

Article

Disturbance History and Dynamics of an Old-Growth *Nothofagus* Forest in Southern Patagonia

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Abstract: The identification of disturbance events using disturbance chronologies has become a valuable tool in reconstructing disturbance history in temperate forests worldwide; yet detailed reconstructions of disturbance history and their effect on the structure and dynamics of the old-growth *Nothofagus* forests in the southern Patagonia are scarce. We reconstructed forest dynamics and disturbance history of an old-growth *N. pumilio* forest in the Toro River Valley, Santa Cruz, Argentina using dendroecological techniques. Since a variation in the disturbance regimes was expected with changing elevation, we sampled at different elevations. We found distinct differences in forest structure, dynamics, and disturbance history with changes in the elevation. The disturbance chronologies provided robust evidence that forests in the study area have been subjected to multiple disturbance events over the last 200 years. Yet, recognizing the agent of disturbance could be difficult in these montane forests and further studies are required. Moreover, disturbances might have varied from frequent, moderate- to high-severity events to less frequent and more severe events. This study represents the first of its kind for the temperate forests of Patagonia.

Keywords: forest structure; disturbance history; dendroecology; old-growth; *Nothofagus pumilio*

1. Introduction

Natural disturbances, a frequent and inherent part of ecosystems, are key drivers of forest dynamics influencing forest structure, composition, and function [1–4]. Thus, knowledge of the natural disturbance regime and the vegetation response to disturbances becomes essential for understanding forest dynamics at both the stand and landscape scale. Furthermore, knowledge of the disturbance regime could also guide forest management as sustainable forest management must integrate ecological, social, and economic aspects. Disturbance-based management that emulates natural ecological processes, such as local disturbance regimes, is viewed as more likely to sustain ecosystem functions and dynamics of forest ecosystems while maintaining biodiversity and ecological resilience to ensure a wide range of service and values to societies [5,6].

Different approaches have been used to study forest structure and dynamics, as well as associated processes such as disturbances. Chronosequences have been useful to describe forest development (e.g., [7]), although this method might be less suitable to study communities subject to frequent disturbances of different severity [8]. Long-term measurements can provide direct evidence of changes in forest structure and dynamics (e.g., [9]) but unfortunately these studies usually provide limited time

scales and lack in interannual variability. Retrospective methods such as dendroecological techniques, on the other hand, have been used to reconstruct both disturbance history and associated vegetation response over larger time scales, providing precise information on the disturbance regimes and forest dynamics (e.g., [10–13]).

Natural disturbances have historically shaped the mountain regions of the Andes of Patagonia, Argentina, playing important roles in the dynamics of these forests [14,15]. Tree rings have been widely used to study diverse disturbance such as fires, avalanches, and insect outbreaks by precisely dating disturbance events (e.g., [16–19]). Other studies, alternatively, have documented vegetation dynamics influenced by recent disturbances such as droughts, fires, landslides, and forest declines (e.g., [20–24]). Yet, few studies have reconstructed both disturbance history and forest dynamics simultaneously [25,26]. A common aspect of most studies in the region is the focus on a single disturbance type and/or forest type. Thus, studies on disturbance regimes and forest dynamics over larger areas where more than one disturbance occur are needed.

Ecological knowledge on disturbances and forest dynamics in the southern part of the Patagonian Andes of Argentina is much less compared to the northern part where most studies have taken place. Over the past decade, there has been an increased interest on the dynamic character of forest ecosystems and the role that natural disturbances have in driving ecosystem change in the southern Patagonian Andes [18,27,28]. Snow avalanches and wind are the most common natural disturbances in these forests [15,18,19,29–31]. Previous and on-going research in the Rio de las Vueltas basin, Santa Cruz province have provided evidence these are not only particularly common in the study area [18,32,33] but also that they could co-occur (Amoroso et al., unpublished), suggesting disturbance regimes in these old-growth forests may be more complex with frequent intermediate intensity disturbance events likely playing an important role in their dynamics. Yet, knowledge is incipient on the different disturbance regimes and their effect on the structure and dynamics of these forests. Therefore, it is of great importance to gain a better understanding of the dynamics of the forests and the history and regimes of the main disturbance agents in the area.

While disturbance-specific chronologies exist [18,27,32], we are not aware of the existence of disturbance chronologies (sensu [10]) developed from changes in tree growth patterns for the Andean-Patagonian forests. A disturbance chronology is a temporal scale estimating the frequency and severity of canopy disturbance events, as well as canopy accession dates using dendroecological techniques [10]. The identification of disturbance events using this approach has become a valuable tool in reconstructing disturbance regimes, and there are many recent examples of its application on the reconstruction of disturbance history in temperate forests of Europe and North America (e.g., [14,34–36]); yet, its usefulness has not been tested in the mountain forests of Patagonia.

The goal of this study was therefore to reconstruct the forest dynamics and disturbance history of an old-growth forest in the Río de las Vueltas basin, Santa Cruz province, Argentina using dendroecological techniques. Since variation in the disturbance regimes is expected with changing elevation (avalanches are likely to affect more higher areas compared to wind), we proposed to assess resulting disturbance history and forest dynamics at different elevations. The specific objectives were to: (1) Reconstruct forest structure and dynamics at different elevations; (2) develop disturbance chronologies based on the study of the abrupt increases in radial growth and the rapid early growth rates of overstory canopy trees; (3) determine whether the temporal variation in the disturbance history affects forest structure and dynamics at different elevations.

2. Materials and Methods

2.1. Study Area

The study site (49° 22' S; 72° 55' O) is located in the southern sector of the Patagonian Andes at the Rio Toro Valley, Santa Cruz, Argentina (Figure 1). The forests in the area are dominated by deciduous broad-leaved *N. pumilio* and they extend along a west-to-east elevation gradient ranging from about

950–1100 to 500 m.a.s.l. Forests present well-developed and erect *N. pumilio* individuals of varying height (10 to 20 m) along the elevational gradient with the exception of the upper altitudinal limit (treeline) where individuals are smaller and become stunted near the upper boundary assuming a multistem krummholz form. The terrain is rugged and steep, represented by mountains, glacial valleys, and rivers. The soils are generally clay loam and characterized by the absence of horizons in their profile [37]. The climate is temperate to cold and the total annual precipitation and the mean annual temperature 30 km to the south at the Los Glaciares National Park office in El Chaltén (405 m.a.s.l.) are 438 mm and 7 °C, respectively.



Figure 1. Study site location (left) and photo of the studied forest (right) in the Toro River Valley, Santa Cruz, Argentina.

The Rio Toro Valley is one of the many transversal valleys in the Rio de las Vueltas basin characterized by steep slopes and strong W-E winds which determine the occurrence of snow avalanches and wind-driven wave mortality (Figure 1). Our study site was an old-growth *N. pumilio* forest on a northeast-facing slope.

2.2. Sampling

With the objective of reconstructing the structure, dynamics, and disturbance history at different elevations of an old-growth forest, we used the point-centered quarter method [38] to sample the elevational gradient excluding the valley bottom (590–630 m.a.s.l.) and the upper altitudinal limit of the forest or treeline (980–1150 m.a.s.l.). Within this elevational gradient, two parallel transects were run and arranged perpendicular to the slope and the direction of the prevailing winds. A random starting point was established at the western end of the sampling area and from there a transect was run of approximately 1750 m (slope distance) and an average elevation of 886 m.a.s.l. (upper transect). Parallel to it, a lower elevation transect was run, averaging 738 m.a.s.l. and a slope distance of 1600 m long. In each transect systematically-located sampling points were placed at 50 m totalizing 65 sampling points (34 for the upper transect and 31 for the lower transect). Each sampling point was divided into four quadrants (W-E and N-S directions) and the nearest live or dead tree ≥ 1.3 m tall in each quarter was tallied. For each tallied tree, we recorded the distance to the center point, species, diameter at breast height (DBH), total height, and whether the individual was alive or dead. For the dead trees we also recorded whether the main stem was complete and standing, snapped/broken, or uprooted. For each sampled tree we extracted cores at a height of approximately 30 cm above the ground and perpendicular to the slope so as to avoid reaction wood. Multiple cores per tree were taken to ensure the sample intercepted or was close to the pith and included sound sapwood and bark so that the outer ring was the last ring formed on living and dead trees. Transverse cross-sections were taken from dead

individuals from which we could not extract good quality cores due to wood decay or the absence of bark. In the center of each sampling point a circular 1 m² plot was placed where the number of seedlings (trees < 1.30 m tall) of the main woody species was documented.

2.3. Dendrochronological Methods

Cores were mounted and cross-sections were glued to wooden boards and sanded following standard dendrochronological methods [39]. For the cross-sections, we selected two radii to be measured using criteria to ensure comparability with the increment cores (perpendicular to the slope to avoid reaction wood and including sound sapwood and bark). Cores and radii were visually crossdated using an existing master chronology (Sruur, unpublished) and ring-width series were measured on a Velmex bench to the nearest 0.01 mm. Ring-width series were statistically crossdated using the program COFECHA [40] with an average inter-series correlation coefficient of 0.568. Ring-width series were standardized using the program ARS41_win [41].

For the cores that did not intercept the pith we estimated the number of missed rings [42]. Of the 264 trees sampled, missing rings were estimated on 110 trees (42%) but could not be estimated on 13 trees (5%) due to the lack of complete arches.

2.4. Analyses

2.4.1. Forest Structure

For each transect, average height, average diameter, age, and basal area per hectare, were calculated for all living trees. Adult and seedlings density of all living and dead trees were also calculated. Height and diameter measurements were categorised in classes in order to build frequency histograms for each transect. The proportion of living and dead trees and the proportion of the stem condition of dead trees (standing, snapped, and uprooted) were also quantified. The Student t-test was used to analyze differences in the mean values. Chi-square and Fisher exact tests were performed to compare the proportions of living and dead trees and the stem condition of dead trees between transects, respectively [43].

2.4.2. Forest Dynamics

Properly crossdated samples and tree-ring measurements were used to build establishment histograms and tree-ring width chronologies for each transect. Establishment dates were calculated as the date of the inner most ring for each sample minus the number of missing rings.

For the disturbance history analysis, we constructed disturbance chronologies for each transect based on the study of the abrupt increases in radial growth (releases due to canopy mortality events) and the rapid early growth rates (gap-recruited trees in gap origin events) [10,12,35,44]. A disturbance chronology is a temporal scale estimating the frequency and severity of past canopy disturbance events from the abrupt changes in radial growth and canopy accession dates of canopy trees [10]. The quantification of the abrupt increases in radial growth (releases) was conducted calculating the percent-growth change (PGC) for individual trees according to the technique of [45] using the JOLTS program [46]. PGC for a year is equal to $(M2 - M1)/M1$, where M1 represents the average growth over the prior 10 years and M2 represents the average growth over the subsequent 10 years. It represents positive (releases), negative (suppression), and no significant changes. A 10-year span for radial-growth averaging was selected since it tends to average out short-term growth responses related to climate, while capturing growth changes associated with canopy disturbance [45,47]. The determination of the release criteria on *N. pumilio* trees was performed combining visual and analytical analyses. Firstly, individual tree-ring series and PGC values were plotted (Figure 2) to enable visual examination of the degree of release and the number of years during which a release event was sustained [25]. Even though the running mean method tends to eliminate growth changes not associated with canopy disturbances, releases sustained for a few years or 'false releases' may still occur from short-term

climatic trends [48]. Visual inspection of the ring-width series confirmed that releases sustained up to three years could be the result of the variability in tree growth and not related to canopy disturbances. Therefore, the minimum period for which an increase in GC must be sustained to be considered a release event resulting from canopy disturbances in this study was four years. The criteria used to classify the degree of release were: (a) Major releases for >100% GC, and (b) moderate releases for 50%–99% GC (e.g., [25,35,45]).

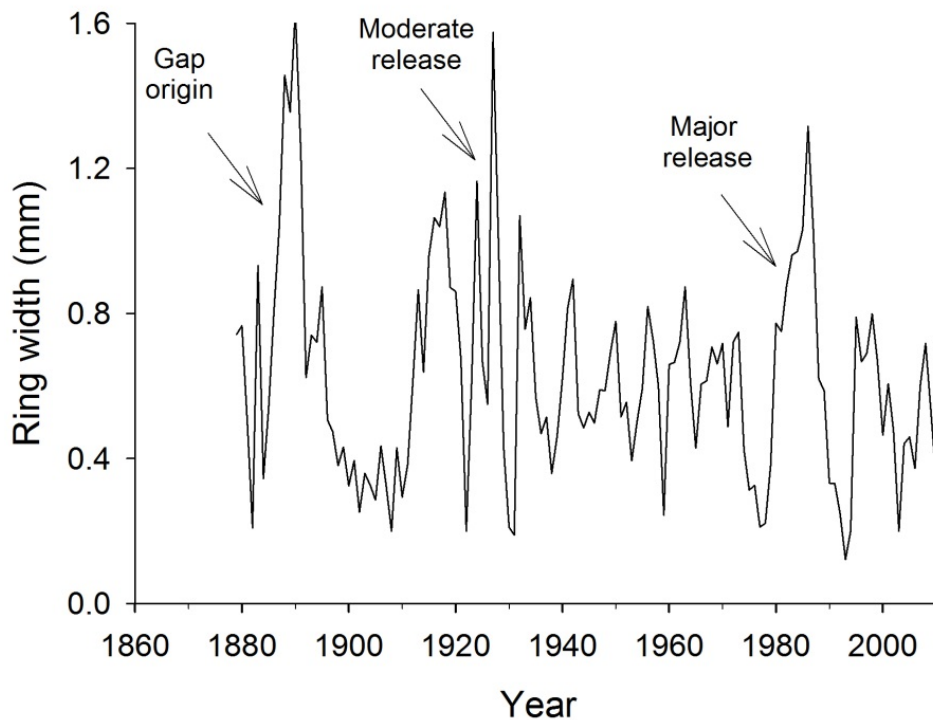


Figure 2. Tree ring width series (mm) for an *N. pumilio* individual in the Toro River Valley, Santa Cruz, Argentina. Arrows indicate gap origin as a result of high initial growth rates and moderate (percentage growth change 50–99) and major (percentage growth change >100) growth releases resulting from abrupt changes in radial growth after the occurrence of a disturbance event in the canopy.

Gap origin events were defined based on the detection of rapid early growth rates of the trees [10,12]. This method uses a radial growth threshold based on the last ten years (extent) of a-priori field-determined groups of suppressed and dominant trees. The threshold for gap origin trees is set as the upper 95th percentile of growth rate of suppressed trees over the last ten years which corresponded closely with the fifth percentile of dominant trees [10,12]. The threshold was 0.96 mm and consequently trees that had rings 6 to 15 (counted from the pith) present (87.8% of the sampled trees) and grew at a higher rate than the threshold between those years (6–15) were considered of gap origin. Visual examination of the individual tree-ring series was used to confirm radial growth threshold and extent on gap origin trees. Establishment dates for gap origin trees were determined to depict gap origin disturbance events [10,44].

Disturbance chronologies for each transect were built by determining the proportion of trees with major and moderate releases and gap origin events relative to the number of trees alive [10,12,36].

3. Results

3.1. Forest Structure

The structure of the forest exhibited differences along with changes in the elevation (Table 1). Living trees in the lower transect were significantly taller than those of the upper transect (t -value = 7.62; $p < 0.012$) and had a similar height class distribution but with different mode (Figure 2). Likewise,

living and dead trees in the lower transect were significantly larger than those of the upper transect (t -value = 5.47; $p < 0.001$) but presented different diameter class distribution (Figure 3). While the average tree age in the lower transect was higher, the difference was not significant (t -value = 1.85; $p = 0.06$; Table 1).

Table 1. Average total height, diameter at breast height, age, overstory and understory density, and basal area at different altitudes for an *N. pumilio* forest in the Toro River Valley, Santa Cruz, Argentina.

	Height (m)	Diameter (cm)	Age (Year)	Overstory Trees (n°/ha)	Understory Trees (n°/ha)	Basal Area (m ² /ha)
Upper transect	5.3 (± 2.6)	16 (± 11.9)	136 (± 61.4)	6455 (± 8063)	(± 31,668)	75.1 (± 58.7)
Lower transect	8.2 (± 3.2)	24.8 (± 14.3)	151 (± 59.3)	4580 (± 11,222)	3437 (± 12,854)	85.9 (± 67.8)
Mean	6.7	20.4	143.5	5517	7601	80.5

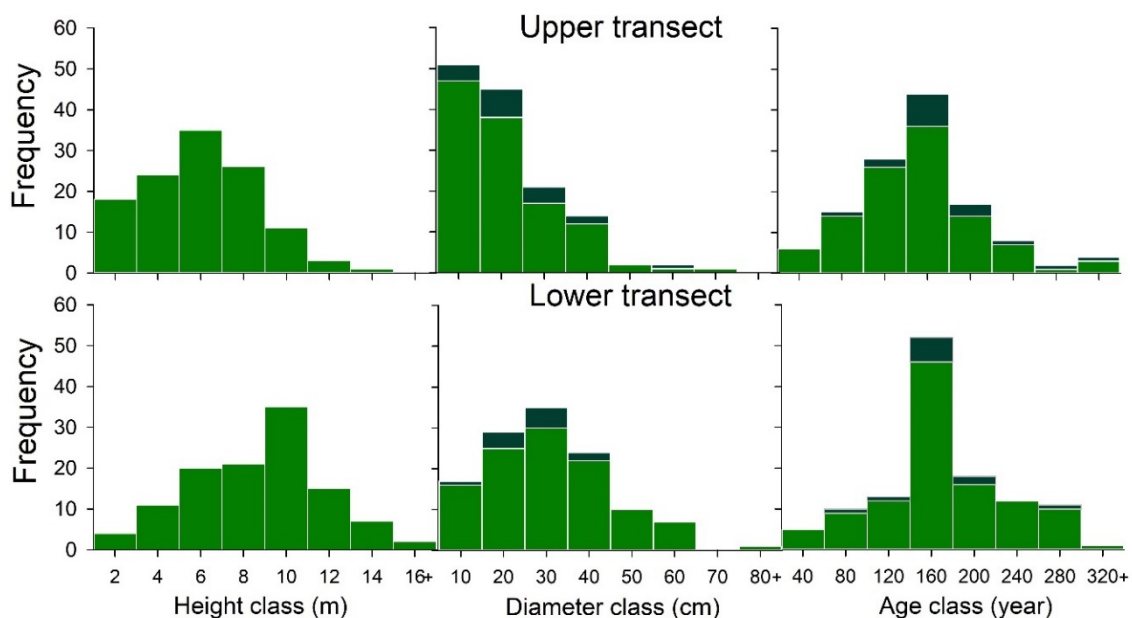


Figure 3. Height, diameter, and age distributions of living (light colors) and dead (dark colors) trees (>1.3 m height) at different altitudes for an *N. pumilio* forest in the Toro River Valley, Santa Cruz, Argentina. Classes indicate the upper limit of each interval.

Average density of adult trees and seedlings was higher in the upper transect but did not differ significantly from those densities of the lower transect due to the high variability present in both transects (Table 1). Alternatively, the transect at the low elevation presented an average basal area significantly higher than that of the upper transect (t -value = 7.45; $p < 0.0001$; Table 1).

The proportion of living and dead trees was 0.87 and 0.13 and 0.90 and 0.10 for the upper and lower transect, respectively, and did not differ significantly ($X^2 = 0.58$, $df = 1$; p -value = 0.89). The stem condition of the dead trees varied with the elevation. While in the upper transect the proportions of standing dead and snapped trees were 0.89 and 0.11, respectively and dead uprooted trees were not present. In the lower transect 0.54 of the dead trees were standing while 0.31 were snapped and only 0.15 were uprooted; differences in the proportions did not differ significantly (p -value Fisher = 0.08).

3.2. Forest Dynamics and Disturbance History

The establishment of trees over time exhibited some differences with the elevation (Figure 4A,C). While at the upper transect establishment was rather sporadic for the first 230 years (1600–1830), at the

lower transect started around 1730 and remained steady before peaking around 1810. Subsequently establishment in the upper transect increased but remained steady to reach peaks around 1840, 1860, 1890, and 1910 before abruptly decreasing (Figure 4A). Establishment in the lower transect, on the other hand, progressively decreased for about two decades and then began increasing in the 1840s to slowly decrease by the late 1920s (Figure 4C). There was no establishment for almost two decades at both transects until 1940 followed by low and steady for almost four decades.

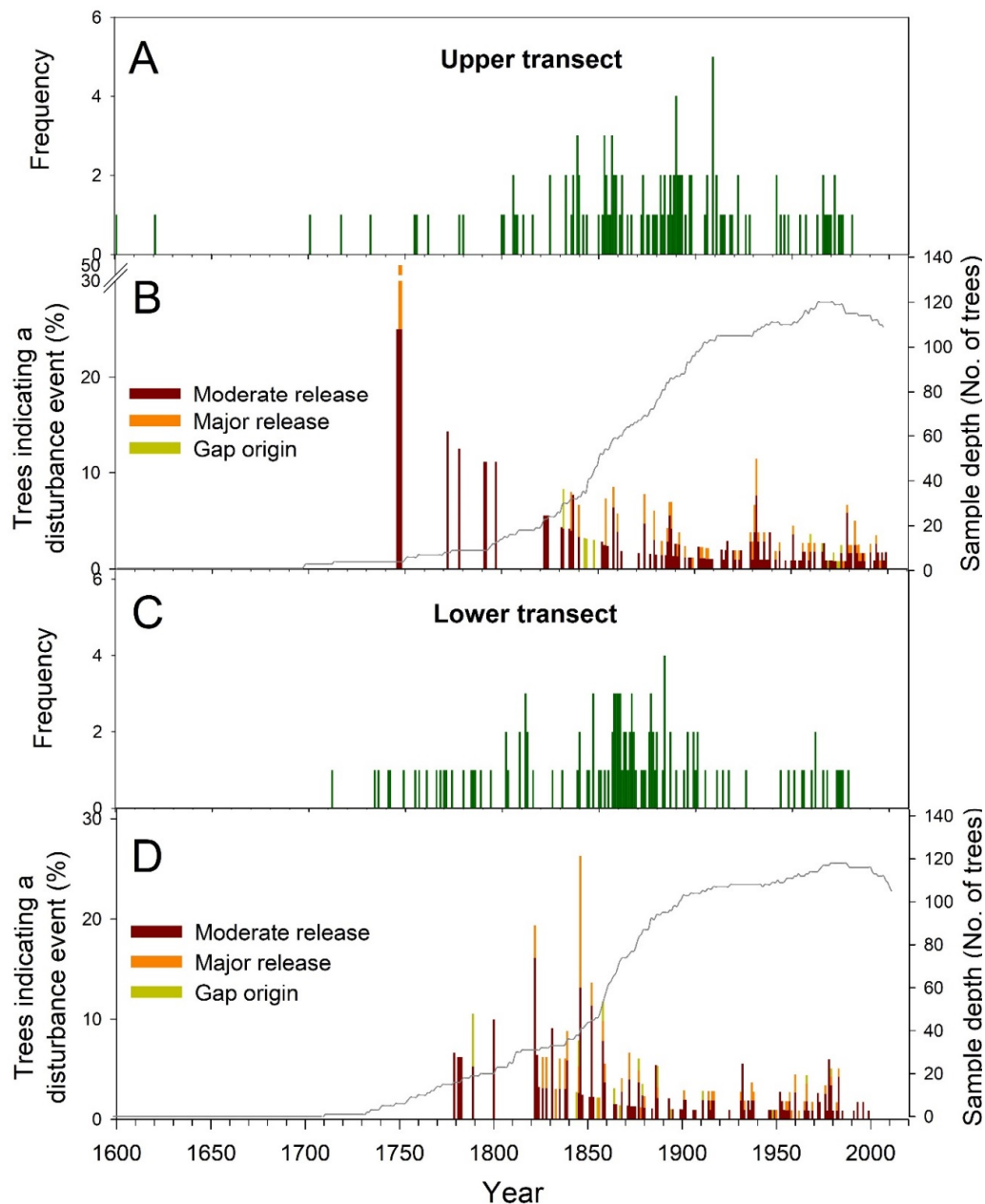


Figure 4. Establishment dates of trees (panels (A,C)) and disturbance chronologies based on the proportion of radial growth releases and gap origin events (panels (B,D)) at different altitudes for an *N. pumilio* forest in the Toro River Valley, Santa Cruz, Argentina. Brown and orange bars represent moderate (PGC 50%–99%) and major releases (PGC > 100%), respectively. Light green bars represent gap origin trees (high initial growth rates). The solid lines indicate the total number of living trees at each year.

The average radial growth of trees was 0.62 and 0.69 mm/year for the upper and lower transect, respectively, and did not differ significantly (t -value = 1.66; p = 0.07). The radial growth patterns,

however, presented distinct patterns (Figure 5). Given the low sample size both chronologies were characterized by high variability during the first 60 years. Starting in 1850, the lower transect chronology exhibited higher values than the upper transect with accentuated differences during some periods (1870–1885, 1890–1930, 1985–2005; Figure 5).

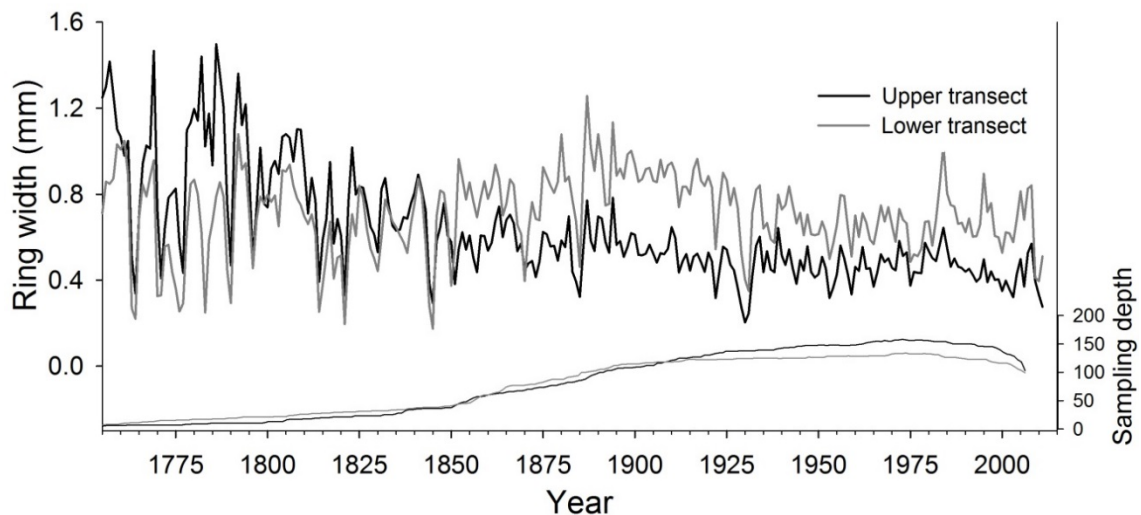


Figure 5. Ring-width mean chronologies of living and dead trees (>1.3 m height) for *N. pumilio* forests at different altitudes in the Toro River Valley, Santa Cruz, Argentina.

The proportion of trees that experienced growth releases and the magnitude of the releases (major and moderate) were similar at both elevations (Table 2). Nevertheless, transects showed distinct temporal patterns of disturbance events in the canopy over the last 200 years (Figure 4B,D). In the upper transect, 79% of all sampled trees exhibited at least growth releases. Although sporadic for the first ca. 100 years, moderate and major releases were common since 1740 with peaks (>10% trees releasing) in the 1740, 1770, 1790, 1940 decades (Figure 4B,D). In the lower transect, alternatively, 76.3% of all sampled trees experienced at least growth releases sporadically between late 1770 and the 1830s, to become later more uniform. High percentages of releases (>10) were recorded for the decades of 1800, 1820, 1830, 1840, and 1850 (Figure 4B,D).

Table 2. Proportion and mean and maximum duration of radial growth releases of different PGC for trees growing at different altitudes in the Toro River Valley, Santa Cruz, Argentina.

	Moderate Release (PGC 50%–99%)			Major Release (PGC > 100%)		
	% Trees	Mean (Year)	Maximum (Year)	% Trees	Mean (Year)	Maximum (Year)
Upper transect	74	6,4	22	26	6,1	13
Lower transect	76	6,7	18	24	5,7	13

The proportion of gap origin trees was smaller compared to that of the growth releases and its temporal patterns differed also greatly between transects (Figure 4B,D). Of all sampled trees in the upper transect, only 9.2% had a gap origin and had established in two distinctive periods (1830–1840 and 1960–1970). Alternatively, 13.6% of all sampled trees in the lower transect indicated a gap origin and gap origin events mainly occurred during the 1780s and the 1840–1880 and 1960–1970 periods.

The disturbance chronologies resulting from both growth release and gap origin events varied with the elevation. Both chronologies reflected the occurrence of different types of canopy disturbances since the second half of the 1700 until the year 2000 with a relative absence of canopy disturbances

during the period 1750–1810 probably due to the small sample size (Figure 4B,D). It was indeed for that period and until the 1860s where differences due to elevation were most remarkable: 1740–1790 and 1820–1850 for the upper and lower elevation transect, respectively. The other distinct difference between elevations was the higher number of canopy disturbances in the decades of 1880 and 1930 in upper transect compared to the lower transect (Figure 4B,D).

4. Discussion

Our study revealed an extensive canopy disturbance history in a montane old-growth *N. pumilio* forest in the Toro River Valley in the southern Patagonia, Argentina. The disturbance chronologies indicated a high proportion of the canopy trees were affected by canopy disturbances (75% radial growth releases and 11% gap origins). While the proportion of individuals which documented the occurrence of past canopy disturbance events was similar at both elevations, the temporal patterns of canopy disturbances differed. At the higher elevation, there were major growth releases and gap origin events in the period of 1830–1860 which might have originated from disturbances that eliminated much of the canopy, this being less marked during the 1960–1980 period. Similarly, and in the absence of gap origin events, a significant proportion of moderate and major growth releases took place between 1870 and 1900. At the lower elevation, alternatively, a higher proportion of trees originated in gaps over several decades (1840–1880 and 1960–1970) and the occurrence of numerous periods with high proportion of growth releases could be attributed to the result of a single or multiple disturbance events of less intensity in the canopy. Yet, the fact that the extension of the pulses of growth releases at lower elevation extended from two to six decades, and also showed distinct fluctuations in the proportion of affected trees, makes the interpretation of these results less accurate. Noteworthy is the occurrence of growth releases and gap origin events for six consecutive decades at the lower elevation forest (1830–1890), that could have resulted from multiple high-frequency disturbance events of varying magnitude but also from a combination of low frequency and high intensity disturbance events combined with more frequent events of lesser intensity. In turn, this highlights the difficulty in identifying the precise moment when the disturbances took place, especially when trees established in gaps for extended periods following apparent high severity disturbances [36]. It is important to note that due to insufficient sample depth prior to 1800, our inferences of disturbance history beyond this point are limited.

Nevertheless, it is possible that this complex combination of disturbances of different frequency, intensity, and magnitude could, in turn, be in part explained by the nature of the disturbance agents. The magnitude, frequency, and area affected by wind events in *N. pumilio* forests in southern Patagonia can vary broadly, ranging from large blowdowns and wave mortality patches to small treefall gaps [15,30,31,49–51]. For the study area in particular, [33] and Amoroso (in preparation) reported moderate and minor (GC of 25%–49%) growth releases in wind-disturbed forest patches as a result of windstorm events. This moderate growth response would likely occur as a result of wind-driven “mortality waves”. Such partial disturbances have been reported in *Nothofagus* forests in southern Patagonia [15,20,29,31] and in particular for the studied area ([33], Amoroso et al. in preparation). The authors of [33] found that the average frequency of wind blowdown events was 6.5 (at 813 m.a.s.l.) and 10.7 years (at 916 m.a.s.l.) for the study area, and 4 (at 640 m.a.s.l.) and 7 years (at 693 m.a.s.l.) a few kilometers south in the valley of the Rio de las Vueltas, resembling the high-frequency canopy disturbances found in this study. Major growth releases (PGC > 100), on the other hand, represent releases generally associated with the total loss of the upper canopy as a result of disturbances of greater magnitude and scale (e.g., [13,44]). For montane *Nothofagus* forests, major releases could result in trees responding to changes in the environment due to tree mortality caused by snow avalanche events [19]. Dendrochronological reconstructions of snow avalanches in the Rio de las Vueltas basin reported average return periods of 19.6 and 18.8 years for Loma de las Pizarras and Lago del Desierto, respectively [18,32]. Similarly, such magnitude of growth releases, while less common, could result from greater intensity wind blowdown events as well ([12,52], Amoroso et al. in preparation). Similar

combinations of frequent, low severity disturbance and less frequent, intermediate severity disturbance events caused by wind are indeed common in other ecosystems where wind is an important disturbance (e.g., [12,34,35]). Yet, recognizing the agent of disturbance of each canopy event might be difficult in these forests as the recolonization dynamic in snow avalanche paths could be similar to what would occur after windthrow events [19,29,30]; while avalanches are less frequent and more intense disturbance events that usually affect areas at higher elevations and may have overlapped with wind blowdown events or vice versa, resulting in the apparent higher frequency of canopy disturbance events at higher elevations.

The condition of the dead trees varied with the elevation and reflected the complex history of disturbance agents in the study area. A greater proportion of standing dead trees was recorded at the higher elevation forest resulting probably from snow avalanches that usually leave standing trees facing their stems down-slope or uproot trees [18,32]. At lower elevations, on the other hand, the greater proportion of snapped and uprooted trees probably resulted from gusty winds that usually knock down trees in the direction of the prevailing winds and produce cracks in the stems [30,33,53]. Yet, it is important to note that snow avalanches could result in a similar type of damage (e.g., [54,55]) making the distinction of a specific causal agent on each tree difficult.

Past canopy disturbances have strongly influenced the structure and dynamics of this forest, and differences in disturbance history with elevation have contributed to significantly different forest structures. On average, individuals at the lower elevation were larger and older, and basal area per hectare was higher at the lower elevation forest. While at the lower elevation the diameter distribution frequency presented a slight asymmetry to the left, at the higher elevation it resulted in an inverted J-shaped distribution resulting from the higher density of saplings compared to the lower elevation forest. Although not distinct, these differences were also observed in the height distribution frequencies.

Tree establishment over the last 280–300 years was characterized by important temporal variations strongly suggesting the occurrence of multiple canopy disturbances (e.g., [56–58]). There were common periods of establishment for both transects with pulses of continuous establishment (1840–1910 and 1940–1980), but also some distinctive periods such as that in the 1740–1810 for the lower transect. Peaks of establishment were, alternatively, different from the upper (1840, 1860, 1890, 1910) and the lower (1810, 1880) transect, respectively. Overall, periods of increasing recruitment and peaks reinforce the occurrence of different canopy disturbances. At higher elevations, some periods of recruitment were nearly contemporaneous with a number of minor and major disturbances periods such as that between 1870 and 1900. Similarly, peaks in recruitment coincided with a high proportion of trees have establishing in gaps over several decades at the lower elevation (1840–1880 and 1960–1970); the origin of this continuing and massive establishment could have resulted as a consequence of successive disturbances of medium-to-high intensity and magnitude. Lags between canopy disturbances and subsequent establishment were common as expected in montane environments where the climate is harsh [59] but also due to methodological sampling aspects as establishment dates represent estimates recorded at ca. 30 cm from the ground. The lack of further establishment since 1980 results from lack of data due to the sampling protocol (only trees ≥ 1.3 m tall were dated).

Differences in forest structure and dynamics in *N. pumilio* forests could be expected with elevation [60–62] as it has also been reported in other *Nothofagus* forests [63]. Nevertheless, the rich and diverse history of canopy disturbances of varying frequency and intensity at different elevations cannot be ignored while assessing the dynamics and the structural differences in these forests. After the occurrence of disturbances such as wind and snow avalanches, differences in forest structure at different elevations are expected [17,27,46], as we reported in this study.

5. Conclusions

Our study unveils important insights of the forest dynamics and disturbance history of old-growth *N. pumilio* forests in southern Patagonia, Argentina. By developing the first disturbance chronologies for these forests, we provided robust evidence that forests in the study area have been subject of

multiple disturbance events over the last 250 years. Moreover, small changes in elevation resulted in disturbance chronologies with slightly different histories. The abrupt increases in radial growth, the rapid early growth rates, and the recruitment over time of overstory canopy trees indicated forest structure and dynamics have been shaped by frequent, moderate- to high-severity disturbance events, but also to less frequent and more severe events. While most events resulted from the effect of wind and snow avalanches, recognizing the agent of disturbance of each event might be difficult in these montane forests. Dendrochronological methods such as disturbance chronologies alone cannot identify the nature of each of the disturbance pulses documented in this study. The identification of the nature of these events indeed requires the use of a proper methodology for each agent and historical record, so as to clarify what kind of disturbance occurred at different times in the history of these stands. Determining the nature and effects of the disturbances in the region, will allow a better understanding of their dynamics and will help determine the frequency and the main disturbance agents in these events. This could in turn be used in forest management that tries to mimic natural forest dynamics. Additional studies in *N. pumilio* old-growth remnants across the region will facilitate a more comprehensive understanding on this issue.

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