



Dendroecological analysis of the remote endemic *Nothomyrcia fernandeziana* forests of Robinson Crusoe Island in the Southeast Pacific

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ABSTRACT

Juan Fernández Archipelago National Park is located in the Southeast Pacific Ocean ~670 km off the coast of Chile. Composed by three islands, encompasses an ecosystem with 208 native plant species of which 64% are endemic. Robinson Crusoe Island (RCI) is the largest and the only with a permanent human population. Among the tree species of RCI, *Nothomyrcia fernandeziana* is the most abundant and dominant forming part of this fragile forest ecosystem. Despite this, there is very little information regarding its autoecology and conservation. Therefore, the objective of this work was to determine the radial growth patterns of *N. fernandeziana* and its longevity using dendrochronological methods. For this purpose, cross sections of trees blown down by wind were collected in conjunction with park rangers from five different sites and analyzed using tree-ring methods. Our results confirm that *N. fernandeziana* is a shade-tolerant species capable of maintaining extremely low initial growth rates under the canopy for several decades. Individual growth series were found to respond rapidly to changes in environmental conditions, revealed by abrupt positive and negative changes in their annual growth. Our data indicate a longevity of up to 450 years, with one *N. fernandeziana* individual established in the mid XVII century before the arrival of humans to the pristine island ecosystem. The results of this study are essential to strengthen RCI conservation plans considering restoration actions based on the autoecology of this rare endemic tree species, and the control of exotic invasive species that presently threatens the RCI forests ecosystems.

1. Introduction

Characterized by unique flora, with up to 70% endemism, the Robinson Crusoe Island (RCI) and the Juan Fernández Archipelago (JFA) is a global biodiversity hotspot located about 670 km offshore from Chile in the southeast Pacific Ocean (Penneckamp, 2018; Fig. 1). It was declared a Chilean National Park in 1935 and a Biosphere Reserve by UNESCO in 1977. RCI is the largest island of the JFA and presents the highest biodiversity, with 1.9 endemic plant species per km² (Bernardello et al., 2006). It is also the only island with a permanent human population. Due to its isolated evolution, the unique biodiversity of the JFA is highly susceptible to the effects of several introduced species, which have rapidly established themselves during the 20th century and severely

threaten the endemic species (Vargas et al., 2013).

After the discovery of the JFA in 1574 and the subsequent establishment of a permanent human population on RCI around 1749 (Cáceres Roque and Saavedra Villanueva, 2004), RCI has been constantly affected by the threats derived from the introduction of invasive exotic species (IES) and anthropogenic land-use changes, which have severely modified the unique ecosystems of the Island (Johow, 1896; Smith-Ramírez et al., 2017). Currently, among the most aggressive IES affecting the endemic flora and wildlife of RCI are mammals, such as *Capra aegagrus* (goat), *Oryctolagus cuniculus* (European rabbit), *Nasua nasua* (South American coati), plant species such as *Ugni molinae* (Chilean guava), *Aristotelia chilensis* (Chilean wineberry), and *Rubus ulmifolius* (Elm-leaf blackberry), and birds such as the *Sephanoides*

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sephanoides (Chilean hummingbird) and *Turdus falcklandi* (Austral Thrush). Misuse of the forest and fires near the human settlement on RCI have reduced the tree cover and replaced the native forest by *Eucalyptus* sp., *Cupressus* sp. and *Pinus* sp. The aggressive establishment and presence of these IES and the human disturbances have generated severe threats to the fragile biodiversity of RCI, altering the dynamics and ecological processes of the endemic forests and threatening the conservation of this unique island ecosystem in the Southeast Pacific (Vargas et al., 2011, 2013).

Presently, the JFA National Park protects 208 native plant species, of which 135 or 64% are endemic (several which are monotypic genus (Penneckamp, 2018)), corresponding to > 5% of the total Chilean endemic vascular flora distributed over just 0.01% of the national territory (Vargas et al., 2011). It should be noted that at least four plant species are extinct on the JFA, among them the Sandal tree (*Santalum*

fernandezianum), which was intensively exploited due to its aromatic and valuable wood until it completely disappeared ca. 1910 (Penneckamp, 2018). The forest type on RCI is known as Myrtisylva because the dominant tree species belong to the Myrtaceae family (Danton et al., 2006), which is largely dominated by the tree species *Nothomyrcia fernandeziana* (Hook. & Arn.) Kausel, locally known as *Luma de Juan Fernández* and classified as *vulnerable* by the International Union for Conservation of Nature (IUCN). *N. fernandeziana* is an evergreen tree that can reach 20–25 m in height and represents a monotypic genus endemic to RCI (Fig. S1; Murillo-Aldana and Ruiz, 2011). It is a shade-tolerant species present in most forest strata and to a lesser extent in exposed sites, growing mainly between 50 and 700 m a.s.l., and forming pure or mixed forests associated with other endemic tree species such as *Zanthoxylum mayu*, *Drimys confertifolia*, *Rhaphithamnus venustus*, *Juania australis*, *Coprosma pyriformis* and *Coprosma olivieri* among others

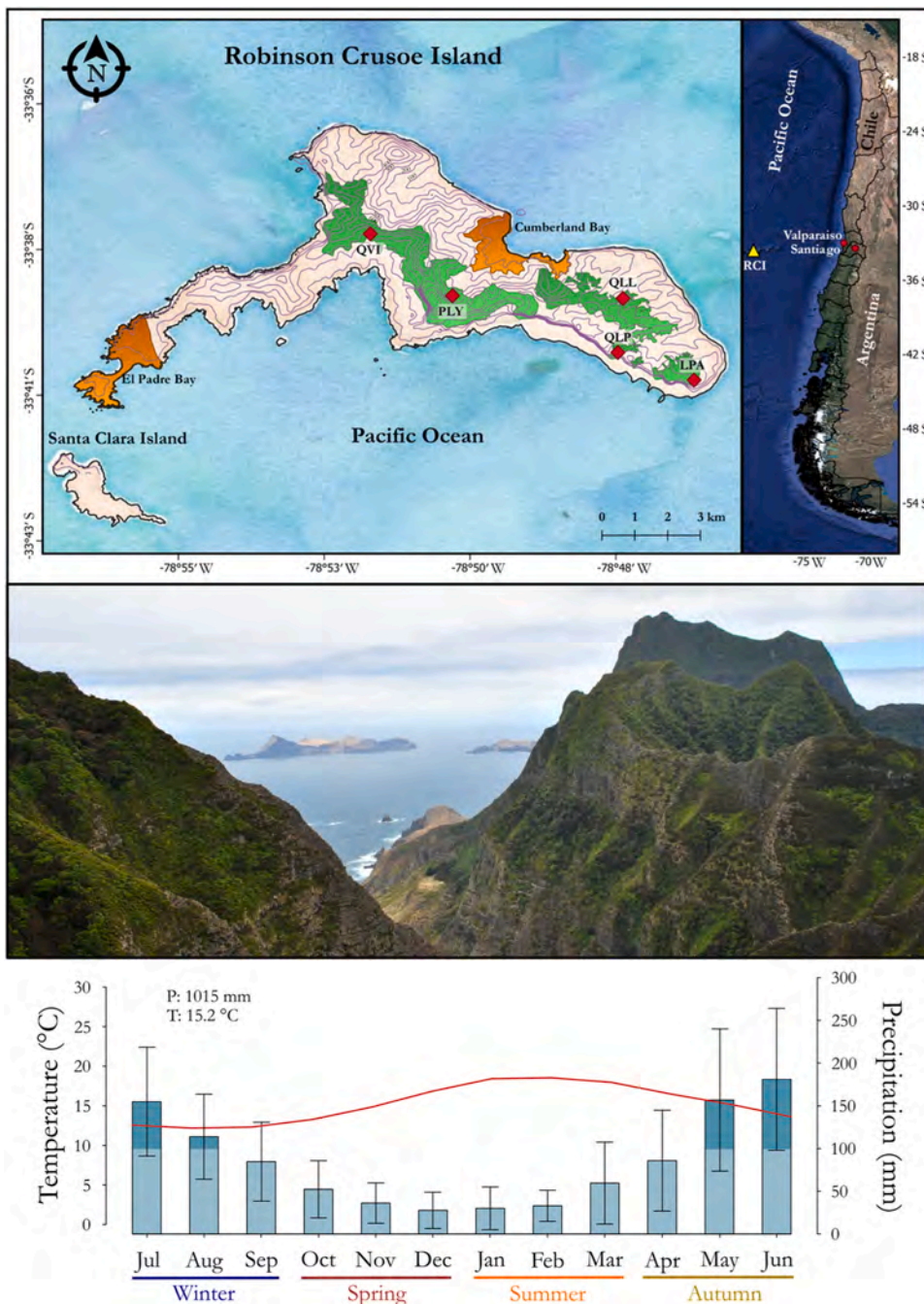


Fig. 1. Panoramic view and location of Robinson Crusoe Island (RCI) in the Southeast Pacific. A) Map with the five sampling sites within the island are highlighted by red diamonds. The orange areas represent the two most important bays of RCI where the human population is concentrated. The green area represents the distribution of *N. fernandeziana* forests. B) Photograph of the geography of the island showing the areas where *N. fernandeziana* grows. C) Climatic graph showing the seasonality of precipitation and the oceanic character of the temperature. (Photo credits: Rodrigo Vargas Gaete).

(Penneckamp, 2018). The wood of *N. fernandeziana* is light-colored and there is no distinction between its sapwood and heartwood; due to its dense and resistant properties it has been used for the construction of boats, posts and agricultural tools (Johow, 1896).

At present, there is scarce information about the natural dynamics of the forests on RCI, which are dominated by tree-fall gaps of small to medium size caused mainly by uprooted and broken trees because of oceanic windstorms (Vargas et al., 2013). The presence of *N. fernandeziana* and the IES *A. chilensis* as gap border trees are indicative of the conservation status of the forests, being positively and negatively correlated with overall native plant species richness, respectively (Vargas et al., 2013). Even though the structure of the Myrtisylva forest on RCI are dominated by *N. fernandeziana*, with an estimated density of > 1000 trees per hectare (Vargas et al., 2010), there is a lack of detailed information regarding the longevity and growth dynamics of this tree species. Preliminary studies about *N. fernandeziana* have demonstrated that tree-ring analysis is a suitable approach to obtain a better ecological insight of this tree species and particular forest type (Rojas-Badilla et al., 2017). Maximum ages have been reported to be about 250 years old, with an average radial growth of 0.16–0.3 cm per year, with minimum and maximum values of 0.07 and 9 mm/year, respectively (Rojas-Badilla et al., 2017). This may indicate that the radial growth of *N. fernandeziana* could be highly variable depending on environmental conditions related to light availability within the closed canopy that characterizes these forests, leading to suppressed growth rates in the initial stages of this species. This tree-ring derived evidence provides valuable biological information about the ecology of *N. fernandeziana* and the dynamics of its ecosystem, with implications for conservation and restoration plans of these rare endemic oceanic forests. Therefore, in the present study we investigate the *N. fernandeziana* forests of RCI based on tree-ring analyses to (i) determine the potential longevity of the species, (ii) characterize the tree growth rates of *N. fernandeziana* according to age, and (iii) examine the tree growth patterns of *N. fernandeziana* during the last centuries on this threatened and unique ecosystem from the Southeast Pacific.

2. Materials and methods

2.1. Study area

The JFA is located in the Southeast Pacific ca. 700 km off the shore of the Chilean coast at a subtropical latitude (33°S; Fig. 1), and was discovered in 1574 by Spanish sailors. RCI and the Scottish sailor Alexander Selkirk who was marooned on the island and lived alone for four years during the early 1700s, inspired Daniel Defoe to write his famous novel "Robinson Crusoe" turning the island into a literary icon. During the XVII and XVIII centuries, RCI served as an intermittent refuge and place of arrival for various navigators, pirates and corsairs, who introduced the first IES, including goats, which had a severe impact on the fragile and isolated ecosystem. The JFA is composed of three islands that emerged from a submarine volcanic cord related to the Juan Fernandez Ridge, corresponding to the Nazca plate (Sepúlveda et al., 2015), with RCI being the largest island. This archipelago encompasses an area of 9967 ha, of which 96% have been protected since 1935 as a Chilean National Park due to the exceptional biodiversity and level of endemism. RCI is the only island with a permanent human population estimated at 926 inhabitants. It possess an area of 4794 ha, of which 1015 ha are covered by the montane forest dominated by the endemic tree species *N. fernandeziana*, *Zanthoxylum mayu*, *Drimys confertifolia* and *Boehmeria excelsa* (Díaz-Vega, 2012; Smith-Ramírez et al., 2013). The tree ferns *Dicksonia berteriana* and *Thyrsopteris elegans*, which occupy the intermediate forest strata are also of particular interest (Stuessy et al., 2017). Their foliage shows simple and leathery leaves with entire margins, reddish-brown petioles, and flowers (up to 12) gathered in inflorescences that are hermaphrodite and produce a reddish-colored berries with several dark seeds (Fig. S1; Ricci, 2006).

2.2. Local climate

RCI is located in a subtropical zone, at the southeastern edge of the South Pacific anticyclone where tropical maritime air masses predominate. RCI has a Mediterranean climate with a strong oceanic influence and a dry season of 4–5 months (Fig. 1). Rainfall is frontal in the winter and convective in the summer, reaching 1015 mm per year (1966–2021), concentrated mainly during the winter months (Hajek and Espinoza, 1987; Novoa et al., 1989). Average minimum and maximum temperatures are about 13 °C and 18 °C, respectively, with an annual average of 15 °C (CR2, 2021). Considering the strong orographic effect, the precipitation on the island is highly variable, and its geography also determines fog and wind exposures according to altitude, orientation and slope, producing diverse microclimates (Hajek and Espinoza, 1987). The dominant winds come from the south and southwest in the summer, and N, NW, SW and W in the winter. Provided the orographic features of the island, the direction and intensity of the winds change according to the surface shape (hills and valleys), altitude and size of the island. This complex orography acts as a barrier, depending on the direction of the mountain ranges that forces the air masses to ascend and condense, forming fog or precipitation at the higher altitudes where the Myrtisylva forest grows (Castro et al., 1996).

2.3. Fieldwork sampling and processing

The collection of tree-ring samples was conducted with park rangers between January and February in 2018 on five populations of *N. fernandeziana* located at Plazoleta El Yunque (PLY), Quebrada Villagra (QVI), Quebrada La Laura (QLL), Quebrada La Piña (QLP) and La Pascua (LPA) sectors, at 340, 320, 370, 320 and 180 m a.s.l. respectively (Fig. 1). Due to the National Park's protection measures samples were only taken from recently uprooted dead *N. fernandeziana* individuals, from which park rangers had carefully registered the years that these trees were blown down by windstorms. These cross sections were obtained between 20 and 30 cm from the base of the tree, considering the loss of information in the wood far from the base. In total, we sampled 24 complete cross-sections (≥ 5 cm in diameter) with bark using a chainsaw close to the base of the stem. Cross-sections were first dried and stabilized with wood glue, dissolved in water to prevent breakage, and then levelled and polished with sandpaper of decreasing grain size from 80 to 800 grains cm^2 .

2.4. Age and growth patterns of *N. fernandeziana*

To identify growth rings, we examined the distribution of the anatomical features of the wood structure, including the distribution and size of the vessels, presence of parenchyma, woody rays and the arrangement within rings under a binocular microscope (Schweingruber, 1996). To determine the age of each individual, the growth rings were counted from the pith to the periphery, assigning the first visible ring with year zero according to Stokes and Smiley (1996). Due to the eccentric growth and wedging observed in some samples, the minimum age of each sample was determined by counting the growth rings from each cross section along two radii to minimize counting errors. For the cases of some cross sections that exhibited micro-rings to the pith, it was established that the first visible ring closest to the pith would be the first year of the individual. After comparing the two radii of each cross-section, annual rings were counted and visually cross-dated. Subsequently, calendar year of each growth ring was assigned from the most recent ring according to the known tree fall information provided by the park rangers and following Schulman's convention for the Southern Hemisphere (Schulman, 1956). Once the tree rings were identified, the tree-ring widths of the two radii of each cross-section were measured under a binocular microscope using a measuring stage (Velmex®, Bloomfield NY, USA) with 0.001 mm of precision. To determine the radial growth patterns according to age, we first calculated the average

growth rate by age among all individuals with complete measures from the pith.

Tree growth releases and suppressions were analyzed to detect abrupt changes in growth produced by canopy disturbances and used to infer stand dynamics (Veblen et al., 1991; Nowacki and Abrams, 1997). We calculated the relative percentage of growth change (GC) for releases and suppression events by calculating the GC when comparing the average of 10 years before and 10 years after each ring. We computed major and moderate releases as $GC > 100\%$ and $> 50\%$ increase in average radial growth, respectively, and suppressions as $GC > 50\%$ decrease in average radial growth (Nowacki and Abrams, 1997; Lamas and Rozas, 2007). We utilized these sustained release criteria (10 years) to avoid short-term climatic pulses and gradual ring-width changes due to tree ageing, stem geometry and long-term climate trends (Nowacki and Abrams, 1997; Gutiérrez et al., 2004).

3. Results

3.1. Descriptions of tree rings

N. fernandeziana forms rings delimited by parenchyma cells, with multi-seriate rays; its rings exhibit clear boundaries between the lighter earlywood with abundant and homogeneously distributed vessels, and the darker latewood with fewer vessels (Fig. 2). These color differences were fundamental to distinguish the limits between one ring and the next when they presented reduced growth during a prolonged period of time. The possibility of examining complete cross-sections allowed for a better exploration of this newly evaluated species, including a clear visualization of the different wood shades, ranging from whitish to dark brown, and the frequent wedging and lobate growth of the rings. Occasionally, a dark color impeded the differentiation of the tree-ring limit. The analyzed cross-sections permitted a selection of paths (radii) that clearly represented the annual growth of *N. fernandeziana*. The average ring width per population considering the measurements of all of the series per site was 1.11 mm in PLY, 0.75 mm in QLL, 0.91 mm in QVI, 0.86 mm in QLP and 0.86 mm in LPA. *N. fernandeziana* exhibited low growth rates and a weak expression of common patterns in growth among trees when comparing trees in individual sampling sites and among trees from all of the sites. On the other hand, the suppression of growth rings due to reduced growth over long periods of time was observed to a lesser or greater extent in all of the studied samples. This makes the visualization of the rings during the early life of the trees complex, due to the compression of the growth rings near the pith.

3.2. Growth rates and longevity

For a better comparison of the tree-ring series and to search for common signals among populations, the samples were grouped by sampling site. The last year of each sample was obtained from the record of discrete wind events that caused uprooting in the different sampling sites, which occurred between the years 2013 and 2017 (Table 1). The mean age of the samples was 178 years, with minimum and maximum ages of 86 and 456 years, respectively. The oldest tree was found in Plazoleta El Yunque, living between 1562 and 2017; it was thus established one year prior to the arrival of humans on RCI. Some samples presented the complete formation of the last (more recent) growth ring, presuming that those trees fell during the autumn-winter period. The analyzed stands differed in age and growth patterns (Table S1).

The analysis of growth according to tree age in terms of the annual growth rate and cumulative growth allowed us to assess the variability of radial growth throughout the life history of each tree and site (Fig. 3). Of the five studied populations, all series in which growth rings could be recognized from the pith were selected. With this data set, the annual radial growth according to tree age (mm/age) and a mean growth curve

Table 1
Radial growth, minimum and maximum ages, and number of *Nothomyrcia fernandeziana* individuals sampled by study site on Robinson Crusoe Island.

	Plazoleta El Yunque (PLY)	Quebrada La Laura (QLL)	Quebrada Villagra (QVI)	Quebrada La Piña (QLP)	La Pascua (LPA)
Number of trees	6	5	4	4	5
Number of series	11	10	8	8	10
Number of rings	1180	986	741	691	894
Minimum age	86	161	122	96	149
Maximum age	456	242	222	195	228
Max. ring width (mm)	5.06	3.14	4.77	3.64	6.34
Min. ring width (mm)	0.05	0.04	0.12	0.07	0.07
First year (series)	1562	1774	1839	1821	1788
Last year (series)	2017	2017	2017	2016	2015

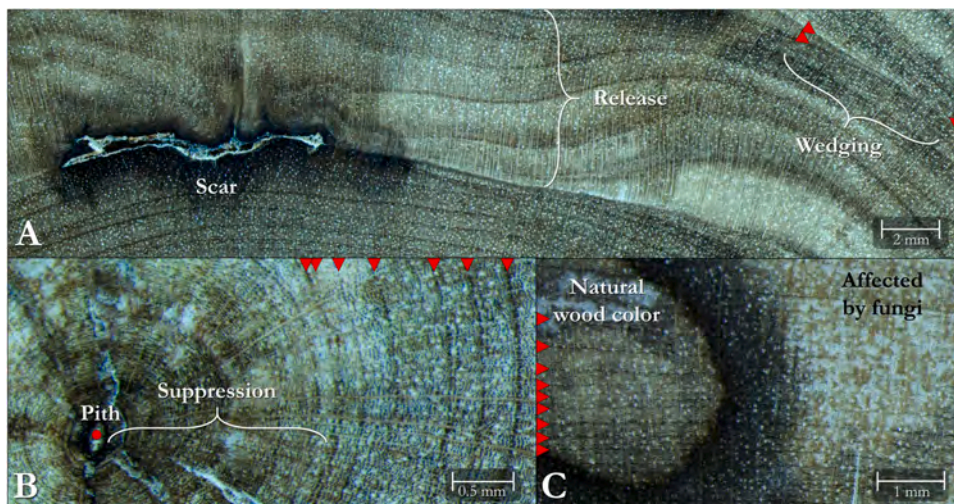


Fig. 2. Annual growth rings in a cross-section of *N. fernandeziana* with clear anatomical differentiation between earlywood, with abundant vessels and a light color, and latewood, with almost absent vessels and a darker color. Each red triangle represents the limit of a growth ring. (a) A small scar is shown at the left side of the image, which causes a release in growth followed by wedging. (b) Growth suppression and subsequent release is verified in the center of the cross section. (c) The left side of the image shows the natural dark colored wood of the species with well-defined rings, while the right side shows a lighter color of the wood with a vague definition of the ring boundaries.

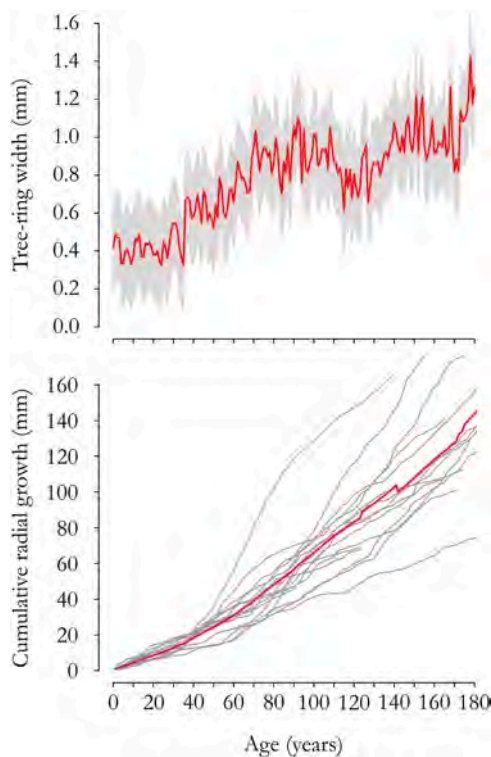


Fig. 3. Average radial growth of *Nothomyrcia fernandeziana* (red line) according to age (top), gray areas represent the standard deviation and cumulative radial growth rate by age (bottom). The red and gray lines represent the average and individual ($n = 16$) measurements. Only tree ring series that presented measurements from the pith were considered. The average curve from the top panel was calculated for the same individuals.

for the species was calculated with its respective standard deviation (Fig. 3). Of the 24 samples, it was possible to identify growth rings from the pith in 16 (66%). Cumulative growth for these series was also computed to better visualize the reduced initial growth of the species. The annual radial growth ranged from 0.04 to 6.34, while the mean annual increment of all trees was 0.86 mm, calculated from 4492 growth rings. The oscillating growth of the species was represented in all of the stands, with reduced growth at the juvenile stages (0.4 mm/yr), followed by an ascending rate (up to 1.4 mm/year) when the trees reached about 180 years old (Fig. 3).

3.3. Releases and suppressions of tree-growth

For the analysis of releases, we considered a total of 47 tree-ring series. The use of suppression and release filters on individual tree-ring series revealed marked variations in growth (Fig. 4). Utilizing the GC to detect releases and suppressions showed that individuals did not always exhibit synchronous responses, which could indicate the occurrence of small-scale disturbances within the forests. It was observed that when one tree exhibited a release in its growth, another might respond in the same way, neutral or with a suppression. In general, the selected series did not show many strong releases; however, moderate releases and suppressions occurred periodically over ca. 240 years for the first four samples and ca. 460 years for IRC011A, which included the oldest sampled individual. The IRC011 series showed profuse releases due to the adaptability of this species to respond to changes in light conditions, along with very well represented suppressions during its lifetime.

By means of the GC, an average suppression of 340% was observed between 1661 and 1666, another 580% between 1867 and 1872 and a last more pronounced 906% between 1990 and 1995. The releases in this series were as recurrent as the suppressions, with the three most

prominent being between 1613 and 1618 (445% GC), 1676 – 1682 (716% GC), and the last between 1969 and 1975 (363% GC), all of which clearly denote canopy disturbances (Fig. 4). The overall analysis of releases and suppressions developed with the 47 series revealed that the *N. fernandeziana* forests exhibit strong and moderate releases throughout most of the studied period, mainly concentrated between the years 1850 and 1960 (Fig. 5). The few releases and suppressions prior to 1850 could be due to the low sample depth. The period with the highest number of moderate and strong releases was between 1950 and 1960, but the early 1900s also exhibited a large number of strong releases. The last period between 1985 and 1995 also stood out in terms of the number of noticeable suppressions.

4. Discussion

N. fernandeziana was formerly found from sea level to approximately 700 m a.s.l. (Johow, 1896; Vargas-Gaete, 2004). Today the Myrtisylva is mainly restricted to between 200 and 700 m a.s.l. (Penneckamp, 2018) due to anthropogenic influences and IES, which have reduced its natural distribution range. Some remnants of low montane forest were found ca. 50 m a.s.l., though they were severely damaged by either degraded soils or herbivory, thus affecting regeneration. For this study, the minimum altitude at which samples were taken was 180 m a.s.l. The longevity of the trees there was between 86 and 456 years, such an amplitude allowed us to analyze aspects of their growth over the last five centuries, exhibiting a minimum and maximum growth of 0.04 and 6.34 mm/year, respectively. The amount and exceptional quality of the material studied positively contributed to the analysis of radial growth patterns and to the description of the characteristics that modulate the growth patterns of *N. fernandeziana*. However, despite the good definition of the limits of the growth rings, it is possible that the age of some individuals could have been underestimated because of the difficulty to identify the rings grouped towards the pith of some cross-sections (Fig. 2). This may imply even lower growth rates of *N. fernandeziana* than those recorded in this study, indicating the capability of this species to withstand adverse environmental conditions and its ability to quickly respond to gap openings. In some portions of the cross-sections, rings completely disappeared because of wedging (Fig. 2), indicating that the tree showed no secondary growth in certain areas of its trunk in a year or group of years. We also observed that the mean *N. fernandeziana* annual growth rate differed from the classic curve expected for a fast-growing tree species compared to the IES of RCI, such as *A. chilensis* (Rojas-Badilla et al., 2017). The classic curve of fast-growing trees is characterized by accelerated growth during the juvenile stage of individuals, a steady growth during the mature stage and finally a decrease in growth that becomes steady during the senescent stage.

Releases and suppressions in tree growth are typically defined as the relative increase or decrease of growth in shade-intolerant species, while shade-tolerant species do not react abruptly to the entrance of light (Veblen et al., 1991). However, being a shade-tolerant species, *N. fernandeziana* has shown abrupt changes in its growth caused by canopy disturbances, mainly originated by oceanic winds that cause tree-fall gaps as a result of tree uprooting or broken branches. Therefore, growth releases have proven to result from an increase in light availability due to a reduction in competition (Arellano-Cataldo, 2012; Smith-Ramírez et al., 2017). For example, the individual analysis of the rings associated with scars could result from impacts of branch falls or neighboring trees, followed by an increase in the growth rate in response to light availability (Fig. 2). This demonstrates the plasticity of *N. fernandeziana* to respond to changes in the light regime.

The adaptation of *N. fernandeziana* to the different light conditions provided by the niche in which it grows would be manifested in the varying periods of releases and suppressions, these traits could explain the abundance of the species across RCI (Vargas-Gaete, 2004). The extremely slow growth rate at the initial (seedling) and juvenile stages of this species may indicate the progressive development of trees under

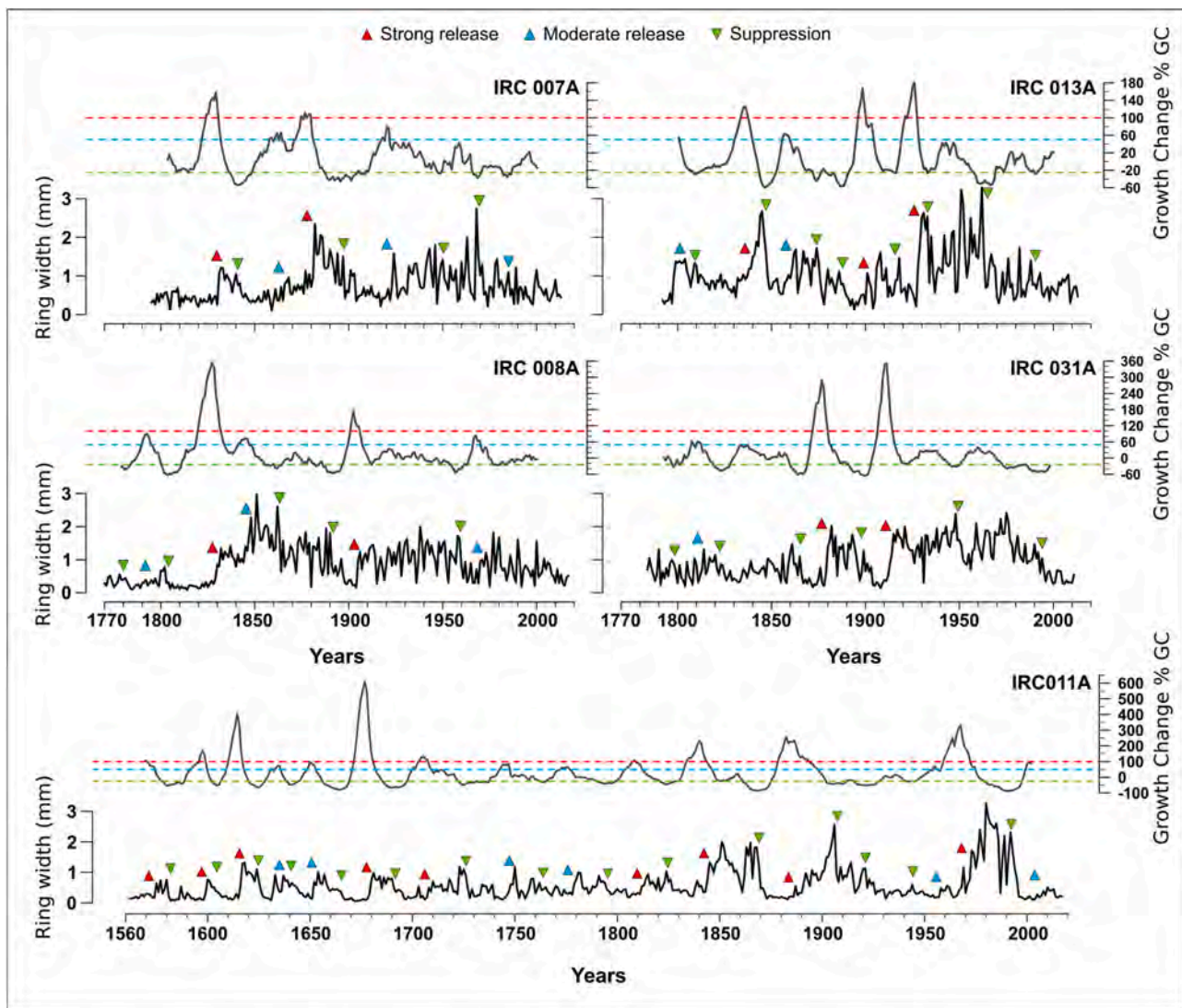


Fig. 4. Radial growth patterns for five selected *Nothomyrcia fernandeziana* individuals on Robinson Crusoe Island, including the oldest sampled tree (bottom). For each individual tree, the percentage of growth change (GC) and the corresponding ring width are shown. Green, red and light-blue triangles (dotted lines) denote the years (threshold) of suppressions (<50% GC), and strong (>100% GC) and moderate (>50% GC) releases, respectively. Data from the IRC007/008/011 series begin from the pith.

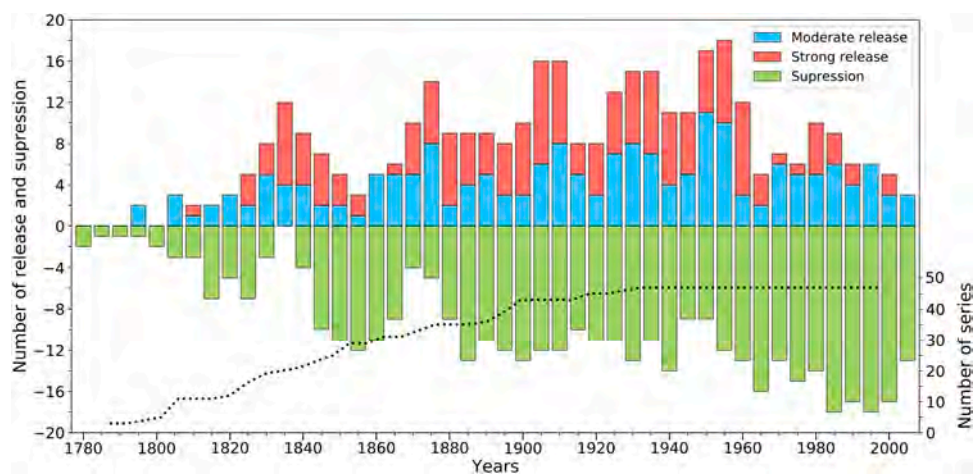


Fig. 5. Chronology (five-year intervals) of suppressions, moderate and major radial growth releases in 24 tree ring series of *Nothomyrcia fernandeziana* trees from Robinson Crusoe Island.

heavy shade within low canopy positions (Rozas, 2005). This reveals a regeneration niche avoiding direct sunlight and a regeneration and establishment strategy under a closed canopy. The reduced growth observed in the rings during the juvenile stage expresses the tree's ability to tolerate shade and determine its germination, establishment, development and competition, as well as its release in growth in response to light limitations (Donoso, 1989). On the other hand, suppression events during the adult stages could be a response to the temporal variation in light conditions surrounding each individual or to the mechanical damage caused by the decline of neighboring trees. Particularly, two relevant periods of releases and one very marked period of suppressions were observed. Both release periods occur at the beginning and middle of the 20th century, the first one characterized by a dominance of strong releases. The second period is dominated by moderate release as well as a decrease in suppressions. This may be due to several factors (Mitchell, 2013), considering that it is difficult to compare releases with wind gusts events (Martin and Ogden, 2006). It can be inferred, according to the Quinta Normal station that records rainfall in central Chile and the recurrence of drought events for Santiago (González-Reyes, 2016), that the periods of releases coincide with increases in rainfall, which is accompanied by strong gusts of wind in addition to softening the substrate leaving it prone to uprooting. It is also worth mentioning that the island's forests were anthropically disturbed before it was named a national park in 1935, which coincides with a period of low releases. Later in 1977 it was named a Biosphere Reserve, coinciding with the beginning of the decline of releases and the increase of suppressions in the island's forests. Therefore, it is likely that the releases and suppressions following the arrival of people on the island are on the one hand of anthropogenic origin and on the other hand of natural origin related to strong wind events.

Considering that RCI forests are mainly dominated by *N. fernandeziana*, and this tree has also been documented as being responsible for at least 50% of the canopy gaps in the forests (Arellano-Cataldo, 2012; Smith-Ramírez et al., 2017), this species plays a key role in the dynamics of the entire forest ecosystem of RCI. However, the formation of canopy gaps also promotes the colonization of IES, thus the conservation, ecosystem health, and restoration of degraded areas of *N. fernandeziana* forests is essential to prevent the establishment of foreign species (Vargas et al., 2013). On the other hand, this species is also able to establish itself under closed canopy conditions, like many native Chilean species belonging to the Myrtaceae family (Peña et al., 2014). This establishment strategy gives *N. fernandeziana* a great advantage over intolerant invasive species.

The regeneration niche of this species could be restricted to principally closed canopies, resulting in limited light capture leading to an initially reduced growth rate in seedlings and juveniles. During fieldwork, abundant cotyledons of *N. fernandeziana* were observed growing below adult trees. Another reason for its slow growth could be the strong herbivory produced by IES, which affects *N. fernandeziana* seedlings (Smith-Ramírez et al., 2017) and causes soil degradation. This ability to maintain extremely low growth rates during the first decades of establishment and during any period of its life demonstrates its resistance as a result of evolution and adaptation to the conditions of the dense evergreen forests of RCI.

Considering the results of the present and previous studies concerning the conservation of *N. fernandeziana* forests and the integrated control of invasive woody species on RCI, it is crucial to develop active restoration actions to protect the biodiversity of this unique ecosystem that is so rich in endemic species. Provided the capability of *N. fernandeziana* to establish in low light conditions and the high light levels required by IES tree species, such as *A. chilensis*, we propose active restorative efforts of *N. fernandeziana* in large tree-fall gaps to prevent the establishment of IES. Some research has proposed decreasing the radiation that reaches the forest floor with ferns to prevent the establishment of IES (Smith-Ramírez et al., 2017; Vargas-Gaete et al., 2018); however, this proposal incorporates the active restoration of individuals

of *N. fernandeziana* larger than 1 or 2 m to protect them from herbivory and thus definitively cover the areas to control the expansion of invasive woody species. In addition, we do not recommend clearing large sectors covered by IES; instead, we suggest planting groups of individuals in small gaps of 5–10 m² and progressively opening the canopy to prevent them from regenerating the IES by self-shading. These active plantations with native trees, combined with soil conservation practices could help restoration programs. Finally, a thorough study of the main woody IES of the island is necessary to first identify their traits in terms of growth, growth patterns and longevity, and to second build a detailed plan to impede the spread of IES and protect the long-lived tree species *N. fernandeziana* and the endangered forest ecosystems of RCI.

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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.

Data availability

The data that has been used is confidential.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dendro.2023.126129](https://doi.org/10.1016/j.dendro.2023.126129).

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