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ORIGINAL PAPER

Pinus contorta invasion in the Chilean Patagonia: local patterns in a global context

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Abstract Alien conifer invasions are affecting ecosystems across the globe, but until recently, reports of such invasions in South America were scarce. *Pinus contorta* was first established in Chilean Patagonia for erosion control caused by historical fires and cattle farming. Recently, the species has been planted over large areas for commercial purposes. It is well adapted to local conditions and is now spreading into natural areas. This study analyzes natural regeneration of *Pinus contorta* around Coyhaique city, Chile, to determine the spatial patterns of invasion. Five study sites were selected, four with grasslands dominated by exotic species and one site in the steppe. In each site, the plantation (seed source) was characterized using morphological attributes and density. Regeneration, density, height and age at different distances from the seed source were recorded, and ground cover was measured as an environmental factor influencing the invasion process. A comparative analysis was also conducted between the situation in Chile and other countries affected by *P. contorta* invasion. In Chile, *P. contorta* regeneration is significantly influenced by distance from the seed source. Higher densities are found close to the parent stand (up to 13,222 trees ha^{-1}), decreasing as distance from the seed source increases. Age and height structure indicate that the invasion process is at an early stage, and this offers a unique opportunity to study the process of invasion and to monitor it over time. In order to preserve the distinctiveness of Patagonian ecosystem, decisive action is required to control invasive conifers, with *P. contorta* as the number one priority. Relative to control, there is much that can be learnt from the experiences of other countries, such as New Zealand.

Keywords Biological invasions · *Pinus contorta* · Pine invasion · Patagonia · Chile

Introduction

The impacts of pine invasions have been widely recognized. According to Richardson and Higgins (1998), the increase in the abundance of trees in habitats where they were previously absent is causing a wide range of changes to various features of the

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invaded ecosystems in many parts of the Southern Hemisphere. This causes the suppression of native plants or the creation of habitats for new species. Other impacts related to pine invasions are the reduction of structural diversity, the increase in biomass, the disruption of prevailing vegetation dynamics, and changes in the nutrient cycling (Mack et al. 2000; Peterken 2001; Richardson 2001). Although alien conifer invasions in South America have not been as widespread as in some other parts of the Southern Hemisphere, their extent is increasing rapidly due to the intensification of commercial forestry and increase in human disturbances (Richardson et al. 2008). There is greatest concern in areas where commercial afforestation with alien conifers occurred only in the last few decades—such as the Chilean and Argentinean Patagonia. However, little is known about the mechanisms and impacts of pine invasion in the region (Simberloff et al. 2010).

Pines show similar invasion processes all over the world involving two main stages: (a) immigration and establishment, and (b) population growth/expansion (Richardson et al. 1994). Immigration and establishment are widely variable among sites and species. However, initial population growth is usually characterized by a dispersal kernel, where dense regeneration is located next to the seed source (short distance dispersal), while medium and long distance dispersal generates scattered outlier trees (Higgins and Richardson 1999; Richardson 2001; Ledgard 2003) (Fig. 1a). In this first stage, intra-specific competition is low and therefore wildings can establish at any distance from the seed source within the first "wave". After some of the trees reach maturity, propagules originate both from the original source, the invasion front and the outlier trees (Fig. 1b). Once the second wave of invasion has started the opportunities for successful control are greatly reduced, increasing the overall impacts of the invasion in the landscape.

Pinus contorta is one of the most invasive plantation trees (Benecke 1967; Ledgard 1988; 2001; Richardson and Bond 1991; Higgins and Richardson 1998; Despain 2001; Richardson and Rejmánek 2004). Its invasiveness is due to its early seed production, small size of seeds (enabling ready dispersal by wind), short time between big seed crops (compared to other pine species), (Rejmánek and Richardson 1996) and the fast growth of seedlings (Grotkopp et al. 2002). Outside South America, *P. contorta* has been classified as a naturalized species in Great Britain, Ireland and Russia, and as invasive species in Australia, New Zealand and Sweden (Richardson and Higgins 1998; Haysom and Murphy 2003; Ledgard 2001; Despain 2001; Richardson 2006; Richardson and Rejmánek 2004) (Fig. 2). In South America, *P. contorta* has been recorded as invasive in Argentina and Chile (Richardson et al. 1994; Peña and Pauchard 2001; Peña et al. 2008).

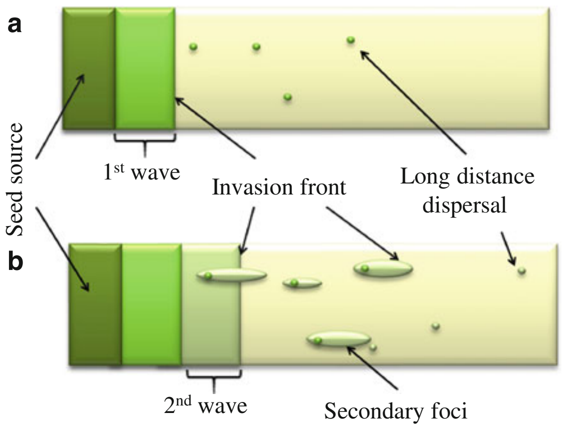


Fig. 1 Diagram of conifer invasion spread in **a** an early stage of invasion where seeds come from a main foci (*above*) and **b** in a secondary phase where seeds come from both the main foci as well as from satellite foci (*below*). Diagram based on Richardson and Higgins (1998), Richardson (2001), and Ledgard (2003)

Invasion success, however, does not only depend on the species attributes, it also depends on site susceptibility to invasion. According to Richardson et al. (1994) ground cover, disturbance and resident biota are the main factors influencing site susceptibility to pine invasions. Richardson and Bond (1991) established that conifer seedling success is determined by how well they compete with resident competing vegetation. For example, the establishment and success of *P. contorta* decreases with an increasing ground cover, and therefore, recruitment is higher where mineral soil is exposed (Ledgard 2001; Engelmark et al. 2001).

The history of *P. contorta* invasion has been well studied in some countries. In New Zealand, for example, *P. contorta* was introduced around 1,880 and by 1960 there were 10,000 ha of pure or mixed stands. From the late 1940's on, there appeared to be an increase in the affected area, so that by 2001, there were 150,000 ha that had a density of at least one

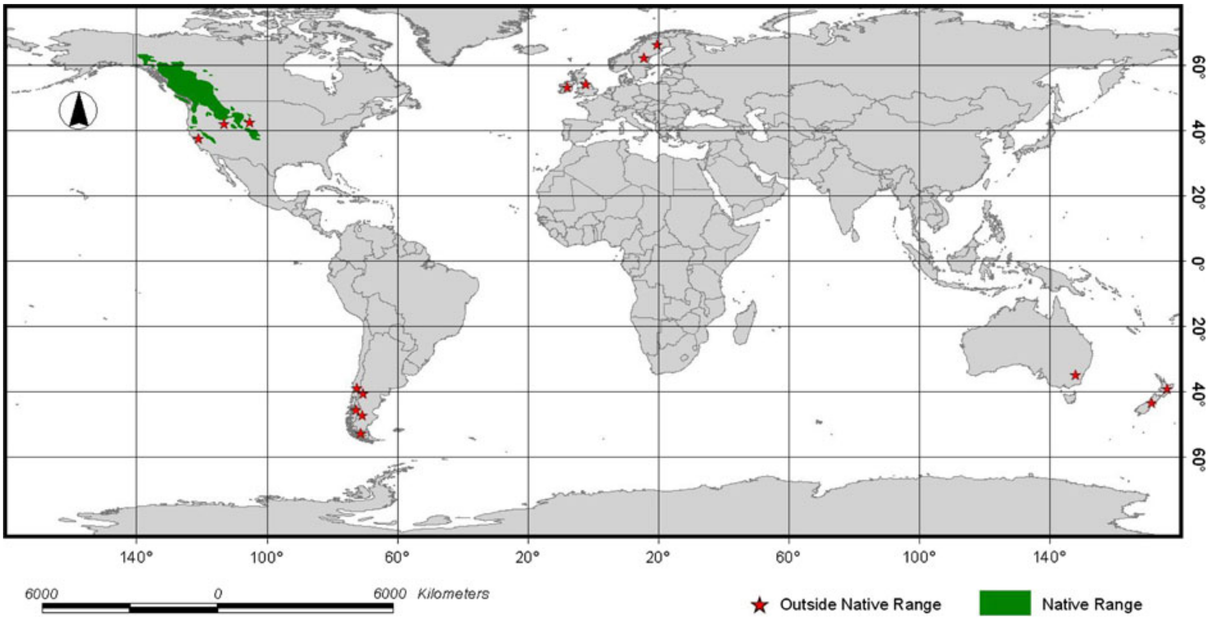


Fig. 2 Global distribution of *Pinus contorta* in and outside its native range. Its habitat is concentrated between 40 and 60 degrees latitude. Information compiled from Richardson and Higgins (1998), Haysom and Murphy (2003), Ledgard (2001), Despain (2001), Richardson (2006), Richardson et al. (1994), Peña and Pauchard (2001), Peña et al. (2008)

wilding per hectare (Ledgard 2001, 2004). The spread has occurred in a step-wise pattern, similar to that recorded for other pines (Richardson et al. 1994; Richardson and Higgins 1998; Richardson 2006). In Sweden, *P. contorta* was introduced in the 1920's on an experimental scale, but from the 1970's on it has been planted for commercial purposes. In the year 2001, 565,000 ha were covered with the species, and environmental effects of the species introduction have not been assessed adequately (Engelmark et al. 2001).

In South America, *P. contorta* has been planted in both Chile and Argentina, especially in harsher and colder environments. In Argentina, *P. contorta* is invading the steppe with natural regeneration first occurring at an age of 12 years (Sarasola et al. 2006). In Chile, the invasive status of *P. contorta* was studied in the Malalcahuello National Reserve by Peña et al. (2008), where the invasion covers 78 ha, with one individual found 1,200 m away from the seed source. Further south around Coyhaique city, Langdon et al. (unpublished) determined that *P. contorta* regeneration has reached densities as high as 16,650 individuals ha^{-1} in less than 30 years, with the most distant seedling found 3 km away from the seed source.

Conifer invasions in the Chilean Patagonia could become a major threat to native ecosystems. In the Aysén Region of Chilean Patagonia, large areas were cleared by fires during the second half of the 20th century), the objective being to create a suitable environment for livestock farming and agriculture. As a consequence of those fires, soil erosion is now a common problem and grasslands dominated by European-herbs have replaced native forests. In the 1970s, the Chilean government started reforestation programs to control erosion in the worst affected areas. The "Corporación Nacional Forestal" (CONAF), established large trial plots in many National Reserves in order to determine suitable species for controlling erosion (Löewe and Murillo 2001). One of them was the Coyhaique National Reserve, where the oldest plantations are located. Lately, conifers have also been planted for commercial purposes. According to CONAF (1999), 180,000 hectares are available for forestry in the Aysén Region, and according to the Forestry Institute (INFOR 2007) only 43,137 ha have been planted (55% corresponds to *Pinus ponderosa* Doug. ex Laws., 15% to *P. contorta*, and 0.1% to *Pseudotsuga menziesii* (Mirb.) Franco).

Based on the relatively short time period (ca. 40 years) since the first introduction of *P. contorta* into the Chilean Patagonia, we hypothesize that its invasion is at an early stage, where plantations are the primary seed source, with plant density numbers decreasing with distance from the plantation edge. Regeneration structure (based on age and height) should therefore not be related to distance from the seed source, because no intra-specific competition has yet occurred, and therefore recruitment should occur close to the seed source but also at longer distances. This situation differs from current reports of massive *P. contorta* invasions in New Zealand and other countries with a much longer history of introductions. Therefore, this study aims to determine the stage of the *P. contorta* invasion process in the Coyhaique Province and by using a comparative analysis shed light onto what we can expect of *P. contorta* invasions in the Chilean Patagonia.

Methods

The species

Pinus contorta is known for its wide ecological amplitude (Lotan and Critchfield 1990; Ledgard 2001). It is naturally distributed in United States and Canada, under a wide variety of climatic conditions. Four varieties can be distinguished based on their geographical range: *P contorta* var. *contorta* (costal form), *P. contorta* var. *bolanderi* (Parl) (California form), *P. contorta* var. *murrayana* (Balf.) (Sierra Nevada form), and *P. contorta* var. *latifolia* (Engelm.) Critchf. (inland form). The natural range, environment and ecology of all four varieties of *P. contorta* are well described by Lotan and Critchfield (1990). Considering the four varieties and their large geographical distribution, minimum temperatures range between −57 and 7°C, and maximum temperatures between 27 and 38°C. Annual precipitation varies between 250 and 500 mm. The seasonal distribution of precipitation is significant, because snowfall supplies most of the soil water used for rapid growth in early summer. The more serotinous variety *latifolia* is the most widely planted in the Chilean Patagonia. Variety *murrayana* was only planted in trial plots, and never for commercial or soil protection purposes.

In its natural range *P. contorta* produces viable seeds at an early age, between 5 to 10 years. Cones withstand temperatures below freezing and are not commonly affected by cone or seed-feeding insects. Cone productions of dominant and codominant trees can vary from a few hundred to a few thousand per tree, accumulating there for decades. Annual crops can vary from 173,000 to 790,000 seed per hectare with half or a third of them available for seedfall. These values are considered typical for those places where some portion of the trees is of the serotinous type. Seed size is relatively small compared to other *Pinus* species. Weight varies from 2.3 to 11.4 mg in different locations of its distributional range (Lotan and Critchfield 1990).

Germination and establishment are enhanced at full sunlight and mineral soil. Favorable temperatures are between 8 and 26°C and adequate soil moisture is required during the critical few weeks after germination. For that reason, germination occurs soon after snow melts (Despain 2001). Seedlings are resistant to freeze damage. *Pinus contorta* is intolerant to shade and grows better under direct sun light (Lotan and Critchfield 1990).

Study area

The study was conducted in southern Chile, in the Coyhaique Province (S 45° 33′ and W72° 04′), in the Aysén Region (Fig. 3). The area encompasses three geomorphological zones: the Andes Mountains (characterized by rugged topography), the oriental subandean range (characterized by open valleys), and the oriental plain-form reliefs (characterized by depositional plains). The first two zones show a continental trans-andean climate characterized, in Coyhaique, by a mean annual precipitation of 1,200 mm, with 50% of the precipitation falling between May and August. Due to low temperatures, a mean of 9°C, precipitations are mainly as snow (DGAC 2009). The main vegetational formation corresponds to the Andean-Patagonian forests, dominated by *Nothofagus pumilio* (Poep. Et Endl Krasser. The vegetation has been severely altered by human-induced fires replacing *N. pumilio* forests with anthropogenic grasslands dominated by exotic European species. The third zone corresponds to the steppe (Gobierno Regional de Aysén 2005) with a cold dry climate characterized by many months with less than 40 mm precipitation. From 55 to 62% of the total annual precipitation falls between May and August. Annual mean temperature ranges from 6 to 9°C (DGAC 2009). The vegetation

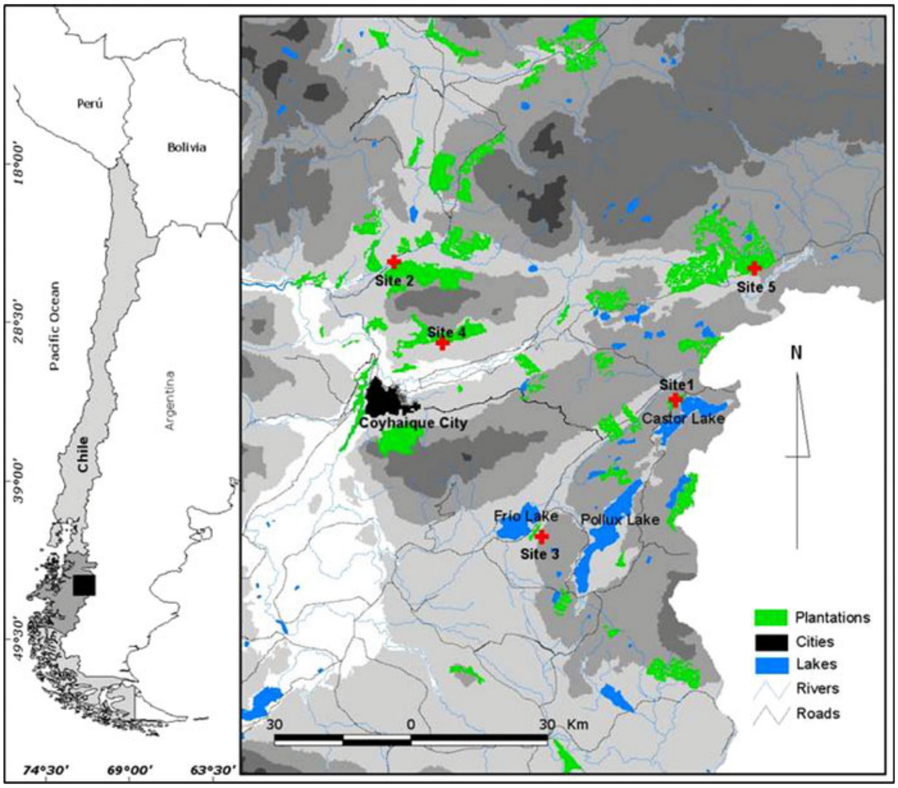


Fig. 3 Study area, study sites and pine plantations within the Coyhaique Province in the Aysén Region, Chilean Patagonia. Sites 1 to 4 are in grasslands and site 5 is in the steppe

is dominated by scarce low stature native species, mainly *Festuca sp.* and cushion plants such as *Baccharis sp.*, *Mullinum sp.*, and *Acaena sp.* (Gobierno regional de Aysén 2005). Browsing and grazing by sheep, rabbits and hares are common disturbances at all sites.

Sampling

We sampled invasion fronts in *P. contorta* plantations in anthropogenic grasslands and the steppe. We selected four replicates in grasslands (Site 1 (S45°35′9.79″; W71°47′17.63″), Site 2 (S45°29′10.75″; W72°2′32.98″), Site 3 (S45°39′53.53″; W71°55′7.63″), and Site 4 (S45°32′23.39″; W71°59′36.38″))), and only one in the steppe ((Site 5—S45°30′2.13″; W71°42′15.07″)), because of the lack of mature plantations in this ecosystem.

We characterized the selected parent stands (seed source) and the regeneration established near them, by recording the number of trees, diameter at breast height (DBH—1.3 m) and total height of a subsample of trees. Where no record of age existed, we extracted increment cores and counted growth rings. In order to characterize the invasion pattern, we established three transects from the edge of *P. contorta* plantations at 50 m intervals. Transects were perpendicular to the edge, 3 m wide and 150 m long, and divided into 15 subtransects of 10 m length each. In each subtransect, we recorded the number of individuals of *P. contorta*, seedling heights (in six categories <0.4, 0.5–0.9, 1–1.4, 1.5–2.9, 3–4.9, and >5 m), and the most distant tree (GPS position using a search distant of 50 m until no individuals were found). We determined cone presence/absence for every tree and aged the highest tree in each subtransect by counting stem tree-rings. We also recorded ground cover in categories 1–24, 25–49, 50–74 and 75–100%. In each site we recorded topography, and predominant wind direction.

Data analysis

We categorized data into grasslands and steppe. Using SAS (Version 9.0), we adjusted a General Linear Model for each ecosystem, considering regeneration density as a function of distance from the seed source and the ground cover variables. We fitted linear regression models for all variables plus distance from the seed source. We reduced height data into only two categories, trees smaller than 1 m and those higher than 1 m. We adjusted an age-height Weibull model using data from the highest tree in each subtransect. Using the model, we estimated mean age for each height class (<0.5, 0.5–1.4 and >1.5 m).

Comparative analysis

We compare our results for the Chilean Patagonia with *P. contorta* invasion in New Zealand, Sweden and Argentina. For each region we used published literature and international sources to compare: mean daily maximum temperature for the warmest month, mean daily minimum temperature for the coldest month, annual precipitation (of invaded areas), total plantation area, year of introduction, purpose of planting, and invaded area.

Results

Parental pine stands

Although all plantations in the five study sites had similar ages (21–22), with the exception of Site 1 (30), there was considerable variation in density, DBH and height (Table 1). DBH and height differences are could be associated with planting density or site conditions.

Spatial patterns

Table 2 GLM results for *Pinus contorta* regeneration density in relation to distance from the parental plantation edge and micro-site vegetation ground cover in grasslands

Source	DF	*F*-Value	Pr > *F*
Site	3	2.55	0.0577
Transect	2	1.79	0.17
Distance	14	5.37	<0.0001
Ground Cover	3	2.21	0.0887

In the steppe, regeneration density showed no significant relationship with any of the tested variables

Distance from the seed source was a significant variable relative to density of regenerated seedlings only for grasslands ($P < 0.0001$ GLM, Table 2). Probably because of insufficient data, the relationship at the steppe is not significant. However, regressions showed a significant relationship between regeneration density and distance from the seed source for both ecosystems (Fig. 4a). Maximum mean density was 5,319 trees ha^{-1} in grasslands and 13,222 trees ha^{-1} for the steppe. In both ecosystems there was regeneration at 150 m from the seed source, with densities of 194 trees ha^{-1} in Grasslands and 1,111 trees ha^{-1} in the steppe. The most distant seedlings were found at a maximum distance from the seed source of 310 m in grasslands and 368 m in the steppe (Table 1). We did not search further afield, because distance between neighbor seedlings was higher than 50 m.

Ground vegetation cover shows no significant relationship with regeneration density ($P = 0.088$ for grasslands and $P = 0.077$ for the steppe).

Regeneration structure

The number of trees in each height category varied considerably within and between ecosystems (Fig. 4b). A linear fit analysis showed no significant relationship between proportions and distance from the seed source ($P > 0.05$ for every height category

Table 1 Age and morphological characteristics of parental stands and maximum distance of continuous regeneration of *Pinus contorta* at each study site

Site	Age (years)	Density (trees/ha)	DBH (cm)	Height (m)	Max. distance (m)
1	30	844	21.47	7.8	199
2	22	1,289	20.46	12.4	223
3	22	889	15.84	6.1	310
4	21	400	22.79	10.7	183
5	22	667	17.3	6.9	368

Sites 1 to 4 are grasslands and site 5 is steppe in all sites). Small trees (<0.5 m) were the most frequent at almost every distance from the seed source. The Weibull model adjusted between height and age was significant for all study sites ($P < 0.0001$). Estimated age categories were: trees less than 3.6 years, between 3.6 and 5.3 years and older than 5.3 years, corresponding to height categories <0.5, 0.5–1.5 and >1.5 m. For tree age, we found no significant relationship with the distance from the seed source. In both grasslands and steppe, younger trees represented the highest proportions (Fig. 4c). Cone presence was low in both ecosystems (Fig. 4d). As occurred with height and age, cone presence did not present a significant relationship with distance from the seed source. The highest cone presence (17%) was found in grasslands.

Comparative analysis

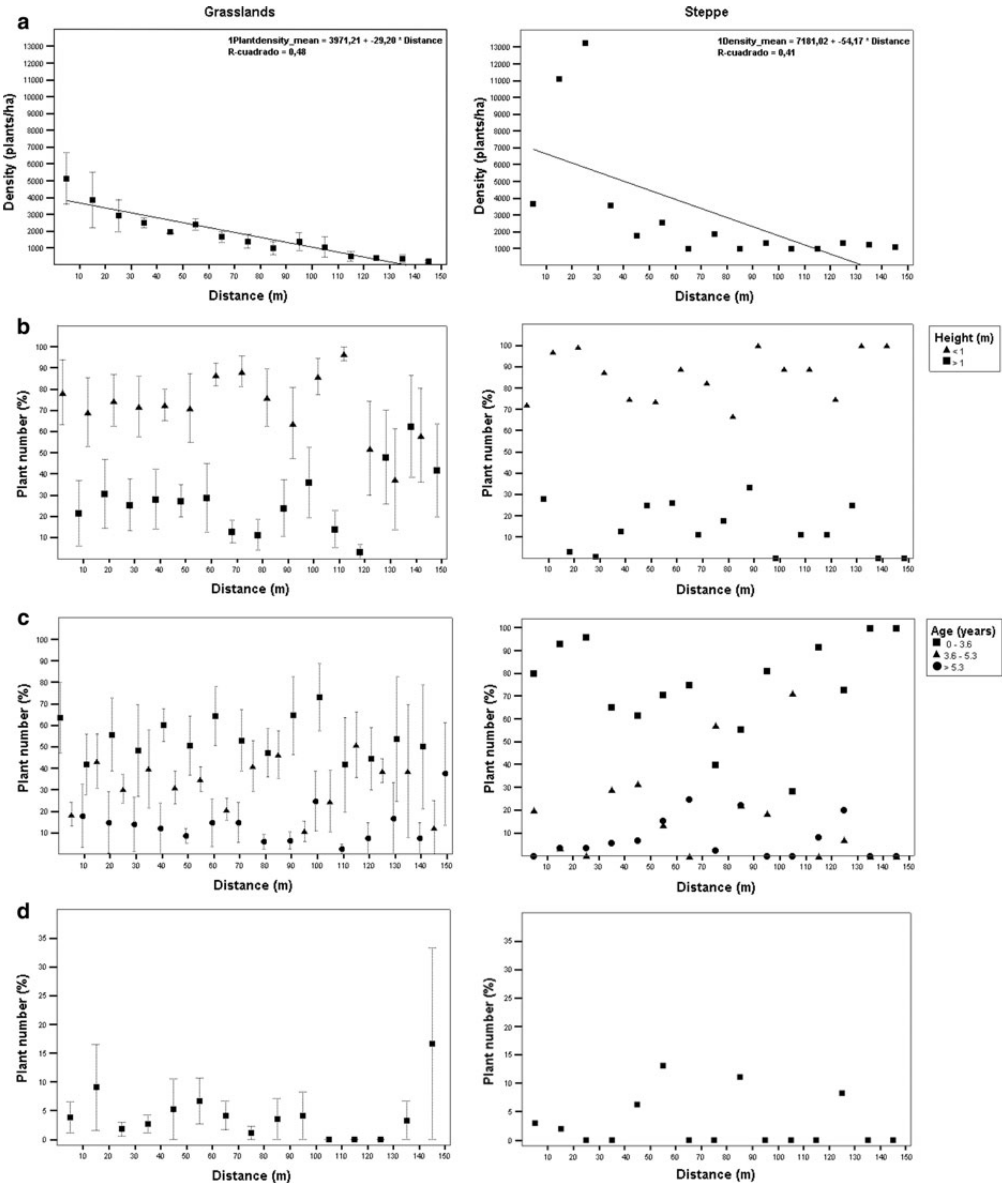
Pinus contorta invasions show historic differences between South America and both Sweden and New Zealand (Table 3), especially in terms of residence time and total area planted. First introductions to New Zealand were made almost 100 years before it was planted in Chile or Argentina. In Sweden, it was planted only 40 years before Chile and Argentina, but the plantation area is significantly larger. The species was introduced for commercial purposes in Sweden and Argentina and for both commercial and erosion control purposes in New Zealand and Chile. Argentina and Chile share similarities in terms of time of residence, but plantation areas are considerably larger in Argentina. Management and control are now fundamental actions to prevent unwanted spread in New Zealand, where natural spread affects at least 300,000 ha (mainly grasslands) (Ledgard 2001). In Sweden, *P. contorta* management is for forest products (pulpwood and saw-timber production) and its regeneration is managed for wood products in the same manner as the native species *Pinus sylvestris* L. (Elfving et al. 2001). No information was found on its the effects on native Swedish ecosystems.

Discussion

For the establishment of a species in a new environment and its spread, several conditions must coexist. The conditions around Coyhaique appear to be adequate for *P. contorta*, allowing for spread and establishment. Although plantations remain the main source of seed, populations have started to expand, and as individuals in the invasive front become reproductive, increasing areas will become affected.

Conifer invasions usually require both short and long distance dispersal events. In the Coyhaique most of the spread occurs over short distances (fringe spread—Ledgard 2001), showed by high regeneration densities within the first 60 m. However, proportions of young, small trees are maintained across all distances from the seed source. The same situation has been reported in several other regions before the site is occupied completely by the species (Ledgard 2001; Despain 2001; Engelmark et al. 2001). The short distance dispersion in Coyhaique is a reflection of an early stage in the growth of the invasive population (sensu Pauchard and Shea 2006). Long distance dispersal events, aided by the strong winds of the steppe, are occurring, but at a much lower rate. According to Ledgard (1988) seeds of *P. contorta* can be transported by wind up to 30 km (Ledgard 2010 personal communication). Langdon et al. (unpublished) found *P. contorta* seedlings 3 km away from the seed source in the steppe of the Aysén Region. Hence, the indications are that new recruitment can occur at any distance from the seed source, meaning that maximum invasion density has not been reached yet—in spite of the fact that regeneration density is now larger than those of the parent stands or any commercial plantation.

Reproductive maturity of the invasion front is a crucial element that determines the second wave of invasions. In North America, the natural range of *P. contorta*, cone production starts as early as 5 to 10 years (Lotan and Critchfield 1990; Engelmark et al. 2001; Ledgard 2001). In New Zealand cones have been reported present at age 3, but with viable seed from age 5 (Weston 1957 and Wardrop 1964 in Ledgard 2001). These findings are similar to what we observed in Coyhaique. At 4 to 5 years old, some seedlings already bear cones, although the viability of the seeds has not been assessed. Periodicity in seed production can also influence the speed of spread. However, *P. contorta* does not have continuous seed production in its home range, where large seed crops occur once every 1 to 3 years (Lotan and Critchfield 1990). In our study, we found wildings of all age categories (between weeks and almost 8 years),



indicating a continuous seed production. In addition, there are a range of cone and seed predators which are not present in S. America. Therefore, as in New Zealand, future seed production will probably be higher than in the species homeland. Probably, half of the trees will be reproductive by the time they are 15 years old. Individuals establishing both close to, and far from, the original seed source will become new dispersers of seed, originating new invasion fronts. Then, the second invasion "wave" will start

◀ **Fig. 4** Mean *Pinus contorta* variables (±SE) in relation to distance from the main seed foci (plantation) in grasslands ($n = 4$) and Patagonian steppe ($n = 1$). Each site value was calculated as the average of three transects. **a** *Pinus contorta* regeneration density. Linear regressions were significant in both cases (Grassland $P < 0.001$, Patagonian steppe P-value = 0.011). **b** *Pinus contorta* plants (±SE) by height class (<1 or >1 m) Linear regressions were not significant in both cases (Grassland $P = 0.166$, Patagonian steppe P-value = 0.401). **c** *Pinus contorta* plants by age class (0–3.6, 3.6–5.3, >5.3). Age classes were estimated using tree height and a Weibull function. Linear regressions were not significant for either ecosystem type or age class ($P > 0.05$). **d** *Pinus contorta* plants with cones. Linear regressions were not significant for either ecosystem type ($P > 0.5$)

and the invasion process will be more difficult to manage.

The two main factors differentiating the *P. contorta* invasion process in Chile and Argentina with that in New Zealand and Sweden are the residence time and the propagule pressure in terms of planted and invaded areas (Table 3). These two aspects could compensate each other: a short residence time with large areas planted could result in the same situation that a long residence time with a smaller planted area. In Chile, the species is still being planted, increasing the propagule pressure and the probability of new invasion fronts.

Within the Chilean Patagonia, susceptibility to pine invasion varies among ecosystems. The steppe (367,322 ha in the Aysén Region) seems to be a more susceptible environment to invasion, mainly because of low competition of resident biota and strong wind, but drought and frosts are potential causes for seedling establishment failure. Grasslands (144, 699 ha in the Aysén Region) may have less stress factors, but competition levels are probably higher. Native forests, on the other side, represent unsuitable ecosystems for pine invasion because of the closed canopy and low levels of light on the forest floor (Lotan and Critchfield 1990). However, gaps, roads and disturbances within forests are more suitable areas for pine regeneration.

The steppe and grasslands are being threatened by *P. contorta* invasion. The ultimate result will be an increased abundance of trees where they were previously absent or less common, and a loss of native vegetation as it is outcompeted (Richardson and Higgins 1998). Another potential effect of *P. contorta* invasion would be an increase in fire intensity. Although there is no current management being conducted on the unintentional spread of pines in the Chilean Patagonia, this situation is likely to change as forest certification requires explicit control of natural regeneration outside the boundaries of the plantation.

The distinctiveness of Patagonian ecosystems both in terms of their biogeography and conservation value requires decisive action relative to the control of invasive conifers, with *P. contorta* as the number one

Table 3 Comparative analysis of the *Pinus contorta* invasion in Chile, Argentina, New Zealand and Sweden

Country	New Zealand	Sweden	Argentina	Chile
Temperatures (°C)				
*Maximum	23	19.6	21.7	18.4
*Minimum	3.8	−9.1	−2.2	−1.6
Annual precipiltation (mm)	875.9	569.1	596.5	908.75
Year of introduction	1880s	1920s	1960s	1970s
Plantation surface (ha)	NA	565,000	49,200	6,546
Purpose of planting	Commercial/erosion control	Commercial	Commercial	Erosion control/commercial
Distance from seed source (km)	8	NA	3	3
Invaded area (ha)	300,000	NA	NA	78
Management and control	Yes	Yes	No	No

*Maximum temperature represents mean daily temperature for the warmest month and minimum temperature represents mean daily minimum temperature for the coldest month of invaded areas in the corresponding countries NA = No available information

Sources: New Zealand: World Weather Information Service, Ledgard 2001; Raal 2009 (pers.com.); Sweden: World Weather Information Service, Engelmark et al. 2001, Elfving et al. 2001; Chile: Departamento de Geofísica de la Facultad de Ciencias Físicas y Matemáticas de la Universidad de Chile Peña et al. 2008, Langdon et al. (not published); Argentina: Sarasola et al. 2006, Servicio Meteorológico Nacional priority. Relative to control, there is much that can be learnt from the experiences of other countries. In addition, as we have shown in this paper, the early invasion stage offers a unique opportunity to study the process of invasion in natural experiments and to monitor it over time.

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