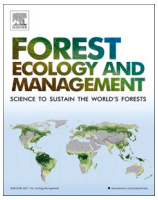
Forest Ecology and Management 524 (2022) 120519



Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco





Impacts of varying precipitation regimes upon the structure, spatial patterns, and productivity of *Nothofagus pumilio*-dominated old-growth forests in Patagonia

Daniel P. Soto [a,*], Christian Salas-Eljatib [b,c,d], Pablo J. Donoso [e], Ángela Hernández-Moreno [f], Dominik Seidel [g], Anthony W. D'Amato [h]

[a] *Departamento de Ciencias Naturales y Tecnología, Universidad de Aysén, Coyhaique, Chile*
[b] *Centro de Modelación y Monitoreo de Ecosistemas, Universidad Mayor, Santiago, Chile*
[c] *Vicerrectoría de Investigación y Postgrado S1, Universidad de La Frontera, Temuco, Chile*
[d] *Departamento de Silvicultura y Conservación de la Naturaleza, Universidad de Chile, Santiago, Chile*
[e] *Instituto de Bosques y Sociedad, Universidad Austral de Chile, Valdivia, Chile*
[f] *Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Coyhaique, Chile*
[g] *Department for Spatial Structures and Digitization of Forests, Faculty of Forest Sciences, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany*
[h] *Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA*

ARTICLE INFO

Keywords:
Climate change
Spatial-point pattern
Uneven-aged forests
Structural heterogeneity

ABSTRACT

Climate is a critical variable in determining the productivity and structural complexity of forest ecosystems. Under similar temperature regimes and other site conditions, precipitation becomes fundamental for forest regeneration and growth, and eventually for the development of structural complexity and patterns in forest productivity. Empirical quantification for this expected response to varying precipitation is needed, especially to provide conservation and management strategies under current and future climate change impacts. To address this need, we evaluated the effects of varying annual precipitation regimes (dry, mesic, and humid sites; all with similar temperature regimes) on three key forest attributes and processes; 1) size and age structure, 2) tree spatial point patterns, and 3) forest stand productivity based on the normalized difference vegetation index (NDVI), in three old-growth lenga (*Nothofagus pumilio*) forests in western Patagonia. Tree-size and age structure were irregular in the humid and mesic sites, and regular (unimodal) in the dry site (based on Weibull probability function). The relationship between tree diameter and age was strongest in the humid site ($r^2 = 0.86$), and weakest in the dry site ($r^2 = 0.36$). Forest stand productivity was significantly higher in the humid site (mean NDVI = 0.73, vs. 0.68 and 0.63 in the mesic and dry sites, respectively). Univariate spatial-point patterns showed that the humid site had the strongest clumped pattern for live trees along all distances analyzed (i.e., 20 m), while the dry site had a fully random pattern for live and dead trees along all distances analyzed. Collectively, these results illustrate different challenges for silviculture in these forests: 1) The multi-aged structure, plus clumped spatial patterns of small trees (following partial overstory disturbance) in the humid and mesic sites, reflect a gap-based regeneration mode, which consequently suggests the feasibility of implementing uneven-aged silviculture in these sites; 2) Dry sites, close to the forest-steppe ecotone (dry, cool and windy) may require a focus on silviculture for adaptation to cope with expected declines in precipitation and to potentially avoid the loss of these ecosystems to woodlands; 3) Dieback of larger trees in mesic sites (presumably due to xylem cavitation) is a reflection of climate change impacts and a warning to implement strategies that may adapt these forests to new climate conditions (transition to dry condition). Consideration of the great variation in structure and productivity in Patagonian lenga forests due to differences in precipitation regimes, is urgently needed to guide the development of site-specific management approaches for this forest type, particularly given expected future declines in precipitation.

* Corresponding author.
E-mail address: daniel.soto@uaysen.cl (D.P. Soto).

https://doi.org/10.1016/j.foreco.2022.120519
Received 25 June 2022; Received in revised form 31 August 2022; Accepted 3 September 2022
Available online 18 September 2022
0378-1127/© 2022 Elsevier B.V. All rights reserved.

1. Introduction

Forest management during times of global change increasingly emphasizes strategies that promote diverse, resilient, complex and adaptive forest ecosystems at the stand (Puettmann et al., 2009; Schütz et al., 2012; Messier et al., 2013; Fahey et al., 2018; Palik et al., 2021; Donoso et al., 2022a) to landscape level (Messier et al., 2019, 2021; Mina et al., 2021). At the stand level, complex forests have many attributes such as rich vertical and horizontal structures, standing dead trees and downed wood, high compositional and functional diversity, and abundant tree regeneration and well-developed understories (Spies, 2004; Puettmann et al., 2009; D'Amato et al., 2009; O'Hara, 2014; Donoso et al., 2020). These attributes are mostly associated with uneven-aged mature and old-growth forests (Bauhus et al., 2009), which contrast with even-aged forests that often lack or have poor representation of these attributes (Bauhus et al., 2009; D'Amato et al., 2009; Ponce et al., 2017; Donoso et al., 2022b). Overall, some work suggests that greater stand structural complexity may provide forests with greater capacity to adapt to disturbances (Puettmann et al., 2009; Messier et al., 2013; Fahey et al., 2018; Ehbrecht et al., 2021). However, climate is a key variable in determining the patterns of stand structural complexity and productivity for different forest ecosystems (Barnes et al., 1999; Ehbrecht et al., 2021). Thus, empirical quantification of how forest structural development and productivity are affected by aspects of a given climate regime, including varying precipitation is needed, especially to inform management strategies designed to address current and future climate change impacts.

The evaluation of disturbance patterns and successional development in forests is commonly done through tree-size distributions, based on the diameter of the stem at 1.3 m (*d*) or total height (*h*) (Goff and West, 1975; Lorimer and Krug, 1983; Donoso et al., 1985; Baker et al., 2005; Zenner, 2005; Müller-Landau et al., 2006; Coomes and Allen, 2007; Wang et al., 2009). Moreover, foresters and forest ecologists have used the diameter/age distribution in a stand to reflect its general structural attributes, such as cohort structure and vertical/horizontal complexity (Tyrrell and Crow, 1994; Zenner, 2005; Fajardo and Alaback, 2005; Soto et al., 2010; Esse et al., 2021). For instance, temperate forests in Chile stands containing a reverse-J diameter distribution and large trees (i.e., >70 cm), are likely uneven-aged, have a high vertical structural diversity (multiple canopy layers; e.g., Parada et al., 2003; Donoso and Soto, 2016), and typically contain more snags and coarse-woody debris than even-aged stands with bell-shaped distributions and relatively small trees (Oliver and Larson, 1996; Franklin et al., 2002). Since most of the studies in South America's temperate forests have proven that the diameter/age relationship is fairly well correlated in uneven-aged stands or reverse-j diameter distributions (Donoso, 2005; Fajardo and Alaback, 2005; Soto et al., 2010; Esse et al., 2021), the diameter distribution can be used as a proxy of the age distribution and the likelihood of old-growth attributes in a forest (Veblen et al., 1996; Zenner, 2005; Donoso and Soto, 2016). Nevertheless, the rate of structural development is highly associated with factors influencing site productivity (Larson et al., 2008), including precipitation regimes. As such, old-growth forests belonging to the same forest type, with a quite similar disturbance regime (i.e., in terms of severity and time since the last disturbance) and stand developmental stage, but under different precipitation regimes may differ in terms of age distribution (e.g., new cohort establishment and development since last disturbance) and structure (e.g., live-tree size-class distribution), a condition that would provide evidence of potential impacts of climate change upon the future of these forests in terms of patterns in structural development and productivity.

Spatial patterns of forest trees (i.e., horizontal tree position in the x and y coordinate) arise from spatially-explicit patterns and processes governing spatial heterogeneity in resource availability over time (Perry et al., 2006; McIntire and Fajardo, 2009; Wiegand and Moloney, 2014). These patterns are also key aspects of forest structure; influencing tree-tree interactions, regeneration patterns, and resilience to disturbance (Salas et al., 2006; Soto et al., 2010; Churchill et al., 2013). While most studies examining tree spatial patterns are site-specific, studying these patterns across multiple sites highlights the influence of broader scale factors, such as site productivity and precipitation regime, upon forest spatial structure (e.g., Iniguez et al., 2019). Nevertheless, a unique combination of factors are needed across multiple sites to isolate the role of precipitation regime in affecting forest spatial structure. This includes examining sites across different climate conditions (e.g., precipitation), but that share a similar development stage (e.g., old-growth) and disturbance history, and are dominated by a single species to reduce variation from interspecific interactions. Such an examination may provide valuable results in terms of management alternatives to increase stand structural complexity and adaptive capacity for monospecific forest ecosystems, such as the widely distributed *Nothofagus pumilio* forests of the Patagonian region, particularly in the context of climate change.

Remote sensing data through the normalized difference vegetation index (NDVI) has been widely used as a proxy to estimate vegetation productivity (Wang et al., 2004; Pettorelli, 2013; Bianchi et al., 2020), and has offered researchers a way to couple this process with forest structure (Pau et al., 2012; Pettorelli, 2013; Asbeck et al., 2021). NDVI is strongly related to above-ground forest productivity through photosynthetic activity because the internal mesophyll structure of healthy green leaves strongly reflects near-infrared radiation, while leaf chlorophyll and other pigments absorb a large proportion of the red visible radiation (Wang et al., 2004; Pettorelli, 2013; Fuenzalida et al., 2019). It is well established that precipitation affects productivity of forest stands (Barnes et al., 1999; Chapin et al., 2011), with several studies demonstrating a relationship between NDVI and climate, i.e., temperature and precipitation (Tang et al., 2017; Lara et al., 2018; Bianchi et al., 2020). For example, Salas-Eljatib (2021) recently showed that decreasing growing season precipitation and increasing temperature in 1 °C by 2100 would cause a decrease in site index (a proxy of forest productivity) by 1.4 m in secondary forests in South-Central Chile. Given the importance of forest productivity upon stand structural development, and the scarcity of studies on this topic worldwide, studying how precipitation declines influence changes in structure for the same forest type in the same development stage, may enable inferences regarding mechanisms, processes and patterns operating across the landscape, and may provide useful insights on the potential impacts of climate change on future forest productivity.

Western Patagonia is largely dominated by cold temperate and pure *Nothofagus pumilio* forests (González et al., 2006). In general, this forest type has a gap-phase regeneration mode, which is consistent with the natural disturbance of the region, allowing the species to naturally regenerate in small-to medium-size gaps (Veblen 1992; Rebertus and Veblen, 1993; Veblen et al., 1996; Fajardo and de Graaf, 2004; Promis, 2018; Donoso et al., 2022a). These small scale disturbances create irregular patchy structures with different sizes, but the effects of precipitation upon forest structural attributes (e.g., size and age, and spatial patterns) and productivity following partial overstory disturbance (i.e., selective cuttings) have not been studied at different sites receiving different levels of precipitation or larger spatial scales. Understanding how stand recovery and development following disturbance varies across precipitation regimes is of importance to refine ecological theory and forest management at different spatial contexts, within these and other forest ecosystems (e.g., Soto and Puettmann, 2020).

These naturally monospecific *Nothofagus pumilio* forests could provide an exceptional opportunity to isolate the effects of large-scale climatic controls upon forest structure and productivity. In western Patagonia, the temperature gradient is very narrow (mostly associated to altitudinal gradient and/or latitude; Fajardo et al., 2019), but precipitation is strongly associated with longitude (2,500 to 400 mm of mean annual precipitation in the west-to-east axis of the eastern slope of the Andes where *N. pumilio* forests grow; Olivares-Contreras et al.,

2019). To this end, recent studies (e.g. Ehbrecht et al., 2021; Seidel et al., 2021) have isolated the effects of large climate factors upon forest structural complexity, unveiling that precipitation has a direct effect on stand structural complexity index (SSCI; Ehbrecht et al., 2021) and understory complexity index (UCI; Seidel et al., 2021). Moreover, Soto et al. (2021) found that varying precipitation in *Nothofagus pumilio* old-growth forests affects both abiotic and biotic understory patterns. Therefore, in this study we sought to further to evaluate the potential effects of precipitation on structure, age/*d* relationships, univariate spatial point pattern, and forest productivity (NDVI) in three distinct *Nothofagus pumilio* old-growth forests growing in sites with differing precipitation and without evident large-scale overstory disturbances at least during the last 50 years. Our specific hypothesis are: H1) There is a monotonic and descendant *d* (live and dead trees) and age distribution in the humid site given the lack of water limitation allows regeneration in gaps (tail in curve) and faster recovery of small tree-size classes, which changes to unimodal in the dry site due to water limitation that inhibits gap-scale regeneration and recruitment into smaller *d* classes, H2) Age and *d* are highly related in humid sites given the absence of water limitation and fewer limits to tree growth, but the relationship becomes weaker towards drier sites due to site-specific controls of regeneration associated with fine scale patterns in soil water availability resulting in a wide range of ages for a given *d*, H3) Distinct univariate spatial point patterns are evident among sites, being highly clumped in the humid site due to no water limitation, which allows clumped regeneration (high competition and mortality) in gaps, and decreasing towards random spacing at the dry site for live and dead trees given the lack of gap-scale recruitment and mortality, and H4) Productivity declines from sites with higher precipitation to sites with lower precipitation due to more rapid stand recovery and growth in humid sites relative to mesic and dry sites, where water limitation limits gap-infilling and tree growth.

2. Methods and material

2.1. Study area

The study area is the geographic region where Patagonian forests develop. We deliberately selected three contrasting precipitation sites -used previously by Soto et al. (2021)- within the temperate bioclimatic gradient transitioning from a rainy and warm climate in the Pacific coast to a cold and drier climate in the Patagonian steppe (Pisano, 1977). It is important to note these sites are different in terms of mean annual precipitation, but not in mean annual temperature (see Soto et al., 2021 and Table 1). The three sites are located in western Patagonia, Aysén Region, specifically as follows: The humid site is located in Lago largo (45°13′S; 71°51′W; 940–970 m a.s.l.), the mesic site located in Reserva Nacional Trapananda (45°21′S; 71°48 W; 950–1050 m a.s.l.), and the dry site in Coyhaique alto (45°24′S; 71°34′W; 1050–1150 m a.s.l.). The humid site has 994 ± 19.3 mm of annual precipitation and a mean annual temperature of 5.1 ± 0.4 °C. The mesic site has 817 ± 20.1 mm of annual precipitation, and a mean annual temperature of 4.8 ± 0.2 °C. The dry site has 613 ± 18.6 mm in mean annual precipitation and a mean annual temperature of 4.6 ± 0.3 °C. Fig. 1 shows average temperature and precipitation at the three locations from 1970 to 2018 based on Worldclim 2.1 (Fick and Hijmans, 2017 details are provided there).

Soils on the dry site correspond to Ñirehuao soil series (CIREN, 2005); they have a sandy loam texture developed over a old glacial material, and are classified as sandy loam in the family of the frigid humic dystrudepts (CIREN, 2005). Soils of mesic and humid sites have sandy textures and finer textures at the superficial soil profile (Inceptisols), and in the lower soil profile the texture becomes finer. This soil has been locally developed from volcanic ashes (Andisols) (CIREN, 2005). Some soil characteristics obtained from raster data from the soilgrid database (https://soilgrids.org/) are displayed per site in Table 1 (further details are given in the footnote of the table).

Table 1
Site and forest characteristics (Mean ± (SD)) for the three forests studied.

	Dry	Mesic	Humid	*F*-value
Overstory Disturbance (based on owner personal communication)				
year	1967	1962	1971	
Climate characteristics				
Mean annual precipitation (mm)	613.0c (18.6)	817.3b (20.1)	994.0a (19.3)	21.7**
Mean annual temperature (°C) 1	5.1(0.4)	5.7(0.1)	6.1(0.4)	1.93 ns
Stand characteristics				
Top-height (m)	12.6c (2.6)	16.7b (2.4)	19.3a (1.8)	24.5**
Density (tree ha^{-1})	1,379b (467)	2,821a (993)	3,280a (1538)	9.9***
Basal area (m^2 ha^{-1})	68.8(8.4)	59.4(4.9)	63.9(25.1)	1.1 ns
Mean dbh (cm)	21.9a(3.8)	12.6b(1.6)	12.4b(1.9)	51.2***
Leaf area index (m^2 m^2)$_3$	2.1c (0.2)	2.5b (0.3)	3.0a (0.2)	34.6***
Understory characteristics				
Cover (%)$_3$	3.6b (0.4)	77.6a (22.2)	81.7a (20.6)	46.7***
Richness (S)$_3$	1.1b (0.04)	5.7a (0.7)	4.9a (0.9)	42.3***
Simpson diversity index (D)$_3$	0.05b (0.03)	0.66a (0.06)	0.64a (0.01)	37.5***
Soil characteristics				
Taxonomic group	Inceptisol	Andisol	Andisol	
Soil texture	Silty loam/ Sandy loam	Silty loam	Silty loam	
Bulk density (cg/cm^3)$_2$	88.5a (0.7)	83.3b (1.2)	86.3b (0.7)	94.1***
Cation exchange capacity (mmol(c)/kg)$_2$	250.5b (1.9)	277.1a (7.9)	275.0a (6.4)	52.6***
Nitrogen (cg/kg)$_2$	4641.3 (265.3)	4689.0 (956.2)	4165.3 (609.4)	2.2 ns
Soil organic carbon (dg/kg)$_2$	1040.0b (54.6)	1045.8b (35.8)	1089.3a (19.9)	5.6*
Volumetric soil water content (%)$_3$	7.8c (1.4)	13.8b (1.9)	19.3a (3.1)	74.4***
Coarse-woody debris (%)$_3$	26.6b (3.3)	37.3a (4.3)	33.7a (5.9)	16.4***
Litter cover (%)$_3$	64.7a (5.7)	54.6b (5.7)	57.2b (8.5)	7.0*

Notes: ns: non significant, * $p < 0.05$, ** $p < 0.01$, ***$p < 0.001$. Different letters show statistical differences obtained through LSD's post hoc test. $_1$ Precipitation and temperature calculations 3 to 5 raster pixels (obtained from WorldClim 2.1) were used (Fick and Hijmans, 2017). $_2$ Soil characteristics were obtained from Soilgrid database (https://soilgrids.org/), where one to two pixels were obtained and averaged (cg = centigram, dg = decigram). $_3$ data obtained from Soto et al. (2021).

2.2. Regeneration dynamics of lenga

Nothofagus pumilio (common name lenga) is a mid-tolerant to shade-tolerant tree species, and can reach approx. 2 m in diameter and 30 m height in forests (González et al., 2006). Its major regeneration mode is through gaps created after the death of one or several senescent trees. This gap-phase regeneration mode (Veblen, 1992; Rebertus and Veblen, 1993; Veblen et al., 1996; Fajardo and de Graaf, 2004; Promis, 2018; Donoso et al., 2022a) is consistent with the dominant natural disturbance of the region, which is tree windfalls. The regeneration ecology of lenga has not been well studied and there are key knowledge gaps due to the different site conditions along the large distributional range of the species (i.e., ~35° to 54° S). However, as mentioned above, it is a species adapted to regenerate under small- to medium-size gaps (Veblen et al., 1996; Promis, 2018) that occur frequently in Patagonia due to the action of winds upon senescent and decaying trees mostly in old-growth forests (Rebertus et al., 1997; Promis, 2018). These usually small-scale autogenic disturbances create a mosaic of different cohorts at the stand scale,

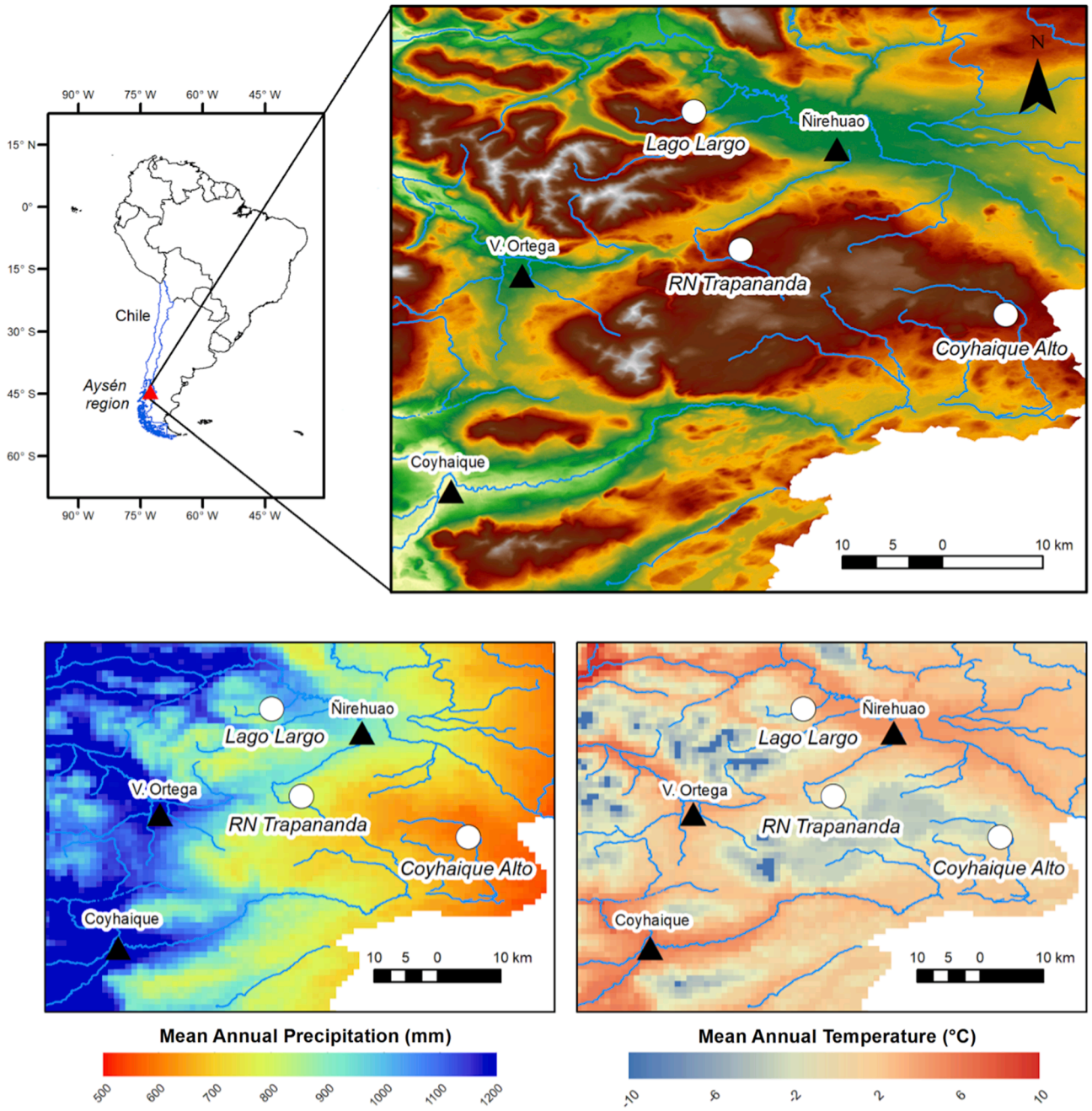


Fig. 1. Upper panel depicts the study area within Southern America and the major geoforms of the Andes in the Aysén region, western Patagonia, Chile. The map was obtained from a digital elevation model obtained from the ASTER sensor with 30 m spatial resolution (NASA et al., 2019). The lower left panel shows the mean annual temperature (mm), and lower right panel shows the mean annual precipitation for a period of 1970–2018 and were obtained by using the raster images from the Worldclim2 (Fick and Hijmans, 2017). The study locations are displayed with white dots and major towns in black triangles.

although winds can occassionally generate stand-scale disturbances (Promis, 2018). These irregular patchy structures have different ages, but the age structure of lenga forest stands remains poorly understood.

There are several factors that influence regeneration dynamics of lenga in these forests. Increased light availability after gap creation has been identified as the major predictor of lenga regeneration (Donoso, 1993; Heinemann et al., 2000; Heinemann and Kitzberger, 2006; Promis 2018), but more detailed works have shown that an increase in light availability is positively correlated with air and soil temperature in small treefall gaps (<700 m^2) in Tierra del Fuego island, and the interaction of these factors may trigger the regeneration of lenga (Promis, 2018). In contrast to shade-intolerant *Nothofagus* species, such as coihue (*Nothofagus dombeyi*), which needs larger canopy gaps or large-scale disturbances, where mineral soil is exposed and the competing understory vegetation is destroyed (Veblen et al., 1996; Soto and Puettmann, 2018), regeneration of lenga is often associated with highly decayed coarse-woody material on the forest floor, and also with abundant litter cover without understory competition (Donoso, 1993; Promis, 2018, Toro-Manríquez et al., 2018). These microsite preferences and findings from work examining regeneration patterns for lenga in relation to soil moisture, highlight the importance of moisture during the growing season in affecting regeneration patterns for this species (Bava and Puig, 1992; Heinemann et al., 2000; Heinemann and Kitzberger, 2006). In general, the successful regeneration of this species appears to require the lack of competition with understory species (Donoso, 1993; Promis, 2018), the proper combination of soil water content and light

availability in the understory (Heinemann et al., 2000; Martínez-Pastur et al., 2007), and the availability of "safe sites'' to environmental extremes to allowing successful regeneration provided by coarse woody debris (Toro-Manríquez et al., 2018). Therefore, we would expect the long-term structural dynamics of lenga forests to vary based upon prevailing precipitation regime; however, such investigations have yet to occur in these forests.

2.3. Study design, data collection and management

Four blocks with three permanent sample plots of 1,600 m^2 (40 × 40 m) were established in 2019 on each site (dry, mesic, and humid). Each site comprises large areas of old-growth forests, with the humid site located within 1,500 ha of continuous forests, mesic site in Reserva Nacional Trapananda within 2,305 ha, and the dry site in Estancia Punta del Monte within >5,200 ha. At each site, blocks were laid out in different aspects and slope conditions within similar developmental stage and disturbance history (Table1). In each plot, diameter at breast height (*d*) of all live and dead trees above 5 cm were measured.

Single-tree selection cuttings were implemented in summer 2020 in two-thirds of the plots (8 plots), leaving the rest as control (4 plots). From the managed plots we collected wood discs at breast-height (1.3 m) of all felled trees. The selection harvesting captured a good representation of trees along the entire diameter distribution, from 5 to 60 cm in *d*. The original and residual diameter distributions and further details about single-tree selection cutting are given in appendix (Fig. S1).

A total of 1,166 tree discs were collected, 243 for the dry site, 522 for the mesic site, and 401 for the humid site. We used geometric radii to determine where to count and measure annual rings. Discs were air-dried in dark and well aerated rooms to avoid wood collapse or fungus proliferation. Later, the dried samples were sanded with increasing grain of sandpaper to ensure the identification of all rings. The samples were scanned and then rings counted (years) and measured (mm) using the Windendro software (Regent instruments, Quebec, Canada). The tree ring series per site were cross-dated using COFECHA software to avoid missing false rings (Holmes, 1983).

One of the four control plots per site was randomly selected to measure the spatial coordinates of all trees. We divided the plots in a grid of 10 × 10 m, where all trees above 5 cm (live and dead) in *d* were measured and their × and y coordinates registered in the horizontal space following the protocols of Salas et al. (2006) and Soto et al. (2010).

To estimate the change in productivity over time in each plot, we used the normalized difference vegetation index (NDVI). NDVI is considered a proxy of above-ground primary productivity (Pettorelli, 2013), and is a very useful tool for studying the integrated effect of the main climatic constraints (temperature and precipitation) on forest dynamics (Lara et al., 2018; Yang et al., 2017). This index uses two bands in a multispectral raster dataset: chlorophyll pigment absorptions in the red band (RED) and the high reflection capability of vegetation in the near-infrared band (NIR) (Pettorelli, 2013). Usually, vegetation with high productivity shows low reflectance in the visible wavelength band (400–700 μm), i.e. RED band, because radiation within these wavelengths is utilized in photosynthesis, while reflectance in the NIR wavelength band is high (750–2600 μm) (Fuenzalida et al., 2019). NDVI was calculated from Landsat 8 Operational Land Imager (OLI) images, obtained between December to February of each year from 2015 to 2020 (Table S.2) because the productivity is maximized in the middle of the southern summer. NDVI data was derived from the surface reflectance products, Level-2 Landsat (imagery with radiometric, atmospheric and geometric corrections), obtained from the U.S. Geological Survey (USGS) web-service (https://glovis.usgs.gov/app). All the scenes were considered Tier 1 (T1), which corresponds to the higher quality data and are considered suitable for time-series analysis. This index is given by Eq. (1) (Rouse et al., 1974):

$$NDVI = \left(\frac{NIR - RED}{NIR + RED}\right) \quad 1$$

Where NDVI is the vegetation index value, which varies between −1 to 1; NIR and RED are reflectance in the near infrared and red wavelength bands. Since this index has a strong relationship with photosynthesis and this in turn with productivity, high values close to 1, indicate high productivity, values close to 0 low productivity, and values close to −1 bare areas or without vegetation (Rouse et al., 1974; Pettorrelli, 2013).

2.4. Analyses

2.4.1. Tree-size distribution among precipitation sites

The size and age structure per site was analyzed by fitting the Weibull density probability function (pdf) using tree *d* (all live and dead trees separately) and age (live trees only, obtained from selection cutting). For the live trees, we used all live trees without segregation of form and health status. The Weibull model represents the symmetric distributions, as well as the asymmetric distribution (Salas-Eljatib et al., 2021). We used the following reparameterization of the Weibull's pdf:

$$f(d) = \frac{\propto}{\beta}\left(\frac{d}{\beta}\right)^{\alpha-1} exp\left[-\left(\frac{d}{\beta}\right)^{\alpha}\right] \quad 2$$

where *d* is the random variable (tree diameter), and α and β are parameters. The advantages of using the Weibull pdf is the interpretation of its parameters. Bailey and Dell (1973) noticed that values of the α parameter lower than 1 describe monotonic and descendant curves, which resembles negative exponential diameter distributions; meanwhile, if α is lower, Eq. (2) depicts a unimodal curve with positive asymmetry. Lastly, when α equals 3.6, Eq. (2) represents a curve similar to those described by the Gaussian's pdf. Values higher than 3.6 describe a normal curve with negative asymmetry. Eq. (2) was fitted by maximum likelihood using the R package *fitdistrplus* (Delignette-Muller and Dutang, 2015).

2.4.2. Age-diameter relationship

We studied the age-size relationship by modeling tree age as a function of its diameter (*d*). Because of the nested structure of the data (trees within sample plots, and those nested within blocks), we fit linear mixed models by maximum likelihood using the *nlme* package (Crawley, 2012) and used findings from previous work to inform the selection of the random structure (Salas-Eljatib et al., 2019). We assessed the model by computing the coefficient of determination (r^2) between the observed and predicted values, and the mean square error of the residuals, based on the fixed-effects.

2.4.3. Spatial point patterns

The univariate spatial distribution patterns for live and dead trees were analyzed with the pair-correlation function ("PCR", Stoyan and Stoyan, 1996; Wiegand and Moloney, 2004). As noted by Salas-Eljatib et al. (unpublished) most of the spatial analyses in forest ecology are based on fitting Ripley's function (Ripley, 1977), but because of its cumulative nature, some criticism has been raised (see Wiegand and Moloney, 2004). To address these issues, the PCR is now one of the functions most used in current ecological studies, as summarized by Wiegand and Moloney (2014). The PCR is estimated from Ripley's function by the following expressions:

$$\widehat{K}(r) = \frac{A}{n^2}\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{1}{w_{ij}}I_r(u_{ij}) \quad 3$$

where u_{ij} is the is the distance (m) between the i-*th* subject tree and the j-*th* tree,

I_r is a counter, equal to 1 if $u_{ij} \leq r$ (the tree is within the circular plot of radius *r*) or zero otherwise, w_{ij} is an edge correction factor. To

compute the PCR and avoid the cumulative nature of $K(r)$, the following equation was conducted:

$$PCR(r) = \frac{d\hat{k}(r)}{dr} \Big/ \pi r \quad (4)$$

where the first term of the function is the derivative of the $K(r)$ on the distance r. PCR(r) is computed between the expected value of rings around the tree of interest (Wiegand and Moloney, 2004). We used 1 m as the interval of incrementing r, and starting with $r = 1$, and ending with a maximum value of $r = 20$ m. Further details about this modeling approach can be reviewed in Wiegand and Moloney (2004). The PCR(r) function was fitted using the live and dead trees per site conditions using the SpPack package (Perry, 2004).

2.4.4. NDVI

The average of the last five years (using the highest NDVI per year, commonly found in December-February-see above section for details) per plot (12 per site) was used to compare sites using ANOVA, with post-hoc Tukey's test performed when ANOVA was significant at a level of 95 %. Previously to running the ANOVA, Levene's test for homogeneity of variance, and Shapiro-Wilk for data normality were performed.

3. Results

3.1. Diameter and age structures among precipitation sites

The scale parameter ($\hat{\alpha}$) fit for live trees through Weibull probability function was 1.18 in the humid site and increased towards the dry site, showing values of 1.38 for the mesic site and 1.68 for the dry site (Fig. 2). High mortality was observed throughout for small diameters, and increased their probability towards the humid site. Specifically, a scale parameter ($\hat{\alpha}$) value of 0.98 was found for dead trees in the humid site, suggesting mortality was intense in $d < 10$ cm. However, in mesic ($\hat{\alpha}$ =1.42) and dry ($\hat{\alpha} = 1.51$) sites the mortality was intense for trees below 20 cm in d, showing higher scale parameters for both sites (Fig. 2).

The Weibull pdf for age had a distinct age pattern among sites (Fig. 3). The scale parameter fit for the dry site was 3.47 and decreased

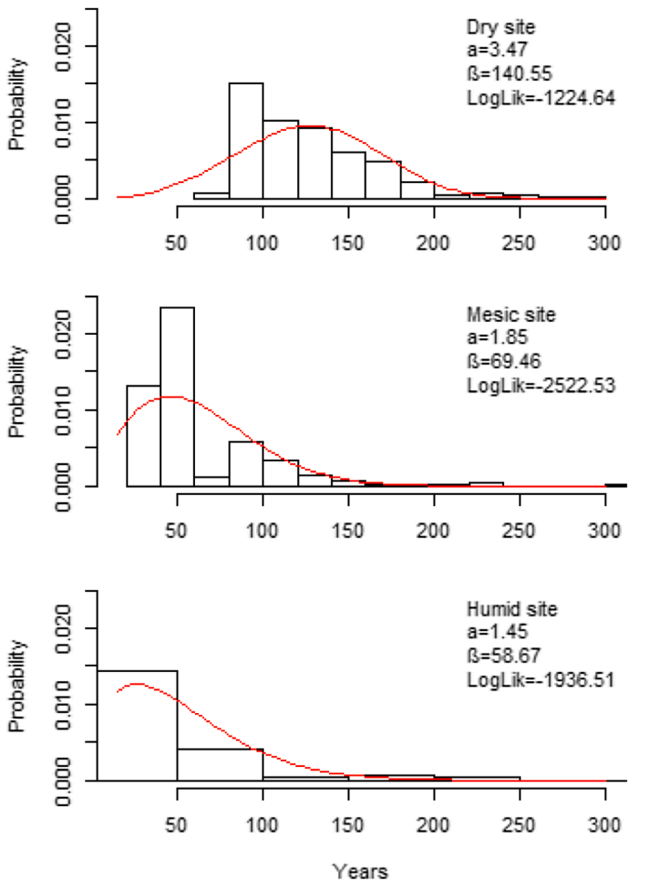


Fig. 3. Weibull probability function for tree age for each site and sorted by precipitation (increasing from left to right panels). The estimated parameters and log likelihood of the Weibull probability density function (Eq. (2)) and the fitted curve in red are also displayed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

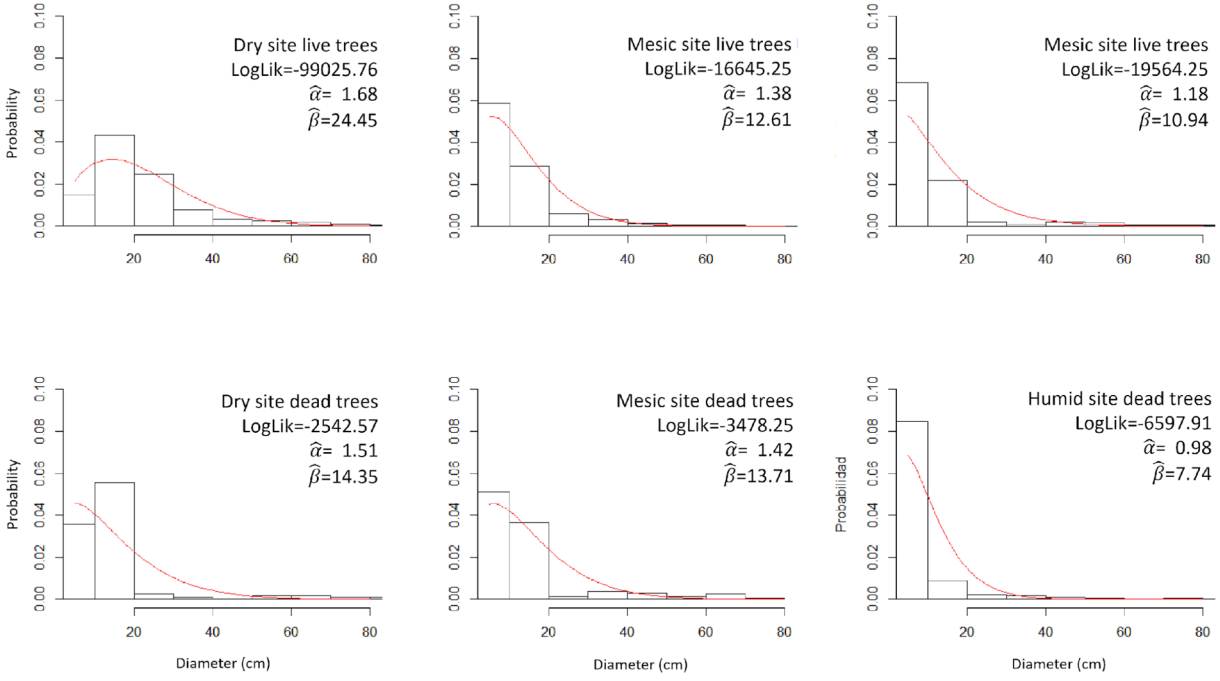


Fig. 2. Density probability function (pdf) for the tree diameters for live (upper panels) and dead trees (lower panels) for each site. The estimated parameters and log likelihood of the Weibull probability density function (Eq. (2)) and the fitted curve in red are also displayed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

towards the mesic (1.85) and humid (1.45) sites. In the same way, the form parameter ($\widehat{\beta}$) was higher for the dry site (140.5) and declined towards the mesic (69.46) and humid (58.6) sites. Specifically, peaks in regeneration occurred 30–50 years ago in the humid site, 40–60 years ago in the mesic site and 80 years ago in the dry site (Fig. 3), which abruptly stopped after this peak of regeneration.

3.2. Age vs. d relationship among precipitation sites

The relationship between age and *d* displayed an exponential versus linear relationship at all studied sites (Fig. 4); however, the strength of this relationship varied. There was a strong relationship of observed vs. predicted values for the humid ($r^2 = 0.865$) and mesic ($r^2 = 0.772$) sites, and a weaker relationship for the dry site ($r^2 = 0.376$). Specifically, trees close to 5 cm in *d* had ages in the range of 50–200 years at the dry site. In contrast, mesic and humid sites had strong age/*d* relationships in small-sized trees, but for larger trees this relationship weakened (Fig. 4).

3.3. Univariate spatial point patterns among precipitation sites

The univariate spatial point pattern for the three sites under study showed different spatial patterns in tree positions (Fig. 5). For the dry site, the null hypothesis of random pattern was met for live and dead trees, whereas the mesic site displayed a clumped pattern until 13 m, and the humid site showed intense clumping for almost the entire distance analyzed (Fig. 5). An irregular spatial point pattern between random and clumped was shown for dead trees along the distance analyzed for the mesic and humid site (Fig. 5). Specifically, the mesic site had clumped dead trees at intermediate distances and the humid site had clumping of dead trees at short distances. In contrast, the dry site displayed a fully random pattern for dead trees (Fig. 5).

3.4. Productivity among precipitation sites

We found significant differences among sites in terms of NDVI (Fig. 6), with the humid site (mean NDVI = 0.73) being different with respect to the mesic (mean NDVI = 0.68) and dry (mean NDVI = 0.63) sites ($p < 0.05$), and the mesic site being different with respect to the dry site ($p < 0.05$). The dispersion of NDVI was narrower in the humid site, and amplified towards the dry site (Fig. 6).

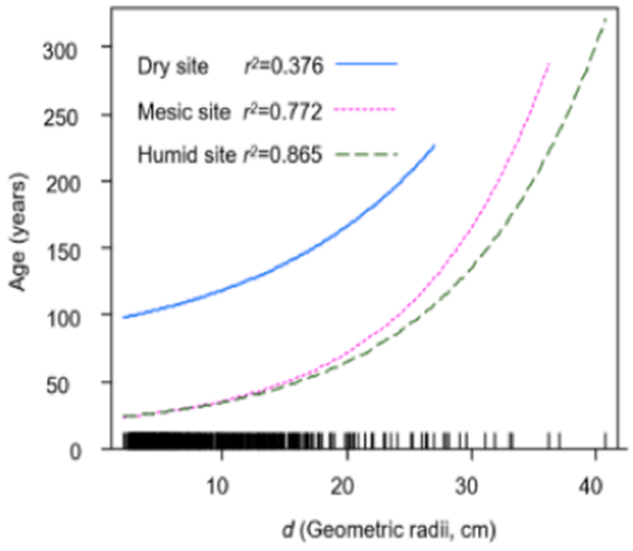


Fig. 4. Age-*d* relationships fitted through GLMMs for the three distinct precipitation sites. r^2 corresponds to the relationship between observed and fitted predicted values.

4. Discussion

The forests studied here showed contrasting size and age distributions, different spatial patterns of stem positions, and also different productivity, despite representing the same stand developmental stage (old growth) for pure *N. pumilio* forests, being at relatively short distances (ca. 30 km), and lacking apparent partial overstory disturbance in the last 50 years (Bernardo Acuña (humid site), Wildo Palma (mesic site), and Alejandro Galilea (dry site), personal communication). Although several studies have documented the influence of disturbance history in generating variation in old-growth structural characteristics and processes in a given forest type (Zenner, 2005; D'Amato et al., 2008), our study is one of few to demonstrate the influence of the underlying precipitation regime in affecting stand structural development and therefore forest productivity. Our findings indicate that the rates of structural development and recovery (i.e., regeneration following partial overstory disturbance) are driven differentially by precipitation regimes in this forest type, which may affect post-disturbance recovery time or even stall recovery by arresting succession when regeneration limitations are present (see Soto and Puettmann, 2020). Such information collected in this study is critical for anticipating changes in forest structural dynamics, and to plan for appropriate adaptation strategies in response to climate change, including precipitation declines.

4.1. Effects of precipitation upon tree size and age distributions.

The scale parameter ($\widehat{\alpha}$) of the Weibull probability function (pdf) for the humid and mesic sites indicated a quite similar monotonic and descendant curve, confirming an irregular tree-size structure or reverse-J diameter distribution for these sites (*sensu* Bailey and Dell, 1973; Lorimer and Krug, 1983). A similar pattern for the age structure was found for the humid and mesic sites, suggesting that these forests are truly uneven-aged. These results confirm our study hypothesis that pure lenga old-growth forests with irregular tree-size structures are uneven-aged; this postulate has remained unresolved until now, assuming the diameter structure can be linked to age structure. However, the scale parameter for the dry site was 1.68 and 3.47 for the size and age structures, respectively. The latter values for the dry site can be considered unimodal with a left asymmetry, indicating that smaller trees (i.e., $d < 10$ cm), as well as those with ages<50 years old are almost absent in that forest condition. Moreover, the age structure showed a lack of relationship between age and *d*, with trees 5 cm in *d* with an age of 20 years or 200 years. Three potential mechanisms can be operating in these dry sites with scarce soil water availability: 1) mortality induced by drought on tree regeneration (seedlings), 2) mortality induced by strong competition to small-trees (established regeneration), and/or 3) seasonal mortality of small regenerating seedlings due to inhibition mechanisms caused by dense and thick litter layers, as found by Soto et al. (2021). This is also consistent with the findings by Hennemann and Kitzberger (2006) in canopy gaps in lenga forests in drier sites in its northern distribution in Argentinean Patagonia. Therefore, competition for soil resources (i.e., soil water availability), which is largely assumed to be size-symmetric (*sensu* Schwinning and Weiner 1998), can be considered as the decisive mechanism operating in the dry site. The same mechanism was claimed by Soto et al. (2021) for understory patterns in lenga forests (i.e., cover, richness and plant diversity) within the same sites under study here. On the other hand, the humid and mesic sites have no apparent water limitation for the studied species, where a prolific regeneration became established and grew following the last partial overstory disturbance. In these sites, high mortality was observed among small *d* sizes (see Weibull pdf for dead trees) presumably indicating greater resource limitation in these size classes relative to larger trees. Since soil water availability is likely not a limiting factor for regeneration and growth in mesic and humid sites for *N. pumilio*, these patterns of mortality are likely driven by asymmetric competition for light instead of symmetric competition for soil resources (Schwinning

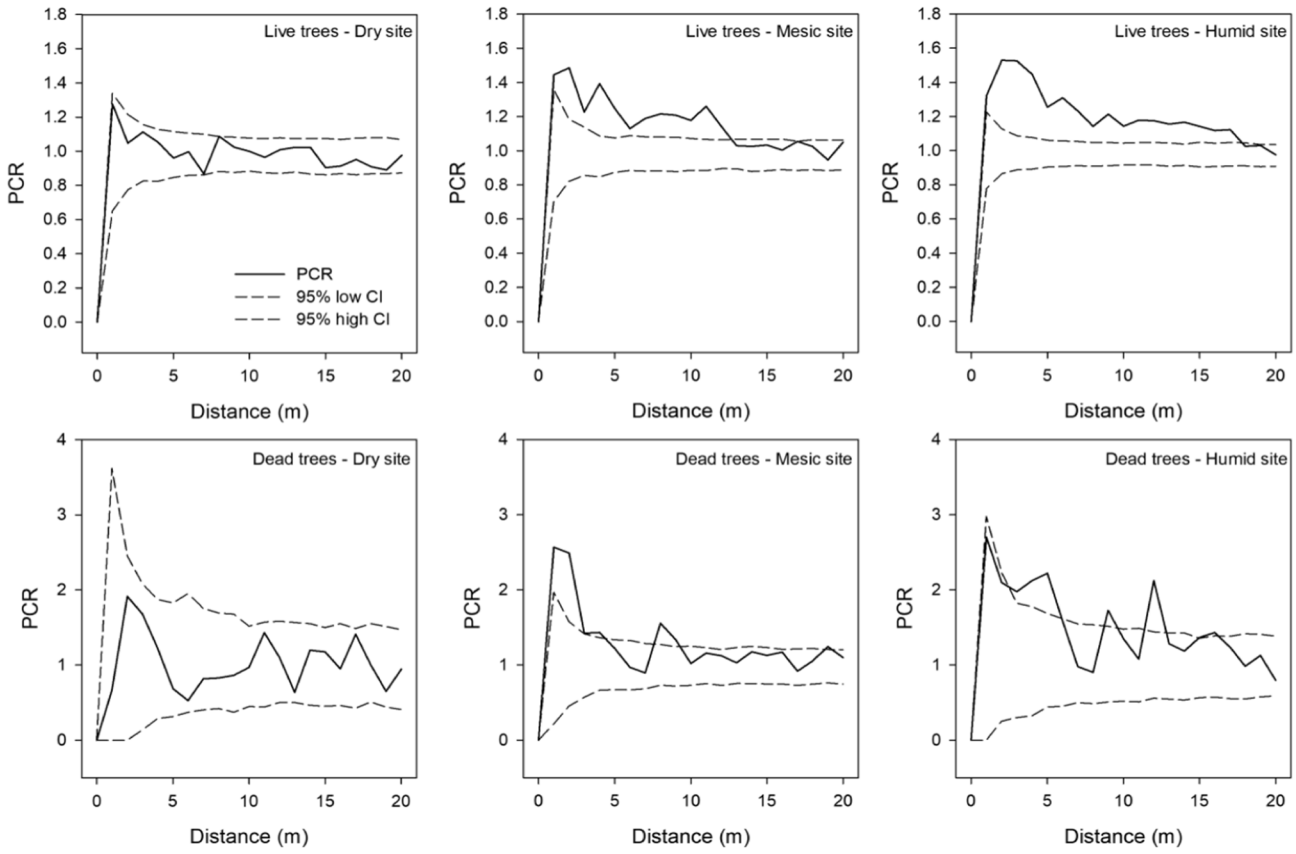


Fig. 5. Univariate pair correlation function (PCR) for the different precipitation sites. Dashed lines represent the 95 % confidence interval (CI) for a random pattern. Continuous line for live and dead trees above the CI represents cluster pattern and below it represents regular pattern.

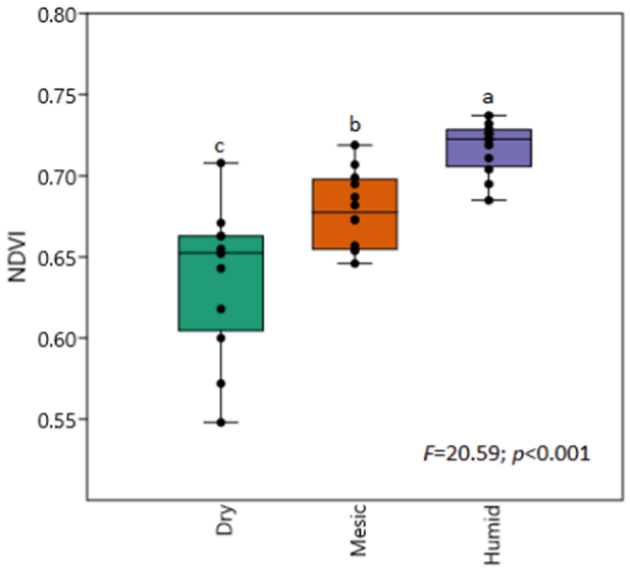


Fig. 6. Distribution of the NDVI per plot (12 per site) by precipitation sites. Different letters show significant differences among sites ($p < 0.05$) based on an one-way ANOVA model.

and Weiner, 1998; Weiner, 1990).

4.2. Age vs. d relationships

In some cases, particularly with species less tolerant to shade, there is often a strong correlation between tree size and age (Witt, 2010). Nevertheless, previous work has demonstrated a weaker relationship for shade-tolerant trees given the ability for individuals to reach advanced ages as smaller, suppressed individuals before ascension to upper canopy positions in humid site conditions (e.g., Seymour and Kenefic, 1998). The high age-*d* correlation in humid and mesic sites in this study ($r^2 = 0.86$ and 0.77) may reflect the rapid development of regeneration in these forests enabled by access to ample soil water availability. In contrast, the lack of a strong age-size relationships observed in old-growth forests under dry conditions suggest variation in access to limiting resources, namely soil water, may have resulted in a wide range of ages for a given size. These patterns are consistent with those observed in response to variability in above-ground resource availability (i.e., light) in more humid forests (Seymour and Kenefic 1998).

Each site had large (>100 cm) and old trees that correspond to structural legacies from past partial overstory disturbance. Recruitment patterns at each site following these events had varying duration, depending on the precipitation regime. The dry site exhibited an extended recruitment period reflected by cohorts establishing between 200 and 80 years ago. In contrast, the recruitment period spanned 100 years at the mesic site (50–150 years ago) and was shortest at the humid site (50 year spanning 50–100 years ago). The differences in recruitment periods between precipitation regimes is consistent with patterns in other temperate forests, where drier sites display extended recruitment patterns due to greater limitations to successful regeneration, namely soil moisture availability (e.g., Millar et al., 2015). Moreover, the multi-decadal recruitment periods documented at all sites are consistent with a growing body of literature highlighting such patterns following stand replacing disturbances and their importance in generating complex forest conditions early in stand development (Tappeiner et al., 1997; Donato et al., 2012; Freund et al., 2014).

4.3. Changes in spatial patterns in lenga forests according to precipitation

A common hypothesis from spatial point patterns of trees is that small trees (e.g., saplings) have a clumpy pattern, middle-age trees have regular patterns, and old trees have a random spatial distribution in old-growth forests (Szwagrzyk and Czerwczak, 1993; Aldrich et al., 2003; Rozas, 2006), which is not consistently supported by our results. Specifically, we found a distinct spatial pattern from complete randomness in the dry site to strong clumping in the mesic and humid sites. This confirmed our hypothesis H3. The process of changing from a clumped (young forest or young trees) to a random pattern (mature and/or old-growth forest or patterns of large trees) (Szwagrzyk and Czerwczak, 1993; Aldrich et al., 2003; Wiegand and Moloney, 2004) is largely linked to mortality that takes place in absence of major endogenic overstory disturbances (Kenkel, 1988; Lepš and Kindlmann, 1987). A generally accepted hypothesis is that dead trees have a clumped pattern in space reflecting the outcomes of mortality at short distances due to strong competition (Kenkel, 1988; Wiegand and Moloney, 2004). Spatial patterns for dead trees at the mesic and humid sites followed this expectation, whereas dead trees at the dry site did not meet this hypothesis and followed a random process consistently along all distances analyzed (20 m). Some work suggests that spatially random mortality patterns, such as those detected at the dry site, are more common in old-growth forest ecosystems than previously expected, and reflect density-independent mortality processes (Larson and Churchill, 2008; Aakala et al., 2012). Undoubtedly, further research is needed to better understand these patterns, and larger plots (e.g., 1 ha) would help for this purpose.

4.4. Productivity of lenga forests across sites with differing precipitation

The difference in NDVI between sites shows that there is an effect of climate (i.e., precipitation) on primary forest productivity. This relationship has been demonstrated in different vegetation types globally (Zhang et al., 2013; Clinton et al., 2014; Tang et al., 2017; Yang et al., 2017; Touhami et al., 2022). Moisture is the main abiotic environmental limitation for regeneration and growth in the dry site, including canopy gaps not filled with regeneration since the last disturbance (ca. 50 years), causing lower productivity. The humid site allows for the development of abundant clumped regeneration in gaps, high tree densities, and large and tall trees. While productivity expectations for the mesic site were similar as for the humid site, and in fact, also had abundant regeneration and high tree densities in small-diameter classes clumped in gaps, there was a massive apical death (that is, upper canopy) of large trees, which started to occur in the mid-90s (Fig. 7). Apical death of these large trees represents an adaptation strategy to new drier conditions in this site, as these individuals would not be able to transport water to the upper canopy from soils with lower moisture than historical levels, i.e., it is a consequence of a cavitation process (*sensu* Ogasa et al., 2013; Olson et al., 2018). This is of particular interest and concern since it can be inferred that forests at this site are transitioning towards a drier condition triggered by changes in precipitation experienced in western Patagonia (Olivares-Contreras et al., 2019). The use of remote sensing and corresponding NDVI in these areas allowed us to capture these dynamics and demonstrate that NDVI works well as a proxy for the forest productivity of the sites studied, being in line with the existing literature (Clinton et al., 2014; Asbeck et al., 2021; Touhami et al., 2022).

4.5. Forest complexity variations according to precipitation

The last partial overstory disturbances at the humid and mesic sites recruited new *d* and age cohorts with the abundance of these trees generally < 20 cm in *d*. This pattern indicates that regeneration was prolific after this disturbance, enhancing an irregular and uneven-aged forest structures in both sites, humid and mesic. The same pattern has been reported in lenga forests with irregular structures at low elevation forests in mesic sites in Argentina (Bava, 1999; López-Bernal et al., 2003). Also, Promis (2018) showed that humid coastal mixed forests of lenga and coihue de Magallanes (*Nothofagus betuloides*) had reverse-J diameter distributions (i.e. negative exponential curve). Moreover, four decades ago Donoso (1981) pointed out in the original Chilean forest types classification that pure lenga forests could have uneven-aged structures, but there was little empirical support for this assertion. In this work, we confirm the uneven-aged condition for old-growth lenga forests and highlight the variation in structures expected under this condition in different precipitation regimes.

Overall, uneven-aged forests are often characterized by complex forest structures (see Puettmann et al., 2009; Messier et al., 2013; Soto and Puettmann, 2020; Stiers et al. 2020) that are linked to several ecosystem services (Fahey et al., 2018; Perles-Garcia et al., 2021). In that matter, recent studies have pointed out that precipitation influences forest structural complexity at global (Ehbrecht et al., 2021) and regional scales (Seidel et al., 2021). As forest structural complexity is linked to several forest functions and services, studying how varying climate components (i.e. precipitation and temperature) affect forest processes and patterns is of great interest to foresters and forest



Fig. 7. Aerial photograph showing the dieback of larger trees of lenga in the mesic site in Reserva Nacional Trapananda. Photograph taken during March 2021.

ecologists (Fahey et al., 2018; Ehbrecht et al., 2021). Old-growth forests without recent past disturbances, such as those examined in this study, provide an excellent opportunity to assess forest structure according to climatic variations. For example, Seidel et al. (2021) found that the understory complexity index of different forest types of Chile can be directly linked to climate factors (i.e., seasonal precipitation) without mediation of canopy openness and basal area in absence of recent major overstory disturbances. In addition, the contrasting patterns of productivity for the three sites we examined, although not unexpected given the well-known linkages between precipitation on above-ground forest productivity (Barnes et al., 1999; Asner et al., 2005), also can be linked to forest structural complexity (Gough et al., 2019), which is related to more densely packed canopy strata (Stiers et al. 2020; Ehbrecht et al., 2021).

4.6. Implications for forest management

An understanding of the structure and dynamics of old-growth forests is central to the development of silvicultural strategies for restoring their complexity and increasing adaptation potential in the face of climate change (Palik et al., 2021). To this end, the natural recruitment process documented at the humid and mesic sites suggest tree regeneration after partial overstory disturbance five decades prior to this study, supporting previous work that old-growth lenga forests follow gap-phase regeneration patterns (sensu Veblen, 1992; Heinemann et al., 2000; Fajardo and de Graaf, 2004; Promis, 2018; Donoso et al., 2022a). This natural disturbance model, which allow regeneration and the establishment of new *d* and age cohorts in these forests, could be emulated with uneven-aged silvicultural systems, such as single-tree selection systems (Nyland, 2002; O'Hara, 2014; Donoso et al., 2020; Soto and Puettmann, 2020; Donoso et al., 2022b) (Fig. 8). This silvicultural option is a great alternative to the traditional shelterwood system (Martínez-Pastur et al., 2000) and seed-tree cutting (Rosenfeld et al., 2006) typically and successful used in lenga forests, since it creates more complex forest structures than these even-aged approaches (Puettmann et al., 2009, 2015; Messier et al., 2013; Stiers et al., 2020; Donoso et al., 2022a). Actually, Bava (1999) suggested the uneven-aged silviculture options for humid sites in northern Patagonia, but it has been rarely used. In contrast, the size and age structures documented for the dry site are more consistent with forest ecosystems experiencing mixed severity disturbance regimes, where extended recruitment periods following partial overstory disturbances can generate complex structures over time (Donato et al., 2012; Fraver and Palik, 2012). Given the recent drought dynamics in our study region, resistance adaptation strategies (see Palik et al., 2021) focused on reducing drought-induced stress on existing trees in these forests will be a critical near-term option to avoid their potential transformation into woodlands. Collectively, these findings underscore the importance of accounting for the influence of varying precipitation upon regeneration dynamics, forest structure and productivity in these Patagonian pure old-growth forests, and argue for the development of site-tailored management strategies that account for underlying climate regime to achieve timber or conservation/adaptation objectives (D'Amato et al., 2011; Palik et al., 2021).



Fig. 8. An example of single-tree selection method based on BDq approach recently implemented at Reserva Nacional Trapananda (mesic site) treated with 45 m^2 of residual basal area with D of 60 cm and q factor of 1.6. It is hypothesized that regeneration will create a new age cohort and understory will increase in species richness and cover due increases in resource availability left soon after harvesting (including downed wood), therefore potentially increasing stand structural complexity.

5. Conclusions

In this study, we show that old-growth lenga forests, from the eastern Andes towards the steppe, are less complex and vigorous as precipitation declines whereas other environmental conditions are similar. Changes in the structure, spatial patterns and productivity in old-growth lenga forests in western Patagonia suggest that the impacts of climate change, especially declines in precipitation expected for the region, must be faced differentially across the region. While humid and mesic sites could be managed with uneven-aged silviculture to promote complex forest structures for a variety of goods and services, our results suggest that climate change adaptation strategies should be considered for dry sites, specifically management strategies aimed at preventing in more extreme cases the potential transformation of pure lenga forest ecosystems to woodlands. In this vein, it is urgent that decision-makers and forest managers take into account these findings to enhance adaptive management of these forests for both conservation or production purposes.

Funding

Fondecyt 1221593 and FIBN 09/2019-CONAF.

CRediT authorship contribution statement

Daniel P. Soto: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Christian Salas-Eljatib:** Formal analysis, Methodology, Writing – review & editing, Visualization. **Pablo J. Donoso:** Methodology, Writing – review & editing. **Ángela Hernández-Moreno:** Formal analysis, Methodology, Writing – review & editing. **Dominik Seidel:** Writing – review & editing. **Anthony W. D'Amato:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the support of project Fondecyt 1221593 and FIBN 09/2019-CONAF. We also thank to Andrea Ríos, Marcelo Sanhueza, Mathias Legue, Manuel Vargas, Jose Manuel Velásquez, Manuel Villalobos, Marcelo González. We also thank the logistic support from CONAF (Patricio Poblete, Julio Molettieri, Wildo Palma, Hernán Herrriquez, Marcela Piñones), Bernardo Acuña and David Muñoz (lago largo site), and Alejandro Galilea (Hacienda Punta del Monte in Coyhaique alto).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120519.

References

Aakala, T., Fraver, S., Palik, B.J., D'Amato, A.W., 2012. Spatially random mortality in old-growth red pine forests of northern Minnesota. Can. J. For. Res. 42, 899–907. https://doi.org/10.1139/x2012-044.

Aldrich, P.R., Parker, G.R., Ward, J.S., Michler, C.H., 2003. Spatial dispersion of trees in an old-growth temperate hardwood forest over 60 years of succession. For. Ecol. Manage. 180 (1–3), 475–491. https://doi.org/10.1016/S0378-1127(02)00612-6.

Asbeck, T., Sabatini, F., Augustynczik, A.L., Basile, M., Helbach, J., Jonker, M., Knuff, A., Bauhus, J., 2021. Biodiversity response to forest management intensity, carbon stocks and net primary production in temperate montane forests. Sci. Rep. 11 (1), 1–11. https://doi.org/10.1038/s41598-020-80499-4.

Asner, G.P., Carlson, K.M., Martin, R.E., 2005. Substrate age and precipitation effects on Hawaiian forest canopies from spaceborne imaging spectroscopy. Rem. Sens. Environ. 98 (4), 457–467. https://doi.org/10.1016/j.rse.2005.08.010.

Bailey, R.L., Dell, T.R., 1973. Quantifying diameter distributions with the Weibull function. For. Sci. 19 (2), 97–104. https://doi.org/10.1093/forestscience/19.2.97.

Baker, P.J., Bunyavejchewin, S., Oliver, C.D., Ashton, P.S., 2005. Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. Ecol. Monogr. 75 (3), 317–343. https://doi.org/10.1890/04-0488.

Barnes, B.V., Zak, D.R., Denton, S.R., Spurr, S.H., 1999. Forest Ecology, Fourth Edition. John Wiley & Sons, New York.

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manage. 258(4), 525-537. https://doi.org/10.1016/j.foreco.2009.01.053.

Bava, J., 1999. Los bosques de lenga en Argentina. In: Donoso, C., Lara, A. (Eds.), Silvicultura de los bosques nativos de Chile. Editorial Universitaria, Santiago, pp. 273–296.

Bava, J.O., Puig, C.J., 1992. Regeneración natural de lenga. Análisis de algunos factores involucrados. Actas Seminario Manejo Forestal de la Lenga y Aspectos Ecológicos Relacionados. Publicación Técnica CIEFAP, Esquel.

Bianchi, E., Villalba, R., Solarte, A., 2020. NDVI Spatio-temporal Patterns and Climatic Controls Over Northern Patagonia. Ecosystems 23, 84–97. https://doi.org/10.1007/s10021-019-00389-3.

Chapin, F.S., Matson, P.A., Vitousek, P., 2011. Principles of Terrestrial Ecosystem Ecology. Second Edition, Springer, New York.

Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., Lutz, J.A., 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. For. Ecol. Manage. 291, 442–457. https://doi.org/10.1016/j.foreco.2012.11.007.

CIREN, 2005. Estudio agrológico XI Región : descripciones de suelos, materiales y símbolos., CIREN N°13. Centro de información de recursos naturales, Santiago.

Clinton, N., Yu, L., Fu, H., He, C., Gong, P., 2014. Global-scale associations of vegetation phenology with rainfall and temperature at a high spatio-temporal resolution. Rem. Sens. 6 (8), 7320–7338. https://doi.org/10.3390/rs6087320.

Coomes, D.A., Allen, R.B., 2007. Mortality and tree-size distributions in natural mixed-age forests. J. Ecol. 95 (1), 27–40. https://doi.org/10.1111/j.1365-2745.2006.01179.x.

Crawley, M.J., 2012. The R book, Second edition. John Wiley and Sons, London.

D'Amato, A.W., Orwig, D.A., Foster, D.R., 2008. The influence of successional processes and disturbance on the structure of *Tsuga canadensis* forests. Ecol. Appl. 18 (5), 1182–1199. https://doi.org/10.1890/07-0919.1.

D'Amato, A.W., Orwig, D.A., Foster, D.R., 2009. Understory vegetation in old-growth and second-growth *Tsuga canadensis* forests in western Massachusetts. For. Ecol. Manage. 257 (3), 1043–1052. https://doi.org/10.1016/j.foreco.2008.11.003.

D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2011. Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. For. Ecol. Manage. 262, 803–816. https://doi.org/10.1016/j.foreco.2011.05.014.

Delignette-Muller, M.L., Dutang, C., 2015. fitdistrplus: An R package for fitting distributions. J. Stat. Softw. 64, 1–34. https://doi.org/10.18637/jss.v064.i04.

Donato, D.C., Campbell, J.L., Franklin, J.F., 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? J. Veg. Sci. 23 (3), 576–584. https://doi.org/10.1111/j.1654-1103.2011.01362.x.

Donoso, C., 1981. Tipos Forestales de los bosques nativos de Chile. Investigación y Desarrollo Forestal. Documento de Trabajo N°. CONAF-FAO-PNUD, Santiago, p. 38.

Donoso, C., 1993. Bosques templados de Chile y Argentina: variación, estructura y dinámica, Segunda ed. Editorial Universitaria, Santiago.

Donoso, C., Escobar, B., Urrutia, J., 1985. Estructura y estrategias regenerativas de un bosque virgen de ulmo (*Eucryphia cordifolia* Cav.)-tepa (*Laurelia philippiana* Phil.) Looser en Chiloé. Chile. Rev. Chil. Hist. Nat. 58 (2), 171–186.

Donoso, P.J., 2005. Crown index: a canopy balance indicator to assess growth and regeneration in uneven-aged forest stands of the Coastal Range of Chile. Forestry 78 (4), 337–351. https://doi.org/10.1093/forestry/cpi046.

Donoso, P.J., Ojeda, P.F., Schnabel, F., Nyland, R.D., 2020. Initial responses in growth, production, and regeneration following selection cuttings in hardwood-dominated temperate rainforests in Chile. Forests 11 (4), 412. https://doi.org/10.3390/f11040412.

Donoso, P.J., Promis, Á., Loguercio, G.A., Beltrán, H.A., Caselli, M., Chauchard, L.M., Cruz, G., González-Peñalba, M., Martínez-Pastur, G., Navarro, C., Núñez, P., Salas-Eljatib, C., Soto, D.P., Vásquez-Grandón, A., 2022a. Silviculture of South American temperate native forests. N. Z. J. Forest. Sci. 52, 2. https://doi.org/10.33494/nzjfs522022x173x.

Donoso, P.J., Soto, D.P., 2016. Does site quality affect the additive basal area phenomenon? results from Chilean old-growth temperate rainforests. Can. J. For. Res. 46, 1330–1336. https://doi.org/10.1139/cjfr-2016-167.

Donoso, P.J., Soto, D.P., Salas-Eljatib, C., Riquelme-Buitano, T., 2022b. Present and prospects for multi-aged silviculture in Chilean temperate forests: Targeting secondary forests in transition and partially harvested old-growth forests. Front. For. Glob. Change 5, 965599. https://doi.org/10.3389/ffgc.2022.965599.

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D.C., Puettmann, K., Nilus, R., Babweteera, F., Willin, K., Stiers, M., Soto, D., Boehmer, H.J., Fisichelli, N., Burnett, M., Juday, G., Stephens, S.L., Ammer, C., 2021. Global patterns and climatic controls of forest structural complexity. Nat. Commun. 12 (1), 1–12. https://doi.org/10.1038/s41467-020-20767-z.

Esse, C., Correa-Araneda, F., Acuña, C., Santander-Massa, R., Los Ríos-Escalante, D., Saavedra, P., Jaque-Jaramillo, X., Moreno, R., Garcia-Meneses, P.M., Soto, D.P., 2021. Structure, diversity, and environmental determinants of high-latitude threatened conifer forests. Forests 12 (6), 775. https://doi.org/10.3390/f12060775.

Fahey, R.T., Alveshere, B.C., Burton, J.I., D'Amato, A.W., Dickinson, Y.L., Keeton, W.S., Kern, C.C., Larson, A.J., Palik, B.J., Puettmann, K.J., Saunders, M.R., Webster, C.R., Atkins, J.W., Gough, C.M., Hardiman, B.S., 2018. Shifting conceptions of complexity in forest management and silviculture. For. Ecol. Manage. 421, 59–71. https://doi.org/10.1016/j.foreco.2018.01.011.

Fajardo, A., Alaback, P., 2005. Effects of natural and human disturbances on the dynamics and spatial structure of *Nothofagus glauca* in south-central Chile. J. Biogeogr. 32 (10), 1811–1825. https://doi.org/10.1111/j.1365-2699.2005.01331.x.

Fajardo, A., de Graaf, R., 2004. Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile. Plant Ecol. 173, 95–105. https://doi.org/10.1023/B:VEGE.0000026333.54741.97.

Fajardo, A., Gazol, A., Mayr, C., Camarero, J.J., 2019. Recent decadal drought reverts warming-triggered growth enhancement in contrasting climates in the southern Andes tree line. J. Biogeogr. 46 (7), 1367–1379. https://doi.org/10.1111/jbi.13580.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

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., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155 (1–3), 399–423. https://doi.org/10.1016/S0378-1127(01)00575-8.

Fraver, S., Palik, B., 2012. Stand and cohort structures of old-growth *Pinus resinosa*-dominated forests of northern Minnesota, USA. J. Veg. Sci. 23, 249–259.

Freund, J.A., Franklin, J.F., Larson, A.J., Lutz, J.A., 2014. Multi-decadal establishment for single-cohort Douglas-fir forests. Can. J. For. Res. 44 (9), 1068–1078. https://doi.org/10.1139/cjfr-2013-0533.

Fuenzalida, T.I., Hernández-Moreno, Á., Piper, F.I., 2019. Secondary leaves of an outbreak-adapted tree species are both more resource acquisitive and more herbivore resistant than primary leaves. Tree Physiol. 39 (9), 1499–1511. https://doi.org/10.1093/treephys/tpz083.

Goff, F.G., West, D., 1975. Canopy-understory interaction effects on forest population structure. For. Sci. 21 (2), 98–108. https://doi.org/10.1093/forestscience/21.2.98.

González, M., Donoso, C., Ovalle, P., Martínez-Pastur, G., 2006. Nothofagus pumilio. In: Donoso, C. (Ed.), Las Especies Arbóreas de Los Bosques Templados de Chile y Argentina. Autoecología, Ediciones Marisa Cuneo, Valdivia, pp. 486–500.

Gough, C.M., Atkins, J.W., Fahey, R.T., Hardiman, B.S., LaRue, E.A., 2019. Community and structural constraints on the complexity of eastern North American forests. Glob. Ecol. Biogeogr. 29 (12), 2107–2118. https://doi.org/10.1111/geb.13180.

Heinemann, K., Kitzberger, T., 2006. Effects of position, understorey vegetation and coarse woody debris on tree regeneration in two environmentally contrasting forests of north-western Patagonia: a manipulative approach. J. Biogeogr. 33 (8), 1357–1367. https://doi.org/10.1111/j.1365-2699.2006.01511.x.

Heinemann, K., Kitzberger, T., Veblen, T.T., 2000. Influences of gap microheterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. Can. J. For. Res. 30, 25–31. https://doi.org/10.1139/x99-181.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree Ring Res. 43, 69–75.

Iniguez, J.M., Fowler, J.F., Moser, W.K., Sieg, C.H., Baggett, L.S., Shin, P., 2019. Tree and opening spatial patterns vary by tree density in two old-growth remnant ponderosa pine forests in Northern Arizona, USA. For. Ecol. Manage. 450, 117502. https://doi.org/10.1016/j.foreco.2019.117502.

Kenkel, N.C., 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69 (4), 1017–1024. https://doi.org/10.2307/1941257.

Larson, A.J., Churchill, D., 2008. Spatial patterns of overstory trees in late-successional conifer forests. Can. J. For. Res. 38, 2814–2825. https://doi.org/10.1139/X08-123.

Larson, A.J., Lutz, J.A., Gersonde, R.F., Franklin, J.F., Hietpas, F.F., 2008. Potential site productivity influences the rate of forest structural development. Ecol. Appl. 18, 899–910. https://doi:10.1890/07-1191.1.

Lara, C., Saldías, G.S., Paredes, A.L., Cazelles, B., Broitman, B.R., 2018. Temporal variability of MODIS phenological indices in the temperate rainforest of northern Patagonia. Remote Sens. 10, 1–12. https://doi.org/10.3390/rs10060956.

Lepš, J., Kindlmann, P., 1987. Models of the development of spatial pattern of an even-aged plant population over time. Ecol. Model. 39 (1–2), 45–57. https://doi.org/10.1016/0304-3800(87)90012-3.

López-Bernal, P.M., Bava, J.O., Antequera, S.H., 2003. Regeneración en un bosque de lenga (*Nothofagus pumilio* (Poepp et Endl.) Krasser) sometido a un manejo de selección en grupos. Bosque (Valdivia) 24 (2), 13–21. https://doi.org/10.4067/S0717-92002003000200002.

Lorimer, C.G., Krug, A.G., 1983. Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. Am. Midl. Nat. 331–345 https://doi.org/10.2307/2425414.

Martínez-Pastur, G., Cellini, J.M., Peri, P.L., Vukasovic, R.F., Fernández, M.C., 2000. Timber production of *Nothofagus pumilio* forests by a shelterwood system in Tierra del Fuego (Argentina). For. Ecol. Manage. 134 (1–3), 153–162. https://doi.org/10.1016/S0378-1127(99)00253-4.

Martínez-Pastur, G., Lencinas, M.V., Peri, P.L., Arena, M., 2007. Photosynthetic plasticity of *Nothofagus pumilio* seedlings to light intensity and soil moisture. For. Ecol. Manage. 243 (2–3), 274–282. https://doi.org/10.1016/j.foreco.2007.03.034.

McIntire, E.J., Fajardo, A., 2009. Beyond description: the active and effective way to infer processes from spatial patterns. Ecology 90 (1), 46–56. https://doi.org/10.1890/07-2096.1.

Messier, C., Puettmann, K.J., Coates, K.D., 2013. Managing forests as complex adaptive systems: building resilience to the challenge of global change. Routledge, New York.

Messier, C., Bauhus, J., Doyon, F., Maure, F., Sousa-Silva, R., Nolet, P.,..., Puettmann, K., 2019. The functional complex network approach to foster forest resilience to global changes. For. Ecosyst. 6(1), 1-16. https://doi.org/10.1186/s40663-019-0166-2.

Messier, C., Betts, M.G., Tittler, R., Paquette, A., 2021. Box C 11: A Novel TRIAD Approach to Increase Resilience of the Forest Landscape to Global Change: Or How to Make a Better Omelette without Cracking Too Many. In Krumm, F.; Schuck, A.; Rigling, A. (eds), 2020: How to balance forestry and biodiversity conservation – A view across Europe. European Forest Institute (EFI); Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf. 640 p.

Mina, M., Messier, C., Duveneck, M., Fortin, M.J., Aquilué, N., 2021. Network analysis can guide resilience-based management in forest landscapes under global change. Ecol. Appl. 31 (1), e2221. https://doi.org/10.1002/eap.2221.

Millar, C.I., Westfall, R.D., Delany, D.L., Flint, A.L., Flint, L.E., 2015. Recruitment patterns and growth of high-elevation pines in response to climatic variability (1883–2013), in the western Great Basin, USA. Can. J. For. Res. 45 (10), 1299–1312. https://doi.org/10.1139/cjfr-2015-0025.

Müller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A., Bunyavejchewin, S., Davis, S., Foster, R., Gunatilleke, S., Harms, K.E., Hart, T., Hubbell, S.P., Itoh, A., Rahman Kassim, A., LaFrankie, J.V., Lee, H.S., Losos, E., Makana, J.R., Ohkubo, T., Sukumar, R., Sun, I.F., Supardi, M.N.N., Tan, S., Thompson, J., Valencia, R., Villa-Muñoz, G.V., Wills, C., Yamakura, T., Chuyong, G., Shivaramaiah Dattaraja, H., Esufali, S., Hall, P., Hernandez, C., Kenfack, D., Kiratiprayoon, S., Suresh, H.S., Thomas, D., Vallejo, M.I., Ashton, P., 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecol. Lett. 9 (5), 575–588. https://doi.org/10.1111/j.1461-0248.2006.00904.x.

NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team. ASTER Global Digital Elevation Model V003. 2019, distributed by NASA EOSDIS Land Processes DAAC, https://doi.org/10.5067/ASTER/ASTGTM.003 (accessed 30 May 2021).

Nyland, R.D., 2002. Silviculture: concepts and applications, 2nd ed. McGraw-Hill, New York.

Ogasa, M., Miki, N.H., Murakami, Y., Yoshikawa, K., 2013. Recovery performance in xylem hydraulic conductivity is correlated with cavitation resistance for temperate deciduous tree species. Tree Physio. 33 (4), 335–344. https://doi.org/10.1093/treephys/tpt010.

O'Hara, K.L., 2014. Multiaged Silviculture: Managing for Complex Forest Stand Structures, first ed. Oxford University Press, London.

Olivares-Contreras, V.A., Mattar, C., Gutiérrez, A.G., Jiménez, J.C., 2019. Warming trends in Patagonian subantartic forest. Int. J. Appl. Earth Obs. Geoinf. 76, 51–65. https://doi.org/10.1016/j.jag.2018.10.015.

Oliver, C.D., Larson, B.C., 1996. Forest stand dynamics, update edition. Wiley Sons Inc., New York.

Olson, M.E., Soriano, D., Rosell, J.A., Anfodillo, T., Donoghue, M.J., Edwards, E.J., León-Gómez, C., Dawson, T., Camarero Martínez, J.J., Castorena, M., Echeverría, A., Espinosa, C.I., Fajardo, A., Gazol, A., Isnard, S., Lima, R.S., Marcati, C.R., Méndez-Alonzo, R., 2018. Plant height and hydraulic vulnerability to drought and cold. Proc. Natl. Acad. Sci. U.S.A. 115 (29), 7551–7556. https://doi.org/10.1073/pnas.1721728115.

Palik, B.J., D'Amato, A.W., Franklin, J.F., Johnson, K.N., 2021. Ecological Silviculture. Foundations and Applications. Waveland Press Inc., Illinois.

Parada, T., Jara, C., Lusk, C.H., 2003. Distribución de alturas máximas de especies en rodales antiguos de selva Valdiviana. Parque Nacional Puyehue. Bosque (Valdivia) 24 (2), 63–67. https://doi.org/10.4067/S0717-92002003000200007.

Pau, S., Gillespie, T.W., Wolkovich, E.M., 2012. Dissecting NDVI–species richness relationships in Hawaiian dry forests. J. Biogeogr. 39 (9), 1678–1686. https://doi.org/10.1111/j.1365-2699.2012.02731.x.

Perles-Garcia, M.D., Kunz, M., Fichtner, A., Härdtle, W., von Oheimb, G., 2021. Tree species richness promotes an early increase of stand structural complexity in young subtropical plantations. J. Appl. Ecol. 58 (10), 2305–2314. https://doi.org/10.1111/1365-2664.13973.

Perry, G.L., 2004. SpPack: spatial point pattern analysis in Excel using Visual Basic for Applications (VBA). Environ. Modell. Softw. 19 (6), 559–569. https://doi.org/10.1016/j.envsoft.2003.07.004.

Perry, G.L., Miller, B.P., Enright, N.J., 2006. A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. Plant Ecol. 187 (1), 59–82. https://doi.org/10.1007/s11258-006-9133-4.

Pettorelli, N., 2013. The normalized difference vegetation index. Oxford University Press, Oxford.

Pisano, E., 1977. Fitogeografía de Fuego - Patagonia chilena. I.- Comunidades vegetales entre las latitudes 52 y 56° S. An. Inst. Patagon. 8, 121–250.

Promis, Á., 2018. Claros de dosel en bosques nativos templados de Chile y Argentina: Conocimientos actuales y desafíos para el futuro. In: Donoso, P.J., Promis, Á., Soto, D.P. (Eds.), Silvicultura En Bosques Nativos: Experiencias En Silvicultura y Restauración En Chile, Argentina y El Oeste de Estados Unidos. College of Forestry-Oregon State University, Corvallis, pp. 23–49.

Puettmann, K.J., Coates, K.D., Messier, C.C., 2009. A critique of silviculture: managing for complexity. Island press, Washington.

Ponce, D.B., Donoso, P.J., Salas-Eljatib, C., 2017. Differentiating structural and compositional attributes across successional stages in Chilean temperate rainforests. Forests 8 (9), 329. https://doi.org/10.3390/f8090329.

Rebertus, A.J., Kitzberger, T., Veblen, T.T., Roovers, L.M., 1997. Blowdown history and landscape patterns in the Andes of Tierra del Fuego, Argentina. Ecology 783, 678–692. https://doi.org/10.1890/0012-9658(1997)078[0678:BHALPI]2.0.CO;2.

Rebertus, A.J., Veblen, T.T., 1993. Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego. Argentina. J. Veg. Sci. 4, 641–654. https://doi.org/10.2307/3236129.

Ripley, B.D., 1977. Modelling spatial patterns. J. R. Stat. Soc. Series B Methodol. 39 (2), 172–192. https://doi.org/10.1111/j.2517-6161.1977.tb01615.x.

Rosenfeld, J.M., Cerrillo, R.N., Alvarez, J.G., 2006. Regeneration of Nothofagus pumilio [Poepp. et Endl.] Krasser forests after five years of seed tree cutting. J. Environ. Manage. 78 (1), 44–51. https://doi.org/10.1016/j.jenvman.2005.03.009.

Rouse, J.W., Haas, R.H., Deering, D.W., Sehell, J.A., 1974. Monitoring the vernal advancement and retrogradation (Green wave effect) of natural vegetation. Final Rep. RSC 1978-4, Remote Sensing Center, Texas A&M University, Austin.

Rozas, V., 2006. Structural heterogeneity and tree spatial patterns in an old-growth deciduous lowland forest in Cantabria, northern Spain. Plant Ecol. 185 (1), 57–72. https://doi.org/10.1007/s11258-005-9084-1.

Salas, C., LeMay, V., Núnez, P., Pacheco, P., Espinosa, A., 2006. Spatial patterns in an old-growth *Nothofagus obliqua* forest in south-central Chile. For. Ecol. Manage. 231 (1–3), 38–46. https://doi.org/10.1016/j.foreco.2006.04.037.

Salas-Eljatib, C., 2021. An approach to quantify climate–productivity relationships: an example from a widespread *Nothofagus* forest. Ecol. Appl. 31 (4), e02285. https://doi.org/10.1002/eap.2285.

Salas-Eljatib, C., Corvalán, P., Pino, N., Donoso, P.J., Soto, D.P., 2019. Modelos de efectos mixtos de altura-diámetro para *Drimys winteri* en el sur (41–43° S) de Chile. Bosque (Valdivia) 40, 71–80. https://doi.org/10.4067/s0717-92002019000100071.

Salas-Eljatib, C., Mehtätalo, L., Gregoire, T.G., Soto, D.P., Vargas-Gaete, R., 2021. Growth Equations in Forest Research: Mathematical Basis and Model Similarities. Curr. Forestry Rep. 7, 230–244. https://doi.org/10.1007/s40725-021-00145-8.

Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113 (4), 447–455. https://doi.org/10.1007/s004420050397.

Schütz, J.P., Pukkala, T., Donoso, P.J., Gadow, K.V., 2012. Historical emergence and current application of CCF. In: Pukkala, T., Gadow, K.V. (Eds.), Continuous cover forestry. Springer, Dordrecht, pp. 1–28.

Seidel, D., Annighöfer, P., Ammer, C., Ehbrecht, M., Willim, K., Bannister, J., Soto, D.P., 2021. Quantifying understory complexity in unmanaged forests using TLS and identifying some of its major drivers. Remote Sens. 13 (8), 1513. https://doi.org/10.3390/rs13081513.

Seymour, R.S., Kenefic, L.S., 1998. Balance and sustainability in multiaged stands: a northern conifer case study. J. For. 96, 12–17. https://doi.org/10.1093/jof/96.7.12.

Soto, D.P., Salas, C., Donoso, P.J., Uteau, D., 2010. Heterogeneidad estructural y espacial de un bosque mixto dominado por *Nothofagus dombeyi* después de un disturbio parcial. Rev. Chil. Hist. Nat. 83 (3), 335–347. https://doi.org/10.4067/S0716-078X2010000300002.

Soto, D.P., Puettmann, K.J., 2018. Topsoil removal through scarification improves natural regeneration in high-graded *Nothofagus* old-growth forests. J. Appl. Ecol. 55 (2), 967–976. https://doi.org/10.1111/1365-2664.12989.

Soto, D.P., Puettmann, K.J., 2020. Merging multiple equilibrium models and adaptive cycle theory in forest ecosystems: implications for managing succession. Curr. Forestry Rep. 6 (4), 282–293. https://doi.org/10.1007/s40725-020-00128-1.

Soto, D.P., Donoso, P.J., Zamorano-Elgueta, C., Ríos, A.I., Promis, Á., 2021. Precipitation declines influence the understory patterns in *Nothofagus pumilio* old-growth forests in northwestern Patagonia. For. Ecol. Manage. 4 (91), 119169. https://doi.org/10.1016/j.foreco.2021.119169.

Spies, T.A., 2004. Ecological concepts and diversity of old-growth forests. J. For. 102 (3), 14–20. https://doi.org/10.1093/jof/102.3.14.

Stiers, M., Annighöfer, P., Seidel, D., Willim, K., Neudam, L., Ammer, C., 2020. Quantifying the target state of forest stands managed with the continuous cover approach–revisiting Möller's "Dauerwald" concept after 100 years. Trees, Forests and People 1, 100004. https://doi.org/10.1016/j.tfp.2020.100004.

Stoyan, D., Stoyan, H., 1996. Estimating pair correlation functions of planar cluster processes. Biom. J. 38 (3), 259–271. https://doi.org/10.1002/bimj.4710380302.

Szwagrzyk, J., Czerwczak, M., 1993. Spatial patterns of trees in natural forests of East-Central Europe. J. Veg. Sci. 4 (4), 469–476. https://doi.org/10.2307/3236074.

Tang, Z., Ma, J., Peng, H., Wang, S., Wei, J., 2017. Spatiotemporal changes of vegetation and their responses to temperature and precipitation in upper Shiyang river basin. Adv. Sp. Res. 60, 969–979. https://doi.org/10.1016/j.asr.2017.05.033.

Tappeiner, J.C., Huffman, D.W., Marshall, D., Spies, T.A., Bailey, J.D., 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. Can. J. For. Res. 27 (5), 638–648. https://doi.org/10.1139/x97-015.

Toro-Manríquez, M., Promis, Á., Huertas-Herrera, A., Martínez Pastur, G., 2018. Influencia del micrositio y la exposición en la regeneración de bosques de *Nothofagus pumilio* afectados por Castor canadensis en Tierra del Fuego: un análisis exploratorio. Bosque (Valdivia) 39 (3), 431–440. https://doi.org/10.4067/S0717-92002018000300431.

Tyrrell, L.E., Crow, T.R., 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75 (2), 370–386. https://doi.org/10.2307/1939541.

Touhami, I., Moutahir, H., Assoul, D., Bergaoui, K., Aouinti, H., Bellot, J., Andreu, J.M., 2022. Multi-year monitoring land surface phenology in relation to climatic variables using MODIS-NDVI time-series in Mediterranean forest. Northeast Tunisia. Acta Oecol. 114, 103804. https://doi.org/10.1016/j.actao.2021.103804.

Veblen, T.T., 1992. Regeneration dynamics. In: Glenn-Lewin, D.C., Peet, R.K., Veblen, T. T. (Eds.), Plant Succession: Theory and Prediction. Chapman and Hall, London, pp. 152–186.

Veblen, T.T., Donoso, C., Kitzberger, T., Rebertus, A.J., 1996. Ecology of Southern Chilean and Argentinean *Nothofagus* Forests. In: Veblen, T.T., Hill, R.S., Read, J. (Eds.), Ecology and Biogeography of *Nothofagus* Forests. Yale University Press, New Haven, pp. 293–353.

Wang, J., Rich, P.M., Price, K.P., Kettle, W.D., 2004. Relations between NDVI and tree productivity in the central Great Plains. Int. J. Remote Sens. 25 (16), 3127–3138. https://doi.org/10.1080/0143116032000160499.

Wang, X., Hao, Z., Zhang, J., Lian, J., Li, B., Ye, J., Yao, X., 2009. Tree size distributions in an old-growth temperate forest. Oikos 118 (1), 25–36. https://doi.org/10.1111/j.0030-1299.2008.16598.x.

Weiner, J., 1990. Asymmetric competition in plant populations. Trends Ecol. Evol. 5 (11), 360–364. https://doi.org/10.1016/0169-5347(90)90095-U.

Wiegand, T., Moloney, K., 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104 (2), 209–229. https://doi.org/10.1111/j.0030-1299.2004.12497.x.

Wiegand, T., Moloney, K.A., 2014. Handbook of spatial point-pattern analysis in ecology. CRC Press, Florida.

Witt, C., 2010. Characteristics of aspen infected with heartrot: Implications for cavity-nesting birds. For. Ecol. Manage. 260, 1010–1016. https://doi.org/10.1016/j.foreco.2010.06.024.

Yang, H., Yang, X., Heskel, M., Sun, S., Tang, J., 2017. Seasonal variations of leaf and canopy properties tracked by ground-based NDVI imagery in a temperate forest. Sci. Rep. 7 (1), 1–10. https://doi.org/10.1038/s41598-017-01260-y.

Zenner, E.K., 2005. Development of tree size distributions in Douglas-fir forests under differing disturbance regimes. Ecol. Appl. 15 (2), 701–714. https://doi.org/10.1890/04-0150.

Zhang, Y., Gao, J., Liu, L., Wang, Z., Ding, M., Yang, X., 2013. NDVI-based vegetation changes and their responses to climate change from 1982 to 2011: A case study in the Koshi River Basin in the middle Himalayas. Glob. Planet. Change 108, 139–148. https://doi.org/10.1016/j.gloplacha.2013.06.012.