Effect of a native tree on seedling establishment of two exotic invasive species in a semiarid ecosystem

Pablo I. Becerra · Ramiro O. Bustamante

Abstract Theory predicts that in more stressful environments, positive plant-plant interactions should be more important than negative ones. For instance, in arid and semiarid regions, amelioration of soil drought produced by the shade of established plants could facilitate establishment of other species, in spite of light reduction. However, this theory has not been tested widely in the context of plant invasion. In this paper we evaluated the hypothesis that in a semiarid ecosystem of central Chile, the native tree, *Lithrea caustica*, should facilitate through positive shading effects, the seedling establishment of two widely planted and invasive forestry species, *Pinus radiata* and *Eucalyptus globulus*. We assessed the seedling establishment examining two processes: seedling recruitment (including germination) and subsequent seedling survival. We sowed seeds (to assess recruitment) and planted 8 months old seedlings (to assess seedling survival) of each exotic species under *Lithrea* patches, open sites and under an artificial shade mimicking *Lithrea* shading. The study was repeated in a north-facing and a south-facing slope in the study area located in a xeric zone within the distribution range of plantations of these species in central Chile. Our results show that in a north-facing slope *Lithrea* had positive effects on recruitment of both species, which was produced by shading. These effects were counteracted by negative effects on seedling survival but through a different mechanism, which suggests that *Lithrea* would have no significant effect on the whole seedling establishment process of *Pinus radiata* nor *Eucalyptus globulus* in this habitat. In turn, in a south-facing slope *Lithrea* had no significant effect on recruitment but had a negative effect on seedling survival, which was not produced by shading. This suggests that in this habitat *Lithrea* has a negative effect on the seedling establishment of these exotic species. Our results suggest that the effect of the native *Lithrea caustica* on the seedling establishment of these exotic species is dependent upon the life-cycle phase (recruitment or seedling survival) and habitat even within the same semiarid ecosystem. In contrast to the expected positive effects *Lithrea* is unlikely to facilitate seedling establishment of these exotic species in this area, and in fact in some habitats this effect could be negative. However, our results also suggest that a common mechanism proposed to resist

P. I. Becerra (✉)
Departamento de Ecosistemas y Medio Ambiente, Facultad de Agronomía e Ingeniería Forestal, Universidad Católica de Chile, Av. Vicuña Mackenna 4860, Santiago, Chile
e-mail: pbecerro@uc.cl

P. I. Becerra · R. O. Bustamante
Instituto de Ecología y Biodiversidad, Las Palmeras 3425, Santiago, Chile

R. O. Bustamante
Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Santiago, Chile

invasion in forest ecosystems such as shading, probably is not sufficient to inhibit invasion in a semiarid region.

Keywords　Alien species · Biotic resistance · Facilitation · Plant invasion · Plant-plant interactions · Shading effects

Introduction

Invasion by exotic species is currently a relevant issue in ecology and a global concern for conservation biology (Mooney and Hobbs 2000; Sax et al. 2005). In particular, the role of native vegetation for plant invasion has widely been debated during recent years (Bulleri et al. 2008). Many studies have observed and proposed that native vegetation inhibits invasion by exotic plant species, mainly based on the evidence that disturbances favour exotic plants (e.g. Richardson et al. 1994; Higgins and Richardson 1998; Davis et al. 2000; Davis and Pelsor 2001; Levine et al. 2004; Mitchell et al. 2006; Dewine and Cooper 2008). However, other studies have recently documented that native vegetation may also facilitate some invaders (e.g. Maron and Connors 1996; Richardson et al. 2000; Lenz and Facelli 2003; Siemann and Rogers 2003; Von Holle 2005; Bruno et al. 2005; Cavieres et al. 2005; Badano et al. 2007; Cavieres et al. 2008). From theory, in habitats considered stressful for a target plant species, resident plant species may facilitate its establishment (Bertness and Callaway 1994; Maestre et al. 2009). For instance, when water limitation is the stress factor, positive effects produced by shading of resident plants such as amelioration of soil drought and high temperatures, would be more important than the negative effects due to decrease in light intensity, producing facilitation (Bertness and Callaway 1994; Holmgren et al. 1997; Holzapfel and Mahall 1999; Holmgren et al. 2000; Hastwell and Facelli 2003; Prider and Facelli 2004; Callaway 2007; Maestre et al. 2009). Thus, in ecosystems with water limitations for exotic species, native plants may facilitate establishment of the exotic due to positive shading effects rather than reduce or inhibit invasion. Whilst many studies have assessed this facilitation

mechanism in xeric ecosystems such as arid and semiarid climate regions (e.g. Fuentes et al. 1984; Holzapfel and Mahall 1999; Holmgren et al. 2000; Hastwell and Facelli 2003; Prider and Facelli 2004; Gómez-Aparicio et al. 2005), very few studies have evaluated it in the context of interactions between native and exotic species (e.g. Lenz and Facelli 2003).

Forestry plantations are a major source of invaders worldwide (Richardson 1998; Mooney and Hobbs 2000). In Chile, forestry plantations are predominantly composed of *Pinus radiata* D. Don (Pinaceae) and *Eucalyptus globulus* Labill. (Myrtaceae). These species are also widely used as forestry trees in other parts of the world, and both *P. radiata* (Richardson and Brown 1986; Richardson and Bond 1991; Higgins and Richardson 1998; Lindenmayer and McCarthy 2001; Rouget et al. 2002; Williams and Wardle 2005) and *E. globulus* (Boyd 1996; Rejmánek et al. 2005), have been recognised as important invasive species in some places where they have been introduced, such as Australia, New Zealand and South-Africa in the case of *P. radiata*, and California (USA) in the case of *E. globulus*. In Chile, plantations of these species are primarily in the Mediterranean region of the country including a wide extension of semiarid zones and providing a tremendous propagule source for invasion there (Figueroa et al. 2004). Invasion in Chile by these species is still incipient, but it is already occurring in several locations in the country (Bustamante et al. 2003; Becerra 2006).

Pinus radiata and *E. globulus* are native to Mediterranean climates, *P. radiata* from California (USA) and *E. globulus* from Tasmania and Victoria (Australia). Although the ecology and physiology of these species is well known (Kaufmann 1977; Richardson and Brown 1986; Correia et al. 1989; Boyd 1996; Keeley and Zedler 1998; Higgins and Richardson 1998; López et al. 2000; Lindenmayer and McCarthy 2001; Close et al. 2002; Humara et al. 2002; Walcroft et al. 2002; Bustamante and Simonetti 2005; Becerra 2006), little is known about the interaction between these species and native species in the exotic and native range. *Pinus radiata* and *E. globulus* are considered shade-intolerant species (Correia et al. 1989; Keeley and Zedler 1998; Walcroft et al. 2002), and consistent with this some studies have documented a greater seedling establishment, density and invasion in open sites or where disturbances have diminished vegetation cover (e.g.

Richardson and Brown [1986](javascript); Lindenmayer and McCarthy [2001](javascript); Close et al. [2002](javascript); Walcroft et al. [2002](javascript); Bustamante and Simonetti [2005](javascript); Williams and Wardle [2005](javascript)). However, these patterns have mainly been evaluated in temperate regions or humid mediterranean zones, where water availability is not an important stress factor. Thus, it is not clear if in more xeric climates within the geographic range of these species, native vegetation will also have a negative effect. In environments where water may be a limiting factor for *P. radiata* and *E. globulus* such as the northern area of plantations in central Chile, resident native plants may facilitate establishment and invasion of these exotic species due to positive shading effects (Bertness and Callaway [1994](javascript); Holmgren et al. [1997](javascript)). In this study we experimentally address whether in a xeric environment for these exotic species, a native species has the potential to facilitate its seedling establishment through positive shading effects. Specifically, we assess the net effect as well as the particular effect produced by shading of the widely distributed and abundant chilean native tree species *Lithrea caustica* (Mol.) H. et A. (Anacardiaceae), on two subsequent phases in the seedling establishment process (recruitment and seedling survival) of *P. radiata* and *E. globulus* in a semiarid ecosystem of central Chile. We predict that in this semiarid ecosystem, *Lithrea caustica* will facilitate the recruitment and seedling survival of *P. radiata* and *E. globulus* due to positive shading effects.

Methods

Study site

The study was carried out in a relatively xeric zone within the Mediterranean region of Chile. The Chilean Mediterranean region is characterised by a semiarid and seasonal climate, with precipitation concentrated in winter although an important increase in precipitation occurs latitudinally. In addition, most of the human population of Chile resides within this region, and therefore it has been intensively disturbed. 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](javascript)).

The study was located in a watershed immediately adjacent to the eastern border of the city of Santiago (33°30′S, 70°30′W), specifically in the San Ramón Creek watershed. This area is located near the northern limit of plantations of *Pinus radiata* (hereafter *Pinus*) and *Eucalyptus globulus* (hereafter *Eucalyptus*) in Chile, representing the most xeric zone where these species are planted. The climate in this locality is semiarid, characterised by 5–6 dry months and precipitation concentrated during winter, reaching an annual average of 347 mm and an annual mean temperature of 15°C (Dirección Meteorológica de Chile [2008](javascript)). The topography of the study site is dominated by north-facing slopes and south-facing slopes. The study was performed during 2004 and 2005. Precipitation during 2004 was 353 mm, and during 2005, 434 mm.

The study site has not been extensively disturbed (logging, fire or livestock) during the past 10 years and currently is protected by the Chilean Forest Service. The vegetation is spatially heterogeneous, composed of herbaceous, shrub and tree patches. Woody (tree and shrub patches) are composed almost exclusively of native species while herbaceous patches are composed of native as well as exotic herbs. Tree patches of the watershed average approximately 30% cover and are dominated by *Lithrea caustica*. The size of herbaceous and tree patches varied naturally between 20 and 150 m^2 approximately. However, for the study we selected tree and herbaceous patches (see Experimental design) between 80 and 120 m^2. Height of these tree patches varied between 5 and 7 m. Plantations of *Pinus* and *Eucalyptus* in the area are small and no individual of these species was present within the area of the experiment.

Experimental design

The experiment was performed under a climate representing a xeric and stressful condition for these exotic species within the mediterranean region of Chile, as it was located at the northern part of the plantation zone of these exotic species. Our results, therefore, may be generalized to this zone and not necessarily the entire Mediterranean region of Chile. Furthermore, within any zone in the Mediterranean region of Chile south-facing slopes are frequently moister than north-facing slopes (Armesto and

Martínez 1978) with potentially important influences in plant-plant interactions and communities (Badano et al. 2005). In order to assess this potential variability, at least at this spatial scale, we repeated the experiment in a north-facing and a south-facing slope (hereafter habitats) located within the study area (0.5 km apart). Both habitats have typical vegetation, fauna, soils, and disturbance history for the region and for central Chile. Thus, our experiment was carried out under the more typical environmental conditions in the region.

Our study was designed to evaluate the net (or total) effect of *Lithrea* as well as the particular effect produced by shading on recruitment and seedling survival of *Pinus* and *Eucalyptus*. We evaluated the net effect of *Lithrea* contrasting recruitment and seedling survival of both exotic species between *Lithrea* patches and nearby open sites (without woody plants). Further, in order to isolate the shading effect, we compared recruitment and seedling survival between sites with artificial shading located in originally open sites with open sites not manipulated. This allows contrasting sites with different shading but equal soil conditions (e.g. Holzapfel and Mahall 1999; Gómez-Aparicio et al. 2005). Artificial shading (hereafter canopy mimic treatment sensu Callaway 2007) consisted of a 4 × 4 m piece of black nylon shade-cloth, suspended 2 m above the ground from iron posts. Our aim was to simulate at least the levels of light and air temperature occurring under *Lithrea* canopies.

In total, we used three canopy treatments: (1) open sites (without woody canopy), (2) *Lithrea* patches and, (3) *Lithrea* canopy mimics. Each canopy treatment was replicated ten times in each habitat, yielding a total of 30 replicates per habitat and 60 replicates in total. Replicates were located at least 10 m apart, and were separated by other patch types in order to maximise statistical independence among them. Each replicate consisted of a 1 × 1.5 m plot, fenced on the sides and the top by a wire mesh in order to exclude mammals and birds. We used this plot size to keep at least 1 or 2 m apart from the edge of shade-cloths (artificial shadings) and *Lithrea* canopies. At the beginning of winter (20–25 June 2004) we planted three seedlings of each exotic species each 30 cm in two rows 30 cm apart, within the 0.5 × 1 m area in each plot. For this size plot we preferred to use only three seedlings in order to

reduce potential competition between them during the period of the experiment. Furthermore, within the 1 × 1 m area in each plot, we sowed 50 seeds of each species (20–25 June 2004) which were placed on the ground to simulate the depth and microhabitat at which seeds are located after a natural seed rain. We preferred to use only 50 seeds spaced 10 cm apart to reduce the probability of competition between them as well as recently germinated seedlings. Seedlings of each species were 8 months old at the time of planting. Seedling heights at time of planting were 19.7 cm ± 0.15 and 22.9 cm ± 0.19 (mean ± 1SE) for *Pinus* and *Eucalyptus*, respectively. This period of sowing is similar to that when seeds are dispersed naturally in central Chile. Seedlings and seeds were obtained from the greenhouse of the University of Chile, Santiago. These seeds are collected from plantations of both species located in the Mediterranean zone of Chile. Seedlings were produced from the same seed types in long tubes so as to not inhibit tap root development.

Microenvironmental measurements

In order to characterise the microenvironment of each canopy treatment in each habitat, we measured photosynthetic active radiation (PAR), soil water content (SWC), soil nutrient concentration (N, P, K), soil pH, air temperature and herb cover. PAR was measured at the soil level and at 30 cm above the ground (in order to differentiate light on the top of seedlings and light for recently germinated seedlings potentially affected by herbs). PAR was quantified using a light sensor (LI-COR, Lincoln, USA) to take instantaneous PAR measurements directly beneath *Lithrea* patches, canopy mimics and in open sites. In each replicate of each canopy treatment we sampled light as the mean of 45 s reading. This procedure was repeated on three different days during the growing season (October 2004) on days with <5% cloud cover between 12:00 PM and 13:00 PM. We assumed that differences between canopy treatments are similar through the year. Air temperature was measured in the same way as light. We used the mean of 45 s reading with an air thermo-hygrometer (Deltatrak 13307, resolution: 0.1°C) in each replicate on three sunny days (<5% cloud cover) in summer (January 2005), between 12:00 PM and 13:00 PM. We evaluated air temperature in summer in order to

describe differences between canopy treatments in the period when temperature differences can be greater in this region. SWC was evaluated using the gravimetric method (by quantifying changes in weight after 48 h drying soil samples at 80°C) and was measured four times (approximately every 3 weeks) in each season for each experimental replicate. Soil samples for moisture evaluation were approximately 250 cm^3, collected from the first 10 cm depth. We used the average from the four measurements to quantify the SWC in each season per replicate. Soil nutrients (N, P, K) and pH were evaluated once by sampling the soil (15 cm of soil without leaf litter) on a summer day in January, 2005. Soil samples for nutrient analyses were collected in eight randomly selected replicates per treatment (four per treatment and habitat). Finally, in order to describe probable differences of herb cover between canopy treatments we evaluated percentage of herb cover in each replicate using the intercept point method.

Measurements of seedling establishment and analyses

Seedling establishment of *Pinus* and *Eucalyptus* was divided into two continuous phases: recruitment and seedling survival. We assessed recruitment probability as the percentage of seeds that germinated and survived from the 50 seeds initially sown in each replicate until 1 year after sowing (June 2005). Seeds were monitored monthly since sowing. All seed germination occurred between 3 and 5 months after sowing. Seedlings germinated from experimental seeds were approximately 8 months old at the end of the experiment (June 2005), a similar age to seedlings planted at the beginning of the experiment. Therefore we were able to evaluate a continuous seedling establishment process including germination and seedling survival until the seedlings were 1 year and 8 months old. Statistical analyses for the recruitment experiment were performed with two-way ANOVA (canopy treatment and habitat as factors) for each exotic species separately and Arc sine-transformed.

Survival of planted seedlings of each exotic species was quantified by the number of living seedlings 1 year after planting from the three originally planted per plot. Seedlings were monitored every 2 months for 1 year after planting (June 2004–June 2005), but we only used survival values 1 year after planting (June 2005) in order to examine the final survival after all seasons. Because seedling survival corresponded to count data, statistical analyses for seedling survival were performed with GLIM (Generalized Linear Models) assuming a Poisson data distribution and an "Identity" function link, with LSD Post-hoc tests, using SPSS 15.0 (SPSS 2006) for each species separately.

Results

Microenvironment

PAR at soil level significantly differed between canopy treatments ($F_{2,54} = 19.17$, $P < 0.001$) but not between habitats ($F_{1,54} = 0.28$, $P = 0.60$). Statistical interaction between these factors was not significant ($F_{2,54} = 0.02$, $P = 0.98$). In both habitats PAR at soil level was significantly higher in open sites than in *Lithrea* patches and canopy mimics, with no significant difference between these two last canopy treatments (Table 1). Similarly, PAR at 30 cm level significantly differed between canopy treatments ($F_{2,54} = 322.24$, $P < 0.001$) but not between habitats ($F_{1,54} = 0.95$, $P = 0.33$), and the statistical interaction between these factors was not significant ($F_{2,54} = 1.17$, $P = 0.32$). In both habitats PAR at 30 cm level was significantly higher in open sites than in *Lithrea* patches and canopy mimics, with no significant difference between these two last canopy treatments (Table 1).

Air temperature differed significantly between canopy treatments ($F_{2,54} = 57.49$, $P < 0.001$) and habitats ($F_{1,54} = 12.45$, $P < 0.001$). Statistical interaction between these factors was not significant ($F_{2,54} = 0.02$, $P = 0.98$). Air temperature was significantly higher in open sites than in *Lithrea* patches and canopy mimics, with no difference between the last two canopy treatments (Table 1). In general, air temperature was higher in the north-facing than in the south-facing slope (Table 1).

Soil water content (SWC) showed different patterns between seasons. In winter (2004), we found no significant differences between canopy treatments ($F_{2,54} = 0.41$, $P = 0.67$), but it was significantly higher in the south-facing than in the north-facing

Table 1 Values (mean ± 1 SD) for each environmental variable compared between canopy treatments [open (O), *Lithrea* (L) and *Lithrea* canopy mimic (M)] and habitats

Variable	North-facing slope habitat			South-facing slope habitat		
	M	L	O	M	L	O
PAR at soil level ($\mu mol\ m^{-2}\ s^{-1}$)	$67.4^{Aa} \pm 23.1$	$54.0^{Aa} \pm 7.8$	$431.1^{Ab} \pm 109.7$	$81.3^{Aa} \pm 32.3$	$67.5^{Aa} \pm 26.4$	$468.6^{Ab} \pm 132.2$
PAR 30 cm level ($\mu mol\ m^{-2}\ s^{-1}$)	$264.3^{Aa} \pm 35.6$	$233.4^{Aa} \pm 28.3$	$1340.8^{Ab} \pm 103.8$	$217.9^{Aa} \pm 38.3$	$192.0^{Aa} \pm 49.8$	$1476.9^{Ab} \pm 45.1$
SWC (winter 2004) (%)	$19.1^{Aa} \pm 0.4$	$20.3^{Aa} \pm 0.8$	$18.2^{Aa} \pm 0.9$	$23.5^{Ba} \pm 0.9$	$23.1^{Ba} \pm 0.7$	$23.5^{Ba} \pm 1.3$
SWC (spring 2004) (%)	$15.5^{Aa} \pm 0.7$	$19.0^{Ab} \pm 1.1$	$10.9^{Ac} \pm 0.5$	$19.3^{Ba} \pm 0.9$	$20.2^{Aa} \pm 0.9$	$18.1^{Ba} \pm 1.0$
SWC (summer 2005) (%)	$3.2^{Aa} \pm 0.2$	$4.6^{Ab} \pm 0.2$	$2.4^{Ac} \pm 0.3$	$3.3^{Aa} \pm 0.2$	$4.4^{Ab} \pm 0.2$	$2.2^{Ac} \pm 0.2$
SWC (autumn 2005) (%)	$15.8^{Aa} \pm 0.9$	$16.9^{Aa} \pm 0.9$	$14.7^{Aa} \pm 1.0$	$20.1^{Ba} \pm 0.9$	$20.6^{Ba} \pm 0.9$	$20.7^{Ba} \pm 0.6$
Air temperature (°C)	$34.8^{Aa} \pm 1.6$	$31.4^{Aa} \pm 1.6$	$44.8^{Ab} \pm 1.8$	$30.8^{Ba} \pm 0.4$	$27.9^{Ba} \pm 0.5$	$41.0^{Bb} \pm 1.1$
Herb cover (%)	$77.5^{Aa} \pm 22.5$	$72.5^{Aa} \pm 11.4$	$70.5^{Aa} \pm 17.7$	$73.5^{Aa} \pm 11.8$	$59.0^{Aa} \pm 12.1$	$62.0^{Aa} \pm 12.5$
Nitrogen (ppm)	$27.7^{Aa} \pm 4.4$	$21.0^{Aa} \pm 1.5$	$20.3^{Aa} \pm 2.9$	$50.0^{Ba} \pm 11.5$	$26.0^{Aa} \pm 4.0$	$39.3^{Ba} \pm 11.6$
Phosphorous (ppm)	$24.0^{Aa} \pm 7.2$	$15.3^{Aa} \pm 6.3$	$21.7^{Aa} \pm 4.8$	$45.7^{Ba} \pm 4.1$	$60.3^{Ba} \pm 2.7$	$59.0^{Ba} \pm 10.2$
Potassium (ppm)	$280.0^{Aa} \pm 42.6$	$305.0^{Aa} \pm 21.4$	$259.3^{Aa} \pm 14.2$	$452.3^{Ba} \pm 80.8$	$587.3^{Ba} \pm 127.3$	$608.0^{Ba} \pm 153.4$
Soil pH	$6.70^{Aa} \pm 0.15$	$6.73^{Aa} \pm 0.23$	$6.67^{Aa} \pm 0.32$	$6.13^{Ba} \pm 0.12$	$6.20^{Ba} \pm 0.21$	$6.33^{Ba} \pm 0.12$

SWC soil water content, *PAR* photosintetically active radiation. For nutrients and soil pH, N = 4 per treatment. For other variables N = 10 per treatment. Different lowercase and uppercase letters indicate significant differences (Tukey-test, $P < 0.05$) between canopy treatments for a single habitat and between habitats for a single canopy treatment, respectively

slope ($F_{1,54} = 33.07$, $P < 0.001$) (Table 1). Statistical interaction between these factors was not significant ($F_{2,54} = 1.02$, $P = 0.37$). In spring (2004), there was significant differences in SWC between canopy treatments ($F_{2,54} = 16.00$, $P < 0.001$), and it was significantly higher in the south-facing slope ($F_{1,54} = 29.58$, $P < 0.001$). However, the statistical interaction was significant ($F_{2,54} = 5.37$, $P = 0.01$). In the north-facing slope the soil in *Lithrea* patches was significantly moister than in canopy mimics and open sites, and under canopy mimics significantly moister than in open sites (Table 1). In turn, in the south-facing slope we found no significant difference between canopy treatments (Table 1). In summer (2005), we found differences in SWC between canopy treatments ($F_{2,54} = 52.20$, $P < 0.001$) but not between habitats ($F_{1,54} = 0.29$, $P = 0.59$), and the statistical interaction was not significant ($F_{2,54} = 0.38$, $P = 0.68$). In both habitats, the soil in *Lithrea* patches was significantly moister than the other two canopy treatments, and canopy mimics significantly moister than open sites (Table 1). Finally, in autumn (2005), we found no significant

difference in SWC between canopy treatments ($F_{2,54} = 0.73$, $P = 0.49$), but it was significantly higher in the south-facing than in the north-facing slope ($F_{1,54} = 41.26$, $P < 0.001$) (Table 1), and the statistical interaction was not significant ($F_{2,54} = 0.88$, $P = 0.42$).

Herb cover did not differ statistically between canopy treatments ($F_{2,54} = 2.25$, $P = 0.12$), nor between habitats ($F_{1,54} = 4.19$, $P = 0.06$). The statistical interaction was not significant ($F_{2,54} = 0.42$, $P = 0.66$).

Soil pH did not differ significantly between canopy treatments ($F_{2,18} = 0.08$, $P = 0.92$). In turn soil pH was significantly higher in the north-facing than in the south-facing slope ($F_{1,18} = 8.18$, $P = 0.01$) (Table 1), and the statistical interaction was not significant ($F_{2,18} = 0.19$, $P = 0.83$).

Nitrogen available in the soil did not differ significantly between canopy treatments ($F_{2,18} = 2.27$, $P = 0.15$). In turn, nitrogen was significantly higher in the south-facing than in the north-facing slope ($F_{1,18} = 6.83$, $P = 0.02$) (Table 1), and the statistical interaction was not significant ($F_{2,18} = 0.81$, $P = 0.47$).

Phosphorus available in the soil did not differ significantly between canopy treatments ($F_{2,18} = 0.82$, $P = 0.46$). In turn, phosphorus was significantly higher in the south-facing than in the north-facing slope ($F_{1,18} = 53.24$, $P < 0.001$) (Table 1), and the statistical interaction was not significant ($F_{2,18} = 3.42$, $P = 0.07$).

Finally, potassium available in the soil did not differ significantly between canopy treatments ($F_{2,18} = 0.46$, $P = 0.64$). In turn, potassium was significantly higher in the south-facing than in the north-facing slope ($F_{1,18} = 13.24$, $P < 0.001$) (Table 1), and the statistical interaction was not significant ($F_{2,18} = 0.49$, $P = 0.63$).

The absence of differences in light intensity and air temperature between *Lithrea* patches and canopy mimics indicates that the artificial shading allowed us to efficiently simulate shading effects of *Lithrea* canopy under similar soil conditions.

Recruitment

For *Eucalyptus,* recruitment percentage differed significatly between canopy treatments ($F_{2,54} = 11.21$, $P < 0.001$) and between habitats ($F_{1,54} = 5.92$, $P = 0.018$). However, we found a significant statistical interaction between both factors ($F_{2,54} = 16.47$, $P = 0.032$). Specifically, we observed that in the north-facing slope recruitment was significantly higher under *Lithrea* canopies and canopy mimics than in open sites, with no significant difference between the first two treatments (Fig. 1). In turn, in the south-facing slope we found no significant difference between canopy treatments (Fig. 1). In addition, recruitment was significantly higher in the south-facing than in the north-facing slope although only in open sites (Fig. 1).

In *Pinus*, recruitment percentage differed significantly between canopy treatments ($F_{2,54} = 15.00$, $P < 0.001$) and between habitats ($F_{1,54} = 47.28$, $P < 0.001$). However, we also found a significant interaction between these two factors ($F_{2,54} = 3.09$, $P = 0.049$). In the north-facing slope, *Pinus* recruitment was significantly higher under *Lithrea* canopies and canopy mimics than in open sites, with no significant difference between the first two treatments (Fig. 1). In turn, in the south-facing slope we found no significant difference between canopy treatments (Fig. 1). In addition, recruitment was significantly
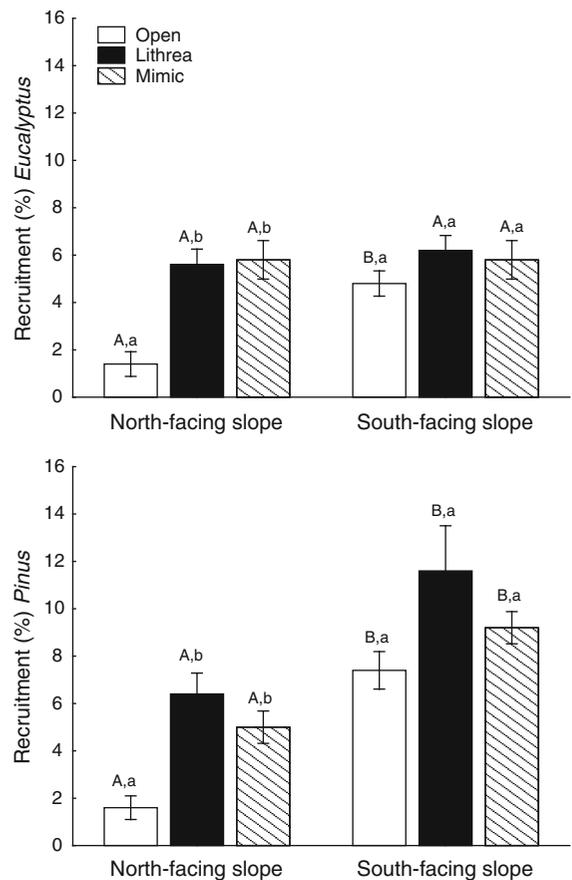
Fig. 1 Recruitment percentage of *Pinus* and *Eucalyptus* (1 year after sowing and approximately 8 months after germination), in each type of canopy treatment (open, *Lithrea*, *Lithrea* canopy mimic) and habitat (North-facing and South-facing slope) (mean ± 1SE). N for each *bar* = 10. Different *elowercas* and *uppercase letters* indicate significant statistical differences (Tukey Post-hoc tests, $P < 0.05$) between canopy treatments within a single habitat and between habitats within a single canopy treatment, respectively

higher in the south-facing than in the north-facing slope in all canopy treatments (Fig. 1).

Seedling survival

For *Eucalyptus*, seedling survival 1 year after planting differed significantly between canopy treatments ($Chi^2 = 20.81$, $N = 60$, $P < 0.001$) with no significant difference between habitats ($Chi^2 = 0.001$, $N = 60$, $P = 0.98$). Furthermore, interaction between these two factors was not significant ($Chi^2 = 1.64$, $N = 60$, $P = 0.44$). In both habitats seedling survival in open sites and canopy mimics

was significantly greater than in *Lithrea* patches, with no difference between the first two treatments (Fig. 2). Similarly, for *Pinus*, seedling survival 1 year after planting differed significantly between canopy treatments (Chi^2 = 16.65, N = 60, $P < 0.001$), with no significant difference between habitats (Chi^2 = 0.01, N = 60, $P = 0.91$), and the statistical interaction between canopy and habitat was not significant (Chi^2 = 0.11, N = 60, $P = 0.95$). In both habitats seedling survival in open sites and canopy mimics was significantly greater than in *Lithrea* patches, with no difference between the first two treatments (Fig. 2).

Discussion

Our results only partially supported the hypothesis that in this semiarid ecosystem representing a xeric and stressful environment for the exotic trees *Pinus radiata* and *Eucalyptus globulus*, the native tree *Lithrea caustica* would facilitate their recruitment and seedling survival due to positive shading effects. Our results indicate that the effect of *Lithrea* depended on the life-cycle stage of the exotic species (recruitment or seedling survival), and habitat (a north-facing or a south-facing slope). Specifically, in the north-facing slope *Lithrea* facilitated the recruitment but inhibited the seedling survival of these species. In contrast, in the south-facing slope *Lithrea* produced no significant net effect on recruitment, but it had a negative net effect on seedling survival of both exotic species. Thus, combining both recruitment and seedling survival, in the north-facing slope *Lithrea* resulted in no significant effect on the whole seedling establishment process of these exotic species. However, our results suggest that in the south-facing slope *Lithrea* has a predominantly negative effect on the seedling establishment process of both species.

In addition, our results suggest that mechanisms by which *Lithrea* affected the recruitment and seedling survival differed. The positive net effect of *Lithrea* on recruitment of the two exotic species in the north-facing slope is likely to be caused by a positive shading effect as we found greater recruitment under canopy mimics than in open sites. On the south-facing slope we found no significant difference between canopy treatments, suggesting that when
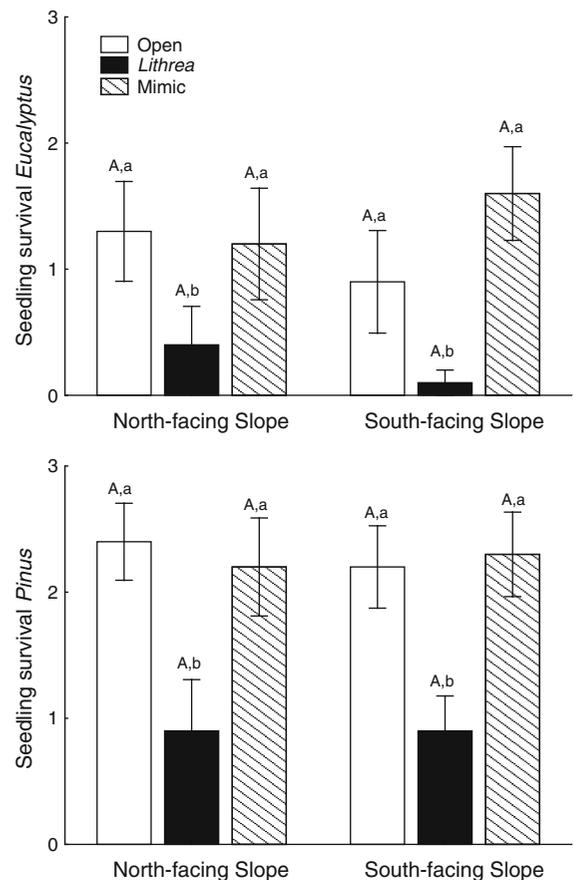

Fig. 2 Seedling survival (number of living seedlings per replicate 1 year after planting) of *Pinus* and *Eucalyptus* in each type of canopy treatment (open, *Lithrea*, *Lithrea* canopy mimic) and habitat (North-facing and South-facing slope) (mean ± 1SE). N for each *bar* = 10. Different *lowercase* and *uppercase letters* indicate significant statistical differences (GLIM, LSD Post-hoc tests, $P < 0.05$) between canopy treatments within a single habitat and between habitats within a single canopy treatment, respectively

there is no significant shading effect there also is no significant net effect of *Lithrea* on recruitment of these exotic species. The positive shading effects may have been produced by greater soil moisture observed under canopy mimics and *Lithrea* patches than in open sites during spring and summer, which has frequently been documented and related to facilitation processes in semiarid ecosystems (e.g. Fuentes et al. 1984; Holzapfel and Mahall 1999; Holmgren et al. 2000; Hastwell and Facelli 2003; Lenz and Facelli 2003; Prider and Facelli 2004; Gómez-Aparicio et al. 2005). Nonetheless, it is not possible to rule out other mechanisms

producing this pattern, for instance, photoinhibition or direct negative effects of high temperatures on recruitment in the open (Callaway 2007), as light and air temperature decreased under canopy mimics and *Lithrea* patches with respect to open sites.

On the other hand, the negative net effect of *Lithrea* on seedling survival of both exotic species in each habitat was not produced by shading as we observed no significant difference between canopy mimics and open sites in seedling survival of either exotic species. We may speculate that some soil-related variable could have a role in this negative net effect. Canopy mimics efficiently simulated shading under *Lithrea* patches and therefore the main differences between these canopy treatments could be related to soil characteristics (e.g. Gómez-Aparicio et al. 2005). Thus, greater seedling survival under canopy mimics than in *Lithrea* patches in both species and habitats suggest that some soil variable related to *Lithrea*, for instance, litter, allelopathic compounds, soil microorganisms, water or nutrient availability below 15 cm in the soil (as above 15 cm deep these treatments did not differ in SWC, nutrients or soil pH), etc., (Callaway 2007), could have produced this negative net effect, although some indirect interaction may have also played a role (Mitchell et al. 2006). Clearly, this requires further research.

Despite both species having been recognized as shade-intolerant species (Correia et al. 1989; Keeley and Zedler 1998; Walcroft et al. 2002), this biological attribute was not the factor triggering negative net effects from *Lithrea* on their seedling survival and with this neutral effects on the whole establishment process. Shading produced no negative effect on the recruitment nor seedling survival of these species, although we can not rule out that negative effects of light reduction could have been counteracted, for example, by beneficial effects of greater soil moisture or less air temperature under canopy (natural or mimic). Martin et al. (2009) documented that while many exotic plants are shade-intolerant and invade mainly disturbed or open habitats, there also are many other shade-tolerant exotic species which frequently invade undisturbed forest ecosystems. In contrast, our results suggest that shading alone will not necessarily inhibit invasion even by shade-intolerant species such as *Pinus radiata* and *Eucalyptus globulus*. These species can successfully recruit and establish under shading produced by the canopy of some plant species in this ecosystem. It is possible that these species are not shade-intolerant during the seed or seedling stages, and that only during older stages they become more shade-intolerant. In fact, canopy treatments had different effects on the recruitment compared with seedling survival for both species, suggesting an ontogenetic shift in the ecological requirements of *Pinus radiata* and *Eucalyptus globulus*. Similarly, several other studies have also documented this type of change in other species (Schupp 1995; Miriti 2006; Schiffers and Tielbörger 2006; Lortie and Turkington 2008; Armas and Pugnaire 2009). Specifically, our results are consistent with the seed-seedling conflict hypothesis proposed by Schupp (1995). Thus, this ontogenetic shift between recruitment and seedling survival suggests that other shifts may arise along the life-cycle of these species, for instance, an increase in shade-intolerance as exists evidence that these species are more shade-intolerant during sapling and adult stages (Correia et al. 1989; Keeley and Zedler 1998; Walcroft et al. 2002).

Because we assessed only a short period along the life-cycle of these species (seedling establishment up to approximately 2 years old seedlings), our results do not allow to predict the total effect of *Lithrea* on them. For instance, the effect of *Lithrea* on reproduction or other older stages in these exotic species is still unknown. Nevertheless, given the great relevance of early life-stages such as seedling establishment for population pattern and processes (Harper 1977), our results suggest that *Lithrea* may help to resist invasion by these exotic species. On the other hand, whilst this experiment was carried out over a single year, our results were produced during a period with climatically average conditions for the region. In particular, rainfall during the experimental period (353 mm in 2004 and 434 in 2005) was very close to the average for the region (347 mm). However, because plant-plant interactions may vary depending on the climate conditions of each year (Callaway 2007; Maestre et al. 2009), our results may vary between years with contrasting climatic conditions, particularly during very dry or wet years.

Overall, our results suggest that even in a stressful environment for these exotic tree species, a native tree such as *Lithrea* may help to resist plant invasion through negative or at least no facilitative effects on

seedling establishment, depending on the habitat. Thus, these results suggest that increasing or at least retaining *Lithrea* cover may help to reduce the probability of invasion of *Pinus radiata* and *Eucalyptus globulus* in the more xeric environments where these species are planted. However, our results also suggest that a common mechanism proposed to resist invasion in forest ecosystems such as shading (Martin et al. 2009), is not sufficient to inhibit invasion by these exotic species in semiarid regions.

References

Armas C, Pugnaire FI (2009) Ontogenetic shifts in interactions of two dominant shrub species in a semi-arid coastal sand dune system. J Veg Sci 20:535–546

Armesto JJ, Martínez J (1978) Relations between vegetation structure and slope aspect in the Mediterranean region of Chile. J Ecol 66:881–889

Badano E, Cavieres LA, Molina-Montenegro MA, Quiroz CL (2005) Slope aspect influences plant association patterns in the Mediterranean matorral of central Chile. J Arid Environ 62:93–108

Badano E, Villarroel E, Bustamante RO, Marquet PA, Cavieres LA (2007) Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. J Ecol 95:682–688

Becerra P (2006) Invasión de árboles alóctonos en una cuenca de Chile central. Gayana Botanica 63:161–174

Bertness MD, Callaway RM (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Boyd D (1996) Eucalyptus globulus: Bluegum *Eucalyptus*. In: Randall JM, Marinelli J (eds) Invasive plants: weeds of the global garden. Science Press, New York, p 32

Bruno JF, Fridley JD, Bromberg KD, Bertness MD (2005) Insights into biotic interactions from studies of species invasions. In: Sax DF, Stachowicz JJ, Gaines SD (eds) Species invasions: insights into ecology, evolution and biogeography. Sinauer Associates, Inc., USA, pp 13–40

Bulleri F, Bruno JF, Benedetti-Cecchi L (2008) Beyond competition: incorporating positive interactions between species to predict ecosystem invasibility. PLOS Biology 6:1136–1140

Bustamante RO, Simonetti JA (2005) Is *Pinus radiata* invading the native vegetation in central Chile?, demographic responses in a fragmented forest. Biol Invasions 7:243–249

Bustamante RO, Serey IA, Pickett STA (2003) Forest fragmentation, plant regeneration and invasion processes across edges in central Chile. In: Bradshaw GA, Marquet PA (eds) How landscape change. Springer-Verlag, Berlin, pp 145–158

Callaway RM (2007) Positive interactions and interdependence in plant communities. Springer, Dordrecth, The Netherlands

Cavieres LA, Quiroz CL, Molina-Montenegro MA, Muñoz AA, Pauchard A (2005) Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native Taraxacum officinale in the high-Andes of central Chile. Perspectives Plant Ecol Evol Syst 7:217–226

Cavieres LA, Quiroz CL, Molina-Montenegro MA (2008) Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: are there differences between nurses? Funct Ecol 22:148–156

Close DC, Beadle CL, Holz GK, Brown PH (2002) Effect of shadecloth tree shelters on cold-induced photoinhibition, foliar anthocyanin and growth of *Eucalyptus globulus* and *E. nitens* seedlings during establishment. Aust J Botany 50:15–20

Correia M, Torres F, Pereira J (1989) Water and nutrients supply regimes and water relations of juvenile leaves of *Eucalyptus globulus*. Tree Physiol 5:459–471

Davis MA, Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. Ecol Lett 4:421–428

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Dewine JM, Cooper DJ (2008) Canopy shade and the successional replacement of tamarix by native box elder. J Appl Ecol 45:505–514

Dirección Meteorológica de Chile (2008) www.meteochile.cl. November, 2008

Figueroa JA, Castro SA, Marquet PA, Jaksic FM (2004) Exotic plant invasion to the Mediterranean region of Chile: causes, history and impacts. Revista Chilena de Historia Natural 77:465–483

Fuentes ER, Otaiza RD, Alliende MC, Hoffmann AJ, Poiani A (1984) Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. Oecologia 62:405–411

Gómez-Aparicio L, Gomez JM, Zamora R, Boettinger JL (2005) Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. J Veg Sci 16:191–198

Harper JL (1977) The population biology of plants. Academic Press, London

Hastwell G, Facelli JM (2003) Differing effects of shade-induced facilitation on growth and survival during the establishment of a chenopod shrub. J Ecol 91:941–950

Higgins SI, Richardson DM (1998) Pine invasions in the southern hemisphere: modeling interactions between organism, environment and disturbance. Plant Ecol 135:79–93

Holmgren M, Scheffer M, Huston MA (1997) The interplay of facilitation and competition in plant communities. Ecology 78:1966–1975

Holmgren M, Segura AM, Fuentes ER (2000) Limiting mechanisms in the regeneration of the Chilean matorral. Plant Ecol 147:49–57

Holzapfel C, Mahall BE (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. Ecology 80:1747–1761

Humara JM, Casares A, Majada J (2002) Effect of seed size and growing media water availability on early seedling growth in *Eucalyptus globulus*. For Ecol Manag 167:1–11

Kaufmann M (1977) Soil temperature and drought effects on growth of Monterey pine. Forest Sci 23:317–325

Keeley JE, Zedler PH (1998) Evolution of life histories in *Pinus*. In: Richardson DM (ed) Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, pp 219–250

Lenz TI, Facelli JM (2003) Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. Austral Ecol 28:480–490

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to alien plant invasions. Ecol Lett 7:975–989

Lindenmayer DB, McCarthy MA (2001) The spatial distribution of non-native plant invaders in a pine-eucalypt landscape mosaic in south-eastern Australia. Biol Conserv 102:77–87

López M, Humara JM, Casares A, Majada J (2000) The effect of temperature and water stress on laboratory germination of Eucalyptus globulus Labill. seeds of different sizes. Annals Forest Sci 57:245–250

Lortie CJ, Turkington R (2008) Species-specific positive effects in an annual plant community. Oikos 117:1511–1521

Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation plant communities. J Ecol 97:199–205

Maron JL, Connors PG (1996) A native nitrogen-fixing shrub facilitates weed invasion. Oecologia 105:302–312

Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers Ecol Environ 7:142–149

Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. J Ecol 94:973–979

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Huafbauer RA, Kironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloon EW, Torchin ME, Vasquez DP (2006) Biotic interactions and plant invasions. Ecol Lett 9:1–15

Mooney HA, Hobbs HA (2000) Invasive species in a changing world. Island Press, California

Prider JN, Facelli JM (2004) Interactive effects of drought and shade on three arid zone chenopod shrubs with contrasting distributions in relation to tree canopies. Funct Ecol 18:67–76

Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ, Grotkopp E (2005) Ecology of invasive plants - state of the art. In: Mooney HA, Mack RN, Mc Neely JA, Neville L, Schei PJ, Waage J (eds) Invasive alien species: a new synthesis. Island Press, Washington, DC, pp 104–161

Richardson DM (1998) Forestry trees as invasive aliens. Conserv Biol 12:18–26

Richardson DM, Bond WJ (1991) Determinants of plant distribution: evidence from pine invasions. American Naturalist 137:639–668

Richardson DM, Brown PJ (1986) Invasion of mesic mountain Fynbos by *Pinus radiata*. S Afr J Bot 52:529–536

Richardson DM, Williams PA, Hobbs RJ (1994) Pine invasions in the southern hemisphere: determinants of spread and invadability. J Biogeogr 21:511–527

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions - the role of mutualisms. Biol Rev 75:65–93

Rouget M, Richardson DM, Milton S, Polakow D (2002) Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecol 152:79–92

Sax DF, Stachowicz JJ, Gaines SD (2005) Species Invasions. Insights into ecology, evolution and biogeography. Sinauer Associates, Inc., USA

Schiffers K, Tielbörger K (2006) Ontogenetic shifts in interactions among annual plants. J Ecol 94:336–341

Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am J Bot 82:399–409

Siemann E, Rogers WE (2003) Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. J Ecol 91:923–931

SPSS (2006) SPSS version 15.0 for Windows. SPSS, Chicago, Illinois, USA

Von Holle B (2005) Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. J Ecol 93:16–26

Walcroft AS, Whitehead D, Kelliher FM, Arneth A, Silvester WB (2002) The effects of long-term, partial shading on growth and photosynthesis in *Pinus radiata* D. Don trees. Forest Ecol Manag 163:151–163

Williams MC, Wardle GM (2005) The invasion of two native Eucalypt forests by *Pinus radiata* in the Blue mountains, New South Wales, Australia. Biol Conserv 125:55–64