

Fire as a driver of pine invasions in the Southern Hemisphere: a review

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Abstract Contrasting evidence in the degree of post-fire conifer invasion reported for different regions of the Southern Hemisphere (SH) raises questions about the role of fire as a presumed driver of invasion. We studied the influence of fire on invasion responses (assessing ‘serotiny’ and ‘time’ as key factors to determine invasion) based on a review of case studies performed in natural habitats of the SH. Our work showed that burned environments have no lag time with respect to invasion and are more susceptible to serotinous pine invasion than are unburned environments. Also, serotinous pines reached extremely high densities in burned habitats, exceeding records for the same species in unburned habitats, as well as for non-serotinous pines in any habitat condition. Therefore, burned environments are impacted by conifer invasion earlier and more intensively than unburned ones. Overall, our work indicates that fire is a leading driver of invasion, but only for serotinous pines. This highlights the importance of considering life history traits of introduced species to determine the

probability and extent of invasion in relation to disturbance. We discuss the implications of introducing serotinous species in regions of the SH where serotiny is absent from native flora. Lastly, we provide suggestions for prioritizing management and further study.

Keywords Disturbance · *Pinus* spp. · *Pseudotsuga menziesii* · Time lag · Tree invasion · Serotiny

Introduction

Land-use change poses an important threat to biodiversity (Sala et al. 2000), mostly due to its contribution in the introduction and spread of non-native invasive species (Moore 2005). In this regard, the worldwide area dedicated to tree plantations (currently 264 million ha) is estimated to grow at a rate of 5 million ha yr⁻¹ (Food and Agriculture Organization 2010). At present, one-quarter of all tree plantations are composed of introduced species, but this proportion increases noticeably when considering regions of the Southern Hemisphere (hereafter SH; 39% for Africa, 77% for Oceania, and 97% for South America; Food and Agriculture Organization 2010). In this hemisphere, the development of extensive exotic tree plantations has seriously impacted diverse components and ecological processes of native ecosystems (Richardson 1998). In many cases, these effects have

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not been limited to tree cultivation areas, but also to the natural habitat surrounding them (Armstrong and van Hensbergen 1996; Raffaele and Schlichter 2000; Paritsis and Aizen 2008; Lantschner et al. 2013). Several pines species (*Pinus* spp., Pinaceae) introduced as forestry species primary (Richardson et al. 1994; Richardson and Higgins 1998), have deeply affected the matrices of native vegetation because of severe invasions generated by propagules dispersed hundreds of meters from plantations (Richardson et al. 1994; Richardson 1998; Williams and Wardle 2005).

Early research on pine invasion drivers in the SH recognized fire as the greatest contributor to the invasion process (Richardson and Bond 1991). However, the evidence for many regions was scarce and represented by a small number of studies and/or anecdotal accounts (Richardson and Bond 1991; Richardson et al. 1994; Richardson and Higgins 1998). A survey that includes more recent case studies from different regions of the SH (Appendix 1 in ESM), reveals a great variation in the degree of post-fire invasion for the same or different species, questioning therefore the role of fire on pine invasion (Raffaele et al. 2016). Considering this scenario, a synthesis of information comparing quantitative data on the invasion between burned and unburned habitats, could explain the relative influence of fire and its interaction with intrinsic and extrinsic factors.

Similar to other non-native plant species (Lockwood et al. 2007), variation in pine invasiveness is determined by intrinsic and extrinsic factors and their interactions (Richardson and Higgins 1998; Procheş et al. 2012). Among the intrinsic factors, the presence of specific adaptations to fire can play an important role in determining the level of post-fire recruitment. In particular, serotiny (the prolonged storage of seeds in the canopy) is a trait closely related to demographic responses of many woody taxa in ecosystems with recurrent fires (Lamont et al. 1991; Keeley et al. 2012). Fire can promote the increase in population size of serotinous species by stimulating a massive release of seeds (Lamont et al. 1991; Lamont and Enright 2000), which maximize their availability when the conditions are most favorable for their establishment (Lamont and Enright 2000). Therefore, unlike other adaptations that allow fire survival (e.g. thick bark, self-pruning), serotiny can promote invasion through a substantial population increase after fire (Richardson and Bond 1991; Higgins and Richardson 1998). On the other

hand, time is an extrinsic key factor in determining the success of plant invasion, but the way it influences invasion can be difficult to determine (Richardson et al. 1994; Lockwood et al. 2007; Procheş et al. 2012). As a generalization, ‘more time since introduction’ means a greater chance or extent of invasion (Richardson et al. 1994; Kowarik 1995) with the minimal lag phase defined by the time needed to produce the first propagules (Richardson et al. 1994; Kowarik 1995). However, for some pine species the occurrence of fire can be sufficient to initiate a rapid invasion (Richardson et al. 1994). The estimation of time lags for woody plants can be useful not only for understanding the dynamics of population growth within a changing environment (e.g. Lediuk et al. 2016), but also as an indicator of a potential starting point for a successful invasion (Kowarik 1995). Therefore, time lag estimation could allow us to anticipate actions to avoid detrimental invasion impacts on natural communities (Larkin 2012).

Despite the existence of some well documented case studies of pine post-fire invasion in their introduced area, there is no data compilation on the relative effects of fire neither on invasion responses nor on the importance of serotiny in shaping these responses. We reviewed the influence of fire on pine invasion by taking advantage of a valuable natural experiment based on pine plantations and pine spreading in the SH (Richardson et al. 1994, 2004; Richardson and Higgins 1998). In addition, we conducted tests to verify if serotinous pines are key drivers of invasion. The focus was particularly on analyzing how invasion degree or probability was affected by fire occurrence, and by time since the last fire and from plantation introduction in unburned habitats. Using these data, we assessed the existence of a threshold response in pine abundance in burned and unburned scenarios to identify lag times associated with invasion.

Methods

To carry out the review, we compiled a set of data from scientific literature that reported density of pines regenerated naturally in burned and unburned natural habitats of the SH. A search of literature was conducted on Google Scholar and Web of Science using a combination of relevant terms such as: pine (*Pinus*), invas*(introduced, alien, exotic or non-

native), fire, lag time (delay time or lag phase), serotin*, and conifer. The reference list from the retrieved articles was reviewed to find other relevant publications not found in the initial searches. Pine density outside plantation boundaries was used as a measure of invasion degree. Most of the density records (78%) came from articles with a similar experimental design, which consisted in transects (or plots) placed perpendicular to the original plantation, from the plantation edge to the natural surrounding habitat. We estimated mean pine density by averaging the number of pines per transect, and when a study reported data for more than one transect per plantation, we averaged density values among transects. In numerous cases, we obtained more than one density datum from a single study (e.g. a study that reported invasion density for different species). When density data from the articles were reported in figures, we extracted them with a graph digitizer software (Digitize It v. 2.1, © 2001–2015 Ingo Bormann). We also recorded pine species, country of introduction, habitat type, habitat condition (burned or unburned), and time since the last fire and plantation introduction (in

unburned habitats). ‘Time lag’ was determined by adding both, the time from first cone production in the introduced area, and the period where the first spontaneous spread was documented. Each pine species was classified as serotinous or non-serotinous based on published literature (see Table 1). We included the records for *Pseudotsuga menziesii* (Pinaceae) in the database, which were not included in all analyses (see “Data analysis”). This species has also been widely used for forestry purposes in many regions of the SH thus becoming an invasive species of natural areas (Richardson and Higgins 1998; Ledgard 2002; Richardson and Rejmánek 2004; Sarasola et al. 2006; Pauchard et al. 2008; Orellana and Raffaele 2010; Simberloff et al. 2010).

Data analysis

We calculated the ‘effect size’ using the log-response ratio (Hedges et al. 1999) to determine the relative importance of invasion for serotinous and non-serotinous pines in burned and unburned habitats. In this study, the response ratio was calculated as $\ln(X_B/X_U)$,

Table 1 List of the conifer species compiled from the literature review (see “Methods”) Source: ^{A1} Richardson et al. (1990), ^{A2} Pausas (2012), ^{A3} USDA Forest Service (2017), ^{Ba} Langdon et al. (2010), ^{Bb} Ledgard (2001), ^{Bc} Peña et al. (2008), ^{Bd} Hunter and Douglas (1984), ^{Be} Sarasola et al. (2006), ^{Bf} Dezzotti et al. (2009), ^{Bg} Richardson et al. (1990), ^{Bh} Zalba et al. (2008), ^{Bi} Richardson and Cowling (1994), ^{Bj} Richardson and Brown (1986), ^{Bk} Catling and Carbyn (2005); ^{B1} Orellana and Raffaele (2010), ^{Bm} Ledgard (2002), ^{Bn} Richardson (1988), ^{Bñ} Gómez et al. (2011), ^{Bo} Dvorak (2002)

Species	Fire trait ^A	Age of first coning (years) ^B
<i>Pinus contorta</i>	Serotinous ¹	4 ^a , 5 ^b , 5 ^c , 5 ^d , 8 ^e , 14 ^f (6.8)
<i>Pinus elliotii</i>	Non-serotinous ¹	8 ⁱ
<i>Pinus glabra</i>	Non-serotinous ¹	10 ^g
<i>Pinus halepensis</i>	Serotinous ¹	5 ^h , 12 ⁱ , <14 ⁿ (10.3)
<i>Pinus oocarpa</i>	Serotinous ²	10 ^o
<i>Pinus pinaster</i>	Serotinous ¹	6 ⁱ , 10 ^d (8)
<i>Pinus pinea</i>	Non-serotinous ¹	15 ⁱ
<i>Pinus ponderosa</i>	Non-serotinous ¹	15 ^e , 15.4 ^f , 17 ^e , 18 ^d (16.3)
<i>Pinus radiata</i>	Serotinous ¹	6 ^j , 6 ⁿ , 8 ⁱ , 9 ^d (7.2)
<i>Pinus sylvestris</i>	Non-serotinous ¹	10 ^k
<i>Pinus taeda</i>	Non-serotinous ¹	5 ^g
<i>Pseudotsuga menziesii</i>	Non-serotinous ³	7 ^m , 10.9 ^l , 11 ^e , 18 ^d (11.7)
Mean reproductive age	Serotinous	8.5
Mean reproductive age	Non-serotinous	10.8

The species were classified as serotinous or non-serotinous, and for each one the reproductive age of individuals regenerated naturally in introduced ranges was reported. We informed the reproductive age for the native range (italics numbers) when data for the introduced range were not found. Mean value of first coning age (shown between parentheses) was calculated for those species with more than one register. Superscripts indicate the data source

where X_B was the mean pine density (response variable) in burned habitats, and X_U was the mean pine density in unburned habitats. A ratio of 0 (or if the confidence interval overlaps 0) indicates that invasion degree does not differ between both conditions. A positive ratio indicates a greater invasion in the burned habitats, whereas a negative ratio indicates a greater invasion in the unburned habitats. To assess the impact of serotiny on the level of invasion, we compared pine density between serotinous and non-serotinous pines within each habitat condition using Mann–Whitney U tests (burned habitats; nonparametric data), and t tests (unburned habitats; parametric data). We performed simple logistic regressions to test how the probability of invasion (using ‘presence/absence of pines’ as the dependent variable) depended on habitat condition (burned or unburned), time since last fire, and time since plantation introduction. To evaluate if time from last fire or from plantation introduction (unburned habitats) can determine a threshold response in the invasion level, we performed simple and piecewise regressions using natural log of pine density as the dependent variable. Piecewise regressions are effective in estimating ecological thresholds by modeling abrupt changes in the dependent variable as a consequence of continuous changes in the explicatory variable (Crawley 2007). We only modeled two linear regressions to the left and right sides of the estimated breaking point (representing the threshold). From piecewise regressions and simple regressions we selected the ones that best fitted the data when significant differences were detected between both models (Crawley 2007). Regressions and model comparisons were performed with R software (lm package; R Development Core Team 2006). Finally, we did not include *Pseudotsuga menziesii* data ($n = 28$) in comparative analysis between burned and unburned habitats since they belonged to one habitat condition only (unburned).

Results

We obtained a total of 125 records for invasion density (Fig. 1; Appendix 1 in ESM) corresponding to eleven pine species and *Pseudotsuga menziesii* (Table 1). Density data were compiled from studies performed in countries distributed in three continents of the SH: South America (Argentina, Brazil, and Chile), Africa

(South Africa), and Oceania (Australia). Less than 30% of the data corresponded to burned habitats (34 out of 125) where the majority of the records belonged to serotinous species (25 out of 34; Fig. 2). On the other hand, most of the records for unburned habitats belonged to non-serotinous species (62 out of 89; Fig. 2).

The response ratio indicated that the invasion degree of serotinous pines was greater in burned habitats than in unburned ones (Fig. 3a). By contrast, non-serotinous pines showed similar natural regeneration in burned and unburned habitats (Fig. 3a). Serotinous pines had a sevenfold greater abundance than non-serotinous pines in burned habitats (serotinous: 7718 ind/ha \pm 3848 vs. non-serotinous: 1194 \pm 1188; mean \pm SE; $U = 40.5$, $p < 0.01$; Fig. 3b), but there were no differences in the invasion degree between both pine types in unburned habitats (serotinous: 1080 ind/ha \pm 291 vs. non-serotinous: 534 \pm 364; mean \pm SE; $t_{59} = 1.59$, $p > 0.05$; Fig. 3b).

The probability of invasion was not affected by the habitat condition (i.e. burned or unburned; $p > 0.05$, Analysis of Deviance) but it was positively affected by the time from last fire and by the time from plantation introduction in unburned habitats ($p < 0.01$, and $p < 0.001$, respectively, Analysis of Deviance) (Figs. 4, 5). The results showed that at similar times, burned habitats had a greater probability of invasion than unburned habitats, which is particularly noticeable up to the first twenty years (Figs. 4, 5).

In burned habitats invasion density was positively related to the lapsed time from last fire ($F_{1,31} = 19.02$, $p < 0.001$; Fig. 6a), and did not show an inflection point (Table 2). Although the first post-fire invasions were recorded one year after the fire and belonged to serotinous species, the majority of the records began 7 years later. On the other hand, in unburned habitats pine density increased at a greater time since plantation introduction, reaching its maximum at a plantation age of 30 years old (Table 2; Fig. 6b). In unburned habitats the estimated time lag was 16 and 17 years for serotinous and non-serotinous species respectively (Fig. 6b).

Discussion

Conflicting evidence from published case studies has questioned the dominant role of fire as a driver of pine

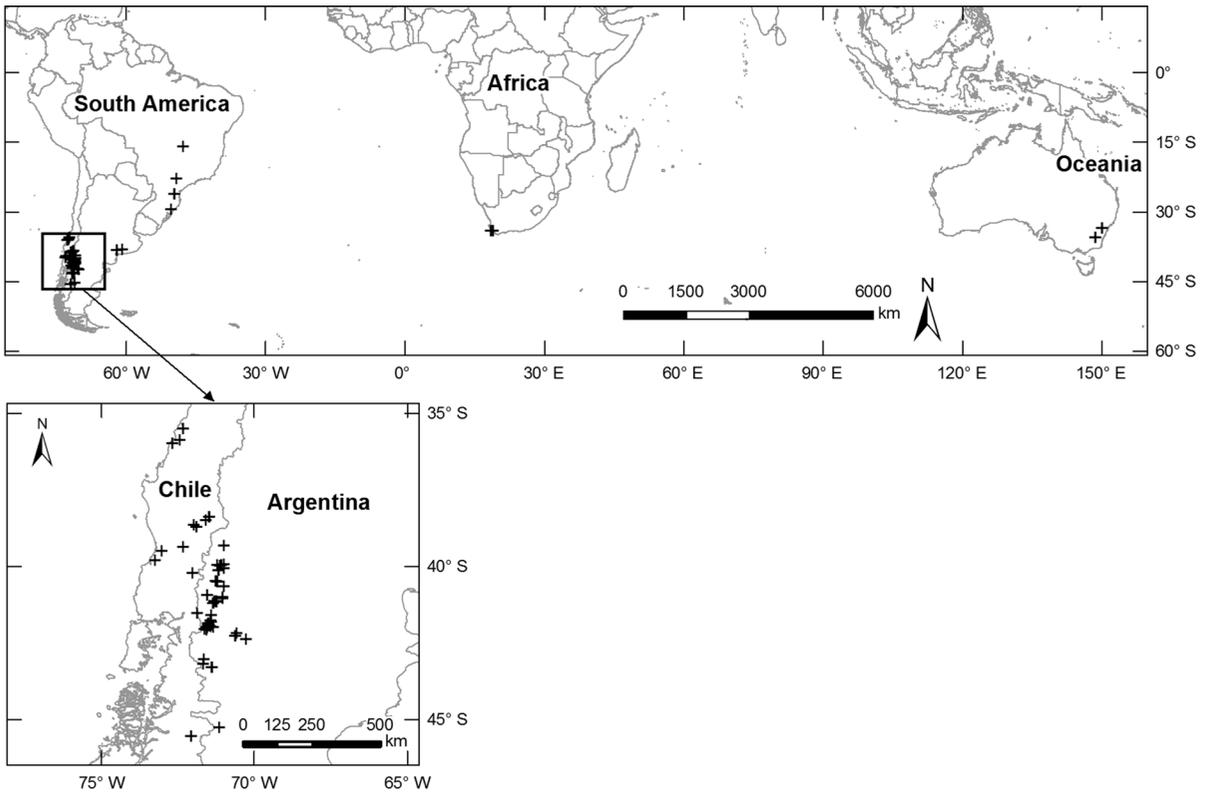


Fig. 1 Geographical location of density records of *Pinus* spp. and *Pseudotsuga menziesii* obtained from studies performed throughout the Southern Hemisphere. A detail is shown for the region that grouped the majority of the sites in South America.

Many data were obtained from one same site or a nearby one; therefore they can overlap on the map (detailed information in Appendix 1 in ESM)



Fig. 2 Percentage of density records for burned and unburned habitats of the Southern Hemisphere. Records for serotinous and non-serotinous species are indicated in grey and white respectively. *Pseudotsuga menziesii* data are included in the figure

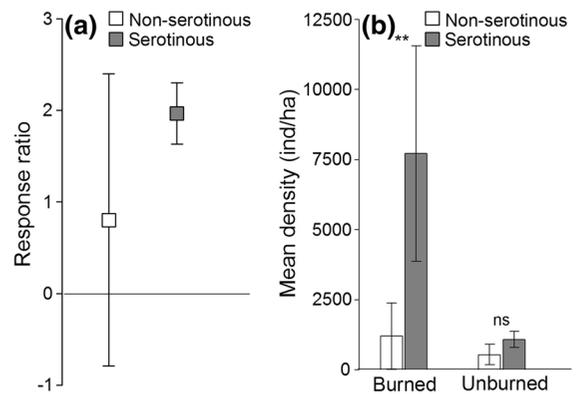


Fig. 3 **a** Response ratio of pine invasion, and **b** mean pine density (\pm SE) in burned and unburned natural habitats of the Southern Hemisphere. Results are shown for non-serotinous pines (in white), and for serotinous pines (in grey). A response ratio of 0 (or if the confidence interval overlaps 0) indicates that invasion level does not differ between both conditions, and a positive ratio indicates a greater invasion in the burned habitats. Square symbols represent the mean effect size, and bar the 95% confidence interval

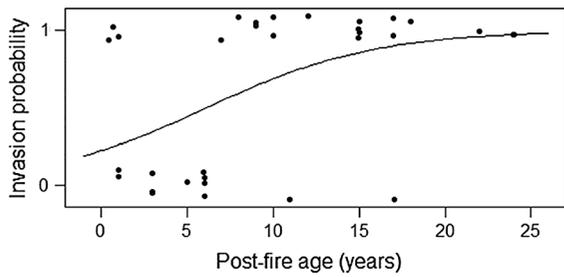


Fig. 4 Invasion occurrence in function of the post-fire age ($n = 34$) of natural habitats of the Southern Hemisphere. Jittered axes ('jitter'-function in R) were used to visualize data in a nonoverlapping way

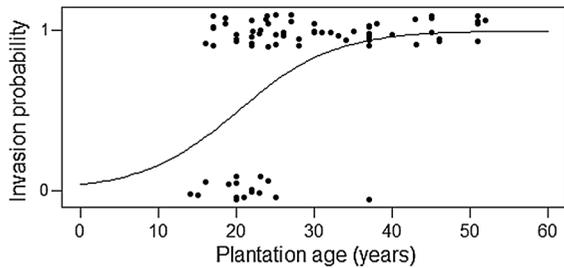


Fig. 5 Invasion occurrence in function of the age of plantations ($n = 76$) in natural habitats of the Southern Hemisphere. Jittered axes ('jitter'-function in R) were used to visualize data in a nonoverlapping way. *Pseudotsuga menziesii* data were included in the analysis

invasions in the SH (Appendix 1 in ESM). We studied the influence of fire on invasion responses (assessing 'serotiny' and 'time' as key factors in determining invasion), based on a review that compared data from burned and unburned natural habitats. Our results indicated that fire is a leading driver of pine invasion in natural habitats of the SH, but only for serotinous species. Fire was also important in determining the absence of a lag time in the invasion.

Serotiny and pine invasion

Serotinous pines reached extremely high densities in burned habitats, far exceeding the densities recorded for the same species in unburned habitats, as well as for non-serotinous pines in any habitat condition. The abundance of density records of serotinous species in burned habitats further supports these findings. These results highlight the importance of considering life history traits of introduced species to determine the invasion degree or probability related to disturbance.

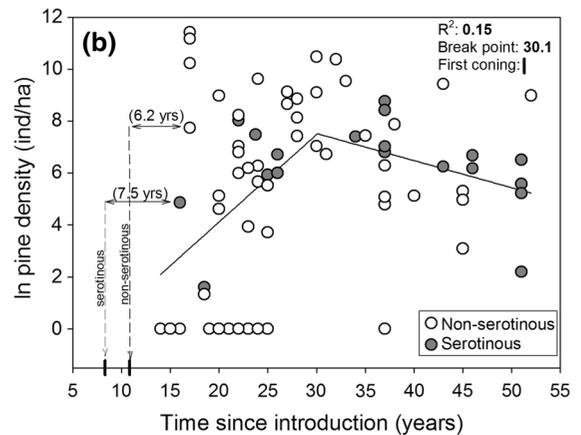
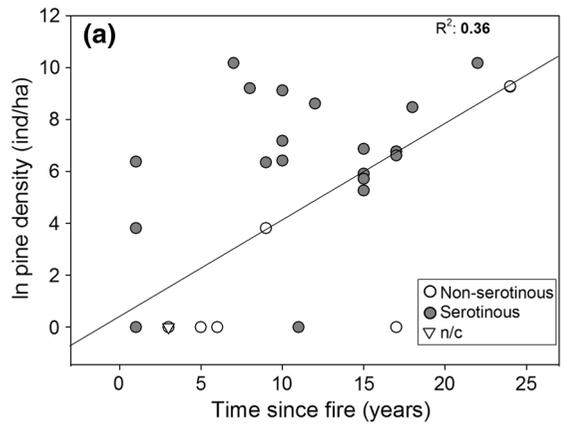


Fig. 6 Invasion (ln pine density) in function of **a** time since fire (simple regression, $n = 33$), and **b** time since plantation introduction in unburned habitats (piecewise regression, $n = 76$). Circles represent the average density value for one or more transects from each reference plantation. Data corresponding to non-serotinous and serotinous pines are showed in white and grey circles, respectively. n/c not classified (mixed plantations). **b** *Pseudotsuga menziesii* data were included in the analysis. Time lag was estimated adding the time of first coning (8.5 and 10.8 years) and the period up to the first documented spontaneous spread (indicated between parenthesis)

In the SH, serotiny is well represented in the native flora of Australia and South Africa (Lamont et al. 1991; Bond and van Wilgen 1996; Pausas 2012), but this is not the case in South America where there are no serotinous species. It may be interesting to examine if communities lacking native serotinous species are more susceptible to the invasion of serotinous species that exploit an empty niche. Rundel et al. (2014) presented this 'empty niche' hypothesis as a key mechanism for tree invasion into tree-less areas, which

Table 2 Adjusted determination coefficients (Adj. r^2) of simple and piecewise regressions of pine density in function of post-fire age and plantation age

Response variable	Independent variable	Adj. r^2 simple regression	Adj. r^2 piecewise regression	p value for model comparison
ln pine density	Postfire age	0.36	0.34	0.527
ln pine density	Plantation age	0.15	0.12	0.017

p value for comparison between models (simple vs. piecewise regressions) is shown. Piecewise regressions were performed when significant differences between models were detected. Bold numbers indicate the selected model for each response variable after model comparisons. See data analysis for a detailed explanation

we also proposed as a valid mechanism for forested areas.

Global warming is expected to increase fire activity in many of the pine introduction areas (Veblen et al. 2008; Flannigan et al. 2009), which could lead to promoting their invasion (Veblen et al. 2011). Moreover, pines are fire-prone species that by themselves contribute to changing the fire regime (Veblen et al. 2008, 2011; Simberloff et al. 2010; Cóbar-Carranza et al. 2014) and creating post-fire conditions unfavorable to the invaded community but conducive to their invasion (Veblen et al. 2011; Cóbar-Carranza et al. 2014; Raffaele et al. 2015). Increased fire occurrence and pine invasion can act synergistically by causing severe habitat degradation in different areas of the SH (Simberloff et al. 2010). For example, in a forest reserve located in the Andean Patagonia of South America (Raffaele et al. 2015), fire has recurrently burned an important area invaded by the serotinous species *Pinus radiata*, with the last two fires occurring only 3 years apart (2012 and 2015; Fig. 7). This area, due to the serious deterioration of native forests, was included in an environmental observatory network (www.desertificacion.gob.ar) to develop prevention and control measures on invasion and improve environmental management decisions. Similar long-term monitoring projects in diverse fire-prone areas of the SH could contribute to the understanding and management of pine invasions.

Lag-time and pine invasion

Wildfires can influence lag phases of species introduced in natural environments of the SH as recently shown for the serotinous tree *Banksia ericifolia* (Proteaceae) in the fynbos of South Africa (Geerts et al. 2013). This species' populations have long lag phases in absence of fire (even under suitable climatic conditions and without limitations for reproduction),

but they can increase rapidly with little or no lag time after fire. Similarly, in our study, burned habitats had no lag time since the first invasion records of serotinous species appeared as early as one year (or less) after fire. Based on how fire negatively affects mycorrhizal fungi (Longo et al. 2014), and that absence or low abundance of proper mycorrhizal fungi can limit the establishment of Pinaceae species (Nuñez et al. 2009, 2013), we could anticipate no pine recruitment in the immediate post-fire phase. While this was true for some sites, there were also other sites with low (44 pines/ha), medium (585 pines/ha), and high (93,000 pines/ha) levels of invasion recorded only a few months after fire (Appendix 1 in ESM). These situations could indicate that burned habitats pose a more complex scenario for interpreting the mycorrhizal fungi–pine interaction in the invaded range. The lack of studies based on the dynamics of this interaction in post-fire environments reveals a knowledge gap in the invasion ecology of exotic conifers.

As expected, the probability of pine invasion increased over time and was particularly higher in burned habitats during the first post-fire years. The increase in pine density in post-fire environments was linear with numerous invasion records observed 7 years after fire. This could be due to the occasional propagule dispersion from the first post-fire recruitment, since some serotinous species can start producing cones long before the mean reproductive age in the introduced range (e.g. *P. contorta* at 4 years, and mean reproductive age for serotinous pines was 8.5 years; Table 1). These results showed that a lack of early pine recruitment control can increase the extent of invasion in a very short time after fire, potentially interfering greatly with the post-fire succession of the invaded communities. By contrast, the absence of fire caused a lag-phase of about 16 years with no differences between serotinous and non-serotinous species.



Fig. 7 Post-fire invasion (carpet of saplings in the understory) originated from an older post-fire invasion (burned trunks) after burning in January 2012. The older post-fire invasion originated from adult plantations of *Pinus radiata* burned in 1987. The

picture was taken in March 2013 in the forest reserve ‘Reserva de Usos Múltiples Lago Epuén’ (Argentina; 42°17’S–71°37’W)

In these habitats, invasion increased year by year reaching a maximum at 30 years after the introduction of plantations. This demonstrates that time is a relevant factor in determining the degree of Pinaceae invasion in the absence of fire.

Concluding remarks

Overall, our work showed that burned environments are more susceptible to invasion by serotinous pines than unburned ones, with no lag time in the post-fire invasion. A correlation between alien species abundance and level of impact (Kumschick et al. 2015; Pearson et al. 2016) suggests that burned environments are impacted by conifer invasion more strongly and earlier than environments not affected by fire. Early control and monitoring of post-fire invasion could avoid the high levels of infestation and pine interference in the secondary succession of natural communities. A first step in diminishing the ecological risks and economic costs associated with invasion could be to avoid establishing new plantations of serotinous pines in fire-prone areas. This measure has

been suggested for the Western Cape of South Africa (van Wilgen and Richardson 2012) as an option to improve the chances of sustainable control of pine invasions in fynbos areas. In particular, land managers should be aware that the introduction of serotinous pines into regions of the SH where serotiny represents a novel trait could result in increased impact on recipient plant communities (Kumschick et al. 2015). In addition, the formulation of consistent management guidelines for plantations in the SH, comparable to those proposed for Europe by Brundu and Richardson (2016), could prevent the intensification of pine invasions in a near future. Finally, considering that burned plantations are expected to be an increasingly common scenario (van Wilgen and Richardson 2012), we emphasize the need for research to focus on aspects related to the ecological mechanisms and impacts of conifer invasion in post-fire natural environments.

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