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Control of invasive conifers in temperate Andean forests promotes native vegetation restoration, but requires continuous management

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ABSTRACT

Non-native conifers have been planted widely because of their growth potential and wood quality. However, many of them have become invasive in the introduced ranges. In Chile, the initial introduction of non-native conifers helped the recovery of degraded land, but today some pine species present a high invasion risk when they are not properly managed, leading to detrimental impacts on natural ecosystems and biodiversity. Such is the case of Douglas fir (*Pseudotsuga menziesii*), a species listed as invasive in south-central Chile, as well as in many other countries, when it establishes beyond the original plantation range. The main goal of this research was to characterize the invasion pattern of *P. menziesii* within a recently-declared protected area nearby the Conguillío National Park in the Andes Cordillera. We aimed at determining the key factors that promote the invasion of *P. menziesii* outside the original plantations. We established five 1,000 m^2 sampling transects (i.e., 100×10 m), considering two invasion conditions: (i) within the native forest and (ii) far into open scrub areas, both adjacent to *P. menziesii* plantations. We measured forest structure, soil nutrients, the floristic composition and pine regeneration before and after controlling the invasion within each study conditions. We found that *P. menziesii* density and soil nutrient availability in the soil decreased with the distance from the plantation. In addition, an increase in native species cover was found after removing pines, but also noted the ability of *P. menziesii* to readily re-invade the native forest after removal. These results indicate the need for continuous control of *P. menziesii*, especially inside the native forest at the early stages of invasion. We discuss the need for better plantation management to prevent its spread into natural areas and protect native forests from non-native conifers invasion.

1. Introduction

Biological invasions have led to rapid range-expansions of thousands of plant and animal species worldwide (Hobbs, 2000; Meyerson and Mooney, 2007; van Kleunen et al., 2015). In spite of the rapid change and the ability of prompting novel interactions, and altering communities and ecosystems (Le Roux and McGeoch, 2008), the ecological impacts of invasive plant species still remain poorly explored (Wallingford et al., 2020; Eckert et al., 2023). Non-native conifers, such as pine species have been planted widely because of their growth potential and good timber quality, however, many of them have become invasive (Ledgard, 2002; Richardson and Rejmánek, 2004; Orellana and Raffaele, 2010). Examples of this issue are well documented for Lodgepole pine (*Pinus contorta* Douglas & Loudon), Monterrey pine (*Pinus radiata* D. Don) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), which outside of their planted ranges, are invading numerous natural ecosystems, including forests, open scrubland areas and treeless steppe (Pauchard and Jimenez, 2010; Pauchard et al., 2016; Núñez et al., 2017;

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García et al., 2018).

Understanding patterns and impacts of conifer invasions is critical for their management and reducing their effects on biodiversity and ecosystem services (Broncano et al., 2005; Núñez et al., 2008). In South America, non-native conifer plantations have been promoted in multiple ecosystems in the last 50 years. However, only recently research has focused on the potential risk of invasion, and even less so in proper management and control of conifer invasions (Evans et al., 2021). Globally, conifer invasion reports approximately 80 species as naturalized somewhere in the world (13 % of the total) and 36 species (6 %) as invasive with direct impacts on biodiversity (Richardson and Rejmánek, 2004).

In Chile, according to recent data published in the catalog of alien species, (Fuentes et al., 2020), there are 1122 naturalized alien species, of which >70 % correspond to terrestrial and aquatic vascular plants. Of this group of species, conifers are one of the most studied (i.e., Pinaceae family, which is native to the Northern hemisphere), considering that they have been planted widely in south-central temperate areas of Chile (Pauchard et al., 2008; Müller-Using et al., 2016). Many of these conifer species have characteristics, associated with high invasiveness (Jaksic and Castro, 2014; Fuentes et al., 2020) such as shade tolerance, enhanced competitive traits and the ability to massively produce viable seeds early. The first non-native conifers planted in Chile were initially introduced as ornamental species, and then used to control soil erosion (Prado, 2015). Afterwards, pine plantations were established in areas where native forests had been exploited, mainly triggered by laws that promoted afforestations with alien tree species, such as *P. radiata* and *P. menziesii* (Jaksic and Castro, 2014). Currently, the area covered by fast-growing conifer plantations in Chile is approximately 3 million ha, equivalent to 17.5 % of the total area covered by forests in Chile (CONAF, 2017), and the forest industry represents 2.1 % of the country's Gross Domestic Product (Promis, 2020).

Pseudotsuga menziesii is a monoecious species native to western North America (Hermann and Lavender, 1990). It has been widely introduced into the world due to its rapid growth, great wood features, and its ability to adapt to various environments (Kannegiesser, 1988), being able to grow in different climatic conditions, with average temperatures between −9° and 30°C (Hermann and Lavender, 1990). According to Richardson and Rejmánek (2004), *Pseudotsuga menziesii* is the species with the highest number of records as an invasive species worldwide, and it has been reported in Europe, New Zealand, Argentina, Chile, among many others (Frank and Finckh, 1997; Ledgard, 2002; Orellana and Raffaele, 2010; Evans et al. 2021). *Pseudotsuga menziesii* (Douglas Fir) is the sixth introduced species with the greatest presence in Chile, and the third planted conifer, covering ca. 21,000 ha between the Maule and Aysén regions (~35°- 45°S). More than 40 % of the national total planted area takes place in La Araucanía region (38°, Sagardía et al., 2022). Outside of its planted range, *P. menziesii* has become an invader in Chile, particularly within temperate forests (Pauchard et al., 2016), with a high invasive potential (Fuentes et al., 2014). Pauchard et al. (2008) indicate that the invasive potential of *P. menziesii* is associated to site factors (i.e., disturbances) as well as intrinsic attributes of the species (i.e., propagule pressure) and high shade tolerance.

The invasion of *P. menziesii* in south-central Chile begins 15 years after the establishment of plantations, which coincide with the maturity age at which the species begins to produce cones and viable seeds. In addition, there are isolated patches nearby plantations that advance as a result of natural regeneration (Pauchard et al., 2008). According to Fuentes et al. (2014), this species is highly invasive due to the massive production of seeds that are easily transported by wind, and whose germination is catalyzed by disturbances in the local environment (Núñez et al., 2009). The main impacts of *P. menziesii* invasion are the formation of dense stands capable of displacing native vegetation, changing the functional and structural diversity of the invaded site, and outcompeting native vegetation for light and soil nutrients (Fuentes et al., 2014; Jaksic and Castro, 2014). Unfortunately, many plantations of *P. menziesii,* as well as other non-native conifers, were established in protected areas of south-central Chile as a method to control soil erosion and recover vegetation in areas affected by fires and logging (Pauchard et al., 2016). Temperate native forests of Chile dominated by *Nothofagus* spp. has shown to be susceptible to invasion by *P. menziesii* (Pauchard et al., 2008), but to date little is known about the invasion degree in natural areas and how effective and efficient are the control methods.

Thus, the main goal of this study is to characterize the invasion of *P. menziesii* within protected areas in south-central Chile that were previously afforested with *P. menziesii*. Specifically, we aimed to (i) evaluate how *P. menziesii* invades across a distance gradient between the source plantation and adjacent native forest dominated by *Nothofagus* spp. as well as into open areas, (ii) identify and characterize key site variables associated with the invasion of *P. menziesii*, (iii) assess the response of the native vegetation 12 months after of *P. menziesii* invasion control, and (iv) evaluate the potential re-invasion of *P. menziesii* after invasion control.

2. Methods

2.1. Study area and species description

This research was conducted within a protected area of south-central Chile, specifically in Marsella sector, which was lately incorporated to Conguillío National Park in 1987 (CONAF, 2006). This area encompasses 5463 ha and is located 17 km from the town of Cherquenco in the municipality of Vilcún, La Araucanía region (38°43′S, 71°51′W; Fig. 1). The study area is located in a hydromorphic biogeographic zone, with vegetation characterized by hydrophytic features, moderate temperatures, and high rainfall (~2500–3000 mm; Pollmann, 2003). This, together with the characteristics of the soil, altitude, and phytogeography, allow the formation of varied forest ecosystems, including mixed and pure forest stands. The most important plant communities where this research was carried out are *Nothofagus obliqua-N. alpina-N. dombeyi* (roble-raulí-coigüe), *N. dombeyi-N. antarctica* (coigüe-ñirre) and *N. dombeyi-N.alpina-Laureliopsis philippiana* (coigue-raulí-tepa) (CONAF, 2006).

Prior to its incorporation into Conguillío National Park, Marsella was subject to successive timber harvests that reached ca. 1900 ha. Between 1970 and 1973, about 200 ha of *P. menziesii* plantations were established in the area. This led to a significant increase in the area covered by the species, beyond the sites originally planted, due to its high propagation capacity (Pérez et al., 2017). In 2015 and 2016, around 30 ha of *P. menziesii* plantations were clearcutted in the area to restore native forest. Plantations were 42 to 44 years old, with dominant individuals of ~30 m in height and a density of 1700 trees/ha.

Pseudotsuga menziesii is a large evergreen coniferous tree up to 50–60 m tall and with a trunk of up to 2.5 m in diameter (Kannegiesser, 1988). In its natural range can grow exceptionally over 100 m in height and with a trunk up to 4 m in diameter, living more than 1300 years. Also, it can occur from 0 to 3200 m a.s.l., reflecting the high plasticity of the species being able to grow under a wide variety of climatic conditions. It is a fast-growing, pioneering tree species following fire and other soil disturbances, but also behaves as shade-tolerant species in secondary successions, so that it may invade in early, mid and late forest stages. Shade tolerance, enhanced competitive features and the ability to massively produce seeds early would facilitate the dispersal and the invasion of the species in natural ecosystems (Pauchard et al., 2008).

2.2. Measurements

In January 2019, five longitudinal transects of 10×100 m (1000 m^2) were established in the study area. Each transect was established between 900 and 1060 m a.s.l., perpendicular to the propagule source, which was defined as the nearest adjacent *P. menziesii* plantation to each sampling transect (Fig. 2). Two study conditions were defined: one

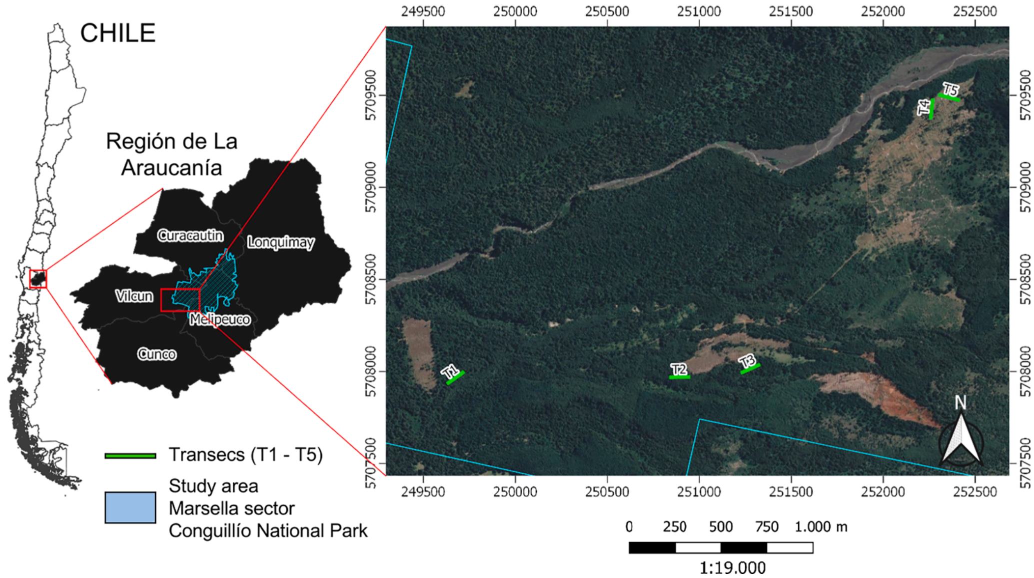

Fig. 1. Study area and sampling transects in Marsella, Conguillío National Park, Araucanía Region (south-central Chile; 38°43′S, 71°51′W). Transects T1 T2 and T3 were established within native forest, while transects T4 and T5 were located in an open scrubland area.

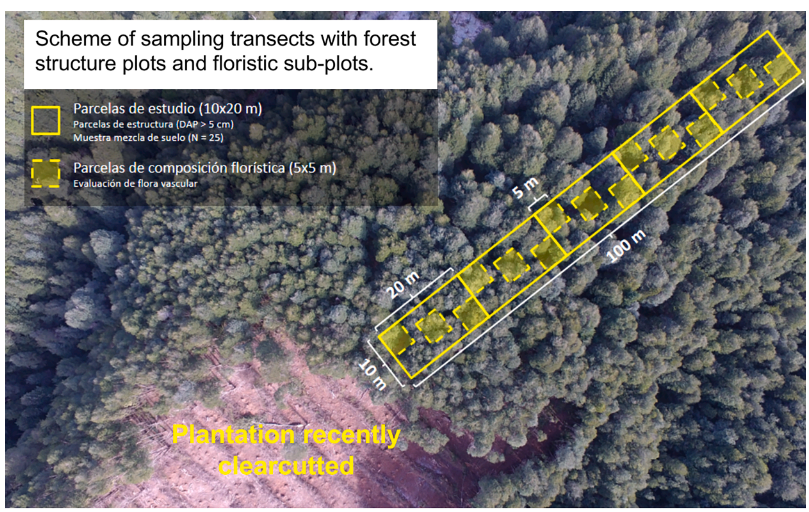

Fig. 2. Scheme of data collection within transects (10×100 m each). Note that in the image the native forests is adjacent to a clear cut area where the plantation originally was. The continuous contour represents the plots that make up the transect, while the squares with the segmented contour represent the sub-plots where floristic composition data was acquired.

under native forest canopy, and another in an open scrubland area. Within the native forest, transects were established adjacent to a recent clearcutted stand of *P. menziesii* that occurred in year 2017, while for open areas transects were established adjacent to a standing *P. menziesii* plantation. Each transect, in the two study conditions, was divided into five nested-plots of 10×20 m (200 m^2), where three square subplots (9 m^2) were systematically distributed along the transect (Fig. 2). Data on the invasion of *P. menziesii*, as well as on the tree structure of the forest were also obtained in each 200 m^2-plot. For the forest, all woody individuals with a diameter at 1.3 m or (DBH) $\geq$ 5 cm were counted and identified. For each tree individual, DBH and height were recorded. In addition, within the subplots of 9 m^2 ($n = 75$), all vascular plants were recorded using the scale of Braun Blanquet (1964) to evaluate the floristic composition. Species not identified in the field were collected for further identification using specialized literature (Riedemann and Aldunate, 2004; Teillier et al., 2014). Nomenclature and taxonomic classification followed Zuloaga et al. (2008).

Furthermore, soil samples were taken to determine the availability of nutrients (i.e., nitrogen [N,] phosphorus [P] and potassium [K]). A mixed random sample was taken in each 200 m^2 plot of approximately 500 g, composed of 5 sub-samples of soil from the first 5 to 10 cm of depth. Analyses were performed by the Nitrogen and Carbon Analysis Service of the Zaidín Experimental Station (CSIC), Granada, Spain (EEZ, 2020). For the analysis, the mean availability of the nutrients was calculated as a function of the distance from the plantation according to each of the study condition (i.e., native forest canopy and open scrubland area).

After measurements in the sampling unit (i.e., transects), all *P. menziesii* individuals were manually and mechanically removed. We performed this activity to record pine density segregated by height classes as follows: seedlings (0–50 cm), juveniles (51–200 cm) and saplings (>2 m). The following year, in January 2020, data were again collected on the same transects, plots and subplots established the previous year. This was carried out to evaluate the re-invasion capacity of *P. menziesii* over time and for assessing the recovery of the native vascular flora 12 months after the invasion control. *Re*-invasion was defined by the presence of new *P. menziesii* individuals in the transects one year after the control, and it was expressed as density (ind./ha^{-1}).

2.3. Data analysis

2.3.1. Forest structure and plant composition

We estimate stand variables such as tree density and basal area for each 200m^2 plot, as well as the richness of all vascular species and their abundance at each 9m^2 subplot. All these variables were computed by species, and for each measurement occasion (i.e., before and after the invasion control). For floristic data, relative cover of each species (%), its phytogeographic origin (i.e., alien or native) and growth form (i.e., herbaceous, shrub and arboreal) were measured. These variables were evaluated before and after the *P. menziesii* control. With the data obtained, species richness was calculated as a function of the distance from the source of *P. menziesii* propagules for each study condition (i.e., native forest canopy and open scrubland area), and species richness according to phytogeographic origin, and the most abundant species for each study condition. The Shannon-Wienner diversity index (H') and Pielou's evenness index (J') were also estimated using the *vegan* package (Oksanen et al., 2018) available in the R statistical program (R Core Team 2023). Additionally, a Non-Metric Multidimensional Scaling (NMDS) analysis was performed using the matrix of species found in each plot, which is based on the level of floristic dissimilarity between plots.

2.3.2. Invasion and re-invasion of P. menziesii

The number of individual *P. menziesii* trees in each plot along each transect was quantified, classifying the plants found according to their stage of development, which are: seedlings (i.e., category 1, between 0 and 50 cm in height), juveniles (i.e., category 2, between 51 and 200 cm in height) and saplines (i.e., category 3, individuals >200 cm in height). Once counted, all *P. menziesii* individuals were extracted by manual or mechanical removal (with pruning shears and/or saws for saplings). The same procedure was repeated the following year after the control to quantify the re-invasion of *P. menziesii*. Before and after the invasion control, the density (i.e., number of individuals/ha) was calculated for each category as a function of the distance gradient.

Additionally, the site variables that have a significant effect on pine density before and after the initial control were evaluated. This analysis was performed using the Kruskal-Wallis test (Kruskal and Wallis, 1952), with a significance level of α=0.05. Subsequently, the Mann-Whitney U test was used to establish comparisons (Mann and Whitney, 1947). We used nonparametric analyses because the response variables were not normally distributed. Finally, Pearson's correlation coefficient was obtained to determine the relationship between site variables and *P. menziesii* density before and after the control. All the statistical analyses were performed using the R software (R Core Team 2023).

3. Results

3.1. Forest structure

A total of 332 tree individuals ($\geq$ 5 cm DBH) were found in the study transects, of which 288 were alive and 44 were standing dead. Of the living individuals, 280 were found in the native forest (97 %), and only 8 (3 %) in the open scrubland zone. Seven native species and one alien species were recorded (i.e., *P. menziesii*). The most abundant native species was *N. dombeyi* in both study conditions, followed by *N. antarctica* in the native forest and *Lomatia hirsuta*, also in the native forest. On average, the diameter (DBH) and total height of individuals were greater in the open zone than in the native forest. The native forest, on the other hand, had a higher density of trees and also a greater basal area than open areas of scrubland (Table 1).

3.2. Availability of soil nutrients

Before the invasion control, higher phosphorus (P), nitrogen (N) and potassium (K) availability was recorded in the native forest when compared to open scrubland areas (Fig. 3a, 3b y 3c, respectively). Likewise, while in the native forest nutrient availability decreased with the distance from the propagule source (i.e., *P. menziesii* plantation), in the open zone nutrients increased in availability as the distance from the plantation as well.

3.3. Floristic composition

Before the invasion control, 66 vascular plant species were found in the sampling subplots. Of these, 42 species occurred in the native forest and 41 in open scrubland areas. Most of the species corresponded to herbaceous and shrubs in the native forest, and mainly to herbaceous in open areas. Then, a total of 66 species were found after the invasion control; 46 of them were found in the native forest (mostly herbaceous and shrubs), and 37 in the open areas (mostly herbaceous). There were no significant differences between the species richness found before and after the control of *P. menziesii* ($P > 0.05$; Table 2), nor when contrasting the native forest with open areas of scrubland. Shannon-Wiener diversity and Pielou's evenness indices also showed no significant differences when comparing study conditions in both periods (before and after de invasion control, $P > 0.05$; Table 2). After the control of *P. menziesii*, in the native forest, six native and two alien species were lost, but in their place, other nine native and three alien species appeared, with a net increase of four species. In the open scrubland zone, two native, seven alien, and two unidentified species were lost, and in their place, two native species appeared to replace the lost ones, resulting in a net decrease of three species between the two study periods (i.e., before and after the control, respectively).

Table 1
Tree structure (> 5 cm DBH) within areas invaded by *Pseudotsuga menziesii* in Marsella. Median (Med.), minimum (Min.) and maximum (Max.) values are presented for each species found on native forests or open conditions.

Native Forest	Trees/ha			Basal area (m^2/ha)			DBH (cm)			Height (m)		
	Med.	Min.	Max.	Med.	Min.	Max.	Med.	Min.	Max.	Med.	Min.	Max.
Embothrium coccineum	20	10	30	0.1	0.02	0,1	7.0	5.0	8.0	4.0	3.5	4,0
Lomatia hirsuta	240	50	390	1.5	0.2	2.6	8.5	5.3	17	5.3	3.0	10
Luma chequen	10	10	10	0.1	0.1	0.1	10	10	10	2.5	2.5	2.5
Nothofagus antarctica	800	800	800	8.2	8.2	8.2	8.7	5.2	33.5	7.0	0.5	25
Nothofagus dombeyi	420	300	540	53.4	27.9	71.3	33	5,1	94	21	2.5	29
Saxegothaea conspicua	10	10	10	0.03	0.03	0.03	6.0	6.0	6.0	4.5	4.5	4.5
Total	820	610	1370	53.7	37.8	73.9	11.5	5.0	94	8.0	0.5	29
Open Scrubland												
Laureliopsis philippiana	10	10	10	1.7	1.7	1.7	46	46	46	9.5	9.5	9.5
Nothofagus dombeyi	50	50	50	9.9	9.9	9.9	48.5	44.7	60.7	21	18	22
Pseudotsuga menziesii	20	20	20	0.4	0.4	0.4	13.8	7.0	20.5	9.5	7.0	12
Total	80	80	80	11.9	11.9	11.9	46	7.0	60.7	19	7.0	22

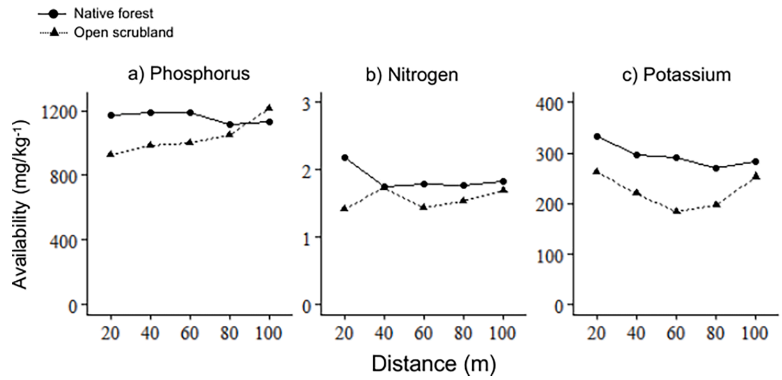

Fig. 3. Concentration of soil nutrients along transects within native forest (continuous line) and within the open scrubland areas (dashed line).

Table 2
Summary results of total species richness, Shannon-Wienner diversity index (H') and Pielou's evenness index (J') before and after control of *Pseudotsuga menziesii* invasion in each study condition (native forest and open scrublands). Capital letters indicate significant differences for the same year ($P > 0.05$). Lowercase letters indicate significant differences for the same condition ($P > 0.05$).

	Total Richness	Study Condition	Richness	Life Forms			H'	J'
				Trees	Shrubs	Herbs		
Before invasion control	66A	Native Forest	42Aa	8	17	17	2,84 Aa	0,90 Aa
		Open Scrubland	42Aa	5	7	30	3,03 Aa	0,89 Aa
After invasion control	66A	Native Forest	46Aa	13	15	18	2,93 Aa	0,89 Aa
		Open Scrubland	37Aa	5	8	24	2,98 Aa	0,90 Aa

Regarding native vascular flora cover, this was higher after the control of the *P. menziesii* invasion, especially in the native forest (Fig. 4b), but did not show differences for alien species (Fig. 4a). In open scrubland areas, the cover of alien species before invasion control was higher at the beginning of the transect (i.e., from 0 to 40 m), decreasing with distance from the plantation, in contrast to the second year where alien cover increased with distance from the plantation (Fig. 4c). Native species also increased after the invasion control in open scrublands (Fig. 4d). Correlation analysis showed a non-significant relationship between the distance gradient and species cover (p-value >0.05). The most abundant species recorded in the native forest were *Gaultheria mucronata* (Chilean pernettya) followed by *Rubus ulmifolius* (wild blackberry) and *Escallonia virgata*, while in the open scrubland zone they were *Agrostis capillaris* (common bent), *N. dombeyi* and *Hypochaeris radicata* (common catsear).

The NMDS ordination analysis showed a clear differentiation of the flora between the two study conditions: native forest and open areas of scrubland. The floristic composition in the open zone before and after the control is very similar, showing no major changes once the *P. menziesii* was removed. This is not the case in the native forest, where there was a greater dispersion of data, possibly related to the short term effect of removal of the invasion (Fig. 5).

3.4. Invasion and re-invasion of P. menziesii

Before the invasion control, and within native forest areas, a high density of pine individuals was found, mainly dominated by seedlings (Fig. 6a), followed by juveniles (Fig. 6b) and saplings at a much lower density (Fig. 6c). In general, *P. menziesii* density decreased as distance from the propagule source increased (i.e., plantation). Only saplings (< 5 cm DBH > to 2 m in height) were found in higher density in intermediate zones of the transect (i.e., from 40 to 60 m).

After invasion control, approximately 40 % of seedlings were found with respect to the previous period, mostly concentrated at the beginning of the distance gradient (i.e., first 20 m from the original plantation). After the control, no saplings were found, and very few juvenile pines were present.

In open scrubland areas, *P. menziesii* density was much lower than in native forest conditions, representing only about 2.5 % of the total number of seedlings found in the transects before the control. In both periods, pine seedlings found in open areas showed an increasing trend as the distance from the plantation increased (i.e., 40–80 m; Fig. 6d-f).

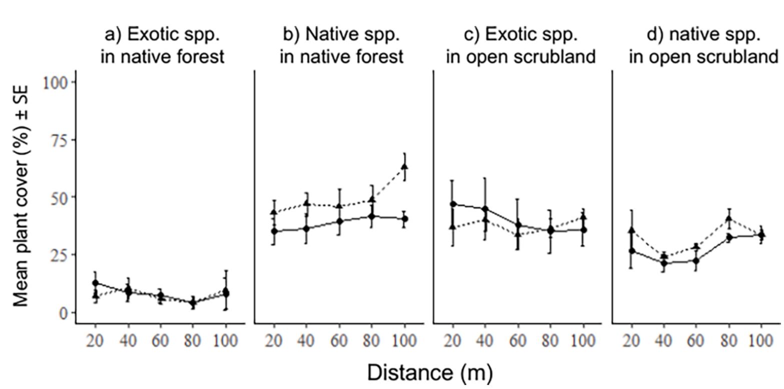

Fig. 4. Mean of vegetation cover (±S.E.) by study condition and plant origin before control (solid line) and after control (segmented line).

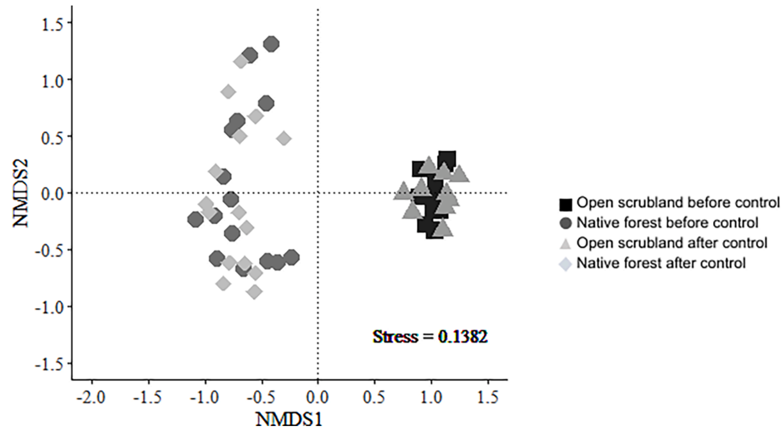

Fig. 5. Non-metric multidimensional scaling (NMDS) analysis of the floristic composition within the open scrubland areas and native forests, differentiating before and after the control of *Pseudotsuga menziesii*.

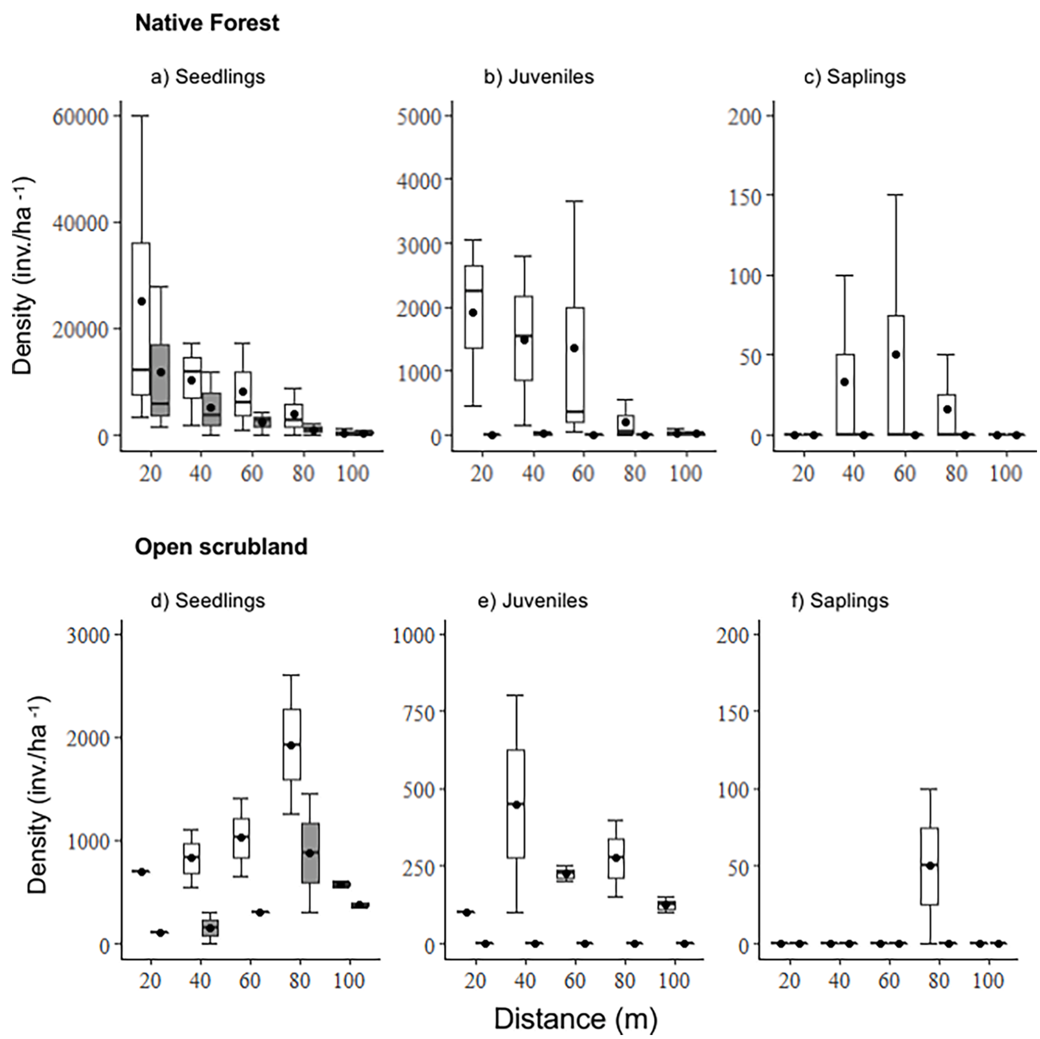

Fig. 6. Regeneration of *Pseudotsuga menziesii* before control, during the first year (white bars) and after control, during the second year of study (gray bars) occurring under the native forest (top panels) and within open scrubland areas (bottom panels). *Pseudotsuga menziesii* individuals were counted and analyzed as seedlings (a,d), juveniles (b,e) and saplings (c,f), respectively.

After the control, during the second year, the density of seedlings accumulated approximately 30 % with respect to the seedlings initially found (Fig. 6a).

The Kruskal-Wallis test showed that condition (i.e., native forest and open area) has a significant effect on *P. menziesii* density (p-value <0.05), as well as when contrasting study periods (p-value <0.01). As for the most important soil variables for vegetation (N, P and K), these have a significant effect on pine density (p-value <0.05), as well as basal area (p-value <0.01), and forest density (i.e., trees per hectare; p-value <0.05).

The correlation analysis showed that the variables which significantly related to pine density before the control were the density of trees per hectare in the forest, basal area and the distance from the *P. menziesii* plantation, the latter being negatively correlated. After the control, the only variables significantly correlated were tree density and basal area in native forest conditions (Table 3).

4. Discussion

In the Marsella area, which now is part of a protected area, the *P. menziesii* plantations were established in the early 1970s, so the invasion process could have begun at least 40 years ago, and with this, successive seeding and recruitment seasons have occurred. This is clearly shown by the large number of pine individuals in different stages of development found in both studied conditions (within the native forest and in open scrubland areas), ranging from seedlings (less than 50 cm in height) to sapling and tree individuals, which can exceed 12 m in height.

Regarding the invasion pattern of *P. menziesii*, there is a clear decrease in the density of seedlings and juvenile individuals while increasing distance from the propagule source in the native forest for both years of study, while in the open area there is not such a clear pattern, which may be due to the high competition with herbaceous and shrub species. In open conditions, the invasion density is lower than in the native forest, although they do not differ significantly. Regarding total invasion, there are significant differences when comparing before and after the control, because after the invasion control, less than half of the *P. menziesii* individuals recorded in the previous year were found.

After the control of juveniles and saplings, no individuals of these categories were observed in the following year, which may be due to the short evaluation time and due to the fact that *P. menziesii* is unable to reproduce vegetatively (Pauchard et al., 2008). Presumably, the large number of seedlings found the following year are due to propagules that were stock in the soil seed bank that are waiting better conditions for germination. This indeed could have occurred once the competition was removed. Mortality of *P. menziesii* seedlings is high in early stages of establishment, once this size is exceeded, individuals have high chances of becoming adults, so it would be recommended to apply a repeated control over time for individuals that exceed 50 cm in height to be effective against invasion (Pauchard et al., 2008).

In a similar study, Burmeister (2017) found that *P. menziesii* invasion in *Nothofagus* forests in New Zealand is strongly influenced by abiotic factors, both those occurring above and below ground, including light, altitude, distance from the propagule source, and soil nutrient availability. In our analysis, the distance from the source of propagules did not show a significant effect on the invasion of *P. menziesii*. However, a negative and significant correlation was found with the density of pines before the control. Furthermore, it was found that the availability of the nutrients evaluated had a significant effect on the density of pines. Studies have reported that nitrogen (N) is the only nutrient that limits the growth of *P. menziesii* in soils of the Pacific Northwest and the Intermountain Northwest (Hermann and Lavender 1990). It was observed that the greatest availability of N occurs in the first 20 m from the propagule source and is where the greatest number of *P. menziesii* individuals was found, at least in the native forest.

Table 3
Correlation analysis of site variables and pine density before and after invasion control. R^2 quantifies the Pearson's correlation coefficient between the density of pines and the site variables considered in the study. *: $P < 0.05$; **: $P < 0.01$.

Variable	Pine density before control (R^2)	Pine density after control (R^2)
Distance from plantation	−0,46 *	−0,16
Basal area	0,49 *	0,48 *
Tree density / ha^{-1}	0,67 **	0,66 **
Soil nitrogen (N)	0,20	0,21
Soil phosphorus (P)	0,37	0,61
Soil potassium (K)	0,21	0,12
Plant cover before pine control	−0,006	0,11
Plant cover after pine control	−0,42	−0,23

As for the floristic composition, species richness and diversity before and after the control would not be very different, nor between the study conditions. However, there was an increase trend in the cover of shrub and herbaceous species in both conditions after the control, especially in plots farther away from the propagule source, where there was also less regeneration of *P. menziesii*. When looking at the ordination data within the native forest, before and after the control, the segregation found in the NMDS analysis may be associated with the increase in the cover of native species. This could indicate that by removing the *P. menziesii*, forest clearings are generated, which allow the regeneration of native species that were limited by the shade of these individuals (Frank and Finckh, 1997).

Acheritobehere and Orellana (2016) observed that the establishment of *P. menziesii* is strongly limited by the presence of other shrub and herbaceous species, which strongly compete for water and nutrients. In contrast, a higher density of *P. menziesii* would be more associated with woody species than with bare soil or herbaceous species. Burmeister (2017) also observed that in New Zealand, *P. menziesii* is established throughout the forest and not only under canopy openings. The aforementioned coincides with the high density of *P. menziesii* found in the native forest in our study, both before and after the control, as it was observed that in the open scrublands trees are older, but are found in smaller numbers, while in the native forest, younger individuals were found, but in greater density.

After the control, *P. menziesii* regeneration seem to be inhibited by competition with native species in the understory, and has been favored by the presence of trees. However, the study period only lasted one year, so it is necessary to continue monitoring over time to determine the success of the native vegetation establishment after the removal of *P. menziesii* (i.e., removal of seed-source trees that further disperse seeds at larger distances). In addition, other types of disturbances caused by silvicultural management of the plantation, such as timber extraction and grazing, must also be considered. As observed by Broncano et al. (2005), these disturbances generate forest clearings, reduce competition between species, and put seeds in contact with the soil that would otherwise be inhibited by vegetation cover. To strengthening the control of *P. menziesii,* it is also important to develop early detection and rapid response actions, especially within the native forest where the invasive conifer is able to establish and prosper. A rapid response capacity implies the availability of skilled personnel, contingency plans, updated technical guidelines, and within an unified framework (Brundu et al., 2020).

The presence of large herbivores, both domestic and wild, can increase the rate of successful introductions of propagules, since they act as transporters of seeds, as well as visitors, especially when they come from different localities, and they can act as vectors of intercontinental dispersal (Pauchard and Jiménez, 2010). However, in the case of grazing in protected areas, it is necessary to consider the role of livestock in the socioeconomic development of the communities involved and to develop strategies that may include zoning and agreements to control the movement of animals. As *P. menziesii* seedlings can eventually outgrow the *Nothofagus* forest canopy, a minimum control strategy could be to cut any visible *P. menziesii* above the canopy (Burmeister, 2017), thus preventing further seed propagation of this species.

According to Llanquilef (2017), and from a restoration perspective with further management, planting monospecific groups of *Nothofagus dombeyi* (coigüe) and/or bispecific groups of *N. dombeyi* and *Embothrium coccineun* (notro) is an innovative restoration technique that yields good results following a clearcut of *P. menziesii*. This, together with a periodic control of juvenile individuals (i.e., height greater than 50 cm), could increase the probability of restoration success after the invasion. Moreover, in order to minimize the propagation of this species through anemochory (seed dispersal through wind), some authors recommend considering the predominant wind directions when establishing plantations and using windbreaks with non-invasive species to prevent invasions (Pauchard et al., 2008; Acheritobehere and Orellana, 2016). However, good prevention is the least costly and most efficient action to prevent the establishment of invasive species, so a national strategy with regard to these species would make it possible to regulate the entry of new species and the spread of those already present in the territory that have a significant invasive potential (Pauchard and Jimenez, 2010). In addition, the plantation matrix should be reoriented and diversified in the country by incorporating native species (Brundu et al., 2020) in order to recover the forests and associated ecosystems that can provide multiple goods and services for the communities (Promis, 2020). It has been warned by experts that the problem of invasive conifers in South America is expected to increase substantially, as plantings have taken place very recently, and on a continental scale that is orders of magnitude larger than early introductions elsewhere (Richardson et al., 2008). This, however, could be tackled by applying approaches to the management of conifer invasions successfully developed in other countries, potentially saving considerable time and expense in finding local solutions to the problem.

5. Conclusions

Invasion of *P. menziesii* in native forest and in open scrubland areas can occur at least up to 100 m from the plantations, and that pattern of invasion decreases with distance from the original plantations. Once *P. menziesii* is removed, the necessary conditions for the native vegetation to be re-instated in both study conditions (native forest can and open scrublands) are provided. Even so, regeneration of pine after control is greater in the native forest than in the open scrubland, likely because there is less competition in the understory, and the light conditions necessary for *P. menziesii* to be established would be present. Furthermore, it was found that, initially, nutrients are more available in the native forest, so an evaluation after the control would be necessary to establish a possible relation with the regeneration of *P. menziesii*. However, according to the results, one year after the control of *P. menziesii*, it is the tree structure of the native forest that would be conditioning the regeneration of *P. menziesii* in our study site. However, the role of the species cover in the understory when determining the re-invasion density should be further evaluated.

In order to reduce the invasion of *P. menziesii* plantations into protected areas, it is recommended to maintain periodic control of the invasion in adjacent areas of at least 100 m. Efficient control methods in early invasion stages include manual and mechanical removal of individuals, especially those over 50 cm in height, so that the control is effective and does not require more effort than necessary. The greatest efforts should be focused on forest areas with high tree density and low understory cover. As the problem of invasive conifers in South America is expected to increase substantially, it is necessary to continue monitoring the response of the vegetation over time to determine the success of the control of *P. menziesii*. Lessons learned from other countries with similar problems could save considerable time and expense in finding local solutions.

CRediT authorship contribution statement

Andrés Fuentes-Ramirez: Conceptualization, Supervision. **Rodrigo Vargas-Gaete:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Octavio Toy-Opazo:** Writing – review & editing, Visualization, Validation, Data curation. **Nayadeth Muñoz-Gómez:** Writing – original draft, Visualization, Formal analysis, Data curation. **Christian Salas-Eljatib:** Writing – review & editing, Methodology. **Aníbal Pauchard:** 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.

Data availability

Data will be made available on request.

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