this thesis showed that long-lived pioneers influence for many centuries (>500 years) the structure and functioning of forests in the studied region. Analyses in *Research paper V* (Fig. 7) also suggested shifts in dominant tree species with different traits that may explain structural and functional changes of studied forests under climate change. The developed model can be used to explore how carbon cycling during the succession is driven by compositional changes involving transitions of species traits. Addressing this question can help to understanding the links between biodiversity, biomass and productivity.

Local processes promoting forest structural variability

Future research should address the spatial interplay of environmental factors and occurring species traits to explain structural variability of old-growth forests in temperate rainforests of SSA. Thereby, the use of point-based statistics (Wiegand *et al.*, 2009) are promising to explore hypotheses outlined in *Research paper IV* on how local processes operating in forests (e.g. changes in demographic rates of species) interact with environmental factors occurring at the stand scale (e.g. soil moisture differences). The gained knowledge should be incorporated in forest dynamic models.

Interactions between disturbances and climate change

Climate change and disturbances may interact to elicit unpredicted shifts in forest composition (Overpeck *et al.*, 1990). According to Overpeck *et al.* (1990), it is likely that disturbances, e.g. forest fires, wind storms, flooding and hurricanes, increase the rate at which forest respond to future climate change. Frequency of such disturbances could change due to global warming (Scholze *et al.*, 2006, Meehl *et al.*, 2007). Therefore, the interaction between forest disturbances and climate require further study for forests in SSA. The developed forest model allows detailed analyses of forest dynamics under different disturbance regimes (e.g. Fig. 7 *Research paper IV*) that can be explore including different climatic scenarios for SSA.

Interactions of multiple global change drivers

Alterations of tree grow could be promoted by nitrogen deposition, accelerated nitrogen mineralization due to global warming and increases in atmospheric CO_2 (Saxe *et al.*, 1998, Aber *et al.*, 2001, Saxe *et al.*, 2001). Additionally in SSA, increased forest fragmentation and introduction of exotic plant species may influence future development of forest remnants (Armesto *et al.*, 2001). Fires can become more frequent and intense as a result of climate change in this region (Scholze *et al.*, 2006) potentially increasing forests susceptibility to environmental change. The interaction of these multiple drivers of global change needs to be explored in temperate rainforests of SSA to complement the gained knowledge of this research. The developed model provides a convenient starting point for future research in this direction.

Long-term monitoring

Modelling studies can be complemented by annual monitoring of forests to study their responses to novel climates (Boisvenue & Running, 2006). Monitoring programs in forests worldwide has been useful to record increases in tree mortality rates (Lorimer *et al.*, 2001, van Mantgem *et al.*, 2009), changes in carbon storage (Lewis *et al.*, 2009), and species compositional (Laurance *et al.*, 2006) and productivity changes (Pretzsch, 2005). Changes in stand structure and species composition, demographic rates and canopy turnover remain poorly documented in temperate rainforests of SSA. Permanent plots networks, such as the one presented in *Research paper II*, should be used as priority sites for such monitoring programs. Long-term studies can be complemented with measurements of important ecosystem functions, using eddy flux towers to determine whole ecosystem carbon and water fluxes. Such information should be incorporated in future model applications.

CONCLUSIONS

Characterization of old-growth forests in southern South America is necessary because of their current decline due to changes in land use. Results from this thesis confirm that many remnant forests in the rural mosaic of Chiloé Island, without evidence of human disturbance (such as selective logging or fire scars), with a complex vertical profile, and having stand ages >200 years can be defined as old growth. Structural variability observed in old-growth forests of Chiloé Island was mainly explained by environmental differences among sites (e.g. air temperature, coastal vs. non-coastal, elevation), and changes in demographic rates due to local environmental factors (e.g. soil moisture). Old-growth forest features described here offer a baseline for managers interested in maintaining and restoring old-growth forest structure in temperate rainforests of SSA.

According to model results, many old unmanaged forests occurring on Chiloé Island and neighbouring areas represent a successional stage in which forests have not reached a steady state. Old-growth temperate rainforests in this region contain large quantities of carbon and can take 500 to 850 years of succession to reach this stage. Despite of the rarity of major disturbances, long-lived pioneers persisted in the old-growth stage because of their long life spans and the occurrence of canopy openings produced by windstorms. Biomass tends to decrease as forests approach steady state because large pioneers are replaced by smaller late-successional trees, potentially resulting in carbon losses. Consequently, long-lived pioneers influence for many centuries (>500 years) the structure and functioning of forests in the studied region.

Results from this thesis strongly suggest that temperate rainforests of SSA will be impacted by climate change. Above ground forest biomass decreased 11% and net primary production was reduced in ~30% for year 2100 under climate change (from 7.6 to 2.4 tC ha/year). As a result of warming alone, i.e. without accounting for the direct effects of CO_2, old-growth forests in this region will become sources of carbon in the current century. Currently, carbon losses from these forests are in average 0.7 tC ha/year but under climate change scenario will be 3.7 tC ha/year for 2100. The model results emphasized complex and variable patterns of carbon cycling among stands related to their successional stage and tree species composition. Climate change can also impact forest water balance and produce progressive shift in composition in the long-term (after year 2200). These results inform the debate about forest responses to climate change in temperate rainforests of SSA.

This thesis highlights the possibilities of using forest models to gain insight into dynamics, functioning and structural complexity of temperate rainforests. This research synthesised the current knowledge of temperate rainforests of Chile and build up a model application. In developing and applying the model, a framework was provided to facilitate the analysis of structure and dynamics of species-rich forest ecosystems and, thereby, to explain complex processes occurring under a transient environment. Models as the one developed here can be used to support the analysis of strategies aiming at sustainable land use planning, forest management and climate change mitigation and adaptation strategies. The results of this thesis encourage future research efforts on assessing global change impacts on forests of SSA. This is especially relevant if current threats to old-growth forests in SSA (e.g. intensive logging, fires, substitution by forestry plantations) still operate during the next decade. The experience gained in the course of this work can support future model applications exploring the impacts of multiple drivers of global change on forests of southern South America.

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APPENDIX

Research paper I

Gutiérrez AG and Huth A. Temperate rainforests under changing climate: a review

Research paper II

Gutiérrez AG, Armesto JJ, Aravena JC, Carmona M, Carrasco NV, Christie DA, Pena MP, Pérez C, Huth A (2009) Structural and environmental characterization of old-growth temperate rainforests of northern Chiloe Island, Chile: Regional and global relevance. *Forest Ecology and Management*, **258,** 376-388.

Research paper III

Gutiérrez AG, Aravena JC, Carrasco-Farias NV, Christie DA, Fuentes M, Armesto JJ (2008) Gap-phase dynamics and coexistence of a long-lived pioneer and shade-tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloé Island, Chile. *Journal of Biogeography*, **35,** 1674-1687.

Research paper IV

Gutiérrez AG, Rüger N, Huth A. Successional stages of temperate rainforests: are old-growth forests at steady state?

Research paper V

Gutiérrez AG and Huth A. Potential impacts of climate change on temperate rainforests of southern South America.

Supplementary Information

The Forest Model `FORMIND-CLIM`

RESEARCH PAPER I

A temperate rainforest in southern Chile
(Chiloé Island, Ahuenco)

A similar version of this research paper will be submitted for publication as

Gutiérrez AG, Huth A. Temperate rainforests under a changing climate

Author contributions

AGG and AH conceived and designed the study. AG wrote the paper. AH contributed to the text.

Photo credit: Pablo Necochea

Temperate rainforests under a changing climate: a review

ABSTRACT

Understanding forest responses to global change is increasingly necessary because of the importance of forests for human well-being and their role for climate change mitigation. Forest types of the world may vary in their responses to climate change and, therefore, contribute differently to climate change mitigation. Temperate rainforests held the world's highest known amount of carbon in their biomass per area and support an endangered biodiversity with high levels of endemism. Both characteristics emphasize the role TRF may play in the carbon cycle and their value for conserving biodiversity under novel climates. However, the role of TRF in climate change mitigation is currently not recognized. Here we provide a synthesis of current ecological knowledge available for this forest type with special focus in the potential impacts of climate change. Using a global forest cover database and the climatic areas where TRF occur, we calculated the TRF cover worldwide. TRF cover a minor global surface compared with other forest biomes representing 0.89% of global forest cover. TRF are located in coastal and rainy areas of the world sharing similar environmental and ecological constraints that determine their similarities in life-history traits and forest structure. All TRF regions are very likely to warm during this century, with warming and rainfall trends varying sub-regionally. Climate change can alter TRF functioning by increasing productivity with contrasting results among and across regions. Climate change may impact mortality rates of TRF trees due to increased drought conditions. However, the impact of extreme climatic events during the next century on TRF is hampered due to uncertainties in possible change in climatic oscillations (e.g. El Niño Southern Oscillation). Fragmentation due to land-use changes and potential shifts in disturbance regimes (e.g. fires) can increase TRF susceptibility to climate change. Little is known about the response of TRF to novel climates in South America encouraging future research efforts in this region. Species traits can provide a framework to simplify the analysis of forest functioning of these species-rich ecosystems and foster the development of predictive models.

INTRODUCTION

Forest ecosystems cover the third part of world land area (FAO, 2005), keep most of the biodiversity of the planet and account approximately for 75% of terrestrial net primary production (Melillo *et al.*, 1993). Human activities, e.g. logging and land use changes, are modifying forest structure and dynamics (Fischlin *et al.,* 2007). Additionally, climate change will alter biogeochemical functioning of forests and their feedbacks with the climatic system (Bonan, 2008, Chapin *et al.*, 2008) Forests have socioeconomic importance not only because of the goods, services, and financial values provided by them but also by their role in climate change mitigation (Nabuurs *et al.*, 2007). Therefore, it is necessary to address forest responses to global change to develop efficient strategies of forest management focused on climate change mitigation.

To inform policy makers, it is relevant to consider how different forest types will respond to climate change and how they can contribute to climate change mitigation. Forest biomes classifications currently do not recognize the potential role of temperate rainforests (TRF) in climate change mitigation. These forests are mainly located in North America (Pacific northwest coast, PNW), southern South America (south-western coast, SSA), New Zealand, and south-eastern Australia (Whittaker, 1975). Temperate rainforests held the world's highest known amount of carbon in their biomass per area and, therefore, they are relevant for maintaining or increasing forest carbon stocks (Keith *et al.*, 2009). Temperate rainforests sustain a biodiversity with high levels of endemism and are located in populated areas where human activities have strongly impacted forest structure and endangered their biodiversity (Myers *et al.*, 2000, Brooks *et al.*, 2006). Temperate rainforests may be sensitive to changes in climate because productivity in these regions is mainly constrained by temperature and radiation (Boisvenue & Running, 2006). These characteristics emphasize the role of temperate rainforests in climate change mitigation and biodiversity conservation, and demand to understand how temperate rainforests will respond to climate change. This review seeks to provide a synthesis of current ecological knowledge available for this forest type with special focus on the potential impacts of climate change. Our main interest is also to propose future research needs for enhancing our understanding of structure and dynamics of this forest type.

WHAT, WHERE AND HOW MUCH?

Temperate rainforests occur in widely separated areas of the world with highly rainy and temperate climatic conditions. Rainfall in these areas is year-around and usually exceeds 1400 mm (annual rainfall) with >10% occurring during summer (Whittaker, 1975, Alaback, 1991, Wright *et al.*, 2004). Main locations of TRF are: the Pacific north-west coast of North America (from mixed coniferous forests of the Olympic Peninsula to the coast redwood forest of California and Oregon), south-eastern Australia (*Eucalyptus regnans* forests), New Zealand, Tasmania and south-western coast of southern South America (Fig. 1, Whittaker, 1975). In the southern hemisphere, TRF are mainly dominated by evergreen broad-leaved *Nothofagus* trees but conifers may be present (Ovington, 1983). TRF areas are found in temperate regions with cool frequently overcast summers (isotherm <16°C), a dormant season caused by low temperatures may be accompanied by transient snow, and absolute minimum temperature ranging from -10 to 0°C (Alaback, 1991, Prentice *et al.*, 1992). Climates in TRF areas have limited oscillations in temperature extremes. For example, the annual temperature range for coastal areas in SSA rarely exceeds 7°C (Arroyo et al., 1996).

It is not well known the geographical global extension of temperate rainforests. Following the methodology of Schmitt *et al.* (2008), we calculated the global surface of TRF. We filtered a global forest cover database (Iremonger *et al.*, 1997) with a global climate database (Hijmans et al., 2005) using the following climatic criteria: annual rainfall >1400 mm, annual mean temperature >16°C and absolute minimum temperature is >-10°C. According to this analysis, global cover of TRF was around 347,100 km². This surface represents 0.89% of total forest cover according to estimations of UNEP-WCMC (2000). Temperate rainforests of North America covered 38.7% of total TRF surface while TRF of southern South America represented 37.8%. TRF of south-eastern Australia, Tasmania and New Zealand TRF represented together 23.5% of total TRF surface.

Temperate rainforest areas covered a minor global surface compared with other forest biomes, such as tropical forests and boreal forests (covering c. 51% and 18% of forested land, respectively).

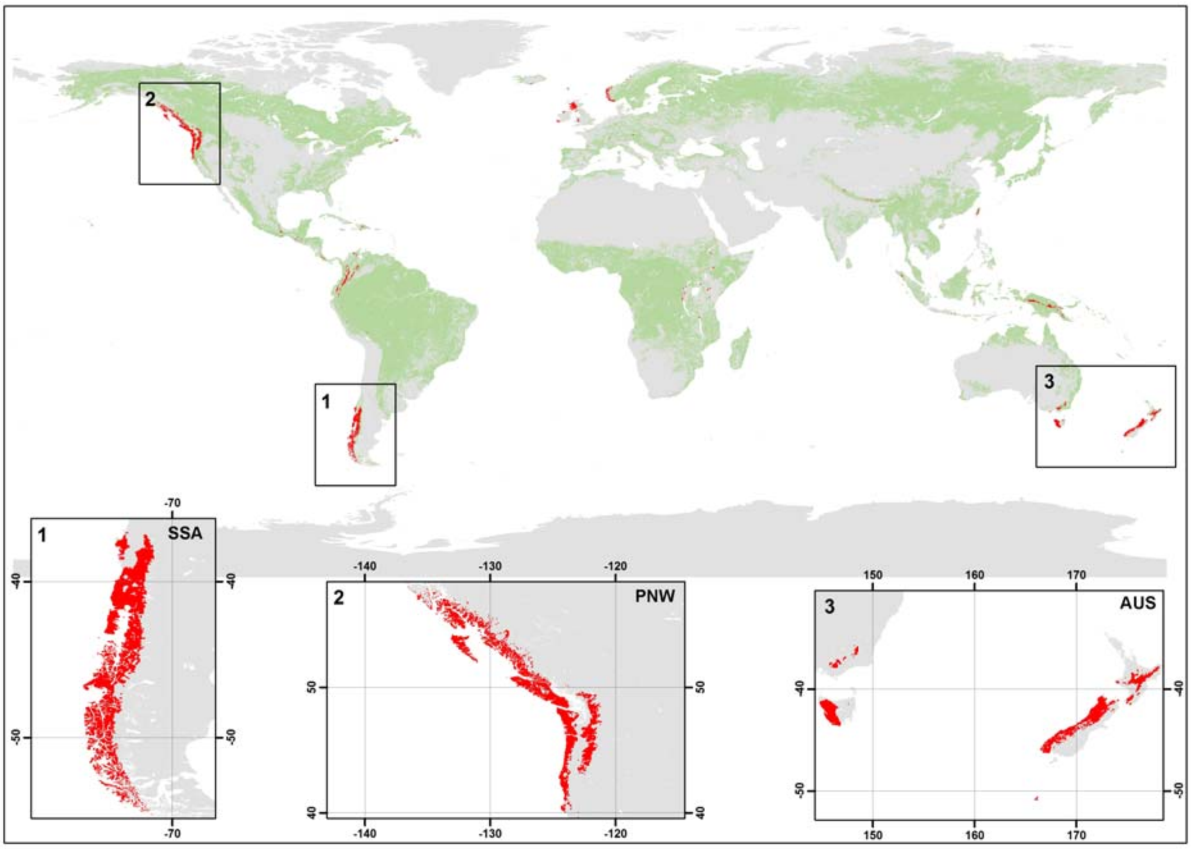

Figure 1. Main temperate rainforest areas of the world. In red are shown locations where annual rainfall exceeds 1400 mm, annual mean temperature >16°C and absolute minimum temperature is > -10°C. Boxes show a detailed map of regions in 1: southern South America (SSA), 2: Pacific Coast of North America (PNW) and 3: south-eastern Australia, Zealand and Tasmania (AUS). Global forest cover (green) according to Iremonger et al. (1997).

FOREST STRUCTURE

Plant diversity

Temperate rainforests exhibit a very rich floristic assemblage with >500, up to 3000 species of vascular plants (including ferns and angiosperms) in each area (Kier et al., 2005), and up to 70 tree species (Table 1). High levels of endemism are common in temperate rainforests, with each area supporting 50 to 200 endemic vascular plant species (Myers *et al.*, 2000, Kier *et al.*, 2009). One of the most conspicuous differences among southern and northern temperate rainforests is the dominance of conifer species in the northern hemisphere and broad-leaved species in the southern hemisphere (Groombridge & Jenkins, 2002). In temperate rainforests located along the PNW, conifer tree species such as Sequoias, Douglas firs (*Pseudotsuga menziesii*), pines (*Pinus spp.*), make up the canopy, but other conifer taxa are also important (e.g. *Larix*, *Abies*, *Tsuga*, Waring & Franklin, 1979, Alaback, 1991). In contrast, temperate rainforests in the Southern Hemisphere are dominated by broad-leaved evergreen tree species. TRF occurring in New Zealand, Tasmania and

SSA have the widespread dominance of the same broadleaved tree genus, *Nothofagus* (Ovington, 1983). Other broad-leaved tree species such as *Eucryphia*, *Weinmannia* and members of the Myrtaceae family are also common in southern TRF occurring in mixtures with conifers of the Araucariaceae, Cupressaceae and/or Podocarpaceae families (Ovington, 1983, Hill & Enright, 1995, Armesto *et al.*, 1996, Veblen *et al.*, 1996b).

Table 1. Structural characteristics of temperate rainforests separated by main regions of the world.

	Units		**Pacific Northwest of North America**[1]	**New Zealand and south-eastern Australia**[2]	**Southern South America**[3]
Tree species richness			40-70	>50	45
Canopy height	m		30 - 100	90	50
Tree life-spans	years		550 - 3500	350 - 1170	250 - 3600
Maximum stem diameter	cm		630	700	500
Basal area	m² / ha		49 - 338	55 - 144	70 - 305
Stem density	stems / ha		373 - 1154	444 - 674	800 - 2300
Stem volume	m³ / ha		1,406 – 10,817	81.7 - 839	200 - 1550
Above ground biomass	t / ha	Typical range	450 - 1500	415 - 950	440 - 880
	t / ha	upper limit	1800 - 3300	1500 - 3600	1470 - 2200
Net productivity	t / ha year		6.6 – 14.3	8 - 10	8.3 - 9.6

References: 1: (Waring & Franklin, 1979, Franklin & Waring, 1980, Spies & Franklin, 1991, Waring et al., 2006, Keeling & Phillips, 2007); 2: (Wardle et al., 1983, Grierson et al., 1992, Neave & Norton, 1998, Silvester & Orchard, 1999, Keith et al., 2009); 3: (Lara, 1991, Donoso et al., 1993, Lara & Villalba, 1993, Villagrán & Hinojosa, 1997, Donoso & Lara, 1999, Lara et al., 2000, Pollmann & Veblen, 2004, Schlegel & Donoso, 2008, Keith et al., 2009)

Different evolutionary histories of temperate rainforest locations may determine these differences in species composition (Ovington, 1983). For example, *Nothofagus* dominance in the southern hemisphere results from the connection of southern land masses as one land area in the late Cretaceous, approximately 100 million years ago (Markgraf et al., 1995, Veblen et al., 1996a). One explanation of conifer dominance in PNW forests is that, during the winter, soil water potential of the unfrozen ground is high and, during summer, drought is severe resulting in few angiosperm tree species that are able to survive (Bugmann & Solomon, 2000). Winters are not as severe for plant growth in the Southern Hemisphere as in North America given the oceanic influence that moderates winter temperatures (Arroyo et al., 1996, Markgraf & McGlone, 2005). This results in the rarity of some functional groups, such as deciduous trees in the southern hemisphere, the lack of species able to tolerate cold and the abundance of lianas, palms, tree ferns at higher latitudes than elsewhere (Markgraf & McGlone, 2005). Differing climatic histories of the southern hemisphere in the past could be also responsible for biotic differences with the northern hemisphere (Alaback, 1991, Markgraf *et al.*, 1995).

Biomass, productivity and carbon storage

As far we know, the highest above-ground forest biomass in the world is found in *Eucalyptus regnans* temperate rainforests of south-eastern Australia (Keith et al., 2009). These forests can reach 3600 t/ha in living above ground biomass (AGB, estimated upper limit between 1500 and 3600 t/ha). The AGB upper limit for temperate rainforests of the PNW is estimated between 1800 and 3300 t/ha (Keeling & Phillips, 2007). In New Zealand, *Agathis australis* forests can store up to 1500 t/ha in AGB and in SSA *Nothofagus* forests held up to 2200 t/ha (Silvester & Orchard, 1999, Schlegel & Donoso, 2008). Typical ranges in AGB found in temperate rainforests are detailed in Table 1. Following the pattern in biomass, basal areas and stand volume of temperate rainforests are among the highest in forests of the world (Table 1). Standing volumes up to 10,817 m³/ha are found in Coast Redwood in the PNW (Waring & Franklin, 1979) and up to 1550 m³/ha in *Fitzroya cuppressoides* forest in SSA (Donoso *et al.*, 1993). Old-growth TRF forests can also hold large amounts of coarse woody debris biomass, with the highest values found in the PNW (>1000 Mg/ha) (Harmon *et al.*, 1986, Schlegel & Donoso, 2008).

Temperate rainforests represent the second most productive ecosystem (net primary production of c. 780 gC m^{-2} yrs^{-1}, gross primary production of c. 1700 gC m^{-2} yrs^{-1}) after tropical humid evergreen forests (Keeling & Phillips, 2007, Luyssaert *et al.*, 2007). Productivity of temperate rainforest is limited by radiation and temperature in winter, by temperature in spring, and water by midsummer (Boisvenue & Running, 2006). Mid fall and winter conditions may facilitate continued tree productivity in TRF (Keith et al., 2009). These climatic conditions and predominant disturbance regimes (see below) coupled with slow decomposition rates of dead biomass are factors explaining high biomass of TRF areas (Smithwick *et al.*, 2002, Keith *et al.*, 2009).

Structural variability

Old-growth temperate rainforests typically have multilayered canopies, large variation in tree sizes, many large live old trees and standing dead trees, and large amounts of coarse woody debris (Franklin & Spies, 1991b, Spies & Franklin, 1991, Armesto *et al.*, 2009, Gutiérrez *et al.*, 2009). These structural components are highly variable among old-growth stands (Franklin *et al.*, 2002, Gutiérrez *et al.*, 2009). For example, in old-growth forests of the PNW total basal area varies from 64 to 338 m²/ha (Waring & Franklin, 1979, Spies & Franklin, 1991). In Chile, total basal area in old-growth stands varies from 80 to 160 m²/ha in average (Gutiérrez et al., 2009) but reach up to 305 m²/ha (Pollmann & Veblen, 2004). The main part of this structural variability in old-growth TRF (ca. 50%) is explained by environmental factors, such as climate (Lusk, 1996, Ohmann & Spies, 1998, Gutiérrez *et al.*, 2009). Other differences among sites, such as successional age, forest management, disturbance regime, and demographic rates variation in different sites have been shown to explain in part the structural variability found in old-growth temperate rainforests (Ohmann & Spies, 1998, Franklin *et al.*, 2002, Gutiérrez *et al.*, in review). The broad range of variation in tree *dbh* distributions (cf. Gutiérrez *et al.*, 2009) and in the amount of coarse woody debris in old-growth temperate rainforests (Spies & Franklin, 1991, Schlegel & Donoso, 2008) are consistent with different patterns of competition and disturbance among stands (Coomes *et al.*, 2003, Coomes & Allen, 2007). Multiple successional pathways to the old-growth stage can also explain structural variability observed in old-growth temperate rainforests (Gutiérrez *et al.*, in review).

FOREST DYNAMICS

Forest succession in temperate rainforests usually vary according to the tree species pool present in each site and site environmental differences, such as soil moisture, disturbance, and climate (Franklin *et al.*, 1991, Bugmann & Solomon, 2000, Hall & Hollinger, 2000, Busing *et al.*, 2007, Gutiérrez *et al.*, in review). Temperate rainforests dynamics are also characterized by diverse interactions among tree species and other vascular plants, and the high diversity of functional traits of tree species. In order to assess this complexity, the patch dynamics perspective of forest succession (Pickett & White, 1985) and the regeneration niche concept (Grubb, 1977) have frequently been used for analyzing stand-level dynamics, particularly in *Nothofagus* forests (Veblen et al., 1996b). From the study of *Nothofagus* forests, the non-equilibrium paradigm of forest dynamics has emerged pointing to the impact of natural disturbance on forests (Veblen et al., 1996a). Current research in TRF dynamics is been focused in understanding the role of functional species traits, species interactions and disturbance regime as discussed below.

Functional traits

A common feature in temperate rainforests worldwide is the large tree heights and sizes of trees (Table 1). Along the PNW, forests with the tallest trees in the world (>100 m) can be found that are only rivalled by *Eucalyptus* forests of south-eastern Australia (Waring & Franklin, 1979, Keith *et al.*, 2009). *Agathis australis* trees up to 7 m in diameter are found in New Zealand (Wardle, 1991). Long lifespans is also a common feature among temperate rainforests (Table 1) with the oldest tress found in SSA (e.g. conifer trees >3600 years-old and broad-leaved trees >600 years-old, Lara & Villalba, 1993, Lusk, 1999). Waring & Franklin (1979) speculate that the elapsed time between stand-replacing disturbances favour the persistence of tree species with long-life spans and large statures in the PNW.

Differences in shade-tolerance among competing tree species were long used to explain regeneration dynamics of temperate rainforests (Franklin & Hemstrom, 1981, Stewart & Rose, 1990, Donoso, 1993). However, in southern temperate rainforests many tree species show similar tolerance to shade in juveniles (Figueroa & Lusk, 2001). In SSA, some shade-tolerant tree species are able to regenerate in canopy gaps (Gutiérrez et al., 2008) and their seed germination is relatively unresponsive to overstorey light conditions similarly to other forests (Swaine & Whitmore, 1988, Figueroa & Lusk, 2001). In contrast to moist tropical forests and other temperate forest ecosystems, a large group of pioneer species that require canopy gaps for successful germination is not evident in temperate rainforests of SSA (Figueroa, 2003). For example, the pioneer tree species *Drimys winteri* seems broadly tolerant to light conditions during the seedling and sapling stages (Figueroa & Lusk, 2001, Chacón & Armesto, 2005). Consequently, the physiological plasticity to light environment of tree species in southern TRF suggests that they are able to respond to slight differences in understorey light levels as has been shown in other broad-leaved temperate forests (Canham, 1989).

Other functional traits can help to explain the coexistence of tree species differing in shade tolerance in old-growth temperate rainforests. Longevity differences among competing tree species have been proposed as a mechanism promoting the coexistence in this forest type (Franklin & Hemstrom, 1981, Stewart & Rose, 1990, Gutiérrez *et al.*, 2008). Old-growth temperate rainforests commonly contain pioneer tree species with long lifespans, such as pioneer conifers >1000 years old (Waring & Franklin, 1979, Franklin & Hemstrom, 1981, Lara, 1991, Lusk & Ogden, 1992, Lusk & Smith, 1998). Broadleaved pioneers >600 years-old are found in SSA (Lusk, 1999, Pollmann & Veblen, 2004, Gutiérrez *et al.*, 2008) and pioneer >450 years-old are also found in TRF of south-eastern Australia and in New Zealand (Stewart & Rose, 1990, Keith *et al.*, 2009). Pioneer tree species may persist in the old-growth stage due to the occurrence of disturbances (Franklin & Hemstrom, 1981) but also by other species-specific traits. For example, the regeneration of light-demanding trees can be facilitated by sprouting from gap makers or trees growing along gap edges in SSA (Veblen *et al.*, 1981, Lusk, 1995, Gutiérrez *et al.*, 2008).

Other traits can be explored to assess tree species coexistence in TRF such as wood properties (e.g. anatomy and density, resistance to decay, Loehle, 1988), reproductive traits (e.g. dispersal distances, Loehle, 2000), and crown plasticity (e.g. Pretzsch & Schutze, 2005, Longuetaud *et al.*, 2008). An association between the mechanism of seed dispersal and chilling requirements may also play a role (Figueroa, 2003). The chilling requirement for germination is common in tree species in the Northern Hemisphere but in contrast, in SSA, there is only a moderate representation of delayed germination enhanced by cold possibly due to lower seasonal temperate fluctuations (Figueroa, 2003).

The above discussion supports the view that multiple life history traits determine the dynamics and structure of temperate rainforests communities. The functional aggregation of tree species into successional roles (e.g. pioneers, intermediate and late successional species) and other traits (e.g. shade-tolerance, life spans, height, dispersal and germination, see also Körner 2005 for a review) can help to simplify the understanding of temperate rainforests dynamics. Similar traits seems to be structuring other forest types (Shugart, 1984, Acevedo *et al.*, 1996). Understanding changes in dominant species with different functional traits during the succession (e.g. height and diameters) is important because they may influence successional trends in biomass of temperate rainforests (Wirth & Lichstein, 2009, Gutiérrez *et al.*, in review).

Disturbance regime

Disturbance regimes have been used to interpret differences in composition and structure of old-growth stands in SSA and in the PNW (Veblen *et al.*, 1981, Franklin *et al.*, 1991, Armesto *et al.*, 1996). It is still under discussion the role of fire regimes in temperate rainforest dynamics. Alaback (1991) disregarded fires as an important evolutionary factor because of the highly rainy conditions of TRF areas. Nevertheless, Franklin *et al.* (1991) argued that a gradient in fire frequency associated with climatic differences exists in the PNW. Model simulations support the importance of fires on forest dynamics in the same region (Busing *et al.*, 2007). Recent studies in southern temperate rainforests have documented high severity widespread events of fires (González et al., 2005) and explored the role of fire regimes in tree regeneration dynamics (Holz, 2009). In general in TRF areas, these catastrophic events tend to be historically infrequent (Franklin *et al.*, 1991, González *et al.*, 2005, Holz, 2009). The low frequency of catastrophic disturbances like fire and hurricane in TRF coupled with favourable climatic regime may determine that tree species persist in the canopy for a long time (c. 500 years on average) (Lertzman & Krebs, 1991, Lusk & Smith, 1998, Ott & Juday, 2002). Koch *et al.* (2004) argued that trees grow tall in TRF areas because storms are not strong enough to produce crown mechanical damage. Despite of the infrequency of catastrophic fires, the role of other disturbances (e.g. landslides, volcanism, earthquakes and windstorms) has been relevant to explaining the dynamics and floristic composition differences across TRF regions. Contrasting disturbance regimes can result in different regeneration modes of tree species and differences in forest community composition. For example, Andean forests of SSA (38°-47°S) are subjected to more frequent cycles of large disturbances (i.e. landslides, volcanism and fire), determining a stand-replacement regeneration mode (Veblen & Ashton, 1978, Veblen *et al.*, 1981). Conversely, in the coastal-range and coastal-lowland forests of the same region these events are rare and forests are mainly subjected to gap phase dynamics (Veblen *et al.*, 1981, Veblen, 1985, Armesto & Figueroa, 1987, Armesto & Fuentes, 1988). As in tropical forests (Schnitzer & Carson, 2001), individual tree-fall gaps (e.g. <300 m^2) can be important sites for the regeneration of most main canopy tree species in temperate rainforests of SSA subjected to gap phase dynamics (Gutiérrez et al., 2008). Local distinctive disturbance histories determine different successional pathways in different sites, as suggested by modelling studies in temperate rainforests of PNW (Busing et al., 2007).

Species interactions

Animal-plant interactions have been recognized as important ecological processes in TRF of the southern hemisphere (Armesto et al., 1987). Compared with temperate forests of the northern hemisphere and some wet tropical forests, temperate rainforests of SSA and New Zealand are characterised by a high proportion of fleshy fruited species (70% of woody flora, Armesto & Rozzi, 1989). Indeed, patterns of seed dispersal, i.e. ornithocory, in temperate rainforests of SSA contrast also with dispersal syndromes found in northern temperate forests and are more similar to dispersal syndromes found in the tropics (Armesto & Rozzi, 1989, Armesto *et al.*, 2001a). This strongly suggests a mutual dependence between plant and birds populations (Armesto & Rozzi, 1989). Biotic pollination is the main syndrome in SSA (Armesto et al., 2009) and emergent trees with profuse and massive flowering might be a pivotal resource for insect pollinators (Smith-Ramirez et al., 2005).

Old-growth TRF usually are complex in term of their vertical canopy structure (Franklin & Van Pelt, 2004, Gutiérrez *et al.*, 2004, Gutiérrez *et al.*, 2009). This structural complexity can have a positive influence on richness and abundance of animal species by determining guild structure (Franklin & Spies, 1991a, Díaz *et al.*, 2005). Old-growth TRF stands have also large, senescent trees and large snags (stem diameter >20 cm) that are key structural attributes providing habitat for bird species (Franklin & Spies, 1991a, Willson *et al.*, 1996, Cornelius, 2008). Snags also provide habitat for vascular and non-vascular epiphytes (Muñoz *et al.*, 2003, Díaz *et al.*, 2005) as well as safe-sites for regeneration of tree species (Lusk & Ogden, 1992, Lusk, 1995, Christie & Armesto, 2003).

The effect of understory species, such as *Chusquea* bamboos proliferating after natural or anthropogenic disturbances, can also be relevant in regeneration dynamics of southern TRF (Veblen, 1982). The abundance of *Chusquea* bamboos have an important role as competitors in gaps, apparently inhibiting the regeneration of pioneers and shade tolerant species in southern TRF (Veblen, 1982, González *et al.*, 1997, Donoso & Nyland, 2005). *Chusquea* bamboos provide protection and food resources for resident birds in old-growth forests in this region (Reid *et al.*, 2004).

CLIMATE CHANGE IMPACTS

Climate change projections in temperate rainforests areas

According to the results of the Intergovernmental Panel of Climate Change (IPCC, Christensen et al., 2007), all temperate rainforests regions are very likely to warm during this century comparable overall to the global mean warming. In all temperate rainforests regions projected temperature changes for the next century are in the range of 2-4°C but up to 6°C in the PNW. Temperature is projected to increase almost linearly with time. The warming varies sub-regionally, with less warming in coastal regions of Australia, Tasmania, the South Island of New Zealand, and SSA.

Models project different rainfall trends for the next century among TRF regions (Christensen et al., 2007). An increase in annual mean precipitation over most of North America is projected excepting the most south-westerly part of the continent. Rainfall during winter is predicted to decrease in 10-15% whereas summer temperature may increase in 5 to 15%. In the PNW, increases in rainfall over snowfall and rain-on-snow events increased extreme runoff by

11%, which would contribute to more severe flooding. Annual mean precipitation is projected to decrease over large parts of SSA, with relative precipitation changes being largest in summer. Although simulation of the regional climate is affected in SSA by model deficiencies, projections are in the range of decreases in precipitation occurred in the century (40%, time period 1901–2005, Christensen *et al.*, 2007, Trenberth *et al.*, 2007). Increased rainfall on the South Island of New Zealand, possibly accompanied by a decrease in the North Island, is expected to occur in the next century. The South Island rainfall increase is likely to occur in the upper part of the main mountain range but modulated by the strong topography of the island. According to seasonal modelling projections for south-eastern Australia (Christensen et al., 2007), rainfall will tend to increase in summer but decrease during winter and spring.

Uncertainties in climatic projections still remain about how climatic oscillations, such as El Niño-Southern Oscillation -ENSO- or the Pacific Decadal Oscillation -PDO-, will respond to climate change (Christensen *et al.*, 2007). ENSO significantly influences rainfall, drought conditions and extreme climatic events in SSA (Garreaud *et al.*, 2009) but models tend to project no significant changes in the frequency of extremely wet or dry seasons over SSA (Christensen et al., 2007). However, these projections are limited by the knowledge available on extremes of temperature and precipitation in SSA (Christensen et al., 2007). In contrast, in Australia and New Zealand is very likely that extreme high daily temperatures become more frequent and cold extremes become uncommon in the next century. Decreases in the annual frequency of days below 0°C and increases in the annual number of days above 25°C are projected for New Zealand. In the PNW, climate change can decrease extreme cold events and increase extreme hot temperature events (California), increase extreme in precipitation during the cold season (British Columbia), and increase the likelihood of severe flooding (Christensen *et al.*, 2007).

Temperate rainforests responses to climate change

Climate-induced tree mortality and forest die-off is relatively well documented for the PNW in the last decade with drought and warmth leading to extensive insect outbreaks (Allen *et al.*, 2010). Regional warming and consequent drought stress are the most likely drivers of changes in tree demographic rates (e.g. increased mortality) currently occurring in TRF of the same region (van Mantgem *et al.*, 2009). Following this line of evidence, it is likely that global warming could increase mortality rates of temperate rainforests elsewhere. Simulation experiments of climate warming impact on forest dynamics in Oregon landscapes (Busing et al., 2007) suggested that rapid climate change could not cause severe shifts in forest composition. Douglas-fir is projected to remain as a dominant species in the landscape while some other species may shift their ranges to higher elevations (Busing et al., 2007). This result lends support to suggestions of a slow, muted response on PNW forests to climate change (Dale & Franklin, 1989, Cumming & Burton, 1996, Zolbrod & Peterson, 1999). Long life spans of tree species and the ability of established trees to accommodate environmental change may explain the slow retreat of range boundaries of temperate rainforests in response to climate change (Franklin et al., 1991). Considering the findings of van Mantgem et al. (2009), it is important to notice that model assumptions such as unlimited dispersal and constant background tree mortality (Busing et al., 2007), may underestimate TRF responses to climate change in the PNW.

Decreased rainfall conditions projected for the next century may have an impact on forests of SSA and New Zealand. In SSA, ENSO-related seasonal droughts in SSA have been found to amplify background tree mortality rates and cause extensive mortality of *Nothofagus* (Suarez *et al.*, 2004). Similar drought-induced mortality has been documented in *Nothofagus* forests in New Zealand (Hosking & Hutcheson, 1988). The influence of current climate change on forests of SSA, i.e. the last 50 years, is also apparent in the unusual increase in tree growth and alterations in forest regeneration (Villalba *et al.*, 1997, Villalba & Veblen, 1997). Markgraf & McGlone (2005) argue that the effects current climate change in southern TRF could be similar to the effects of warming in the past (i.e. last 16,000 years), such as immigration of new taxa and elimination of old, cool-adapted taxa. However, it should be considered that forests in SSA have reduced and isolated geographical range and forestry plantations of exotic timber species could limit the potential migration of tree species to southern areas due to climate warming (Armesto *et al.*, 2001b). We are not aware of modelling studies in SSA projecting TRF responses to climate change. In New Zealand upwards migration of lowland dominant species into montane areas may occur (Leathwick et al., 1996). In this region, it is predicted the invasion of broad-leaved species in large areas dominated by *Nothofagus* and the southwards migration of northern species into areas with higher solar radiation (Leathwick et al., 1996). According to Leathwick et al. (1996), an increase of 2°C in mean annual temperature may cause disequilibrium in forests of New Zealand.

A climate-change risk analysis for world ecosystems projects more frequent wildfires in much of South America forced directly by climate (Scholze *et al.*, 2006). In this region, climatic regime and major climatic oscillations (e.g. ENSO) can create dry conditions resulting in widespread fires in SSA (Kitzberger & Veblen, 1997, Holz, 2009). Holz (2009) emphasized that current climate trends in the last 60 years appear more conducive for a higher frequency of fires. As consequence, drying conditions projected in SSA may promote an upward trend in wildfire activity, with potential impacts on temperate rainforest dynamics.

An overall increase in forest productivity due to climate change has been found in temperate rainforests of the PNW but this increase is not consistent across the region (Boisvenue & Running, 2006, Latta *et al.*, 2010). Radial growth increases detected in tree lines of SSA (Villalba *et al.*, 2003) may agree this trend of increased tree productivity but contrasting results (no trend related to global warming) have been found in New Zealand (Cullen *et al.*, 2001). Therefore, complex patterns of forest responses to climate change could operate locally in TRF regions despite of their similar climatic constraints to plant growth (cf. Boisvenue & Running, 2006). Limited information is available about productivity changes in lowland and mid-altitude temperate rainforests of the Southern Hemisphere.

RESEARCH NEEDS

Addressing the impacts of climate change on temperate rainforests will require empirical information on forest processes (e.g. demographic rates and below-ground net primary production) and carbon balance under changing environmental conditions. Global warming and rising carbon dioxide concentration in the atmosphere could impact forest's carbon fluxes through changes in carbon uptake and loss (Boisvenue & Running, 2006, Gough *et al.*, 2008). Although warming and consequent increases in water deficits are likely contributors to increases in tree mortality rates (van Mantgem *et al.*, 2009), it is not clear how these factors alter forest structure, composition and carbon sequestration. As in other forest biomes (Chapin *et al.*, 2009), it is still uncertain how environmental changes will impact global forest productivity mainly because of the lack of reliable data on below-ground microbial processes.

The determination of the forest processes discussed above and their responses under novel climates will require long-term monitoring of forests in representative sites (Boisvenue & Running, 2006). Forest monitoring should consider large scale field experiments (e.g. >1 ha) that include the range of variability of forest ecosystems and, in this way, reduce the uncertainty of forest productivity projections (Dixon *et al.*, 1994, Boisvenue & Running, 2006). Continuous forest monitoring programs are still not uniformly and globally available (Dixon *et al.*, 1994). The lack of monitoring and data from temperate rainforests of developing countries, i.e. Chile and Argentina, is evident in global dataset (e.g. Luyssaert et al., 2007) particularly in data of gross primary production, net ecosystem exchange and ecosystem respiration. In developing countries, monitoring programs are difficult to sustain because of day-to-day management of natural resources by poor rural people, availability of permanent local funds and human resources (Danielsen *et al.*, 2003). As a consequence, studies addressing changes in stand structure over time, i.e. tree mortality, canopy turnover, and snag formation rates, are rare in this region (Gutiérrez *et al.*, 2009).

Forest models can provide relevant information for scenario assessments of the impact of global change on forest ecosystems, especially in those areas where monitoring data is still missing. Models also provide a synthesising tool of the current knowledge and allow to examine multiple and interacting effects of climate change (Gough *et al.*, 2008). Individual oriented forest models (i.e. gap models Bugmann, 2001) has been applied in temperate rainforests facilitating detailed analyses of forest dynamics (Pausas *et al.*, 1997, Bugmann & Solomon, 2000, Hall & Hollinger, 2000, Busing *et al.*, 2007, Rüger *et al.*, 2007, Gutiérrez *et al.*, in review). Currently, there is a strong scientific focus on implementing individual-based models, primarily developed for doing local dynamic simulations, at regional and global scales (see for example Purves & Pacala, 2008).

In order to reduce the uncertainties of these models, more information is needed at the level of species or groups of species (Purves & Pacala, 2008). TRF are commonly included in dynamic global vegetation models as part of other forest biomes with contrasting disturbance and climatic regimes, for example with boreal forests dominated by fire disturbances or with mediterranean forests with a strong drought season. Forest responses to climate change also vary among TRF regions; therefore, these models may oversimplify possible trends in these regions. Considering the features of TRF described here, a separation TRF in these global biome assessments could reduce modelling uncertainties to project vegetation responses to climate change at the global scale.

OUTLOOK

The main characteristics of temperate rainforests have been discussed here with emphasis on their response to climate change. Old-growth temperate rainforests represent an important natural heritage due to the high number of species endemism, trees characteristics and forest structure. The features of TRF discussed here can help to better characterize this forest type in general classifications of global forests (e.g. Groombridge & Jenkins, 2002) and consider a separation of these forests in biome classifications (Keith *et al.*, 2009). Comparatively with other forests biomes, the surface of TRF is low (0.89% of total forest cover) but rates of deforestation are as high as in tropical forests in some TRF regions (e.g. southern Chile Echeverría *et al.*, 2007). This may interact with the current process of fragmentation increasing their susceptibility to climate change. TRF may play an important role in carbon cycling because of the high amount of carbon store in their biomass and high forest productivity. Additionally, structural variability of old-growth TRF provides an interesting framework to test hypotheses about environmental influence, successional pathways and species interactions along the succession.

All temperate rainforests regions are very likely to warm during this century, with warming and rainfall trends varying sub-regionally. How extreme climatic events could change appear unclear mainly due to uncertainties in possible shifts of climatic oscillations during the next century (e.g., ENSO, PDO). Current empirical evidence and projected responses of TRF to climate change strongly suggest that TRF can be impacted through changes in mortality rates of trees mainly due to increased drought conditions. Changes in species composition appear lagged by the long life-span of dominant trees. Climate change can alter TRF functioning by increasing productivity but contrasting results can be expected among and across regions.

We encourage future research efforts in TRF located in the Southern Hemisphere focusing on expanding long-term monitoring programs into these areas and conducting experimental climate change research. Although such research programs are challenging in the developing countries, we believe that expanding current research efforts of global change impacts (e.g. eddy-flux towers monitoring and free-air CO_2 enrichment -FACE- experiments) on species-rich southern TRF will improve our understanding of complexity in global forest functioning and their response to climate change. Future research focusing on role of functional species traits can also be important to enhance predictive tools to analyze the response of TRF to climate change.

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RESEARCH PAPER II

Interior of an old-growth temperate rainforest in southern Chile
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Author contributions

AGG conceived and designed the study, performed research, analyzed data, and wrote the paper. NVC, DAC and MP analyzed data and performed the research. JCA, MC, and CP performed research and provided data. JJA and AH conceived and designed the study. All authors contributed to the text.

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Structural and environmental characterization of old-growth temperate rainforests of northern Chiloé Island, Chile: Regional and global relevance

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ABSTRACT

Old-growth forests are ecologically relevant reservoirs of biodiversity and provide valuable and unique ecosystem functions in the landscape. However, what constitutes an old-growth stand is confusing because the definition depends largely on the forest type under study. Despite the ecological importance of old-growth temperate rainforests in southern Chile in comparison to other global forests, no attempts have been made to characterize them as a way to assess their structural variability. Here, we characterized old-growth stands of Valdivian and North Patagonian rain forest types located in Chiloé Island (Chile, 42°30′S) using inventory data from 23 permanent plots (0.1 ha each) located in rural landscapes and protected areas of northern Chiloé Island. For each stand, its age (average age of the oldest trees present in each stand) and disturbance regimes (evidence of recent human impact, e.g. cuttings or fires, and tree growth rates) were used as defining old-growth criteria. We characterized the structure (tree species richness, size-density distributions, vertical stratification and presence of snags) and floristic composition of each stand. Environmental variables (i.e. temperature, distance to coastline and elevation) were related to stand structure using multivariate constrained correspondence analysis. Old-growth forests were commonly characterized by (a) tree basal areas >80 m^2/ha; (b) density of shade-tolerant tree species in the emergent and dominant canopy layer >36%; (c) higher tree species richness (>7 tree species) than successional stands; (d) presence of large canopy emergents (>80 cm dbh, >25 m tall); (e) high vertical heterogeneity; and (f) minimum stand ages older than 200 years. Old-growth forests showed a distinctive structural variability and floristic diversity influenced both by stand age and disturbance history of the stands. Structural variability was also related to environmental differences among sites (e.g. air temperature, distance to coastline, soil types). Old-growth forest features described here can offer a baseline for managers interested in maintaining and restoring old-growth forest structure in southern temperate rain forests.

1. Introduction

What constitutes an old-growth stand is usually confusing because there is no generally accepted or universally applicable definition (Hunter, 1989; Foster et al., 1996; Franklin and Van Pelt, 2004; Spies, 2004). In general, old-growth forests can be defined by low rates of human disturbance and the dominance of old canopy trees (Hunter, 1989). Old-growth forests under this broad definition often have a complex structure and a heterogeneous spatial arrangement that varies depending on the forest type (Foster et al., 1996; Franklin and Van Pelt, 2004; Spies, 2004). There is a renewed interest in the unique structural and functional characteristics of old-growth forests because of their diminishing land cover, high relevance for the conservation of regional biodiversity and their value for global carbon storage (Harmon et al., 1990; Lindenmayer and Franklin, 2002; Van Pelt, 2007). As forests over vast areas of the world become logged and maintained in young successional stages (Laurance et al., 2006), unique services provided by old-growth ecosystems are increasingly imperilled.

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Few areas of the world within the temperate zone still maintain old-growth forest ecosystems and only in the southern hemisphere such forests are dominated by broad-leaved, evergreen tree species. Among the last remnants of temperate old-growth rain forests in southern South America are significant areas along the coast of south-central Chile, 37–43°S (Smith-Ramírez, 2004). Interest in conservation of these last remnants of endemic-rich old-growth forests increased in recent years (Dinerstein et al., 1995; Armesto et al., 1998; Olson et al., 2001; Smith-Ramírez, 2004) because of growing threats due to logging, fire, the construction of new access roads into remote coastal areas (Smith-Ramírez, 2004), and expanding exotic forestry plantations (Armesto et al., in press), leading to fast rates of land-use change (Echeverría et al., 2007). In particular, in northern Chiloé Island (40–42°S), the progressive loss, fragmentation and subsequent degradation of forest cover is reducing the original biodiversity and ecological complexity (Echeverría et al., 2007; Jaña-Prado et al., 2007). Moreover, rapidly expanding eucalyptus plantations in northern Chiloé Island in the past decade are threatening the integrity of ecosystem functions in the rural landscape.

Knowledge of old-growth forest structure and function in temperate rainforests of South America remains sparse (but see Armesto et al., in press). As a consequence, limited conceptual and empirical understanding of old-growth forest functioning has been applied to policy decisions about land cover inventories, regional conservation of biodiversity and forest management. As in other parts of the world (Hendrickson, 2003), national forest inventories (e.g., CONAF-CONAMA-BIRF, 1999) have significant gaps in their ability to identify remnant old-growth stands. Consequently, proper identification and characterization of remnant old-growth rain forests is a key national priority for the long-term protection of forest-dwelling biological diversity (Armesto et al., 1998; Smith-Ramírez, 2004), the maintenance of carbon storage, and other relevant ecosystem services, such as hydrologic balance and soil nutrient cycling (Lara et al., 2003).

Despite the global importance of old-growth temperate rainforests in southern Chile because of their highly endemic and endangered biodiversity (Armesto et al., 1998) and unique nature of unpolluted biogeochemical cycles (Hedin et al., 1995), no attempts have been made to characterize them in terms of their structural variability and ecological values for regional conservation, ecosystem management and long-term ecological research. Here, we characterize old-growth forests of two major forest types in south-central Chile: Valdivian and North Patagonian temperate rainforests (Veblen et al., 1983; Armesto et al., 1996). The analysis is based on floristic, structural and environmental parameters shared by remnant forest stands found in protected and rural areas of northern Chiloé Island. Our main goal is to identify structural attributes that are most valuable for the biodiversity conservation and integrity of ecosystem services in these temperate rainforests. We also discuss the potential role of our characterization for regional conservation and management strategies. We specifically addressed the following questions relative to old-growth forest stands: (1) What structural features are common and unique to old-growth temperate rainforests in Chiloé Island?; (2) Is there a characteristically distinct tree species composition of old-growth Valdivian and North Patagonian temperate rainforests compared to younger forests of Chiloé Island?; (3) Is there a relationship between old-growth forest structure and local environment? These questions provide valuable information for policy decisions regarding improvement of national forest inventories and for enhancing the societal appreciation of the heritage represented by the last old-growth forests.

2. Material and methods

2.1. Study area

The predominant topography in northern Chiloé Island is low-elevation, rolling hills over highly organic postglacial soils (<1 m deep) or gentle sloping coastal mountains up to heights of

Table 1
Study site locations in northern Chiloé Island, Chile. Distance to coastline was estimated using GPS location and the orthogonal distance to the nearest coastline on the Pacific Ocean. Data sources: (1) this study; (2) Aravena et al. (2002); (3) Gutiérrez et al. (2008).

Study site	Plot name	Location	Elevation (m.a.s.l.)	Distance to coastline of Pacific Ocean	Reference
Abtao	MIXTO	42°22′S–74°02′W	540	7.2	(1)
Aguila	AGC	41°54′S–73°35′W	60	34.5	(2)
Ahuenco	AHUEN1	42°06′S–74°03′W	80	1.2	(1)
	AHUEN2		80		(1)
Caulin	CAULIN	41°50′S–73°36′W	26	30	(1)
Cole-Cole	COLE1	42°30′S–74°11′W	80	0.7	(1)
	COLE2		80		(1)
Guabun	GUAB1	41°46′S–74° W	130	1.2	(3)
	GUAB2		130		(3)
Koenig	KOENIG	41°58′S–73°35′W	74	36	(2)
Melleico	BRIGIDA	42°35′S–73°56′W	280	14.4	(1)
	ELI		280		(1)
	MELISA		280		(1)
	MELL1		200		(1)
	MILENA		280		(1)
	PILLO		145		(1)
Quemado	QUEM1	41°51′S–73°36′W	40	34.3	(2)
Rapoport	RAP1	41°53′S–73°39′W	60	29	(2)
	RAP2		60		(2)
Senda Darwin	PAPIC	41°52′S–73°39′W	60	26.8	(2)
	SUCRE		60		(2)
	TEPU1		60		(2)
	TEPU2		60		(2)

Table 2
Climatic data from meteorological stations considered in the constrained correspondence analysis of forest stands in northern Chiloé Island (see Section 2).

		Meteorological station		
		Senda Darwin^1	Punta Corona^2	Castro^3
Location		41°52′S–73°39′W	41°47′S–73°52′W	42°29′S–73°48′W
Elevation		60	56	24
Recording period		1996–2006	1911–2005	1950–2000
Yearly mean temperature	T (°C)	9.1	10.8	10.4
Yearly mean maximum temperature	t_{max} (°C)	13.9	17.6	14.7
Yearly mean minimum temperature	t_{min} (°C)	4.2	5.2	6.2
Annual rainfall	ppt (mm)	2157.8	1744.3	1920.6
Summer rainfall (% of annual rainfall)		25	13	19
Winter mean temperature	JJA (°C)	8.1	8.5	7.4
Summer mean temperature	DJF (°C)	12.5	13	15.8

Data source: (1) Estación Biológica Senda Darwin; (2) Armada de Chile; (3) Dirección Metereológica de Chile. JJA: June to August; DJF: December to February.

600 m (Table 1). In rural landscapes old-growth forest stands are part of a mosaic of bogs, remnant and secondary forest, shrublands, exotic plantations and artificial grasslands. The present rural landscape has been shaped by a recent history (less than 200 years) of widespread use of fire and logging to clear land for pastures and selective logging of many forest patches (Willson and Armesto, 1996; Torrejón et al., 2004). Prevailing climate is wet-temperate with strong oceanic influence (di Castri and Hajek, 1976). Rainfall, about 2000 mm annually, occurs all year round, but 13–25% falls during summer (January–March). The mean annual temperature is 9.1–10.8 °C. Mean monthly maximum temperature is 17.6 °C in coastal sites and 14.4 °C in inland sites (January). Minimum monthly temperature is 6.9 °C (coast) and 4.2 °C (inland, both in July) (Table 2).

2.2. Main forests types

Chiloé Island has a mixed composition of broad-leaved evergreen rain forests depending on topography, elevation and soils (Holdgate, 1961; Veblen et al., 1983; Armesto et al., 1996; Table 3). The North Patagonian forest type is found predominantly on relatively poorly drained flat areas, in the southern sector of the island, and at elevations above 400 m on the coastal range. This forest type is floristically defined by the dominance of shade-tolerant conifers (Podocarpaceae), in addition to *Drimys winteri* (Winteraceae) and *Nothofagus nitida* (Nothofagaceae) in the main canopy, together with *Tepualia stipularis* and other Myrtaceae tree species in the understory (Veblen et al., 1983; Donoso, 1993; Armesto et al., 1996). In contrast, Valdivian rain forests are largely concentrated in northern and low-elevation sites (below 400 m), slopes facing the Pacific Ocean, and well-drained soils. These forests are generally dominated by a different set of broad-leaved evergreen tree species, such as the canopy emergents *Eucryphia cordifolia* (Eucryphiaceae) and *Aextoxicon punctatum* (Aextoxicaceae), several Myrtaceae species in the main canopy and subcanopy and often lack *Nothofagus* spp. (Veblen et al., 1983; Donoso, 1993; Armesto et al., 1996). In both forest types, tree trunks and branches are profusely covered with epiphytic ferns (e.g. *Hymenophyllum* spp., *Hymenoglosum cruentum*, *Polypodium feullei*) and several species of flowering epiphytes and climbers (e.g. species of Gesneriaceae and Bromeliaceae), including the hemiepiphytic tree *Raukaua laetevirens* (Araliaceae). The presence of dense thickets of native *Chusquea* bamboos is important in large canopy openings formed by natural tree falls and in logged forests, where the canopy has been opened. Shrubs are uncommon, except along forest margins and on coastal cliffs.

2.3. Forest sampling

Forest stands sampled in northern Chiloé Island (Fig. 1), were selected on the bases of accessibility from nearby roads, landowners' willingness to grant access to their properties and visual attributes (e.g. tree sizes, stratification, logging or fire marks, trails) that allowed us to estimate age since last disturbance. We selected forests stands ($n = 9$) that represented a successional chronosequence from 30 to 200 years as described by Aravena et al. (2002) and an additional group of stands, selected from rural and protected areas in northern Chiloé ($N = 14$). The latter stands had an average canopy height of at least 12 m, and therefore are classified as mature forests by current national inventories (Fig. 1, CONAF-CONAMA-BIRF, 1999). Structural characteristics of these mature forests (e.g., presence of large emergent trees, a patchy canopy including tree-fall gaps, tree-size distribution, and absence of logging and fire) suggested an old-growth condition.

In each selected forest, we set up one to four 20 m × 50 m (0.1 ha) permanently marked plots for assessing forest structure and species composition. The number of plots per stand was mainly constrained by accessibility and forest patch size. Plots

Table 3
Tree species present in North Patagonian and Valdivian forest types in northern Chiloé Island, following Veblen et al. (1983) and the authors personal observations. Life-span is the mean estimated maximum longevity in Chiloé Island following (1) Veblen (1985); (2) Lusk (1996b); (3) Gutiérrez et al. (2008) and data from this study. Shade-tolerance according to Figueroa and Lusk (2001), Aravena et al. (2002), Donoso (2006) and personal observations.

Tree species	Family	Abbrev.	Life-span	Shade-tolerance
North Patagonian forests				
Podocarpus nubigena	Podocarpaceae	Pn	500^2	To
Myrceugenia chrysocarpa	Myrtaceae	Mc	nd	To
Nothofagus nitida	Nothofagaceae	Nn	193	I
Saxegothaea conspicua	Podocarpaceae	Sc	600^2	To
Tepualia stipularis	Myrtaceae	Ts	nd	Int
Valdivian forests				
Aextoxicon punctatum	Aextoxicaceae	Ap	349^3	To
Amomyrtus meli	Myrtaceae	Am	113^3	Int
Dasyphyllum diacanthoides	Asteraceae	Dd	nd	Int
Luma apiculata	Myrtaceae	La	nd	To
Myrceugenia ovata	Myrtaceae	Mo	nd	To
Myrceugenia planipes	Myrtaceae	Mpl	nd	To
Rhaphithamnus spinosum	Verbenaceae	Rs	nd	Int
Shared species				
Amomyrtus luma	Myrtaceae	Al	nd	To
Caldcluvia paniculata	Cunoniaceae	Cp	68	Int
Crinodendron hookerianum	Elaeocarpaceae	Ch	nd	Int
Drimys winteri	Winteraceae	Dw	250^1	I
Eucryphia cordifolia	Eucryphiaceae	Ec	329	I
Gevuina avellana	Proteaceae	Ga	82	Int
Laureliopsis philippiana	Monimiaceae	Lp	307	To
Myrceugenia parviflora	Myrtaceae	Mp	140	Int
Raukaua laetevirens	Araliaceae	Pl	nd	Int
Weinmannia trichosperma	Cunoniaceae	Wt	404	Int

nd: no data available; To: shade-tolerant, I: shade-intolerant, Int: intermediate tolerance; Abbrev.: abbreviation code according to the first letters of the binomial species name.

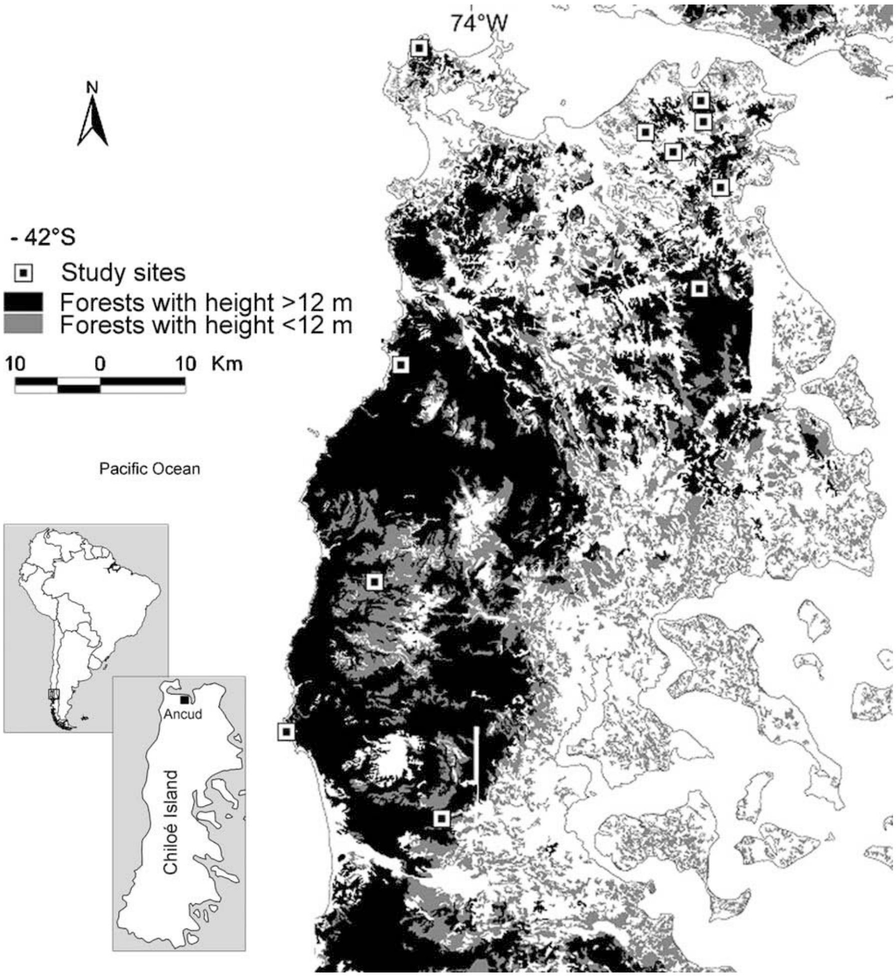


Fig. 1. Study site locations (squares) on northern Chiloé Island, Chile. Forest cover data from CONAF-CONAMA-BIRF (1999).

were set up between 1998 and 2005 and located at least 200 m away from edges with adjacent open areas. All trees rooted within each plot with stems >1.3 m height and >5 cm diameter at 1.3 m height (dbh) were permanently marked with numbered aluminium tags, identified to species, and their dbh measured to the nearest cm. Canopy classes for each tree were recorded as: (1) emergent, above canopy height; (2) dominant, in the canopy tier; (3) subcanopy, directly under the canopy with light only from above; and (4) understory, permanently shaded. Additionally, each tree was classified as (1) alive (healthy); (2) some branches dead; or (3) standing dead (snags).

Increment cores were obtained from a sample of >10 of the largest trees in each stand to estimate the minimum stand age. Tree cores were processed following standard dendrochronological techniques (Stokes and Smiley, 1968) and tree ages were assessed by counting annual growth rings. When mean age of the 10 oldest trees was <100 years, we classified the stand as young forests, representing the building phase of stand development, and mean age of all trees provided a suitable estimate of stand age (Aravena et al., 2002). When the mean age of the 10 oldest trees was >100 years, the stand was classified as mature. In the latter case, we considered the mean age of the 10 oldest trees as an estimate of stand age. Using the mean of all cored trees would underestimate the stand age for mature forests because of their skewed age distributions due to the numerous presence of juvenile trees (Aravena et al., 2002). For young stands, the age of the 10 oldest trees would overestimate stand age because of the presence of few remnant old trees (Aravena et al., 2002).

We characterized stand structure in terms of tree species richness, size (dbh) distribution, canopy heterogeneity (number of tiers) and frequency of snags. To provide a quantitative basis for comparing dbh distributions (trees >5 cm dbh) among plots, we fitted Weibull functions to the dbh frequency distribution of all trees in each plot (Bailey and Dell, 1973). Probability density distributions were fitted to each diameter distribution using a maximum-likelihood algorithm (Cohen, 1965). Weibull distributions can accommodate a wide variety of shapes as indicated by the shape parameter "c". When $c = 1$, dbh distribution fits a negative exponential, when $c > 1$, the function is unimodal, either positively skewed ($1 < c < 3.6$), normal ($c = 3.6$), or negatively skewed ($c > 3.6$) (Bailey and Dell, 1973).

2.4. Old-growth criteria

The old-growth condition was defined by the assessment of stand age and the evidence of disturbance in each stand (Hunter, 1989; Foster et al., 1996). Stand ages were used to determine whether dominant canopy trees reached their average life expectancy. In Chiloé, life spans of conifer tree species (Podocarpaceae) can be >500 years whereas most angiosperms have average life spans of about 300 years (Table 3). Following Lorimer et al. (2001), estimated stand ages representing at least one-half of the estimated life span of the main canopy tree species were considered indicators of old-growth condition. Because extensive land-use change in Chiloé Island dates back only to the late 19th and early 20th century (Willson and Armesto, 1996; Torrejón et al., 2004), a stand age >150 years strongly suggest that the stand has remained largely unaffected by direct human impact over the past two centuries. We further evaluated the undisturbed condition of mature forest stands (Hunter, 1989) by searching for stumps from selective logging and scars from human-set fires. Only stands without evidence of disturbance were considered old-growth.

A heterogeneous canopy structure is also a relevant attribute characterizing old-growth forests (Spies and Franklin, 1991). Based on the canopy classes defined above, we assessed the heterogeneity of vertical canopy structure using the Berger-Parker diversity index d (Magurran, 2004). This index provides a measure of stratification and canopy heterogeneity through the proportional importance of the most abundant canopy class: $1/d = 1/(N_{\max}/N)$, where $N_{\max}$ is the number of individuals in the canopy class with the highest number of individuals and N is the total number of individuals in the stand. A high value of this index would reflect greater vertical heterogeneity, which is often associated with the old-growth status (Aber, 1979; Spies and Franklin, 1991).

Tree basal area, density, the c parameter of dbh distributions, dbh range, the number of canopy tiers, presence of snags, and tree species richness per plot were parameters used to characterize old-growth stands, previously defined by using the above criteria. In addition, the presence of shade-tolerant tree species in the dominant canopy layers (emergent and dominant) was used as an indicator of advanced successional age (Oliver and Larson, 1990). Linear regressions between each structural characteristic and stand age were used to assess the change of old-growth structural attributes through the advanced stages of stand development.

2.5. Multivariate analysis

We conducted floristic analyses for all plots sampled ($N = 23$) and then separately for those plots identified as old growth by the criteria specified above ($N = 11$, Table 4). Cluster analyses based on tree species presence (dbh >5 cm) in stand inventories were used to define species associations. Cluster analyses were based on Jaccard distances using the unweighted pairing with arithmetic mean (UPGMA) as the linkage method (Kaufman and Rousseuw, 1990). The groups defined by clustering were tested using the Partitioning Around Medoids (PAM) method, with the number of clusters determined by maximizing the average silhouette (Kaufman and Rousseuw, 1990).

Multivariate analysis was used to relate differences in tree species composition and forest structure to environmental factors and stand age. We carried out a gradient analysis using a Constrained Correspondence Analysis (CCA, a.k.a. canonical correspondence analysis) (Ter Braak, 1986) as a direct ordination method to relate environmental variables to basal area and density of tree species per plot. Environmental variables considered in the CCA were elevation, distance to the coastline (estimated using the plot GPS location and the orthogonal distance to the nearest coastline of the Pacific Ocean) and climatic variables for each sampled stand (Table 2). CCA is robust and usually preferable to other ordination methods (i.e. Detrended Correspondence Analysis). Some advantages of CCA are its good performance with highly inter-correlated environmental variables, and with situations where some factors determining tree species composition are unknown (Palmer, 1993). CCA calculates the proportion of the variation explained by each axis, the correlation between each canonical axis and each species axis, and the variation of species composition explained by the stand variables. The correlation between each variable and the canonical axes provides insights into factors that influence vegetation structure. According to Legendre and Legendre (1998), rare species that have little influence on vegetation structure may cause ordinations to be artificially aligned. Therefore, we removed from the analysis those species only found in one site. We performed Monte Carlo permutation tests ($n = 10{,}000$) (Legendre and Legendre, 1998) to

Table 4
Plot classification according to old-growth criteria discussed in this study for forests of northern Chiloé Island (see Section 2).

Plot name	N	Basal area (m^2/ha)	Tree ages (years)			Stand-age	%Shade-tolerants	Evidence of human impact	Classification
			Mean	10 oldest	The oldest (species[a])				
QUEM1	39	72.9	88.8	175.7	404 (Wt)	2[b]	0.0	Fire	Young
PAPIC	10	22.0	11.2	11.2	14 (Dw)	11	0.0	Fire	Young
RAP2	30	44.8	33.3	40.2	46 (Dw)	33	1.4	Fire	Young
CAULIN	65	98.3	42.3	85.4	118 (Pn)	42	37.9	Selective cuttings	Young
PILLO	10	107.0	47.6	47.6	68 (Dw)	47	84.1	Selective cuttings	Young
RAP1	38	16.7	49.3	104.8	329 (Ec)	49	0.0	Fire	Young
SUCRE	31	60.2	61.5	111.7	200 (Pn)	112	16.2	Fire	Mature
MELISA	10	102.8	112.7	112.7	157 (Lp)	113	96.2	None	Mature
ELI	11	109.9	119.0	127.2	211 (Lp)	127	92.2	None	Mature
TEPU1	40	71.9	67.2	129.1	174 (Lp)	129	25.5	None	Mature
AGC	37	105.3	79.8	132.7	234 (Ec)	133	2.2	Selective cuttings	Mature
KOENIG	39	137.6	68.9	134.0	336 (Sc)	134	30.6	Selective cuttings	Mature
BRIGIDA[c]	4	96.5	172.8	–	192 (Lp)	173	97.0	None	Old-growth
MILENA	12	123.0	166.7	189.1	239 (Lp)	189	100.0	None	Old-growth
TEPU2	40	80.5	96.0	204.6	311 (Sc)	205	41.7	None	Old-growth
MELL1	48	56.4	123.8	217.1	307 (Lp)	217	84.0	None	Old-growth
AHUEN2	30	162.4	153.9	242.7	308 (Ec)	243	76.9	None	Old-growth
COLE1[c]	–	100.3	–	–	–	250	97.6	None	Old-growth
COLE2[c]	–	122.5	–	–	–	250	100.0	None	Old-growth
GUAB2	29	91.1	168.4	276.9	325 (Ap)	277	97.6	None	Old-growth
GUAB1	31	109.0	171.1	282.9	349 (Ap)	283	81.1	None	Old-growth
AHUEN1	49	120.6	160.4	283.2	297 (Ec)	283	92.3	None	Old-growth
MIXTO	20	82.0	202.0	308.6	399 (Pn)	309	36.2	None	Old-growth

N: number of cored trees. Mean age represents the average of all trees cored. %Shade-tolerants is the percentage of shade-tolerant trees in the dominant and emergent canopy layers.

[a] Represents the species of the oldest tree found in the plot.

[b] Known age since the last stand-devastating anthropogenic fire to the time of plot sampling.

[c] Limited or no age data were obtained because of high wood density of main canopy species. Mature: stand age >100 years but not fulfilling the structural criteria for old-growth.

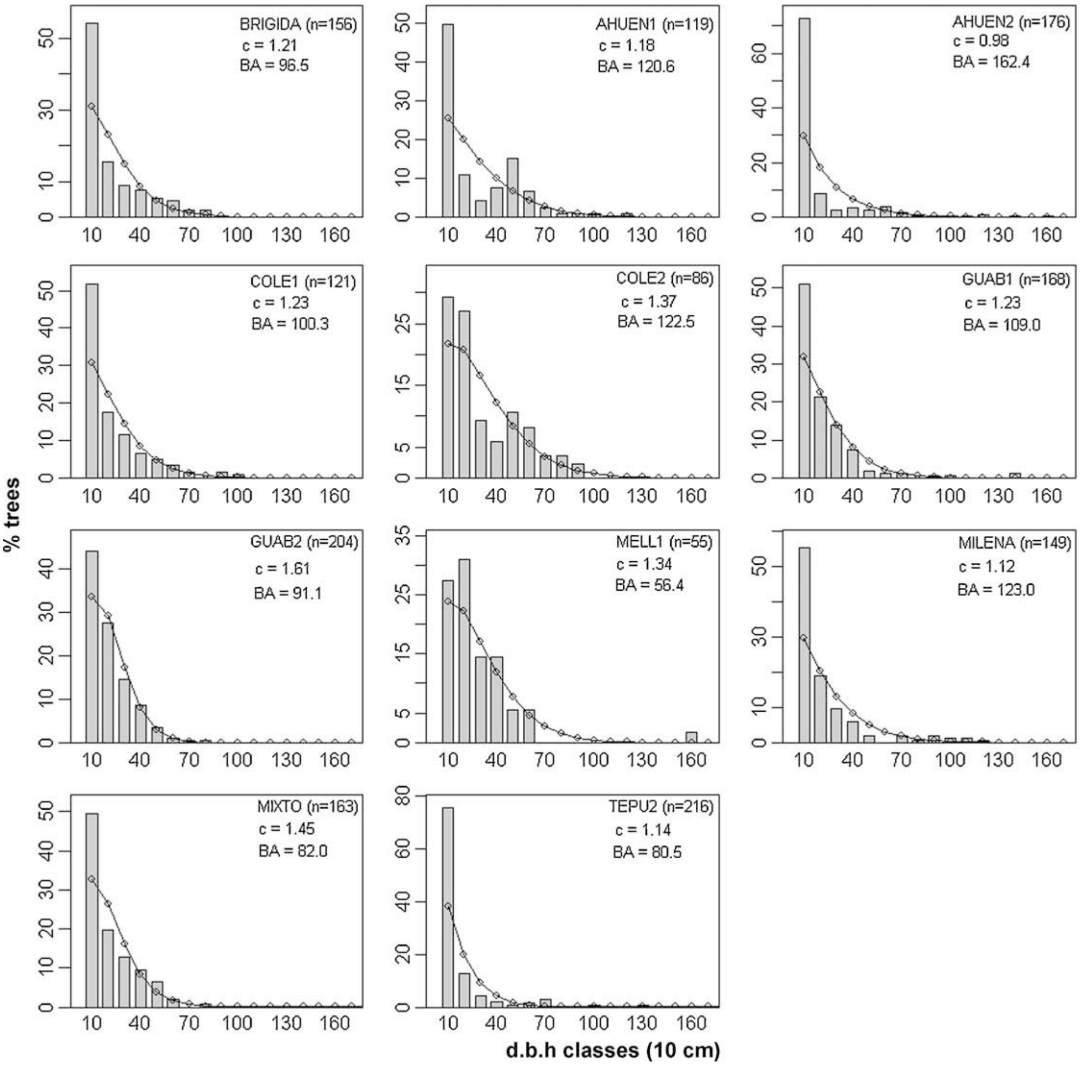


Fig. 2. Tree-size structure (trees >5 cm dbh) in old-growth forest plots on northern Chiloé Island. Lines indicate the Weibull function fitted to each size distribution. N = number of trees; BA = total basal area (m^2/ha); c = shape parameter c of the Weibull distribution. Note different scale on the y-axis.

assess whether the observed patterns differed from random. Statistical analyses were conducted in R statistical environment (R-Development-Core-Team, 2005). Species nomenclature follows Marticorena and Quezada (1985) and Mabberley (1997).

3. Results

3.1. Old-growth forest structure

From the 23 plots sampled, 11 fitted the multiple criteria used to define old-growth status (Table 4). Mean minimum ages of the 10 oldest trees in these 11 stands were >189 years, with maximum values >239 years (Table 4). These results suggest that estimated stand ages of >150 years are good indicators of old-growth condition, as most canopy trees have reached their average life expectancy. These 11 stands represented forests without evidence of human disturbance through logging or fire. Although no tree age data were available for COLE1 and COLE2 plots, they were also classified as old-growth stands because their density, basal area and dbh distributions strongly suggested an uneven age structure (Fig. 2). Moreover, these stands are found within a remote and unbroken forest sector of Chiloé National Park, without human occupation or transit and had significant presence of shade-tolerant tree species in emergent and dominant canopy tiers (>97% of emergent and canopy tree densities). This canopy structure suggests that the first cohort of pioneers had disappeared and the stand taken over by mid and late-successional tree species, a process that would take about three hundred years. Shade-tolerant species accounted for 36–100% of emergent and canopy dominant tree densities in all old-growth stands inventoried (Table 4) and the proportion of shade-tolerant tree species in the canopy increased linearly with stand age ($r^2 = 0.37$, $P < 0.005$, $n = 23$, Fig. 3).

Tree species richness in the canopy of 11 plots classified as old-growth ranged from 5 to 12 (mode = 7 tree species in 0.1 ha). Despite some exceptions (AHUEN2, TEPU2), Berger-Parker index was usually high in old-growth plots (median = 3.4, Table 5, Appendix A) and its value increased linearly with increasing stand age ($r^2 = 0.28$, $P = 0.005$, $n = 23$, Fig. 3). Tree-size (dbh) distributions for the 11 old-growth plots had c parameters ranging from 0.98 to 1.6, representing steeply descending, negative exponential, and unimodal (positively skewed) dbh distributions (Fig. 2). Tree densities (>5 cm dbh) of old-growth forest plots ranged from 1075 to 2160 individuals per hectare. Total tree basal area (Fig. 3) increased linearly with increasing stand age ($r^2 = 0.20$, $P < 0.05$, $n = 23$, Fig. 3). Particularly one site, MELL1 had a low basal area and tree density because of the large area of tree-fall gaps in the stand (ca. 50% of plot area). Excluding MELL1, basal area of old growth

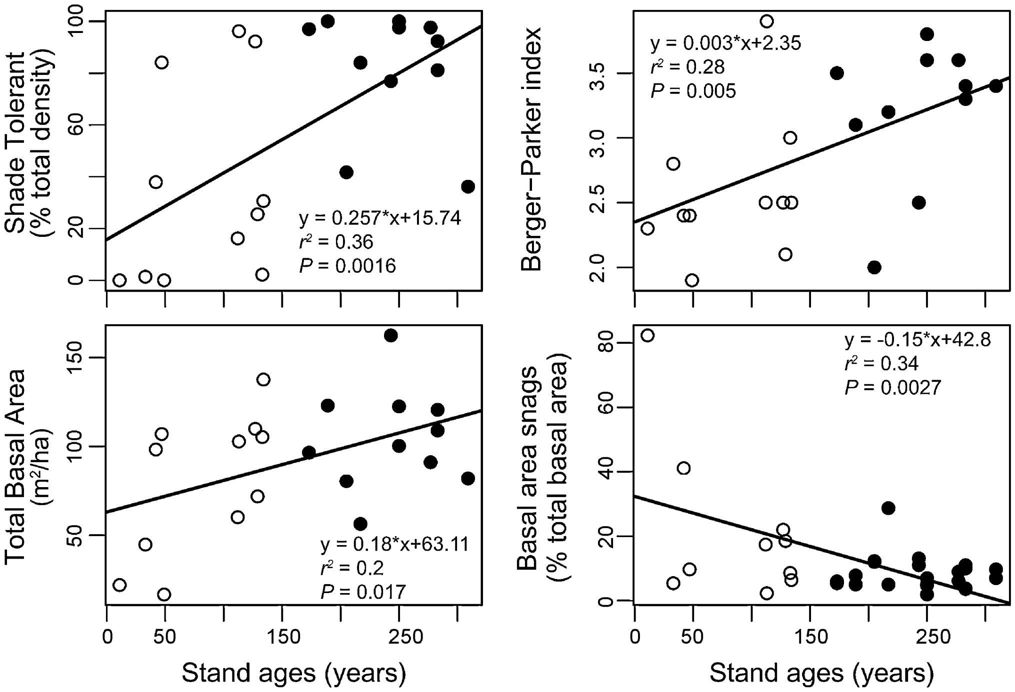


Fig. 3. Structural attributes of forest stands related to their estimated stand ages. Filled circles represent old-growth stands; open circles indicate non old-growth stands based on evidences of disturbance.

stands ranged from 80.5 to 162 m^2/ha (including snags). Large old trees (>80 cm dbh), occupying the emergent tree layer, represented up to 5.8% of total stem density. Snags represented at least 29% of stem density and 28% of total basal area in all old-growth stands and their abundance decreased linearly with stand age ($r^2 = 0.34$, $P < 0.005$, $n = 23$, Fig. 3). Mean quadratic dbh of snags ranged from 16.7 to 54.9 cm (Table 5).

3.2. Floristic composition

The distinction of floristic groups was similar between all plots surveyed and plots classified as old-growth (Fig. 4). These main floristic groups identified were rather consistent with the distinction of Veblen et al. (1983, see also Armesto et al., 1996) between North Patagonian (Groups B and C; Fig. 4a and b) and Valdivian coastal rain forests (Groups A, D and E; Fig. 4a and b). PAM component analyses showed that plot clusters accounted for 38.6% (all forest plots) and 46.9% (old-growth plots only) of the variation in floristic composition, whereas species clusters accounted for 24.4% (all forest plots) and 35.1% (old-growth plots analysis) of the point variability.

Plots belonging to Valdivian rain forests (Fig. 4a and b) were characterized by tree species, such as *A. punctatum*, *Luma apiculata*, *Myrceugenia ovata*, *Myrceugenia planipes* and *Rhaphitamnus spinosus*, which are absent from North Patagonian forest plots. In contrast, the group of plots belonging to North Patagonian rain forests (Fig. 4a and b) were characterized by the presence of the conifer *Saxegothaea conspicua* which is absent from groups A, D and E (Fig. 4a and b). Some species such as the understory shrub *Crinodendron hookerianum*, the canopy trees *N. nitida*, *Podocarpus nubigena* and *T. stipularis* were always present in plots of groups II and III (i.e. North Patagonian rain forest) but were occasionally present in groups I and IV (i.e. Valdivian rain forest) (Fig. 4). *Amomyrtus luma, D. winteri, Caldcluvia paniculata*, *Laureliopsis philippiana* and *Weinmannia trichosperma* were shared between both plot groups. *Myrceugenia chrysocarpa* was only present in the understory of old-growth North Patagonian forest plots, whereas *Dasyphyllum diacanthoides* was represented only in old-growth Valdivian rain forests. *Amomyrtus meli* was also absent from old-growth North Patagonian forests.

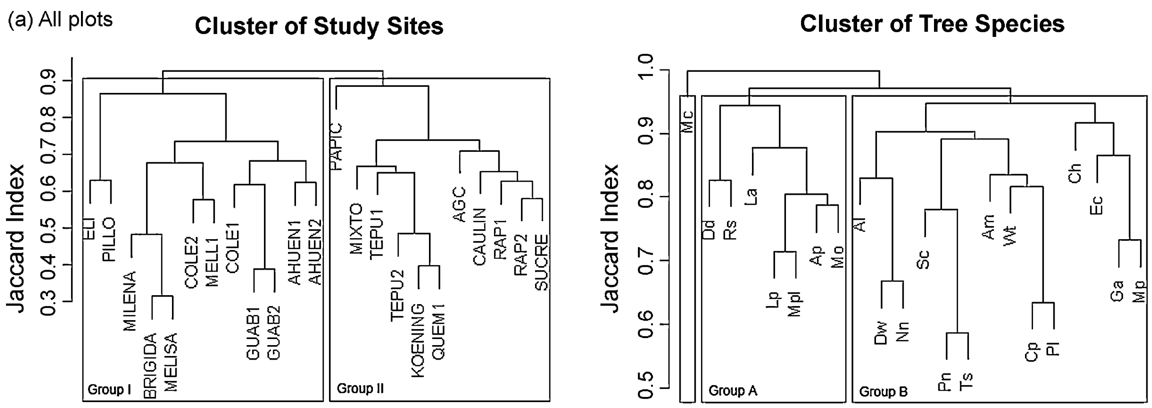
Based on the floristic classification of forest types described above, we averaged the density and basal area of old-growth stands belonging to Group III (North Patagonian rain forest type, $n = 2$), and old-growth stands belonging to Group IV (Valdivian rain forest type, $n = 9$) (Table 6). North Patagonian old-growth forests were numerically dominated by the understory tree species *T. stipularis*, the main canopy shade-tolerant conifer *P. nubigena* (shade-tolerant) and by the semi-tolerant *D. winteri*. Valdivian old-growth forests were numerically dominated by shade-tolerant tree species such as *A. luma*, *M. ovata* and *L. philippiana*. Density of all Myrtaceae tree species pooled represented the 59% of stem density in old-growth Valdivian rain forests, whereas in North Patagonian plots it was only 33%. Basal area of old-growth North Patagonian rain forests was largely accounted by canopy emergents such as *N. nitida* (shade-intolerant), *P. nubigena* and *D. winteri*. In Valdivian old-growth forests, basal area was dominated by shade-tolerant tree species such as *L. philippiana*, *A. punctatum* and *A. luma*. The large emergent,

Table 5
Range of structural attributes (median value in parenthesis, stems >5 cm dbh) in old-growth forest stands of northern Chiloé Island. MQD: mean quadratic diameter.

Stand variables	
Estimated stand age (years)	173–309 (242)
Basal area[a] (m^2/ha)	80.5–162 (104.7)
Density[a] (N/ha)	1075–2160 (1513)
Canopy composition	
Tree species (species)	5–12 (7)
Berger-Parker index (–)	2.0–3.8 (3.4)
Shade-tolerant tree species (% trees in emergent and dominant canopy layer)	36–100 (92.3)
dbh structure	
Shape parameter *c* of the Weibull distribution (–)	0.98–1.6 (1.2)
% of trees dbh > 80 cm (% of total stem density)	0–5.4 (2.4)
Snags	
MQD (cm)	16.7–54.9 (30.8)
Density (%)	3.2–29.1 (5.8)
Basal area (%)	2–28 (6.1)

[a] Excluding MELL1 because it has 50% of plot area in canopy gap.

(a) All plots



(b) Old-growth plots

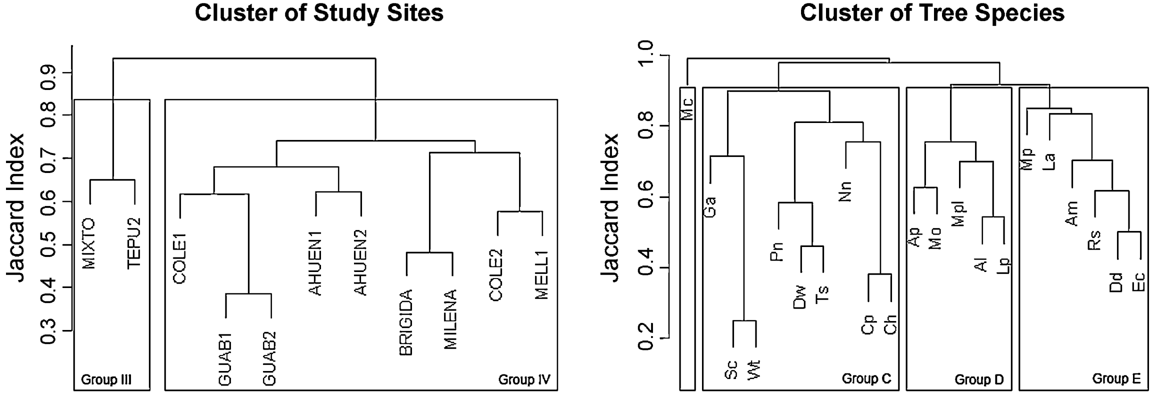


Fig. 4. Cluster analysis of floristic compositions of sites and tree species associations (>5 cm dbh) for (a) all plots and (b) old-growth plots sampled in temperate rainforests of northern Chiloé Island. Dendrogram was based on Jaccard's distance calculated from tree species densities (stems >5 cm dbh) using UPGMA as the linkage method. Boxes represent clusters determined after testing the groups detected using the Partitioning Around Medoids method, with the number of clusters determined by maximizing average silhouette (Kaufman and Rousseuw, 1990).

shade intolerant tree species *E. cordifolia* (Table 3), was rarely present in old-growth North Patagonian forests, while having low density and basal area in old-growth Valdivian forests sampled (Table 6). North Patagonian forests were characterized by lower presence of shade-tolerant tree species in the main canopy (Table 4).

3.3. Forest structure and the environmental gradient

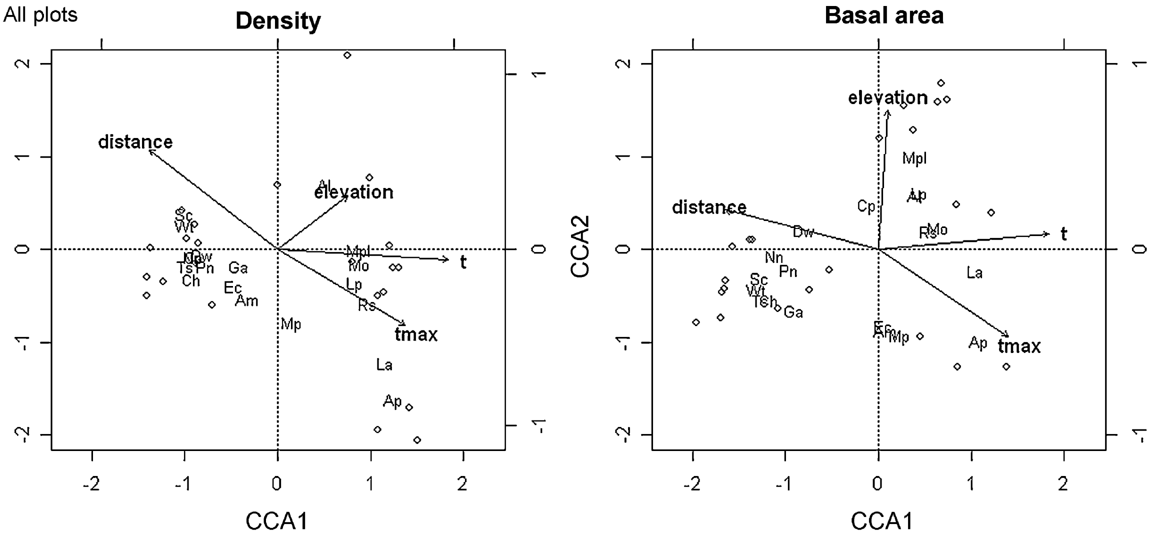
Examination of the constraining variables (Fig. 5a and b; Table 7) showed that there are two main gradients associated with major changes in tree species density and basal area in the studied forest

Table 6
Mean density of trees (stems >5 cm dbh, *N*/ha) and mean basal area (m^2/ha ± standard error) of main canopy tree species in old-growth stands of northern Chiloé Island.

Tree species	North Patagonian (*N* = 2)		Valdivian (*N* = 9)	
	Density	Basal area	Density	Basal area
A. punctatum	[a]	[a]	126 ± 53	21.6 ± 10.3
A. meli	[a]	[a]	28 ± 12	1.2 ± 0.7
L. apiculata	[a]	[a]	73 ± 31	9.3 ± 5.9
M. ovata	[a]	[a]	207 ± 107	3.4 ± 1.4
M. planipes	[a]	[a]	283 ± 85	7.5 ± 2.9
R. spinosum	[a]	[a]	17 ± 8	0.1 ± 0.1
M. chrysocarpa	10 ± 10	0.03 ± 0.03	[a]	[a]
W. trichosperma	17 ± 12	9.2 ± 6.3	0 ± 0	0 ± 0
S. conspicua	23 ± 12	1.4 ± 1.3	[a]	[a]
N. nitida	167 ± 38	20.2 ± 6.1	0 ± 0	0 ± 0
C. hookerianum	97 ± 49	0.4 ± 0.2	0 ± 0	0 ± 0
P. nubigena	517 ± 80	15.8 ± 3.1	1 ± 1	0.7 ± 0.7
T. stipularis	620 ± 376	7.5 ± 4.5	1 ± 1	0.04 ± 0.04
M. parviflora	7 ± 7	0.02 ± 0.02	19 ± 18	0.2 ± 0.2
D. winteri	367 ± 116	12.4 ± 7.4	27 ± 17	2.3 ± 1.4
A. luma	117 ± 29	1.1 ± 0.5	375 ± 154	13.1 ± 2.8
L. philippiana	40 ± 26	1.4 ± 0.8	380 ± 51	32.6 ± 7.0
G. avellana	10 ± 10	1.4 ± 1.4	6 ± 5	0.1 ± 0.1
C. paniculata	217 ± 148	1.4 ± 1.0	6 ± 5	2.2 ± 1.9
E. cordifolia	0 ± 0	0 ± 0	9 ± 6	9.8 ± 6.1
Others[b]	3 ± 3	0.01 ± 0.01	41 ± 41	0.4 ± 0.4

[a] Absent in the forest type.
[b] *D. diacanthoides* and *R. laetevirens*.

(a) All plots



(b) Old-growth plots

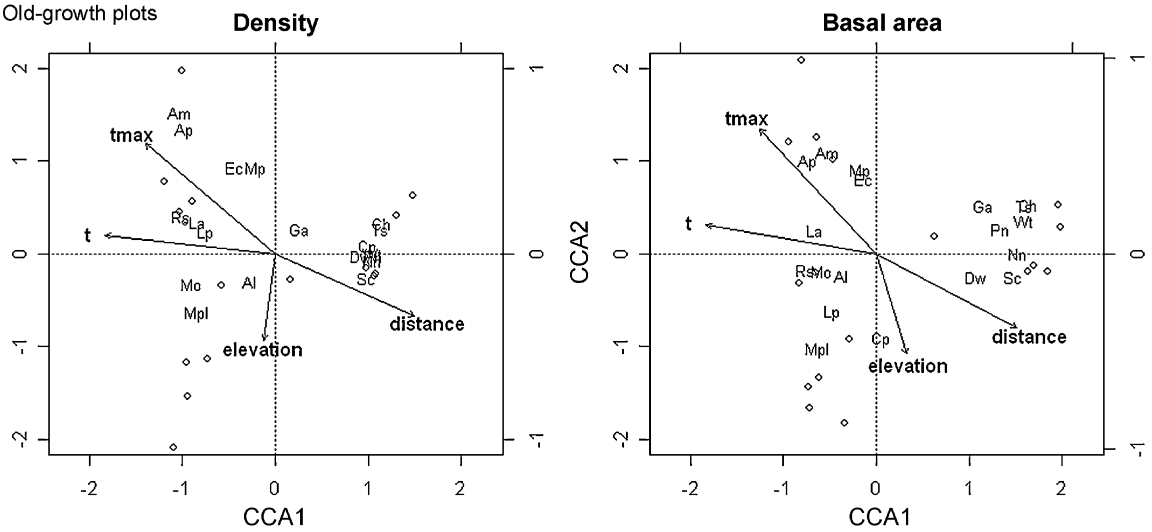


Fig. 5. Canonical correspondence analysis ordination diagrams (biplots) of basal area and density for (a) all forest plots and (b) old-growth forest plots. Sites are represented by circles, species are represented by their name abbreviations from Table 3. The proximity between species indicates occurrence in similar environments. Constrained variables are represented by arrows, which point toward increasing values of that variable and extend in both directions. The arrow relative length is directly proportional to the importance of the variable in influencing community structure. A smaller angle between the arrow and the constrained ordination axis indicates greater relationship of the variable to the derived CCA gradient. Distance: distance to the nearest coastline.

stands: one of decreasing temperatures with distance from the coast (first constrained axis, CCA1) and one of decreasing temperature with altitude (second constrained axis, CCA2). In both analyses (all plots and old-growth plots), the best environmental predictors were mean air temperature, mean maximum temperature and distance to the coastline for CCA1; and elevation and mean maximum temperature for CCA2 (Fig. 5a and b; Table 7). Other variables (Table 2) were discarded because they were collinear (redundant). The amount of the total variation in both basal area and density explained by environmental parameters was >41% and significant in both analyses (Monte Carlo permutations, $P < 0.005$).

4. Discussion

4.1. Structural attributes and heterogeneity of old-growth southern forests

Our results confirm that many remnant forests in the rural mosaic of Chiloé Island and forests protected in private and public parks, without evidence of human disturbance (such as selective logging or fire scars), with a complex vertical profile, and having stand ages >200 years old can be defined as old growth. Old-growth stands in northern Chiloé Island are also characterized by (a) tree basal areas of at least 80 m^2/ha; (b) density of shade-tolerant tree species in the emergent and dominant canopy layer >36%; (c) seven or more tree species represented in the main canopy; (d) presence of large, often emergent, trees (>80 cm dbh); and (e) a high vertical heterogeneity indicated by a high value of Berger-Parker index. These stand attributes are consistent with other old-growth stand descriptions in Chiloé and in the mainland (Table 8). We propose to use these structural attributes in future forest inventories for the recognition of the old-growth condition and for mapping old-growth evergreen, broadleaved temperate rainforests in Chile. Tree species richness, densities and basal areas of old-growth forest stands in Chiloé Island are also comparable to old-growth forests elsewhere in the temperate region (Table 8). From these comparisons, old-growth forests of Chiloé Island had lower basal areas than old-growth evergreen forests located at similar latitudes in the Andes of the Chilean Lake District and much lower than old-growth coniferous forests of the Pacific Northwest in North America. Tree species richness was also lower than in other old-growth coastal evergreen forests found in the Coastal Range near Valdivia, at 40°S (Table 8).

Table 7
Biplot scores for tree species and constraining variables after obtaining a significant overall trace (after 10,000 Monte Carlo permutations, $P < 0.005$) for the constrained correspondence analysis (CCA) of all forest plots and old-growth plots. CCA1 and CCA2 are constrained axes that accounted for most of the explained variation (species data and species–environment relationship). The best predictors of tree species densities and basal areas along the constrained axes are in bold. Tree species order follows Table 6. Rare species (species occurring only in one site) were excluded from the analysis (see Section 2 for details).

	All plots				Old-growth plots			
	Basal area		Density		Basal area		Density	
	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2
Explained variation (%)	20.7	12.4	23.9	10.1	23.4	13.6	33.6	9.4
Tree species								
A. punctatum	1.08	−1.00	1.24	−1.63	−0.74	1.00	−0.98	1.33
A. meli	0.08	−0.88	−0.33	−0.53	−0.52	1.10	−1.03	1.53
L. apiculata	1.04	−0.23	1.15	−1.23	−0.67	0.26	−0.85	0.34
M. ovata	0.64	0.24	0.88	−0.15	−0.60	−0.18	−0.91	−0.33
M. planipes	0.40	0.98	0.87	−0.03	−0.63	−1.03	−0.84	−0.64
R. spinosum	0.55	0.20	0.97	−0.58	−0.76	−0.17	−1.01	0.40
W. trichosperma	−1.31	−0.43	−1.00	0.26	1.60	0.35	1.06	0.00
S. conspicua	−1.29	−0.31	−1.01	0.38	1.47	−0.25	0.98	−0.27
N. nitida	−1.12	−0.06	−0.91	−0.08	1.52	0.00	1.04	−0.07
C. hookerianum	−1.19	−0.54	−0.93	−0.32	1.63	0.53	1.15	0.33
P. nubigena	−0.97	−0.22	−0.78	−0.17	1.33	0.27	1.05	−0.02
T. stipularis	−1.27	−0.54	−0.99	−0.18	1.60	0.52	1.13	0.27
M. parviflora	0.23	−0.95	0.15	−0.80	−0.18	0.89	−0.22	0.92
D. winteri	−0.80	0.20	−0.82	−0.05	1.07	−0.25	0.91	−0.02
A. luma	0.39	0.59	0.50	0.70	−0.38	−0.23	−0.27	−0.30
L. philippiana	0.44	0.60	0.82	−0.37	−0.48	−0.63	−0.76	0.22
G. avellana	−0.91	−0.66	−0.41	−0.18	1.16	0.52	0.26	0.27
C. paniculata	−0.12	0.47	−0.90	−0.10	0.05	−0.92	0.99	0.08
E. cordifolia	0.04	−0.82	−0.48	−0.39	−0.14	0.81	−0.44	0.93
Constraining variables								
Distance to coastline	**−0.82**	0.21	**−0.73**	**0.57**	**0.72**	−0.38	**0.75**	−0.34
Elevation	0.05	**0.75**	0.40	0.30	0.15	**−0.51**	−0.06	−0.47
Mean temperature	**0.92**	0.09	**0.97**	−0.05	**−0.87**	0.15	**−0.92**	0.10
Mean maximum temperature	**0.70**	−0.47	**0.72**	−0.43	**−0.60**	**0.64**	**−0.70**	**0.59**

Our results also support the view that old-growth forests are often highly variable in structure and tree species composition (Foster et al., 1996). Dbh distributions generally fitted a broad range of functions, as suggested by c-Weibull parameters. Such structural differences among stands may reflect differences in disturbance regimes (Coomes et al., 2003), which in forests presented here vary from light to moderate canopy disturbances (Veblen et al., 1981; Veblen, 1985; Armesto and Fuentes, 1988; Gutiérrez et al., 2004; Gutiérrez et al., 2008). Disturbance regimes (i.e. tree-fall gaps of different sizes generated by emergent and canopy trees) play a fundamental role in producing variable canopy structure of old-growth stands, as documented by the plot MELL1 (50% of its area in canopy gaps). Canopy disturbance may drastically change other structural attributes (e.g. stem density, basal area, and vertical stratification). Because of the differences in life spans among main canopy tree species in North Patagonian and Valdivian forests (Table 3), the stand age criterion should be used with caution. For example, some forest plots which were dominated by *L. philippiana* (MELISA, ELI) coincided in most old-growth criteria, as described above, but their stand age was <150 years and accordingly did not classify as old growth (Table 4). A more precise determination of the time elapsed since the last coarse-scale disturbance would be necessary to assess the old-growth condition in these stands. Dendroecological analysis (Fritts and Swetnam, 1989) provide a valuable tool to conduct such analyses.

Old-growth forests are critical for implementing biodiversity conservation strategies at a regional scale (Hunter and White, 1997). In general, tree species richness was higher in old-growth than in younger stands suggesting an increasing trend in tree species richness with stand age reported for Chiloé Island by Aravena et al. (2002). Additionally, some tree species (i.e. *D. diacanthoides* and *M. chrysocarpa*) were recorded only in old-growth stands. *D. diacanthoides* is a common species of Chilean temperate rainforest in the mainland (Veblen et al., 1981) but rare in Chiloé Island. It has been suggested that the persistence of this tree species in lowland forests may be threatened by intense anthropogenic disturbance (e.g. fire) (Abarzúa et al., 2006), but we currently have no clue about its possible decline. *M. chrysocarpa* is a common tree species of the understory of old-growth *Fitzroya cuppressoides* (Cupressaceae) forests on the coastal range of Chiloé Island.

The high vertical heterogeneity of stands classified as old-growth has been shown to have a positive influence on bird species richness and abundance (Díaz et al., 2005). Old-growth stands often had numerous senescent trees as well as large snags (dbh >20 cm) that are considered key structural elements for forest biodiversity, as they provide habitat for woodpeckers and other cavity nesters (Willson et al., 1996; Cornelius, 2008). Such habitat structures are also important in Subantartic rain forests (Vergara and Schlatter, 2004) and North American temperate forests (Spies and Franklin, 1991). Furthermore, snags also provide important habitat for a significant diversity of vascular and non-vascular epiphytes (Muñoz et al., 2003; Díaz et al., 2005) and logs offer safe-sites for regeneration of most tree species in these rain forests (Lusk, 1995; Christie and Armesto, 2003).

The ongoing process of forest fragmentation in Chiloé Island, which often is accompanied by substantial changes in forest structure and tree species composition (Echeverría et al., 2007; Jaña-Prado et al., 2007) can compromise the habitat structure provided by old-growth forests. Under this changing scenario, the identification of remnant old-growth stands, especially in accessible areas, is an urgent task for conservation planning. In our study, six of the 17 mature stands sampled did not fit the old-growth structure criteria. This result documents that current national inventories of Chilean forests (CONAF-CONAMA-BIRF,

Table 8
Comparison of structural attributes of old-growth forests in Chile, New Zealand and North America. Sampling method refers to the minimum size of the stems considered.

Forest type	Sampling method	Tree species richness	Stand ages (years)	Density (*N*/ha)	Basal area (m^2/ha)	Reference
North American temperate rainforests						
Coniferous Pacific Northwest	d.b.h >5 cm	5–17	>400	–	98–338	(1)
Douglas-fir forests	d.b.h >5 cm	4–6	>195	394–551	64–74	(2)
North American temperate forests						
Hemlock – hardwood	d.b.h. >10 cm	2–3	290–390	200–500	50–60	(3)
Quercus – hardwood	d.b.h. >8 cm	5–12	>250	385–590	17–61	(4)
New Zealand temperate rainforests						
Nothofagus–Weinmania	>2 m tall	12	>800	444.7	55.9	(5)
Podocarp/broadleaved	d.b.h. >1 cm	14	>400	6015	144.5	(6)
Chilean temperate rainforests						
Andean forests						
Evergreen broadleaved	d.b.h >5 cm	8–9	>380	1451–2343	207–305	(7)
Nothofagus – dominated	d.b.h >5 cm	4	>570	1162–1478	175–273	(7)
Nothofagus – dominated	d.b.h >5 cm	5	–	501	126	(8)
Nothofagus – dominated	d.b.h >5 cm	6	>300	200–1200	31–245.8	(9, 10)
Evergreen broadleaved	d.b.h >5 cm	5	>300	160–1760	43.4–221.3	(9, 10)
Chiloé forests						
Evergreen broadleaved	d.b.h. >30 cm	8–10	>500	271–494	–	(9)
Evergreen broadleaved	d.b.h. >5 cm	8–10	–	883–1179	56–90	(11)
Evergreen broadleaved	d.b.h. >5 cm	5–6	–	1095–1541	77.9–111.3	(12)
Evergreen broadleaved	d.b.h. >10 cm	6–9	200	750–1436	32.3–78.4	(13)
Coastal forests						
Podocarp dominated stand	>2 m tall	7	>200	–	77.7	(14)
Evergreen broadleaved	d.b.h. >5 cm	10–16	–	499–939	63.1–113.8	(15)
North Patagonian forests	d.b.h >5 cm	7	–	500–690	64.3–94	(16)

Data sources: (1) Waring and Franklin (1979); (2) Spies and Franklin (1991); (3) Ziegler (2000); (4) Orwig et al. (2001); (5) Lusk and Smith (1998); (6) Smale et al. (1997); (7) Pollmann and Veblen (2004); (8) Donoso and Lusk (2007); (9) Veblen (1985); (10) Schlegel and Donoso (2008); (11) Donoso et al. (1984); (12) Donoso et al. (1985); (13) Armesto and Figueroa (1987); (14) Lusk (1995); (15) Donoso and Nyland (2005) and Donoso (2002); (16) Innes (1992) and Donoso (1993).

1999) fail to properly identify old-growth stands. Using their mature forest category will greatly overestimate old-growth forest cover. The attributes of old-growth forests identified here may help to accurately map rapidly declining old-growth forests in southern Chile and adjacent Argentina. These structural attributes of old-growth may also be used to develop forest management protocols aimed at restoring or reproducing old-growth structure in logged or disturbed stands. With regard to hydrologic cycles, the large intercepting surface and evapotranspiration rates of the old-growth forest canopy (Díaz et al., 2007) in this high rainfall area may be relevant to regulating soil water infiltration and maintaining the depth of the water table in poorly drained sites of Chiloé Island and the Lake District.

4.2. Environmental gradients

According to bi-plots of tree species (Fig. 4, Table 7) a high degree of variance was explained by a well-defined floristic dichotomy between Valdivian and North Patagonian rain forest species, which is mainly driven by differences in the mean air temperature among sites occupied by each forest type. This dichotomy is consistent with previous studies of forest composition in this region (Veblen et al., 1983; Villagrán, 1991; Armesto et al., 1996). Floristic differences were associated primarily with latitudinal and altitudinal gradients in the Chilean Lake District (Schmithüsen, 1956; Oberdorfer, 1960; Villagrán, 1991, 2001). Valdivian rain forest species are classified as thermophilic (i.e. *E. cordifolia*, *A. punctatum*), some are thermally intermediate (*N. nitida*, *W. trichosperma*, *L. philippiana* and Myrtaceae species) and North Patagonian species are classified as cold-resistant (Podocarpaceae species, *D. winteri*, *T. stipularis*) (Heusser et al., 1999). Our results were also consistent with morphological adaptations of North Patagonian tree species to cold temperatures (e.g. high plasmatic resistance to desiccation and a high sclerophyll index of leaves) and/or acclimation to winter temperatures (Alberdi, 1995). Further sampling should be conducted especially in the North Patagonian forest type to characterize variation of its floristic composition and stand structure along climatic and edaphic gradients.

Structural variability among old-growth forest stands of Chiloé Island was also related to site differences (e.g. air temperature, coastal vs. non-coastal, edaphic conditions). In coastal sites the dominance of *A. punctatum* may be related to its ability to tolerate salt spray (Pérez, 1994). In contrast, *W. trichosperma* and *P. nubigena* are rare in coastal areas (Donoso et al., 1985; Veblen, 1985; Gutiérrez et al., 2008). Basal area of *E. cordifolia* seemed unresponsive to the temperature gradient, but more responsive to elevation differences. It has been suggested that enhanced soil drainage on hillsides improves the performance of *E. cordifolia* (Donoso et al., 1984; Donoso, 1993). The association of *P. nubigena*, *D. winteri*, *N. nitida* and *T. stipularis* is more characteristic of poorly drained soils (Armesto et al., 1995; Lusk, 1996a) and in soils characterized by high C/N ratios and lower N availability (Pérez et al., 1998; Pérez et al., 2004).

4.3. Long-term research in old-growth forests

Old-growth forests are priority sites for ecological monitoring because they can be used to test hypotheses about complexity, stability, resilience, and ecosystem change (Hendrickson, 2003). Few studies in southern Chile have compared old-growth stands to young stands with regard to structural attributes, composition and ecosystem functions (Aravena et al., 2002; Carmona et al., 2002; Pérez et al., 2004). Changes in stand structure and species composition over time (Laurance et al., 2006), demographic rates of tree species (Lorimer et al., 2001; van Mantgem et al., 2009), and canopy turnover (Runkle, 2000) remain poorly documented for temperate rainforest of southern Chile. Most monitoring experiments (Lara et al., 2000) have been conducted to test silvicultural practices in second-growth stands, particularly to follow tree growth and regeneration. The present study contributes to identifying state variables of significant ecological value for old-growth forests in Chiloé Island, based on a pilot permanent plot network. This network provides a useful baseline for addressing the dynamic behaviour of unmanaged forests in the face of prospective climate change, biotic effects of herbivores and pathogens, and rapid changes in land use. Additionally, old-growth forests characteristics described here can serve as natural models to restore critical structural features to second-growth, managed, or highly degraded forests (Foster et al., 1996) or for developing management strategies focused on native tree species and uneven-aged forest structures (Rüger et al., 2007).

5. Conclusions

Characterization of old-growth forests is necessary because of their current decline due to changes in land use. Valdivian and North Patagonian old-growth forests in Chile showed a distinctive structural heterogeneity and floristic diversity influenced both by stand age and disturbance history of the stands. Structural heterogeneity was also related to environmental differences among sites (e.g. air temperature, coastal vs. non-coastal, soil types). To prevent the rapidly declining trend in old-growth forest area in Chile, which affects their role as repositories of species genetic information, carbon stores, biodiversity, and sources of baseline data on the dynamics and biogeochemical function of forest ecosystems, it is necessary to recognize their status and educate the public on understanding their unique ecological values. Such recognition should be manifested in future national inventory which should assess the changes in cover of threatened remnants of old-growth forest stands at regional and local scales.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.03.011.

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Supplementary data

Summary of structural attributes of plots sampled in northern Chiloé Island, Chile. n.d. = no data available. c is the shape parameter of Weibull distribution function fixed for each plot. MQD: Mean quadratic dbh.

Plot name	**Canopy composition**		**Stand variables**		**Dbh structure**		**Snags**		
	Number of tree species	**Berger Parker index [-]**	**Basal area [m^2 / ha]**	**Density [stems/ ha]**	**% trees with dap>80 [%total density]**	**c Weibull [-]**	**MQD [-]**	**Density (%)**	**% total basal area**
AGC	9	3.0	105.3	1710	1.8	1.34	28.7	8.2	8.6
AHUEN1	10	3.3	120.6	1190	3.4	1.18	31.2	5.0	3.8
AHUEN2	11	2.5	162.4	1760	3.4	0.98	54.9	5.1	13.1
BRIGIDA	6	3.5	96.5	1560	1.3	1.21	30.8	4.5	5.4
CAULIN	12	2.4	98.3	2640	1.9	1.18	71.5	3.8	41.1
COLE1	7	3.8	100.3	1210	2.5	1.23	16.7	5.8	1.9
COLE2	5	3.6	122.5	860	3.5	1.37	25.4	11.5	4.8
ELI	7	2.5	109.9	4250	0.2	1.52	27.4	9.5	22.0
GUAB1	11	3.4	109.0	1680	2.4	1.23	19.6	7.7	3.6
GUAB2	9	3.6	91.1	2040	0.0	1.61	17.5	11.2	6.1
KOENING	13	2.5	137.6	2560	2.0	1.11	25.0	4.7	6.4
MELISA	6	3.9	102.8	1210	4.1	1.22	31.6	2.5	2.3
MELL1	5	3.2	56.4	550	1.8	1.34	35.9	29.1	28.7
MILENA	5	3.1	123.0	1490	5.4	1.12	41.8	4.7	7.8
MIXTO	7	3.4	82.0	1630	0.0	1.45	18.4	17.4	9.7
PAPIC	3	2.3	22.0	250	4.0	1.13	45.8	44.0	82.3
PILLO	8	2.4	107.0	5620	0.0	1.47	13.3	13.1	9.7
QUEM1	8	2.9	72.9	2290	0.4	1.4	20.3	88.7	90.4
RAP1	6	1.9	16.7	2450	0.0	2.63	n.d.	n.d.	n.d.
RAP2	10	2.8	44.8	2120	0.5	1.56	18.5	4.2	5.4
SUCRE	9	2.5	60.2	3920	0.0	1.71	24.6	5.6	17.4
TEPU1	9	2.1	71.9	3080	1.0	1.37	37.6	3.9	18.5
TEPU2	12	2.0	80.5	2160	0.9	1.14	42.4	3.2	12.3

RESEARCH PAPER III

An dominant tree of Eucryphia cordifolia
in the old-growth forest of Guabún
(Chiloé Island, Chile)

Please cite this research paper as:

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Author contributions

AGG conceived and designed the study, performed research, analyzed data, and wrote the paper. NVC, DAC and MF analyzed data and performed the research. JCA provided data and suggested the study site. JJA conceived and designed the study. All authors contributed to the text.

Photo credit: Juan L. Celis-Diez

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ORIGINAL ARTICLE

Gap-phase dynamics and coexistence of a long-lived pioneer and shade-tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloé Island, Chile

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SUMMARY

Aim A major question with regard to the ecology of temperate rain forests in south-central Chile is how pioneer and shade-tolerant tree species coexist in old-growth forests. We explored the correspondence between tree regeneration dynamics and life-history traits to explain the coexistence of these two functional types in stands apparently representing a non-equilibrium mixture.

Location This study was conducted in northern Chiloé Island, Chile (41.6° S, 73.9° W) in a temperate coastal rain forest with no evidence of stand disruption by human impact.

Methods We assessed stand structure by sampling all stems within two 50 × 20 m and four 5 × 100 m plots. A 600-m long transect, with 20 uniformly spaced sampling points, was used to quantify seedling and sapling densities, obtain increment cores, and randomly select 10 tree-fall gaps. We used tree-ring analysis to assess establishment periods and to relate the influences of disturbances to the regeneration dynamics of the main canopy species.

Results Canopy emergent tree species were the long-lived pioneer *Eucryphia cordifolia* and the shade-tolerant *Aextoxicon punctatum*. Shade-tolerant species such as *Laureliopsis philippiana* and several species of Myrtaceae occupied the main canopy. The stem diameter distribution for *E. cordifolia* was distinctly unimodal, while for *A. punctatum* it was multi-modal, with all age classes represented. Myrtaceae accounted for most of the small trees. Most tree seedlings and saplings occurred beneath canopy gaps. Based on tree-ring counts, the largest individuals of *A. punctatum* and *E. cordifolia* had minimum ages estimated to be > 350 years and > 286 years, respectively. Shade-tolerant Myrtaceae species and *L. philippiana* had shorter life spans (< 200 years). Most growth releases, regardless of tree species, were moderate and have occurred continuously since 1750.

Main conclusions We suggest that this coastal forest has remained largely free of stand-disrupting disturbances for at least 450 years, without substantial changes in canopy composition. Release patterns are consistent with this hypothesis and suggest that the disturbance regime is dominated by individual tree-fall gaps, with sporadic multiple tree falls. Long life spans, maximum height and differences in shade tolerance provide a basis for understanding the long-term coexistence of pioneer and shade-tolerant tree species in this coastal, old-growth rain forest, despite the rarity of major disturbances.

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Chile, dendroecology, disturbance regime, regeneration modes, shade tolerance, temperate rain forest, tree life history, tree-fall gap dynamics, tree-species coexistence.

INTRODUCTION

The coexistence of tree species is often explained by shifts in species composition and dominance in response to local disturbance regimes. Such shifts are often associated with contrasting life-history traits of tree species (e.g. functional types) (Bazzaz, 1979; Noble & Slatyer, 1980). Because tree life cycles encompass diverse growth and developmental strategies over several centuries, different mechanisms of coexistence may operate on the various life-history stages (Nakashizuka, 2001). For example, responses to canopy gaps and understorey environments may differ between juvenile and adult trees (Veblen, 1986; Lusk & Smith, 1998). Such differences could be important for understanding the coexistence of tree species in the forest canopy. An unresolved question concerning the dynamics of southern temperate rain forests at coastal sites in Chile is the unexpected persistence of shade-intolerant tree species in old-growth forests (Lusk, 1999; Aravena *et al.*, 2002). Species-specific differences in patterns of tree regeneration (Christie & Armesto, 2003; Saldaña & Lusk, 2003), seed dispersal (Armesto & Rozzi, 1989; Armesto *et al.*, 2001) and longevity (Lusk, 1999) have all been recognized as relevant for explaining the canopy composition of old-growth southern temperate rain forests. However, the correspondence between disturbance regimes and species-specific life-history traits is not well understood (e.g. Loehle, 2000) and may explain the coexistence of tree species with markedly different shade tolerances in the canopy of these forests.

Temperate rain forests in southern South America are subjected to contrasting disturbance regimes. Andean forests occurring at mid and high elevation are subjected to repeated cycles of catastrophic disturbances (i.e. landslides, volcanism and fire), determining a stand-replacement regeneration mode (Veblen & Ashton, 1978; Veblen *et al.*, 1981) with a canopy dominated by pioneer *Nothofagus* species (e.g. *Nothofagus dombeyi*) (Veblen *et al.*, 1981). Conversely, in coastal-range and coastal-lowland forests of the same region (38–47° S), subjected to gap phase dynamics, the canopy is generally dominated by evergreen broad-leaved, shade-tolerant tree species (Veblen *et al.*, 1981; Donoso *et al.*, 1985; Veblen, 1985; Armesto & Figueroa, 1987; Armesto & Fuentes, 1988; Bustamante & Armesto, 1995) often lacking *Nothofagus* and other pioneer, shade-intolerant tree species. However, some old-growth temperate rain forest stands in coastal areas present a mixed canopy of pioneer, shade-intolerant trees (such as *Eucryphia cordifolia*) together with shade-tolerant tree species (Aravena *et al.*, 2002).

In the present work, we seek to understand the mechanisms explaining the long-term persistence of pioneer tree species (in particular, large individuals of *Eucryphia cordifolia*) in the canopy of an old-growth coastal rain forest in Chiloé Island, Chile (42° S). We examined the patterns of tree growth and recruitment of the main canopy species in this forest using a dendroecological reconstruction of long-term regeneration dynamics and historical disturbance regimes that prevail in this forest. Specifically, we addressed the following questions: (1) what is the predominant disturbance regime in this forest, (2) do canopy-emergent tree species differ in life spans and other important life-history traits related to regeneration strategies under the current disturbance regime, and (3) is there a correspondence between disturbance and species-specific life-history traits that may explain the coexistence of pioneer and shade-tolerant species in the canopy of this rain forest?

MATERIALS AND METHODS

Study site

The study was conducted in a coastal remnant of old-growth Valdivian rain forest in Guabún, 30 km north-west of Ancud, northern Chiloé Island, Chile (41.6° S, 73.9° W; Fig. 1). The landscape is a mosaic of patches of second-growth and old-growth forests over rolling hills of low altitude (50–100 m), dispersed in a matrix of anthropogenic grazing pastures. The present landscape has been shaped by a history of forest clearing through the use of fire and logging in the past half century, followed by occasional selective logging of the remaining forest patches (Willson & Armesto, 1996). Soils are generally deep (> 1 m), originating from Pleistocenic moraine fields and glacial outwash plains or coastal marine terraces (Denton, 1999). The prevailing climate is wet-temperate with a strong oceanic influence (Di Castri & Hajek, 1976), with rainfall throughout the year, but with less rainy summers (December–March). The nearest meteorological station in Punta Corona (41°47′ S, 73°52′ W, 48 m elevation, period 1911–2005) has an annual average rainfall of 2444 mm and a mean annual temperature of 10.8°C. Mean monthly maximum and minimum temperatures are 17.6°C (January) and 4.9°C (July), respectively.

Coastal forests are dominated by evergreen broad-leaved tree species, primarily the canopy emergents *E. cordifolia* (Eucryphiaceae) and *Aextoxicon punctatum* (Aextoxicaceae), reaching heights of > 25 m, and several species of Myrtaceae in the canopy and subcanopy (12–25 m). Tree trunks and branches are profusely covered with epiphytic ferns (e.g. *Hymenophyllum* spp., *Hymenoglosum cruentum*, *Polypodium feullei*) and several species of vascular epiphytes and climbers

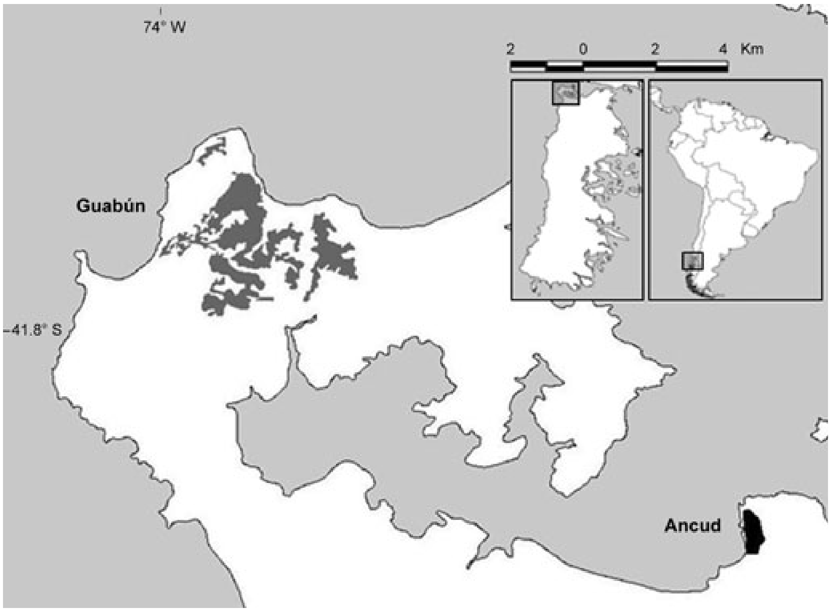

Figure 1 Location and extent of the coastal old-growth forest studied (shaded areas) in the Guabún Peninsula, northern Chiloé Island, Chile.

(e.g. species of Gesneriaceae and Bromeliaceae), including the hemi-epiphyte *Pseudopanax laetevirens* (Araliaceae). The stand selected for study has been free of fire or logging impacts for several centuries. *Chusquea* bamboos in this forest were confined to the forest edge and large canopy openings (> 1000 m^2). Because of intense clearing and logging of lowland coastal forests, including selective logging of *E. cordifolia* and *A. punctatum*, this forest is one of the last remnants of Valdivian coastal rain forest in northern Chiloé Island and resembles coastal rain forests in less accessible areas of Chiloé National Park (Armesto *et al.*, 1996) and coastal forests on the mainland (Smith-Ramírez, 2004) in both structure and floristic composition. Old-growth forests resembling the forest in Guabún have been described by Veblen (1985), Donoso *et al.* (1984, 1985), Armesto & Figueroa (1987) and Armesto *et al.* (1996) on Chiloé Island.

Field methods

Tree-species composition, age structure and regeneration

All sampling was conducted within an old-growth forest stand of about 200 ha. To sample a homogeneous area of this forest stand, our surveys were located > 100 m from any forest edge adjacent to the anthropogenic landscape matrix, and generally on gently sloping or relatively flat land. Canopy cover and old-growth forest structure were taken into account to define the environmental homogeneity of the studied stand. Because most spatial variability is generated by the presence of small tree-fall gaps (Armesto & Fuentes, 1988), sampling methods were designed to capture the structural and floristic composition presented in stands of this forest type (i.e. Donoso *et al.*, 1985; Veblen, 1985). To determine the stand structure and tree community composition, we randomly set up two 50 × 20 m plots, with an additional sampling of four 5 × 100 m strips, covering a total of 0.4 ha. Other studies in Chilean temperate rain forests have used similar sampled areas as representative of stand floristic composition and structure (Veblen *et al.*, 1977, 1980; Donoso *et al.*, 1985; Lusk, 1995). Our data, however, may not fully represent the structural heterogeneity at large spatial scales, which is associated with different disturbance histories and soil conditions (Lusk, 1996; Rüger *et al.*, 2007).

In each 50 × 20 m and 5 × 100 m plot, we identified and recorded the diameter at breast height (d.b.h.) of all adult trees (stems > 1.3 m tall and > 5 cm d.b.h.) rooted within the plot. Stems were classified as: (1) alive (healthy), (2) some branches dead, or (3) snags. Additionally, we utilized a 600-m long transect with 20 uniformly spaced (30-m apart) sampling points, to quantify seedling and sapling densities under closed canopy and within 10 randomly select tree-fall gaps (see below). The strip transect began at one arbitrarily selected point within the forest, far from any forest edge, and was run in a randomly selected compass direction. At each sampling point we identified and counted all tree seedlings (stems < 1.3 m in height) occurring within a 1 × 1 m plot, and all saplings (stems > 1.3 m in height but < 5 cm d.b.h.) occurring within a circular plot of radius 2 m. At each of the 20 sampling points, we obtained core samples of the nearest two to four adult trees (> 5 cm d.b.h.) within a distance of 10 m, using increment borers at a height of about 1.3 m from the trunk base. Additionally, we harvested cross sections from the two nearest saplings to each sampling point, one at ground level and the second one at 1.3 m above the ground to assess the minimum age of trees at breast height. Additional cores were obtained from the largest trees encountered along the strip transect, totalling four cores overall. We used both cores and cross sections to assess stand age structure, to analyse tree radial growth patterns, and to reconstruct the stand history.

Nomenclature for species names follows Marticorena & Quezada (1985) and Mabberley (1997).

Sampling under canopy gaps

We randomly selected 10 tree-fall gaps which intercepted the 600-m long strip transect or were located < 15 m away from this line. We defined canopy gaps as the area of the forest floor directly underneath a canopy opening produced by a single or a multiple tree fall (Runkle, 1992). In order to sample tree regeneration under canopy gaps produced by a single disturbance event, we sampled canopy gaps produced by single tree falls, as indicated by the presence of logs. Canopy gaps were defined as openings $< 1000\ \mathrm{m}^2$ that remained unfilled (tree regeneration > 2 m height, covering < 75% of the area under the gap; Brokaw, 1982). Canopy gap area was adjusted to an ellipsoid determined by the vertical projection of the canopy leaves of trees adjacent to the gap (Runkle, 1992). The expanded gap area was determined by the trunks of the edge trees (Runkle, 1992). Total gap area was determined by the sum of the gap area and the expanded gap area. Following Runkle (1992) we recorded for each gap its originating process (uprooting, snapping or standing dead trees), gap maker identity and gap maker stem diameter. To assess seedling densities within gaps, we set up four 1-m^2 quadrats in each of the 10 gaps, two in the centre of each gap and two in the expanded gap area. Saplings were counted within one circular plot of radius 2 m placed at the gap centre. The total area of all tree-fall gaps (individual tree-fall gaps and multiple tree-fall gaps $> 1000\ \mathrm{m}^2$) occurring along the transect divided by the strip-transect area (600 × 30 m) provided a rough estimate of the fraction of forest in gaps (Runkle, 1992). Gap ages were estimated by coring the trees bordering the gap and fallen gap makers, and from estimated ages of saplings growing on tree-fall mounds and nurse-logs.

Data analyses

Forest structure

The densities and basal areas of each tree species in the plots were added. Density of seedlings and saplings in areas under canopy gaps (gap centre + extended gaps) and under closed canopy were compared using the Kruskal–Wallis rank sum test. Because of possible confusion among seedling and sapling classes of *Amomyrtus luma*, *Amomyrtus meli* and *Luma apiculata*, their densities were combined in one group (Myrtaceae; Myrt) for the statistical analysis of regeneration. To provide a quantitative basis for comparing d.b.h. structures among tree species (Bailey & Dell, 1973), Weibull functions were fitted to the d.b.h. frequency distributions of tree species with > 20 sampled individuals > 5 cm d.b.h. Probability density functions were fitted to each diameter distribution using a maximum-likelihood algorithm (Cohen, 1965). Weibull distributions can accommodate a wide variety of shapes as indicated by the shape parameter, c. When $c \leq 1$, a descending monotonic distribution is indicated; when $c > 1$, the function is unimodal, either positively skewed ($1 < c < 3.6$), normal ($c = 3.6$), or negatively skewed ($c > 3.6$) (Lorimer & Krug, 1983). We use the shape parameter to compare the observed d.b.h. frequency distributions to models often assumed to represent a continuously regenerating population (Veblen, 1992).

Dendroecology

A total of 270 cores were obtained and processed following the techniques outlined by Stokes & Smiley (1968). We discarded cores ($n = 14$) with fewer than 25% of the stem radii intact. All discarded cores corresponded to *E. cordifolia* because of its greater tendency to have rotten tree centres with indistinguishable tree rings. Therefore, old trees (d.b.h. > 100 cm) of *E. cordifolia* may not be well represented in the age structure of this species. Because Myrtaceae tree species usually have extremely hard wood, i.e. $> 900\ \mathrm{kg\ m}^{-3}$ (Hall & Witte, 1998), few cores ($n = 4$) were obtained to estimate ages of the largest trees. Because increment cores were collected at 1.3 m above the ground, we considered the ages obtained as the minimum age of trees at breast height. Minimum tree ages were estimated by counting the annual tree rings in each core ($n = 256$). Rings were visually cross-dated using signature rings and assigning a calendar year according to the date of the latest ring (Stokes & Smiley, 1968). We assigned to each tree ring the date in which radial growth started (Schulman, 1956). For cores where the pith was missing and ring width geometry allowed us to correct ages, the number of rings to the pith was estimated following Duncan (1989). We used this method when ring width geometry implied an addition of < 15 rings. Cores where ring-width geometry would imply a larger correction were considered as incomplete ages. Ages obtained from cross sections, cores with pith and cores aged according to Duncan (1989) were considered as complete ages and were used to estimate recruitment dates. We defined recruitment date as the year when the tree reached coring height, corrected according to cross sections of saplings. Annual radial growth increments were measured to the nearest 0.01 mm with an increment-measuring device and recorded on a computer. We used the computer program COFECHA (Holmes, 1983) to detect measurement and cross-dating errors. After cross-dating, annual increments were standardized by dividing the measured growth by the average radial growth of the series. This standardization procedure facilitates detection of past disturbances because it preserves the growth trend, which can be due both to the stem geometry (i.e. the inherent growth trend) and to disturbance/competition (Veblen *et al.*, 1991) and allows for trees with different growth rates to be combined into a standardized mean chronology (Fritts, 1976). Tree-ring chronologies were produced for the canopy species with a sample size of > 15 trees (*A. punctatum* and *E. cordifolia*).

Each core sampled was examined for releases in radial growth. Releases provide evidence of enhanced tree radial growth presumably associated with canopy opening, and were used to make inferences about historical disturbance regimes and long-term stand dynamics. We defined a major release as an increment of > 100% in average radial growth lasting for at least 15 subsequent years and a moderate release as an increment > 50% in average radial growth lasting for at least 15 years afterwards (Lorimer & Frelich, 1989). To distinguish the effect of canopy disturbance from transient effects of climatic fluctuations on tree growth, we searched for sustained releases (15 years' enhanced growth) coinciding in several trees within the stand. This criterion ruled out short-term climatic pulses and gradual changes in ring width due to tree ageing, bole geometry and long-term climate shifts (Lorimer & Frelich, 1989; Nowacki & Abrams, 1997).

RESULTS

Tree-species composition and stand structure

A total of 14 evergreen, broad-leaved tree species made up the canopy of this old-growth forest (Table 1). Large individuals of *E cordifolia* and *A punctatum* occupied the emergent stratum (> 25 m tall). *Laureliopsis philippiana* together with several Myrtaceae species (including *A. luma*, *Myrceugenia planipes*, *Myrceugenia ovata* and *L. apiculata*) occupied the main canopy (20–25 m). A few large trees of *E. cordifolia* contributed disproportionately to the stand basal area (Table 1). *Laureliopsis philippiana* and *A. luma* contributed rather equally to forest structure in terms of both the density and basal area. Two species of *Myrceugenia*, *M. planipes* and *M. ovata*, had a high stem density in the forest, mainly in the subcanopy. Combining all species of Myrtaceae, they made up 47.5% of the stand tree density but < 30% of the basal area. Despite its uniform presence in the emergent and canopy layer, *A. punctatum* contributed only a small fraction of both density and stand basal area. Standing dead trees (snags) were common within the stand, accounting for 16% of total basal area (Table 1). Other tree species, such as *Drimys winteri* and *Rhaphithamnus spinosus*, were minor components of this old-growth forest.

Seedlings and saplings were numerically dominated by Myrtaceae tree species in this old-growth forest. Regeneration of *A. luma* was the most abundant (Table 2). *A. punctatum*, *L. philippiana* and *M. ovata* had lower densities of seedlings but they were well represented in the sapling size classes. Neither *Drimys winteri* nor *Pseudopanax laetevirens* had any saplings under the forest canopy or in gaps, although these tree species were present as seedlings. The hemi-epiphyte *P. laetevirens* was never found rooted to the ground (Table 1). In the plots, this tree typically adopted a hemi-epiphytic growth habit on large emergent trees of *E. cordifolia*.

The d.b.h. distributions of canopy trees in this forest presented the characteristic shape of an old-growth uneven-aged stand, which significantly departed from a negative exponential distribution (typical of actively growing stands) by the higher fraction of trees in the larger d.b.h. classes (Weibull *c* = 1.13). The largest-diameter classes (> 80 cm d.b.h., > 25 m tall trees) were numerically dominated (Fig. 2) by *E. cordifolia* (maximum recorded d.b.h. 243 cm) and *A. punctatum* (maximum d.b.h. 136 cm). The d.b.h. distribution of *E. cordifolia* was distinctly unimodal with a positive skew (*c* = 2.48; Fig. 2). Despite its importance as an emergent, *E. cordifolia* was poorly represented in the stand by stems < 30 cm d.b.h. In contrast, *D. winteri* had a unimodal d.b.h.

Table 1 Density, basal area, relative density and relative dominance (% of basal area) of tree species (stems > 5 cm d.b.h.) in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile.

Species	Abbrev.	Family	Density (No. ha^{-1})	Basal area (m^2 ha^{-1})	Relative density (%)	Relative dominance (%)
Eucryphia cordifolia	Euco	Eucryphiaceae	72	40.7	3.5	32.5
Amomyrtus luma	Amlu	Myrtaceae	425	18.7	20.7	15.0
Laureliopsis philippiana	Laph	Monimiaceae	432	13.7	21.0	11.0
Myrceugenia planipes	Mypl	Myrtaceae	290	7.4	14.1	5.9
Aextoxicon punctatum	Aepu	Aextoxicaceae	116	11.1	5.6	8.9
Myrceugenia ovata	Myov	Myrtaceae	160	3.2	7.8	2.5
Amomyrtus meli	Amme	Myrtaceae	58	5.2	2.8	4.2
Rhaphithamnus spinosus	Rhsp	Verbenaceae	123	0.9	6.0	0.7
Luma apiculata	Luap	Myrtaceae	43	2.4	2.1	1.9
Drimys winteri	Drwi	Winteraceae	36	1.4	1.8	1.1
Ovidia pillo-pillo	Ovpi	Thymeliaceae	40	0.1	1.9	0.1
Pseudopanax laetevirens	Psla	Araliaceae	0†	0.0	0.0	0.0
Other species*			120	0.2	5.8	0.2
Dead trees			140	20.3	6.8	16.2
Total			2055	125.2		

Abbrev.: species code name corresponding to the first two letters of each part of the binomial name.

*Includes: *Dashypyllum diacanthoides* and *Caldcluvia paniculada.*

†Found only as seedlings.

Table 2 Number of seedlings (mean ± standard error of n = 60 1-m^2 plots) and saplings (mean of 30 circular plots) in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile.

	Seedlings		Saplings	
Species	Density ± SE (No. ha^{-1})	Relative density (%)	Density ± SE (No. ha^{-1})	Relative density (%)
Eucryphia cordifolia	11,803 ± 4420	4.1	55 ± 55	1.7
Amomyrtus luma	129,016 ± 17,995	44.4	357 ± 109	10.9
Laureliosis philippiana	1967 ± 837	0.7	110 ± 86	3.4
Myrceugenia planipes	26,721 ± 4074	9.2	220 ± 67	6.7
Aextoxicon punctatum	10,000 ± 2024	3.4	604 ± 200	18.5
Myrceugenia ovata	3443 ± 1651	1.2	439 ± 183	13.4
Amomyrtus meli	74,426 ± 14,003	25.6	466 ± 192	14.3
Rhaphithamnus spinosus	27,213 ± 5063	9.4	357 ± 140	10.9
Luma apiculata	2951 ± 2628	1.0	439 ± 156	13.4
Drimys winteri	2295 ± 887	0.8	0	0.0
Ovidia pillo-pillo	328 ± 230	0.1	220 ± 152	6.7
Pseudopanax laetevirens	492 ± 364	0.2	0	0.0
Total	290,655		3265	

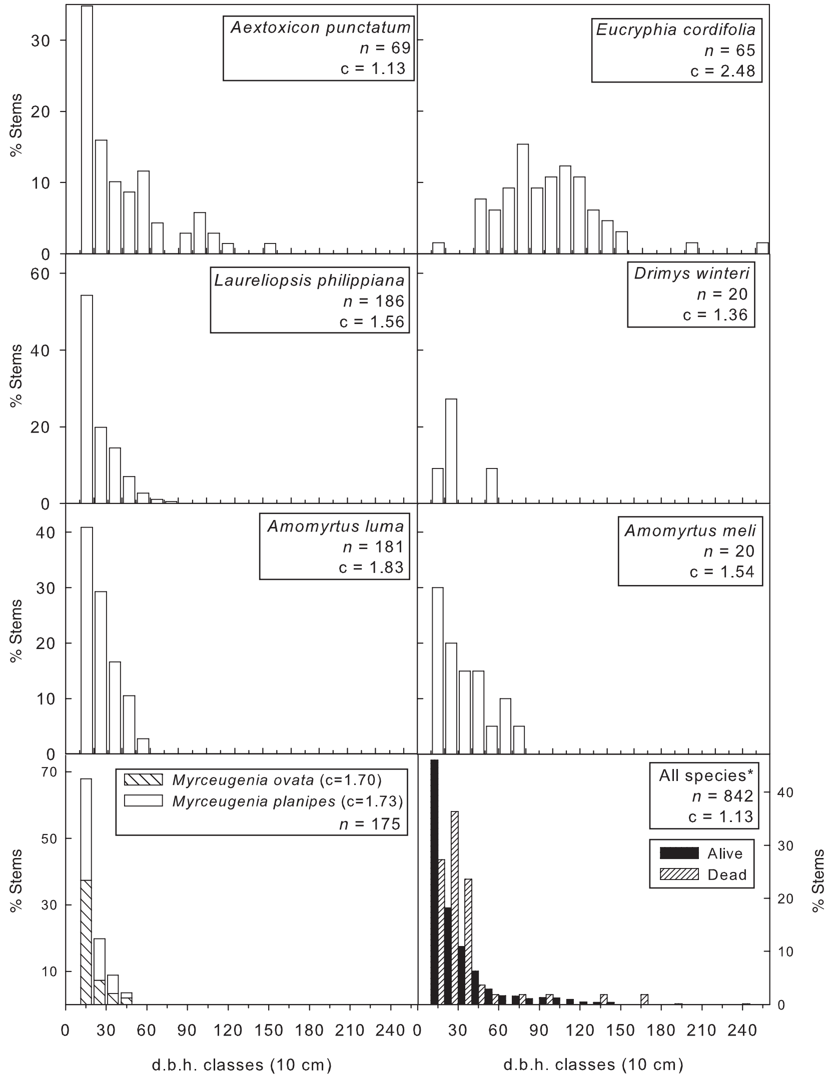

Figure 2 Diameter (d.b.h.) class distribution for the main canopy tree species (trees with d.b.h. > 5 cm; $n > 20$) in the coastal temperate rain forests of Guabún, in northern Chiloé Island, Chile. See details about Weibull shape parameter c in text. All species* includes all tree species listed in Table 1. Note different scales for the y-axes.

distribution (Weibull $c = 1.36$) dominated by small sized individuals (d.b.h. < 60 cm). *Aextoxicon punctatum* on the other hand was represented in the entire range of d.b.h. intervals < 60 cm, with a distinct secondary peak for d.b.h. > 70 cm (Weibull $c = 1.13$; Fig. 2). Intermediate size classes (30–70 cm d.b.h.) within this old-growth stand were almost entirely

Table 3 Characteristics of tree-fall gaps in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile. The total gap area is the sum of gap area plus expanded gap (see Materials and Methods for definitions).

Gap maker	Number of gaps	Gap maker stem diameter (cm)	Gap size range (m^2)			Origin
			Gap	Expanded gap	Total gap	
Eucryphia cordifolia	5	30–111	31–137	261–350	291–476	Snapping, uprooting
Laureliopsis philippiana	2	53–75	53–104	136–159	212–239	Snapping
Aextoxicon punctatum	1	59	211.7	88.8	122.9	Uprooting
Amomyrtus luma	1	45	230.1	58.9	171.2	Snapping
Amomyrtus meli	1	78	292.1	184.5	107.6	Uprooting

dominated by Myrtaceae species and *L. philippiana* (Fig. 2), which had similar d.b.h. distributions (Weibull $c = 1.54–1.83$). Myrtaceae (four tree species combined) accounted for most individuals under the canopy in the smallest stem diameter classes (< 30 cm d.b.h.; 30% of all trees). Snags were more frequent in the smaller d.b.h. classes (< 40 cm, Fig. 2).

Regeneration in tree-fall gaps

Eucryphia cordifolia was the most frequent gap maker and produced the largest canopy gaps (Table 3). Most gap-makers had estimated trunk diameters > 50 cm. Including two large gaps recorded as > 1000 m^2, the total fraction of forest area in gaps was nearly 8%. Individual tree-fall gaps ranged in age between 31 and 115 years with an average age of 55 years, and ranged in size from 107–476 m^2, all of them formed by uprooting or snapping of canopy trees (Table 3). The total gap area for expanded gaps averaged 215.3 m^2 for all gaps sampled.

Most seedlings occurred under light-exposed canopy gaps, with much lower densities under closed canopies (Kruskal–Wallis $\chi^2 = 6.9$, d.f. = 1, $P < 0.01$; Fig. 3a). The combined density of seedlings of *A. luma*, *A. meli* and *L. apiculata* was significantly higher under tree-fall gaps than under the continuous forest canopy (Kruskal–Wallis $\chi^2 = 6.9$, d.f. = 1, $P < 0.01$; Fig. 3a). *Eucryphia cordifolia*, *R. spinosus* and *L. philippiana* had higher seedling densities under canopy gaps than under the shade (Kruskal–Wallis $\chi^2 = 6.3$, d.f. = 1, $P < 0.01$ for *E. cordifolia*; Kruskal–Wallis $\chi^2 = 5.2$, d.f. = 1, $P < 0.05$ for *L. philippiana*, Kruskal–Wallis $\chi^2 = 10.1$, d.f. = 1, $P < 0.01$ for *R. spinosus*). In this old-growth stand, saplings of *E. cordifolia* were not found under the closed canopy but they were present beneath gaps. *Ovidia pillo-pillo*, which is a tree species occurring mainly in secondary forests, and which was absent from old-growth forest canopy, had seedlings and saplings under canopy gaps only (Fig. 3). Saplings of *R. spinosus* were more abundant under tree-fall gaps than under the forest canopy (Kruskal–Wallis $\chi^2 = 11.7$, d.f. = 1, $P < 0.01$; Fig. 3b).

Tree age structures

Age structures were constructed for the four main canopy tree species, including the two emergents (Fig. 4). Age structures were also indicative of the old-growth condition of this forest, characterized by multi-aged cohorts (Fig. 4). The oldest tree recorded in the stand belonged to *A. punctatum* (minimum tree age > 350 years) followed by *E. cordifolia* (minimum tree age > 286 years) (Table 4). However, considering the maximum d.b.h. of *A. punctatum* (136 cm in this forest), the recorded minimum ages are likely to underestimate the age of

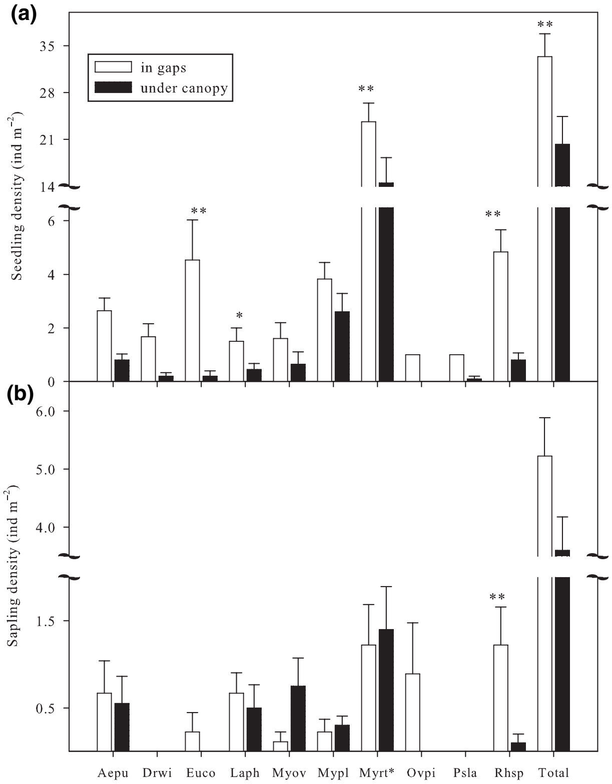

Figure 3 Mean seedling and sapling densities (individuals m^{-2}) recorded under the forest canopy ($n_{\text{seedling}} = n_{\text{sapling}} = 20$ plots) and within tree-fall gaps (gap centre + expanded gap) ($n_{\text{seedlings}} = 40$ plots; $n_{\text{saplings}} = 10$ plots) in Guabún, northern Chiloé Island, Chile. Abbreviations of species correspond to the first two letters of each part of the binomial name as listed in Table 1. Myrt* represents the pooled density of seedlings and saplings of *A. luma*, A. *meli* and *L. apiculata*. Significant differences in density of seedlings and saplings between closed and open habitats (Kruskal–Wallis test) are indicated: *$P < 0.05$ and **$P < 0.01$.

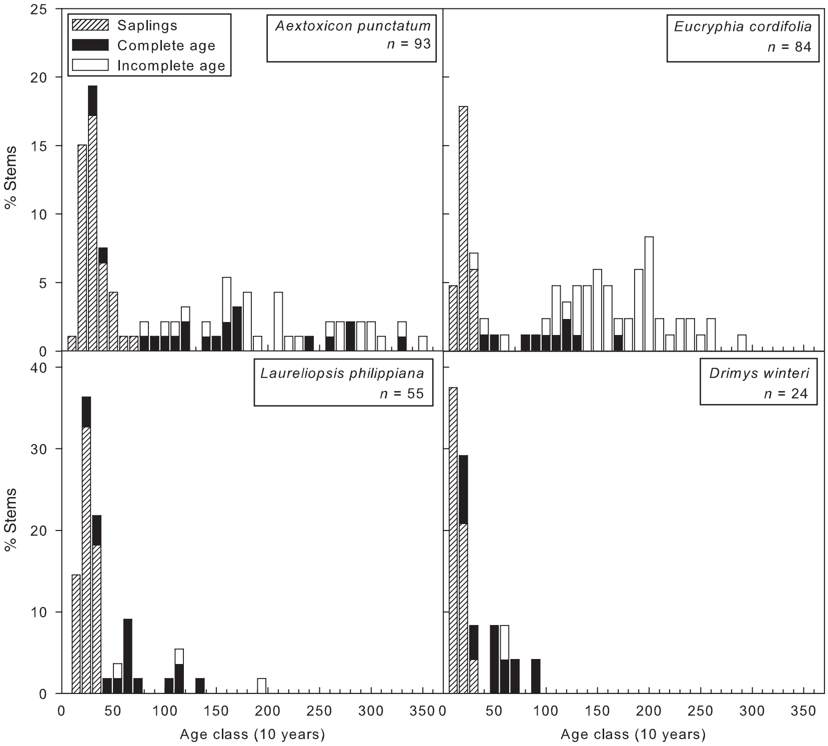

Figure 4 Age class distribution (at 0.3 m above the ground) of saplings (individuals < 5 cm d.b.h.) and adult trees (d.b.h. > 5 cm) in an old-growth coastal temperate rain forest, Guabún, northern Chiloé Island, Chile. Ages of saplings were obtained using cross sections. Complete ages were obtained from cores with pith and cores aged according to the method of Duncan (1989). Incomplete ages were obtained from cores where the pith was missing and ring width geometry did not allow a correction using Duncan (1989).

Table 4 Minimum ages and life-history traits of main canopy tree species in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile. The age at coring height (1.3 m) was obtained using cross sections from saplings, one at the ground level and the second one at 1.3 m above the ground.

Species	Shade tolerance	Mean age at coring height (years ± SD)	Minimum age range (years)*	Life span† (years)	Maximum height (m)‡	Maximum d.b.h. recorded (cm)§
Aextoxicon punctatum	To	16 ± 10 [19]	8–349 [93]	480	34	136*
Amomyrtus luma	To	–	–	200	22	137
Amomyrtus meli	Int	–	113 [1]	113*	26*	59
Drimys winteri	In	7 ± 3 [11]	5–89 [24]	280	22*	104
Eucryphia cordifolia	In	11 ± 3 [18]	8–286 [70]	650	38	243*
Laureliopsis philippiana	To	8 ± 6 [21]	6–187 [55]	657	34	121
Luma apiculata	Int	–	–	n.d.	23	84
Myrceugenia ovata	To	–	–	n.d.	22	44
Myrceugenia planipes	To	–	73–140 [3]	260	17	39

To, shade-tolerant; In, shade-intolerant; Int, intermediate (after Figueroa & Lusk, 2001; and authors' personal observations).

SD, standard deviation of the mean. Number of trees sampled is indicated in brackets [ ]. n.d. indicates no data available.

*Data from this study.

†Life span (or mean estimated maximum longevity) follows the literature (Lara, 1991; Lusk & Del Pozo, 2002; Pollmann & Veblen, 2004; Veblen, 1985).

‡Data from Parada *et al.* (2003).

§Gutiérrez *et al.*, unpublished data.

the oldest tree because the longest tree core obtained represented only 33% of the stem radius. Fig. 4 also shows that at least three trees more of *A. punctatum* had ages > 300 years (35–40% stem radii intact). These two canopy emergent tree species had numerous individuals established in the last 30 years, but they were well represented across all age intervals, showing uneven-aged structures (Fig. 4). The multimodal age distribution of *E. cordifolia* indicated a distinctive recruitment pulse about 150–200 years ago. Other canopy trees, *A. meli*, *L. philippiana* and *M. planipes*, had life spans of about 100 years, whereas all *D. winteri* stems were younger than 90 years (Table 4). *Laureliopsis philippiana* and *D. winteri* had similar monotonically descending age distributions, with a large proportion of young individuals (Fig. 4).

Tree radial growth and regeneration modes

The number of radial growth releases recorded since 1670 differed among species (ANOVA $F_{3,152} = 101.9$, $P < 0.01$; Table 5). Radial growth patterns of the four canopy species analysed produced sustained releases to a level defined here as a major release (Table 5). However, release frequencies, indicative of synchronous growth releases among nearby trees within the stand, were much higher for moderate than for major releases (Table 5). A low frequency of synchronous major releases suggests that large tree-fall gaps are infrequent in this old-growth forest. This is supported by the fact that only moderate releases were detected in cores obtained from trees located along the edges of current tree-fall gaps (Fig. 5). Shade tolerant *A. punctatum* and *L. philippiana* had a greater frequency of moderate growth releases than *E. cordifolia* (Table 5).

Growth releases were compared for the oldest trees ($n = 44$, minimum age > 150 years; Fig. 6a) in the forest for every 10-year interval from 1750 to 1990. The number of growth releases fluctuated greatly, with higher frequencies recorded in 1790, 1840, 1890–1900, 1930 and 1970. Tree-fall gap dates coincident with release events were obtained for the period between 1940 and 1970 and for one tree-fall gap dated in the 1890s (Fig. 6b). The highest frequency of major releases in the entire period analysed was detected in the 1930s (coincident in eight trees).

The recruitment of canopy-dominant tree species was fairly constant over the past 300 years of forest history, except for an apparent gap in the number of trees established during the period 1920–50 (Fig. 6c). Lower establishment in the period between 1920 and 1950 was more noticeable for *E. cordifolia* and may be responsible for the two distinct cohorts of trees identified in the age structure of this species (Figs 4 & 6c). Radial growth of *A. punctatum* and *E. cordifolia* generally increased in contrasting periods during the recent history of the stand (Fig 6c) and both species presented a strong growth decline during the period 1870–1900, with similar levels of radial growth suppression.

DISCUSSION

Tree regeneration patterns

The long-term patterns of regeneration of tree species in this old-growth coastal rain forest suggest that most tree species responded to small canopy openings (Figueroa & Lusk, 2001). As in tropical forests (Schnitzer & Carson, 2001), individual tree-fall gaps < 300 m^2 in their expanded area were important sites for the regeneration of most tree species in the forest canopy (Fig. 3a). This lends support to the idea that tree-fall gaps play a major role in the maintenance of tree-species composition in the canopy of this temperate old-growth forest. Although the light requirements reported for seedlings of shade-tolerant *A. punctatum*, *L. philippiana* and Myrtaceae species are relatively lower than those of shade-intolerant tree species (Figueroa & Lusk, 2001), seedlings and saplings of both functional types were more frequently found in tree-fall gaps than under the continuous forest canopy. The regeneration of shade-tolerant tree species under canopy gaps (Fig. 3) suggests that they are able to respond to slight differences in understorey light levels, as has been shown in other temperate forests (Canham, 1989). This physiological plasticity is also supported by the fact that seed germination of shade-tolerant tree species in Chilean and other forests is relatively unresponsive to overstorey light conditions (Swaine & Whitmore, 1988; Figueroa & Lusk, 2001). Although both *E. cordifolia* and *D. winteri* are generally considered pioneer tree species, which regenerate more frequently in large openings (Donoso, 1993), in this coastal forest both species regenerate within small canopy openings. Shade-intolerant species may be restricted to small canopy gaps largely due to their higher light requirements for regeneration (Canham, 1989). *Drimys winteri* seems broadly tolerant to light conditions during the seedling and sapling stages (Figueroa & Lusk, 2001; Gutiérrez *et al.*, 2004; Chacón & Armesto, 2005). However, the regeneration pattern of *E. cordifolia* contrasts with the findings for lowland (but not coastal) Chiloé forests where the regeneration of this species appeared to depend on larger gaps (Donoso *et al.*, 1985; Veblen, 1985). The sprouting ability of *E. cordifolia* (Veblen

Table 5 Radial growth patterns for the main canopy tree species in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile. Major and moderate releases defined as in Lorimer & Frelich (1989).

	Aextoxicon punctatum	*Eucryphia cordifolia*	*Laureliopsis philippiana*	*Drimys winteri*
Number of trees	38	35	14	5
Mean radial growth (mm $year^{-1}$) ± SD	0.96 ± 0.69	1.04 ±0.72	1.15 ± 0.74	1.08 ± 0.58
Maximum radial growth (mm $year^{-1}$)	7.24	6.64	5.15	3.65
Maximum sustained release*	5.27	4.54	8.54	1.67
Moderate release frequency (releases 100 $year^{-1}$)†	2.4	1.66	2.16	0.9
Major release frequency (releases 100 $year^{-1}$)†	0.76	0.34	1.13	0

SD, standard error of the mean.

*Maximum sustained release was calculated as the growth rate for the 15-year period following the release event, divided by the growth rate for the 15 years prior to release.

†Release frequencies for the past 350 years were calculated by averaging the number of growth releases recorded for each tree and dividing by tree age.

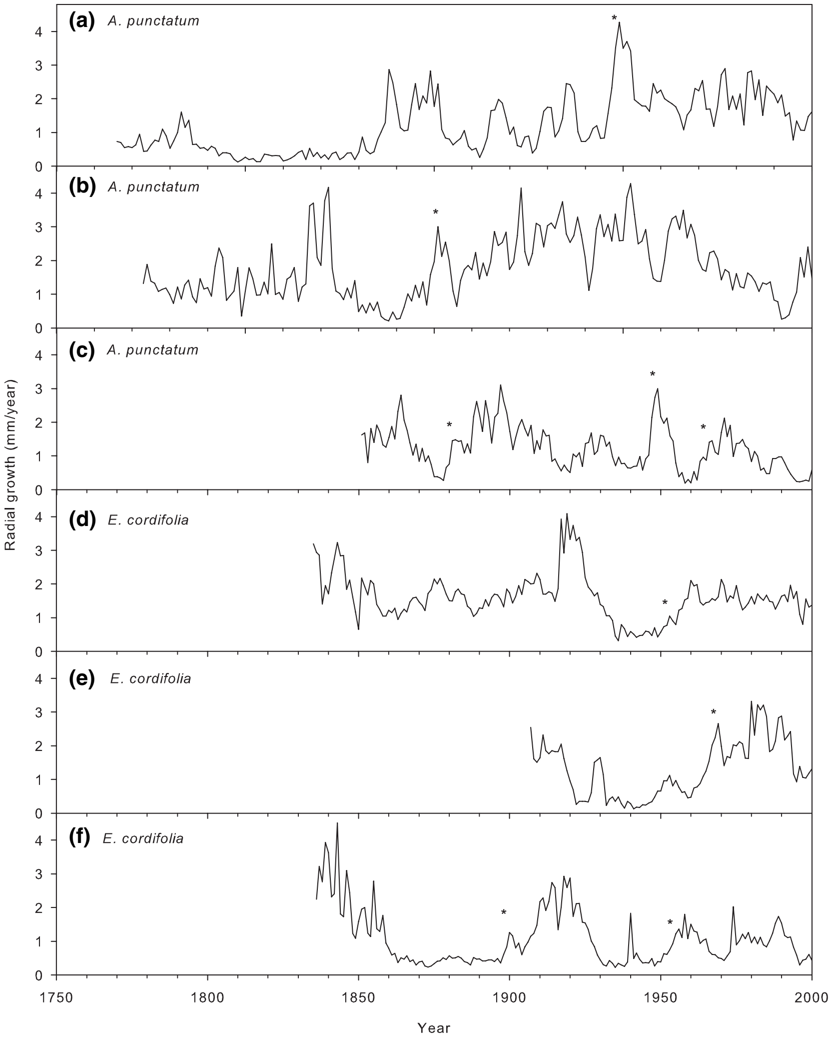

Figure 5 Radial growth rates (mm year^{-1}) for selected trees located along canopy gap edges. Data are for *Aextoxicon punctatum* (a–c) and *Eucryphia cordifolia* (d–f) in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile. Asterisks indicate years of moderate releases defined following Lorimer & Frelich (1989).

et al., 1981; Donoso *et al.*, 1985; Veblen, 1985) may facilitate regeneration from gap makers or trees growing along small gap edges. A similar regeneration pattern was found by Veblen *et al.* (1981) in the Cordillera Pelada, Chile (40°10′ S, elevation of 260 m) as suggested by the size structure and clustered spatial pattern of *E. cordifolia*.

Some differences emerge between this coastal forest and lowland (but not coastal) forests located in Chiloé Island (Donoso *et al.*, 1985; Veblen, 1985). We found a high relative dominance by *A. punctatum* in our study area versus its absence in the two cited studies that may be related to its ability to tolerate salt spray in coastal areas (Pérez, 1994). Also, the pioneer tree species *Weinmannia trichosperma* (Cunoniaceae) was absent or rare in our study area whereas it is present in lowland Chiloé forests (Donoso *et al.*, 1985; Veblen, 1985; Aravena *et al.*, 2002; Gutiérrez *et al.*, 2004). A possible explanation is that *E. cordifolia* can be a pioneer where soil conditions do not allow the establishment of *W. trichosperma* or *Nothofagus* spp. (Donoso *et al.*, 1984). The abundance of *Chusquea* bamboos may also have an important role as competitors in gaps in other forests, apparently inhibiting the regeneration of *E. cordifolia* and the shade-tolerant *A. punctatum* (González *et al.*, 1997; Donoso & Nyland, 2005). These differences reflect important site differences (e.g. coastal vs. non-coastal, soil differences) as well as differences in disturbance regime.

Disturbance regime and regeneration dynamics

The mean canopy gap area in this old-growth forest (< 300 m^2) was smaller than that reported for coastal, montane evergreen forests of Chiloé Island (Armesto & Fuentes, 1988). However, the fraction of the area in canopy gaps (8% in this old-growth forest), which included multiple tree-fall gaps, was consistent with previous estimates for lowland old-growth forest in Chiloé Island (Veblen, 1985). Large canopy openings (> 1000 m^2), produced by multiple tree falls, were infrequent and spatially confined to specific areas as reported in other Chiloé forests (Veblen, 1985; Armesto & Fuentes, 1988). Presumably, such openings are caused by infrequent, but severe, wind storms (Veblen, 1985). Trees growing along the edge of the extant tree-fall gaps did not show evidence of major growth releases (Fig. 5), indicating that single tree falls are more likely to produce moderate

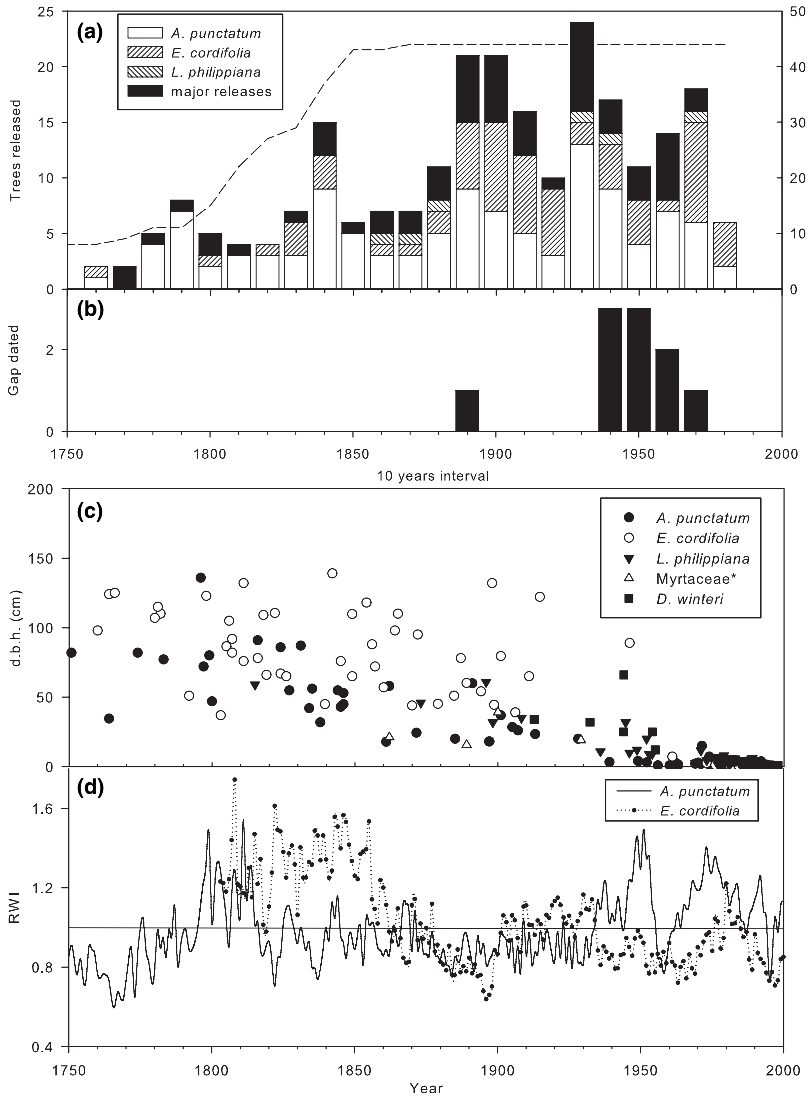

Figure 6 (a) Decadal distribution of major and moderate radial growth releases (after Lorimer & Frelich, 1989) in the oldest trees cored ($n = 44$, indicated by dotted line). (b) Frequency distribution of gap ages ($n = 10$). (c) Age–diameter (d.b.h.) relationships showing the minimum recruitment date and the present d.b.h. of sampled trees ($n = 256$). Myrtaceae* includes *M. planipes* and *A. meli*. (d) Radial growth index (RWI, estimated for periods with $n > 5$ trees) of *A. punctatum* and *E. cordifolia* [same trees as in (a)]. Note that the *x*-axis ticks don't line up for all of the graphs in this figure.

releases in the affected trees. Hence, the dominance of moderate releases in the release chronology and the observed tree recruitment patterns (Fig. 6) in this forest are consistent with a disturbance regime dominated by frequent, low-intensity disturbances (i.e. gap-phase dynamics), with sporadic large-scale disturbances (i.e. multiple tree falls).

The regeneration modes of canopy tree species and the disturbance regime in this old-growth coastal forest both resembled those documented for other southern temperate rain forests (Stewart & Rose, 1990; Lusk & Smith, 1998; Gutiérrez *et al.*, 2004; Pollmann & Veblen, 2004). The disturbance regime in these coastal forest differed from even-aged *Nothofagus* stands in the Andes, with catastrophic recruitment modes induced by large-scale disturbances (i.e. fires, mass movements induced by earthquakes) (Veblen & Ashton, 1978; Veblen *et al.*, 1992). Although extensive land-use changes on Chiloé Island started in the late 19th century (Willson & Armesto, 1996; Torrejón *et al.*, 2004), large disturbances were infrequent in this coastal forest as suggested by the presence of few major releases in the chronology. No shifts in tree-species composition are inferred from the recruitment patterns (Figs 4 & 6). Shade-tolerant tree species (Myrtaceae, *L. philippiana*, *A. punctatum*) (Table 4) are able to regenerate continuously under this disturbance regime, germinating and recruiting to sapling stage in both small canopy gaps and under a closed canopy. The largest and presumably oldest trees of shade-tolerant tree species (i.e. *A. punctatum*) may reach ages > 450 years (Fig. 4, Table 4). In contrast, most of the extant population of the comparatively shade-intolerant *E. cordifolia* was established sporadically (intermittently) in response to both small and larger gaps (Fig. 4). Based on these results, we propose that the canopy composition of the forest has remained relatively unchanged for at least 450 years.

Gap-phase dynamics and the coexistence of *A. punctatum* and *E. cordifolia*

Our results support the idea that long life spans, coupled with differences in sapling shade tolerance, and the creation of canopy gaps of different sizes by emergent and canopy trees are important factors for the non-equilibrium persistence of tree species mixtures (Lusk & Smith, 1998; Loehle, 2000). A long residence time in the canopy for *E. cordifolia* ensures that at least one gap of sufficient size will be produced to facilitate its recruitment (Loehle, 2000). Because of the large individual sizes that this species attains (Table 4) and its frequency as a gap-maker (Tables 3 & 6; see also Veblen, 1985), it is suggested that the death of large, emergent individuals of *E. cordifolia* creates conditions that favour its own regeneration mode (Shugart, 1984). Other traits of *E. cordifolia* that may enhance its long-term persistence in the canopy until the old-growth stage include its sprouting ability in small canopy openings, its rapid establishment immediately following a large disturbance event, its ability to tolerate long periods of growth suppression (Fig. 5f), and its rapid radial growth following release (Fig. 5d–f). These traits are comparable with those seen for *Weinmannia trichosperma*, which is a long-lived pioneer (Lusk, 1999) not present (or rare) in this coastal forest. In contrast, shade-tolerant *A. punctatum* persists and dominates the canopy because of its lower light requirement for germination (Figueroa & Lusk, 2001) and seedling growth compared with that of *E. cordifolia*, and its capacity to recruit (Fig. 2) and survive (Fig. 5a–c) both under canopy gaps and under the continuous forest canopy. Additionally, the long life span of *A. punctatum* increases its chances of survival in the understorey until the overtopping tree dies and a canopy gap forms in which an established subordinate tree can succeed.

Species-specific life-history traits (such as life spans, maximum height and shade tolerance) provide a basis for understanding the long-term coexistence of pioneer and shade-tolerant tree species in this coastal, old-growth rain forest, despite the rarity of major disturbances. To better understand the mechanism of tree-species coexistence, it would also be important to assess the importance of other reproductive traits, such as seed dispersal distances, under disturbance regimes varying in spatial and temporal scales (i.e. turnover rate, gap size distribution). Expanding these reconstructive studies of old-growth rain forests in coastal areas will also yield valuable insights for the protection and management of these threatened forests.

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RESEARCH PAPER IV

Interior of an old-growth temperate rainforest in southern Chile (Ahuenco, Chiloé Island)

A similar version of this research paper has been submitted for publication as

Gutiérrez AG, Rüger N, Huth A. Successional pathways to the old-growth stage in temperate rainforests of Chiloé Island, Chile.

Author contributions

AGG conceived and designed the study, performed research, analyzed data, and wrote the paper. NR contributed to data analysis and new methods. AH conceived and designed the study. All authors contributed to the text.

Photo credit: Pablo Necochea

Successional stages of temperate rainforests: Are old-growth forests at steady state?

ABSTRACT

Old-growth forests are commonly assumed at steady state, representing a final successional stage where in the absence of major disturbance forests remain stable in structure (e.g. biomass). In forests containing pioneer tree species with long lifespan (>450 years), the time taken to enter this stage can be long. As a consequence, old-growth stands containing long-lived pioneers may differ in features commonly associated with the old-growth stage. Here, we propose a method for identifying forest successional stages using a dynamic forest model. We examined the successional stages of 13 old-growth temperate rainforests on Chiloé Island, Chile. We parameterized the model for 17 tree species using field data and values given in the literature. Model performance was evaluated comparing structural patterns observed in the field and the patterns predicted by the model. The model reproduced the structural and compositional variability of the studied forest stands when variable successional pathways to the old-growth stage had been considered. The long-term dominance of pioneers emerged during the first 500 years of succession because of their long lifespans and the occurrence of canopy openings produced by windstorms. Our results suggest that 6 of the 13 old-growth forests represent a transient successional stage. Biomass tends to decrease as forests approach steady-state because large pioneers are replaced by smaller late-successional trees, potentially resulting in carbon losses. Temperate rainforests in this region contain large quantities of carbon and can take 500 to 850 years of succession to reach the old-growth stage. This dynamic behaviour should be considered in assessments of carbon storage in temperate rainforests.

INTRODUCTION

The global trend of diminishing cover of old-growth forests and the importance of these forests for the global carbon cycle (Luyssaert et al., 2008) demand to analyze the dynamics of old-growth forest remnants. It is often assumed that old-growth forests are in a steady state (Odum, 1969), representing a final successional stage where in the absence of major disturbance forests are stable in composition, structure and biomass over long periods (Oliver & Larson, 1990, Franklin & Spies, 1991). Forests enter the old-growth stage only after the pioneers have been replaced (Wirth et al., 2009). In forests containing pioneer tree species with long lifespan (>450 years), the time taken to reach this stage can be long hampering recognition of old-growth forests. Pioneer tree species may persist in the old-growth stage due to the occurrence of disturbances or specific life-history traits (Franklin & Hemstrom, 1981). As a consequence, old-growth stands containing long-lived pioneers may differ in structural and functional features commonly associated with the old-growth stage, such as reduced net primary production (Franklin & Spies, 1991, Ryan *et al.*, 1997).

Individual-oriented forest models (i.e. gap models, Botkin et al. 1972, Shugart 1984) provide a tool for analyzing the structure and dynamics of forests and for exploring the thresholds at which a forest enters the old-growth stage. Individual-oriented forest models simulate the fate of single trees on the basis of species' life-history traits and limited resource availability (e.g. light, Pacala et al. 1994), thereby facilitating detailed analyses of forest dynamics by tracking individual trees. Forest models have successfully simulated long-term forest dynamics in a variety of forest types by synthesizing current ecological knowledge (Shugart, 1998, Bugmann, 2001, Pretzsch *et* *al.*, 2008). This modeling approach has been mainly used to model forest dynamics in temperate and boreal forests of the northern hemisphere (Shugart, 1998, Bugmann, 2001). Some individual-oriented forest model applications are found in southern temperate rainforests (Pausas *et al.*, 1997, Hall & Hollinger, 2000) but, to our knowledge, only one study has modelled temperate rainforests of southern South America (Rüger et al., 2007).

Temperate rainforests can play an important role in the carbon cycle due to the large amounts of carbon stored in their biomass (Keith *et al.*, 2009). Temperate rainforests occur around the world in coastal areas with temperate climates and annual rainfall >1400 mm (with >10% of rainfall occurring in summer), such as the Pacific Northwest of North America, the western coast of southern South America, south-eastern Australia, and New Zealand (Alaback, 1991). Globally, temperate rainforests support a highly endemic and endangered biodiversity (Myers et al., 2000) and typically contain large trees (Waring & Franklin, 1979). Long-lived pioneer trees are a common feature of temperate rainforests and they often persist in the old-growth stage (Franklin & Hemstrom, 1981, Veblen *et al.*, 1981, Lusk & Smith, 1998, Gutiérrez *et al.*, 2009). Tree species characteristics may be due to similar factors that operate to varying degrees in temperate rainforests areas, such as environmental conditions, disturbance regimes, and land-use history (Keith et al., 2009). Significant areas of old-growth temperate rainforests remnants dominated by broadleaved evergreen tree species are found along the western coast of southern South America (37°45’-47°30’S, SSA, Veblen *et al.*, 1983, Armesto et al., 2009). In this region, old-growth forests can store up to 2200 t/ha in above-ground biomass (Schlegel & Donoso, 2008). Clearing of land for pastures, the pressure for wood production from natural forests and rapidly expanding forestry plantations of exotic tree species have degraded and increased old-growth forest losses (Lara *et al.*, 2003), and demand to enhance our understanding of old-growth forest remnants.

Old-growth temperate rainforests are commonly variable in terms of structure and composition (Franklin *et al.*, 2002, Gutiérrez *et al.*, 2009). This variability can be partly related to environmental differences between sites, successional age, forest management, and disturbance regimes (Ohmann & Spies, 1998, Franklin *et al.*, 2002). In temperate rainforests of Chile (37-43°S), only 50% of the variability in old-growth forest composition and structure can be attributed to environmental factors (Lusk, 1996, Gutiérrez *et al.*, 2009). Old-growth structural variability may be also an indication of multiple successional pathways to the old-growth stage (Glenn-Lewin & van der Maarel, 1992). We hypothesize that the unexplained structural variability of old temperate rainforests in Chile is related to different successional stages of forest stands and local variation (i.e. stand scale) in forest processes, such as demographic rates of tree species.

In this study, we used the forest model `FORMIND` to analyze the dynamics of 13 temperate rainforest stands previously described as old-growth forests on Chiloé Island, Chile. We parameterized the model for 11 species groups (representing 17 tree species) common to the main canopy of these forests. We examined how well the model reproduced forest stand characteristics based on current knowledge of forest processes in Chilean temperate rainforests. In doing so, we developed a new model parameterization to increase the applicability of the model over a variety of forest stands and a larger set of species. In an effort to gain further insight into ecological processes in temperate rainforest dynamics, we focused in the following questions: 1) How can the structural variability observed in old-growth forests of Chiloé Island be explained? and 2) Are the investigated old-growth forests at steady state?

MATERIAL AND METHODS

Study area

We studied old-growth temperate rainforests on northern Chiloé Island, Chile (42° S, Fig.1). The predominant topography of northern Chiloé Island is low elevation, rolling hills over highly organic postglacial soils (< 1 m deep), rising to low coastal mountains up to 600 m high. In rural landscapes old-growth forest stands are part of a mosaic of bogs, secondary forests, shrublands, plantations of exotic tree species, and artificial grasslands. The present rural landscape has been shaped by a recent history (< 200 years) of widespread use of fire and logging of many forest patches (Willson & Armesto, 1996). The prevailing climate is wet-temperate with a strong oceanic influence (di Castri & Hajek, 1976). Rainfall - about 2000 mm annually - occurs all year round, but 13-25% falls during summer (January-March). Mean annual temperature is 9-10.8º C, varying between coastal and inland sites (Gutiérrez et al., 2009).

Main forest types

Forests on Chiloé Island belong mainly to the North Patagonian and Valdivian forest types (Veblen *et al.*, 1983, Armesto *et al.*, 1996) with a mixed composition of broadleaved evergreen tree species (Table 1), depending on topography, elevation, soils, and distance to the Pacific Ocean coast (Holdgate, 1961, Gutiérrez *et al.*, 2009). The North Patagonian forest type is found predominantly on relatively poorly drained flat areas, in the south of the island (Fig. 1), and at elevations above 400 m on the coastal mountain range (Veblen *et al.*, 1983, Armesto *et al.*, 1996). North Patagonian forests support a canopy with mixed dominance of shade-tolerant conifers (Podocarpaceae, Table 1) and light-demanding *Nothofagus* spp. (Nothofagaceae) together with other evergreen tree species (Veblen *et al.*, 1983, Armesto *et al.*, 1996). In contrast, Valdivian rain forests are largely concentrated in northern and low-elevation sites (below 400 m), slopes facing the Pacific Ocean, and well-drained soils. Valdivian coastal forests are generally dominated by broadleaved evergreen tree species (Table 1), often lacking *Nothofagus* (Veblen *et al.*, 1983, Armesto *et al.*, 1996). In both forest types, tree trunks and branches are profusely covered with epiphytic plants and climbers (e.g. Hymenophyllaceae ferns and species of Gesneriaceae and Bromeliaceae). Shrubs and bamboo species (e.g. *Chusquea spp.*) are uncommon in undisturbed old-growth forests of the study area except along forest margins and on coastal cliffs (Gutiérrez et al., 2009).

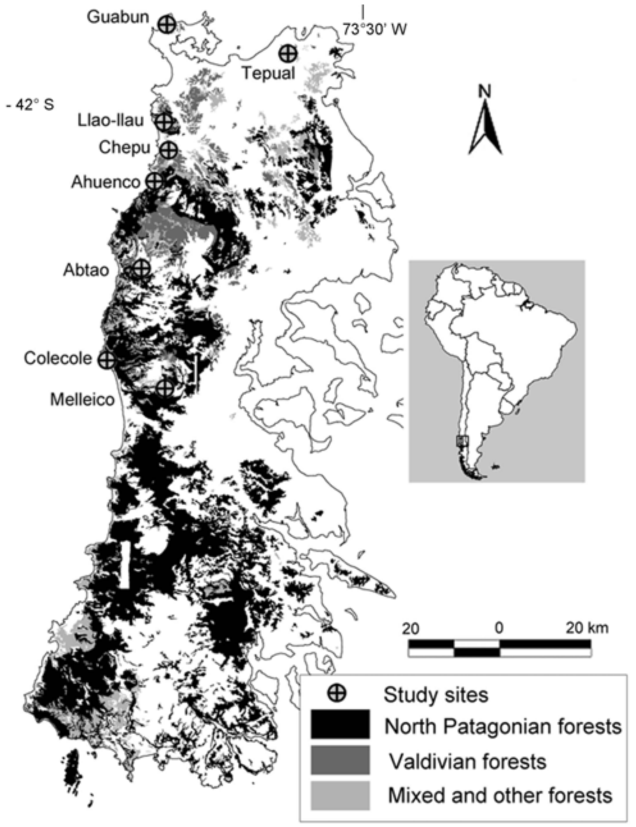

Figure 1. Study site locations (circles) and distribution of main forest types of temperate rainforests on northern Chiloé Island, Chile.

We focused on 11 species groups (Table 1) common to the Valdivian and North Patagonian forests on Chiloé Island. These species groups represent 17 main canopy tree species that are important to the composition, structure, functioning, and management of these forest ecosystems (Veblen *et al.*, 1983, Donoso, 1993, Armesto *et al.*, 1996).

The model

`FORMIND` is a forest growth model that simulates the spatial and temporal dynamics of uneven-aged mixed species forest stands (Köhler & Huth, 1998, Köhler, 2000). The model has been successfully applied to simulate dynamics in tropical (Köhler & Huth, 1998, Köhler *et al.*, 2000, Huth *et al.*, 2005, Groeneveld *et al.*, 2009) and temperate rainforest ecosystems (Rüger et al., 2007). The model simulates forest dynamics as a mosaic of interacting forest patches of 20 m × 20 m, which is the approximate crown size of a large mature tree. Within these patches, forest dynamics are driven by tree competition for light and space following the gap model approach (Shugart, 1984, Botkin, 1993, Pretzsch, 2009). The model is individual-oriented, i.e. light availability is considered to be the main driver of individual tree growth (Pacala et al., 1994). The competition for light is modeled by dividing each patch vertically into height layers. In each height layer the leaf area is summed up and the light climate in the forest interior is calculated via a light extinction law. The carbon balance of each individual tree is modeled explicitly, including the main physiological processes (photosynthesis, respiration). Growth process equations are modified from the models `FORMIX3` and `FORMIX3-Q` (Huth & Ditzer, 2000, Huth & Ditzer, 2001, Rüger *et al.*, 2007).

Table 1. Life-history attributes of species groups and their correspondence with species names. N: North Patagonian, V: Valdivian

Species groups	**Species names**	**Family**	**Shade tolerance**	**Life-span** (years)	**Max. height** (m)	**Max dbh** (cm)	**Forest type¶**	
							N	**V**
Aextoxicon	*Aextoxicon punctatum*	Aextoxicaceae	Tolerant	480*	35	136		x
Amomyrtus	*Amomyrtus luma, A. meli*	Myrtaceae	Tolerant	200*	22	135	x	x
Drimys	*Drimys winteri*	Winteraceae	Intolerant	250	30	104	x	x
Eucryphia	*Eucryphia cordifolia*	Cunoniaceae	Intolerant	650	38	200	x	x
Laureliopsis	*Laureliopsis philippiana*	Monimiaceae	Tolerant	657	34	121	x	x
Luma	*Luma apiculata*	Myrtaceae	Intermediate	400*	27	84		x
Myrceugenia	*Myrceugenia ovata, M. parviflora, M. planipes, M. chrysocarpa*	Myrtaceae	Tolerant	260	22	60	x	x
Nothofagus	*Nothofagus nitida, N. dombeyi*	Nothofagaceae	Intolerant	600	35	126	x	x
Podocarps	*Podocarpus nubigena* *Saxegothaea conspicua*	Podocarpaceae	Tolerant	750	27	102	x	
Tepualia	*Tepualia stipularis*	Myrtaceae	Intermediate	n.d.	15	75	x	
Weinmannia	*Weinmannia trichosperma*	Cunoniaceae	Intolerant	730	34	197	x	x

* for these tree species there is a high probability that the maximum published ages underestimate potential lifespan. n.d.: no data available. ¶ after Veblen et al. (1983) and Gutiérrez et al. (2009).

Allometric functions and geometrical relations are used to calculate above-ground biomass, tree height, crown diameter, and stem volume from the dbh (stem diameter at 1.3 m height) of the tree. Tree mortality can occur either through self-thinning in densely populated patches, senescence, impact of large falling trees, slow tree growth, or external disturbances (e.g. wind throws). Gap formation links neighbouring patches by allowing large falling trees to damage trees in neighbouring patches. Tree regeneration rates are maximum rates of establishment of small trees at a dbh threshold of 1 cm, with seed loss through predation and seedling mortality being incorporated implicitly. These maximum rates are reduced by shading. Nutrient availability is considered to be homogeneous at the stand scale. Inter-annual variability in climatic conditions is not included in the model. A detailed description of the model can be found in Köhler (2000), and Rüger et al. (2007).

Model parameterization

The model was parameterized on the basis of values given in the literature and calibrated using field data on stand structure, tree growth, and tree allometry. The model parameters, their description, calibration method and selected values are summarized in Table 2 and Table S1 (*Supporting information*).

Environmental parameters. – We used meteorological data collected during the growing season (September until March) from the *Senda Darwin* station (41°52'S, 73°39'W, 60 m a.s.l., period 1996-2006) for calculating average irradiance above canopy, length of the daily photosynthetic active period, and the relative length of the season. The light extinction coefficient (k) was chosen according to standard values found in stands with large-stature canopies and in an intermediate or late-successional stage (Pierce & Running, 1988).

Tree geometry parameters. – Model parameters related to species' life-history attributes such as maximum height, maximum dbh, lifespan and shade-tolerance were obtained from the literature and from the available field data (Table 1). Parameters of crown-dbh relationship, crown depth factor, fraction of stem wood biomass were set according to Rüger et al. (2007). Leaf area index (*LAI*) differs significantly between tree species in Chilean temperate rainforests (Saldaña & Lusk, 2003). Therefore, we used a species-specific parameter for maximum leaf area index (L_{max}). L_{max} values for *Aextoxicon, Laureliopsis, Eucryphia* and *Nothofagus* followed Saldaña & Lusk (2003). The estimated L_{max} for *Weinmannia* was set according to the value reported for the New Zealand temperate rainforests species *Weinmannia racemosa* (White & Scott, 2006). We used foliage mass to derive the *LAI* of the other species groups where information was lacking. The *LAI* value was calculated by multiplying leaf lifespan, litter production, and specific leaf area (DeLucia *et al.*, 2002, Moser *et al.*, 2007) according to species estimates reported in the literature (Table S2). With the exception of *Aextoxicon*, this approach underestimated the value observed for tree species with a known *LAI* (Table S2). Therefore, estimated *LAI* values were taken as a reference and the L_{max} values were set taking into account the crown architecture and foliage characteristics of tree species. Information on foliage mass was lacking for *Tepualia stipularis* and *L. apiculata* and their L_{max} values were set according to the estimated *LAI* for *Myrceugenia* and *Amomyrtus* (all members of Myrtaceae).

Biomass production parameters. – The values for maximum rate of photosynthesis (p_{max}) followed values reported in the literature (Table 2). For *Amomyrtus* we used the shade-tolerant Myrtaceae value estimated by Rüger et al. (2007). The value for *Tepualia*, p_{max} was estimated according to tree species with similar shade tolerance. For *Weinmannia*, we used estimates for *Weinmannia racemosa* in New Zealand forests as a reference (Whitehead et al., 2005), but we chose a higher value because of its high demand for light. Species light-use efficiency (α) estimates were not available and were estimated according to species shade-tolerance following reported values (Eschenbach *et al.*, 1998, Carswell *et al.*, 2005). Accordingly, fast-growing pioneer tree species with a high maximum assimilation rate (up to 14.2 µmol $CO_2m^{-2}s^{-1}$) would have lower light-use efficiency ($\alpha \sim 0.03$-0.06) when irradiance is low. Shade-tolerant tree species with low assimilation rates (4.9-7.2 µmol CO_2 $m^{-2}s^{-1}$) would have higher ($\alpha > 0.05$) light-use efficiency (Eschenbach et al., 1998). For tree species with intermediate shade tolerance, we selected an intermediate value ($\alpha \sim 0.06$-0.13). These values were taken as a reference and were calibrated using observed tree growth data (see *Model calibration*). We assumed that 20% of the carbon produced by annual photosynthesis is used for the build-up of new biomass (Ryan, 1991). Wood density values followed Karsulovic *et al.* (2000) and Hall and Witte (1998). The transmission coefficient of leaves and the parameter for conversion of CO_2 into organic dry matter are from Larcher (2001).

Establishment and mortality parameters. – The species pool for each site was set according to observed species presence in North Patagonian and Valdivian forests following Tables 1 and 3. Minimum light intensity for establishment (I_{min}) followed Lusk et al. (2006, 2008) and maximum light intensity for establishment (I_{max}) were estimated according to the shade tolerance of tree species (Table 1). Small trees (dbh <10 cm) experience an additional mortality that strongly declines with increasing dbh (Coomes & Allen, 2007). Accordingly, we set the maximum mortality of small trees to 0.05 per year. A constant mortality rate was assumed for trees >10 cm dbh. To our knowledge, establishment rates and mortality rates of adult trees are not available for temperate rainforests in Chile, therefore these parameters were calibrated against field data (see *Model calibration*).

We included stress-induced mortality (Shugart, 1984, Bugmann, 1994) analogous to the size-related mortality of the model (cf. Rüger et al. 2007). This stress-induced mortality (m_{stress}) is based on the assumption that only a small fraction of trees will survive a given number of years when subjected to stress:

$$m_{stress} = \begin{cases} m_{sup}, & Yrs_{sup} > MaxYrs_{sup} \\ 0 & \text{else} \end{cases}$$

where m_{sup} is the probability of mortality of slow growing trees, Yrs_{sup} is the number of consecutive years the tree has survived under suppression (i.e. radial increment <0.1 cm/years), and $MaxYrs_{sup}$ is the maximum number of years recorded under suppression for a given tree species. Stress-induced mortality is added to basic and size-dependent mortality. The m_{sup} was set to 2% according to Wyckoff and Clark (2002), and $MaxYrs_{sup}$ was determined from tree-ring datasets from the study area (Table S3). *Luma apiculata* and *Tepualia stipularis* lacked information on $MaxYrs_{sup}$ and their values were estimated by personal observations of the authors. Minimum dbh of falling trees followed values reported in the literature (Table 2) and the probability of dying trees falling followed Rüger et al. (2007).

Disturbances. – Several studies have documented the disturbance regime on Chiloé Island (Veblen *et al.*, 1981, Veblen, 1985, Armesto & Fuentes, 1988, Gutiérrez *et al.*, 2004, Gutiérrez *et al.*, 2008). According to these studies, the disturbance regime is dominated by frequent, low-intensity disturbances (i.e. gap-phase dynamics, <500 m^2), with sporadic large canopy openings (> 1000 m^2), produced by multiple tree falls. Presumably, large canopy openings are caused by infrequent but severe wind storms but are infrequent and spatially confined to specific areas of the forests. Occasional wind throw events creating canopy openings (800–1600 m^2) were modeled by removing all trees in an area comprising 2–4 neighbouring patches. Disturbance size (i.e. 2, 3, or 4 patches) is drawn from a uniform distribution. We conducted experiments to compare forest succession given different windstorms frequencies ($Dist_f$). First, we assumed that the probability that a certain hectare is affected by wind throw is 0.8% per year (Rüger et al., 2007). Then, we conducted experiments without windstorms ($Dist_f = 0$ per year) and with a higher windstorm disturbance frequency ($Dist_f = 1.6\%$ per year). We assessed the simulation results as described below (*Model calibration*).

Model calibration

Parameters with no available data for the species studied or those that strongly influenced model results were subjected to parameter calibration (Table 2) with optimization techniques and local sensitivity tests. We conducted this calibration comparing model outputs with available field data at (1) individual, (2) species, and (3) community level.

Individual level. – Allometric parameters for tree geometry were determined using field data obtained from forest stand inventories (Table 2). We conducted a non-linear minimization of a likelihood algorithm (Dennis & Schnabel, 1983) to obtain estimates of allometric function parameters (e.g. dbh - height, Fig. S1). We adjusted the form factor such that simulated stem volume corresponded to empirical volume functions available in the literature (Table 2, Fig. S2).

We fitted parameters of maintenance respiration (r_0, r_1, r_2) such that simulated stem diameter increments of trees under full light conditions generated an upper envelope for the measured diameter increments of trees (Fig. S3). For this analysis, we selected trees cored in the study area (Table S3) growing under high light conditions (i.e. fast-growing trees in forest edges, outside forests, and inside canopy gaps). Calibration was conducted, first by using a genetic algorithm (Rüger et al., 2007) and second by visual inspection of diameter increment simulations. Annual diameter increment was approximated by multiplying tree ring width by two.

Table 2. Parameter descriptions and parameterization method used for selecting parameters. *Method: (1) estimated, (2) field data, (3) literature, (4) calibrated with field data, (5) calibrated using literature. Full list of parameters used in the model and references are given in Table S1.

	Description	Units	*		Description	Units	*
Biomass production				**Environment**			
p_{max}	Maximum rate of photosynthesis	µmol(CO$_2$) m^{-2} s^{-1}	3, 5	k	Light extinction coefficient for leaves	m^2 m^{-2}	3
α	Light-use efficiency	µmol(CO$_2$) µmol(photons)$^{-1}$	1	I_o	Average irradiance above canopy	µmol (photons) m^{-2} s^{-1}	2
r_g	Growth respiration	-	3	Sd	Length of daily photosynthetic active period	hours	2
r_0, r_1, r_2	Maintenance respiration	-	4	$seal$	Relative length of seasons (wet/dry)	year	2
ρ	Wood density	t m^{-3}	3	**Mortality**			
m	Light transmission coefficient of leaves	-	3	m_B	Basic mortality	years^{-1}	4
$codm$	Conversion of carbon in organic dry matter	t µmol(CO$_2$)$^{-1}$	3	m_{max}	Maximum mortality of small trees	years^{-1}	3
Establishment				D_{mort}	dbh up to which mortality is increased	m	3
N_{max}	Maximum establishment rates of small trees	N ha^{-1} years^{-1}	4	D_{fall}	Minimum dbh of falling trees	m	2, 3
I_{min}	Minimum light intensity	% of I_o	5	p_{fall}	Probability of dying trees to fall per year	-	1
I_{max}	Maximum light intensity	% of I_o	1	m_{sup}	Mortality of slow growing trees	years^{-1}	3
Tree geometry				$MaxYrs_{sup}$	Maximum number of years under suppression	years	1, 2
D_{max}	Maximum dbh diameter	m	2	**Disturbances**			
H_{max}	Maximum height	m	2, 3	$Dist_f$	Proportion of years in which windstorm disturbance occurs	years^{-1}	1
h_0	dbh-height relationship	cm m^{-1}	4	**Technical**			
h_1	dbh-height relationship	m	4	D_s	Diameter of ingrowing trees	m	3
f	Form factor		5	a	Patch size	m^2	3
cd	dbh-crown diameter relationship	m cm^{-1}	1	Δh	Step width of vertical layering	m	3
c	Crown depth factor		1				
sw	Fraction of stem biomass to total wood biomass		1				
L_{max}	Maximum *LAI*		5				

Species and community level. – For testing model outputs we selected forest stands previously identified in the literature as old-growth forests on northern Chiloé Island (e.g. stand ages >170 years, containing trees >300 years old, N=13, Table 3). All stands used for this analysis were sampled using a similar sampling design, i.e. plots of 0.1 to 0.5 ha where all stems (dbh > 5 cm) found in the plot were identified according to species and their dbh was recorded. We ran

Table 3. Forests selected in Chiloé Island (Chile) to test model outputs

Stand[†]	Forest type	Sampling area (ha)	Drainage	Slope (%)	Altitude (m.a.s.l.)	Oldest tree (years)	Estimated successional age (years)[¶]	Old-growth index[¶]	Similarity[γ]	Basal area[¢]	P	Density[¢]	P
ABTAO	NP	0.1	good	14	540	399	>450	1.6	0.66	0.99	***	0.56	0.08
AHUENCO	V	0.4	good	flat	80	308	300	0.5	0.82	0.98	***	0.71	*
CHEPU1	V	0.4	poor	flat	40	no data	>450	1.9	0.7	0.99	***	0.63	*
CHEPU2	V	0.4	poor	0-10	80	no data	>500	1.8	0.97	0.99	***	0.95	***
CHEPU3	V	0.4	poor	flat	120	no data	>450	1.4	0.91	0.99	***	0.88	***
CHEPU4	V	0.4	poor	0-5	120	no data	250	0.4	0.85	0.99	***	0.79	***
COLE-COLE	V	0.1	good	30	80	no data	>400	1.6	0.94	0.99	***	0.9	***
GUABUN	V	0.4	good	flat	130	349	540	0.6	0.92	0.97	***	0.87	***
LLAOLLAU1	V	0.4	good	flat	150	no data	350	0.5	0.95	0.99	***	0.94	***
LLAOLLAU2	V	0.4	poor	flat	150	no data	360	0.6	0.85	0.99	***	0.81	***
LLAOLLAU3	V	0.4	good	18 - 40	150	no data	350	0.5	0.82	0.96	***	0.75	***
MELLEICO	V	0.5	good	20-40	280	307	>350	1.6	0.91	0.99	***	0.87	***
TEPUAL	NP	0.2	poor	flat	70	499	>450	1.2	0.96	0.99	***	0.95	***

[†] References: Donoso *et al*. (1984, 1985), Gutiérrez *et al*. (2009). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. NP: North Patagonian, V: Valdivian forest type. [¶] 20 model simulations of each stand (average value, see Materials and Methods). [γ] Morisita-Horn index of similarity. [¢] Pearson correlations between observed data and simulated results.

simulations of 25 ha (i.e. 625 patches of 400 m²) and results were subsequently averaged every 50 years. All model simulations were started from bare ground, assuming that succession had started after a stand-replacing disturbance. To allow the model to reach dynamic equilibrium, we ran simulations to exceed the longest possible lifespan of any of the potential dominant tree species in the study area (Table 1). This required simulations of forest succession for periods covering 1500 years, similar to simulation runs conducted for temperate rainforests elsewhere (Hall & Hollinger, 2000, Busing *et al.*, 2007).

We first compared observed values of total basal area (community level) with model outputs for the validation of simulated total basal area. Then we conducted a systematic comparison (Wiegand et al., 2003) to calibrate the stand-specific parameters of establishment and basic mortality rate (N_{max} and m_B) using the patterns observed in the field and the patterns predicted by the model (species level). Because shade-intolerant species would represent the time elapsed after the occurrence of a stand-replacing disturbance (Molino & Sabatier, 2001), their dominance through the succession can be assumed to be an estimator of the successional age of the forest stand. For estimating stand successional age, we used the basal area of shade-intolerant tree species as the observed pattern (*BAobs*). We ran simulations where establishment rate and basic mortality (N_{max} and m_B) were simultaneously varied, and assessed model performance by systematically comparing species-level basal area of shade-intolerant tree species of the simulated forest (*BAsim*) through the simulated succession. We determined the best match by minimizing the error ε:

$$\varepsilon(t)=\sum_{i=1}^{\text{int}}\frac{\left|BAsim_i(t)-BAobs_i(t)\right|}{BAobs_i(t)}$$

where *i* indicates the shade-intolerant species under analysis and *int* the number of shade-intolerant species in the stand. We defined the estimated successional age of the stand as the time when the simulated pattern best approximated (minimum ε found) the observed pattern of each forest stand. Using this procedure of parameter adjustment would eliminate N_{max} and m_B sets that do not reflect an overall successional trend in the stands observed and would, in this way, distinguish between probable (''small'' ε) and improbable (''large'' ε) parameter sets (Wiegand et al., 2003). Model predictions for species lifespan and diameter increments were also checked for correspondence with the observed data. We used the Morisita-Horn index of similarity (Horn, 1966) to evaluate the forest composition similarity at the estimated successional age of simulated and observed stands. Pearson correlations were used to evaluate the agreement between observed and simulated community structure (basal area and density) at the estimated successional age of stands.

Old-growth stage evaluation

We tested the hypothesis that the focal stands were at steady state by determining whether they had entered the successional stage in which forests have stable composition, structure (basal area and density), and biomass over long time periods (Franklin & Spies, 1991). We developed an old-growth index (*OGI*) that can be expressed as:

$$OGI = \frac{SAGE}{TES}$$

where *SAGE* is the predicted successional age of the forest stand (in years) and *TES* is the predicted time taken to reach stability (in years). Thus, $OGI < 1$ represent forests that have not reached the steady state while $OGI > 1$ characterizes old-growth forests in a steady state. We estimated the *SAGE* of each stand as above (*Model calibration*), but using the calibrated N_{max} and m_B sets of each stand studied. Simulations were run under a windstorms frequency ($Dist_f$) of 0.8 % per year because under this windstorm frequency the simulated pattern best approximated (minimum ε found) the observed pattern of each forest stand. In order to determine *TES*, we simultaneously analyzed the simulated density, basal area and biomass at the community and species level through the simulated succession of each stand. We compared the absolute difference (Δ_t) of these variables at times t and $t+1$ with the standard deviation (σ) of the simulated variables at steady state (i.e. years 1000-1500). When $\Delta_t < \sigma$, we considered that the variable was stabilized at the time t. *TES* was then determined as the earliest time t when all analyzed variables were simultaneously stabilized ($\Delta_t < \sigma$). We ran 20 simulations of 25 ha for each stand with different random number seeds and the results of each simulation were subsequently averaged every 50 years. The starting point for all model simulations was bare ground, assuming that succession started after a stand-replacing disturbance, and all models were run for 1500 years of succession. We averaged the predicted *SAGE* and *TES* values because results may vary from one run to the next due to stochastic variation of simulated dynamics.

RESULTS

Stand structural variability and model performance

The variability in stand structure and composition of the forest stands studied was illustrated by the observed range of variation in total basal areas (54.7 to 115.5 m²/ha) and total density (871-2100 trees/ha, Fig. 2). Stands also varied in terms of forest composition, with some forests dominated in terms of basal area by *Eucryphia cordifolia* while others were dominated by *Laureliopsis philippiana* or Myrtaceae tree species (Fig. 2). Most of the stands studied were dominated in terms of density by *Amomyrtus* species and other Myrtaceae tree species (*Tepualia stipularis*, *Myrceugenia spp.*), but *L. philippiana* and Podacarpaceae tree species were also important (Fig. 2).

Estimated successional age was >250 years and varied among stands (Table 3). At the estimated successional age of simulated forest stands and under windstorm frequencies of 0.8% per year, similarity in species composition ranged from 66 to 97% (Fig. 3, Table 3). Pearson correlations of observed vs. simulated species basal areas was >96% (P <0.001, Table 3). The model produced some overestimation of simulated density of tree species (Fig. 3b) but it was mainly concentrated in trees with dbh <15 cm. With the exception of Abtao, we found significant correlations >63% between observed and simulated species density ($P < 0.05$, Table 3).

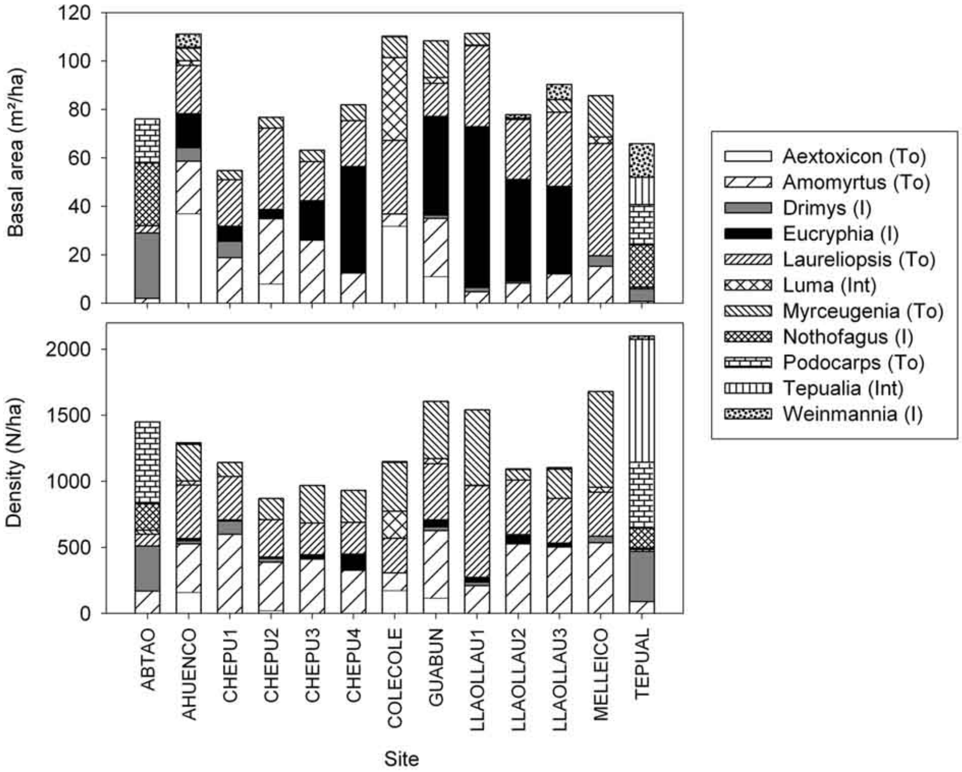

Figure 2. Basal area and density (field data) of studied forest stands on northern Chiloé Island, Chile (trees >5 cm dbh). Shade tolerance is indicated in brackets in the legend according to Table 1. To: tolerant, I: intolerant, Int: intermediate.

Variability of forest attributes for both total basal areas and densities decreased with increasing spatial scale of simulations (Fig. 4). In general, total basal area and density values indicated in field inventories were in the range of variation predicted by the model at the spatial scale of their respective sampling plot. Total basal area varied between 40 and 92 m²/ha, and total density varied between 781 and 3344 trees/ha among stands for a spatial scale of 0.64 ha. For the forests with the best simulated results (e.g. Fig. 4a-c), the observed data agreed with the median of simulation results at all spatial scales (0.04 to 1 ha). In some stands (e.g. Fig. 4d-f) the observed value was close to the extreme value of simulations or represented possible simulated outliers at the field sampling scale.

General patterns of forest succession

The model predicted varied successional pathways for reproducing the observed structural variability of forests studied on Chiloé Island (Fig. 5). Successional patterns simulated for podocarp-broadleaved mixed forests (e.g. Fig. 5a, S4) showed the dominance of *Drimys* and

Nothofagus in the early successional stage. *Drimys* decreased in dominance after 250 years because of its short lifespan, but persisted because of canopy openings produced by the death of large emergent *Nothofagus*. After the death of the first cohorts of pioneers (after 250 - 500 years of succession), Podocarps and *Tepualia* increased in dominance. The pioneer *Weinmannia* was not able to dominate, but it was able to persist in the late succession because of its long lifespan (Fig. 5a). *Nothofagus* persisted in the late-succession of the stand.

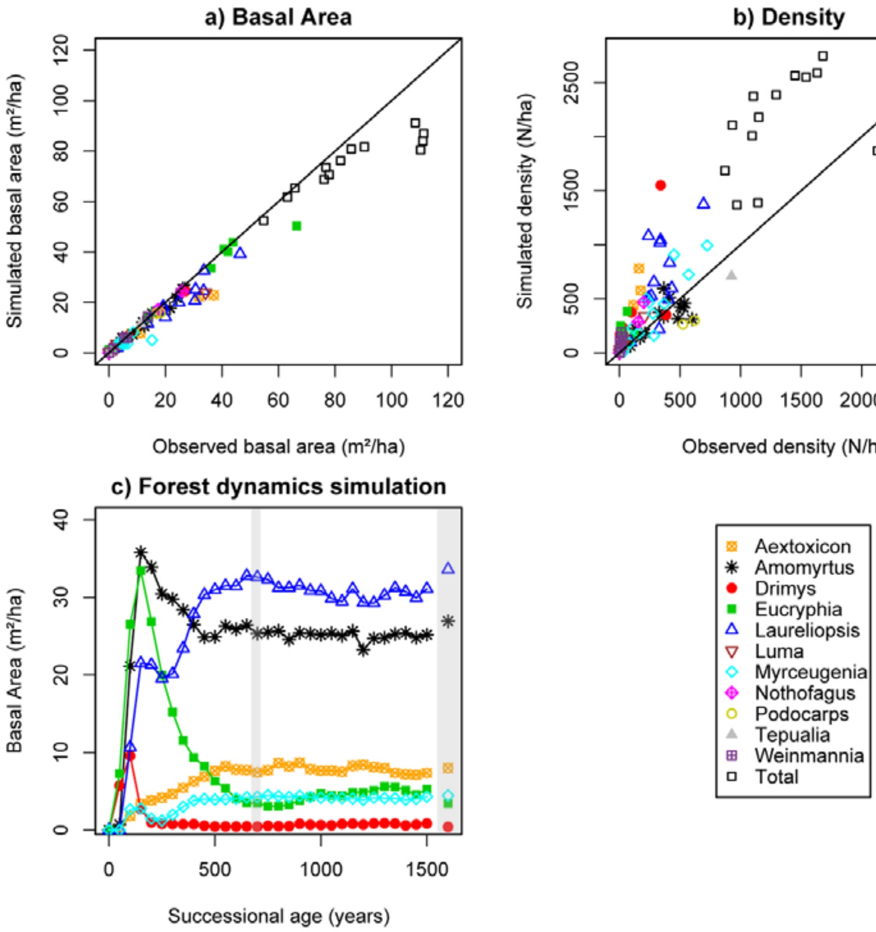

Figure 3. a-b) Comparison of structural patterns observed in field and model predictions (trees >5 cm dbh at the estimated successional age of each stand). **c)** Example of simulated forest dynamics following a large-scale disturbance in one of the studied stands (Chepu2). The grey bar illustrates how the successional age of the simulated stand was obtained by matching the field data (grey bars on the right side of the chart) with predicted forest succession. Species groups names according to Table 1.

A different successional pattern was predicted by the model for coastal sites (Fig. 5b-c), the presence of the long-lived pioneer *Eucryphia* and the shade-tolerant *Aextoxicon*. In some coastal forests (Fig. 5b, Guabun in Fig. S4), *Drimys* and *Eucryphia* dominated the first 250 years of succession until *Aextoxicon* and other shade-tolerant species (*Laureliopsis*, *Amomyrtus*) took over the canopy and dominated the stand after 500 to 800 years of succession. In other coastal forest, *Luma* (intermediate shade-tolerance, Fig. 5c) dominated the stand after 300 years of succession, sharing canopy dominance with the shade-tolerants *Aextoxicon* and *Laureliopsis* in the late succession. At Chepu (Fig. 5d, S4), the model predicted the rapid establishment of *Eucryphia* and

Amomyrtus in the early succession (<200 years of succession). In several forest stands the pioneer *Eucryphia* persisted in the late succession (>500 years of succession, Fig. 5, S4) sharing canopy dominance with the shade-tolerant species.

The pattern-oriented calibration of stand-specific establishment and mortality parameters (N_{max} and m_B) revealed a wide variation in parameter values for some species groups (e.g. *Myrceugenia*, *Drimys*, *Laureliopsis*, Fig. 6). At Colecole, low establishment and high mortality rates for pioneer species at this site were needed in order to reproduce the observed pattern. At the Melleico, Llaollau and Chepu sites an increased establishment rate for *Laureliopsis* and *Amomyrtus* compared to coastal sites determined their dominance in the late succession. Additionally, a low establishment rate was imposed at these sites for *Eucryphia* in order to reduce its chances of being present, as was indicated by field data (Fig. 2).

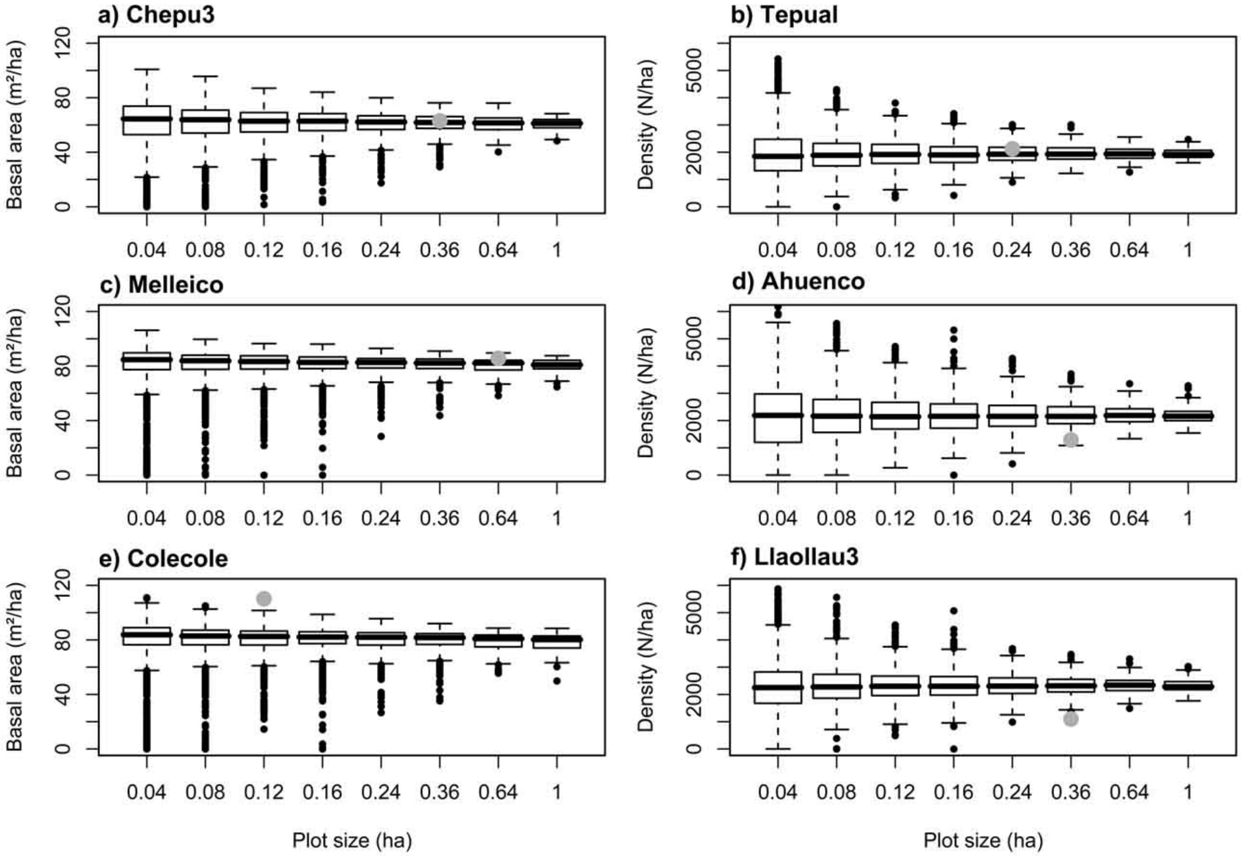

Figure 4. Simulation results at different spatial scales (plot size) of total basal area and total density for selected old-growth stands located in northern Chiloé Island. Runs are for 100 ha and results are presented as samplings plots of different sizes (0.04 – 1 ha, note not linear categories on x-axis). Simulations results were obtained at the estimated successional ages of stands (see Table 3). Selected stands represent those with **a-c)** the best matches, and **d-f)** the highest departures between simulated and observed data. Inventory data from each study site are depicted by the grey dots at a spatial scale used in the field sampling. The boundary of the box indicates the 25th and 75th percentile, the line within the box marks the median (50th percentile) of the data. Points above and below the box indicate possible outliers.

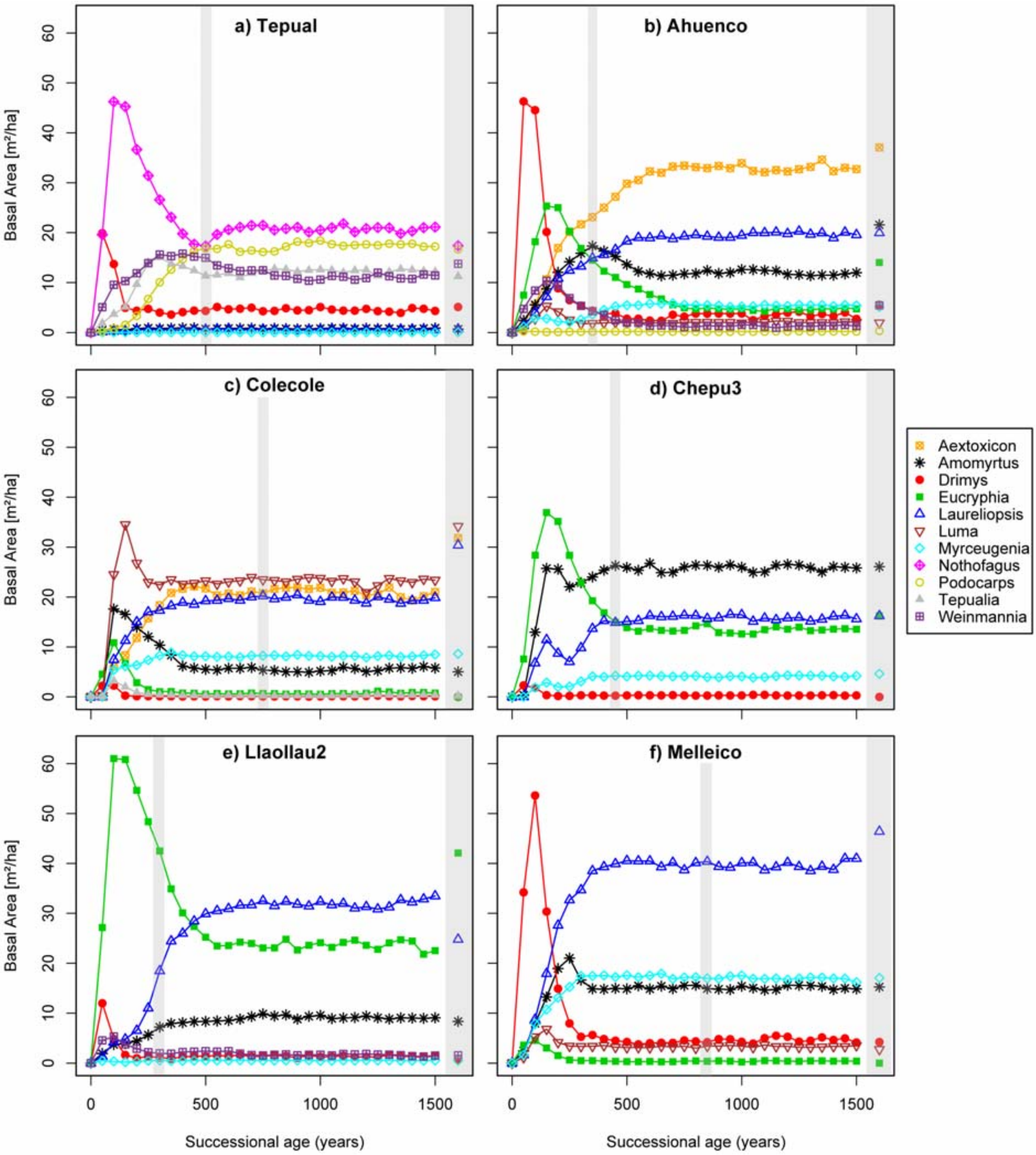

Figure 5. Forest dynamics simulation following a stand-replacing event for forest stands located in northern Chiloé Island, Chile. Simulations were run for 25 ha and 1500 years, results are presented as the running mean over a 50-year period. The grey bars indicate the best agreement obtained with field data at the successional age of simulated stands (see methods). Inventory data from each study site are shown in the grey bars on the right side of each chart. Species groups names according to Table 1.

Effects of disturbance frequency

Canopy openings of 800 to 1600 m^2 produced by windstorms were required to reproduce the structure of the forests studied. Simulated patterns best approximated (minimum ε found) the observed pattern of each forest stand under windstorm frequencies of 0.8% per year (Fig. 2, 3, 7a). The model predicted that tree species composition differed in simulated late-successional forest stands (i.e. after 1500 years) when windstorm disturbances were excluded (Fig. 7b). Simulated

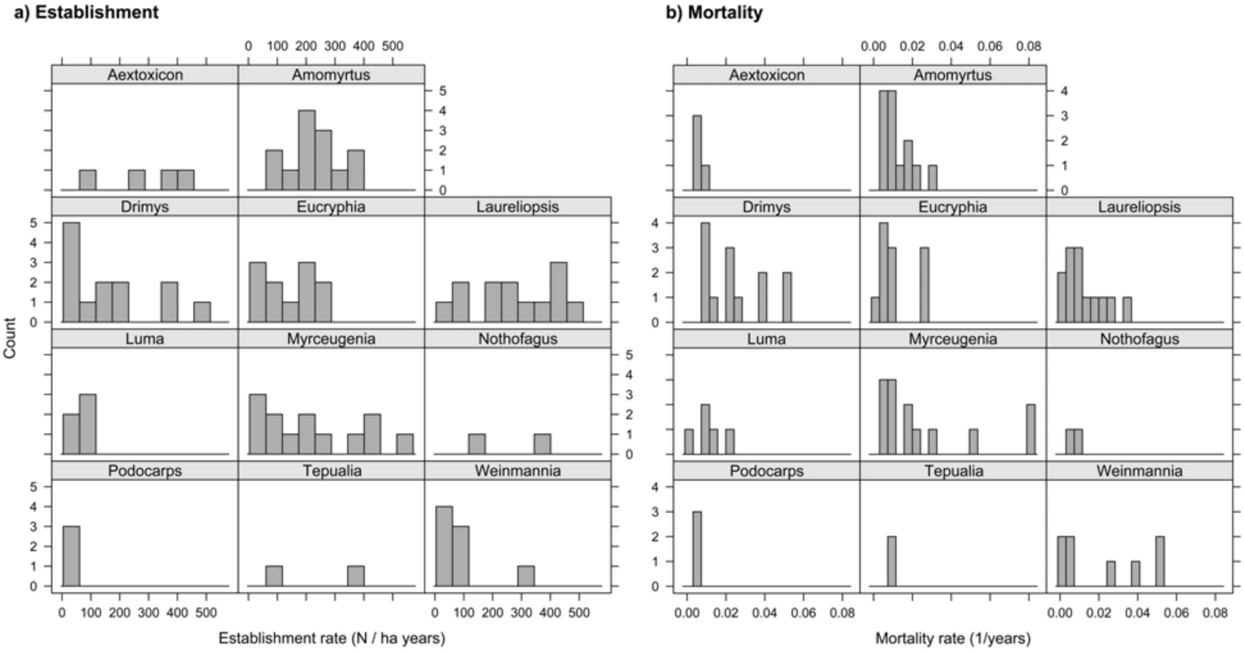

Figure 6. Histograms of **a)** Maximum establishment rate of small trees (N_{max}) and **b)** Basic mortality rate (m_B) parameters selected for reproducing stand structure and composition in 13 forest stands located in northern Chiloé Island. Species groups names according to Table 1.

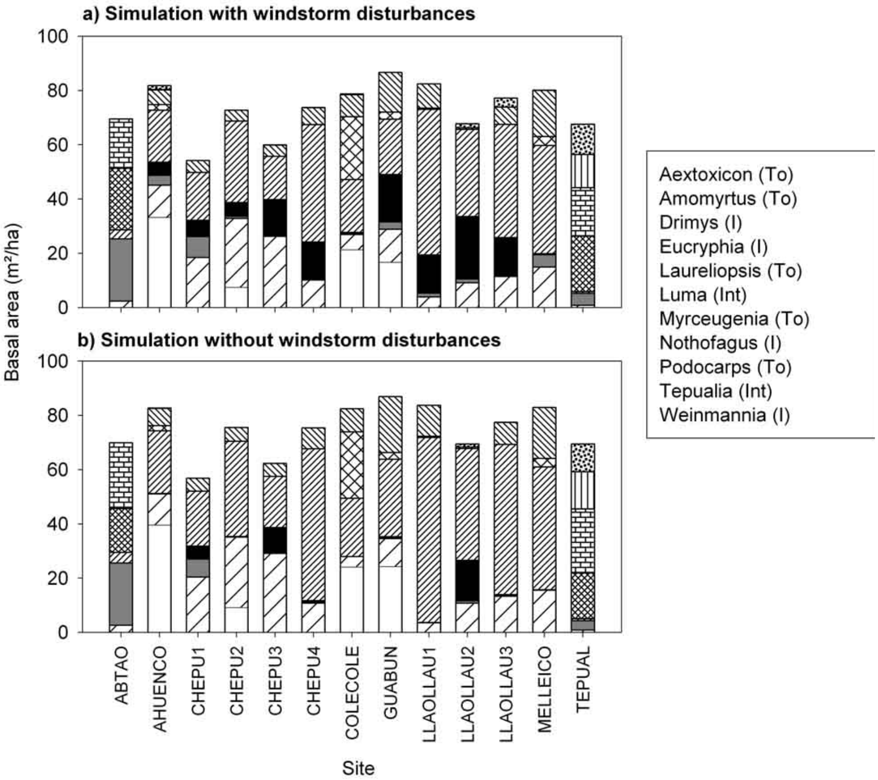

Figure 7. a) Simulated basal area at successional ages of stands (see methods) with a disturbance frequency of 0.8 % per year. **b)** Simulated basal area after 1500 years of succession with a disturbance frequency of 0 % per year. Species groups names according to Table 1. Shade-tolerance is indicated in brackets in the legend according to Table 1. To: tolerant, I: intolerant, Int: intermediate.

stands differed slightly in late-successional composition when the windstorm disturbance frequency was varied from 0.8 to 1.6% (data not shown). In simulations without windstorm disturbances the short-lived pioneer *Drimys* tended to disappear in most Valdivian forests (Fig. 7b). Shade-tolerant species increased in dominance with decreasing disturbance frequency. Intermediate species were unresponsive to changes in windstorm disturbance frequency (Fig. 7b). Some pioneers (e.g. *Eucryphia, Weinmannia, Nothofagus*) decreased in basal area with decreasing windstorm disturbance frequency, but they were able to persist in some of the simulated forest stands without the influence of windstorm disturbances (Fig. 7). Under a disturbance regime without windstorms, pioneer species could reach simulated biomass of up to 250 t/ha in those stands where they attained higher maximum sizes (height and dbh) and longer lifespans than shade-tolerant and intermediate species (data not shown).

Old-growth stage assessment

Model simulations showed that, on average, forest stands reached stability after 500 to 850 years of succession (625 ± 141 years, mean ± standard deviation). Simulated total biomass decreased with increasing old-growth index of the forest stands studied ($P < 0.001$, Fig. 8a). Several studied stands ($N = 6$) had old-growth index <1 indicating that they have not reached stability (Table 3, Fig. 8b). Estimated successional ages for stands with $OGI < 1$ were 250 to 550 years whereas stands with $OGI > 1$ had minimum successional ages >350 years (Table 3). Observed total basal area of stands decreased with increasing *OGI* ($P < 0.05$, Fig. 8c). As expected from our calibration method, the *OGI* decreased linearly with the observed basal area of pioneers ($OGI = -0.02\ BAobs + 1.68$, $F_{(1, 11)} = 14.14$, $r^2 = 0.38$, $P < 0.05$, Fig. 8d).

DISCUSSION

Old-growth stage assessment

Our study provides an example of how forest models can be applied to assess the degree of stability in community structure and the functioning of old-growth forests. Here we propose a method for identifying successional stages based on field data (basal area of pioneer trees, Fig. 8d) and predict the time needed by forests to reach the steady state. This successional criterion can be complemented by other structural and/or biochemical criteria (e.g. Wirth et al. 2009).

According to our analysis, around half of the forests studied on Chiloé Island (6 out of 13 stands) already considered in the literature as old-growth represent a transient successional stage. Biomass tends to decrease as forests approach steady-state (Fig. 8a), potentially resulting in carbon losses. Biomass decline with successional age would result from the death of massive trees of pioneer species, which are replaced by smaller late-successional trees (e.g. *Eucryphia* trees with tree stem volumes >30 m^3 replaced by *Laureliopsis* with tree stem volumes <15 m^3, Fig. S2). This result support the idea that many old-growth forests are not at equilibrium (Luyssaert *et al.*, 2008). In these stands carbon losses may also occur in the future as a consequence of major disturbances (e.g. fires, logging). Our study also suggests that some old-growth forests in Chiloé have reached steady state, a process that can take between 500 and 850 years in this region. It is reasonable to expect future compositional and functional change in these steady-state forests, mainly due to the potential impact of climate change on tree species demographic rates (van Mantgem et al., 2009) and human activities.

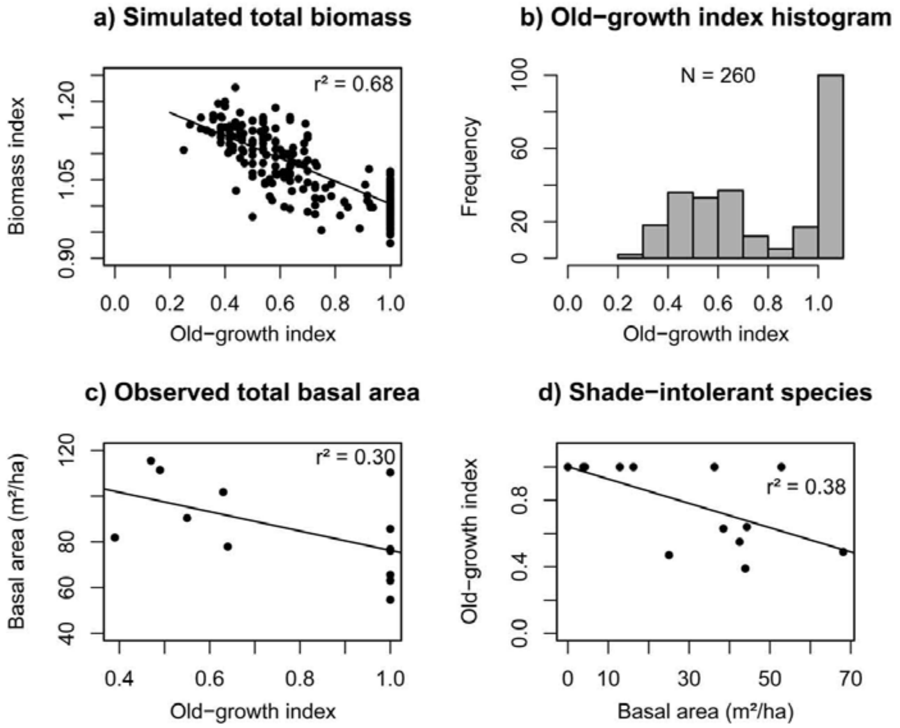

Figure 8. Structural attributes related to the old-growth index (*OGI*, see methods for details) of studied forest stands in northern Chiloé Island, Chile. **a)** Total biomass related to *OGI*. Biomass index is the proportion between total biomass at successional age and total biomass after 1500 years of succession (20 simulations per stand, N = 260); **b)** histogram of old-growth index values obtained after 20 simulations of studied stands (right bar corresponds to *OGI* >1.0), **c)** observed total basal (field data) related to *OGI*, **d)** *OGI* related to observed basal area of shade-intolerant species (BAobs, field data, shade-tolerance according to Table 1). r^2 is the correlation coefficient of the adjusted linear regression model ($p < 0.05$, lines).

Successional pathways and variability of old-growth forests

The model reproduced the observed variability in structure and composition of varied forest stands on Chiloé Island. Main trends of successional dynamics in temperate rainforests of Chile were captured by the model according to current knowledge of tree species and forest dynamics (Veblen *et al.*, 1981, Donoso, 1993, Armesto *et al.*, 1996, Smith-Ramirez *et al.*, 2005, Donoso, 2006). Our results confirmed the importance of canopy openings (i.e. <1.6 ha) produced by occasional windthrow events for the persistence of pioneer tree species in old-growth forests of Chiloé (Veblen, 1985, Gutiérrez *et al.*, 2008).

In temperate rainforests, successional pathways vary according to the tree species pool present at each site, soil conditions, and local distinctive disturbance histories (Franklin *et al.*, 1991, Bugmann & Solomon, 2000, Hall & Hollinger, 2000, Busing *et al.*, 2007). The variety of simulated successional pathways in our study mimic those observed in these studies. In our simulations, windstorm frequencies were kept similar across all sites. Species performance at different sites could be also related with variation in tree growth, which was kept constant for each species group among sites in our simulations. The reasonable match between simulated and observed forest structure in our simulations (Fig. 3, Table 3) suggest that environmental effects on tree growth may only be important at a larger spatial scales than those taken for our analysis (e.g. regional scale). Other studies have shown that changes in recruitment and mortality rates can strongly affect forest composition and dynamics in forests elsewhere (Kobe *et al.*, 1995, Pacala *et al.*, 1996, Wyckoff & Clark, 2002). We propose that multiple successional pathways to the old-growth stage in Chiloé (Fig. 5, S4) are related to autogenic successional mechanisms driven by demographic rates (mortality and establishment) and competition among tree species.

We suggest that variation in soil moisture at stand scale (<50 ha) is the strongest factor impacting the demographic rates of tree species and explaining structural variability of old-growth forests in Chiloé. For example, simulated successional patterns at Chepu and Colecole agreed with field observations that soil drainage may modify the establishment of tree species and potentially alter succession at these sites and elsewhere in Chiloé (Donoso, 1993). Structural and compositional changes can be observed at stand scale in Guabun and Ahuenco in relation to soil drainage (see also *Supporting information*). Similar to temperate rainforests elsewhere, other environmental factors, such as climate, may play a role in the observed variability in forest composition at regional spatial scale in the temperate rainforests of Chile (Ohmann & Spies, 1998). However, according to forest inventories in the north of Chiloé Island (Gutiérrez et al., 2009), only part (*c.* 50%) of the observed structural and compositional variability of old-growth forests can be explained by regional environmental factors (e.g. temperature, elevation, distance to the Pacific Ocean coast). These observations and our model simulations suggest that changes in demographic rates of tree species due to *local* environmental site characteristics (e.g. excessive soil moisture) would explain the high variability in structure and composition of the forests investigated.

Interactions of species with different traits, such as shade tolerance, tree size and lifespan (Table 1) with the predominant disturbance regime in this region provide a basis for simplifying the understanding of species-rich forest dynamics. In our study, species lifespans are not considered explicitly as inputs, therefore, differences in tree species lifespan emerged in our simulations because of their ability to persist under suppression ($MaxYrs_{sup}$, obtained from tree-ring records, Table S3). For pioneer tree species, a long residence time would increase the likelihood of persistence by increasing the probability of a new canopy gap opening nearby, where these species could regenerate. The long residence time predicted in our study (*c.* 500 years on average) for the initial cohort of pioneer trees in forests of Chiloé (e.g. *Nothofagus*, *Eucryphia*, *Weinmannia,* Fig. 5) was in agreement with estimated residence time in the canopy of tree species in temperate rainforests elsewhere (Lertzman *et al.*, 1996, Lusk & Smith, 1998). Accordingly, conifer pioneer trees >1000 years old are commonly found in all temperate rainforests regions of the world (Waring & Franklin, 1979, Franklin & Hemstrom, 1981, Lusk & Ogden, 1992, Lara & Villalba, 1993, Lusk & Smith, 1998). Long-lived broadleaved pioneers >450 years old also occur elsewhere in temperate rainforests of southern South America, south-eastern Australia and New Zealand (Stewart & Rose, 1990, Lara, 1991, Lusk, 1999, Keith *et al.*, 2009). Some shade-tolerant species in the study region can spend long time (>100 years) as saplings before reaching the canopy (Gutiérrez *et al.*, 2004, Gutiérrez *et al.*, 2008) and have long lifespans (750 years, Table 1). For shade-tolerant species, an extended lifespan could be crucial for taking advantage of the death of pioneer tree species to reach the canopy.

Species turnover during succession may involve shifts in species traits inducing gains or losses in biomass in the late succession (Wirth & Lichstein, 2009). In our simulations, after the c. 500 years of pioneers dominance, shade-tolerant species were able to increase in dominance and take over the canopy in the late succession. This general pattern of succession predicted by the model is in line with successional dynamics of other temperate rainforests containing long-lived pioneers (Franklin & Hemstrom, 1981) and similar species traits appear to structure forest communities elsewhere (Purves & Pacala, 2008, Wirth & Lichstein, 2009). According to our simulations, changes in dominant tree species with specific traits during forest succession can take over 500 years (e.g. pioneer species with long life span, Fig. 5) influencing biomass trajectories of forests in the study region for a long time (>500 years).

Model performance

We demonstrated good performance of the model by the significant correlations between observed and simulated forest structures and reasonable predictions of species composition and structure in a variety of sites in Chiloé (Fig. 3 and 7a). This supports the importance of the species life-history traits used as input for the model. The parameter sets presented here can be improved by addressing the main knowledge gaps, such as by empirically quantifying leaf area index and, most importantly, demographic rates of tree species (mortality and recruitment rates, see also *Supporting information*).

Spatial variation in forest structure may generate sampling uncertainty that is relevant for the estimation quality of structural variables in the field (Chave et al., 2003). We suggest that sampling uncertainty in temperate rainforest in Chile can be reduced by using a sampling spatial scale >0.6 ha (Fig. 4, see also *Supporting information*). Different pathways of succession could also occur by chance due to demographic processes, but this was prevented by the spatial scale of our simulations (25 ha). Regardless of this sampling uncertainty, we conclude that the match between simulated and observed data is adequate, especially since we are comparing simulations of 25 ha against measured samples from considerably smaller areas (<0.5 ha).

Application of the modelling approach

The diminishing cover of old-growth forests at global scale (Luyssaert et al., 2008) demands the development of efficient strategies for sustainable management, conservation, and restoration of these endangered ecosystems. Assessments of carbon storage in forests should consider a proper definition of the old-growth stage in order to understand the role that old-growth forests play in the carbon cycle. Our method for assessing the successional stages of forests can facilitate the identification of old-growth remnants. In Chile, old-growth forests are being logged or replaced by plantations of exotic tree species (Lara et al., 2003), particularly in accessible forested areas such as those found on Chiloé Island and along the Chilean Coastal Range. Our results illustrate that forests in this region take a long time to reach the old-growth stage and, therefore, this should be considered in forest management policies, conservation, and restoration strategies of natural forest remnants. The model developed in this study is also a starting point for exploring the effects of old-growth forest fragmentation due to land-use changes (Echeverría et al., 2007) and the impact of exotic tree plantations (e.g. water use by *Eucalyptus* plantations) in natural forests functioning in this region. The development of further model applications and increasing ecological knowledge on tree species would also enhance understanding the impact of biodiversity losses on forests functioning in southern South America.

The climate changes predicted for southern South America increase the need for forest modelling analyses aimed at enhancing our understanding of the dynamic behaviour of these forest ecosystems in a changing environment. Here, we successfully simulated forest development in a stationary climate, providing a starting point for the prediction of forest responses to climate change in forests of Chiloé Island. Because climate and disturbance frequencies may play a role in the forest structure and composition of Chilean old-growth forests, models considering large spatial scales should include forest dynamics simulations under different climatic and disturbance regimes (e.g. Smith et al., 2001).

CONCLUSIONS

Our modelling approach supports the validity of using individual-oriented forest models to analyze the dynamics of old-growth temperate rainforests of southern South America. We propose a method for identifying the successional stages of forests using a forest model to estimate the time taken to reach a structural steady state following a stand-replacing disturbance. By using this method, we found that in Chiloé around half of the studied forests (6 out of 13 stands) would represent a successional stage in which forests have not reached a steady-state. Different successional stages and changes in demographic rates of tree species in different stands explain structural variability observed in old-growth forests of Chiloé. Biomass tends to decrease as forests approach steady-state because large pioneers are replaced by smaller late-successional trees, potentially resulting in carbon losses. Temperate rainforests in this region contain large quantities of carbon and can take 500 to 850 years of succession to reach this stage. This dynamic behaviour should be considered in assessments of carbon storage in temperate rainforests.

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Supporting information

Table S1. Selected parameters values of `FORMIND` used for running simulations in forest of Chiloé Island, Chile. *EBSD: Meteorological station of Estación Biológica Senda Darwin. Full description and calibration method detailed in Table 2 and in the text. Species groups and their correspondence with tree species are detailed in Table 1.

		Species groups											**Reference**
		Aextoxicon	*Amomyrtus*	*Drimys*	*Eucryphia*	*Laureliopsis*	*Luma*	*Myrceugenia*	*Nothofagus*	*Podocarpus*	*Tepualia*	*Weinmannia*	
Environmental													
k	0.5												Pierce & Running, 1988
I_o	1065												EBSD
S_d	14												EBSD
$Seal$	0.5												EBSD
Tree geometry parameters													
D_{max}		1.36	1.35	1.04	2	1.21	0.84	0.6	1.26	1.02	0.75	1.97	Echeverría unpublished, Gutiérrez *et al.* unpublished
H_{max}		35	21.9	30	38	34	27	21.5	35	27	15	34	Lusk 1996a, del Fierro *et al.* 1998, Lusk and Del Pozo 2002, Parada *et al.* 2003, Gutiérrez *et al.* 2004
h_0	2												-
h_1		32.20	22.71	26.87	38.91	27.16	28.76	21.43	32.20	25.96	17.57	32.87	Echeverría unpublished, Gutiérrez *et al.* unpublished, Gutiérrez *et al.* 2004, 2009
f		0.38	0.37	0.38	0.25	0.39	0.34	0.35	0.38	0.44	0.35	0.43	Brun 1969, Emanuelli and Pancel 1999, Salas 2002, Drake *et al.* 2003
cd	0.12												Rüger *et al.* 2007
c	0.37												Rüger *et al.* 2007
SW	0.7												Rüger *et al.* 2007
L_{max}		4.8	4	3.9	4.1	4.3	4	3.8	3.7	4.7	4	3.7	Saldaña and Lusk 2003, White and Scott 2006
Biomass production parameters													
p_{max}		5.6	8.2	8.8	11.1	6.4	8.2	6.2	14	7.9	11	14	Lusk *et al.* 2003, Wright *et al.* 2004, Zuñiga *et al.* 2006, Whitehead *et al.* 2005
α		0.13	0.13	0.11	0.06	0.11	0.13	0.13	0.08	0.13	0.13	0.08	-

r_g	0.2	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Ryan 1991
r_0		0.055	0.03	0.15	0.099	0.06	0.019	0.07	0.096	0.095	0.07	0.06	-
r_1		0.003	0.0055	0.003	0.00021	0.0082	0.016	0.043	0.0027	0.009	0.023	0.00055	-
r_2		-0.0001	-0.00015	-0.00029	-0.000007	-0.00035	-0.0009	0	-0.00011	-0.0007	-0.0015	-0.0000055	-
ρ		0.6	1	0.44	0.696	0.527	0.91	0.57	0.6	0.546	1.06	0.776	Hall and Witte 1998, Karsulovic *et al.* 2000
m	0.1	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Larcher 2001
$codm$	6.34E-13	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Larcher 2001
Establishment													
D_s	0.01	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	-
N_{max}		0 - 450	80 - 380	25 - 470	0 - 270	25 - 500	0 - 100	25 - 550	0 - 400	0 - 130	0 - 275	0 - 300	-
I_{min}		2.2	3.3	3.3	2.2	2.2	3.3	1.3	6.5	3.5	4	2.2	Lusk *et al.* 2006, Lusk *et al.* 2008
I_{max}		70	90	100	100	70	90	70	100	70	80	100	-
Mortality parameters													
m_B		0.004 - 0.008	0.004 - 0.03	0.009 - 0.05	0.002 - 0.05	0.003 - 0.036	0.003 - 0.02	0.004 - 0.08	0.005 - 0.017	0.01 - 0.012	0.002 - 0.05	0.003 - 0.008	-
m_{max}	0.05	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Coomes and Allen 2007
D_{mort}	0.1	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Coomes and Allen 2007
D_{fall}		0.6	0.45	0.4	0.9	0.55	0.4	0.2	0.4	0.4	0.3	0.8	Veblen 1985, Armesto and Fuentes 1988, Gutiérrez *et al.* 2008
p_{fall}	0.3	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Rüger *et al.* 2007
m_{sup}	0.02	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Wyckoff and Clark 2002
$MaxYrs_{sup}$		48.0	100	22	95	56	50.0	22	40	127	50	134	-
Disturbance													
$Dist_f$	0.008	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Rüger *et al.* 2007
Technical parameters													
a	400	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Rüger *et al.* 2007
Δh	0.5	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Rüger *et al.* 2007

FIGURES AND TABLES ILLUSTRATING THE CALIBRATION OF MODEL PARAMETERS

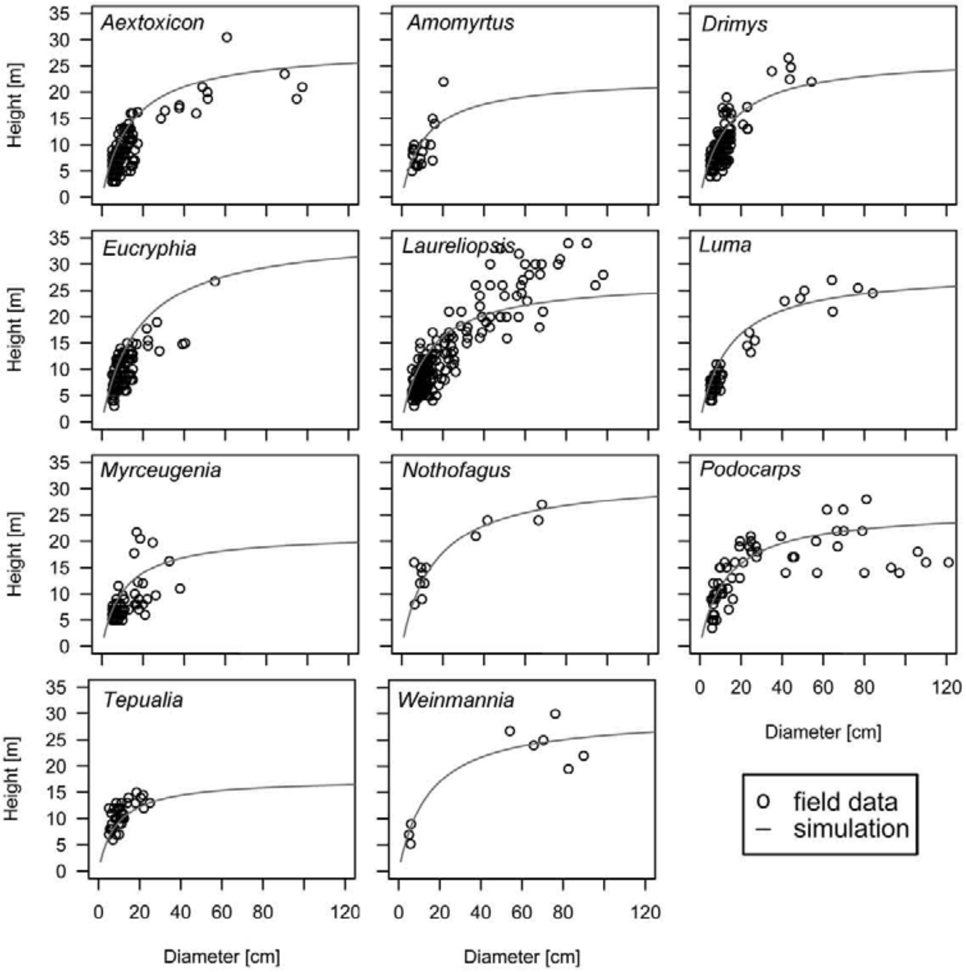

Figure S1. Relationship between tree diameter (dbh) and tree height for the calibration of the parameter h1 of species groups (names according to Table 1).

Table S2. Leaf traits of the parameterized species groups. Estimated leaf area index was calculated multiplying leaf lifespan, litter production and specific leaf area. Species groups names according to Table 1.

Species group	Leaf lifespan [a]	Specific leaf area [a]	Litterfall [b]	Leaf area index	
	(years)	(cm^2 g^{-1})	(g m^{-2})	Observed [c]	Estimated
Aextoxicon	3.7 – 5.3	74 - 78.9	129.4	4.8	3.5 – 5.4
Amomyrtus	3.3 – 3.5	70.9	146.4	no data	3.4 - 3.6
Drimys	2.3 – 3.5	55 - 73	181.3	no data	3.0 - 3.6
Eucryphia	2.3 – 3.6	74 - 81.6	128.1	4.1	2.1 - 3.7
Laureliopsis	2.3 – 4.7	62 - 74.7	113.2	4.3	1.6 - 4
Luma	1.7 – 3.8	61 - 72	no data	no data	-
Myrceugenia	3 – 5	75 - 90.5	101	no data	2.3 – 4.6
Nothofagus	3.2	66.4	149.9	3.7	3.2
Podocarps	6.5 – 7.3	48.9 - 50	130	no data	4.2 - 4.7
Tepualia	no data	no data	no data	no data	-
Weinmannia	2	67	154	no data	2.1

References: (a) Wright *et al.* (2004), Lusk *et al.* (2008); (b) Lusk & Contreras (1999), Pérez *et al.* (2003); (c) Saldaña & Lusk (2003)

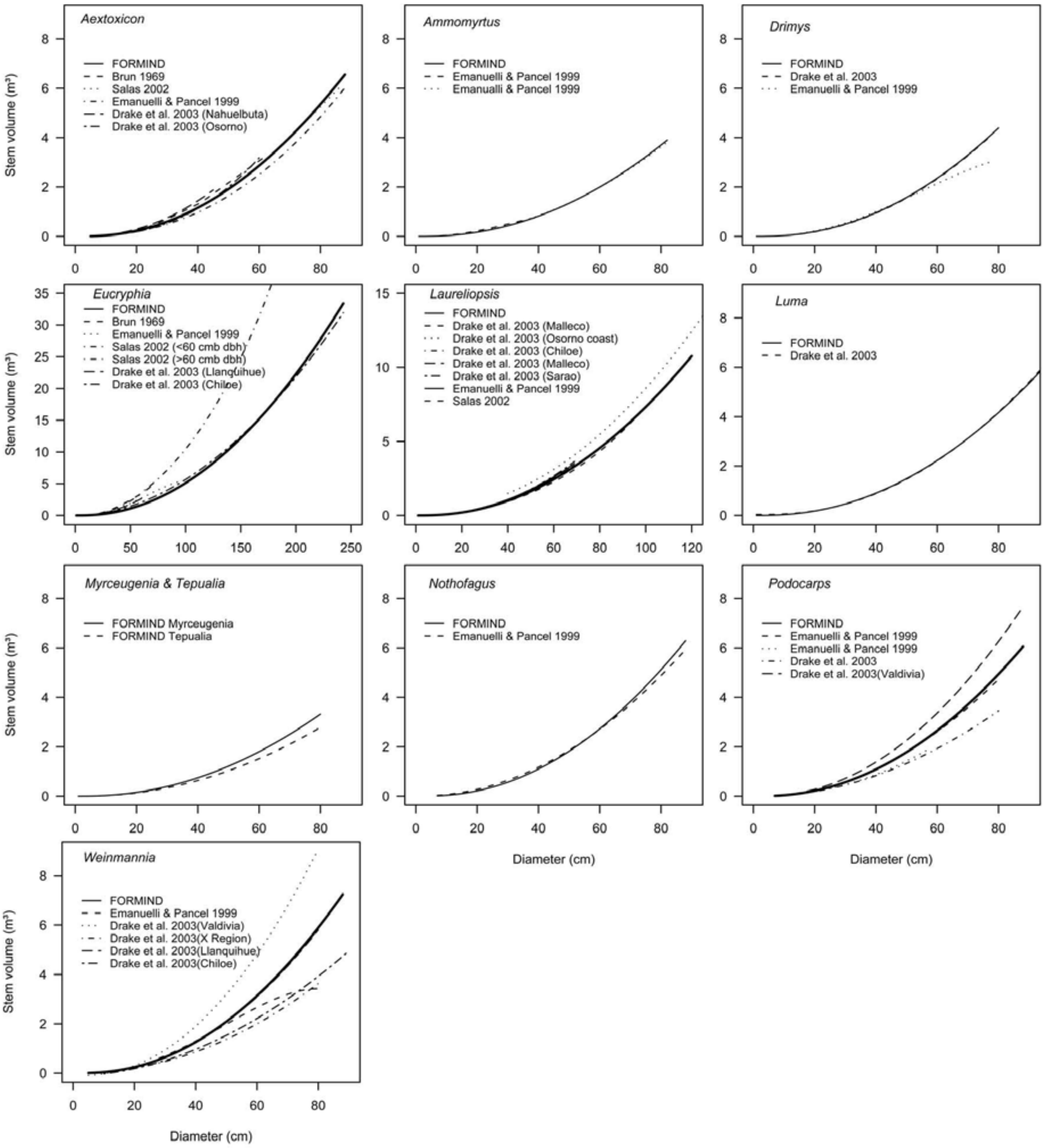

Figure S2. Stem volume of single trees calculated with `FORMIND` and empirical volume functions taken from the literature for the calibration of the parameter form factor (f) of species groups (names according to Table 1). Note different scales on the y- and x-axes.

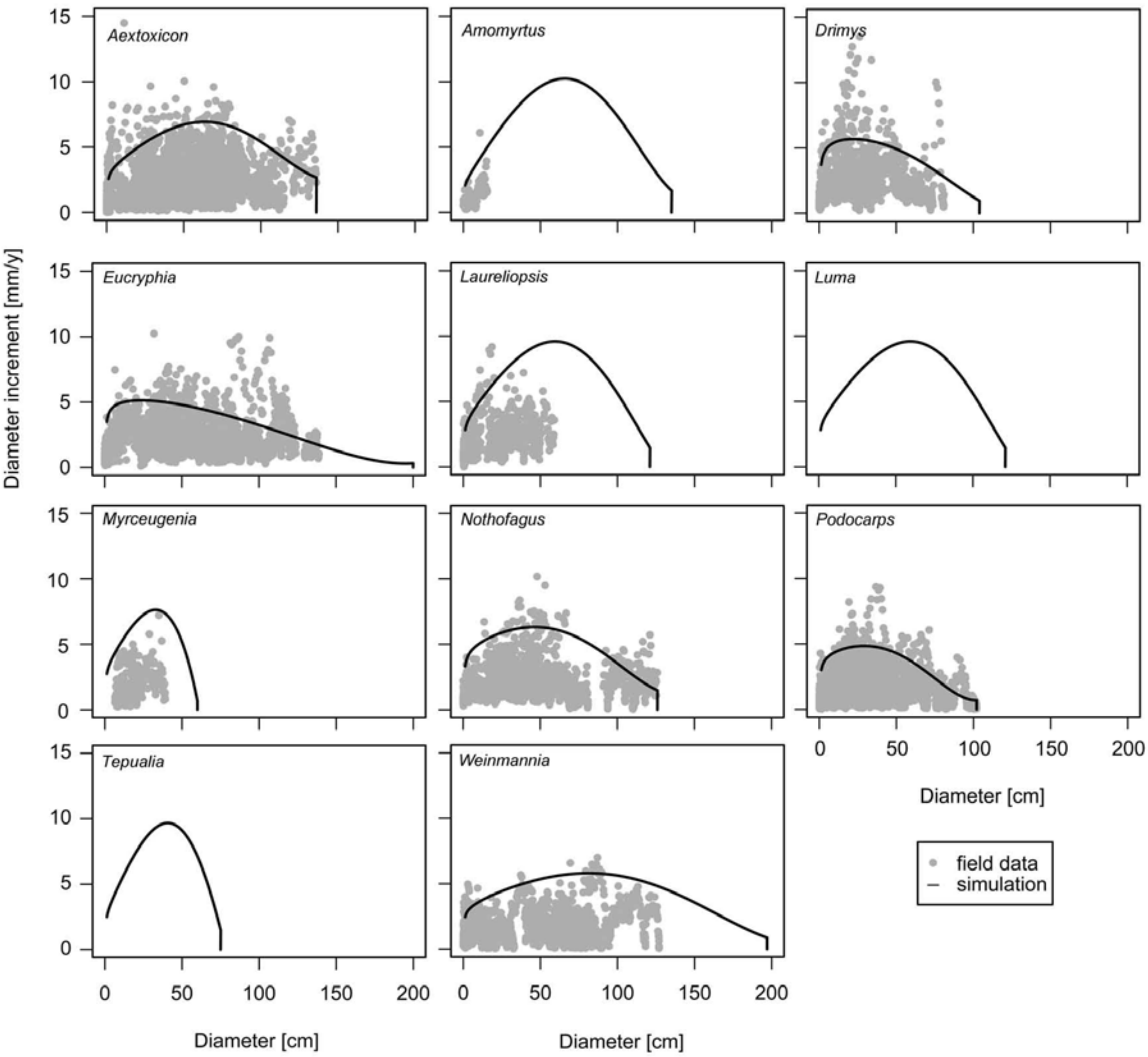

Figure S3. Simulated (lines) and measured (dots) annual diameter increment for the calibration of parameters of maintenance respiration (r0, r1, r2). Simulations were carried out under full light conditions and represent maximum potential growth. Field data are derived from radial growth measurements of trees from the study area (Table 5) growing under high light conditions. Species groups names according to Table 1.

Table S3. Radial increment (*Rinc*) statistics for species groups on Chiloé Island, Chile. Sd: standard deviation of the mean, $Rinc_{sup}$: is the quartile 25% of the observed *Rinc*, $MaxYrs_{sup}$ is the maximum number of years recorded under growth suppression (i.e. *Rinc* <0.1 cm/yrs) as estimated from tree-ring datasets in the study area (Gutiérrez *et al.* 2004, Gutiérrez *et al.* 2008 and A.G. Gutiérrez unpublished). no data: no data available.

Species Groups	Trees N	Mean *Rinc* (cm/yrs)	Sd *Rinc* (cm/yrs)	Maximum *Rinc* (cm/yrs)	$Rinc_{sup}$ (cm/yrs)	$MaxYrs_{sup}$ (years)
Aextoxicon	133	0.17	0.13	1.75	0.082	48
Amomyrtus	1	0.13	0.09	0.61	0.07	22
Drimys	115	0.28	0.24	2.99	0.122	23
Eucryphia	122	0.19	0.14	1.33	0.094	95
Laureliopsis	126	0.19	0.13	1.65	0.1	56
Luma	no data	no data	no data	no data	no data	no data
Myrceugenia	4	0.17	0.11	0.72	0.086	15
Nothofagus	65	0.22	0.20	1.96	0.102	40
Podocarps	129	0.11	0.10	0.82	0.038	127
Tepualia	no data	no data	no data	no data	no data	no data
Weinmannia	25	0.12	0.10	0.70	0.048	134

FIGURES ILLUSTRATING FOREST DYNAMICS SIMULATIONS OF TEMPERATE RAINFORESTS IN NORTHERN CHILOÉ ISLAND, CHILE

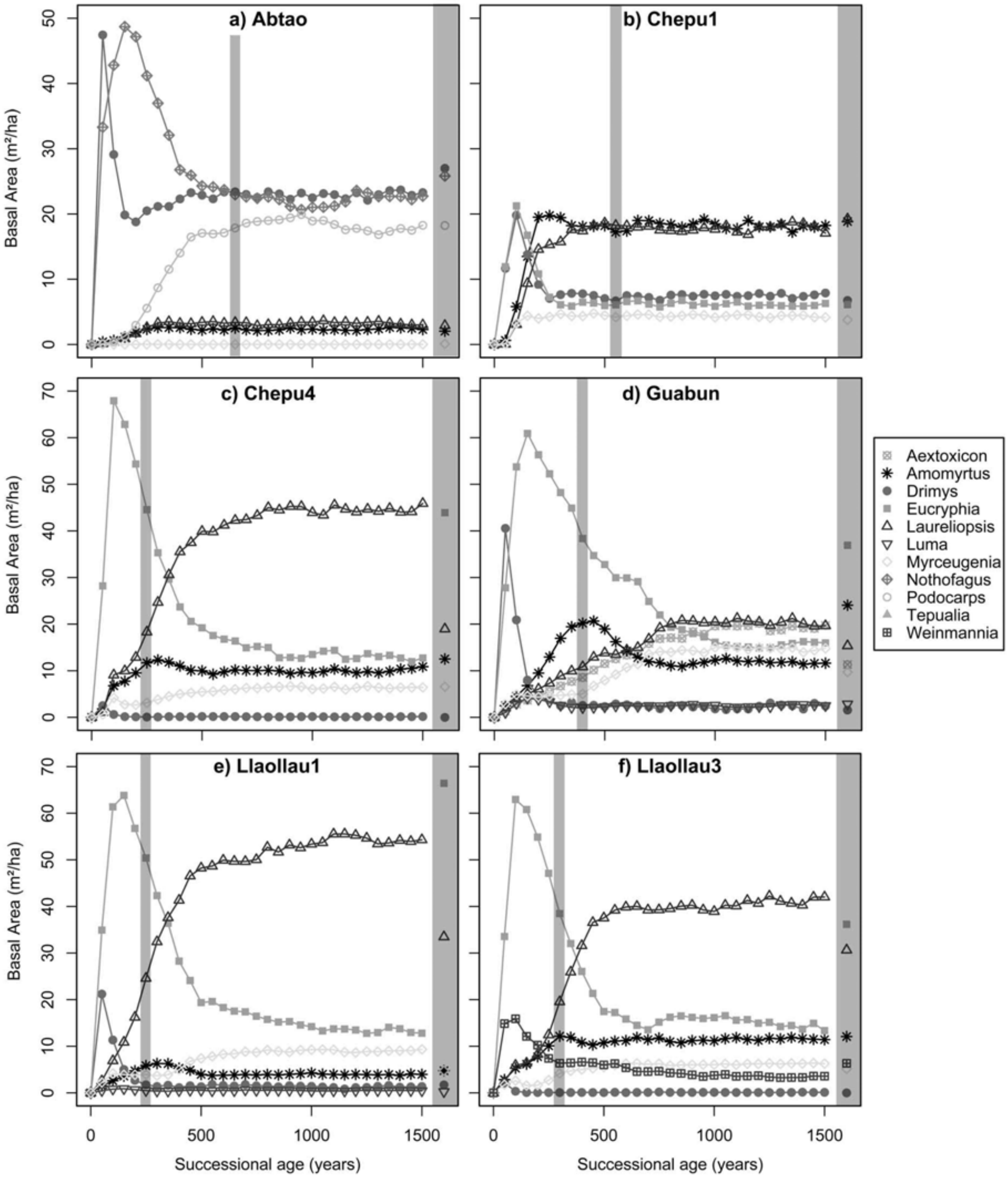

Figure S4. Forest dynamics simulation following a large-scale disturbance (e.g. stand-replacing event) for old-growth forests stands in northern Chiloé Island, Chile. Simulations were run for 25 ha and 1500 years with a windstorm frequency of 0.8 % per year. Results are presented as the running mean over a 50-year period. The grey bars indicate the best agreement obtained with field data at the successional age of simulated stands (see *Materials and Methods*). Inventory data from each study site are shown in the grey bars on the right side of each chart. Species groups names according to Table 1. Note different scale on the y-axis.

SUPPORTING DISCUSSION ON MODEL PERFORMANCE AND FURTHER IMPROVEMENTS TO THE MODELING APPROACH

Examples of the impact of soil moisture on the establishment of tree species in forests of Chiloé include the spatial distribution of tree species associated to excessive soil humidity (Donoso *et al.*, 1984); the enhanced performance of some species (e.g. *Eucryphia cordifolia*) in well drained soils on hillsides (Donoso, 1993); and the particular association of *Podocarpus nubigena*, *Drimys winteri*, *Nothofagus nitida* and *Tepualia stipularis* in poorly drained soils (Armesto *et al.*, 1995, Lusk, 1996b). On some sites (e.g. Ahuenco, Colecole) forest structural patterns were not reproduced exactly by the model, suggesting particular local site conditions that may influence species performance. For example, at Colecole the observed dominance of *Luma apiculata* can be explained because this species occurs mainly in soils subject to long periods of saturation with water (Donoso *et al.*, 2006). At Ahuenco, the observed dominance of *Aextoxicon punctatum* can be explained by its ability to tolerate salt spray (Pérez, 1994).

Some parameters used in this study were selected from temperate rainforests elsewhere, estimated on the basis of reasonable assumptions (e.g. light-use efficiency) and indirect measurements (e.g. *LAI*). Model predictions will be improved by empirically quantifying demographic rates (i.e. mortality and establishment) of main canopy tree species of Chilean temperate rainforests. Further research should address tree species biomass production (photosynthetic rates and slope of light response curve). Leaf area index should be quantified more precisely for each tree species because it strongly influences simulation results (Rüger *et al.*, 2007). Further research is needed for Myrtaceae tree species, specifically with regard to stem volume functions of tree species, biomass production of *Myrceugenia* species, and tree growth of *T. stipularis*, *Amomyrtus spp*. and *L. apiculata*. Additional tree species commonly found in Chilean temperate rainforests, such as the pioneer *Embothrium coccineum* (Proteaceae) and the intermediate *Caldcluvia paniculata* (Cunoniaceae), were not included in this study because of insufficient knowledge about most of the parameters required by the model. In our simulations we did not include the understory bamboo species *Chusquea spp.* because it mainly proliferates after anthropogenic disturbances in the study area (Pérez *et al.*, 2009). *Chusquea* bamboos could lead to stalled gap-phase regeneration (Schnitzer *et al.*, 2000) by restricting the establishment of some tree species in logged forests or after stand-replacing disturbances in Andean forests (Veblen, 1982, Donoso & Nyland, 2005). However, tree regeneration following the synchronous death of *Chusquea* appears to be determined by a complex combination of factors (González *et al.*, 2002). For example, gap colonization by root suckers (both new establishment and advance regeneration) of the main canopy species *E. cordifolia* is more likely after the *Chusquea* dieback (González *et al.*, 2002). Further research should focus on the probability of gap colonization, demographic rates, and growth of *Chusquea* to simulate dynamics in logged forests in the study region. Expanding monitoring studies of regeneration in gaps after *Chusquea* dieback may provide information about alternative pathways of gap-phase regeneration (cf. Schnitzer *et al.* 2000) caused by *Chusquea* bamboos mainly in temperate rainforests of the Andes mountain.

Long-term monitoring in young forests or in forest stands of known successional age should be expanded (in spatial sampling scale and number of experiments) to reduce the uncertainty and variability of field data. Sampling uncertainty can also be improved by increasing the replication number of small sampling plots until a sampling spatial scale >0.6 ha is reached or by using sampling plots of >0.6 ha. Observed basal area may be overestimated in sampling plots by selecting forested areas without including gaps. For example, field sites are commonly established in places with few gaps (higher basal area, lower density) and where large old trees suggest that this part of the forest is old-growth. Thus, the real frequency of gaps may be underrepresented in the field data and the frequency of large old trees may be overrepresented. Additionally, field sampling generally does not take into account that the density of small trees (<5 cm *dbh*) occurring inside gaps can be high (see Gutiérrez *et al.* 2008). Forest sampling should capture the spatial variability inside natural forests by including forest areas of different ages (e.g. canopy gaps).

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RESEARCH PAPER V

A canopy dominant tree of Luma apiculata
in the old-growth forest of Guabun
(Chiloé Island, Chile)

A similar version of research paper will be submitted for publication as

Gutiérrez AG and Huth A. Potential impacts of climate change on temperate rainforests of southern South America.

Author contributions

AGG and AH conceived and designed the study. AG performed research, analyzed data, and wrote the paper. AH contributed to the text.

Photo credit: Juan L. Celiz-Diez

Potential impacts of climate change on temperate rainforests of southern South America

ABSTRACT

Forest responses to climate change may vary among regions of the world demanding to analyze climatic-induced changes in forests for each region in particular. Little is known about future changes that climate change could exert on temperate rainforests ecosystems of southern South America (SSA). Here, we developed an individual oriented process-based forest model and explore forest functioning (e.g. productivity, carbon and water balance) in temperate rainforests of SSA under a business-as-usual scenario of climate change. We parameterized the model using field data and values from 17 tree species given in the literature. Field data from mature undisturbed forests located in Chiloé Island, Chile (42°S, N=12, >250 years-old) were used to evaluate model performance and project responses to climate change. Model results showed that climate change projected for the next century in Chiloé Island will impact forest functioning by modifying water fluxes. Climate change will decrease above ground forest biomass in ~11% and net primary production in ~30% (from 7.6 to 2.4 tonnes of carbon - tC - ha/year) for year 2100. As a result of warming alone, i.e. without accounting for the direct effects of carbon dioxide, temperate rainforests in SSA will become sources of carbon in the next century (average among forest stands of -3.7 tonnes of carbon -tC- ha/year). The model predicted complex and variable patterns of carbon cycling among stands related to their successional stage and structural variability. Climate change can cause a shift in forest composition in the long term due to the establishment of species not occurring previously in the stands. Physiological traits of mid-successional species, medium sizes and potentially long lifespans were relevant for explaining species dominance under novel climate. The model developed here can support future modelling applications to explore impacts of multiple drivers of global change on temperate rainforests of southern South America.

INTRODUCTION

Understanding how forests might respond to climate change is important because they store around half of terrestrial carbon (Bonan, 2008) and play a role in climate change mitigation by sequestering carbon (Nabuurs *et al.*, 2007). Many uncertainties exist regarding climate-forest interactions because our limited knowledge on how individual-level processes can lead to ecosystem-level responses (Purves & Pacala, 2008). Mechanistic, individual-oriented forest models, allow to examining the multiple, interacting effects of climate change on forest dynamics by simulating the fate of each individual tree on small patches as a function of biotic and abiotic factors (Botkin *et al.*, 1972, Loehle & LeBlanc, 1996, Shugart & Smith, 1996, Kahn & Pretzsch, 1997, Pretzsch *et al.*, 2008). Thereby, individual-oriented forest models can help to explore uncertainties regarding the impact of climate change on forest ecosystems.

It is likely that global warming has increased forest productivity at a global scale in recent decades (Nemani *et al.*, 2003). However, forest responses may vary at local scales, such as either increases or decreases in forest productivity (Running & Nemani, 1991, Boisvenue & Running, 2006). For example, an overall increase in forest productivity due to climate change has been found in temperate forests of North America but this increase is not consistent across the region (Running & Nemani, 1991, Latta *et al.*, 2010). In addition, climatic trends expected to occur in the next century can vary among temperate regions of the world (Christensen *et al.*, 2007). As a consequence, contrasting responses of temperate forests are possible to occur with climate change regardless their similar climatic constraints to plant growth. This demands to analyze climate change impact on forest functioning for each region in particular.

Temperate rainforests can play an important role in climate change mitigation because of the large amounts of carbon stored in their biomass (average of 642 tC ha-1, Keith *et al.*, 2009). These forests represent the second most productive ecosystem after tropical humid evergreen forests (net primary production of c. 780 gC m^{-2} yrs^{-1}, gross primary production of c. 1700 gC m^{-2} yrs^{-1}, Keeling and Phillips, 2007, Luyssaert *et al.*, 2007) and held a highly endemic and endangered biodiversity (Myers *et al.*, 2000). All temperate rainforests regions of the world are very likely to warm during this century, with warming and rainfall trends varying sub-regionally (Christensen *et al.*, 2007). Little is known about future impacts of climate change on temperate rainforests, which cover significant areas along the western coast of southern South America (37°45'-47°30'S, SSA). In this region, temperature has increased around 0.25°C per decade (time period 1976–2006, Falvey and Garreaud, 2009) and annual precipitation has decreased c. 40% in the last century (Trenberth *et al.*, 2007). Increase of temperatures in SSA in the last 50 years has produced an unusual increase in tree growth and alterations in tree regeneration (Villalba *et al.*, 1997, Villalba & Veblen, 1997). Extreme climatic events, such as strong droughts driven by El Niño-Southern Oscillation in SSA, have been observed to cause extensive tree mortality at certain sites (Villalba & Veblen, 1998, Suarez *et al.*, 2004). However, it is lacking to understand changes in forest functioning (e.g. productivity, carbon and water balance) due to climatic trends projected for the next century in this region.

Here, we analyzed how temperate rainforests of SSA will be impacted by climate change over the next century. We developed an individual oriented process-based forest model that integrates climatic variability allowing to project forest responses to climate change in temperate rainforests of SSA. We calibrated and evaluated the model using field data from Chiloé Island (Chile, 42°S) and simulated forest dynamics under different scenarios of climate. We particularly explored climate change impacts on forest biomass, productivity, carbon and water balance, and composition in the next century. We further discuss potential applications and further model development for addressing global change impacts on forests of SSA.

MATERIALS AND METHODS

Study area

We studied temperate rainforests occurring on northern Chiloé Island, Chile (42° S, Fig.1).The predominant topography in northern Chiloé Island is low-elevation, rolling hills over highly organic postglacial soils (< 1 m deep), rising to low coastal mountains up to 600 m high. Prevailing climate is wet-temperate with strong oceanic influence (di Castri & Hajek, 1976). Rainfall, about

2000 mm annually, occurs all year round, but 13-25% falls during summer (January-March) and mean annual temperature is 9-10.8ºC (Gutiérrez *et al.*, 2009). In rural landscapes forest stands are part of a mosaic of bogs, shrublands, plantations of exotic tree species and artificial grasslands. The present rural landscape has been shaped by a recent history (< 200 years) of widespread use of fire and logging to clear land for pastures (Willson & Armesto, 1996).

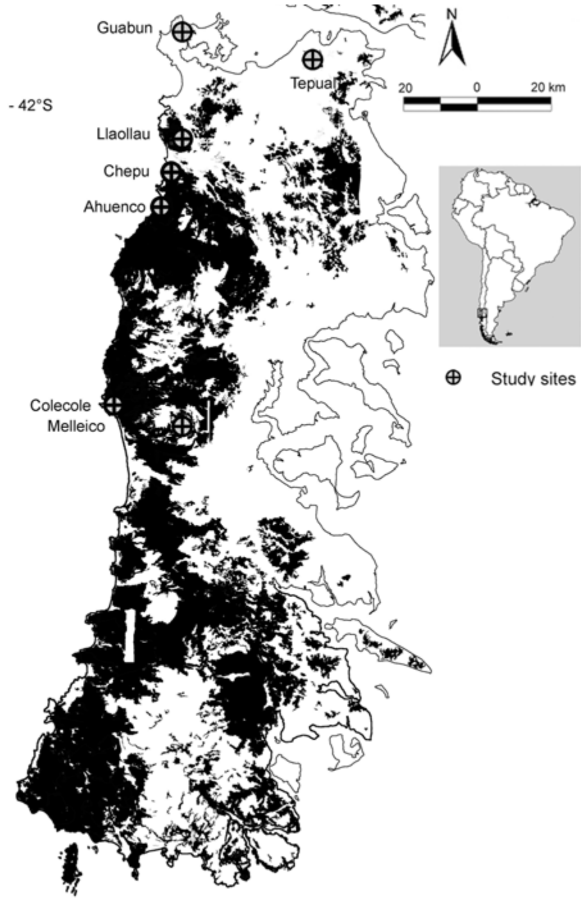

Figure 1. Study site locations (circles) and distribution of main forest types of temperate rainforests on northern Chiloé Island, Chile

Forests in Chiloé Island have a mixed composition of broad-leaved evergreen tree species (Veblen *et al.*, 1983, Armesto *et al.*, 1996). Forest species composition (~ 30 species) vary depending on topography, elevation, soils and distance to the coast of the Pacific Ocean (Holdgate, 1961, Gutiérrez *et al.*, 2009). Forests dominated by shade-tolerant conifers (Podocarpaceae) and broad-leaved *Nothofagus* spp. (Nothofagaceae) are found in the southern sector of the island, and at elevations above 400 m (Veblen *et al.*, 1983, Armesto *et al.*, 1996). Forests dominated by broadleaved evergreen tree species and lacking *Nothofagus* are generally found in northern and low-elevation sites (below 400 m), slopes facing the Pacific Ocean, and well-drained soils (Veblen *et al.*, 1983, Armesto *et al.*, 1996). Tree trunks and branches are profusely covered with epiphytic plants and climbers (e.g. Hymenophyllaceae ferns and species of Gesneriaceae and Bromeliaceae). Shrubs and bamboo species (e.g. *Chusquea spp.*) are uncommon in undisturbed old-growth forests of the study area except along forest margins and on coastal cliffs (Gutiérrez *et al.*, 2009).

The forest model

Here, we present an individual-oriented forest model (`FORMIND-CLIM`) that includes the effect of inter-annual climatic variability on forest processes. The model is based on `FORMIND` (Köhler & Huth, 1998, Köhler *et al.*, 2000), a model successfully applied to simulate dynamics in tropical (Köhler *et al.*, 2000, Huth *et al.*, 2005, Rüger *et al.*, 2008, Groeneveld *et al.*, 2009) and temperate rainforests (Rüger *et al.*, 2007, Gutiérrez *et al.*, in review). Extensions added to the previous model version and its equations are fully described in *Research paper VI.*

`FORMIND` is a forest growth model that simulates the spatial and temporal dynamics of uneven-aged mixed species forest stands. The model simulates forest dynamics (in annual time steps) as a mosaic of interacting forest patches of 20 m × 20 m, which is the approximate crown size of a large mature tree. Within these patches, forest dynamics is driven by tree competition for light and space following the gap model approach (Shugart, 1984, Botkin, 1993, Pretzsch *et al.*, 2008). The model is individual-oriented, i.e. light availability is considered the main driver of individual tree growth (Pacala *et al.*, 1994). For the explicit modelling of the competition for light, each patch is divided vertically into height layers. In each height layer, the leaf area is summed up and the light environment in the forest interior is calculated via a light extinction law. The carbon balance of each individual tree is modelled explicitly, including the main physiological processes (photosynthesis, respiration). Growth process equations are modified from the models `FORMIX3` and `FORMIX3-Q` (Huth & Ditzer, 2000, Huth & Ditzer, 2001, Rüger *et al.*, 2007).

Allometric functions and geometrical relations are used to calculate above-ground biomass, tree height, crown diameter and stem volume from the *dbh* of the tree (i.e., stem diameter at 1.3 m height). Tree mortality can occur either through self-thinning in densely populated grid cells, senescence, gap formation by large falling trees, slow tree grow, or external disturbances (e.g. wind throws). Gap formation links neighbouring grid cells. Tree regeneration rates are formulated as maximum rates of recruitment of small trees at *dbh* threshold of 1 cm, with seed loss through predation and seedling mortality being incorporated implicitly (Rüger *et al.*, 2007). These maximum rates are reduced by shading. Nutrient availability is considered to be homogeneous at the stand scale. A detailed description of the core model and its equations can be found in Köhler (2000) and Rüger *et al.* (2007).

Forest carbon exchange

Forest net flux of carbon is calculated based on processes of carbon acquisition and loss (Woodwell & Whittaker, 1968, Chapin *et al.*, 2009), and integrated into the model after Pinard and Cropper (2000). The main carbon acquisition process, the forest annual gross photosynthetic production (*PB*), is obtained from the amount of carbon assimilated in the photosynthesis of every tree in the forest. Carbon losses occur by forest gross respiration (*R*), the decomposition of coarse woody debris (*CWD*), and soil organic matter decomposition. Annual inputs to the *CWD* pool include biomass from dying trees such as leaves, branches, logs and snags. Forest gross respiration is explicitly obtained from individual tree respiration, i.e. growth respiration during the build-up of new biomass and maintenance respiration of living biomass (Rüger *et al.*, 2007). Soil carbon below 50 cm depth and root biomass are assumed to be static and are not included in the model. In temperate rainforests, they probably represent about 6% and 17% of total ecosystem carbon, respectively (Smithwick *et al.*, 2002).

Water balance

The soil moisture dynamics is modelled considering the soil water content as the state variable and treating the soil as a reservoir that is intermittently filled by rainfall events (Rodriguez-Iturbe *et al.*, 1999, Porporato *et al.*, 2004). Water losses occur via interception by the forest canopy, drainage, runoff, and transpiration. Interception by the forest canopy is calculated relating the canopy retention capacity to leaf area index (*LAI*) of each forest patch (Rey, 1999, Wattenbach *et al.*, 2005). Net precipitation to the soil surface can exceed the soil infiltration capacity and leave the system through runoff. Drainage out of the root zone is calculated using an empirical relationship (Neilson, 1995) broadly applied in vegetation modelling (Smith *et al.*, 2001, Sitch *et al.*, 2003). The water-use efficiency concept (Lambers *et al.*, 1998) is used to compute forest transpiration from the proportion of water used for each tree to assimilate a unit of carbon in the photosynthesis. Maximum water loss by the canopy is limited by the difference between daily potential evapotranspiration and the canopy interception of the day. Current and future climatic time series are constructed in the model using probability distributions (Kumagai *et al.*, 2004, see also *Research paper VI*) based on current climatic statistics and expected tendencies for the study area.

Climatic effects on trees

Model formulations of temperature and soil moisture impact on tree regeneration and growth are based on those generally employed in forest gap models (Aber *et al.*, 1982, Pastor & Post, 1986, Prentice *et al.*, 1993, Pretzsch, 2009) and dynamic global vegetation models (Sykes *et al.*, 1996, Smith *et al.*, 2001). These formulations are also based on functions widely accepted by ecophysiologists and are well supported experimentally (Loehle, 2000, Saxe *et al.*, 2001). The effect of temperature on tree biomass production is computed as a temperature response function (Haxeltine & Prentice, 1996). The effect of soil water scarcity on tree biomass production is implemented as a reduction factor based on soil properties (e.g. field capacity and permanent wilting point, see also *Research paper VI*) and the water demand for photosynthetic production. Both water scarcity and temperature response functions are combined in a multiplier representing different climatic controls on biomass production (Prentice *et al.*, 1993). Tree respiration is assumed to increase exponentially with temperature (Prentice *et al.*, 1993). Climatic limits for the regeneration are represented by the boundary temperate values of each species groups (Sykes *et al.*, 1996, Smith *et al.*, 2001) that are combined in a multiplier applied to tree regeneration rates to determine the number of new stems per species in every time step (Aber *et al.*, 1982, Pastor & Post, 1986, Prentice *et al.*, 1993).

Model calibration

The robustness of `FORMIND` in predicting forest dynamics in the study area without considering climatic variability has been demonstrated in two previous studies (Rüger *et al.*, 2007, Gutiérrez *et al.*, in review). Here, we will address model calibration related to the inclusion of climatic variability and carbon balance into the model (see also *Research paper VI*). We developed a model parameterization for 11 species groups (Table 1), representing 17 main canopy tree species that are important to the functioning of broad-leaved evergreen temperate rainforests in Chile (Veblen *et al.*, 1981, Donoso, 1993, Armesto *et al.*, 1996). Table 2 details parameters needed for running the hydrological, bioclimatic and carbon flux calculations.

Table 1. Main traits of species groups and their correspondence with tree species found in temperate rainforests located in northern Chiloé Island, Chile. Species traits were grouped according to model parameter values from Gutiérrez *et al.* (in review).

Species groups	**Species names**	**Family**	**Life-span**[a]	**Size**[b]	**Grow**[c]	**Successional status**[d]	**Climatic Tolerance**[e]
Aextoxicon	*Aextoxicon punctatum*	Aextoxicaceae	Long	Large	Slow	Late	Narrow, thermophilic
Amomyrtus	*Amomyrtus luma, A. meli*	Myrtaceae	Short	Medium	Slow	Mid	Broad, thermophilic
Drimys	*Drimys winteri*	Winteraceae	Short	Large	Fast	Early	Broad
Eucryphia	*Eucryphia cordifolia*	Cunoniaceae	Long	Large	Fast	Early	Narrow, thermophilic
Laureliopsis	*Laureliopsis philippiana*	Monimiaceae	Long	Large	Fast	Late	Broad, thermophilic
Luma	*Luma apiculata*	Myrtaceae	Long	Medium	Fast	Mid	Narrow, thermophilic
Myrceugenia	*M. ovata,* *M. parviflora,* *M. planipes,* *M. chrysocarpa*	Myrtaceae	Short	Small	Slow	Late	Broad, thermophilic
Nothofagus	*Nothofagus nitida*	Nothofagaceae	Long	Large	Fast	Early	Narrow
Podocarps	*Podocarpus nubigena* *Saxegothaea conspicua*	Podocarpaceae	Long	Large	Slow	Late	Narrow
Tepualia	*Tepualia stipularis*	Myrtaceae	Short	Small	Fast	Mid	Broad
Weinmannia	*Weinmannia trichosperma*	Cunoniaceae	Long	Large	Slow	Late	Broad, thermophilic

a: mean estimated maximum longevity, classed in long (≥500 years) and short (<500 years); **b**: classed with the maximum reported tree *dbh* and height (large *dbh* >100 cm and height >26 m, medium *dbh* >100 cm or height >26 m, small *dbh* <100 cm and height <26 m); **c:** classed with radial increment (fast, radial increment ≥0.19 cm/year, slow <0.19 cm/year); **d:** expected arrival during the succession, classed according to shade-tolerance and light-intensity limits needed for establishment; **e:** classed using parameters in Table 4, narrow $T_w - T_c < 13.5$°C, broad $T_w - T_c \geq 13.5$°C; thermophilic: the species group is found in climates with $T_w > 16$°C and $T_c > 4$°C.

Table 2. Parameter descriptions and parameterization methods used for running simulations of temperate rainforests located in northern Chiloé Island, Chile. (a) literature, (b) calibrated with field data, (c) calculated, (d) calibrated using literature, (e) Meteorological data from EBSD.

	Description	Value	Units	Method	Reference
Carbon Balance					
k_D	Decay rate of coarse woody debris (*CWD*)	0.05	% mass loss years^{-1}	a, d	1, 2, 3
t_A	Transitional rate of soil biomass to the atmosphere	0.038	% mass loss years^{-1}	a	4
t_S	Transitional rate of *CWD* biomass into the soil organic matter pool	0.05	% mass loss years^{-1}	a	5
Climate					
$1/\lambda$	Mean interval time between rainfall events[¥]	[†]	day^{-1}	e	
η	Mean depth of rainfall events[¥]	[†]	mm day^{-1}	e	
Rn_μ	Mean light intensity above canopy[¥¶]	[†]	μmol(photons) m^{-2} s^{-1}	e	
Rn_σ	Standard deviation light intensity above canopy[¥¶]	[†]	μmol(photons) m^{-2} s^{-1}	e	
T_μ	Mean daily temperature[¥§]	[†]	°C	e	
T_σ	Standard deviation daily temperature[¥§]	[†]	°C	e	
Hydrologic Balance					
n	Vertically averaged porosity of the soil	0.757	-	a	6
z	Soil depth	70	cm	a	7
k_{soil}	Soil texture dependent percolation rate at field capacity	4	mm day^{-1}	a	8, 6
α_h	Slope of the canopy saturation curve	0.7	-	a, b	9
f_h	Parameter of the relationship *LAI* and canopy storage capacity	3	-	b	10
LAI_{max}	Maximum *LAI* of the studied forest type	5.5	m² m^{-2}	a	11
WUE	Water-use efficiency	9	g CO_2 kg^{-1}H_2O	d	7
γ	Psychometer constant	65	Pa K^{-1}	a	12, 13
L	Latent heat of vaporization of water	2.56x10^{6}	J Kg^{-1}	d	12, 13
Δ	Rate of change of saturated vapour pressure with temperature	c	Pa K^{-1}	c	12
Bioclimatic model					
T_{Clow}	Lower temperature limit for CO_2 assimilation	-10	°C	a	14
T_{Chigh}	Maximum mean temperature for photosynthesis	37	°C	a	14
T_c	Mean temperature of the coldest month	[††]	°C	e	[††]
T_w	Mean temperature of the warmest month	[††]	°C	e	[††]
T_{ref}	Reference temperature respiration	10.8	°C	a	12
Q_{10}	Short-term respiration response to temperature	1.8	-	a	15
θ_{wp}	Wilting point of the soil	0.125	%	a	16
θ_{fc}	Field capacity of the soil	0.3	%	a	16

¥ per season; §calculated for dry ($P_d < 1$ mm), wet ($1 \leq P_d < 20$ mm) and stormy days ($P_d \geq 20$ mm); ¶calculated for dry ($P_d < 1$ mm) and wet days ($P_d \geq 1$ mm). †see table 4, ††see table 5. References: (1) Carmona *et al.*, 2002; (2) Schlegel & Donoso, 2008; (3) Keith *et al.*, 2009; (4) Raich & Schlesinger 1992; (5) Carmona *et al.* 2006; (6) Jansen *et al.* 2004; (7) Diaz *et al.* 2007; (8) Sitch *et al.*, 2003; (9) Wattenbach *et al.* 2005; (10) Rey 1999; (11) Lusk 2001; (12) Prentice *et al.* 1993; (13) Haxeltine & Prentice 1996; (14) Larcher, 2001, Smith *et al.*, 2001, Sitch *et al.*, 2003; (15) Saxe *et al.* 2001; (16) Maidment, 1993.

We used climatic daily records of rainfall and temperature from the meteorological station *Estación Biológica Senda Darwin* (EBSD, 42º 53’ S, 73º 40’ W, 60 m.a.s.l, period from May 1998 to February 2009) to derive climatic parameters under current climate on a daily basis for each season

(Table 3). Climatic parameters were assumed representative for the spatial scale of the study area, i.e. northern Chiloé Island. Climatic predictions were then compared with observed climatic records at EBSD (see also *Research paper VI*).

The decay rate of coarse woody debris (k_D) was calibrated comparing predicted coarse woody debris biomass at the successional age of studied stands with reported data from old-growth temperate rainforests in the study area, elsewhere in Chile (Carmona *et al.*, 2002, Schlegel & Donoso, 2008) and other temperate rainforests (Keith *et al.*, 2009). *CWD* and soil heterotrophic respiration followed estimates in temperate forests (Raich & Schlesinger, 1992) and in temperate rainforests of Chiloé Island (Carmona *et al.*, 2006), respectively.

The parameter describing the relationship between increasing *LAI* and canopy storage capacity was calibrated assuming that storage capacity reaches 4.9 mm at a *LAI* 5.0 (Diaz *et al.*, 2007). The slope of the saturation curve of the canopy rain retention capacity (*α)* was set following values of broad-leaved temperate trees (Wattenbach *et al.*, 2005).

Table 3. Parameter values for running the weather generator under the studied climatic scenarios (see Climatic scenarios). Current climate calculated from instrumental records from meteorological station EBSD, time period 1998 – 2009. Radiation parameters Rn_μ and Rn_σ (the latter in brackets) were considered the same for both scenarios but were related to daily rainfall (P_d).

	Current climate		**Climate change**	
Rainfall	$1/\lambda$ (1/days)	η (mm)	$1/\lambda$ (1/days)	η (mm)
DJF	0.90	8.3	0.95	4.2
MAM	0.55	12.8	0.64	10.2
JJA	0.29	16	0.29	16.0
SON	0.54	9.5	0.77	4.7
Temperature	(mean °C)		(mean °C)	
DJF	12.5		16.5	
MAM	10.1		13.1	
JJA	8.4		10.4	
SON	9.8		11.8	
Radiation	$P_d < 1$ *mm*	$P_d \geq 1$ *mm*		
DJF	1413.9 (317.0)	986.9 (378.2)		
MAM	701.2 (294.1)	398.8 (261.6)		
JJA	408.9 (159.1)	229.7 (139.4)		
SON	1065.5 (348.7)	640.8 (320.1)		

DJF: December to February (austral summer, growing season), MAM: March to May, JJA: June to August (austral winter), SON: September to November (growing season).

The water-use efficiency (*WUE*) was calibrated using transpiration estimates of Diaz *et al.* (2007) in Chiloé Island (296 mm/year) and the potential canopy photosynthetic rate estimated by the model at this site (Tepual, 41.8 tC ha^{-1}, without climatic variability). The obtained *WUE* was then confirmed with observed *WUE* of Chilean tree species and temperate rainforests elsewhere (Brodribb & Hill, 1998, Cunningham, 2005, Zuñiga *et al.*, 2006, Piper *et al.*, 2007). Soil characteristics (porosity and depth) followed field descriptions from Chiloé Island (Janssen *et al.*, 2004). Water-retention and percolation properties of the soil (parameters θ_{wp}, θ_{fc} and k_{soil}) were set using average parameter values (Maidment, 1993, Sitch *et al.*, 2003) according to soil texture classes (loam to silty loam) described by Janssen *et al.* (2004).

The parameters of temperature effects on tree biomass production T_{Clow} and T_{Cwarm} follow the literature (Larcher, 2001, Smith *et al.*, 2001, Sitch *et al.*, 2003). T_c and T_w were chosen matching observed limits of species groups and available meteorological records from the nearest station (Table 4). The Q_{10} value and reference temperature (T_{ref}) follow Saxe *et al.* (2001).

Table 4. Boundary temperature values for the regeneration of species groups. Northern and southern limits follow those reported by Donoso (2003) and Heusser (2006). Meteorological records were taken from Luebert & Pliscoff (2006) and instrumental records from Dirección Metereológica de Chile (Fray Jorge and Isla Navarino).

Species group	T_w	T_c	Latitudinal limits		Warmest station	Coldest station
Aextoxicon	16.9	7.3	30°40' -	43°34'	Fray Jorge	Isla Guafo
Amomyrtus	18.2	4.1	35°30' -	47°	Constitucion	Abtao
Drimys	16.9	2.2	30°40' -	55°95	Fray Jorge	Isla Navarino
Eucryphia	19.5	6.9	37°17' -	42°50'	Angol	Castro
Laureliopsis	19.5	4.1	37°30' -	47°30'	Angol	Abtao
Luma	17.8	4.5	33°06' -	45°43'	Valparaíso	Puerto Aysén
Myrceugenia	18	4.1	36°67' -	44°33'	Concepción	Abtao
Nothofagus	16.5	4.1	40°20' -	48°30'	La Unión	Abtao
Podocarpus	17	4.1	39°83' -	50°38'	Valdivia	Abtao
Tepualia	16.5	2.4	35°30' -	53°20'	Constitucion	Cabo San Isidro
Weinmannia	22.1	5.5	35°58' -	48°83'	Cauquenes	Puerto Aysén

Model verification

The verification of the hydrological model was done for a secondary forest stand (ca. 70 years old), where the hydrological cycle has been studied in detail (see also *Supporting Information*). We selected forest stands (Table 5, N=12) free of recent fire or logging impacts, representing stand ages >250 years, containing trees >300 years old, and occurring under similar climatic conditions. We considered these stands representative of the current composition and structure of old-growth forests in the study area (Gutiérrez *et al.* 2009). Observed forest structure and composition of these stands were used to evaluate the performance of the model after including climatic variability. All stands were sampled using similar sampling design, i.e. plots of 0.1 to 0.5 ha where all stems found in the plot were identified to species and their sizes recorded. A detailed description of field sampling methods is found in references in Table 5. Demographic rates (recruitment and mortality rates) of each stand follow Gutiérrez *et al.* (in review).

Climatic scenarios

Climate change scenarios were selected using precipitation and temperature shifts for Chiloé Island projected by the regional climatic model `PRECIS-DGF` (DGF & CONAMA, 2006). The `PRECIS-DGF` model provides high-resolution climate information and predictions of climate in

Chile on a daily basis and at 25 km² space resolution. The expected climatic tendency projected for northern Chiloé Island, i.e. comparing the climate in 1961–1990 with the climate in 2071–2100 using severe greenhouse gases concentrations as specified by A2 scenario of IPCC (2007), are hotter and dryer growing seasons (DFJ and SON, austral summer and spring), and hotter winter (JJA, Table 3).

Model experiments of forest dynamics under climate change were ran considering the following scenarios. First, reference simulations were run using current climatic conditions based on daily instrumental record from EBSD. Second, simulations were run under expected climatic scenarios for the period 2070-2100 (Table 3). We explored the impacts of future changes in rainfall and temperature first separated and then together. Current temperature and rainfall parameters were changed assuming a linear increase with time until year 2100 based on the rate of change in climate projections for SSA (Christensen *et al.*, 2007). We analyzed changes in net carbon flux (as a surrogate of net ecosystem carbon exchange, *NEE*), gross primary production (*GPP*, estimated using forest gross photosynthetic production), and net primary production (*NPP*, estimated from the balance between forest gross photosynthetic production and respiration) under the different climatic scenarios. We used `R` statistical environment (R-Development-Core-Team, 2005) for all statistical analyses and the `lattice` package (Sarkar, 2008) for data visualization.

Table 5. Old-growth temperate rainforests studied on Chiloé Island (42°S, Chile). *SAGE* is the estimated successional age and *OGI* is the old-growth index taken from Gutiérrez *et al.* (in review). Similarity is the Morisita-Horn index of similarity, correlations are Pearson correlations between observed and simulated basal area and density (trees dbh >5 cm) of different species groups after the inclusion of climatic variability in the model.

Stand	**Sampling area (ha)**	**SAGE (years)**	**OGI**	**Similarity**	**Correlation**			
					Basal area	***P***	**Density**	***P***
AHUENCO†	0.4	300	0.5	0.84	0.90	***	0.75	**
CHEPU1¥	0.4	>450	1.9	0.72	0.96	***	0.66	*
CHEPU2¥	0.4	>500	1.8	0.98	0.99	***	0.97	***
CHEPU3¥	0.4	>450	1.4	0.87	0.99	***	0.82	**
CHEPU4¥	0.4	250	0.4	0.88	0.99	***	0.82	**
COLECOLE†	0.1	>400	1.6	0.93	0.98	***	0.88	***
GUABUN†	0.4	540	0.6	0.91	0.98	***	0.85	**
LLAOLLAU1δ	0.4	350	0.5	0.97	0.96	***	0.95	**
LLAOLLAU2δ	0.4	360	0.6	0.87	0.99	***	0.82	**
LLAOLLAU3δ	0.4	350	0.5	0.82	0.99	***	0.75	**
MELLEICO†	0.5	>350	1.6	0.89	0.99	***	0.85	**
TEPUAL†	0.2	>450	1.2	0.97	0.95	***	0.96	***

Field data sources: (†) Gutiérrez *et al.* 2009; (¥) Donoso *et al.* 1984; (δ) Donoso *et al.* 1985. *** P <0.001, ** P <.01, * P < 0.05.

Simulations

All simulations of forest dynamics began on a bare ground. Simulations were run until the estimated successional age of the focal stand (*SAGE* from Table 5) under current climatic conditions for characterizing the current structural variability (Solomon, 1986). After reaching the *SAGE*, the forests underwent a period of transient climate reaching after 100 years the projected climate for year 2100. Climate stabilized after this period and the simulation continued for 500 years more. Windstorms frequency were kept constant (0.8 % per year) among scenarios and forest sites. We ran 20 simulations of 25 ha per stand (i.e. 625 patches of 400 m² each) with different random number seeds and results were subsequently averaged every 50 years. Results of the different scenarios were compared at the expected successional age of each stand at year 2100 (i.e., *SAGE*+100 years).

We assumed that, under future climatic conditions, all main canopy tree species could regenerate. Under this assumption, all species would have a probability of dispersal in future climates from parent trees located somewhere in the study area. The latter simplifies the problem of estimating which species would enter a patch under novel climatic regimes, but it eliminates any transients related to slow tree immigration (Solomon, 1986). Demographic rates (regeneration and mortality) of species before the stand reaches the *SAGE* were the same as calibrated in Gutierrez *et al.* (in review). After the stand has reached the *SAGE* (1000 years of succession in the case of steady-state forests), we calculated recruitment rates of species (N_{max}) using density probability functions adjusted to recruitment rates for each species in all the sites (Table S1 in *Supporting information*). This assumption was taken because demographic rates of species may vary in relation to local environmental characteristics of each study site (Gutierrez *et al.* in review). Non-lineal regression analyses were used to calculate basic mortality of species (m_B) assuming that a trade-off between demographic rates of tree species occurs (Fig. S1).

RESULTS

Model verification

The match between observed and simulated basal area and density of the stands and different species groups after the inclusion of the climatic variability in the model is shown in Figure 2. The similarity between observed and simulated forest composition after the inclusion of climate ranged from 72 to 98% (Table 5; Morisita-Horn index of similarity; Horn, 1966). Pearson correlations were high between field data and simulations after the inclusion of climate (>90% for species basal areas and >66% for density, respectively, $P<0.001$ for both analyses, Table 5). These results lend support to model predictions of forest dynamics in northern Chiloé Island after the inclusion of inter-annual climatic variability effects on tree growth.

Forest water fluxes

Model results under the climate change scenario compared to current climate for year 2100 showed diminished net precipitation (~10% reduction), ~20% reduction in mean soil water content, ~10% increase in forest evapotranspiration and ~10% reduction of forest water balance (*EVTP*, Fig. 3, $P < 0.001$, Mann-Whitney *U*-test, all analyses, average values among stands). Soil water content was reduced as low as 30% in some forest stands (Fig. 3). Evapotranspiration and soil water content was mainly driven by the change in precipitation and did not change when considering only changes in temperature ($P = 0.055$, Mann-Whitney *U*-test, both analyses).

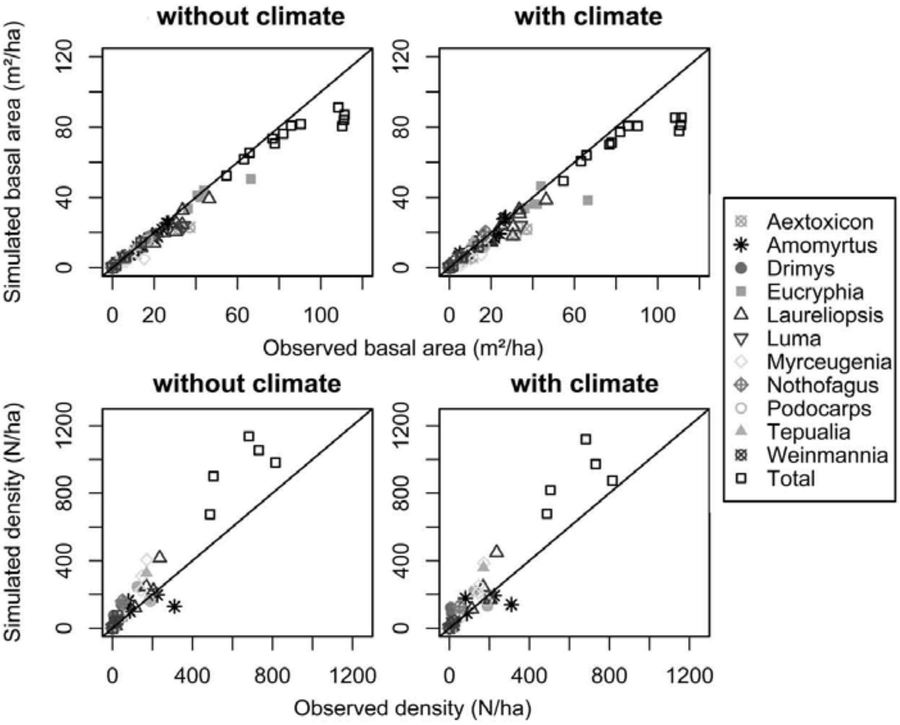

Figure 2. Comparison of structural patterns observed in the field and model predictions before and after including climatic variability in the model. Comparisons were conducted at the estimated successional age of each stand (see Table 5). Observed density are available field data of trees with dbh >15 cm. Species density was not used as calibration variable and represents an independent result.

Forest biomass

Forest above ground biomass (*AGB*) under current climatic conditions averaged 520.4 t/ha among forest stands (range 352.9 – 642.7 t/ha). The model predicted 530.1 t/ha in mean *AGB* for year 2100 under current climate but lower mean *AGB* under climate change for year 2100 (11% less *AGB*, $P < 0.001$, Mann-Whitney *U*-test, Fig. 4). *AGB* reduction ranged 30.1 to 106.2 t/ha among forest stands. *AGB* reductions due to changes in temperature were higher than reductions due to rainfall changes ($P < 0.001$, Mann-Whitney *U*-test, Fig. 4).

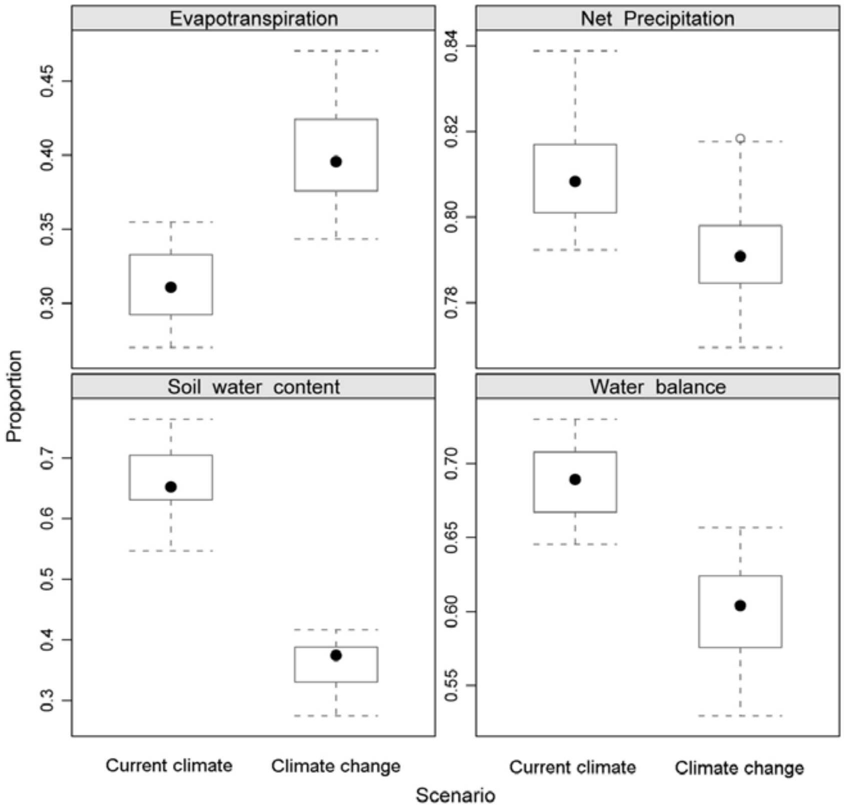

Figure 3. Main components of the hydrologic balance and their variation predicted by the model under climate change compared to current climate. Data is expressed as proportions of the component in relation to annual rainfall. Note different scales on y-axes. Water balance is the difference between rainfall input and water return in evapotranspiration.

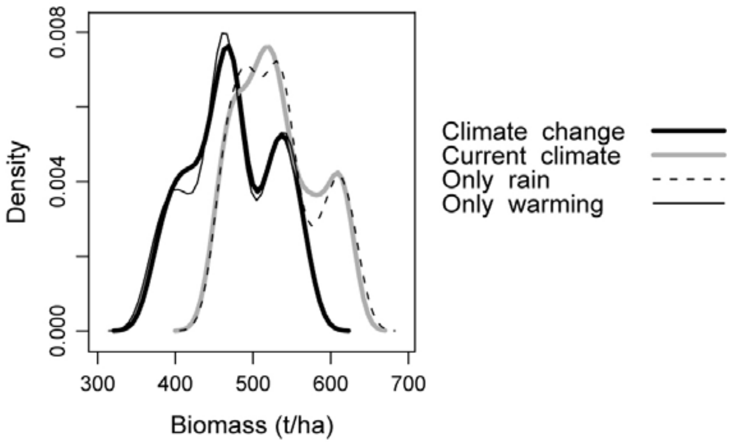

Figure 4. Density distribution of forest above ground biomass (*AGB*) predicted by the model in all studied forest stands under different climatic scenarios for year 2100 (240 simulations). Simulations were run under expected climatic scenario for year 2100 (Climate change), changing only rainfall patterns according to expected climatic scenario for year 2100 (only rain), changing temperature according to expected climatic scenario for year 2100 (only warming) and under current climatic tendencies (current climate).

Forest productivity and net carbon flux

Current *GPP* ranged 34 – 51.8 tC ha/year (mean of 43.5 tC ha/year) and *NPP* ranged 2.9 – 10 tC ha/year among stands (6.5 tC ha/year mean value, Fig. 5). The model projected reduced *GPP* and *NPP* at year 2100 due to climate change (both analyses P <0.001, Mann-Whitney U-test). Mean *GPP* was reduced from 45.4 tC to 40.5 tC ha/year and mean *NPP* value was reduced from 7.6 to 2.4 tC ha/year (Fig. 5). Net ecosystem exchange predicted by the model decreased significantly from -0.2 to -3.7 tC ha/year (mean value) at year 2100 under the climate change scenario (P <0.001, Mann-Whitney U-test, range across stands of 0.2 to -7.1 tC ha/year, Fig. 5). Large variability and complex patterns of carbon fluxes among the studied scenarios and forest stands were predicted by the model (Fig. 6). Regardless of this complexity, shifts in temperature for 2100 drove stronger changes in all analyzed variables than shifts in rainfall (all analyses, P <0.001, Mann-Whitney U-test).

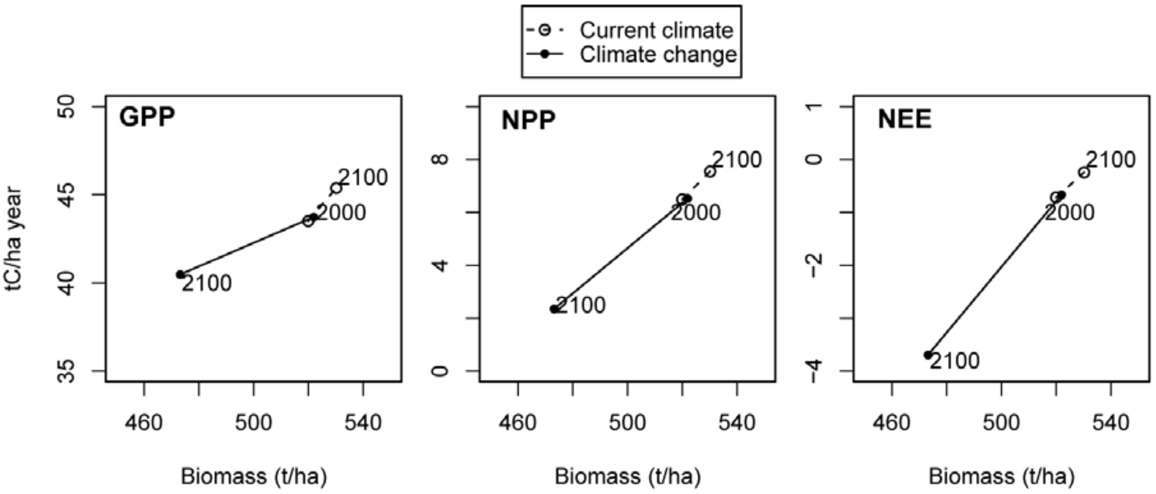

Figure 5. Forest carbon fluxes predicted by the model in all studied forest stands (mean values of 12 sites, N=240) under current climate and climate change scenario for year 2000 and 2100. *GPP*: Gross Primary Production; *NPP*: Net Primary Production, *NEE*: Net ecosystem exchange. Biomass is forest above ground biomass (*AGB*). Note different scales on the y-axes.

Simulated successional pathways

Predicted changes in tree species composition for year 2100 under climate change were modest in comparison with current climate scenario (Fig. 7). Changes in composition for year 2500 were stronger compared to year 2100 (Fig. 7) and mainly in response to shifts in temperature (P <0.001, Mann-Whitney U-test, data not shown). Changes in early-successional species *AGB* at year 2100 under climate change (Fig. 7) were mainly driven by *Eucryphia*, which had the strongest *AGB* reductions among species groups (averaged *AGB* reduction of 21.8 t/ha). Reductions in *AGB* of early successional species due to climate change were stronger in the long term (i.e. at year 2500, Fig. 7). *AGB* of mid- and late-successional species did not change under climate change scenario at year 2100 (Fig. 7) but *AGB* of mid-successional species increased for year 2500 (Fig. 7). In general, successional pathways predicted by the model for the next century under climate change scenario were similar to those predicted under current climate but varied among focal stands (Fig. S2, S3). In the long term, different successional pathways emerged under the climate change scenario with potential compositional shifts mainly as a result of the slow but successful establishment of new tree species under the novel climatic regime (Fig. S2, S3).

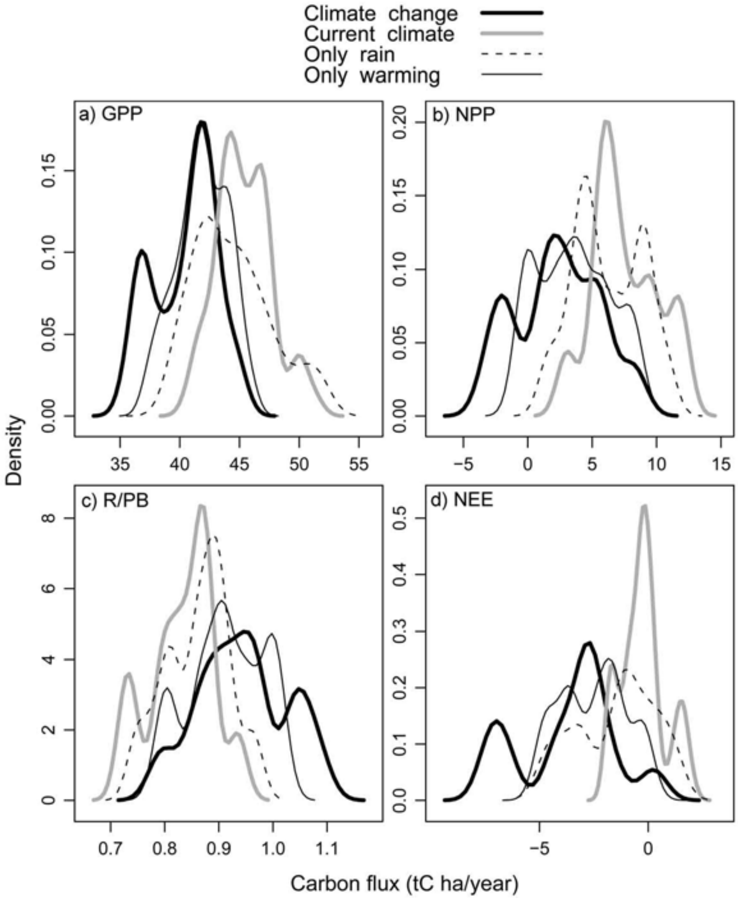

Figure 6. Density distribution of forest carbon fluxes predicted by the model in all studied forest stands under different climatic scenarios for year 2100 (240 simulations). *GPP*: Gross Primary Production; *NPP*: Net Primary Production, *R/PB*: proportion of stand-level autotrophic respiration (*R*) and forest gross photosynthetic production (*PB*); *NEE*: net ecosystem exchange. Note different scales on the axes. Climatic scenarios as in figure 4.

DISCUSSION

Impacts on forest functioning

According to our simulations, climate change expected for year 2100 will impact forest functioning (e.g. carbon balance) in Chiloé Island. Despite of simplified assumptions in the water balance model, we believe model results emphasise changes in water fluxes that can be a direct impact of climate change during the next century and constrain ecosystems services provided by natural forests in the study area, such as water supply (Lara *et al.*, 2009). Increases in 10% of *EVTP* projected by the model are consistent with impacts of climate change on this hydrological component in other temperate forests in North America (Running & Nemani, 1991, Aber *et al.*, 1995). Forest water fluxes alterations due to climate change and their influence on forest functioning suggest that the impacts of climate change can be broader than those commonly proposed for the study region, such as compositional shift and tree migration (Armesto *et al.*, 2001, Markgraf & McGlone, 2005)

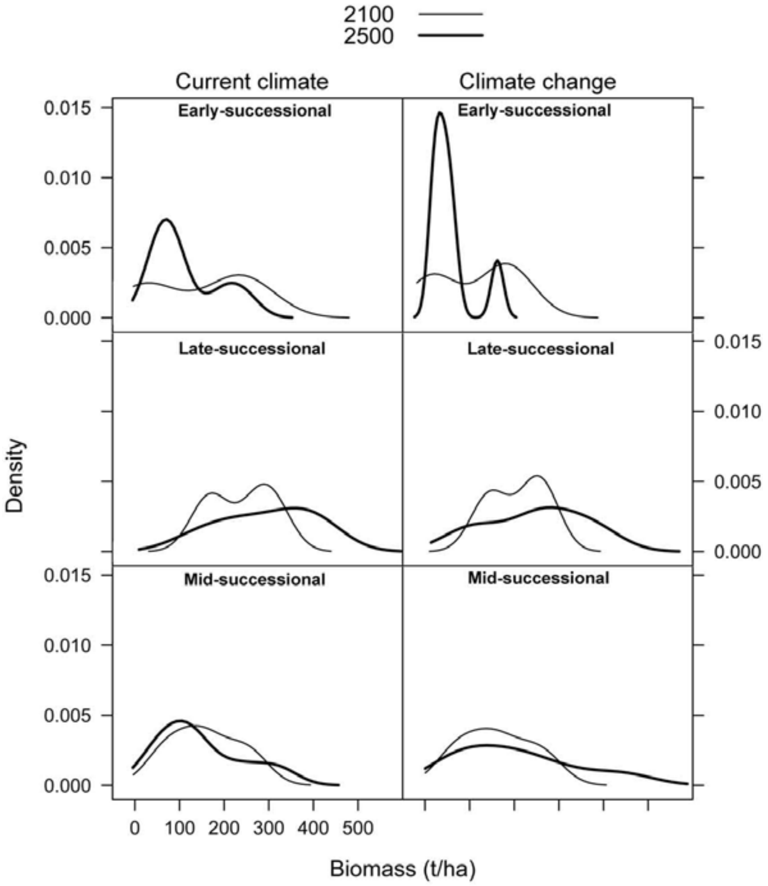

Figure 7. Density distribution of tree species above ground biomass (*AGB*) for year 2100 and 2500 under current climate and climate change. Species *AGB* was aggregated by successional status of tree species according to Table 1.

Climate change can decrease ~30% *NPP* in temperate rainforests of Chiloé Island (decrease of 7.6 to 2.4 tC ha/year, Fig. 5). This result contrasts to a global trend toward increased forest productivity under altered climates (Nemani *et al.*, 2003) and an overall increase in forest productivity due to climate change projected in temperate rainforests of the Pacific Northwest of North America (Lata *et al.* 2010). However, climate change can promote either increases or decreases in temperate forest productivity at local scales (Running & Nemani, 1991, Boisvenue & Running, 2006, Latta *et al.*, 2010). Latta *et al.* (2010) found declining productivity in forests located in low elevation areas experiencing water deficits during the growing season. Our results suggest that hotter and dryer growing seasons projected for Chiloé Island for the next century (Table 3) lead to strong reductions in soil water content, reducing biomass production due to water scarcity (Fig. 4). Warming impacted *NPP* by changing the proportion of photosynthesis and autotrophic respiration (from 0.83 to 0.94, *R/PB* in Figure 6). It has been proposed that process-based forest models can be simplified using a constant ratio of *NPP/GPP* that eliminates the uncertainties in the estimation of respiration (Waring *et al.*, 1998, Landsberg *et al.*, 2003). However, our simulation results showed complex responses of forest autotrophic respiration occurring at the stand level, varying among forest stands and under different scenarios of climate (Fig. 6). We suggest that process-based models assessing climate change impacts on forests should consider this local variability in processes of carbon acquisition and loss in order to reduce uncertainties in projections of forest responses to climate change across regions.

Our simulation experiments allow to assessing the role future forests of SSA may play in the carbon cycle. Carbon fluxes among the studied scenarios and across forest stands (Fig. 6d) revealed a variation related to the successional age and structural variability of studied stands. The model projected that climate change alone, without accounting for the direct effects of carbon dioxide (CO_2), can result in a net loss of carbon in all forest stands for year 2100 (average value of -3.7 tC ha/year). Warming produced carbon loss from forests due to increased autotrophic respiration (Fig. 6c). Decreased *GPP* due to water scarcity (Fig. 5) and biomass reductions in response to climate change were also predicted by the model (Fig. 4). Loss of carbon from forests may be reduced if N-mineralization is greatly accelerated and/or forests adapt to warmer temperatures (Saxe *et al.*, 2001). Additional carbon losses may occur in the future by the incidence of human-set disturbances (e.g. fires, logging, Smithwick *et al.* 2009) or climate-driven natural disturbances (Dale *et al.*, 2001), such as high intensity wind storms, extreme climatic events (e.g. droughts) and climate-driven changes in the dynamics of forest insects and pathogens. Carbon gain could also occur in the future by increased radiation driven by less cloud cover (Nemani *et al.*, 2003) but this was avoid in our model by relating radiation to rainfall occurrence. Increased CO_2 could promote faster forest grow and increase carbon storage but may confound the effects of climatic impacts on forest productivity (Smithwick *et al.*, 2009). We consider, however, the model results informative because document alterations in forest productivity related to climatic shifts projected for year 2100. The model also provides a starting point to explore these and other additional effects of climate change on forests of SSA.

Projected forest composition and dynamics

According to our simulations, climate change will not cause large shifts in forest composition in the study area during the next century. Forest compositional changes are projected by the model in the long term because of the establishment of tree species not present in the stands under current climate (Fig. S2, S3). Alternatively, this slow response of old-growth forests can be due to the long life spans of tree species (cf. Table 1). Long-lived tree species could remain in the canopy several centuries after climate change makes local conditions unsuitable for establishment (Franklin *et al.*, 1991). Similar results of a slow response to climate change has been projected in temperate rainforests of the Pacific Northwest where the long-lived pioneer *Pseudotsuga menziesii* remains as dominant species in the landscape (Busing *et al.*, 2007).

Functional grouping of tree species with emphasis on environmental influence on traits across many species provides a mechanistic understanding of climate change impacts on these species-rich ecosystems. As expected, climate change promoted in our simulations the dominance of thermophilic species (e.g. *Aextoxicon, Amomyrtus* and *Luma,* Table 1) and prejudiced species intolerant to warm climates (e.g. Podocarps, Fig. S2, S3). Furthermore, from our results, other traits appear relevant for species persistence such as physiological traits associated to mid-successional species and medium sizes (cf. Table 1, Fig. 7). In some stands, climate change seems to benefit late-successional species with potentially long lifespans (Fig. 7, e.g *Laureliopsis* and *Aextoxicon*). Long-life spans and slow grow seem to also promote the persistence of early successional species under climate change (e.g. *Weinmannia*). Regardless the preference of *Eucryphia* for warmer climates, this species declined in all forest stands suggesting that reductions in soil moisture due to climate change can be also a strong disadvantage for large and fast growing pioneers (Table 1, Fig. 7). Late successional species, such as *Myrceugenia,* with slow grow, short life-span and small sizes appear competitive excluded regardless its preference for warmer climates. However, future species composition under climate change appears to differ in relation to the successional stage of the stands. Thermophilic species (e.g. *Aextoxicon* and *Luma*) were not able to take over stands dominated by pioneer or mid-successional species (Fig. S3). Additionally, the predicted shift in composition in some stands occurs only after the decline of large and long-lived pioneer species (*Eucryphia*, *Nothofagus*, cf. Fig. S3). The occurrence of these individuals is more common in forests in mature forests in transition to the old-growth stage (Gutiérrez *et al.* in review, see also Fig. S3). Therefore, successional age of stands appears relevant to understanding potential compositional shifts in response to climate change. The model predicted that climate change can disrupt the dynamic equilibrium of steady-state forests, which enter a transient period of succession before reaching again stability (Fig. S2). Similar forest-climate disequilibrium has been projected for temperate rainforests of New Zealand (Leathwick *et al.*, 1996) and other temperate forests (Solomon, 1986).

Model performance and research needs

Here, we presented an individual-oriented process-based forest model that allows detailed analyses of forest dynamics under climatic variability in temperate rainforests of southern South America. We are not aware of other study attempting to project forest dynamics and forest functioning under climate change in this region. The model was calibrated using hydrological field data, the current knowledge of species groups and forest ecology in the study area and, therefore, represents the current “best guess” of forest responses to novel climatic conditions. The model provides projections for this region about the fate of 17 main canopy tree species for year 2100. The model can be used for projecting forest dynamics under climate change scenarios in northern Chiloé Island and neighbouring areas in the mainland, where the same species groups dominate the forests and where model assumptions held. The validity of the model is supported by significant correlations with field data from a set of 12 old undisturbed forest stands (Fig. 2) when running simulations under current climate. Given the studied climate change scenario (A2 business-as-usual scenario of IPCC, 2007), our projections can be considered as estimates of maximum rate of change expected for forests in the study area.

Our forest dynamics projections are limited by the degree of uncertainty generated by available climate models in this region (Christensen *et al.*, 2007) mainly due to the quality and availability of instrumental records. Changes in frequency of wind storms strongly determine composition and structure of forests in the study area (Gutiérrez *et al.* in review) but, to this point, climate projections for SSA do not provide information of the changes in wind storms frequencies and intensities in the future. It is relevant to understanding wind storm formations and their interaction with climatic anomalies such as ENSO and the Antarctic Oscillation, which also affect climatic regimes in the study area (Garreaud *et al.*, 2009). Climatic simulators for SSA provide limited information exist on extreme climatic events. Additionally, the tolerance of tree species to extreme climatic events (Zimmermann *et al.*, 2009) should be studied more in detail. It is expected that fires will become more frequent and intense in SSA as a result of climate change (Scholze *et al.*, 2006), and forest degradation and fragmentation is likely to continue in the next decade. Consequently, future model applications should consider the impact of human-set fires and forest fragmentation on forest dynamic projections under climate change.

Based on our results, we strongly encourage the development of experimental studies focusing in determine whole ecosystem carbon and water fluxes. These data are essential to understanding carbon cycling processes under a changing environment (Gough *et al.*, 2008). It would be useful to conduct experimental studies and establish long-term monitoring programs in representative sites because the determination of forest responses to climate change will require periodical data (Boisvenue & Running, 2006). At this point, continuous forest monitoring programs and studies addressing forest processes over time are incipient in SSA. In the meantime, forest models provide an alternative to long-term forest monitoring especially in forests of SSA where these datasets will be not available in the next decades.

CONCLUSIONS

In this study, we have projected the response of temperate rainforests in southern Chile to a business-as-usual scenario of climate change using an individual-oriented process-based forest model. Forests in this region can become sources of carbon in the next century as a result of climate change alone, i.e. without accounting for the direct effects of CO_2. Climate change can also decrease NPP, impact forest water balance by increasing water return in evapotranspiration and reducing rainfall input, and produce progressive shift in composition in the long-term. The patterns of carbon cycling under climate change emphasize intricate relationships between climate and forests related to the successional age and structural variability of stands. Knowing that our study is based on several assumptions, we believe that our results are helpful to inform the debate about forests responses to climate change in SSA. Future research should focus on conducting experimental studies and obtaining long-term monitoring data still not available in this region. The model developed here can support future modelling applications to explore impacts of multiple drivers of global change on temperate rainforests of southern South America.

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Supporting information

CALIBRATION OF DEMOGRAPHIC RATES

Table S1. Parameter estimates of the probability distribution and functions (m_B~N_{max}) used for calculating demographic rates of species groups under future climatic conditions

	Establishment rate (N_{max})			**Mortality rate (m_B)**		
Species group	**Probability Distribution**	**Parameters**		**Function**	**Parameters**	
		a	**b**		**a**	**b**
Aextoxicon	Exponential	0.02	-	Logarithmic	-0.002	0.02
Amomyrtus	Normal	229.2	88.2	Logarithmic	-0.013	0.08
Drimys	Exponential	0.006	-	Power	0.192	-0.48
Eucryphia	Normal	111.2	94.8	Logarithmic	-0.006	0.04
Laureliopsis	Normal	279.6	155.6	Logarithmic	-0.008	0.06
Luma	Exponential	0.04	-	Logarithmic	-0.004	0.03
Myrceugenia	Uniform	25	550	Logarithmic	-0.018	0.12
Nothofagus	Exponential	0.024	-	Uniform	0.006	0.009
Podocarpus	Exponential	0.096	-	Uniform	0.005	0.007
Tepualia	Exponential	0.03	-	Uniform	0.01	0.01
Weinmannia	Exponential	0.019	-	Power	5.670	-1.53

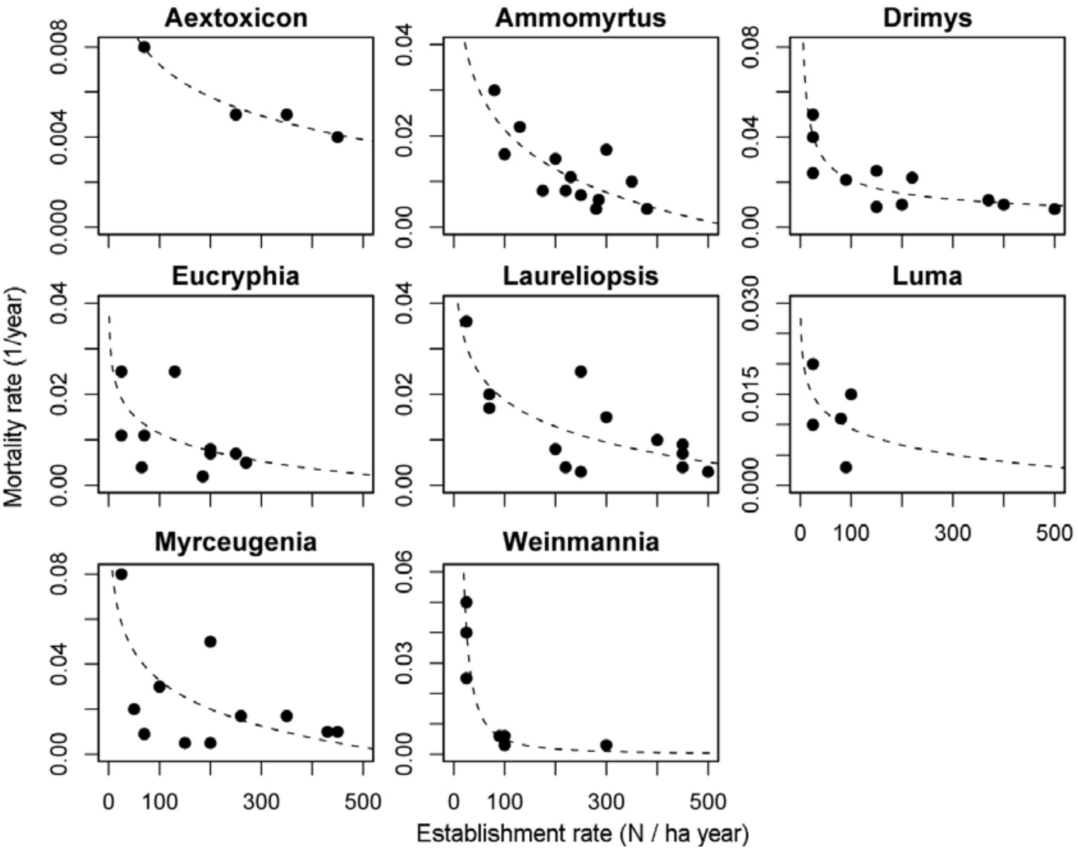

Figure S1. Relationships describing the trade-off between demographic rates of tree species. *Nothofagus*, Podocarps and *Tepualia* are not shown because relationships were uniform.

SUCCESSIONAL PATHWAYS UNDER DIFFERENT CLIMATIC SCENARIOS

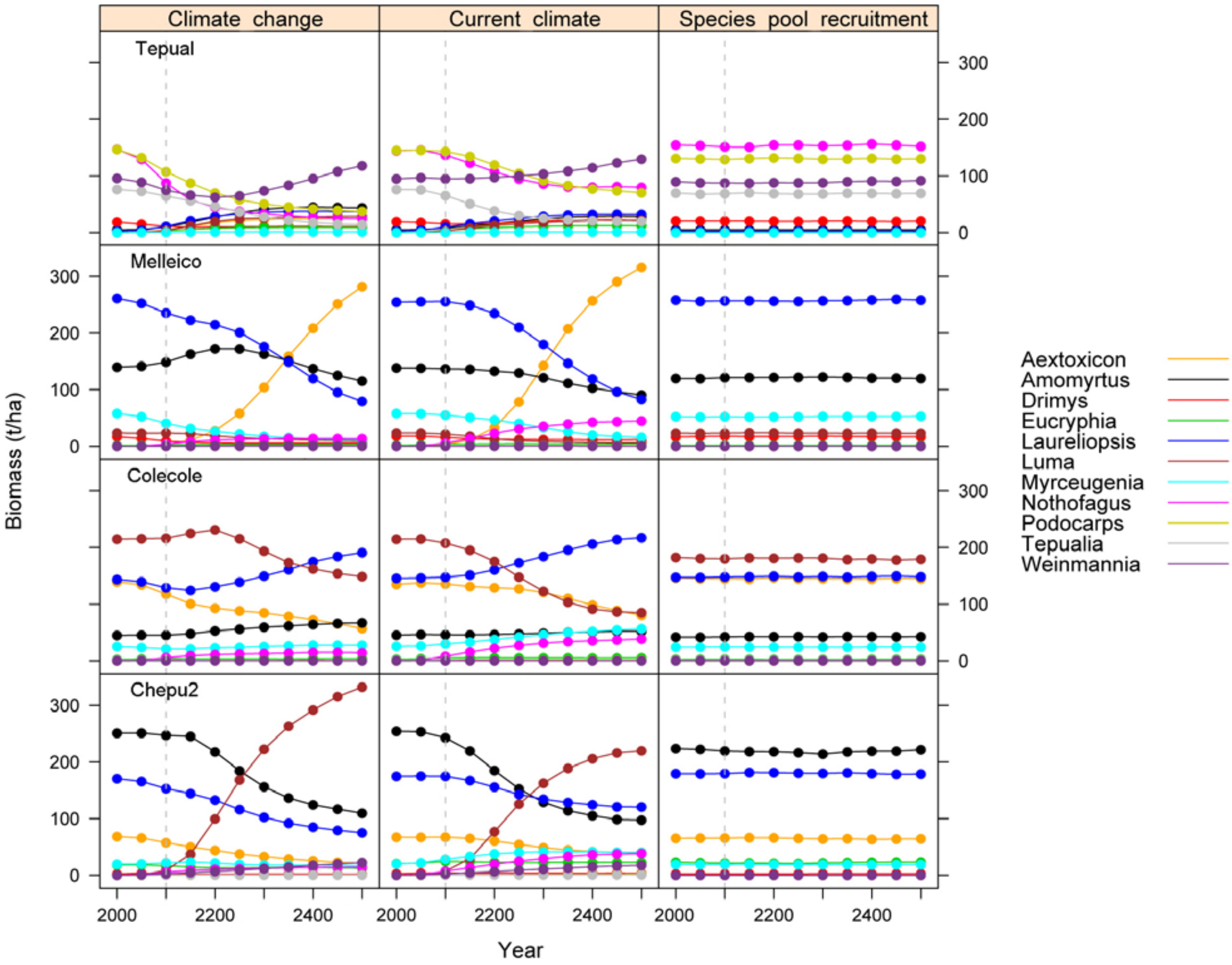

Figure S2. Successional pathways in old-growth forests (*OGI*>1, forest at steady state, Table 5). Climate change scenario includes changes in both rainfall and temperature according to Table 3 that were applied until year 2100 (gray line) and then climate was stabilized. Current climate is the climatic scenario under current climatic tendencies and assuming that all tree species can regenerate after year 2100. Species pool recruitment is the current climatic scenario but demographic rates were kept as Gutiérrez *et al.* (in review) according to the species pool in each stand. Results are the mean of 20 simulations of 25 ha for each stand.

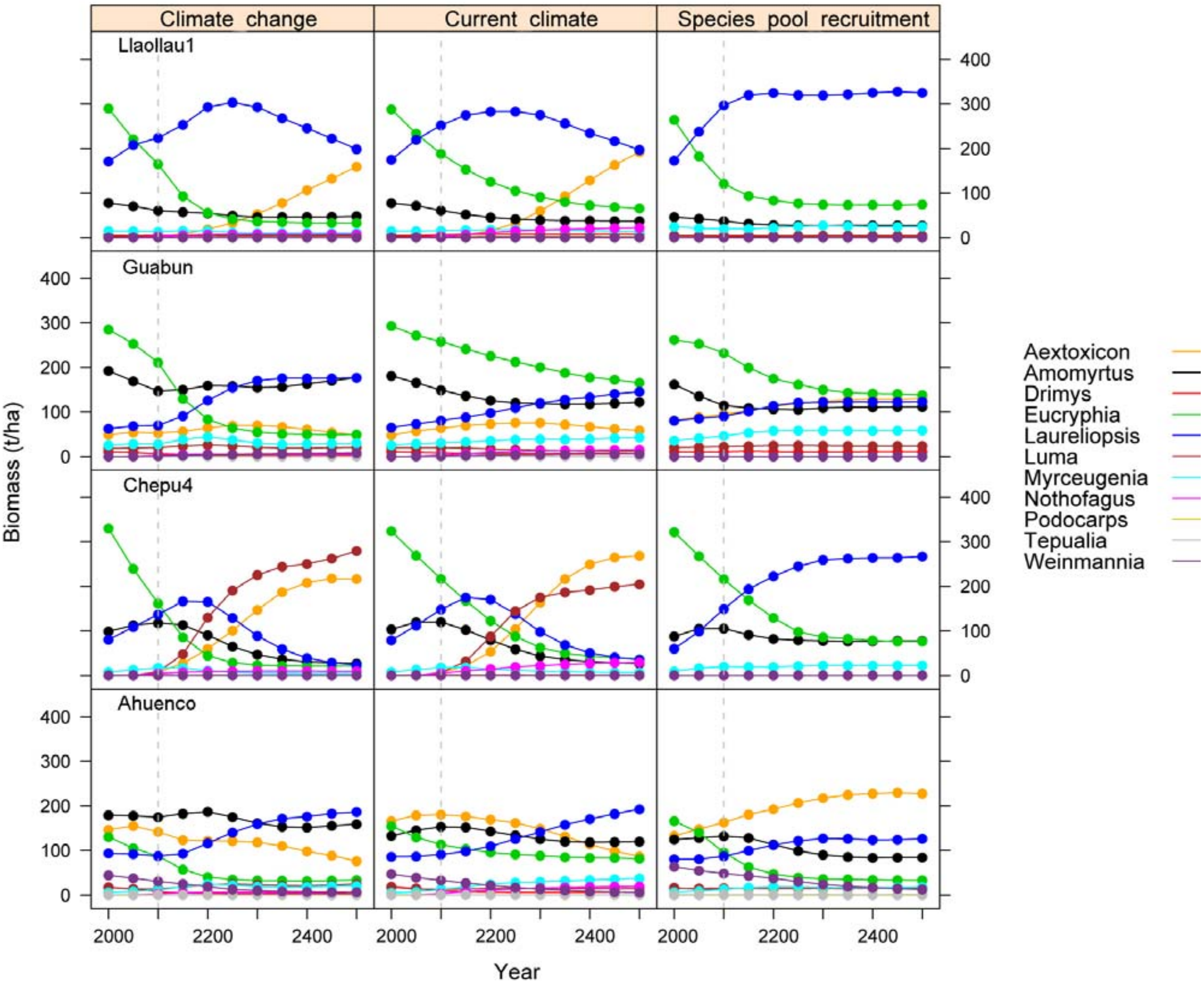

Figure S3. Successional pathways in forests in transition to old-growth (*OGI*<1, Table 5). Transient climate change scenario, including changes in both rainfall and temperature according to Table 3, was applied until year 2100 (gray line) and then climate was stabilized. Current climate is the climatic scenario under current climatic tendencies and assuming that all tree species can regenerate after year 2100. Species pool recruitment is the current climatic scenario but demographic rates were kept as Gutiérrez *et al.* (in review) according to the species pool in each stand. Results are the mean of 20 simulations of 25 ha for each stand.

SUPPLEMENTARY INFORMATION

An abstraction of reality

Contributions

AGG wrote the paper, programmed the model extensions and performed research. AGG and AH conceived the model. Francisca M. Díaz and Juan J. Armesto designed the hydrologic field sampling, performed field research and provided field data.

Photo credit: Alvaro G. Gutiérrez

The forest model `FORMIND-CLIM`

ABSTRACT

An individual-oriented process-based forest model (`FORMIND-CLIM`) is described that includes the effect of inter-annual climatic variability on forest processes. Extensions added to the core model `FORMIND` allow calculations of temperature influences on tree grow, forest carbon cycling and forest water fluxes. The model was calibrated using detailed field measurements of water cycling in a lowland temperate rainforest located on northern Chiloé Island, Chile. This data and independent data from temperate rainforests elsewhere were used to evaluate model performance. Results lend support to the validity of the model to simulate the hydrologic balance in temperate rainforests on Chiloé Island under current climatic conditions. The model allows detailed analyses of forest dynamics under current climatic variability and climate change scenario assessments.

THE MODEL

Here, an individual-oriented process-based forest model (`FORMIND-CLIM`) is described that includes the effect of inter-annual climatic variability on forest processes. The model is based on `FORMIND` (Köhler & Huth, 1998, Köhler *et al.*, 2000), a model successfully applied to simulate dynamics in tropical (Köhler *et al.*, 2000, Huth *et al.*, 2005, Rüger *et al.*, 2008, Groeneveld *et al.*, 2009) and temperate rainforests (Rüger *et al.*, 2007, Gutiérrez *et al.*, in review). Extensions added to the core model `FORMIND` allow calculations of temperature influences on tree grow, forest carbon cycling and forest water fluxes.

`FORMIND` is a forest growth model that simulates the spatial and temporal dynamics of uneven-aged mixed species forest stands (Köhler & Huth, 1998, Köhler *et al.*, 2000). The model simulates forest dynamics (in annual time steps, *t*) as a mosaic of interacting forest patches of 20 × 20 m, which is the approximate crown size of a large mature tree. Within these patches, forest dynamics is driven by tree competition for light and space following the gap model approach (Shugart, 1984, Botkin, 1993, Pretzsch, 2009). The model is individual-oriented, i.e. light availability is considered the main driver of individual tree growth (Pacala *et al.*, 1994). For the explicit modelling of the competition for light, each patch is divided vertically into height layers. In each height layer, the leaf area is summed up and the light environment in the forest interior is calculated via a light extinction law. The carbon balance of each individual tree is modelled explicitly, including the main physiological processes (photosynthesis, respiration). Growth process equations are modified from the models `FORMIX3` and `FORMIX3-Q` (Ditzer *et al.*, 2000, Huth & Ditzer, 2000, Huth & Ditzer, 2001, Rüger *et al.*, 2007). Allometric functions and geometrical relations are used to calculate above-ground biomass, tree height, crown diameter and stem volume from the *dbh* of the tree (stem diameter at 1.3 m). Tree mortality can occur either through self-thinning in densely populated grid cells, senescence, gap formation by large falling trees, slow tree grow, or external disturbances (e.g. wind throws). Gap formation links neighbouring grid cells. Tree regeneration rates are maximum rates of recruitment of small trees at *dbh* threshold of 1 cm, with seed loss through predation and seedling mortality being incorporated implicitly (Rüger *et al.*, 2007). These maximum rates are reduced by shading. Nutrient availability is considered to be homogeneous at the stand scale. A detailed description of `FORMIND` core model and its equations are found in Köhler & Huth (1998), Köhler (2000), Rüger *et al.* (2007). Here, new extensions to the previous model version (Rüger *et al.*, 2007) are described. A description of new parameters needed for running the model is found in Table 1.

Stress-induced mortality

A stress-induced mortality (Shugart, 1984, Bugmann, 1994) was included in `FORMIND` analogous to the size-related mortality of the model. This stress-induced mortality (m_{dinc}) is based on the assumption that only a small fraction of trees will survive a given number of years when they are subject to stress:

$$m_{dinc} = \begin{cases} m_{stress}, & Yrs_{stress} > MaxYrs_{sup} \\ 0 & \text{else} \end{cases}$$

where m_{stress} is the probability of mortality of slow growing trees, Yrs_{stress} is the number of consecutive years the tree has survived under suppression (i.e. diameter increment <0.1 cm years^{-1}) and $MaxYrs_{sup}$ is the maximum number of years recorded under suppression for a given tree species. Stress-induced mortality (m_{dinc}) is added to basic and size-dependent mortality (cf. Rüger *et al.* 2007).

Calculation of carbon fluxes

Forest net flux of carbon is calculated based on processes of carbon acquisition and loss (Woodwell & Whittaker, 1968, Chapin *et al.*, 2009), and integrated into the model after Pinard and Cropper (2000). The net flux of carbon in the atmosphere is interpreted in a yearly timescale. Under conditions where there are no changes in carbon availability in the atmosphere, the forest net carbon flux in each time step can be expressed as:

$$C_{flux} = PB - R - k_D D - t_A S \tag{1}$$

where C_{flux} is the forest net carbon flux (tC, tonnes of carbon hereafter, ha^{-1} year^{-1}), PB is the forest annual gross photosynthetic production (tC ha^{-1} year^{-1}), R is the forest total gross respiration (tC ha^{-1} year^{-1}), D is of the total biomass in coarse woody debris (tC ha^{-1} year^{-1}) and S is the total soil organic matter (tC ha^{-1} year^{-1}). k_D represents the decay rate of coarse woody debris and t_A is the transitional rate of soil biomass to the atmosphere (years^{-1}).

Table 1. Description of new parameters included in FORMIND-CLIM.

	Description	Units
Carbon Balance		
k_D	Decay rate of coarse woody debris (*CWD*)	% mass loss years^{-1}
t_A	Transitional rate of soil biomass to the atmosphere	% mass loss years^{-1}
t_S	Transitional rate of *CWD* biomass into the soil organic matter pool	% mass loss years^{-1}
Climate		
$1/\lambda$	Mean interval time between rainfall events	day^{-1}
η	Mean depth of rainfall events	mm day^{-1}
Rn_μ	Mean light intensity above canopy	µmol(photons) m^{-2} s^{-1}
Rn_σ	Standard deviation light intensity above canopy	µmol(photons) m^{-2} s^{-1}
T_μ	Mean daily temperature	°C
T_σ	Standard deviation daily temperature	°C
Hydrologic Balance		
n	Vertically averaged porosity of the soil	-
z	Soil depth	cm
k_{soil}	Soil texture dependent percolation rate at field capacity	mm day^{-1}
α_h	Slope of the canopy saturation curve	-
f_h	Parameter of the relationship LAI and canopy storage capacity	-
LAI_{max}	Maximum LAI of the studied forest	m² m^{-2}
WUE	Water-use efficiency	g CO_2 kg^{-1}H_2O
γ	Psychometer constant	Pa K^{-1}
L	Latent heat of vaporization of water	J Kg^{-1}
Δ	Rate of change of saturated vapour pressure with temperature	Pa K^{-1}
Bioclimatic model		
T_{Clow}	Lower temperature limit for CO2 assimilation	°C
T_{Chigh}	Maximum mean temperature for photosynthesis	°C
T_c	Mean temperature of the coldest month	°C
T_w	Mean temperature of the warmest month	°C
T_{ref}	Reference temperature respiration	°C
Q_{10}	Short-term respiration response to temperature	-
θ_{wp}	Wilting point of the soil	%
θ_{fc}	Field capacity of the soil	%

Annual gross photosynthetic production of the forest is calculated for each individual tree explicitly and is based on species-specific photosynthetic capacity (following a light response curve), total layer leaf area, incident solar radiation, light attenuation through the canopy, length of the photosynthetic active period per year, and the crown area of the tree (Köhler, 2000, Rüger *et al.*, 2007). Respiration is calculated for each individual tree explicitly and is divided into growth respiration during the build-up of new biomass and maintenance respiration of living biomass (Köhler, 2000, Rüger *et al.*, 2007). Growth respiration is assumed to be a fixed fraction of *PB* (Ryan, 1991), whereas maintenance respiration is assumed to be linearly dependent on the living biomass of the tree. A complete description of *PB* and *R* calculations is found in Rüger *et al.* (2007).

Necromass is divided into coarse woody debris and soil organic matter. Dead roots are not included in the model. Annual inputs to the coarse woody debris pool include biomass from dying trees such as leaves, branches and logs. A proportion of the coarse woody debris pool is decomposed into the soil organic matter pool. Accordingly, necromass dynamics is modelled by:

$$\frac{\mathrm{dD}}{\mathrm{d}t} = B_M - k_D D - t_S D \tag{2}$$

where B_M is the total biomass of death trees during the year (t ha^{-1} year^{-1}) and t_S is the transitional rate of *CWD* biomass into the soil organic matter pool (years^{-1}). Soil organic matter receives annual inputs of *CWD*. A proportion of the soil carbon is evolved as carbon dioxide (CO_2) and it is modelled by:

$$\frac{\mathrm{dS}}{\mathrm{d}t} = t_S D - t_A S \tag{3}$$

In temperate rainforest biomes, soil carbon below 50 cm depth probably represents about 6% of total ecosystem carbon (Smithwick *et al.*, 2002). Therefore, soil carbon below 50 cm depth is assumed to be static and is not included in the model. Root biomass is also not included in the model and probably represents 17% of total ecosystem carbon in these ecosystems (Smithwick *et al.*, 2002).

CLIMATIC MODELLING

Current and future rainfall time series were constructed as series of random numbers generated by probability distributions. The frequency and amount of rainfall events are assumed to be stochastic variables. Following the approach of Laio *et al.* (2001), the interval between precipitation events, τ (day) can be expressed as an exponential distribution given by

$$f_T(\tau) = \lambda \cdot e^{-\lambda\tau}, \qquad \text{for } \tau \geq 0 \tag{4}$$

where $1/\lambda$ is the mean interval time between rainfall events (day). The amount of rainfall when rainfall occurs, h (mm day^{-1}), is also assumed as an independent random variable, expressed by an exponential probability density function (Laio *et al.*, 2001):

$$f_H(h) = \frac{1}{\eta} \cdot e^{-\frac{1}{\eta}h}, \qquad \text{for } h \geq 0 \tag{5}$$

where η is the mean amount of rainfall (mm day^{-1}). Using this type of rainfall model is particularly useful because the parameters can be directly interpreted. Furthermore, it accounts explicitly for changes in frequency and amount of rainfall events (Laio *et al.*, 2001, Kumagai *et al.*, 2004, Porporato *et al.*, 2004).

Daily temperature (T_d, °C) was simulated via a Gaussian random variable with parameters (mean, μ, and standard deviation, σ) that vary according to season of the year. According to meteorological records from Chiloé Island, daily global radiation (Rg_d) varied among seasons in relation to daily rainfall (T-test, p <0.001, Fig. 1). Therefore, Rg_d was related to daily rainfall (P_d) via Gaussian random variable with parameters (mean, μ, and standard deviation, σ) that vary according to P_d ($P_d < 1$ mm and $P_d \geq 1$ mm) and the season of the year.

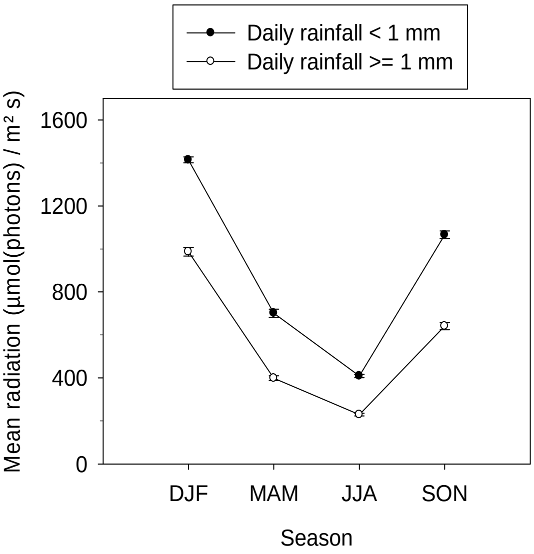

Figure 1. Mean radiation during the seasons related to amount of daily rainfall (observed data). Error bars represent standard error of the mean. DJF: December to February (austral summer, growing season), MAM: March to May, JJA: June to August (austral winter), SON: September to November (growing season

THE HYDROLOGIC MODEL

The soil moisture dynamics is interpreted at a daily timescale, treating the soil as a reservoir with an effective storage capacity that is intermittently filled by rainfall events. Soil water losses occur via transpiration, interception by the forest canopy, runoff and drainage below the root zone. Both the local vertical and horizontal spatial variability of soil moisture are considered negligible at the daily timescale, assuming an equal propagation of the wetting front and equal soil moisture redistribution over the rooting zone (Kumagai *et al.*, 2004, Porporato *et al.*, 2004). We neglected lateral water flow, thus the model applies mainly to terrains without marked topographic effects

The soil saturation s (volume/volume, i.e. dimensionless), vertically averaged over the soil depth z (cm), was considered as the state variable describing the dynamics of the soil water balance (Porporato *et al.*, 2004). Under conditions where there are no lateral contributions, the soil moisture balance equation at a point (Rodriguez-Iturbe *et al.*, 1999) is expressed as:

$$n \cdot z \cdot \frac{\mathrm{d}s}{\mathrm{d}d} = I_d - T_d - Q(s,d) \tag{6}$$

where d is the Julian day of the year, n is the vertically averaged porosity (volume of voids/total volume of soil, i.e. dimensionless); I_d is the net precipitation to the soil surface (mm day^{-1}); T_d is the transpiration rate (mm day^{-1}); and $Q(s,d)$ is the drainage below the root zone (mm day^{-1}). Following

Rodriguez-Iturbe *et al.* (1999), both n and z are assumed to be time-invariant parameters. Accordingly, the total volume of soil water per unit ground area at a given day d is $s \times n \times z$.

Soil saturation s is expressed as a fraction of pore space occupied by water, or volumetric water content divided by porosity,

$$s = \frac{\theta}{n} \tag{7}$$

where, θ is the volumetric water content (m³ water / m³ soil, i.e. dimensionless) so that $0 \leq s \leq 1$ (Rodriguez-Iturbe *et al.*, 1999). The normalized version of equation (6) is used through the text where all terms are divided by $n \cdot z$.

Net precipitation

Net precipitation to the soil surface (I_d) is described by,

$$I_d = P_d - Ec_d \tag{8}$$

where, Ec_d is the canopy interception (mm day^{-1}), defined here as the total amount of rainfall that is retained by the canopy and is evaporated so that it does not reach the ground. P_d is the daily rainfall obtained from equations 4 and 5. Following Rutter and Morton (1977), it is assumed that Ec_d asymptotically approaches the canopy storage capacity (Fig. 2a) and can be modelled at the daily time scale as:

$$Ec_d = S_t \cdot (1 - e^{-\alpha_h \cdot P_d}) \tag{9}$$

where S_t is the canopy water storage capacity of the stand at year t and α_h is a parameter describing the slope of the saturation curve for representing, in a simplified way, the complex process of water partitioning into throughfall and stem flow (Wattenbach *et al.*, 2005). S_t is calculated by the expression (Rey, 1999):

$$S_t = \frac{LAI_t}{LAI_{\max}} \cdot Sc_t \tag{10}$$

where LAI_t is the leaf area index of the forest at simulated year t, LAI_{max} is the maximum LAI of the forest type and Sc_t represents the maximum storage capacity at LAI_t. According to Wattenbach *et al.* (2005), a logarithmic relation between Sc_t and LAI_t can be assumed:

$$Sc_t = f_h \cdot (\log(1 + LAI_t) \tag{11}$$

where f_h describes the relationship between increasing LAI and storage capacity (Fig. 2b).

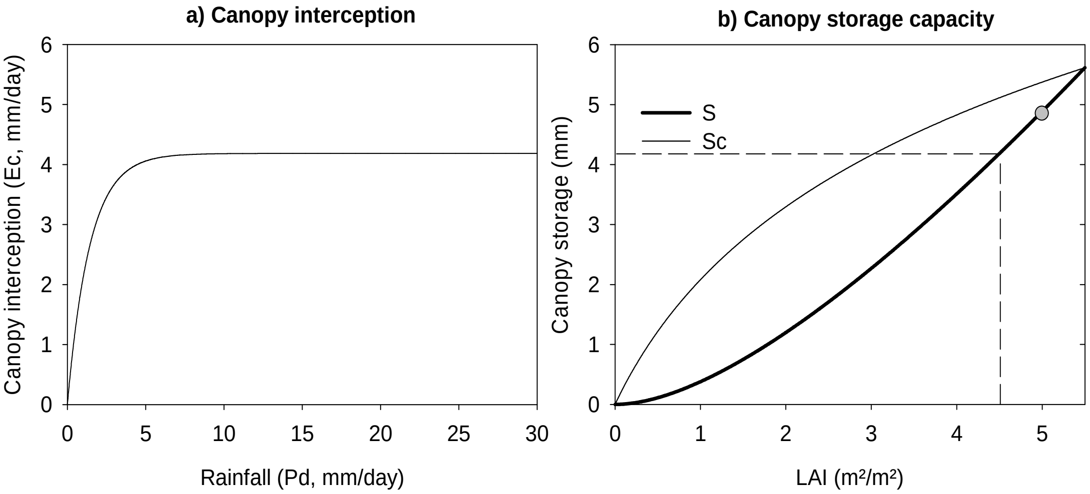

Figure 2. Examples of the relationships used to calculate the canopy interception of a forest patch. **a)** Canopy interception of a forest patch with *LAI* = 4.5 under different rainfall intensities. **b)** Canopy storage related to *LAI*. S represents the canopy storage capacity and Sc the maximum storage capacity at a determined *LAI*. The dashed line exemplifies the maximum canopy storage capacity attainable by a forest patch with *LAI* = 4.5 (c. 70 years-old). The grey dot shows the estimated canopy retention capacity for a forest stand of *LAI* = 5 calculated from field data (Diaz *et al.*, 2007).

Soil moisture modelling

Given the large rainfall intensity in the study area, it is reasonable to assume that net precipitation to the soil surface can exceed the soil infiltration capacity and leave the system through runoff. Field data of soil moisture are measured at a daily basis, and therefore, can be used on a daily time step to calibrate soil moisture and runoff calculations. Runoff occurs when the soil is saturated and no more water can be held by the soil porosity (i.e. $s = 1$). The excess of water is assumed to leave the system. Drainage out of the root zone ($Q(s,d)$) was modelled according to Rodriguez-Iturbe (1999). When the soil is saturated ($s = 1$), soil water is permitted to percolate at rate equivalent to the soil hydraulic conductivity of the given soil at field capacity (k_{soil}, mm d^{-1}). When $s < 1$, soil depth percolation rate is calculated using the empirical relationship of Neilson (1995), which has been broadly applied in vegetation modelling (Smith *et al.*, 2001, Sitch *et al.*, 2003),

$$Q(s,d) = k_{soil}\, s^2 \tag{12}$$

Transpiration

The water-use efficiency (WUE mmol H_2O m^{-2} s^{-1}) describes the proportion of water used for the assimilation of a unit of carbon in the photosynthesis (Lambers *et al.*, 1998). This concept can be used to compute transpiration of the forest from:

$$T_d = \frac{PB_d}{WUE} \tag{13}$$

where, PB_d is the forest gross photosynthetic production (µmol CO_2 m^{-2} s^{-1}) at day d.

Limitation of transpiration by the potential evapotranspiration

The daily potential evapotranspiration (PET_d, mm/day) describes a physical maximum that limits transpiration of the forest because only a certain amount of water can be held and transported away form the canopy under given climatic conditions. Generally, evapotranspiration consists of the total water vapour flux away from the canopy. Thus, it comprises evaporation from the vegetation and soil as well as transpiration. Evaporation is neglected in the model, therefore, it is assumed that maximum water losses by vegetation is limited by the difference between PET_d and the canopy interception of the day (Ec_d), as following:

$$PET_d - Ec_d \geq T_d \tag{14}$$

Daily potential evapotranspiration is calculated using a modified Penman-Monteith expression following the standard calculations of dynamic global vegetation models (Gerten *et al.*, 2004, Venevsky & Maksyutov, 2007). The variation of PET_d is determined by the variation of the daily net radiation flux (Rn_d, W/m²):

$$PET_d = (\frac{\Delta}{\Delta + \gamma})Rn_d / L \tag{15}$$

where γ is the psychrometric constant (ca. 65 Pa/K, slightly depends on temperature), L is the latent heat of vaporization of water (ca. $2.56\text{x}10^6$ J/Kg slightly depends on temperature) and Δ is the rate of change of saturated vapour pressure with temperature (Pa/K, Prentice *et al.*, 1993, Haxeltine & Prentice, 1996). Rn_d was calculated from latitude, day of the year, sunshine hours and air temperature following Prentice *et al.* (1993) and Venevsky and Maksyutov (2007). The rate of increase of saturated vapour pressure was calculated by,

$$\Delta = \frac{2.503 \times 10^6 \exp(17.269 \frac{T_d}{237.3 + T_d})}{(237.3 + T_d)^2} \tag{16}$$

THE BIOCLIMATIC MODEL

Climatic effects on forest processes

Climatic effects on tree biomass production, respiration and regeneration are modelled by combining functions representing different climatic controls, following the approach of Prentice *et al.* (1993):

$$m_P = \varphi(T_d) * \omega(s) \tag{17}$$

$$m_R = \phi(T_d) \tag{18}$$

$$m_E = \delta_{tc} * \delta_{tw} * \varphi(T_d) * \omega(s) \tag{19}$$

Where the m_P, m_R, m_E are composite multipliers for photoproduction, respiration and establishment, respectively. δ are functions taking values 0 or 1, and ω, φ and ϕ are non-negative, real-valued functions, as described below. Figure 3 shows the interaction of these multipliers with other variables calculated by the model.

Effects of temperature on tree biomass production and respiration

The effect of temperature on tree biomass production is computed as a daily temperature response function. Following Haxeltine & Prentice (1996), the effect of low temperatures on photosynthesis is calculated by a inhibition function (Fig. 4a):

$$\varphi_{Tlow} = (1 + \exp(k_1 * k_2 - T_d))^{-1} \tag{20}$$

where T_d is the daily mean temperature at day d, and k_1 and k_2 are calculated as follows:

$$k_1 = \frac{2 \log(0.01 / 0.99)}{T_{Clow} - T_c} \tag{21}$$

$$k_2 = 0.5 * (T_{Clow} + T_c) \tag{22}$$

where T_{Clow} and T_c are parameters representing the lower temperature limit for CO_2 assimilation and the mean temperature of the coldest month where the tree species can cop, respectively. Similarly, the effect of high temperatures on photosynthesis is calculated by:

$$\varphi_{Thigh} = 1 - 0.01 * \exp(k_3 * (T_d - T_w)) \tag{23}$$

where k_3 is calculated as follows:

$$k_3 = \frac{\log(0.99 / 0.01)}{T_{Chigh} - T_w} \tag{24}$$

where T_{Chigh} and T_w are parameters representing the higher temperature limit for CO_2 assimilation and the mean temperature of the warmest month where the tree species can cop, respectively. Respiration is assumed to increase exponentially with temperature (Prentice *et al.*, 1993):

$$\phi(T_d) = Q_{10}^{(T_d - T_{ref})/10} \tag{25}$$

where T_{ref} is a reference temperature.

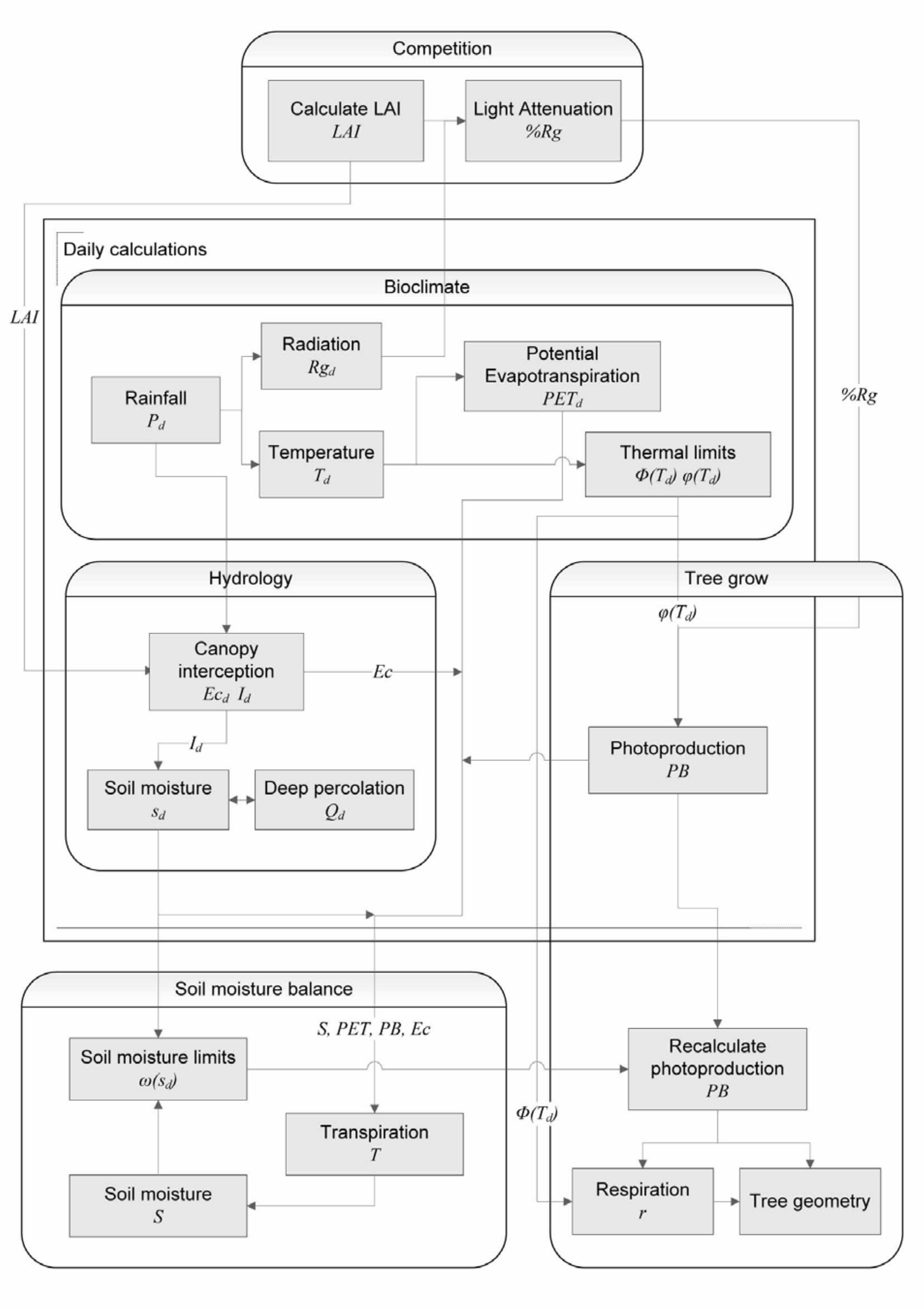

Figure 3. Representation of submodels interactions and variable dependencies in the model. Arrows indicate whether the results of a submodel influence the calculations of another submodel.

The approach described above is a simplified approach for constructing a mechanistic photosynthesis model, and equally simple models of respiration (Prentice *et al.*, 1993, Schenk, 1996). These models are based on functions widely accepted by ecophysiologists (Saxe *et al.*, 2001) and are well supported experimentally for short-term measurements of photosynthesis or for whole plants growing under a constant temperature regime (Loehle, 2000).

Soil moisture limits

The dependence of water uptake for tree biomass production on soil water content s is described by a function representing a reduction factor due to water scarcity ($\omega(s)$, $0 \le \omega(s) \le 1$). This factor accounts indirectly for the impact of water demand on potential photosynthetic production and it is implemented as a daily reduction factor due to water scarcity by,

$$\omega(s) = \begin{cases} 0, & s \le \theta_{wp} \\ (s - \theta_{wp})/(\theta_{msw} - \theta_{wp}), & \theta_{wp} < s \le \theta_{msw} \\ 1, & s > \theta_{msw} \end{cases} \qquad (26)$$

where, θ_{fc} is the soil field capacity (i.e. the soil moisture level when drainage becomes negligible) and θ_{wp} is the wilting point (i.e. minimal point of soil moisture the plant requires not to wilt). θ_{msw} represents a threshold when enough soil moisture is available for the potential biomass production of plants, defined as (all in percentage of soil water volume):

$$\theta_{msw} = \theta_{wp} + \tfrac{1}{3}(\theta_{fc} - \theta_{wp}) \qquad (27)$$

If the soil water content is between the θ_{msw} and θ_{wp}, a linear reduction of biomass production is assumed including soil moisture and the water demand for potential transpiration of leaves (Fig. 4b).

The required water for biomass production is completely removed from the soil water content when soil moisture reach θ_{msw} (i.e., $\omega(s) = 1$), both before the calculation of potential transpiration and after maximum possible transpiration of the leaves. Trees can only take soil water when soil moisture is higher than the wilting point, therefore, θ_{wp} represents the lowest soil moisture content needed for biomass production of trees. If water content falls below the θ_{wp}, transpiration is reduced until soil moisture reach exactly the critical value θ_{wp}. To avoid that soil water content is under θ_{wp} before the uptake of water by transpiration (e.g. due to deep percolation), transpiration is set to zero assuming that trees can not uptake soil water anymore.

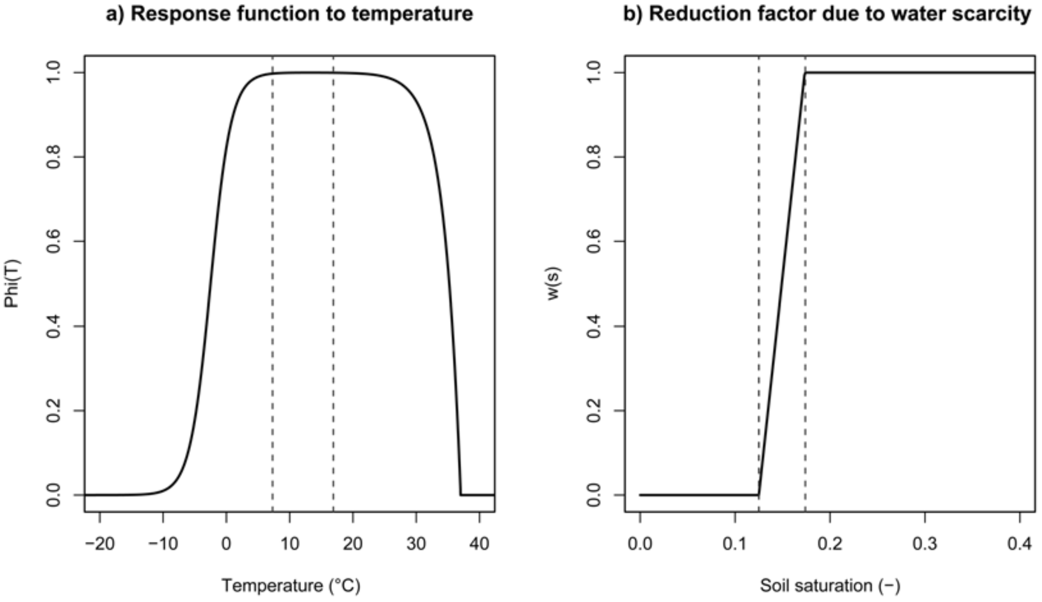

Figure 4. Climatic controls on forest processes. **a)** Daily temperature response function (φ) of photosynthesis. The dashed lines indicate optimal grow conditions for a tree species. **b)** Reduction factor of photosynthesis (ω) due to water scarcity. The dashed lines indicate the permanent wilting point and the minimum soil water for potential photosynthesis.

Regeneration filters due to temperature and soil moisture

Model formulations of temperature and soil moisture impact on regeneration are based on those generally employed in forest gap models (Aber *et al.*, 1982, Pastor & Post, 1986, Prentice *et al.*, 1993) and successfully extended to represent global forest biomes by dynamic global vegetation models (Sykes *et al.*, 1996, Smith *et al.*, 2001). In these models, minimum winter temperatures are used to predict the cold limit of many tree species distributions and appear to reflect seed-setting requirements (Smith *et al.*, 2001). This limit is represented in the model by the mean temperature of the coldest month (T_c), and is applied as follows:

$$\delta_{tc} = \begin{cases} 1, & T_c \leq T \\ 0, & \text{else} \end{cases} \tag{28}$$

where T is the predicted mean temperature of the month. The mean temperature of the warmest month (T_w) is used to predict the warm limit distribution of tree species. Following Prentice *et al.* (1993), above this limit no regeneration can occur (i.e. $\delta_{tw}=0$ if $T > T_w$) and under this limit regeneration is not limited ($\delta_{tw}=1$). If growth is limited by temperature or by soil moisture (ω and φ functions), the regeneration is also limited. The above climatic limits of species are combined in a multiplier (m_E, Eq. 19) that is multiplied by tree regeneration rates in every time step to determine the number of new stems per species.

MATERIALS AND METHODS

We used the field data described below to calibrate the hydrologic model. In 2007, two plots of 20 x 20 m were located to measure the hydrologic balance of a secondary forest stand (ca. 70 years old) located in a flat area at *Estación Biológica Senda Darwin* (EBSD, Chiloé Island, Chile, 41°50' S). The stand was dominated in the canopy by *D. winteri* and *N. nitida* (Table 2) with structure and composition similar to that described for secondary young North Patagonian rainforests elsewhere on Chiloé Island and on the mainland (Navarro *et al.*, 1999, Donoso *et al.*, 2007, Gutiérrez *et al.*, 2009). Net precipitation at this site was estimated using measurements of throughfall (i.e. rainfall that falls through canopy gaps and leaf drip), and stemflow. Stemflow and throughfall of the forest stand were measured for rainfall events (N = 14) occurring between June to October 2007 and April to November 2008. During the same time period, hourly records of rainfall from the meteorological station at EBSD were analyzed to obtain daily incident rainfall above the canopy. Rainfall events considered in the analysis occurred at least with a separation time of two hours without rainfall to allow the full drip from forest canopy. Stemflow collectors consisted of a 2 mm thick smooth polycarbonate sheet that was moulded around the stem to form a funnel to collect the stemflow. A hose led from the lowest point of the funnel to a 25 l polythene container, where the stemflow water was periodically collected after each rainfall event. Stemflow collectors were located in 10 trees randomly selected per plot with *dbh* >10 cm (i.e., stem diameter at 1.3 m height) of the main canopy tree species. Two trees were eliminated because they died during the study period. The amount of collected water was transformed to mm of rainfall assuming that the surface of the collectors equals the projected tree crown area. Crown area was approximated by the area of an ellipse. Throughfall collectors 0.12 x 2 m (total area of 0.7 m² per plot) long gutters were held, with a slight inclination, 0.5 m above the ground in three different areas of each plot. Collectors were connected with a funnel to a 25 l polythene container. Soil matric potential was measured with four sensors per plot (*WatchDog Data Loggers* 450 and 800). Sensors were approximately located in every quarter of each plot and beneath the canopy. Continuous soil moisture measurements were obtained every 30 minutes for the period January 2007 to January 2008. Hydrologic balance predicted by the model was also compared with estimates conducted in other temperate rainforests elsewhere in Chiloé Island and the mainland.

RESULTS AND DISCUSSION

Climatic modelling

Figure 5 compares probability density distributions of observed and measured daily climatic records. The computed probability distributions were similar to recorded data and had only some departures at the tail of predicted distribution for temperature (>25°C). Because the projected scenarios of climatic warming are provided at seasonal timescales, it is also instructive to compare how well the measured and modelled climatic patterns agree for all four seasons. Figure 6 shows that the weather generator reproduced well the seasonal fluctuations in rainfall, temperature and radiation during the year with no significant departures from observed climatic records.

Table 2. Structure of the secondary forest used for the measurement of hydrologic fluxes.

Species	Density (N/ha)	Basal area (m^2/ha)
Amomyrtus spp.	388	1.4
Drimys winteri	1550	32.3
Eucryphia cordifolia	175	0.9
Myrceugenia spp.	88	0.2
Nothofagus nitida	713	17.7
Podocarpaceae	38	0.1
Tepualia stipularis	538	1.9
Weinmannia trichosperma	88	0.3
Total	**3575**	**54.8**

Hydrologic modelling

Predicted infiltration from rainfall (throughfall plus stemflow) was significantly correlated with measured values for several rainfall events (Fig. 7a, N=14, r^2 = 0.57, p <0.01). The model also simulated realistically the values of infiltration from rainfall when compared with the amount of rainfall occurred in each event (Fig. 7b). Predicted values of interception ranged from 38.3% to 49.7% of rainfall occurred in the studied events (forest patches ranging in *LAI* from 4.0 to 5.0), which were in the range of the estimated value from field measurements (40.6%).

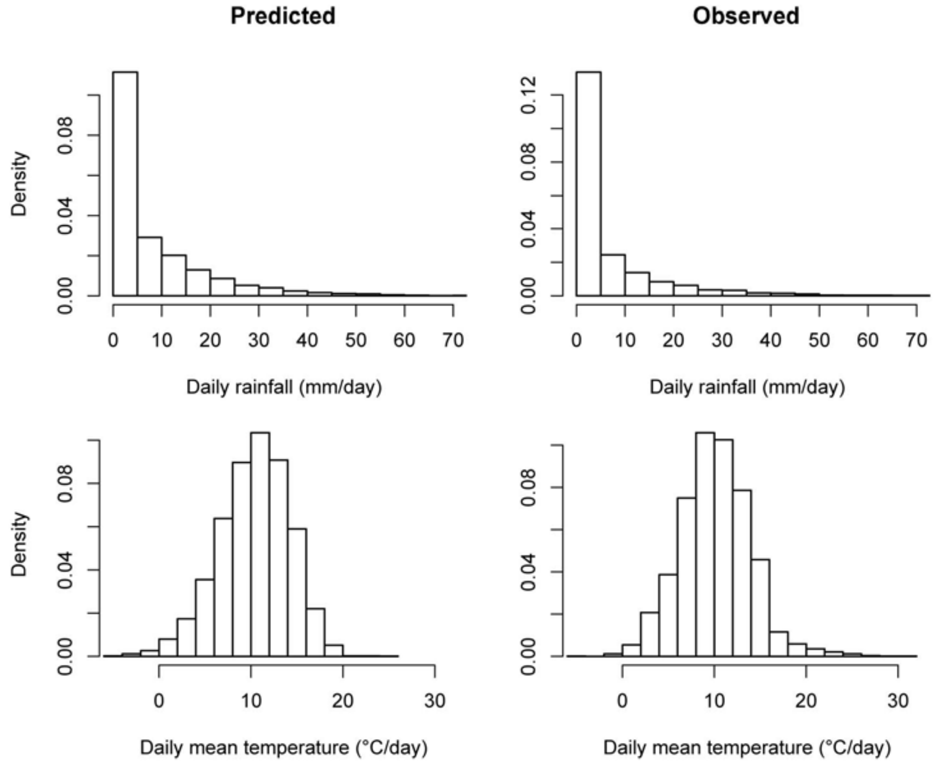

Figure 5. Probability density functions of daily rainfall and daily mean temperature calculated using climatic parameters from EBSD meteorological station, time period 1998 – 2009

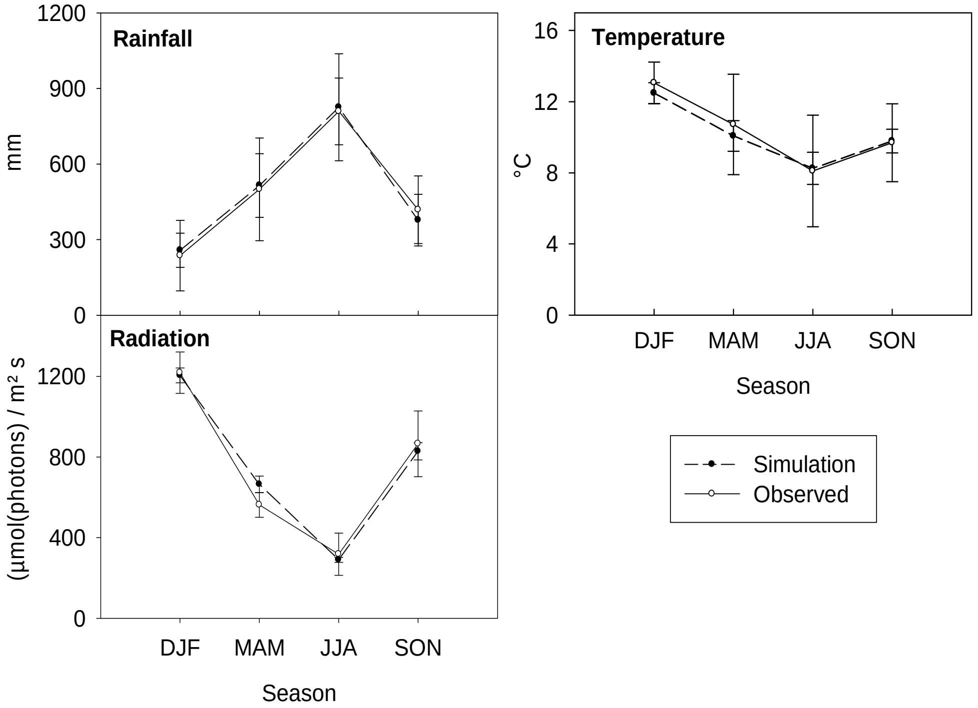

Figure 6. Comparison between simulated and observed climatic patterns during the year. Simulations were run for 100 years using parameters in Table 3 and daily data were averaged by seasons (mean daily temperature and daily radiation). Rainfall is the amount of rainfall during each season. Radiation and temperature are mean of daily values. Weather data are from EBSD meteorological station (N=14, period 1996-2009). Season according to table 3.

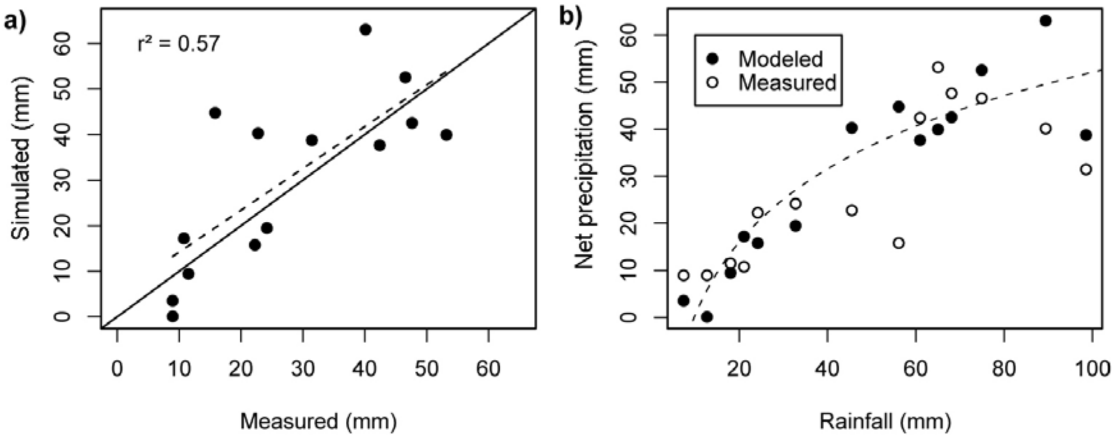

Figure 7. Comparison between measured and modelled net precipitation. **a)** Simulated net precipitation related to measured values, the solid line represents the 1:1 relationship, the dashed line in represents a linear regression between simulated and measured values. **b)** Net precipitation related to rainfall events. The dashed line represents the trend of simulated net precipitation in the studied rainfall events (non linear regression). All values are accumulated rainfall for every rainfall event (N=14). Model results are for a forest patch of 400 m² with a *LAI* = 4.5

Soil moisture dynamics during the year was compared using field measurements of soil matric potential (Fig. 8). Soil matric potential represents the adsorptive forces of the soil matrix, with a value near zero when the soil is saturated. As the soil dries, the matric potential increases. The model predicted an increased pattern of soil moisture after finishing the growing season (Figure 8a, 59< julian day< 242). This increase in soil moisture was triggered by a higher frequency of rainfall events and by decreased transpiration of trees. In contrast during the growing season, predicted soil moisture strongly decreased. The fluctuation in daily soil moisture in relation with the occurrence of rainfall was also realistically simulated by the model with increased soil moisture (decreases in soil matric potential) when rainfall occurs as shown in the measured soil moisture dynamics (Fig. 8b). Simulated soil moisture was also significantly correlated with the measured pattern of soil moisture during the year (Fig 8a, b, r^2 = -0.65, p <0.001). In summary, the hydrologic model simulates acceptably well the hydrologic balance for the North Patagonian forest where the hydrologic measurements were conducted.

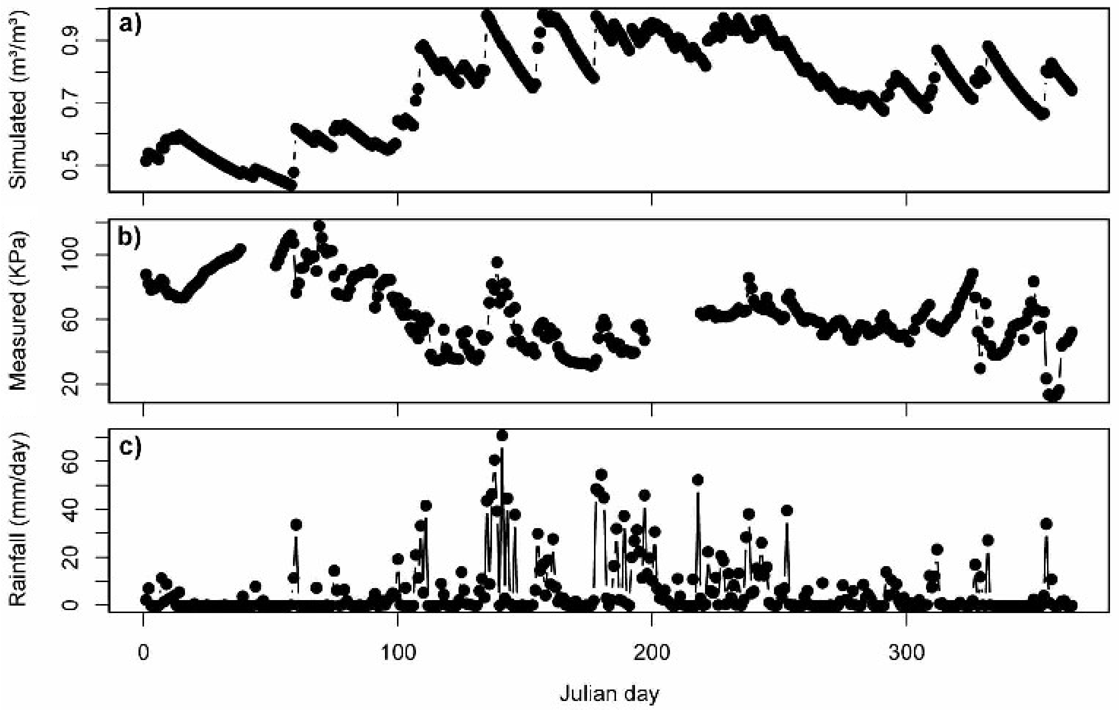

Figure 8. Comparison between **a)** simulated soil saturation and **b)** measured soil matric potential during 2008. Data in **(a)** are results for a forest patch of 400 m² with successional age of 70 years (LAI = 4.7). Data in **(b)** are daily mean values of 3 soil moisture sensors located randomly inside a plot of 400 m². Soil parameters are the same as described in Table 2. Daily rainfall events during 2008 are shown in **(c)** for reference.

The model estimated that annual transpiration and interception of the secondary forest under study was 238 ± 21.8 mm/year and 394 ± 18.5 mm, respectively. Evapotranspiration, computed as the sum of transpiration and interception, account for about 30% of total rainfall (i.e., 631.9 mm/year, Table 3). Predicted values of *EVTP* were similar to estimates by CIREN (1994) for Chiloé Island ranging between 576 to 724 mm.

Model predictions for the major components of forest water balance were in agreement with estimated values in the field by independent studies for broad-leaved temperate rainforests in Chile and elsewhere (Table 4). The only exception was depth percolation rate, which is mainly depending in k_{soil} that was calibrated for *Ñadi* soils of Chiloé Island according to values reported by Janssen *et al.* (2004). Physical characteristics of *Ñadi* soils such as high total pore volume, granular structure and high content of organic matter may affect the water-retention-curve, saturated hydraulic conductivity, infiltration, hydrophobic and the thermal properties of the soils (Janssen *et al.*, 2004). Field measurements of depth percolation are scarce for the studied forest type. Therefore, model results were compared with independent data from a forest developed in a soil type with different physical properties (*Trumao* soils) and with a mixed composition of broadleaved and caducifolius tree species (*Nothofagus obliqua*, Echeverría *et al.*, 2007). Regardless these differences, model predictions of depth percolation were reasonable. Model predictions for runoff were also realistic when comparing data from watershed forested with evergreen temperate rainforests in southern Chile (Lara *et al.*, 2009). These results lend support to the validity of the model to simulate the hydrologic balance in temperate rainforests in the study area.

Table 3. Model estimates of the components of forest water balance in a 70 years-old secondary forest located in northern Chiloé Island, Chile. Data are averaged results of 20 simulations (sd: standard deviation. *EVTP*: Evapotranspiration, sum of interception and transpiration)

Variable	mm/year		sd	%
Depth percolation	984.6	±	57.1	46.4
EVTP	631.9	±	20.7	29.8
Net precipitation	1733.0	±	125.3	81.4
Interception	393.7	±	18.5	18.6
Rainfall	2126.7	±	131.4	-
Runoff	833.4	±	140.3	39.0
Transpiration	238.1	±	21.8	11.3

Table 4. Comparison of major components of forest water balance predicted by the model and independent data of temperate rainforests.

		Model results (mm/year)			(%)	Literature (%)	Source
Canopy Interception	Run200	378.7	±	20.3	20.6	22	(1)
	RunOG	385.8	±	25.9	21.5	17.8	(2)
Evapotranspiration	RunOG	657.6	±	23.1	37.1	19.9 - 33.3	(2, 3)
Net precipitation	Run200	1522.8	±	368.4	79.4	78	(1)
Depth percolation	RunOG	866.3	±	187.3	45.8	66.5	(2)
Potential evapotranspiration		768.3	±	3.7		576-724	(4)
Runoff	RunOG	648.6	±	448.8	30.0	30-55	(5)

(1) Broad-leaved evergreen forest, ~200 years old. Annual rainfall 2500 mm (Huber & Iroume, 2001) . (2): Mixed deciduous-broad-leaved old-growth forest. Annual rainfall 2400 mm (Echeverría *et al.*, 2007). (3) Mixed broad-leaved and conifer forest, ~200 years old in New Zealand. Annual rainfall 3400 mm (Barbour *et al.*, 2005). (4) Annual rainfall 2427 – 3991 mm (CIREN, 1994). (5) Annual rainfall 1700 – 4500 mm, data from evergreen forests with 90% cover (Lara *et al.*, 2009). Results are running mean over a 50 years period (± standard deviation) and simulations were assessed at 200 years and when the forest reaches steady state (Run200 and RunOG, respectively). Simulations were run for 25 ha under a windstorms frequency of 0.8 % per year. % is the percentage of annual rainfall

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The ecologist cannot remain
a voice crying in the wilderness
if he is to be heard and understood.
(M.W. Hodgate)