

The effect of herbivory on seedling survival of the invasive exotic species *Pinus radiata* and *Eucalyptus globulus* in a Mediterranean ecosystem of Central Chile

Pablo I. Becerra*, Ramiro O. Bustamante

Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Instituto de Ecología y Biodiversidad (IEB), Las Palmeras 3425, Santiago, Casilla 653, Chile

ABSTRACT

Herbivory may be an important factor affecting seedling survival of exotic species invading new habitats. We evaluated the effect of vertebrate herbivory on the seedling survival of two widely planted and invasive tree species (*Pinus radiata* and *Eucalyptus globulus*), in a Mediterranean-type ecosystem of central Chile. An important role of herbivory on seedling survival of these two species in their introduced ranges has previously been documented. However, this has mainly been evaluated in forest plantations where habitat and vegetation conditions differ from wild habitats in which invasion occurs. We planted seedlings with and without protection against vertebrate herbivores in different aspects (a mesic south-facing slope and a xeric north-facing slope) and vegetation cover (open sites and sites with patchy tree cover). We found that regardless of aspect or vegetation cover, herbivory, in this case mainly caused by exotic vertebrates, significantly and negatively affected seedling survival of both species. However, while the effect of herbivory on *P. radiata* was significant in every vegetation and habitat condition, for *E. globulus*, the effect of herbivory was significant only for open sites in the mesic habitat. These results suggest that, as observed in forestry plantations, vertebrate herbivory may constrain seedling establishment of these two exotic trees and potentially impede the invasion. However, the importance of herbivory in controlling exotic species may vary depending on the vegetation and habitat conditions in some species such as *E. globulus*.

Keywords:

Biological invasions
Biotic resistance
Chile
Herbivory
Invasive plant species

1. Introduction

Invasion of exotic species is considered a worldwide ecological phenomenon and a relevant conservation issue (Drake et al., 1989; Mooney and Hobbs, 2000). Thus, the study of factors affecting invasion acquire high importance both to answer ecological questions and to address conservation actions. Forestry plantations of exotic tree species are one of the main sources of invasive species (Richardson, 1998). In Chile, the most common tree species used by the forestry industry are *Pinus radiata* D. Don (Pinaceae), originally from Monterey (California, USA), and *Eucalyptus globulus* Labill. (Myrtaceae), originally from Tasmania and Victoria (Australia). The extent of these plantations has grown rapidly during the last decades, covering more than two million hectares, especially in the Mediterranean region of the country. These species are also widely planted throughout the world, especially in the southern hemisphere. However, both *P. radiata* (Richardson

and Brown, 1986; Richardson and Bond, 1991; Rouget et al., 2002; Williams and Wardle, 2005a,b) and *E. globulus* (Boyd, 1996; Rejmánek et al., 2005), have been recognised as important invasive species in different countries 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, invasion by these species is still incipient but it is already occurring in several locations in the country (Bustamante et al., 2003; Becerra, 2006).

A number of environmental factors such as climate, vegetation cover and vegetation type, are known to be related to the success of *P. radiata* (e.g. Richardson and Brown, 1986; Higgins and Richardson, 1998; Rouget et al., 2002; Williams and Wardle, 2005a,b; Becerra, 2006) and *E. globulus* (Boyd, 1996; Becerra, 2006) invasions. In contrast, the role of herbivory on the invasive capabilities of these species has yet to be experimentally assessed. Herbivory may be a major factor affecting the success or failure of the invasion process by exotic species (Maron and Vilà, 2001; Keane and Crawley, 2002; Shea and Chesson, 2002; Levine et al., 2004; Bruno et al., 2005; Parker et al., 2006; Nuñez et al., 2008). Invasion of a plant species may be hindered by herbivory due to

* Corresponding author. Tel.: +56 2 9787384; fax: +56 2 2727363.
E-mail address: pbecerra@icaro.dic.uchile.cl (P.I. Becerra).

direct consumption, or facilitated by it, if resident herbivores preferentially consume competitive resident plants (Maron and Vilà, 2001; Colautti et al., 2004; Joshi and Vrieling, 2005; Parker et al., 2006; Vavra et al., 2007; Nuñez et al., 2008). Until now, the role of herbivory on the survival of *P. radiata* (Ferriere et al., 1983; Muñoz and Murúa, 1990; Richardson and Bond, 1991) and *E. globulus* (Ferriere et al., 1983; O'Reilly and McArthur, 2000; McArthur and Appleton, 2004) within their exotic ranges has been evaluated mainly in forestry plantations, and only some suggestions of an important role of vertebrate herbivores as invasion controllers under natural conditions have been proposed in the case of *P. radiata* (e.g. Richardson et al., 1994). However, within forestry plantations natural vegetation has generally been logged or eliminated and habitat conditions selected or altered to improve productivity. Therefore, environmental conditions in plantations are very different from environmental conditions where invasion occurs. Furthermore, under invasion conditions, seedling abundance is normally low and seedling distribution generally clumped (e.g. Williams and Wardle, 2007). In contrast, seedlings in forestry plantations are generally planted at high densities and are regularly spaced. Thus, the behaviour of herbivores, and the extent of herbivory on exotic species, may differ between natural habitats and plantations.

In central Chile, exotic vertebrates such as rabbits (*Oryctolagus cuniculus*), cows (*Bos taurus*), horses (*Equus caballus*) and goats (*Capra hircus*), are the main potential vertebrate browsers of exotic and native woody seedlings (Fuentes et al., 1983; Jaksic, 1998; Henríquez and Simonetti, 2001; Vásquez, 2002). Nonetheless, some native rodents such as *Octodon degus*, *Octodon bridgesii* and *Abrocoma bennetti* have also been documented to browse seedlings of tree species (Fuentes et al., 1983; Muñoz and Murúa, 1990). Of these animals, at least rabbits are known to browse on seedlings of both *P. radiata* and *E. globulus* in forestry plantations in Chile (Ferriere et al., 1983). In this paper, we experimentally assessed the effect of vertebrate browsing on seedling survival of *P. radiata* and *E. globulus*. We performed this study under natural vegetation and habitat conditions of a Mediterranean ecosystem in central Chile in order to simulate natural conditions where invasion occurs, and used different habitat and vegetation types to examine the context-dependence of this plant-herbivore interaction. We expect that high browsing by vertebrate herbivores in this environment may significantly diminish seedling survival of these exotic trees.

2. Methods

2.1. The study area

The study was carried out in the San Ramón watershed, located on the eastern border of the city of Santiago (33°30'S, 70°30'W), central Chile. The climate is semiarid and Mediterranean-like, with 5–6 dry months and precipitation concentrated during winter, reaching an annual average of 330 mm. The annual mean temperature is 15 °C (Di Castri and Hajek, 1976). In the watershed, there are two main aspects: a north-facing slope and a south-facing slope. These habitats generally differ significantly in moisture conditions in the Mediterranean region of Chile, being moister on the south-facing slope than on the north-facing one (Armesto and Martínez, 1978). In all these habitats vegetation is composed of tree, shrub and herbaceous patches. Sizes of tree as well as herbaceous patches vary between 20 and 150 m² approximately. However, for the study we selected tree and herbaceous patches between 80 and 120 m². Tree patches are dominated by the native tree species *Lithrea caustica*, shrub patches by native species such as *Colliguaya odorifera* and *Retanilla trinervia*, and herbaceous

patches are composed of native species including *Pasithea coerulea* and *Bromus berteroaenus*, as well as exotic herb species including *Fumaria* spp., *Centaurea melitensis* and *Conium maculatum*.

The watershed has been protected (from logging, cattle and fires) for the past 10 years by the national forest service. Large exotic herbivores have been completely excluded (cows and goats) from the study site by forest service management, although on rare occasions, horses coming from nearby ranches are observed in the watershed. Evidence of their presence in the study area is provided in Table 1. On the other hand, the presence of another potential herbivore, the native diurnal caviomorph *O. degus*, can be established either directly by visual observation, or indirectly by burrows, faeces and bare zones produced by their activities (Fuentes et al., 1983). In order to evaluate the presence of *O. degus* we established 20 transects of 200 m × 2 m each (10 on a north-facing and 10 on a south-facing slope) to record some of these indicators. We observed no evidence of any of these indicators of *O. degus* in the study site, hence we are confident that they are not present in the study area or at least their abundance is very low. In addition, this rodent has been documented to be a less important seedling consumer of native trees than rabbits in central Chile (Fuentes et al., 1983). Other species of the *Octodon* genus are not present in this locality (Saavedra, 2003). Finally, another potential seedling predator, the rodent *A. bennetti*, seems to be scarce in central Chile (Iriarte et al., 1989), especially in the pre-Andean zone of Santiago and its influence (if any) as a seedling predator may be negligible (Fuentes et al., 1983). Thus, the main herbivore tree seedling browser in the study area is the European rabbit (*O. cuniculus*), although horses may also play a minor role. The presence of rabbits is documented in Table 1 by faeces frequency.

2.2. Experimental design

We established monitoring stations in the field containing protected (excluded from herbivores) and unprotected (non-excluded from herbivores) seedlings of these exotic trees. We distributed these stations in herbaceous (open sites) and tree patches (dominated mainly by the native tree *L. caustica*), in a xeric (north-facing slope) and a mesic (south-facing slope) habitat. Exclusions consisted of 1.0 m × 1.5 m plots, fenced on the sides and the top by a wire mesh to exclude mammals and birds. In each station, non-excluded seedlings were located next to the fence corresponding to the station. We planted three seedlings per species (each separated by 20 cm from each other) outside the exclusions and three seedlings per species inside them. We used clumps of three seedlings to partially simulate the clumping of seedlings during the invasion process, as it has been documented for *P. radiata* (Williams and Wardle, 2007). However, in order to avoid pseudoreplication we randomly selected only one excluded and one non-excluded seedling from each station to perform statistical analyses. In total, we used 10 stations in open sites and 10 in tree patches (*Lithrea* patches) in each habitat. Thus, we

Table 1
Frequencies (%) of rabbit and horse faeces in each type of habitat and vegetation patch

Habitat-vegetation patch	Rabbits, Mean (%) ± 1 S.E.	Horses, Mean (%) ± 1 S.E.
Mesic-Lithrea	28 ± 6.79	2 ± 1.33
Mesic-Open	63 ± 6.33	3 ± 1.53
Xeric-Lithrea	50 ± 5.96	5 ± 2.24
Xeric-Open	75 ± 3.73	11 ± 3.14

Values correspond to percentage of ten 10 cm × 10 cm plots with presence of faeces. Plots per 4.5 m long transects were separated by 0.5 m ($N = 10$ transects per type of vegetation patch in each habitat).

established 20 stations in each habitat and 40 in total. Within each habitat, stations were located at least 10 m apart and separated by a different vegetation patch type, to minimize spatial dependence among stations. Preliminary observations confirmed the efficacy of fences as we observed no excluded seedlings with signs of browsing.

Planting was carried out during winter (20–25 June 2004). Seedling height at time of planting was 19.7 ± 0.15 cm and 22.9 ± 0.19 cm (mean \pm 1 S.E.) for *P. radiata* and *E. globulus*, respectively. Seedlings were obtained from the greenhouse of the Faculty of Forest Sciences, University of Chile. These seedlings are produced from seeds collected from plantations located in the Mediterranean region of Chile. Seedlings were monitored every 2 months, from 30 June 2004 until 30 June 2005. Thus, we obtained six records of survival for each seedling across this period.

2.3. Herbivory assessments and analyses

We performed two analyses in order to describe the effect of herbivory on seedling survival of these two exotic species. First, we described the seedling mortality effectively produced because of herbivory. In this study the damage caused by vertebrate herbivores was considered as browsing which can include eating as well as only cutting seedlings. Every seedling registered as browsed on one monitoring date, was found dead on the following date. Then, every browsed seedling was registered as dead. In addition, we were able to distinguish when a seedling was effectively browsed and when it died due to desiccation because browsing by these herbivores left a remnant piece of the stem with evidence of having been cut. To describe mortality caused by browsing, we quantified the percentage of browsed seedlings using only non-excluded seedlings at the end of the experiment (1 year long), in the studied habitat and vegetation conditions. This percentage was obtained from 10 seedlings of each species randomly selected per combination of vegetation patch and habitat (one from the three non-excluded originally planted in each station). In order to examine differences between vegetation patch-types and habitats we performed logistic regressions (GLZ procedure, logit function) considering each one of 10 selected seedlings per treatment as a replicate and assigning 0 if the seedling was alive and 1 if it was browsed at the end of the experiment.

Secondly, in order to evaluate if this browsing had significant consequences for seedling survival, we compared survival between protected seedlings from herbivores and unprotected seedlings in the studied habitat and vegetation conditions. Here we performed two evaluations: one general per species (pooling data of different vegetation and habitat conditions) in which we compared all excluded seedlings (40) with all non-excluded seedlings (40). The second analysis was also performed separately for each species, comparing excluded with non-excluded seedlings per vegetation patch-type and habitat, and using 10 seedlings of each species as replicates. All comparisons of seedling survival between excluded and non-excluded seedlings were performed by Log-rank survival curve tests and Holm-Sidak post hoc tests.

3. Results

3.1. Seedling browsing

By the end of the experiment, browsed seedlings reached 92.5% for *P. radiata* and 57.5% for *E. globulus*. Considering each vegetation patch and habitat separately, browsing on *P. radiata* was 100% in both vegetation patch-types in the mesic habitat and 90% and 80% in open sites and *Lithrea* patches, respectively in the xeric habitat

(Fig. 1). Browsing on *E. globulus* showed a different pattern: it reached 90% in both vegetation patch-types of the mesic habitat, but only 40% and 10% in open and *Lithrea* patches, respectively in the xeric habitat (Fig. 1). Thus, in *P. radiata* ($\chi^2 = 4.43$; $P = 0.035$) as well as in *E. globulus* ($\chi^2 = 19.79$; $P < 0.0001$), we observed significant differences between habitats in seedling browsing. Overall, browsing on both species was significantly higher in the mesic than in the xeric habitat (Fig. 1). In turn, we observed no significant difference in seedling browsing for *P. radiata* ($\chi^2 = 0.37$; $P = 0.545$) nor for *E. globulus* ($\chi^2 = 0.93$; $P = 0.336$) between vegetation patch-types. Also, no significant statistical interaction between habitat and vegetation patch-type was detected for *P. radiata* ($\chi^2 = 0.001$; $P = 0.999$) nor for *E. globulus* ($\chi^2 = 0.86$; $P = 0.352$). However, this is clearer in the case of *P. radiata* than for *E. globulus* (Fig. 1). It is probable that in the latter species there was a low statistical power to detect a significant interaction.

3.2. Survival of protected and unprotected seedlings

Considering the two pooled habitats and vegetation patch-types, survival of excluded seedlings was significantly higher than non-excluded seedlings in both *E. globulus* (Log-rank test: $\chi^2 = 19.73$; d.f. = 1; $P < 0.001$) and *P. radiata* (Log-rank test: $\chi^2 = 58.31$; d.f. = 1; $P < 0.001$) (Fig. 2). In *E. globulus*, excluded seedlings had a survival probability of 15% while only 2.5% of non-excluded seedlings were present at the end of the experiment. In *P. radiata*, survival of excluded seedlings was 27.5% while no non-excluded seedling survived by the end of the experiment (Fig. 2).

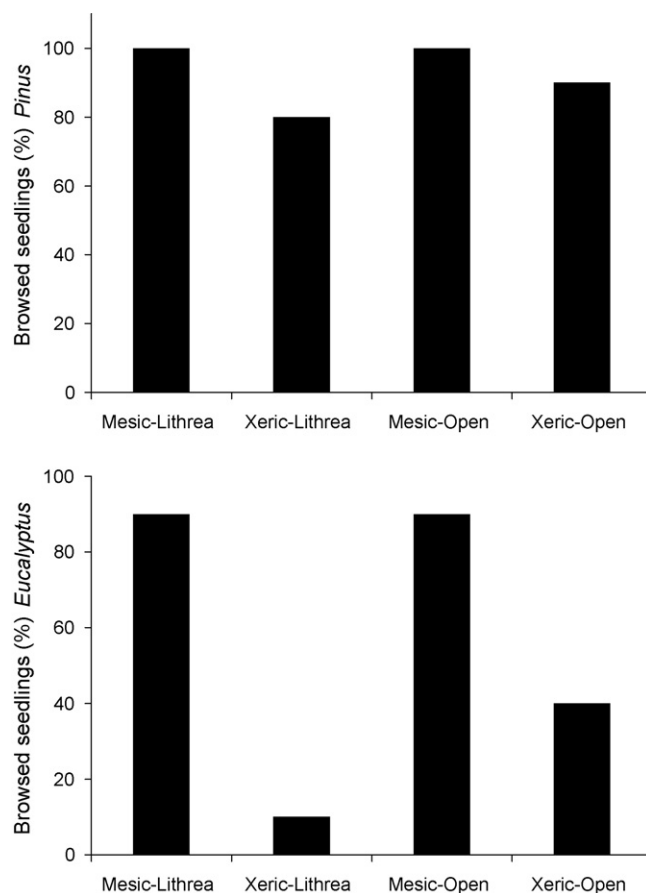


Fig. 1. Seedling browsing percentage of *Pinus radiata* and *Eucalyptus globulus* in open and *Lithrea* patches of a mesic and a xeric habitat. Each value corresponds to the proportion of browsed (killed) seedlings from the 10 originally non-excluded seedlings at the end of the experiment (June, 2005).

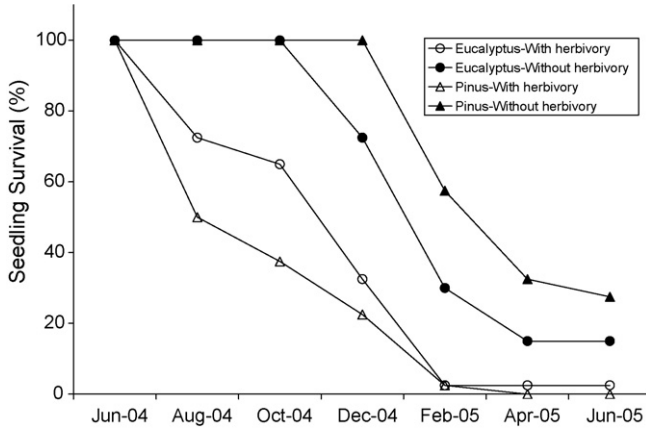


Fig. 2. Seedling survival curves of excluded (without herbivory) and non-excluded (with herbivory) seedlings of *P. radiata* and *E. globulus*. Each point corresponds to the percentage of living seedlings from a total of 40 originally planted per species and herbivory treatment.

Regarding the comparison between excluded and non-excluded seedlings for each species, per habitat and vegetation patch-type separately, we observed that in *P. radiata* survival of excluded seedlings was significantly higher than non-excluded seedlings in all types of habitats and vegetation patch-types (Table 2, Fig. 3). In *E. globulus*, excluded seedlings showed a significantly higher survival than non-excluded seedlings only in open sites of the mesic habitat (Table 2, Fig. 3).

4. Discussion

We observed that vertebrate browsing had an important negative effect on seedling survival of both *P. radiata* and *E. globulus*. This effect was stronger in *P. radiata* than in *E. globulus* as

Table 2

Effect of herbivory on seedling survival (excluded vs. non-excluded seedlings) per species, habitat and vegetation patch-type

Species	Habitat	Patch	χ^2	P	P critical
<i>P. radiata</i>	Xeric	Lithrea	8.56	0.0034	0.0051
		Open	17.75	<0.0001	0.0023
	Mesic	Lithrea	11.11	0.0009	0.0037
		Open	21.19	<0.0001	0.0021
<i>E. globulus</i>	Xeric	Lithrea	1.88	0.17	0.0057
		Open	0.32	0.5720	0.0170
	Mesic	Lithrea	4.36	0.0367	0.0037
		Open	21.19	<0.0001	0.0019

Results correspond to Holm-Sidak post hoc tests from a Log-rank test of survival curves. Significant differences between excluded and non-excluded seedlings are in bold.

differences between survival curves of excluded and non-excluded seedlings for all monitoring times were greater in *P. radiata* than in *E. globulus*. Significant effects of vertebrate herbivory on seedling establishment of these species have already been documented in forestry plantations (Ferriere et al., 1983; Muñoz and Murúa, 1990; Richardson and Bond, 1991; O'Reilly and McArthur, 2000; McArthur and Appleton, 2004). However, our results suggest that in natural plant communities with higher woody plant cover than forestry plantations, vertebrate herbivores may strongly reduce the chances of seedling establishment of *P. radiata* and *E. globulus*.

In addition to these general findings, we also observed some species-specific differences with respect to the effect of herbivory on seedling survival. While the effect of herbivory on seedling survival of *P. radiata* was significant throughout the different vegetation and habitat conditions, the role of herbivory on *E. globulus* survival differed depending on the vegetation patch-type and habitat. In this case, herbivory on *E. globulus* was significant only in open sites of the mesic habitat. The absence of differences in survival between protected and unprotected seedlings of *E.*

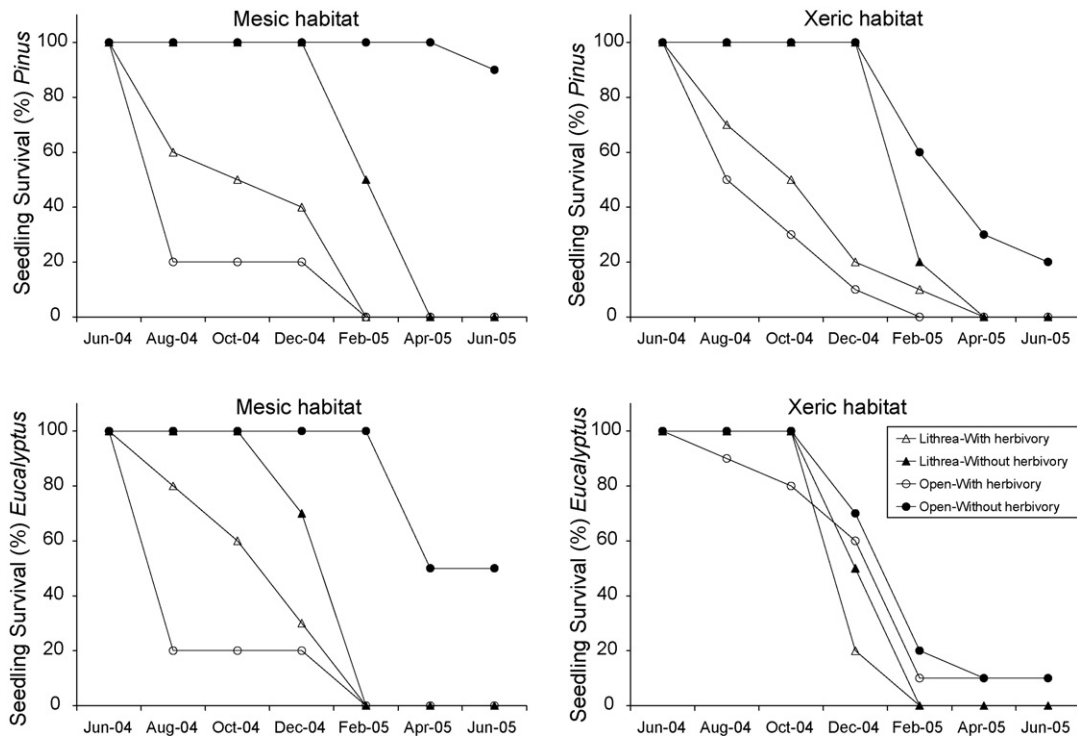


Fig. 3. Survival curves of excluded (without-herbivory) and non-excluded (with-herbivory) seedlings for each species (*P. radiata* and *E. globulus*), habitat and vegetation patch. Each point corresponds to the percentage of living seedlings from a total of 10 originally planted per species, herbivory, habitat and vegetation patch treatment.

globulus in both vegetation types of the xeric habitat could have been produced by the low rate of browsing observed on seedlings of this species in general in this habitat. In contrast, in spite of the high browsing on *E. globulus* seedlings observed in *Lithrea* patches of the mesic habitat, survival of protected and unprotected seedlings did not differ, due to high mortality of protected seedlings. This could have been produced by low light availability under *Lithrea* patches. In this case, it is possible that abiotic factors overshadowed herbivory effects. Similarly, other studies have also documented an important role of habitat, plant productivity or vegetation physiognomy in modulating the importance of the effect of herbivory on performance of native and exotic plants (Fuentes et al., 1986; Hobbs, 2001; Fowler, 2002; DeWalt et al., 2004; Kuijper et al., 2004).

Our observations indicate that the main seedling browser on our study site is the European rabbit. The higher seedling browsing level in the mesic habitat in both species contrasts with a previous study which documented higher browsing on native trees by this herbivore in xeric habitats of central Chile (Fuentes et al., 1983). We cannot infer differences in rabbit abundance between habitats based on frequency of faeces due to possible differences in faeces decay rates between them (Simonetti, 1989). Even, if faeces frequency were an efficient indicator of rabbit abundance, rabbit populations should be higher in the xeric habitat and not in the mesic habitat where browsing was higher. Thus, difference in rabbit abundance between habitats is only a possible cause for the different seedling browsing levels between habitats, which should be evaluated more directly. On the other hand, other studies have found that rabbits have preferences for certain plants (Crawley, 1990). Thus, the higher seedling browsing observed in the mesic habitat may be related to a lower availability of some of their more important and preferred food sources (e.g., some herbs) in this habitat, which might have forced rabbits to feed on these exotic trees there.

Despite the great number of studies assessing the effect of herbivory on plant invasion (D'Antonio, 1993; Holmgren et al., 2000; Maron and Vilà, 2001; Bellingham and Coomes, 2003; Levine et al., 2004; Parker et al., 2006), the role of exotic vertebrate herbivores on the invasion of exotic plant species has been poorly studied (Parker et al., 2006). In general, the effect of exotic herbivores on exotic plants has been observed to be mainly positive, determined indirectly by higher predation on native plants relative to exotic plants, thus reducing competition on exotics (Parker et al., 2006; Vavra et al., 2007; Nuñez et al., 2008). The main herbivores on our study site (the European rabbit and secondarily horses) were exotic species. However, we cannot fully assess the final or net effect of herbivory on *P. radiata* and *E. globulus* and, thus, the role of these exotic vertebrates on invasion of these exotic trees in this ecosystem. In order to test if these herbivores are actually controlling plant invasion, a field experiment would need to evaluate the effect of the herbivores on the dominant native plant species of this area as well. If the tested herbivores (in this case mostly introduced rabbits) have a stronger effect on native plants than they do on both exotic trees, then they would actually facilitate instead of control plant invasion despite the fact of consuming the exotic species. However, this situation would occur if native species affect negatively or compete with these exotic tree species. If native species do not negatively affect these exotic tree species or if this effect is positive, then, regardless the effect of herbivores on native species, this herbivory will control invasion by these exotic trees. This ecosystem is dominated mainly by one native tree (*L. caustica*), some native shrub species (which form several shrubby patches) and many native and exotic herbs which dominate open sites; although they are also present under woody canopy. While

we do not know the interaction between native woody species and these exotic tree species, we may state some conclusions about the net effect of these exotic vertebrate herbivores on both exotic tree species mediated by herbs. Because of we did not control herb species in our treatments, the negative effect of these exotic herbivores on both exotic trees we observed, would correspond to a net effect mediated by interactions between herbivores and herbs (exotics and natives) and between herbs and seedlings of *P. radiata* and *E. globulus*. Thus, we may conclude that there was no important indirect positive effect of exotic herbivores on *P. radiata* and *E. globulus* through their predation upon herbs. This result contrasts with findings in central Chile, in which the same herbivores were found to indirectly facilitate survival of exotic herbs by preferentially preying on native herbs (Holmgren et al., 2000; Holmgren, 2002). In turn, our results are consistent with other studies where negative effects of exotic herbivores on exotic plants were more important than any possible positive indirect effect (e.g. Chaneton et al., 2002; Fowler, 2002; Valone et al., 2002; DeWalt et al., 2004). Therefore, our results contrast with the meltdown hypothesis that exotic species (herbivores in our case) facilitate indirectly invasion of other exotic species (in this case *P. radiata* and *E. globulus*) (Simberloff and Von Holle, 1999). However, additional studies are needed to establish the net effect of these exotic herbivores on both exotic tree species mediated by the interactions between these herbivores and native woody species.

The importance of native herbivores as resistance agents against plant invasion has recently been highlighted (Maron and Vilà, 2001; Levine et al., 2004; Parker et al., 2006; Nuñez et al., 2008). Likewise, the role of exotic herbivores on native plants is also a relevant ecological and conservation issue (Jaksic and Fuentes, 1980; Relva and Veblen, 1998; Cabin et al., 2000; Holmgren et al., 2000; Vásquez, 2002; Parker et al., 2006; Nuñez et al., 2008). In the latter case, a logical conservation action would be to eradicate exotic herbivores if these negatively affect native plant species. However, if exotic herbivores also have a negative effect on exotic plants, their exclusion may have undesirable consequences, for example, an increase of plant invasion (e.g. Cabin et al., 2000). Therefore, control strategies of exotic species must consider controlling exotic plants as well as exotic herbivores.

Acknowledgements

We thank Aguas Andinas S.A., PROTEGE and the Chilean forest service CONAF, for allowing us to work in the study area, and to MITIGA Ltda. for helping in the installation of the experiment. This investigation was supported by a FONDECYT doctoral fellowship. R.O. Bustamante has been partially supported by BBVA prize in Conservation Biology, 2004 and by ICM-P05-002 GRANT from the Institute of Ecology and Biodiversity. We thank Moira Williams, Wouter van Dongen, Juan Armesto, Javier Simonetti, Mary T. Kalin, Lohengrin Cavieres and Lafayette Eaton for their comments on the manuscript. We also thank three anonymous reviewers whose observations significantly collaborated to improve this manuscript.

References

- Armesto, J.J., Martínez, J., 1978. Relations between vegetation structure and slope aspect in the mediterranean region of Chile. *J. Ecol.* 66, 881–889.
- Becerra, P.I., 2006. Invasión de árboles alóctonos en una cuenca pre-andina de Chile central. *Gayana Bot.* 63, 161–174.
- Bellingham, P.J., Coomes, D.A., 2003. Grazing and community structure as determinants of invasion success by scotch broom in a New Zealand montane shrubland. *Divers. Distrib.* 9, 19–28.

- Boyd, D., 1996. *Eucalyptus globulus*: Bluegum Eucalyptus. In: Randall, J.M., Marinelli, J. (Eds.), *Invasive Plants: Weeds of the Global Garden*. Science Press, New York, p. 32.
- Bruno, J.F., Fridley, J.D., Bromberg, K.D., Bertness, M.D., 2005. Insights into biotic interactions from studies of species invasions. In: Sax, D.F., Stachowicz, J.J., Gaines, S.D. (Eds.), *Species Invasions: Insights into Ecology, Evolution and Biogeography*. Sinauer Associates, Inc., USA, pp. 13–40.
- Bustamante, R.O., Serey, I.A., Pickett, S.T.A., 2003. Forest fragmentation, plant regeneration and invasion processes across edges in central Chile. In: Bradshaw, G.A., Marquet, P.A. (Eds.), *How Landscape Change*. Springer-Verlag, Berlin, pp. 145–158.
- Cabin, R.J., Weller, S.G., Lorence, D.H., Flynn, T.W., Sakai, A.K., Sandquist, D., Hadway, L.J., 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Conserv. Biol.* 14, 439–453.
- Chaneton, E.J., Perelman, S.B., Omacini, M., León, R., 2002. Grazing, environmental heterogeneity and alien plant invasions in temperate Pampa grasslands. *Biol. Invasions* 4, 7–24.
- Colautti, R.I., Ricciardi, A., Grigorovich, I.A., MacIsaac, J., 2004. Is invasion success explained by the enemy release hypothesis? *Ecol. Lett.* 7, 721–733.
- Crawley, M.J., 1990. Rabbit grazing, plant competition, and seedling recruitment in acid grassland. *J. Appl. Ecol.* 27, 803–820.
- D'Antonio, C.M., 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* 74, 83–95.
- DeWalt, S.J., Denslow, J.S., Ickes, K., 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* 85, 471–483.
- Di Castri, F., Hajek, E., 1976. *Bioclimatología de Chile*. Universidad Católica de Chile, Chile.
- Drake, J., Mooney, H.A., Di Castri, F., Groves, R., Kruger, F., Rejmanek, M., Williamson, M., 1989. *Biological Invasions: A Global Perspective*. John Wiley, Chichester, UK.
- Ferriere, G., Cerda, J., Roach, R., 1983. El conejo silvestre en Chile. *Boletín Técnico N°8*. CONAF, Santiago, Chile.
- Fowler, N.L., 2002. The joint effects of grazing, competition and topographic position of six savanna grasses. *Ecology* 73, 2477–2488.
- Fuentes, E.R., Jaksic, F.M., Simonetti, J.A., 1983. European rabbits versus native rodents in Central Chile: effects on shrub seedlings. *Oecologia* 58, 411–414.
- Fuentes, E.R., Hoffmann, A.J., Poiani, A., Alliende, M.C., 1986. Vegetation change in large clearings: patterns in the Chilean matorral. *Oecologia* 68, 358–366.
- Henríquez, C.A., Simonetti, J.A., 2001. The effect of introduced herbivores upon an endangered tree (*Beilschmiedia miersii* Lauraceae). *Biol. Conserv.* 98, 69–76.
- Higgins, S.I., Richardson, D.M., 1998. Pine invasions in the southern hemisphere: modeling interactions between organism, environment and disturbance. *Plant Ecol.* 135, 79–93.
- Hobbs, R., 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in Southwestern Australia. *Conserv. Biol.* 15, 1522–1528.
- Holmgren, M., 2002. Exotic herbivores as drivers of plant invasion and switch to ecosystem alternatives states. *Biol. Invasions* 4, 25–33.
- Holmgren, M., Avilés, R., Sierralta, L., Segura, A.M., Fuentes, E.R., 2000. Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients and fire. *J. Arid Environ.* 44, 197–211.
- Iriarte, J.A., Contreras, L.C., Jaksic, F.M., 1989. A long-term study of a small-mammal assemblage in the central Chilean matorral. *J. Mammal.* 70, 79–87.
- Jaksic, F.M., 1998. Vertebrate invaders and their ecological impacts in Chile. *Biodivers. Conserv.* 7, 1427–1445.
- Jaksic, F.M., Fuentes, E.R., 1980. Why are native herbs in the Chilean matorral more abundant beneath bushes: microclimate or grazing? *J. Ecol.* 68, 665–669.
- Joshi, J., Vrieling, K., 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecol. Lett.* 8, 704–714.
- Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17, 164–169.
- Kuijper, D.P.J., Nijhoff, D.J., Bakker, J.P., 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. *Oecologia* 141, 452–459.
- Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* 7, 975–989.
- Maron, J.L., Vilà, M., 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypothesis. *Oikos* 95, 361–373.
- McArthur, C., Appleton, R., 2004. Effect of seedlings characteristics at planting on browsing of *Eucalyptus globulus* by rabbits. *Aust. Forestry* 67, 25–39.
- Mooney, H.A., Hobbs, H.A., 2000. *Invasive Species in a Changing World*. Island Press, California.
- Muñoz, A., Murúa, R., 1990. Control of small mammals in a pine plantation (central Chile) by modification of the habitat of predators (*Tyto alba*, Strigiforme and Pseudolopex sp., Canidae). *Acta Oecolog.* 11, 251–261.
- Núñez, M.A., Relva, M.A., Simberloff, D., 2008. Enemy release or invasional meltdown? Deer preference for exotic and native trees on Isla Victoria. *Argentina. Austral Ecology* 33, 317–323.
- O'Reilly, J., McArthur, C., 2000. Damage to and intake of plantation seedlings by captive European rabbits (*Oryctolagus cuniculus*). *Aust. Forestry* 63, 1–6.
- Parker, J.D., Burkepile, D.E., Hay, M.E., 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science* 311, 1459–1461.
- Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J., Grotkopp, E., 2005. Ecology of invasive plants—state of the art. In: Mooney, H.A., Mack, R.N., Mc Neely, J.A., Neville, L., Schei, P.J., Waage, J. (Eds.), *Invasive Alien Species: A New Synthesis*. Island Press, Washington, DC, pp. 104–161.
- Relva, M.A., Veblen, T.T., 1998. Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. *Forest Ecol. Manage.* 108, 27–40.
- Richardson, D.M., 1998. Forestry trees as invasive aliens. *Conserv. Biol.* 12, 18–26.
- Richardson, D.M., Brown, P.J., 1986. Invasion of mesic mountain Fynbos by *Pinus radiata*. *S. Afr. J. Bot.* 52, 529–536.
- Richardson, D.M., Bond, W.J., 1991. Determinants of plant distribution: evidence from pine invasions. *Am. Nat.* 137, 639–668.
- Richardson, D.M., Williams, P.A., Hobbs, R.J., 1994. Pine invasions in the Southern Hemisphere: determinants of spread and invadability. *J. Biogeogr.* 21, 511–527.
- Rouget, M., Richardson, D.M., 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.
- Saavedra, B., 2003. Disminución en tamaño poblacional y asimetría fluctuante en *Octodon bridgesi* (Rodentia), taxón especialista de hábitat. Thesis. Facultad de Ciencias, Universidad de Chile.
- Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176.
- Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1, 21–32.
- Simonetti, J.A., 1989. Microhabitat use by *Oryctolagus cuniculus* in central Chile: a reassessment. *Mammalia* 53, 363–368.
- Valone, T.J., Meyer, M., Brown, J.H., Chew, R.M., 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. *Conserv. Biol.* 16, 995–1002.
- Vásquez, D.P., 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. *Biol. Invasions* 4, 175–191.
- Vavra, M., Parks, C.G., Wisdom, M.J., 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecol. Manage.* 246, 66–72.
- Williams, M.C., Wardle, G.M., 2005a. The invasion of two native Eucalypt forests by *Pinus radiata* in the Blue mountains, New South Wales, Australia. *Biol. Conserv.* 125, 55–64.
- Williams, M.C., Wardle, G.M., 2005b. The influence of vegetation structure and composition on invasibility by *Pinus radiata* in the Blue Mountains, NSW. *Cunninghamia* 9, 285–294.
- Williams, M.C., Wardle, G.M., 2007. The spatial pattern of invading *Pinus radiata*. *Proceeding of the Linnean Society of New South Wales* 128, 111–122.