



The widely invasive tree *Pinus radiata* facilitates regeneration of native woody species in a semi-arid ecosystem

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Keywords

Exotic plants; Facilitation; Invasion; Mediterranean climate-type ecosystem; Restoration; Sclerophyllous forest

Nomenclature

Marticorena & Quezada (1985)

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Abstract

Question: What is the effect of invading individuals of the widely invasive species *Pinus radiata* D. Don on regeneration of native woody species in a semi-arid ecosystem?

Location: A semi-arid ecosystem in central Chile.

Methods: We sampled natural regeneration of native woody species in 40 plots in each of three canopy types: (1) under young adult invading trees of *P. radiata* located in formerly open (disturbed) sites; (2) in patches of native trees; and (3) in open (disturbed) sites, in two localities where this exotic tree is invading. Additionally, we carried out a field experiment in one of these localities; in eight of each of these canopy types we sowed seeds of ten widely distributed woody native species and monitored their recruitment. We also assessed different biotic and abiotic variables in these canopy types.

Results: We found that soil water content, depth and cover of leaf litter were higher and photosynthetically active radiation was lower under *P. radiata* trees and native patches than in open sites. In the natural regeneration study, species richness of seedlings was higher in native patches and under *P. radiata* trees than in open sites, and total abundance of seedlings (including all species) was higher only in native patches than in open sites. In the field experiment, both species richness and total abundance of seedlings were higher in native patches and under *P. radiata* trees than in open sites. Moreover, in the field experiment species richness recruiting in native patches was higher than under *P. radiata* trees.

Conclusions: We suggest that native patches as well as *P. radiata* trees invading open sites facilitate or have the potential to facilitate regeneration of native species, although facilitation produced by native trees was stronger than that produced by *P. radiata*. Thus, in sites where nurse plants are not available, invasion by this exotic tree may be exploited in restoration processes through sowing or planting native species under the canopy of invading young trees of *P. radiata*, eliminating *P. radiata* individuals after native regeneration has established.

Introduction

Invasion by exotic species is currently a relevant issue of research in ecology and a global concern for conservation biology (Sax et al. 2005). Knowledge about the impacts of exotic invasive species on native species acquires relevance in establishing the need for control and management of invasions (D'Antonio & Meyerson 2002; Levine et al. 2003). Despite many studies reporting strong negative

effects from exotics on native species (e.g. Minchinton et al. 2006; Mason & French 2008; Hejda et al. 2009; Rudgers & Orr 2009; Flory & Clay 2010), positive effects have also been documented (Rodríguez 2006; Fischer et al. 2009). In particular, degraded areas where cover of woody native species has been eliminated or significantly reduced, are typically invaded by woody exotic plants (Higgins & Richardson 1998; Davis et al. 2000; Levine et al. 2004; Mitchell et al. 2006). These exotic plants may

inhibit or delay recolonization, secondary succession and restoration of native species, and in this case eradication of exotics should be carried out as soon as possible. Nevertheless, in other cases some exotics may facilitate recolonization and recovering of native species (D'Antonio & Meyerson 2002).

The net negative or positive effect of an exotic plant on native plant species will depend on different mechanisms. For instance, shade produced by exotic species has been documented to affect native species negatively due to light reduction (Craine & Orians 2004; Wearne & Morgan 2004; Reinhart et al. 2005; Minchinton et al. 2006; Williams 2007), as well as positively when soil moisture stress is reduced (Walker & Vitousek 1991; Dewine & Cooper 2008). Similarly, leaf litter and soil produced under an exotic plant has been documented to have negative (Callaway & Aschehoug 2000; Abhilasha et al. 2008; Gómez-Aparicio & Canham 2008), as well as positive (Quinos et al. 1998; Siemann & Rogers 2003; Lindsay & French 2005; Williams 2007) effects on native species. In arid and semi-arid ecosystems, plant–plant interactions are frequently facilitative (Callaway 2007; Maestre et al. 2009). In dry environments, positive effects produced by shading from some plants, such as amelioration of soil drought, are more important than the negative effects due to decreases in light intensity, competition for soil resources or other inhibitory effects, resulting in facilitation (Holmgren et al. 1997; Holzapfel & Mahall 1999; Castro et al. 2002; Hastwell & Facelli 2003; Prider & Facelli 2004; Maestre et al. 2009). Thus, in ecosystems with water constraints for native species, and particularly in degraded areas, exotic plants growing in sites without cover of native woody species may facilitate recolonization of natives due to positive shading effects (Levine et al. 2003; Rodríguez 2006). Whilst many studies have assessed the effect of nurse plants on regeneration and succession in arid and semi-arid ecosystems (e.g. Fuentes et al. 1984, 1986; Holzapfel & Mahall 1999; Castro et al. 2002; Hastwell & Facelli 2003; Prider & Facelli 2004; Gómez-Aparicio et al. 2005), very few studies have evaluated the effects in the context of interactions between native and exotic species (e.g. Lenz & Facelli 2003; Becerra & Bustamante 2011).

Forestry plantations are a major source of invaders worldwide (Richardson 1998). In Chile, forestry plantations are predominantly composed of *Pinus radiata* D. Don (Pinaceae), which is native to California, USA. This species is also widely used as a forestry tree in many other parts of the world (Lavery & Mead 1998), and it has been recognized as an important invasive species in several places where it has been introduced, such as Australia, New Zealand and South Africa (Higgins & Richardson 1998; Lindenmayer & McCarthy 2001; Williams & Wardle

2005). In Chile, plantations of this species are primarily in the mediterranean region of the country, including a wide extent of semi-arid zones. Invasion in Chile by this species is already occurring in several locations in the country, mainly near plantations (Bustamante et al. 2003; Bustamante & Simonetti 2005; Becerra 2006; Becerra & Bustamante 2008, 2011).

Although this forest species is one of the most planted in the world and has been observed invading several countries where it has been introduced, the effects of *P. radiata* on native species have scarcely been assessed. Some observational studies have documented lower species diversity within plantations of this tree than in adjacent sites with natural vegetation (e.g. Richardson & Van Wilgen 1986; Brockerhoff et al. 2003). Additionally, there are only two experimental studies assessing the effects of *P. radiata* on other species, in particular leaf litter effects (Guerrero & Bustamante 2007; Williams 2007), generally reporting weak effects on recruitment of natives. In turn, no study has experimentally evaluated the net effect of *P. radiata* on native species. In semi-arid regions where this species has invaded, shading produced by the canopy of individuals growing in open areas may ameliorate water stress. In central Chile most tree and many shrub species are facilitated by other woody native species (Fuentes et al. 1984, 1986; Armesto & Pickett 1985; Badano et al. 2005). Therefore, given that soil and litter effects of *P. radiata* seem to be weak (Guerrero & Bustamante 2007; Williams 2007), individuals of this exotic species growing in sites without native tree cover may facilitate recruitment of native species through amelioration of water stress through shading, similar to the effect produced by other native nurses.

In this paper we assessed the net effect of invading individuals of *P. radiata* on the recruitment of woody native species from central Chile. In addition, we compared the effect of this exotic tree on native species with the effect produced by native trees. We first evaluated the pattern of natural regeneration of native woody species under invading individuals of *P. radiata* growing in formerly open areas, in patches of native trees and in open sites in two localities of central Chile. We also report the results of a field experiment in which we sowed seeds of several woody native species under these same canopy conditions. We expect that in this semi-arid and water-stressed area, both *P. radiata* and native trees will facilitate the recruitment of woody native species.

Methods

Study area

The study was carried out in a relatively xeric zone in central Chile, which is characterized by a semi-arid and

seasonal mediterranean-type climate (Luebert & Pliscoff 2005). Most of the human population of Chile resides within this region, and hence it has been intensively degraded. Tree vegetation has been the most affected, resulting in a current distribution as isolated patches surrounded by patches of shrubs and grassland (Fuentes et al. 1984).

The study of natural regeneration was carried out in two nearby localities (40 km apart) in central Chile: Lago Peñuelas Natural Reserve (33°11'S, 71°28'W, 340 m a.s.l.) and Lagunillas (33°25'S, 71°26'W, 200 m a.s.l.), both in the Coast Range of central Chile, where most pine plantations are distributed. Close to both localities there are plantations of *P. radiata*. This area is located near the northern limit of plantations of *P. radiata* in Chile. The climate in both localities is semi-arid, characterized by 5–6 dry months and precipitation concentrated during winter, reaching an annual average of 372 mm, and an annual mean temperature of 14.02 °C (Dirección Meteorológica de Chile 2011). The topography of both localities is dominated by flat areas and slight slopes. The study was performed during 2010, and precipitation during this year was 362 mm in Lago Peñuelas (Dirección Meteorológica de Chile 2011).

In both localities vegetation is spatially heterogeneous, composed of herbaceous, shrub and tree patches. Originally, both localities probably had continuous sclerophyllous forests, which were deforested and/or burned. The resulting open sites are areas where native trees can establish through successional processes (Armesto & Pickett 1985; Fuentes et al. 1986). Woody (tree and shrub) patches are composed almost exclusively of native species (mainly *Quillaja saponaria*, *Lithrea caustica*, *Schinus latifolius*, *Acacia caven*, *Maytenus boaria*) except patches with *P. radiata* which are monospecific or mixed (with some native woody species). Herbaceous patches are composed of native herbs, such as *Pasithea coerulea*, as well as exotic herbs, such as *Erodium* spp and *Fumaria* spp. The herbaceous layer is less diverse and abundant under *P. radiata* individuals and native trees than in open areas, but similar between the two tree patch types. Nomenclature of species follows Marticorena & Quezada (1985).

Natural regeneration

In each locality, between January and February 2010, within an area 4-km long and 1-km wide we selected the first 20 invading young adult individuals (8–14-m high) of *P. radiata* located at least 200 m apart growing in formerly open sites with no individual of a native species higher than 2 m under the canopy. In general, in both localities, density of invading pines was low (<1 individual ha⁻¹). Additionally, selected pine individuals were no more than

5 m from a patch with native trees, to ensure a source of propagules for each invading pine. The canopy diameter of selected pine trees varied between 5 and 8 m. Within this area we also selected 20 patches of native trees as similar to the selected pine trees as possible. These patches had a similar range of canopy diameter (5–8 m) and height (8–12 m), although most of them were composed of one or two tree species. These selected patches were also distributed at least 200 m apart, although other patches with native trees were present within this range. Finally, next to each of these native patches we also selected one open site (20 open sites overall per locality). The sampling in these open sites was no more than 5 m from a patch with native trees, to ensure some source of propagules for them.

For each *P. radiata* individual, patch with native trees and open site (hereafter: canopy types), we sampled natural regeneration within a 1 m × 1 m plot per patch. Each plot was located on the south side of the canopy of each pine tree, native patch, and on the south side from the nearest native patch in open sites. In each plot we recorded the number of seedlings (<50-cm high) of each woody species. These seedlings could be at least 1 yr old, although in general probably no more than 5 yr old. We statistically compared species richness of naturally regenerating woody species and total abundance (number) of seedlings (including all species), between these three canopy types using ANOVA. Data on species richness and total abundance of seedlings were square root-transformed. We also report values of seedling abundance for particular species observed in each canopy type. However, we did not perform statistical analyses separately for each species because for most of the species we observed seedlings in only one or two canopy types or in very few plots within a canopy type. In other cases we observed an identical number of seedlings in all plots between the two canopy types.

Field experiment

In the Lago Peñuelas National Reserve, we selected 16 patches with native trees from the 20 used in the natural regeneration study. We also selected 16 open sites and 16 *P. radiata* individuals separated by at least 50 m from any patch of native trees (different from those used in the natural regeneration study). This method was used to avoid or at least reduce seeds coming from native patches, contaminating the experimental sowing. In each of these three canopy types we installed a 0.5 m (width) × 1 m (height) × 0.5 m (depth) plot, fenced on the sides and the top with a wire mesh in order to exclude mammals and birds (16 per canopy treatment overall). In each plot we sowed seeds of ten typical and widely distributed woody

native species from central Chile with different numbers of seeds, having a wide range of shade tolerance and life form (Table 1). Differences in number of seeds among species was based on proportional differences observed in preliminary samplings of seed banks in the area (Peñuelas), averaging the three canopy types. These differences are not relevant for our analyses as we were not interested in differences in the probability of recruitment between species, but only between the three canopy types, either in species richness, total abundance of seedlings or recruitment pattern separately for each species.

Seeds were deposited on the soil or leaf litter to mimic natural dispersal. Nonetheless, all seeds were dropped between the leaf litter and herbs and hence were not blown away by the wind. The sowing was carried out in May 2010 (when the dispersal period mainly occurs in this area) and recruitment was monitored in late September and late December 2010. However, all analyses were performed with data from December, as in September germination had just started and some species were taxonomically unidentified. In each plot we recorded the number of seedlings of each experimentally sown species. With these data we calculated species richness and total abundance (number) of seedlings (including all species) recruiting in each plot. In open sites and under individuals of *P. radiata* it is unlikely that seeds not experimentally sown would disperse into the experimental plots. However, it is highly probable that some seed, especially from the species present in the canopy of patches of native trees dispersed into experimental plots of this canopy type. Therefore, we excluded from analyses sown species present in the canopy of each native patch in all the plots located in the canopy type corresponding to native trees. Thus, richness analyses were performed using the percentage of species recruiting from all included in the analyses. We compared species richness and total abundance of seedlings between canopy types (*P. radiata* individuals, native patches and open sites) using ANOVA. Data on species richness as well as total abundance of seedlings

were normally distributed. We also report the number of recruited seedlings of each species experimentally added in experimental plots. However, we did not perform statistical analyses separately for each species because for most of the species we observed seedlings in only one or two canopy types, in very few plots within a canopy type or an identical number of seedlings in all plots between canopy types.

Environmental assessment

In plots used either in the study of natural regeneration or field experiment we assessed several environmental variables, in order to characterize the microenvironment of each canopy type. We measured photosynthetic active radiation (PAR), soil water content (SWC), depth and cover of leaf litter, soil nutrient concentrations (N, P, K, Zn, B), organic matter and soil pH. PAR was measured at 30 cm above the ground and quantified using a light sensor (Li-Cor, Lincoln, NE, US) to take instantaneous PAR measurements directly beneath *P. radiata* individuals, native patches and open sites. In each plot used in the study of natural regeneration in Peñuelas ($n = 20$ per canopy type) we sampled light as the mean of a 45-s reading. This procedure was repeated on three different days during the growing season (October, 2010) on days with <5% cloud cover between 12:00 and 13:00 h. We assumed that differences between canopy types are similar through the year as all native species and *P. radiata* are evergreen. SWC was evaluated using the gravimetric method (by quantifying changes in weight after 48 h drying soil samples at 80 °C) and was measured during early September and early December. In both months we measured SWC three times (approximately every 5 d) in each plot used in the study of natural regeneration in Peñuelas ($n = 20$ per canopy treatment), and calculated the average of the three measurements. We separately analysed SWC during late winter (September) and late spring (December) in order to assess temporal variation in this factor in seasons with different rainfall regimes, within a period in the year when germination and recruitment mainly occur in this region. Soil samples for moisture evaluation were approximately 250 cm³, collected from the first 10-cm depth. Depth of leaf litter was measured at five points within each plot used in the study of natural regeneration (corners and midpoint) in Lago Peñuelas and then averaged to obtain one value per plot. Cover percentage of leaf litter per plot was estimated visually in these same plots. Soil nutrients and pH were evaluated once by sampling the soil (15 cm of soil without leaf litter) on a summer day in January 2011. Soil samples were collected in four randomly selected plots per canopy type in Lago Peñuelas. We were interested in

Table 1. Species used in the field experiment. Biological attributes and number of seeds added per plot in the field experiment are indicated.

Species	Shade tolerance/life form	No. of seeds added
<i>Cryptocarya alba</i>	Shade-tolerant tree	10
<i>Peumus boldus</i>	Shade-tolerant tree	30
<i>Quillaja saponaria</i>	Shade-semi-tolerant tree	50
<i>Lithrea caustica</i>	Shade-semi-tolerant tree	50
<i>Azara celastrina</i>	Shade-tolerant tree	20
<i>Maytenus boaria</i>	Shade-semi-tolerant tree	50
<i>Kageneckia oblonga</i>	Shade-semi-tolerant tree	50
<i>Schinus molle</i>	Shade-semi-tolerant tree	50
<i>Acacia caven</i>	Shade-intolerant tree	50
<i>Baccharis paniculata</i>	Shade-intolerant shrub	50

exploring whether some macro- (N, P, K) and micronutrients (B, Zn) were affected by acidification, as predicted in soils influenced by leaf litter produced by species from the genus *Pinus* because some studies have observed and predicted that nutrient availability is reduced in soils with reduced pH, such as soils of pine forests (Scholes & Nowicki 1998). Finally, we characterized the herb abundance in each plot used in the study of natural regeneration in Lago Peñuelas by evaluating total percentage of herb cover using the point intercept method. For all variables, comparison between canopy types was carried out with ANOVA. All variables were distributed normally, except PAR, N, depth of leaf litter and cover of leaf litter, which were square root transformed.

Results

Environmental variables

PAR significantly differed between canopy types ($F_{2,57} = 139.86$, $P < 0.001$), being significantly higher in open sites than in patches of native trees and *P. radiata* individuals, with no significant difference between these two last canopy types (Table 2).

Soil water content (SWC) differed significantly between canopy types (repeated measures ANOVA, $F_{2,57} = 6.56$, $P < 0.001$). However, SWC showed different patterns between seasons. In September 2010, we found no significant differences between canopy types (Table 2), while in December 2010 there were significant differences between canopy types (Table 2); SWC was significantly higher in patches of native trees than in the other two canopy types, and significantly higher under individuals of *P. radiata* than in open sites (Table 2).

Soil pH did not differ significantly between canopy types ($F_{2,9} = 0.73$, $P = 0.51$; Table 2). Organic matter differed significantly between canopy types ($F_{2,9} = 7.55$, $P = 0.011$);

it was significantly higher in patches of native trees than under individuals of *P. radiata* or open sites, with no significant difference between these two last canopy types (Table 2). Although concentration of all nutrients was higher in native patches than in the other two canopy types (Table 2), N available in the soil did not differ significantly between canopy types ($F_{2,9} = 2.46$, $P = 0.14$), nor did P ($F_{2,9} = 2.27$, $P = 0.16$), K ($F_{2,9} = 0.49$, $P = 0.62$) or B ($F_{2,9} = 3.78$, $P = 0.064$) available in the soil. Only zinc available in the soil significantly differed between canopy types ($F_{1,9} = 8.44$, $P = 0.008$), being significantly higher in patches of native trees than under *P. radiata* individuals or open sites, with no significant difference between these two last canopy types (Table 2).

Depth of leaf litter significantly differed between canopy types ($F_{2,57} = 52.31$, $P < 0.001$), being significantly deeper in patches of native trees and *P. radiata* individuals than in open sites, with no difference between the two-first canopy types (Table 2). Similarly, cover of leaf litter significantly differed between canopy types ($F_{2,57} = 384.38$, $P < 0.001$), being significantly higher in patches of native trees and *P. radiata* individuals than in open sites, with no difference between the two-first canopy types (Table 2). Finally, cover of herb species significantly varied between canopy types (ANOVA, $F_{2,57} = 13.99$, $P < 0.001$). In particular, cover in open sites was significantly higher than in patches of native trees and *P. radiata* individuals, with no significant difference between these two last canopy types (Table 2).

Natural regeneration

We observed that species richness of naturally regenerating woody species varied significantly between canopy types (ANOVA, $F_{2,114} = 22.22$, $P < 0.001$), but not between localities (ANOVA, $F_{1,114} = 1.47$, $P = 0.23$), and the interaction between canopy type and locality was not

Table 2. Environmental characteristics (mean \pm 1 SE) of patch types (*Pinus*, Native, Open) (N for soil water content, leaf litter, herb cover and photosynthetic active radiation (PAR) = 20 per patch type; N for chemical soil variables = 4 per patch type), observed in the site Peñuelas.

Environmental variable	<i>Pinus</i>	Open	Native
PAR ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	49.21 \pm 5.57 ^a	1497.10 \pm 21.30 ^b	50.00 \pm 6.46 ^a
Soil water content (%) September	11.89 \pm 2.36 ^a	10.07 \pm 1.91 ^a	13.59 \pm 1.34 ^a
Soil water content (%) December	3.82 \pm 0.48 ^a	1.01 \pm 0.07 ^b	7.07 \pm 1.12 ^c
Soil pH	5.37 \pm 0.2 ^a	5.43 \pm 0.1 ^a	5.19 \pm 0.2 ^a
Organic matter (%)	3.66 \pm 0.3 ^a	3.34 \pm 0.5 ^a	6.03 \pm 0.7 ^b
Nitrogen ($\text{mg}\cdot\text{kg}^{-1}$)	16.3 \pm 2.3 ^a	17.0 \pm 3.5 ^a	29.0 \pm 6.7 ^a
Phosphorus ($\text{mg}\cdot\text{kg}^{-1}$)	3.50 \pm 0.3 ^a	3.50 \pm 0.5 ^a	5.75 \pm 1.38 ^a
Potassium ($\text{mg}\cdot\text{kg}^{-1}$)	67.3 \pm 22.1 ^a	61.5 \pm 5.1 ^a	81.5 \pm 11.2 ^a
Zinc ($\text{mg}\cdot\text{kg}^{-1}$)	2.64 \pm 0.6 ^a	1.78 \pm 0.5 ^a	6.09 \pm 1.1 ^b
Boron ($\text{mg}\cdot\text{kg}^{-1}$)	0.30 \pm 0.01 ^a	0.32 \pm 0.06 ^a	0.57 \pm 0.12 ^a
Depth leaf litter (cm)	5.08 \pm 0.81 ^a	0.17 \pm 0.11 ^b	4.67 \pm 0.57 ^a
Cover leaf litter (%)	89.58 \pm 4.41 ^a	3.41 \pm 1.18 ^b	95.83 \pm 1.72 ^a
Herb cover (%)	26.66 \pm 8.55 ^a	82.50 \pm 5.78 ^b	28.75 \pm 8.98 ^a

Different lowercase letters indicate significant statistical differences (Tukey tests, $P < 0.05$) between patch types for a single variable.

significant (ANOVA, $F_{2,114} = 1.82$, $P = 0.17$). In general, species richness recruiting under native patches and individuals of *P. radiata* was significantly higher than in open sites. In Peñuelas, species richness in patches of native trees was significantly higher than in open sites, but not under *P. radiata* individuals, although slightly higher (Fig. 1a). Species richness of woody species regenerating under *P. radiata* individuals was only marginally significantly higher than in open sites ($P = 0.08$, HSD Tukey *post hoc* test; Fig. 1a). In Lagunillas, naturally regenerating species richness both in patches of native trees and under *P. radiata* individuals was significantly higher than in open sites, and there was no significant difference in species richness between native patches and *P. radiata* individuals (Fig. 1a).

Of the ten woody species observed naturally regenerating among the two localities, eight species

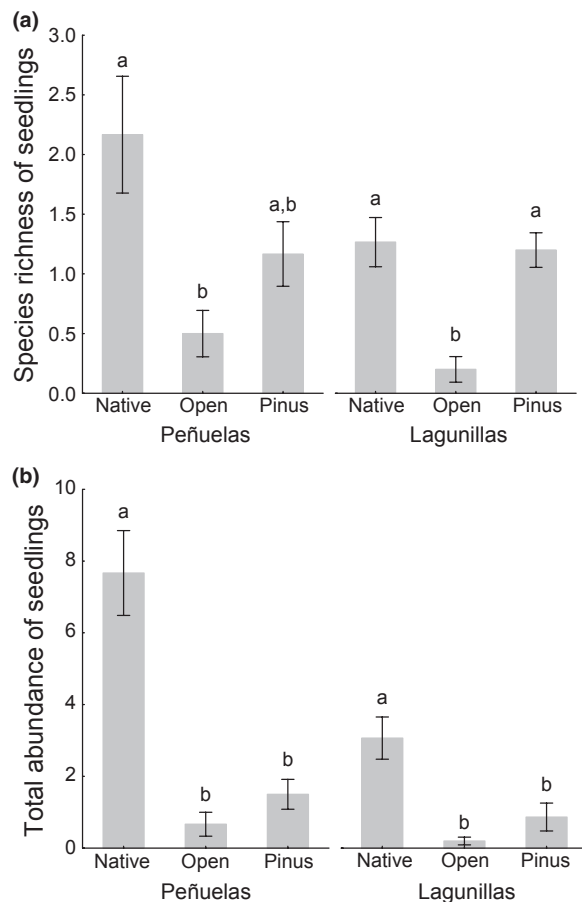


Fig. 1. Species richness (a) and total abundance (N) (b) of seedlings of woody species naturally growing in 1-m² plots under canopy types (mean \pm 1 SE) (invading individuals of *Pinus radiata*, patches of native trees and open sites) ($n = 20$ per canopy type) in each locality (Peñuelas and Lagunillas). Different letters indicate statistically significant differences (Tukey tests, $P < 0.05$) between canopy types for a single locality.

(*M. boaria*, *B. linearis*, *A. dentata*, *S. latifolius*, *P. boldus*, *L. caustica*, *Q. saponaria* and *C. alba*) showed higher abundance of seedlings under native trees than in open sites, and among them, five species showed higher abundance under individuals of *P. radiata* than in open sites (Appendix S1). Only *A. caven* showed higher abundance in open sites than under the canopy of *P. radiata* or native trees (Appendix S1).

Total abundance (including all species) of naturally regenerating seedlings of woody species significantly varied between canopy types (ANOVA, $F_{2,114} = 35.06$, $P < 0.001$), as well as between localities (ANOVA, $F_{1,114} = 12.80$, $P = 0.006$), but the interaction between these two variables was not significant (ANOVA, $F_{2,114} = 1.77$, $P = 0.18$). Specifically, in both localities total abundance of seedlings in patches of native trees was significantly higher than in open sites and *P. radiata* individuals (Fig. 1b), while total abundance of seedlings under *P. radiata* individuals, although higher, did not differ from that observed in open sites (Fig. 1b).

Field experiment

Percentages of species richness recruiting under all canopy types were in general low (<40% of species experimentally added). We observed that species richness recruiting from experimentally sown woody species varied significantly between canopy types (ANOVA, $F_{2,45} = 25.45$, $P < 0.001$). In particular, species richness in patches of native trees was significantly higher than under individuals of *P. radiata* and open sites (Fig. 2a). In addition, species richness recruiting under *P. radiata* individuals was significantly higher than in open sites (Fig. 2a).

Of the ten woody species experimentally sown in the field experiment, eight species (*M. boaria*, *K. oblonga*, *A. celastrina*, *S. latifolius*, *P. boldus*, *L. caustica*, *Q. saponaria* and *C. alba*) showed higher densities of seedlings under native trees than in open sites, and among them, five species (except *P. boldus*, *Q. saponaria*, *A. celastrina*) showed higher densities under individuals of *P. radiata* than in open sites (Appendix S2). Only *B. paniculata* and *A. caven* showed higher densities in open sites than under the canopy of *P. radiata* or native trees (Appendix S2).

Percentage of seedlings recruiting from the 410 originally sown per plot (including all species) was in general very low (<4%). Total abundance of seedlings of woody species experimentally sown varied significantly between canopy types (ANOVA, $F_{2,45} = 10.62$, $P < 0.001$). Specifically, abundance of seedlings in open sites was significantly lower than in patches of native trees or *P. radiata* individuals, with no significant difference between these two last canopy treatments (Fig. 2b).

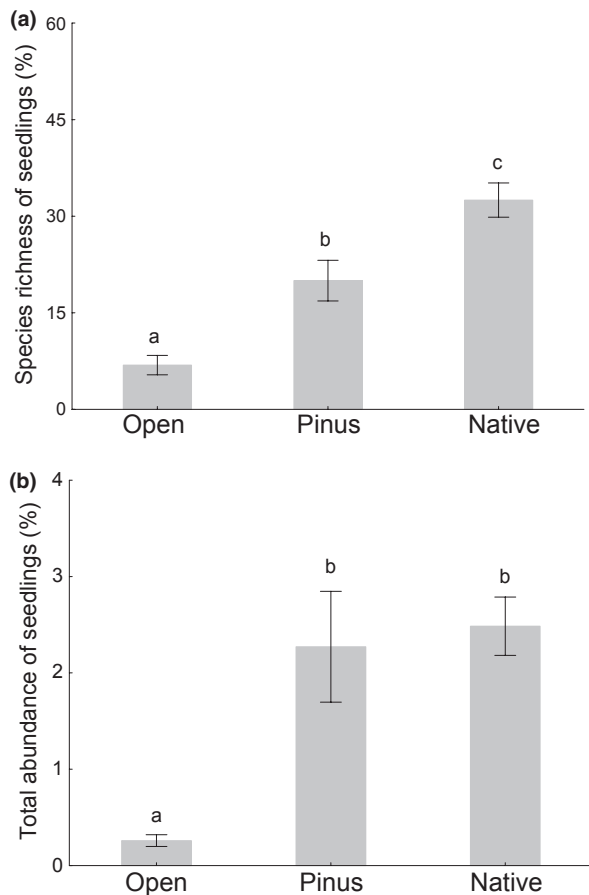


Fig. 2. Species richness (a) and total abundance (b) of seedlings (mean \pm 1 SE) coming from seeds experimentally added in 0.5-m² plots under canopy types (invading individuals of *Pinus radiata*, patches of native trees and open sites) ($n = 16$ per canopy treatment). Species recruiting with presence of conspecific adult individuals in the native canopy were excluded from the analysis. Then, the species richness values correspond to the percentage of new species recruiting in each canopy type from ten species originally sown and abundance values correspond to the percentage of seedlings of new species recruiting in each canopy type from 410 seeds originally sown. Different letters indicate statistically significant differences (Tukey tests, $P < 0.05$) between the canopy types.

Discussion

The results in the study of natural regeneration suggest that, as expected, patches of native trees facilitated regeneration of woody species in terms of both species richness and total abundance of seedlings. In turn, only species richness of natural regeneration of woody species was facilitated by individuals of *P. radiata*. Total abundance of naturally regenerating seedlings under individuals of *P. radiata* was higher than in open sites, but not statistically different. However, most of the species observed in each locality showed higher abundance under individuals of *P. radiata* than in open sites, suggesting facilitation of many species. On the other hand, results observed in our field

experiment suggest that both *P. radiata* and native trees facilitate richness as well as abundance of woody species recruiting in this semi-arid ecosystem. Moreover, in terms of species richness, facilitation produced by patches of native trees was significantly stronger than that produced by invading individuals of *P. radiata*. Thus, our results suggest that native trees as well as *P. radiata* have a positive net effect on regeneration of most woody species of this semi-arid ecosystem, increasing species richness and abundance of recruitment. Although we did not assess the stress gradient hypothesis since we did not include an abiotic gradient (Holmgren et al. 1997; Callaway 2007; Maestre et al. 2009), this general result agrees with part of its assertions, since in this semi-arid, water-stressed ecosystem for these native species, we observed a higher frequency of positive effects on woody native species produced by native trees as well as *P. radiata*.

Despite these general trends, we observed some differences between the natural regeneration pattern and results from the field experiment. Specifically, total abundance of seedlings was significantly higher under *P. radiata* individuals than in open sites only in the field experiment. Probably, natural dispersal of seeds under *P. radiata* was lower than in native patches, preventing the establishment of a higher abundance than in open sites, although this would occur only in terms of abundance and not in terms of the number of species. In turn, when the initial number of seeds was equal (field experiment), facilitation by *P. radiata* effectively produced an increase in total abundance of seedlings.

We observed that in patches of native trees and *P. radiata*, PAR was lower and soil moisture was higher, at least during the main period of recruitment (spring), than in open sites, such as is typically produced by shading in semi-arid ecosystems (Holmgren et al. 1997; Castro et al. 2002; Callaway 2007). Furthermore, leaf litter was more abundant in patches of native trees and *P. radiata* than in open sites, which could also increase soil moisture (e.g. Xiong & Nilsson 1999; Hastwell & Facelli 2000). Thus, the increased soil moisture may have produced facilitation on richness as well as abundance of woody species by native trees as well as *P. radiata*, although we cannot differentiate the role of shade from leaf litter in this experiment. The relevance of soil moisture in facilitative interactions has already been documented in many studies in semi-arid environments (Holzapfel & Mahall 1999; Castro et al. 2002; Hastwell & Facelli 2003; Prider & Facelli 2004; Gómez-Aparicio et al. 2005), some of them carried out in central Chile (Fuentes et al. 1984, 1986; Becerra & Bustamante 2011). On the other hand, we also observed that herb cover was higher in open sites than under the canopy of *P. radiata* individuals and patches of native

trees. Therefore, we cannot rule out the possibility that some indirect interaction mediated by herbs contributes to the facilitation observed (Levine et al. 2003; Rodríguez 2006). In this case, it is possible that herb species negatively affect regeneration of native woody species and, hence, a potential negative effect of *P. radiata* individuals and patches of native trees on herbs (given the lower herb cover under these canopy types; e.g. Craine & Orians 2004) produced the facilitation.

Species showing higher recruitment under *P. radiata* or native patches than in open sites were mainly those typically classified as shade-tolerant or semi-tolerant (*Cryptocarya alba*, *Peumus boldus*, *Azara celsastrina*, *Lithrea caustica*), which, in general, are also more water-demanding species (Armesto & Pickett 1985; Luebert & Plissock 2005). In contrast, typically pioneer and shade-intolerant species from central Chile, such as *Acacia caven*, *Aristotelia chilensis* and species from the genus *Baccharis* (Armesto & Pickett 1985; Luebert & Plissock 2005) seemed to be inhibited or unaffected by the canopy of native trees and *P. radiata*. Therefore, it is probable that water and light requirements of species, and hence differences in SWC and PAR between canopy types, play an important role in recruitment patterns and facilitation interactions.

Even though our data suggest both native trees and *P. radiata* increased species richness of seedlings, we observed significantly higher species richness in patches of native trees than under the canopy of *P. radiata* individuals in the field experiment. Additionally, more species showed higher abundance values in patches of native trees than under individuals of *P. radiata*. A primary factor probably producing this difference in facilitation could be soil moisture, since moisture in patches of native trees was higher than under *P. radiata* individuals, at least during spring, when germination and recruitment mainly occur in this region. A higher SWC in native patches could be related to increased organic matter observed in soils of native patches than under *P. radiata* trees. Nonetheless, other factors could also be involved. For instance, although leaf litter depth and cover under *P. radiata* individuals did not significantly differ to that of patches of native trees (although slightly deeper under *P. radiata* individuals), density of leaf litter could be higher in *P. radiata* soils, reducing root penetration or shoot emergence. This would need further research. On the other hand, it has been documented that leaf litter of species from the genus *Pinus* contains different chemical compounds (e.g. terpenes) as well as acidifying soils with the consequent loss of nutrients (Lill & McWha 1976; Lill et al. 1979; Scholes & Nowicki 1998; Amioti et al. 2007). However, Guerrero & Bustamante (2007) and Williams (2007) did not find biochemical effects of leaf litter from *P. radiata* on native species from Chile and Australia, respectively.

Therefore, it is unlikely that biochemical factors have an important role in the lower facilitation produced by *P. radiata* than that from native patches, although in our study we cannot rule out this possibility. Furthermore, although we observed no significant difference in soil pH between canopy types, we effectively observed that in all nutrients the concentration was higher in native patches than in the other canopy types, although statistically only for Zn. Probably the low number of replicates influenced the absence of statistically significant differences; therefore, we cannot rule out increased nutrient limitation under *P. radiata* trees than in native patches in our system.

Stronger facilitation produced by native trees than by *P. radiata* individuals suggests that the ecological functions of native trees and individuals of *P. radiata* are not equal. Similarly, in this same region, other native pioneer species, especially shrubs, facilitate native woody species less efficiently than native tree patches (Fuentes et al. 1986). Thus, typical native pioneer species (mainly shrubs) and *P. radiata* may be similar as nurse species for native trees in this region. This suggests that the presence of invading individuals of *P. radiata* may be analogous to other pioneer species from central Chile. Probably, in terms of biological conservation, it would be preferable to have native pioneer species rather than *P. radiata* as nurse plants. However, in terms of ecological restoration, given that *P. radiata* can facilitate many mid-successional (e.g. *Lithrea caustica*, *K. oblonga*, *S. latifolius*) and even some late-successional (e.g. *Cryptocarya alba*, *Peumus boldus*, *Azara celsastrina*) species from central Chile (successional status sensu Armesto & Pickett 1985; Fuentes et al. 1986), invasion of *P. radiata* in open degraded sites where native nurse species are not available, could be exploited for reforestation processes in semiarid regions (e.g. D'Antonio & Meyerson 2002). The use of shrubs as nurse plants for reforestation and restoration processes has been widely recognized (Gómez-Aparicio et al. 2004). Sowing or planting native woody species under invading individuals of *P. radiata* may favour regeneration of native vegetation, with no need to wait for the establishment of native pioneer species to act as nurse plants. Then, after regeneration of native vegetation is established, invading individuals of *P. radiata* should be eliminated. Conservation of some young adult *P. radiata* trees, which probably produce fewer seeds than older trees, for their use as nurse plants during reforestation would not entail increased regeneration and invasion by this species. It would not be advisable to use older adult trees since, although these also may facilitate regeneration of native species, larger seed production may entail higher costs for their elimination. Moreover, the amount of time using young adult pine trees should not be more than 3 or 4 yr, sufficient to

ensure establishment of seedlings of native species, followed by elimination of the pines. During this time, seed production of young adult pine trees would not be high. In fact, among all plots sampled in the two localities (120) for the natural regeneration study, we observed only one seedling of *P. radiata* (0.8% frequency). This result, in addition to the low density of adult trees of *P. radiata* in the two localities, suggest that in this relatively xeric area for this species (north part of pine plantations), its invasion is low or occurs very slowly. Hence, seed production and invasion by new pine individuals should not be a big problem counteracting this proposed restoration strategy. Furthermore, this restoration strategy does not imply that new invading individuals of this exotic species should not be continuously eliminated. Only some of the individuals currently present in the area should be used as nurse plants.

Other studies have also observed that other invasive exotic species may facilitate native species (Walker & Vitousek 1991; Quinos et al. 1998; Siemann & Rogers 2003; Lindsay & French 2005; Rodríguez 2006; Dewine & Cooper 2008). Thus, facilitation from exotic plant species on native plant species may be more common than previously assumed, especially regarding the commonness of positive interactions between plants in stressful environments (Callaway 2007; Maestre et al. 2009). Therefore, restoration processes should first assess the effect of exotic species present in the ecosystem, before establishing the eradication timing of exotic species, with the aim of assessing the potential use of these plants for restoration actions.

Conclusion

The results described in this paper suggest that individuals of the widely invasive species *P. radiata* invading open sites of degraded ecosystems in semi-arid regions do not inhibit or delay the recolonization and secondary succession of native species. In contrast, this exotic species seems to facilitate, or has the potential to facilitate, these processes. Therefore, for restoration practices, when native nurse plants are not available, individuals of this exotic species may be used to accelerate establishment of regeneration of mid- or late-successional species, and once this has occurred, invading individuals of *P. radiata* should be eliminated.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Natural regeneration per canopy type in two localities of central Chile.

Appendix S2. Number of seedlings recruited of species experimentally added 7 mo after sowing per patch type.

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