

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at SciVerse ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.de/ppees

Research article

Successional stages of primary temperate rainforests of Chiloé Island, Chile

Alvaro G. Gutiérrez*, Andreas Huth

Department of Ecological Modeling, Helmholtz Centre for Environmental Research (UFZ), Permoserstr. 15, 04318 Leipzig, Germany

ARTICLE INFO

Article history:

Received 29 September 2010

Received in revised form 24 January 2012

Accepted 30 January 2012

Keywords:

Forest gap model

Life-history traits

Chile

Old-growth forests

Structural variability

Forest turnover

ABSTRACT

Understanding forest succession is required when designing management strategies, analyzing forest functioning, and forecasting the effects of changes in disturbance regime of forests. However, assigning a certain successional stage to forests in nature is challenging, especially when long-lived tree species dominate succession. Temperate rainforests commonly harbor emergent pioneer trees with long lifespans (>500 years) and may persist even when forest have reached stability in tree species composition (compositional equilibrium) and stability in structure (e.g. biomass). Thus, it is difficult to locate stands along a successional trajectory. Here, we propose a method for identifying the successional stages of forests using a dynamic forest model that estimate the time taken for a forest to reach the late successional stage, i.e. when forests have reached stability. Using this method, we examined the successional stages of 13 old, unmanaged stands of temperate rainforests located on Chiloé Island (Chile, 42°S). We parameterized the model for 17 tree species using field data and a comprehensive literature search. The model predicted varied successional pathways for reproducing the observed structural variability of studied forests stands. Model results suggest that forests in this region can take 490–850 years to reach the late successional stage. We found 6 out of the 13 studied forests represent a transient successional stage. Forest stands in the late successional stage commonly contained pioneer species with basal area <20 m²/ha. According to our simulations, pioneers can persist until the late successional stage because of their long lifespans and the occurrence of small canopy openings (<1.6 ha) produced by windstorms. Above-ground biomass in the studied forests (estimated at 539 t/ha, average among stands) tended to decrease as forests approach the late successional stage because large pioneers are replaced by smaller late-successional trees. These results can assist in the classification of natural forest according to their successional stages as well as in developing management and conservation strategies of primary forests in this region.

© 2012 Elsevier GmbH. All rights reserved.

Introduction

Forest composition and structure change during the development of stands (Oliver and Larson, 1996; Franklin et al., 2002). These changes have been used to locate stands along a successional trajectory, and to analyze changes in forest functions, e.g. carbon storage and exchange, define management strategies and forecast effects of changes in disturbance regime of forests (Pickett, 1989; Franklin et al., 2002; Pregitzer and Euskirchen, 2004; Luyssaert et al., 2008). However, it is difficult to assign a certain successional stage to forests in nature especially when long-lived tree species dominate succession. In theory, as forest succession advances, the first cohort of pioneers tends to disappear and the stand is taken

over by mid- and late-successional species (Oliver and Larson, 1996; Franklin et al., 2002; Wirth et al., 2009). Forests reach the late successional stage when the tree species composition is stable (i.e. compositional equilibrium, White, 1979) and forest structure is stable (e.g. biomass, Odum, 1969; Franklin and Spies, 1991). In forests containing pioneer tree species with long lifespans (>500 years), the time taken to reach stability can be long (Franklin et al., 2002; Wirth et al., 2009) thereby hampering the ability to recognize forests in the late successional stage.

In temperate rainforests, conifer pioneer trees >1000 years old and broadleaved pioneer trees >500 years old are not uncommon in old forest stands (Franklin and Hemstrom, 1981; Lara, 1991; Lusk and Ogden, 1992; Lusk and Smith, 1998; Gutiérrez et al., 2008; Wood et al., 2010). As consequence it is difficult to determine whether old stands harboring pioneers represent the late successional stage. Several studies conducted in temperate rainforests have addressed the question of how long-lived shade-intolerant tree species are maintained in forests where many co-occurring species are shade tolerant (Lusk and Ogden, 1992; Coomes et al.,

* Corresponding author. Current address: Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Sciences, ETH Zürich, 8092 Zürich, Switzerland. Tel.: +41 44 632 07 65; fax: +41 44 632 13 58.

E-mail address: bosqueciencia@gmail.com (A.G. Gutiérrez).

2005; Gutiérrez et al., 2008). Pioneer trees may persist in old stands due to their specific life-history traits (e.g. long life spans, Gutiérrez et al., 2008; Wirth et al., 2009) and the occurrence of infrequent large-scale disturbances events (Franklin and Hemstrom, 1981; Veblen et al., 1981; Franklin et al., 2002). Temperate rainforests are found in coastal areas with temperate and humid climates (annual rainfall > 1400 mm), such as the Pacific Northwest of North America, southern South America, south-eastern Australia, and New Zealand (Alaback, 1991). Significant areas of primary temperate rainforests harboring emergent pioneer trees are found along the western coast of southern South America (37–43°S, Donoso, 1993; Armesto et al., 2009). In this region, pioneer tree species may coexist with shade-tolerant tree species in mature forest stands even under a small-scale disturbance regime, such as canopy openings <1.6 ha produced by windstorms (Veblen et al., 1981; Veblen, 1985; Armesto et al., 1986; Gutiérrez et al., 2004, 2008). Although studies in this region have compared old and young stands with regard to their structural attributes (e.g. basal area) and composition (Aravena et al., 2002; Gutiérrez et al., 2009) no attempts have been made to explore the thresholds at which a forest enters the late successional stage. Similar to other temperate rainforests (Ohmann and Spies, 1998; Franklin et al., 2002), old stands in this region are commonly variable in terms of structure and composition (Lusk, 1996a; Gutiérrez et al., 2009). The extent to which structural variability of old stands reflects particular site conditions rather than different initial conditions that influenced successional pathways remains poorly understood (Lusk, 1996a; Aravena et al., 2002).

Individual-based forest successional models (i.e. gap models) provide a tool to explore thresholds at which a forest enters a certain successional stage. Gap models simulate the fate of single trees on the basis of species' life-history traits and limited resource availability (e.g. light, Botkin et al., 1972; Shugart, 1984; Bugmann, 2001), thereby facilitating detailed analyses of forest successional trajectories. Gap models have synthesized current ecological knowledge to analyze dynamics of temperate and boreal forests of the northern hemisphere (Shugart, 1998; Bugmann, 2001) but also in southern temperate forests (Pausas et al., 1997; Hall and Hollinger, 2000). To our knowledge, only one forest gap model has been applied in the temperate rainforests of southern South America to study a primary stand (Rüger et al., 2007). In the present work, we used a forest gap model to analyze the successional stages of 13 old unmanaged forest stands located on Chiloé Island, Chile (42°S, >170 years-old). We examined how well the model reproduced structure and composition of forest stands. In doing so, we extended the applicability of the original model by Rüger et al. (2007) including a much larger set of tree species (11 species groups, representing 17 tree species). Using the model, we analyzed the thresholds at which forests enter the late successional stage and explored the following questions: (1) Is the observed structural variability of the studied forests explained by different successional stages? (2) Can a small-scale disturbance regime (i.e. canopy openings <1.6 ha) maintain the current tree species composition in primary forest stands? (3) What structural changes are expected to occur as forests approach the late successional stage?

Methods

Study area

We studied old unmanaged stands located 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. Forest stands in rural landscapes 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 and Armesto, 1996). The prevailing climate is wet-temperate with a strong oceanic influence (di Castri and Hajek, 1976). Rainfall – about 2000 mm annually – occurs all year round, with 13–25% falling during the summer (January–March). Mean annual temperature is 9–10.8°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). These forests are composed of a mixture of broadleaved evergreen tree species (Table 1), with the relative contribution of the different species 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, often lacking *Nothofagus* (Table 1; 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 primary forests of the study area except along forest margins and on coastal cliffs (Gutiérrez et al., 2009). 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 and Huth, 1998; Köhler, 2000). The model has been successfully applied to simulate dynamics in tropical (Köhler and Huth, 1998; 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 is driven by tree competition for light and space following the gap model approach (Shugart, 1984; Botkin et al., 1972). 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. Light availability is considered the main driver of individual tree growth (Pacala et al., 1994) and carbon balance of each individual tree is modeled

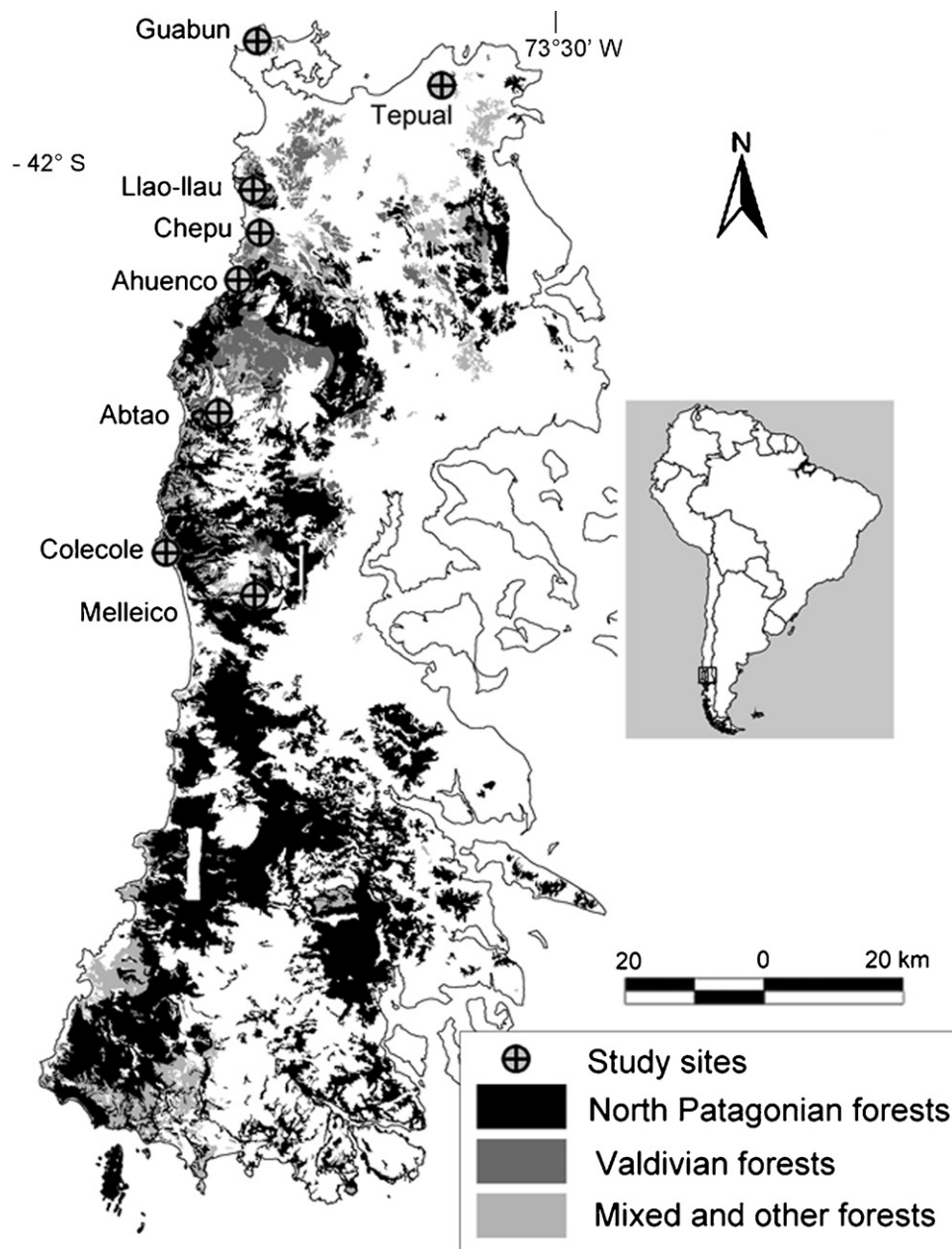


Fig. 1. Study site locations (circles) and distribution of main forest types of temperate rainforests on Chiloé Island, Chile.

explicitly, including the main physiological processes (photosynthesis, respiration). Growth process equations are modified from the models FORMIX3 and FORMIX3-Q (Huth and Ditzer, 2000, 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 (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, growth stress, or external disturbances (e.g. wind throws). Gap formation links neighboring patches by allowing large falling trees to damage trees in neighboring patches. Extensions to tree mortality calculations included in the model are detailed in Appendix A. 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 using an extensive field database on stand structure (4823 trees sampled), tree growth (based on tree-ring measurements of 720 trees), tree allometry (>600 trees sampled), and a comprehensive literature search. The model parameters, their description, calibration method and selected values are found in Table 2 and Appendix B (Table B1).

Table 1
Main life-history attributes of species groups and their correspondence with tree species found in temperate rainforest located on Chiloé Island, Chile. The occurrence of tree species in the main forest types (North Patagonian and Valdivian) follows Veblen et al. (1983) and Gutiérrez et al. (2009).

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

^a For these tree species there is a high probability that the maximum published ages underestimate potential lifespan. n.d., no data available.

^b According to section 'Establishment and biomass production' parameters listed in Table B1.

^c References: Lara (1991), Lusk (1996b), Lusk (1999), Lusk and del Pozo (2002), Pollmann and Veblen (2004), Veblen (1985).

^d References listed in Table B1.

Environmental parameters

We used data collected during the growing season from the Senda Darwin station (41°52'S, 73°39'W, 60 m a.s.l., period 1996–2006, September until March) 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 and 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 followed Rüger et al. (2007). We used a species-specific parameter for maximum leaf area index (L_{max}) according to reported values for *Aextoxicon*, *Laureliopsis*, *Eucryphia* and *Nothofagus* (Saldaña and Lusk, 2003). For *Weinmannia* we followed as a reference L_{max} reported for the New Zealand temperate rainforest species *Weinmannia racemosa* (White and Scott, 2006). We corroborated L_{max} values using foliage mass as an approximation to derive the leaf area index (DeLucia et al., 2002; Moser et al., 2007). Accordingly, we obtained the leaf area index (LAI) by multiplying leaf lifespan, litter production, and specific leaf area according to species estimates reported in the literature (Table B2). Information on foliage mass was lacking for *Tepualia stipularis* and *Luma apiculata*. For these species L_{max} were set using the estimated LAI of species with similar foliage characteristics and crown architecture (i.e. *Myrceugenia* and *Amomyrtus*, all members of Myrtaceae). We fitted allometric function parameters (e.g. dbh–height, Fig. B1) using a non-linear minimization of a likelihood algorithm (Dennis and Schnabel, 1983) and using an individual tree dataset obtained from forest stand inventories (>600 trees sampled, Fig. B1). We adjusted the form factor such that simulated stem volume corresponded to empirical volume functions available in the literature (Fig. B2).

Biomass production parameters

The values for maximum rate of photosynthesis (p_{max}) followed values reported in the literature. 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 followed estimates for *W. racemosa* in New Zealand forests (Whitehead et al., 2005) and values of species with high demand for light to set lower and upper limits to p_{max} . Species light-use efficiency (α) estimates were not available. The relationship of species light-use is well established for species differing in shade tolerance (Lambers et al., 1998), therefore these values can be approximated following species assimilation rate and shade tolerance. Accordingly, fast-growing pioneer tree species with a high maximum assimilation rate (up to 14.2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) would have lower light-use efficiency ($\alpha \sim 0.03$ – 0.06) when irradiance is low (Eschenbach et al., 1998). Shade-tolerant tree species with low assimilation rates (4.9–7.2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) 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). Both selected p_{max} and α values were taken as a reference and were finally set after comparing predicted growth by the model under full light conditions and observed tree growth data (Fig. B3). We fit parameters for maintenance respiration (r_0 , r_1 , r_2) using tree-ring measurements from Chiloé Island (Table B3). We selected trees that were growing under full or high light conditions, i.e. fast-growing trees in forest edges, outside forests, and inside canopy gaps. We fitted r_0 , r_1 , and r_2 parameters by simulating stem diameter increments of trees under full light conditions until they generated an upper envelope for the measured diameter increments of trees (Fig. B3, annual diameter increment was approximated by multiplying tree ring width by two). Calibration was conducted, first by using a genetic algorithm and second by visual inspection of diameter increment simulations. 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).

Table 2

Parameter descriptions of FORMIND and parameterization method used for running simulations of temperate rainforests located on Chiloé Island, Chile. Full list of parameters used in the model and references are given in Appendix B.

	Description	Units	Method		Description	Units	Method ^a
Environment				Biomass production			
<i>k</i>	Light extinction coefficient for leaves	m ² (ground) m ⁻² (leaf)	3	<i>p_{max}</i>	Maximum rate of photosynthesis	μmol (CO ₂) m ⁻² s ⁻¹	3, 5
<i>I_o</i>	Average irradiance above canopy	μmol (photons) m ⁻² s ⁻¹	2	<i>α</i>	Light-use efficiency	μmol (CO ₂) μmol (photons) ⁻¹	1
<i>Sd</i>	Length of daily photosynthetic active period	h	2	<i>r_g</i>	Parameter of growth respiration		3
<i>seal</i>	Relative length of seasons (wet/dry)	year	2	<i>r₀</i>	Parameter of maintenance respiration		4
				<i>r₁</i>	Parameter of maintenance respiration		4
				<i>r₂</i>	Parameter of maintenance respiration		4
Tree geometry				<i>ρ</i>	Wood density	t m ⁻³	3
<i>D_{max}</i>	Maximum dbh diameter	m	2	<i>m</i>	Light transmission coefficient of leaves		3
<i>H_{max}</i>	Maximum height	m	2, 3	<i>codm</i>	Conversion of carbon in organic dry matter	t μmol (CO ₂) ⁻¹	3
<i>h₀</i>	dbh–height relationship	cm m ⁻¹	4	Establishment			
<i>h₁</i>	dbh–height relationship	m	4	<i>N_{max}</i>	Maximum establishment rates of small trees	N ha ⁻¹ years ⁻¹	4
<i>f</i>	Form factor		5	<i>I_{min}</i>	Minimum light intensity	% of <i>I_o</i>	5
<i>cd</i>	dbh–crown diameter relationship	m cm ⁻¹	1	<i>I_{max}</i>	Maximum light intensity	% of <i>I_o</i>	1
<i>c</i>	Crown depth factor		1	Disturbances			
<i>sw</i>	Fraction of stem biomass to total wood biomass		1	<i>Dist_f</i>	Proportion of years in which windstorm disturbance occurs	years ⁻¹	1
<i>L_{max}</i>	Maximum LAI per tree		5	Technical			
Mortality				<i>D_s</i>	Diameter of ingrowing trees	m	3
<i>m_B</i>	Basic mortality	years ⁻¹	4	<i>a</i>	Patch size	m ²	3
<i>m_{max}</i>	Maximum mortality of small trees	years ⁻¹	3	<i>Δh</i>	Step width of vertical discretization	m	3
<i>D_{mort}</i>	dbh up to which mortality is increased	m	3				
<i>D_{fall}</i>	Minimum dbh of falling trees	m	2, 3				
<i>p_{fall}</i>	Probability of dying trees to fall per year		1				
<i>m_{sup}</i>	Mortality of slow growing trees	years ⁻¹	3				
<i>MaxYrs_{sup}</i>	Maximum number of years under suppression	years	1, 2				

^a 1, estimated; 2, field data; 3, literature; 4, calibrated with field data; 5, calibrated using literature.

Establishment and mortality parameters

The species pool for each site was set according to observed species presence/absence in North Patagonian and Valdivian forests following Tables 1 and 3. Minimum light intensity for establishment (I_{min}) followed Lusk et al. (2006, 2008). Maximum light intensity for establishment (I_{max}) was estimated according to the shade tolerance of tree species (Table 1). The model includes a size-dependent mortality (m_D) because small trees (dbh < 10 cm) experience additional mortality that strongly declines with increasing dbh (Coomes and Allen, 2007). m_D is calculated from the maximum mortality of small trees (m_{max}) set to 5% (see also Appendix A). When trees >10 cm dbh are subjected to stress, mortality is increased in the model (m_{stress} , Appendix A). m_{stress} is calculated from the mortality probability of slow growing trees (m_{sup} , set to 2% according to Wyckoff and Clark, 2002) and the maximum number of years under slow grow ($MaxY_{sup}$), here determined using tree-ring datasets from the study area (Table B3, Appendix A). *L. apiculata* and *T. stipularis* lacked information on $MaxY_{sup}$ and their values were estimated by personal observations of the authors. m_{stress} and m_D are added to a basic probability to die (m_B , species-specific, see also Appendix A). To the best of our knowledge, establishment rates and m_B of adult trees are not available for temperate rainforests in Chile, therefore these parameters were calibrated against field data (see section 'Model calibration'). Minimum dbh of falling trees followed values reported in the literature (Table B1) and the probability of dying trees falling followed Rüger et al. (2007).

Field data for model calibration

For testing model outputs at species and community level, we selected old forests located on northern Chile Island (N=13, Table 3 and Fig. 2, field data). All stands represented forests without evidence of human disturbance through logging or fire. Detailed disturbance histories were only available for Tepual and Guabún (Gutiérrez et al., 2004, 2008), and suggested stand ages of >350 years. All studied stands had forest attributes indicative of mature conditions, such as presence of large emergent trees, patchy canopy including tree-fall gaps, tree-size distribution typical of uneven aged stands, canopy height >12 m, stand ages >170 years, and the presence of old canopy trees (Table 3). Overall these attributes are indicative of the lack of coarse-scale disturbances (>25 ha) for at least 200 years (i.e. prior to Chilean settlement on Chile Island). All stands used for this analysis were sampled using a similar sampling design, i.e. plots of 0.1–0.5 ha. All trees found in the plots (dbh > 5 cm) were identified according to species and their dbh was recorded. A detailed description of stand structure, disturbance history and field inventory methods are found in references provided in Table 3.

Successional age assessment

We defined the successional age of forest stands (SAGE) as the time elapsed since stand initiation, i.e. when trees colonize a treeless site resulting from a stand-replacing disturbance (>25 ha). The timing and spatial patterns of tree colonization during stand initiation leave structural imprints that can persist for centuries in temperate rainforests (Winter et al., 2002). Consequently, we assumed that the observed forest structure can be used as indicator for the successional age of forest stands. Under this assumption pioneer tree species can represent the time elapsed since stand initiation (Molino and Sabatier, 2001; Bongers et al., 2009). In order to determine SAGE, we systematically compared the observed basal area of all shade-intolerant pioneer tree species (BAobs) with their basal area through the simulated succession (Basim). We obtained

Table 3
Forest stands used for testing model outputs in temperate rainforests of Chiloé Island, Chile.

Stand ^a	Forest type ^a	Sampling area (ha)	Drainage	Slope (%)	Altitude (m.a.s.l.)	Oldest tree (years)	Basal area of pioneers (m ² /ha)	SAGE (years) ^b	LSI ^b	Above-ground biomass (t/ha)	Sørensen's index of similarity	Pearson correlations ^c	P
ABTAO	NP	0.1	Good	14	540	399	52.8	>670	1.6	446	0.66	0.56	0.08
AHUENCO	V	0.4	Good	Flat	80	308	25.0	300	0.5	662	0.82	0.71	.
CHEPU1	V	0.4	Poor	Flat	40	No data	12.9	>490	1.9	384	0.7	0.63	.
CHEPU2	V	0.4	Poor	0–10	80	No data	3.8	>580	1.8	543	0.97	0.95	.
CHEPU3	V	0.4	Poor	Flat	120	No data	16.2	>590	1.4	471	0.91	0.88	.
CHEPU4	V	0.4	Poor	0–5	120	No data	43.9	250	0.4	542	0.85	0.79	.
COLE-COLE	V	0.1	Good	30	80	No data	0.0	>550	1.6	597	0.94	0.9	.
GUABUN	V	0.4	Good	Flat	130	349	38.5	540	0.6	657	0.92	0.87	.
LLAOLLAU1	V	0.4	Good	Flat	150	No data	68.1	350	0.5	560	0.95	0.94	.
LLAOLLAU2	V	0.4	Poor	Flat	150	No data	44.3	360	0.6	499	0.85	0.81	.
LLAOLLAU3	V	0.4	Good	18–40	150	No data	42.5	350	0.5	583	0.82	0.75	.
MELLEICO	V	0.5	Good	20–40	280	307	4.2	>550	1.6	504	0.91	0.87	.
TEPUAL	NP	0.2	Poor	Flat	70	499	36.3	>590	1.2	554	0.96	0.95	.

^a P<0.05.

^{**} P<0.001.

^a References: Donoso et al. (1984, 1985), Gutiérrez et al. (2009). NP, North Patagonian, V, Valdivian forest type.

^b SAGE: minimum successional age of the stand, LSI: late successional index (average value of 20 model simulations per stand, see section 'Methods').

^c Pearson correlations between observed and simulated species density.

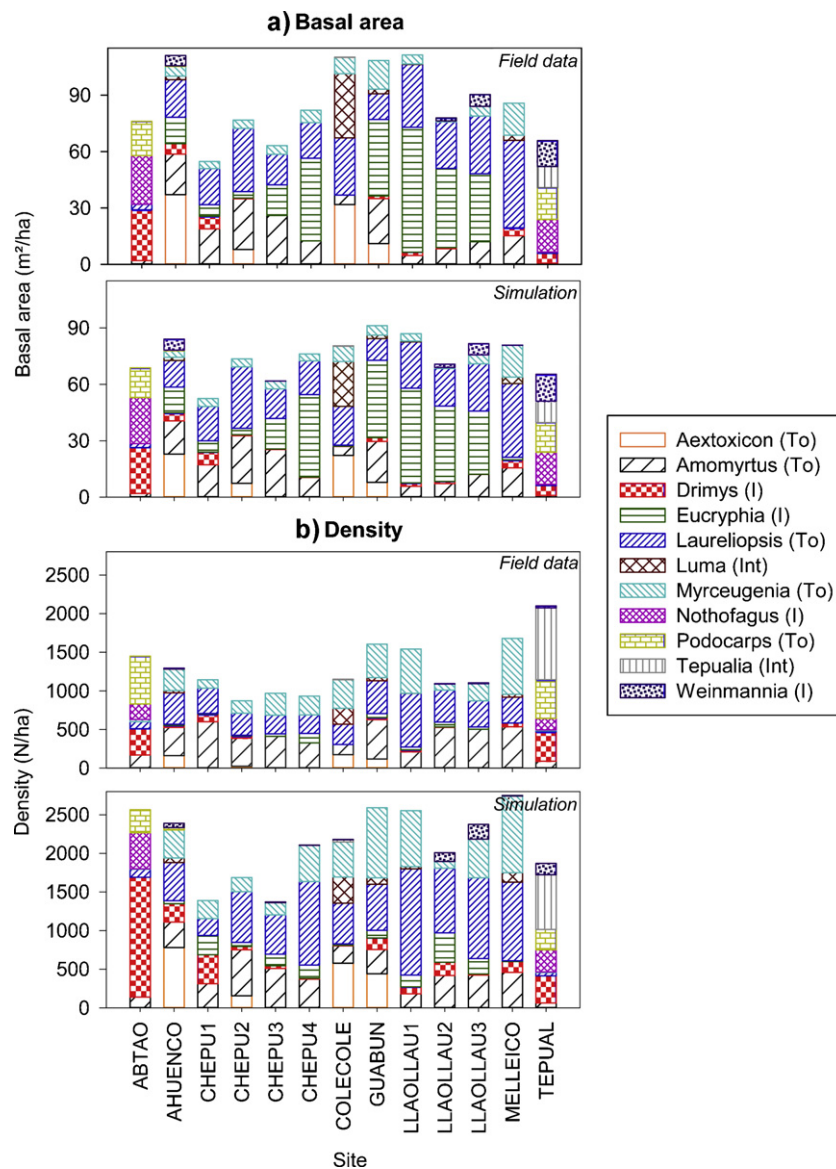


Fig. 2. Comparison of structural patterns obtained from field data and model results (simulation) for trees >5 cm dbh at SAGE of each stand. Model results represent the best agreement at SAGE (see section ‘Methods’ for details) between observed and simulated community structure. Table B1 details the selected values for model parameters used to run these simulations. Species group names according to Table 1.

the minimum SAGE by minimizing the error ε , i.e. the time when the simulated pattern best approximated the observed pattern of each forest stand:

$$\varepsilon(t) = \sum_{i=1}^{int} \frac{|BASim_t(t) - BAobs_i(t)|}{BAobs_i(i)}$$

where i indicates the shade-intolerant pioneer species under analysis and int , the number of shade-intolerant pioneer species in the stand. By simultaneously comparing basal areas of all shade-intolerant pioneer tree species, this method ensures that the obtained matches represent the first occurrence of such a forest structure and composition.

Calibration of demographic parameters

To calibrate the species-specific demographic parameters for each stand (N_{max} and m_B), we conducted a systematic

comparison of the patterns observed in the field (species-level basal area) and the patterns predicted by the model (Wiegand et al., 2003). We first varied demographic parameters of shade-intolerant pioneer species and ran simulations until we minimized $\varepsilon(t)$ for each stand. We recorded t as the minimum SAGE of each stand. We then ran simulations varying demographic parameters of the other species until we got the best agreement at SAGE between observed and simulated community structure. We compared the agreement (basal area of all species groups) using Pearson correlations and the Sørensen’s index of similarity, respectively. Table 3 details independent results for species density (not used as calibration variable) and similarity using the demographic parameter set (i.e. N_{max} and m_B) that best approximated the observed pattern of each forest stand. This procedure of parameter adjustment eliminated N_{max} and m_B sets that do not reflect an overall successional trend in the observed stands and would distinguish between probable (“small” ε) and improbable (“large” ε) parameter sets (Wiegand et al., 2003). The most probable parameter set was kept (i.e. N_{max}

and m_B sets of each stand that minimized the error ε as detailed above, Table B1) and used for analyses described below (see section 'Late successional stage evaluation'). Model predictions for species lifespans were also checked for correspondence with the observed data.

Simulations

We ran simulations for 25 ha (i.e. 625 patches of 400 m²) and for simulation periods exceeding the longest possible lifespan of any of the potential dominant tree species in the study area (Table 1). This required simulations of forest succession covering 1500 years. We assumed that the simulated stands were away from forest edges because all field sampling plots were located >100 m from adjacent open areas (see references in Table 3). Treeless states were used to initialize all simulations. Under these initial conditions, SAGE represents a theoretical estimate of the time taken for a stand to reach the observed structure and composition since stand initiation. We ran simulations trying to mimic the disturbance regime documented on Chiloé Island (Veblen et al., 1981; Veblen, 1985; Armesto and Fuentes, 1988; Gutiérrez et al., 2004, 2008). According to these studies, the disturbance regime is dominated by frequent, small canopy openings produced by individual tree falls (i.e. gap-phase dynamics, <500 m², but large canopy openings (>800 m²) can be produced by multiple tree falls during infrequent, severe wind storms. These wind throw events are spatially confined to specific areas of the forests. The model includes gap-phase dynamics by gap formation produced by dying trees (Rüger et al., 2007). In addition, we simulated wind throw events creating canopy openings after Rüger et al. (2007), i.e. by killing all trees in an area of 0.4–1.6 ha comprising neighboring patches. The size of wind throw events (i.e. 0.4, 0.6 or 1.6 ha) was drawn from a uniform distribution with windstorms frequencies defined by the parameter $Dist_f$ (i.e. the probability that a certain hectare is affected by wind throw). We set $Dist_f$ to 0.8% per year as estimated by Rüger et al. (2007). More than 200 simulations per stand were needed to obtain simulated patterns that approximated the observed pattern of each forest stand.

Late successional stage evaluation

In order to test the hypothesis that the focal stands were in the late successional stage, we concentrated on stability in tree species composition (i.e. compositional equilibrium, White, 1979), and stability in structure (here aboveground biomass). We used the concept of stability in the sense that forest structure stays essentially unchanged at large spatial scales (here 25 ha) despite the presence of disturbance (Grimm and Wissel, 1997; Shugart, 1998). Consequently, we defined that a forest was in the late successional stage when it has reached compositional equilibrium and stability in structure over long time period (i.e. >500 years of succession). Please notice that our definition does not imply that pioneers have been replaced in the late successional stage as assumed by Oliver and Larson (1996). We tested the hypothesis that the focal stands were in the late successional stage using the following index:

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

where LSI is the late-successional index, $SAGE$ was obtained as described above and TES is the predicted time taken to reach stability (in years). Thus, $LSI > 1$ represents forests in the late successional stage while $LSI < 1$ characterizes forests in transition to the late successional stage. 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 between years 1000 and 1500 of succession. We selected this time period because prior visual inspection of successional pathways showed that all studied stands reached stability within 1000 years. 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 ($\Delta_t < \sigma$). Simulations were run under the same conditions that were used for section 'Calibration of demographic parameters'. We averaged TES values because results may vary from one run to the next due to stochastic variation of simulated dynamics.

Results

Model performance

The studied forest stands showed a range of variation in total basal areas of 54.7–115.5 m²/ha, (Fig. 2a, field data) and in total density (871–2100 trees/ha, Fig. 2b, field data). Stands also varied in terms of forest composition, with observed mean compositional similarity of 0.69 among stands (Sørensen's index). Some forests were dominated in terms of basal area by the pioneer *Eucryphia cordifolia* while others were dominated by the shade-tolerants *Laureliopsis* or Myrtaceae tree species (Fig. 2a, field data). Most of the stands studied were dominated in terms of density by *Amomyrtus* species and other Myrtaceae tree species (*T. stipularis*, *Myrceugenia* spp.), but *Laureliopsis philippiana* and Podocarpaceae tree species were also important (Fig. 2b, field data).

Similarity in species composition ranged from 66 to 97% comparing field data with simulated stands at SAGE and under windstorm frequencies of 0.8% per year (Table 3). Species basal area predicted by the model corresponded well with field inventory data (Fig. 2a). With the exception of Abtao, we found significant correlations between observed and simulated species density (>63%, $P < 0.05$, Table 3, variable not used in model calibration). The model somewhat overestimated tree density for some species (Figs. 2b and C1), with overestimation primarily occurring in trees with dbh < 15 cm. Also, a deviation of observed from simulated total basal occurred for stands with the highest basal area (>100 m²/ha, $N=4$, Figs. 2a and C1). However, total basal area and density values indicated in field inventories were all in the range predicted by the model at the spatial scale of their respective sampling plot (Fig. C2). Stands with basal area > 100 m²/ha were close to the extreme value of simulations or represented possible simulated outliers at the field sampling scale (e.g. Fig. C2e). For all the other stands, the median of simulations results at all spatial scales agreed with the observed data (e.g. Fig. C2a–c). This suggests that model predictions were accurate at the spatial scale used in our analyses (25 ha).

General patterns of forest succession

The model predicted a range of successional pathways of primary forests studied on Chiloé Island (Figs. 3 and C3). A wide variation of demographic parameters in some species groups (e.g. *Myrceugenia*, *Drimys*, *Laureliopsis*, Fig. B4) was revealed by our stand-specific calibration in order to reproduce the observed structural variability in the studied stands. Successional patterns simulated for North Patagonian forests (e.g. Figs. 3a and C3a) showed that the pioneer *Drimys* decreased in dominance after 250 years whereas pioneer *Nothofagus* dominated the stand in the late successional stage. Both the pioneers persisted in these stands until the late successional stage (Fig. 3a). In several Valdivian coastal forests (Figs. 3b, d–f and C3d–g) the pioneer *Eucryphia*

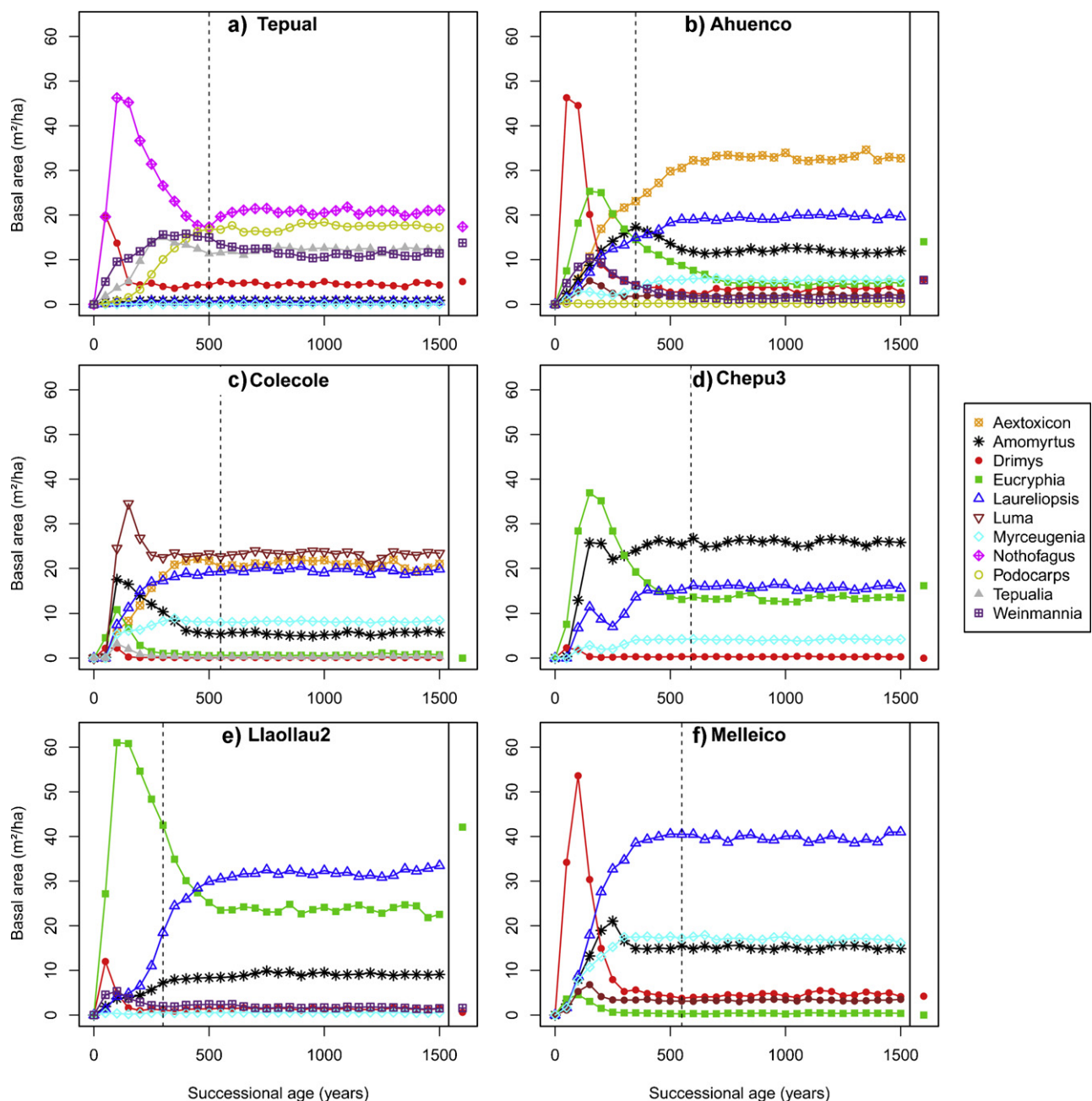


Fig. 3. Forest dynamics simulation for North Patagonian (a) and Valdivian (b–f) forest stands located on Chiloé Island, Chile. Simulations were run for 25 ha and 1500 years, results are presented as the running mean over a 50-year period. The dashed lines indicate the SAGE of simulated stands obtained matching inventory data for pioneer tree species from each study site (shown in the box on the right side of each chart, see section ‘Methods’ for details). Species group names according to Table 1. Dynamics for the remaining sites are shown in Fig. C3 (see Appendix).

persisted for more than 500 of succession. In one Valdivian forest stand, pioneers were excluded after 300 years of succession by *Luma* (intermediate shade-tolerance, Fig. 3c). Low establishment and high mortality rates for pioneer species at this site were needed in order to reduce their chances of being present, as was indicated by field data (Fig. 3c). An increased establishment rate for shade-tolerants *Laureliopsis* and *Amomyrtus* determined their dominance in the late successional stage of Valdivian forest stands (Fig. 3d–f).

Late successional stage assessment

The minimum successional ages were always >250 years but varied among studied stands (Table 3). Model simulations showed

that, on average, forest stands reached stability after 490–850 years of succession (625 ± 141 years, mean \pm standard deviation). According to our analyses, six out of 13 stands have not reached the late successional stage ($LSI < 1$, SAGE ranging 250–540 years, Table 3 and Fig. 4a). Simulated total biomass in stands with $LSI < 1$ was 570 t/ha (on average) and significantly higher than in forests in the late successional stage (488 t/ha, $P < 0.001$, Fig. 4b). Observed total basal area of stands decreased with increasing LSI ($P < 0.05$, Fig. 4c). As expected from our calibration method, the LSI decreased linearly with the observed basal area of pioneers ($LSI = -0.02 BA_{obs} + 1.68$, $F_{(1,11)} = 14.14$, $r^2 = 0.38$, $P < 0.05$, Fig. 4d). Valdivian forest stands in the late successional stage ($LSI > 1$) had observed basal area of pioneers $< 25 \text{ m}^2/\text{ha}$ (Table 3).

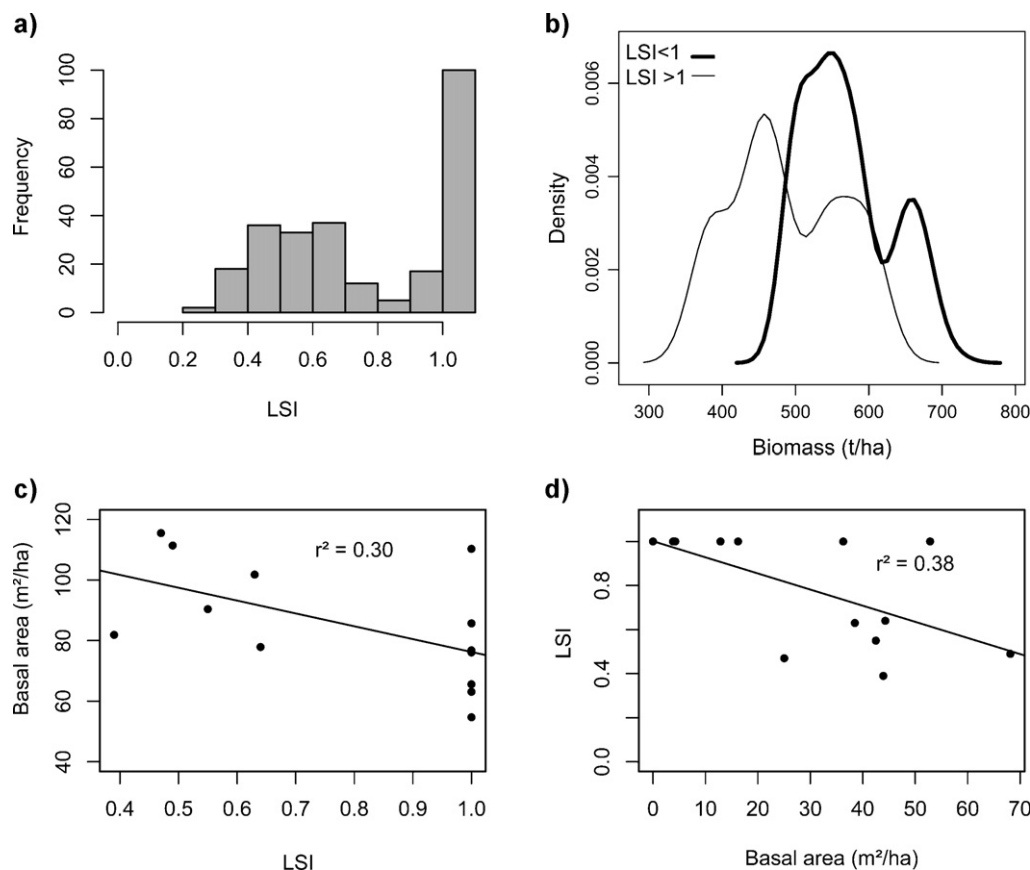


Fig. 4. Structural attributes related to the late successional stage index (*LSI*) of studied forest stands on Chiloé Island, Chile (see section ‘Methods’ for details on *LSI* calculations). (a) Successional stages of studied stands as indicated by their *LSI* values (20 simulations per stand, 260 in total, right bar corresponds to *LSI* > 1.0); (b) frequency distribution of total above-ground biomass related to *LSI* (20 simulations per stand); (c) observed total basal (field data) related to successional stage (*LSI*), (d) relation between observed basal area of pioneers and successional stage (*LSI*, *BAobs* corresponds to field data observations, shade-tolerance according to Table 1). r^2 is the correlation coefficient of the adjusted linear regression model ($P < 0.05$, lines).

Discussion

Late successional stage assessment

Our study exemplifies how models can be applied to assess the degree of stability in community structure of forests and to evaluate the time needed by forests to reach the late successional stage. This method for assessing the successional stages of forests can facilitate and complement studies based on forest structure (cf. Wirth et al., 2009b) or reconstructive tree-ring analyses (Fritts and Swetnam, 1989). For example, our modeling approach suggested that many forests on Chiloé Island >250 years old still represent a transient successional stage (Table 3). Our study also suggests that some forests on Chiloé Island have reached compositional equilibrium and stability in structure (Table 3), a process that can take between 490 and 850 years in this region. Accordingly Valdivian forests containing pioneers that accounted for <25 m²/ha of basal area (Table 3) had an estimated successional age >490 years and would represent forests in the late successional stage. It is reasonable to expect future compositional and functional change in these forests, mainly due to the potential impact of climate change on forest processes, e.g. recruitment rates (van Mantgem et al., 2009), and human activities (e.g. fires, logging).

Successional pathways to the late successional stage

The model reproduced the structural and compositional variability of the studied forest stands when variable successional

pathways had been considered (Figs. 3 and C3). The variety of simulated successional pathways in our study mimic those in other temperate rainforests, where succession varies according to the tree species pool present at each site, soil conditions, and local disturbance histories (Franklin et al., 1991; Bugmann and Solomon, 2000; Hall and Hollinger, 2000; Busing et al., 2007). In our simulations, both windstorm frequencies and species performance (i.e. biomass production) at different sites were kept similar across all sites. Based on the reasonable match between simulated and observed forest structure in our simulations (Fig. 2), we propose that multiple successional pathways to the late successional stage on Chiloé Island are driven by demographic rates (mortality and establishment, Fig. B4) and competition for light and space among tree species.

It has been observed that variations in soil moisture at stand scale (<1 ha) due to poor drainage may modify the establishment of tree species and potentially alter succession in forests of Chiloé Island (Donoso et al., 1984, 1985; Donoso, 1993). Simulated successional patterns in Valdivian forests (Fig. 3c,d) agreed with these field observations and indicated that tree establishment limitation alters succession in these stands. Other study in temperate rainforests in the mainland (Lusk, 1996a) and field observations of the authors also suggest tree establishment limitations and compositional changes at stand scale in relation to soil drainage (Guabún and Ahuenco, see also Appendix D). Similar to temperate rainforests elsewhere (Ohmann and Spies, 1998), other environmental factors, such as climate, may play a role in the observed

variability of primary forest composition at a regional spatial scale in the study region. However, in northern Chiloé Island, analyses of forest inventories showed that about 50% of the observed structural (basal area and density) and compositional variability of old forests can be explained by regional environmental factors (e.g. temperature, elevation, distance to the Pacific Ocean coast, Gutiérrez et al., 2009). According to our results the unexplained variability in structure and composition of the investigated forests is related to changes in demographic rates of tree species due to local site characteristics (e.g. excessive soil moisture).

Interactions of species with different traits, such as shade tolerance, tree size and lifespan (Table 1) with the predominant disturbance regime provide a basis for understanding the persistence of pioneers in forests in this region. Some pioneers, e.g. *Nothofagus* and *Weinmannia*, could persist for long time in the succession even when windstorms were excluded (data not shown). This result demonstrates the role of particular traits of these species allowing them to attain higher sizes (height and dbh) and longer lifespans than shade-tolerant and intermediate species in some sites. In contrast, the pioneer *Eucryphia* was dependent on the occurrence of windstorms to persist. Differences in tree growth among pioneers, particularly in old trees, may explain these contrasting patterns (Table B3). Other traits (e.g. sprouting ability, seed rain) may also facilitate the persistence of *Eucryphia* in the late successional stage when a wind throw event occurs (Veblen et al., 1981; Gutiérrez et al., 2008). Longevity has also been suggested to explain persistence of pioneers in temperate rainforests (Franklin and Hemstrom, 1981; Ogden and Stewart, 1995; Lusk and Smith, 1998; Gutiérrez et al., 2008). Longevity may confer to pioneer tree species a storage effect to disturbances occurring within the lifespan of trees, allowing population maintenance between infrequent disturbances and coexistence with shade-tolerant species in mature stands (Chesson, 2000). In our study, species lifespans are not considered explicitly as model inputs, therefore, long lifespans of pioneer tree species emerged in our simulations mainly because of their ability to persist under grow stress ($MaxYrs_{sup}$, obtained from tree-ring records, Table B3).

According to our simulations, successional pathways to the late successional stage in forests of Chiloé Island are influenced by the long dominance of pioneer trees (Fig. 3). This general pattern of forest succession is in line with successional dynamics proposed for other temperate rainforests containing long-lived pioneers (Franklin and Hemstrom, 1981; Franklin et al., 2002; Lindenmayer, 2009). In our study the initial cohort of pioneer trees (e.g. *Nothofagus*, *Eucryphia*, *Weinmannia*, Figs. 3 and C3) was predicted to persist for about 500 years (on average). This result agrees with the estimated residence time in the canopy of tree species in temperate rainforests elsewhere (Lertzman et al., 1996; Lusk and Smith, 1998). In our simulations, the replacement of the initial cohort of pioneers by late-successional species involved the death of massive trees. For example, pioneer trees of *Eucryphia* with tree stem volumes $>30\text{ m}^3$ are replaced by the late-successional *Laureliopsis* with tree stem volumes $<15\text{ m}^3$ (Fig. B2). As a consequence, biomass tends to decrease as forests approach the late successional stage in this region (Fig. 4b). This result is consistent with biomass trajectories in other temperate rainforests that reflect changes in species traits following species turnover during succession (Wirth and Lichstein, 2009).

Model performance and limitations of the modeling approach

The model performed reasonable well with respect to reproducing species composition and structure at the investigated scale in

a variety of sites on Chiloé Island (Fig. 2 and Table 3). Main trends of successional dynamics in temperate rainforests of Chile (Veblen et al., 1981; Donoso, 1993; Armesto et al., 1996; Smith-Ramirez et al., 2005; Donoso, 2006) were captured by the model according to the current knowledge of tree species and forest dynamics. Our results confirmed the importance of canopy openings produced by occasional wind throw events (i.e. $<1.6\text{ ha}$) for the persistence of pioneer tree species in old forest stands of Chiloé (Veblen, 1985; Gutiérrez et al., 2008).

Our modeling approach reflects the current knowledge on the physiology and demography of studied tree species. Further empirical research is needed particularly on some parameters set used in this study (e.g. parameters calibrated using literature, Table 2, see also Appendix D). For example, the influence of leaf area index of single trees on simulation results (cf. Rüger et al., 2007) demands more precise quantification for tree species in the study area. Photosynthesis parameters in this study were estimated on the basis of reasonable assumptions (e.g. light demands) and few empirical measurements (e.g. p_{max} , Table 2). These parameters can influence model results (e.g. basal area, Rüger et al., 2007), therefore future research should work towards obtaining empirical physiological data for tree species lacking information. Using a pattern-oriented calibration, we provide a set of demographic parameters that account for the impact of local processes on forest dynamics. These local processes can strongly affect forest composition and dynamics of temperate rain forests (Figs. 3 and C3), similar to findings in other forest ecosystems (Kobe et al., 1995; Pacala et al., 1996; Wyckoff and Clark, 2002). However, to test our predictions it would be necessary to monitor demographic rates of tree species in the study area (see also Appendix D). In addition, spatial heterogeneity in forest structure may generate sampling uncertainty that is relevant when estimating structural variables in the field (Chave et al., 2003). Model predictions showed that sampling uncertainty in the studied forests can be reduced by a sampling at a spatial scale $>0.6\text{ ha}$ (Fig. C2, see also Appendix D). Accordingly, in this study we used a large spatial scale in our simulations (25 ha) to prevent different pathways of succession occurring by chance at small spatial scales (e.g. $<1\text{ ha}$). We conclude that the match between simulated and observed data is adequate, considering that we compared simulations of 25 ha against measured samples from considerably smaller areas ($<0.5\text{ ha}$, Table 3).

Our theoretical estimate of the time taken by forests in the studied region to reach the late successional stage was based on simplifications related to disturbance regimes during succession, the initial condition of simulations, and other site factors (e.g. soil nutrients, drainage, see also Appendix D) that should be taken into account when applying this method in other study areas (see also Appendix D). Other processes could be incorporated in the model, such as climatic variability, seed dispersal, sapling banks and other biological legacies (e.g. Franklin et al., 2002). Such model applications should, however, evaluate the benefits of using a complicated model compared to simpler approaches. For example, some deliberately simple modeling approaches using few life history traits (e.g. maximum height, Wirth and Lichstein, 2009) can be easy to interpret but fail to simulate local successional patterns due to over-simplification of the systems under study. On the other hand more complex models can become difficult to interpret due to the increased number of parameters that must be estimated (Reynolds et al., 2001). We believe that model performance in the variety of sites analyzed in our study supports the validity of the gap model approach (particularly, its simplicity and generality Bugmann, 2001) and represent the current state of knowledge on temperate rainforests of southern Chile.

Application of the modeling approach

Primary forests play an important role for the mitigation of climate change by storing carbon (Ditzer et al., 2000; Franklin et al., 2002; Luyssaert et al., 2008). However, this ecosystem service provided by primary forests is imperilled due to their global trend of diminishing cover (FAO, 2010). Primary forests in Chile, particularly those still found in accessible areas of Chiloé Island and the Coastal Range, are being logged or replaced by plantations of exotic tree species (Echeverría et al., 2007; Armesto et al., 2010). However, limited information exists on carbon emissions that accompany their degradation and loss. Using the model, we estimated a large amount of above-ground biomass stored in old unmanaged forests in this region (539 t/ha in average among studied stands, Table 3). Assuming a 50% carbon concentration, above-ground carbon stocks in these forests can range from 187 to 361 tC/ha, i.e. higher than many tropical and boreal forests (cf. Keith et al., 2009). In addition, our method to locate stands along successional trajectories can serve to explore carbon fluxes during succession. The model can be easily extended so as to calculate carbon pools and fluxes (cf. Gutiérrez, 2010).

The method we have developed provides an estimate of how long it might take for a hypothetical stand to reach a certain successional stage. Using the model, we found that forests in the studied region take a long time (>500 years of succession) to reach the late successional stage (Table 3). This result is particularly relevant given the increasing trend of degraded old stands and forests maintained in young successional stages in the study region. On one hand, forest management strategies should recognize that changes in the attributes of natural forests can persist for centuries in this region. On the other hand, the long-time that it takes for a forest to develop the structurally diverse attributes of old stands (cf. Franklin et al., 2002; Gutiérrez et al., 2009) provides additional rationale for their preservation. Our finding that many old unmanaged stands >250 years-old represent a successional stage in which forests have not reached stability (Fig. 4a) also contributes to understand carbon exchange in old forest remnants (e.g. Luyssaert et al., 2008).

Forest fragmentation is an ongoing process on Chiloé Island (Echeverría et al., 2007; Armesto et al., 2010). The model includes a module that facilitate fragmentation analyses (Groeneveld et al., 2009), such as increased tree mortality in forest edges (Laurance et al., 2000). Therefore, future applications can be conducted using the model presented here to explore the impacts of the current forest fragmentation processes, biodiversity losses and introduction of exotic tree plantations (e.g. *Eucalyptus* plantations) in the study region. Our modeling approach provides important information on local forest dynamics which are required to successfully predict succession in the studied landscape. Caution should be taken when analyzing functional patterns of forests beyond the spatial applicability of the model (i.e. about 100 ha). Such model applications should consider a different modeling framework dealing with the spatial variability of forests at a landscape scale (Ditzer et al., 2000; Smith et al., 2001; Schumacher et al., 2004). Some factors that should be included at landscape scales are the variation in disturbance regimes among lowland and Andean forests in Chile, impacts of other types of disturbances (e.g. fire, insect pests), and variation in tree species fitness due to different climatic regimes. Here, we successfully simulated forest development in a stationary climate, providing a starting point for the prediction of forest responses to climate change on Chiloé Island. Current warming and drying trends in the study area (Falvey and Garreaud, 2009) may alter mortality, growth or recruitment of trees, similar to what has been observed in other temperate forests (van Mantgem et al., 2009). Another study is currently underway that incorporates climatic

variability effects on forest processes in the model (cf. Gutiérrez, 2010).

Conclusions

Our modeling approach supports the validity of using forest gap models to analyze the dynamics of temperate rainforests. The model performed reasonably well with respect to reproducing species composition and structure in a variety of sites on Chiloé Island. We propose a method to assess the successional stages of forests and provide an estimate of how long it might take for a hypothetical stand to reach a certain successional stage. By using this method, we found that on Chiloé Island many stands >250 years-old have not reached the late successional stage, a process that can take over 500 years in this region. The model also predicted varied successional pathways to the late succession stage. Above-ground biomass in the studied forests tended to decrease as forests approach the late successional stage because large pioneers are replaced by smaller late-successional trees. These results can assist in the classification of natural forests into successional stages to support management and conservation strategies of primary forests in this region.

Acknowledgments

We thank Nadja Rüger for her support during the development of this model application. We acknowledge the comments provided by Hans Pretzsch, Ché Elkin, Jürgen Groeneveld, Chris H. Lusk, Christian Wirth, Deborah Goldberg (Editor) and anonymous reviewers. We thank Sandro Pütz, Jordi Ferrer, Antonio Lara and Juan J. Armesto for helpful discussions, Cristián Echeverría and Nadja Rüger for providing data, and Natalia V. Carrasco and María-Paz Peña for literature search in Chile. Financial support was provided by DAAD and the ERC advanced grant 233066.

Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ppees.2012.01.004.

References

- Alaback, P.B., 1991. Comparative ecology of temperate rain-forests of the America along analogous climatic gradients. *Rev. Chil. Hist. Nat.* 64, 399–412.
- Aravena, J.C., Carmona, M.R., Perez, C.A., Armesto, J.J., 2002. Changes in tree species richness, stand structure and soil properties in a successional chronosequence in northern Chiloé Island, Chile. *Rev. Chil. Hist. Nat.* 75, 339–360.
- Armesto, J., Aravena, J.C., Villagrán, C., Pérez, C., Parker, G., 1996. Bosques templados de la Cordillera de la Costa. In: Armesto, J., Villagrán, C., Arroyo, M.K. (Eds.), *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, pp. 199–213.
- Armesto, J.J., Fuentes, E.R., 1988. Tree species regeneration in a mid-elevation, temperate rain-forest in Chiloé Island, Chile. *Vegetatio* 74, 151–159.
- Armesto, J.J., Manuschevich, D., Mora, A., Smith-Ramírez, C., Rozzi, R., Abarzua, A.M., Marquet, P.A., 2010. From the Holocene to the Anthropocene: a historical framework for land cover change in southwestern South America in the past 15,000 years. *Land Use Policy* 27, 148–160.
- Armesto, J.J., Mitchel, J.D., Villagrán, C., 1986. A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica* 18, 1–11.
- Armesto, J.J., Smith-Ramírez, C., Carmona, M.R., Celis-Diez, J.L., Díaz, I., Gaxiola, A., Gutiérrez, A.G., Núñez-Avila, M., Pérez, C., Rozzi, R., 2009. Old-growth temperate rain forests of South America: conservation, plant–animal interactions, and baseline biogeochemical processes. In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), *Ecol. Stud.-Anal. Synth.* Springer, New York/Berlin, Heidelberg, pp. 367–390.
- Bongers, F., Poorter, L., Hawthorne, W.D., Sheil, D., 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecol. Lett.* 12, 798–805.
- Botkin, D.B., Wallis, J.R., Janak, J.F., 1972. Some Ecological Consequences of a Computer Model of Forest Growth. *Journal of Ecology* 60 (3), 849–872.
- Bugmann, H., 2001. A review of forest gap models. *Climatic Change* 51, 259–305.

- Bugmann, H.K.M., Solomon, A.M., 2000. Explaining forest composition and biomass across multiple biogeographical regions. *Ecol. Appl.* 10, 95–114.
- Busing, R.T., Solomon, A.M., McKane, R.B., Burdick, C.A., 2007. Forest dynamics in Oregon landscapes: evaluation and application of an individual-based model. *Ecol. Appl.* 17, 1967–1981.
- Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B., Hubbell, S.P., 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *J. Ecol.* 91, 240–252.
- Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343.
- Coomes, D.A., Allen, R.B., 2007. Mortality and tree-size distributions in natural mixed-age forests. *J. Ecol.* 95, 27–40.
- Coomes, D.A., Allen, R.B., Bentley, W.A., Burrows, L.E., Canham, C.D., Fagan, L., Forsyth, D.M., Gaxiola-Alcantar, A., Parfitt, R.L., Ruscoe, W.A., Wardle, D.A., Wilson, D.J., Wright, E.F., 2005. The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. *J. Ecol.* 93, 918–935.
- DeLucia, E.H., George, K., Hamilton, J.G., 2002. Radiation-use efficiency of a forest exposed to elevated concentrations of atmospheric carbon dioxide. *Tree Physiol.* 22, 1003–1010.
- Dennis, J.E., Schnabel, R.B., 1983. Numerical Methods for Unconstrained Optimization and Nonlinear Equations. Prentice-Hall, Englewood Cliffs, New Jersey.
- di Castri, F., Hajek, E., 1976. Bioclimatología de Chile. Universidad Católica de Chile, Santiago.
- Ditzer, T., Glauner, R., Forster, M., Kohler, P., Huth, A., 2000. The process-based stand growth model Formix 3-Q applied in a GIS environment for growth and yield analysis in a tropical rain forest. *Tree Physiol.* 20, 367–381.
- Donoso, C., 1993. Bosques templados de Chile y Argentina. Variación, estructura y dinámica. Editorial Universitaria, Santiago, Chile.
- Donoso, C. (Ed.), 2006. Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología. Maria Cuñeo Ediciones, Valdivia, Chile.
- Donoso, C., Escobar, B., Urrutia, J., 1985. Estructura y estrategias regenerativas de un bosque virgen de Ulmo (*Eucriphia cordifolia* Cav.)-Tepa (*Laurelia philippiana* Phil.) Looser en Chiloé, Chile. *Rev. Chil. Hist. Nat.* 58, 171–186.
- Donoso, C., Grez, R., Escobar, B., Real, P., 1984. Estructura y dinámica de bosques del Tipo Forestal Siempreverde en un sector de Chiloé insular. *Bosque* 5, 82–104.
- Echeverría, C., Newton, A.C., Lara, A., Benayas, J.M.R., Coomes, D.A., 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Global Ecol. Biogeogr.* 16, 426–439.
- Eschenbach, C., Glauner, R., Kleine, M., Kappen, L., 1998. Photosynthesis rates of selected tree species in lowland Dipterocarp rainforest of Sabah, Malaysia. *Trees-Struct. Funct.* 12, 356–365.
- Falvey, M., Garreaud, R.D., 2009. Regional cooling in a warming world: recent temperature trends in the southeast Pacific and along the west coast of subtropical South America (1979–2006). *J. Geophys. Res.-Atmos.* 114, D04102.
- FAO, 2010. Global Forest Resources Assessment. Progress Towards Sustainable Forest Management. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Franklin, J.F., Hemstrom, M.A., 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), *Forest Succession*. Springer-Verlag, New York, USA, pp. 212–229.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecol. Manag.* 155, 399–423.
- Franklin, J.F., Swanson, F.J., Harmon, M.E., Perry, D.A., Dale, V.H., Mckee, A., Ferrell, W.K., Means, J.E., Gregory, S.V., Lattin, J.D., Schowalter, T.D., Larsen, D., 1991. Effects of global climatic-change on forests in northwestern North-America. *Northwest Environ. J.* 7, 233–254.
- Franklin, J.F., Spies T.A., 1991 Ecological definitions of old-growth Douglas-Fir forests. Wildlife and vegetation of unmanaged Douglas-fir forests. In: Ruggiero L.F., Aubry K.B., Carey A.B., Huff M.H. (Eds.). General Technical Report PNW-GTR-285. U.S. Forest Service, Pacific Northwest Research Station. Portland, USA, pp. 71–80.
- Fritts, H.C., Swetnam, T.W., 1989. Dendroecology – a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* 19, 111–188.
- Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109, 323–334.
- Groeneveld, J., Alves, L.F., Bernacci, L.C., Catharino, E.L.M., Knogge, C., Metzger, J.P., Putz, S., Huth, A., 2009. The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. *Ecol. Model.* 220, 2450–2459.
- Gutiérrez, A.G., 2010. Long-term dynamics and the response of temperate rain-forests of Chiloé Island (Chile) to climate change. PhD Thesis. Technische Universität, München.
- Gutiérrez, A.G., Aravena, J.C., Carrasco-Farias, N.V., Christie, D.A., Fuentes, M., Armesto, J.J., 2008. Gap-phase dynamics and coexistence of a long-lived pioneer and shade-tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloé Island, Chile. *J. Biogeogr.* 35, 1674–1687.
- Gutiérrez, A.G., Armesto, J.J., Aravena, J.C., 2004. Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *J. Ecol.* 92, 598–608.
- Gutiérrez, A.G., Armesto, J.J., Aravena, J.C., Carmona, M., Carrasco, N.V., Christie, D.A., Peña, M.P., Pérez, C., Huth, A., 2009. Structural and environmental characterization of old-growth temperate rainforests of northern Chiloé Island, Chile: regional and global relevance. *Forest Ecol. Manag.* 258, 376–388.
- Hall, G.M.J., Hollinger, D.Y., 2000. Simulating New Zealand forest dynamics with a generalized temperate forest gap model. *Ecol. Appl.* 10, 115–130.
- Hall, M., Witte, J., 1998. Maderas del sur de Chile. Árboles, aplicaciones y procesos. Editorial Universitaria, Santiago.
- Holdgate, M.W., 1961. Vegetation and soils in the South Chilean Islands. *J. Ecol.* 49, 559–580.
- Huth, A., Ditzer, T., 2000. Simulation of the growth of a lowland Dipterocarp rain forest with FORMIX3. *Ecol. Model.* 134, 1–25.
- Huth, A., Ditzer, T., 2001. Long-term impacts of logging in a tropical rain forest – a simulation study. *Forest Ecol. Manag.* 142, 33–51.
- Huth, A., Drechsler, M., Kohler, P., 2005. Using multicriteria decision analysis and a forest growth model to assess impacts of tree harvesting in Dipterocarp lowland rain forests. *Forest Ecol. Manag.* 207, 215–232.
- Karsulovic, J.T., Gaete, V.H., León, A., 2000. Estudio de la factibilidad de uso de maderas nativas chilenas en la construcción de instrumentos musicales. *Cienc. Forest.* 14, 19–28.
- Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences of the United States of America* 106 (28), 11635–11640.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5, 517–532.
- Köhler, P., 2000. Modelling anthropogenic impacts on the growth of tropical rain forests – using an individual-oriented forest growth model for the analyses of logging and fragmentation in three case studies. PhD Thesis. Center for Environmental Systems Research and Department of Physics, University of Kassel, Der Andere Verlag.
- Köhler, P., Huth, A., 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model FORMIND. *Ecol. Model.* 109, 301–321.
- Lambers, H., Chapin, F.S., Pons, T.L., 1998. *Plant Physiological Ecology*. Springer, New York.
- Lara, A., 1991. The dynamics and disturbance regime of *Fitzroya cupressoides* in the south-central Andes of Chile. PhD Thesis. University of Colorado.
- Larcher, W., 2001. *Ökophysiologie der Pflanzen*, 6th ed. Verlag Eugen Ullmer, Stuttgart.
- Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Conservation – rainforest fragmentation kills big trees. *Nature* 404, 836.
- Lertzman, K.P., Sutherland, G.D., Inselberg, A., Saunders, S.C., 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* 77, 1254–1270.
- Lindenmayer, D.B., 2009. Old forest, new perspectives – insights from the Mountain Ash forests of the Central Highlands of Victoria, south-eastern Australia. *Forest Ecol. Manag.* 258, 357–365.
- Lusk, C., Ogden, J., 1992. Age structure and dynamics of a podocarp broadleaf forest in Tongariro-national-park, New-Zealand. *J. Ecol.* 80, 379–393.
- Lusk, C.H., 1996a. Gradient analysis and disturbance history of temperate rain forests of the coast range summit plateau, Valdivia, Chile. *Rev. Chil. Hist. Nat.* 69, 401–411.
- Lusk, C.H., 1996b. Stand dynamics of the shade-tolerant conifers *Podocarpus nubi-gena* and *Saxegothaea conspicua* in Chilean temperate rain forest. *J. Veg. Sci.* 7, 549–558.
- Lusk, C.H., 1999. Long-lived light-demanding emergents in southern temperate forests: the case of Weinmannia trichosperma (Cunoniaceae) in Chile. *Plant Ecology* 140 (1), 111–115.
- Lusk, C.H., Chazdon, R.L., Hofmann, G., 2006. A bounded null model explains juvenile tree community structure along light availability gradients in a temperate rain forest. *Oikos* 112, 131–137.
- Lusk, C.H., Falster, D.S., Jara-Vergara, C.K., Jimenez-Castillo, M., Saldana-Mendoza, A., 2008. Ontogenetic variation in light requirements of juvenile rainforest evergreens. *Funct. Ecol.* 22, 454–459.
- Lusk, C.H., del Pozo, A., 2002. Survival and growth of seedlings of 12 Chilean rain-forest trees in two light environments: Gas exchange and biomass distribution correlates. *Austral Ecology* 27 (2), 173–182.
- Lusk, C.H., Smith, B., 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology* 79, 795–806.
- Luyssaert, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmoller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature* 455, 213–215.
- Molino, J.F., Sabatier, D., 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294, 1702–1704.
- Moser, G., Hertel, D., Leuschner, C., 2007. Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pan-tropical meta-analysis. *Ecosystems* 10, 924–935.
- Ogden, E.P., 1969. Strategy of Ecosystem Development. *Science* 164 (3877), 262–270.
- Ogden, J., Stewart, G.H., 1995. Community dynamics of the New Zealand conifers. In: Enright, N., Hill, R.S. (Eds.), *Ecology of the Southern Conifers*. Melbourne University Press, Melbourne, Australia, pp. 81–119.
- Ohmann, J.L., Spies, T.A., 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecol. Monogr.* 68, 151–182.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. John Wiley, New York.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43.

- Pacala, S.W., Canham, C.D., Silander, J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. Forest Res.* 24, 2172–2183.
- Pausas, J.G., Austin, M.P., Noble, I.R., 1997. A forest simulation model for predicting eucalypt dynamics and habitat quality for arboreal marsupials. *Ecol. Appl.* 7, 921–933.
- Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), *Long-term Studies in Ecology. Approaches and Alternatives*. Springer-Verlag, New York, pp. 110–135.
- Pierce, L.L., Running, S.W., 1988. Rapid estimation of coniferous forest leaf-area index using a portable integrating radiometer. *Ecology* 69, 1762–1767.
- Pollmann, W., Veblen, T.T., 2004. Nothofagus regeneration dynamics in South-central Chile: A test of a general model. *Ecological Monographs* 74 (4), 615–634.
- Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biol.* 10, 2052–2077.
- Reynolds, J.F., Bugmann, H., Pitelka, L.F., 2001. How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations, and potentials. *Climatic Change* 51, 541–557.
- Rüger, N., Gutiérrez, A.G., Kissling, W.D., Armesto, J.J., Huth, A., 2007. Ecological impacts of different harvesting scenarios for temperate evergreen rain forest in southern Chile – a simulation experiment. *Forest Ecol. Manag.* 252, 52–66.
- Ryan, M.G., 1991. Effects of climate change on plant respiration. *Ecol. Appl.* 1, 157–167.
- Saldaña, A., Lusk, C.H., 2003. Influence of overstorey species identity on resource availability and variation in composition of advanced regeneration in a temperate rainforest in southern Chile. *Rev. Chil. Hist. Nat.* 76, 639–650.
- Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecol. Model.* 180, 175–194.
- Shugart, H.H., 1984. *A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models*. Springer, New York.
- Shugart, H.H., 1998. *Terrestrial Ecosystems in Changing Environments*. Cambridge University Press, Cambridge.
- Smith-Ramirez, C., Armesto, J., Valdovinos, C., 2005. Historia, biodiversidad y ecología de los bosques costeros de Chile. Editorial Universitaria, Santiago.
- Smith, B., Prentice, I.C., Sykes, M.T., 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecol. Biogeogr.* 10, 621–637.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the Western United States. *Science* 323, 521–524.
- Veblen, T.T., 1985. Forest development in tree-fall gaps in the temperate rain forests of Chile. *Natl. Geogr. Res.* 1, 161–184.
- Veblen, T.T., Donoso, C., Schlegel, F.M., Escobar, B., 1981. Forest dynamics in south-central Chile. *J. Biogeogr.* 8, 211–247.
- Veblen, T.T., Schlegel, F.M., Oltremari, J.V., 1983. Temperate broad-leaved evergreen forest of South America. In: Ovington, J.D. (Ed.), *Temperate Broad-Leaved Evergreen Forest*. Elsevier Science Publishers, Amsterdam, pp. 5–31.
- White, P.S., 1979. Pattern, Process, and Natural Disturbance in Vegetation. *Botanical Review* 45 (3), 229–299.
- White, J.D., Scott, N.A., 2006. Specific leaf area and nitrogen distribution in New Zealand forests: species independently respond to intercepted light. *Forest Ecol. Manag.* 226, 319–329.
- Whitehead, D., Boelman, N.T., Turnbull, M.H., Griffin, K.L., Tissue, D.T., Barbour, M.M., Hunt, J.E., Richardson, S.J., Peltzer, D.A., 2005. Photosynthesis and reflectance indices for rainforest species in ecosystems undergoing progression and retrogression along a soil fertility chronosequence in New Zealand. *Oecologia* 144, 233–244.
- Wiegand, T., Jeltsch, F., Hanski, I., Grimm, V., 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos* 100, 209–222.
- Willson, M.F., Armesto, J.J., 1996. The natural history of Chiloé: on Darwin's trail. *Rev. Chil. Hist. Nat.* 69, 149–161.
- Winter, L.E., Brubaker, L.B., Franklin, J.F., Miller, E.A., DeWitt, D.Q., 2002. Initiation of an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records. *Can. J. Forest Res.* 32, 1039–1056.
- Wirth, C., Lichstein, J.W., 2009. The imprint of species turnover on old-growth forest carbon balances – insights from a trait-based model of forest dynamics. In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), *Ecol. Stud.-Anal. Synth.* Springer, New York/Berlin, Heidelberg, pp. 81–114.
- Wirth, C., Messier, C., Bergeron, Y., Frank, D., Fankhänel, A., 2009. Old-growth forest definitions: a pragmatic view. In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), *Ecol. Stud.-Anal. Synth.* Springer, New York/Berlin, Heidelberg, pp. 11–34.
- Wood, S.W., Hua, Q., Allen, K.J., Bowman, D., 2010. Age and growth of a fire prone Tasmanian temperate old-growth forest stand dominated by Eucalyptus regnans, the world's tallest angiosperm. *Forest Ecol. Manag.* 260, 438–447.
- Wyckoff, P.H., Clark, J.S., 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *J. Ecol.* 90, 604–615.