

Seed predation as a barrier to alien conifer invasions

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Received: 4 December 2007 / Accepted: 28 December 2007 / Published online: 12 January 2008
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Abstract Interactions between exotic plants and animals can play a major role in determining success or failure of plant introductions. Seed predation has been seen as important in explaining biotic resistance to plant invasion, but this hypothesis has rarely been tested. We studied seed predation on exotic forest plants on an island in Patagonia, Argentina where 43 pine species, including 60% of the world's known invasive Pinaceae, were introduced ca. 80 years ago, but where exotics attain relatively high densities only near the original plantings. To test if seed predation limits exotic conifer establishment in this area, we compared seed predation in areas close to plantations (colonized by exotics) and far from them (not invaded). Seeds of exotics were preferred over seeds of native species, possibly because exotic seeds are bigger. Predation was more intense in areas far from plantations than in areas close to them, substantially reducing the chances of exotic seed establishment. Using automatic cameras, we found that both rodents and birds preyed on exotic seeds. This study suggests

that native seed predators can be an important component of biological resistance to plant invasion.

Keywords Biological invasions · Biotic resistance · Patagonia · Pinaceae · Pine invasion · Seed size · Seedling herbivory

Introduction

Biological invasions are a leading cause of global change: they eliminate native species, degrade habitat, change ecosystem function, and facilitate further invasions (D'Antonio et al. 2001). However, most introduced species fail to establish and spread (Williamson and Fitter 1996). Among many hypotheses proposed to explain the success or failure of invasive species are two prominent ones, with opposite predictions: the enemy release hypothesis and the biotic resistance hypothesis (Lockwood et al. 2007). The enemy release hypothesis states that exotic species in their new ranges are less strongly regulated by natural enemies (e.g., herbivores, seed predators, parasites), resulting in an increase in their abundance and distribution (Agrawal et al. 2005; Colautti et al. 2004; Keane and Crawley 2002; Williamson 1996). By contrast, the biotic resistance hypothesis (Elton 1958; Levine et al. 2004; Parker and Hay 2005) states that native interactions with exotics can impede invasions.

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For plants, seed predation is proposed as a major impediment to establishment (Orrock et al. 2006). Seed destruction can reduce and even stop recruitment and expansion of native species (Jules and Rathcke 1999; Maron and Simms 2001; Ostfeld et al. 1997) and has been suggested as a potential mechanism controlling invasion and spread of exotic plant species (Maron and Vilá 2001). However, its importance in controlling invasions is not yet clear owing to the lack of direct evidence that seed predators halt invasions (Bossard 1991; Hoffmann and Moran 1998; Parker 2000; Vila and Gimeno 2003). In theory, changes in degree of seed predation can promote or halt the establishment and spread of introduced species depending on its relative effects on natives and exotics. If an exotic species suffers less seed predation in its introduced than in its native range, this can be evidence for enemy release (see Hierro et al. 2005). On the other hand, seed predators may prefer exotic seeds over native seeds and thus restrict exotic establishment, a form of biotic resistance.

On an Argentinean island with plantations (ca. 80 years old) of many exotic tree species adjacent to native temperate forest, only a few exotic species have begun to invade, and they are found in high densities only near plantations (Simberloff et al. 2002). We sought to determine the effect of seed predation on conifer invasion. For conifers, Castro et al. (2002) showed that seed predation by rodents can limit the distribution of *Pinus sylvestris* in its native range. Also, post-dispersal predation has been recognized as a major source of seed loss in temperate forests (Caccia et al. 2006; Diaz et al. 1999; Schnurr et al. 2004).

In northwestern Patagonia, rodents consume seeds of exotic Pinaceae at very high rates (Caccia and Ballare 1998). A tentative hypothesis for the pattern observed by Simberloff et al. (2002) is that plantations and areas influenced by plantations offer less suitable habitat for native animals and contain fewer seed predators, as has been found in other areas (see Estades 1994; Lindenmayer and Hobbs 2004; Muñoz and Murúa 1989, 1990; Sykes et al. 1989). Another potentially important factor influencing the pattern of invasion on Isla Victoria is that these seeds are wind-dispersed and there is no evidence of secondary dispersal by rodents in this area (Caccia and Ballare 1998; Diaz et al. 1999). Thus, seed predators could be contributing to the observed patterns of few

established populations outside the plantations and a rapid decrease in number of individuals of species that do establish with increasing distance from plantations. Our hypothesis is that post-dispersal seed predation limits establishment of exotic Pinaceae. We predict that seed predation will be more intense in areas far from plantations of exotics trees and that exotic seeds will be preferred over the abundant seeds of native trees. Here we present results from two experiments and an observational study designed to test this hypothesis.

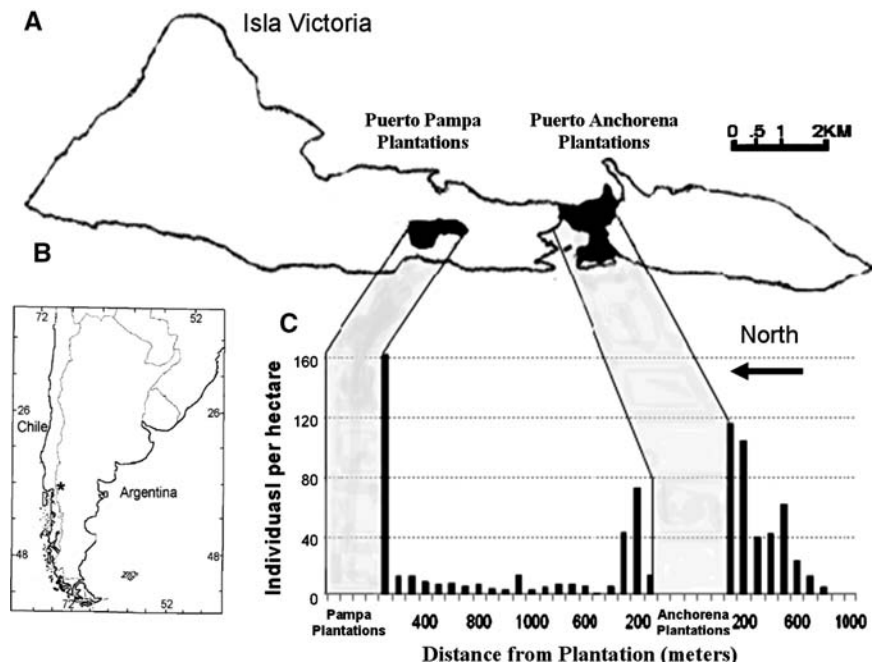
Methods

Study system

Isla Victoria (40°57' S, 71°33' W), in Nahuel Huapi National Park, Argentina (Fig. 1), is 20 km long and 4 km wide. Beginning in 1902, Isla Victoria experienced logging, cattle ranching, and fires, which together affected 50–60% of its total area. These activities decreased when Nahuel Huapi National Park was established in 1934, although there was a functioning plant nursery and cattle ranching into the 1960s (Basti 1988). Today Isla Victoria is dominated by primary or secondary forest of coihue (*Nothofagus dombeyi*) and ciprés (*Austrocedrus chilensis*) trees with a dense understory vegetation composed mostly of shrubs, but several roads, trails, buildings, and abandoned pastures remain (Simberloff et al. 2003).

The Argentine government established a nursery on Isla Victoria in 1925, planting forestry and fruit trees potentially suitable for the region. A variety of exotic species were introduced beginning in 1910 (APNA 1988; Koutché 1942) and planted until 1939. At least 73 conifers, including 60% of known invasive conifer species, and 62 broad-leaved species were on the island. Among the species planted were 21 species of *Pinus*, including 9 of the 12 species that Rejmánek and Richardson (1996) cite as having invasive qualities, and 43 species of Pinaceae, including 17 of the 28 species of Pinaceae for which Richardson and Rejmánek (2004) found evidence of invasiveness somewhere in the world. Despite a large introduction effort, only a few species have been able to disperse from where they were initially planted, and most that have dispersed attain very low densities (Simberloff et al. 2002, 2003) (Fig. 1).

Fig. 1 Map of Isla Victoria with abundance of exotic conifers outside plantations. (a) Map of Isla Victoria with plantations of exotic Pinaceae in black (Puerto Pampa and Puerto Anchorena plantations). (b) Location of the study area (black star). (c) Density of seedlings, saplings, and adults of exotic conifers outside plantations from the Puerto Pampa plantations southward through the Puerto Anchorena plantations, from Simberloff et al. (2002)



Experiments on seed predation

Seed removal

With a seed-removal experiment, we compared seed predation in native habitats in areas containing established exotic species adjacent to plantations (<100 m from a plantation boundary) and areas far from plantations with low densities of invaders (>1,500 m from a plantation boundary). We conducted the experiment during winter (June–August 2005) after seed release to explore the period during which rodents are famished and seed search is more intense. We set 60 seeds per species (five species) per treatment (near and far). We conducted this study from the Puerto Pampa plantations southward through the Puerto Anchorena plantations. Seeds were haphazardly placed over the ground in different sites (60 sites per treatment per species). We placed only one seed per site to mimic conditions after long distance dispersal and also to avoid density-dependent attacks. Long distance dispersal is uncommon but is a key mechanism for pine invasion (see below). We studied five different species—three exotics that are known to be highly invasive elsewhere (*Pseudotsuga menziesii*, *Pinus contorta* and *Pinus ponderosa*) and the two dominant natives (*Austrocedrus chilensis* and *Nothofagus dombeyi*)—to test if local seed predators

prefer exotic seeds. We expect such a preference because exotic seeds are bigger and thus more evident and attractive than those of the native species (Reader 1993). We recorded seed removal 20 days after we set them out. Seeds were glued to wooden flat stakes (1 cm × 10 cm) with a nontoxic odorless adhesive and manipulated with forceps to avoid scent contamination. Because seeds were glued to a stake, we can assume missing seeds were preyed upon.

Seed predator exclosures

To determine the overall effect of seed predation on conifer early establishment, we set up rodent- and bird-exclosures, constructed of metal-mesh (1 × 1 cm, with 0.06 cm wire width), and controls (without the fence). We analyzed seed predation in three species (*Pseudotsuga menziesii*, *Pinus contorta* and *Pinus ponderosa*). Treatments consisted of a factorial combination of three factors: seed species, distance, and exclosure. For each species and at each location (adjacent to and far from plantations), we set up 50 10-cm × 10-cm × 15-cm tall exclosures. Each wire exclosure was embedded 5 cm into the soil to avoid rodent penetration and firmly fixed to the ground. For controls a 10 cm × 10 cm × 6 cm tall wire fence without a covered top was embedded 5 cm into the

ground to minimize losing seeds to runoff and to mimic treatment conditions as closely as possible. We planted one seed per plot per species in 50 randomly selected locations far from (>1,500 m) and adjacent to (<100 m) plantations. Seeds were deposited on the surface on the plots, but with time they were naturally covered by litter or soil. Every 15 days for the first 4 months of the growing season (September–December 2005) and every month thereafter until June 2006, we surveyed seedling emergence in all plots, because we expected variance in time of germination of seeds throughout the year. We measured emergence only once a month from January to June because emergence rates diminished notably, although we found some newly emerged seedlings. In areas adjacent to plantations we also measured seedling establishment at sites where we did not add seeds, to control for seed addition from neighboring exotic trees. To this end we randomly selected an area the same size as the established plots, in which we recorded seedling emergence. We assessed maximum seedling emergence rates using data from a companion study in which we planted 400 seeds of each species used in this experiment in 40 pots (1 l each) and grew them in a greenhouse with soil from the island and water ad libitum. Seeds were cold-stratified to mimic natural germination conditions and manipulated using forceps to avoid scent contamination.

Identification of seed predators

We haphazardly distributed forty automatic cameras (CamTrakker Wildlife Pro Camera[®]) with movement sensors in areas both adjacent to plantations and far from them to record seed predator identities. Each system consisted of a fully automatic camera combined with a passive infrared motion detector. We arranged four cameras per tree species. We aimed four cameras at bait stations consisting of one gram of seeds of each of five species (*Pseudotsuga menziesii*, *Pinus contorta*, *P. ponderosa*, *Austrocedrus chilensis* and *Nothofagus dombeyi*) in two different areas close to and far from plantations (4 cameras per species, two areas, five species; total = 40 cameras). We left the cameras for approximately one week during spring. We were able to identify birds to species and the presence of rodents. Camera resolution prohibited us from distinguishing

rodent species, although size and morphological characteristics enabled us to identify likely candidates.

We did not study the role of arthropods on seed predation, because we did not observe any seed-predator arthropods on the island in any of our multiple visits to the site in winter or early spring (possibly owing to cold temperatures), when seed predation is most important in determining plant establishment. In this region, insect abundance is always extremely low during this period (P. Sackmann personal communication), and rodents are believed to be the main post-dispersal predators in the system (Bustamante 1996; Caccia et al. 2006).

Statistical analyses

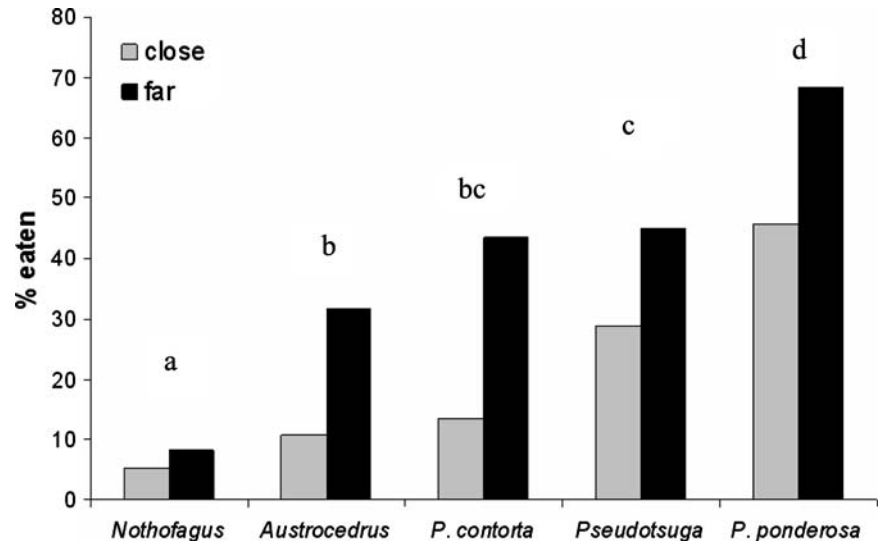
We analyzed results of the seed removal experiment using binary logistic regression, since our response variable was binary (eaten or not eaten) and the independent variables (fixed effects) were categorical; distance was binary and species had five categories (Hosmer and Lemeshow 2000). We also tested for differences between native and exotic species and differences among the different species, using contrast tests in the logistic procedure of SAS 9.13 (SAS 2003). In these models we analyzed both main effects and interaction effects. In the seed exclosure experiment we tested for the effect of species (three categories), exclosures (presence–absence), and location (close to and far from plantations) on seedling establishment using binary logistic regression. We tested for the main effect and for interactions between different variables (Logistic Procedure in SAS 9.13 (SAS 2003)).

Results

Seed removal

Predation rate was higher at areas located far from the plantations than at sites adjacent to them ($\chi^2 = 14.94$, $DF = 1$, $P < 0.001$) (Fig. 2). Also, seeds from exotic species were preferred over seeds from native species ($\chi^2 = 24.77$, $DF = 1$, $P < 0.001$). Seed predators preferred seeds in the following order: *Pinus ponderosa* (exotic), *Pseudotsuga menziesii* (exotic), *Pinus contorta* (exotic), *A. chilensis* (native), and

Fig. 2 Seeds removed in areas close to and far from plantations after 20-day trials. Different letters in the graph represent statistically significant differences



N. dombeyi (native) (Fig. 2). Seed predation was closely related to seed mass; seeds with higher masses were preferred (Table 1). The interaction between species type and distance from the plantation was not significant ($\chi^2 = 4.26$, DF = 4, $P > 0.37$).

Seed predator enclosures

We found significant effects of distance from the plantation ($\chi^2 = 7.85$, DF = 1, $P < 0.005$) and the presence of a protective cage ($\chi^2 = 19.93$, DF = 1, $P < 0.001$) on seedling emergence. However, we found no differences among tree species in the number of seedlings emerged ($\chi^2 = 2.91$, DF = 2, $P > 0.232$), although in areas far from plantations the

trend was consistent with the results of the seed removal experiment. The interaction between the two variables (distance and cage) was marginally significant ($\chi^2 = 3.00$, DF = 1, $P > 0.083$) (Figs. 3 and 4), and the interactions between species and distance and between species and presence of a protective cage were not significant ($\chi^2 = 0.55$, DF = 2, $P > 0.76$; and $\chi^2 = 1.49$, DF = 2, $P > 0.47$ respectively). Also, the 3-way interaction among the variables was not significant ($\chi^2 = 0.568$, DF = 2, $P > 0.753$).

Seedling emergence outside cages was four times higher in areas adjacent to plantations than in areas far from them (27 vs. 6 seedlings, respectively), in accord with the results of the seed removal experiment. Emergence in cages was also higher in areas adjacent to plantations than in areas far from them (55 vs. 33 seedlings, respectively) (Fig. 3). This change in proportion of seedling emergence may explain the marginal significance of the interaction terms. In areas near plantations we found only five emerged seedlings in the 300 plots without seed addition, suggesting a minimal effect from natural seed addition in our experiment. From the companion greenhouse study, we obtained seedling emergence rates of at least 85% for all three species.

The seed removal experiment and the seed predation experiment produced similar results. Despite the differences in methods, seed predation was more intense in areas farther from plantations and heavier seeds were preferred over lighter ones (Figs. 2 and 4).

Table 1 Approximate weight and average seed predation rates for the species studied in the seed removal experiment

Species	Average predation (%)	Seed weight (mg)
<i>Nothofagus dombeyi</i>	6.752874	2.4
<i>Austrocedrus chilensis</i>	21.19048	4.3
<i>Pinus contorta</i> *	28.44633	5.7
<i>Pseudotsuga mensiezii</i> *	36.90678	13.7
<i>Pinus ponderosa</i> *	57.04802	45.45

Sources: Caccia et al. 2006, Sarasola et al. 2006

Exotic species are denoted by *

Fig. 3 Percent of seedlings emerged among the different treatments for all species pooled. Seedling emergence rates were statistically different between areas close to and far from plantations and between caged and uncaged treatments (see text for details)

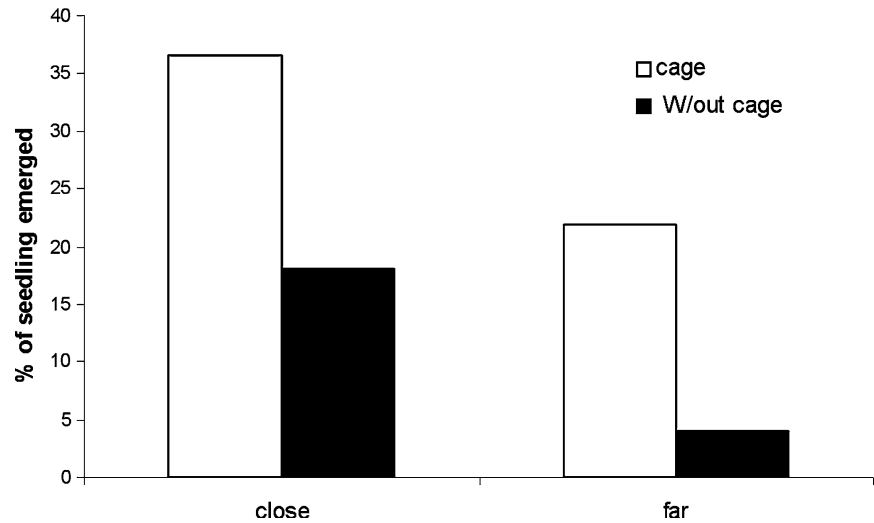
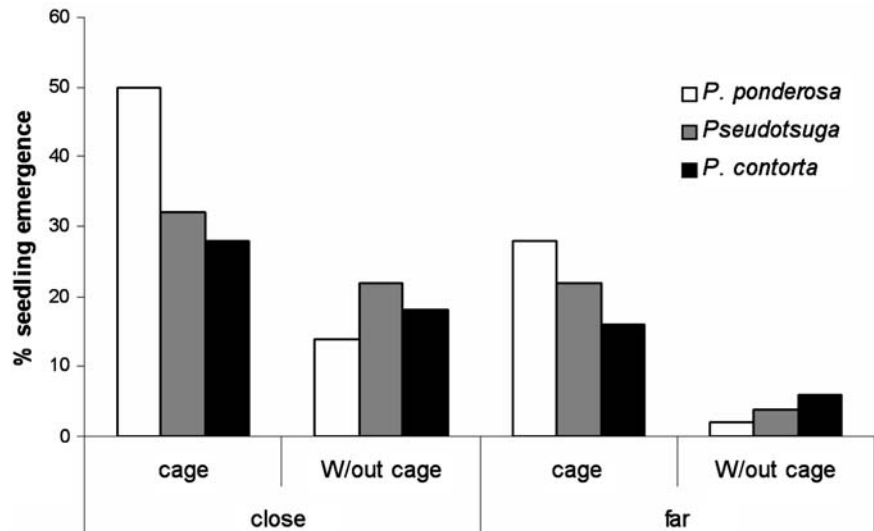


Fig. 4 Percent of seedlings emergence for each species in each treatment. There was a statistical difference between the distance treatments but not among the species. There was also a significant effect of caging (see Fig. 3)



Identification of seed predators

Using cameras, we identified two bird species as seed predators: *Scelorchilus rubecula* and *Phrygilus patagonicus*. Owing to camera limitation, we were unable to identify rodents to species. However, based on the size and morphology of the rodents in the photographs and on previous studies in the area, rodent seed predators were most likely *Abrothrix olivaceus* and *Oligoryzomys longicaudatus* (cf. Caccia et al. 2006). We were able to get pictures of birds or rodents consuming seeds of all species in the different areas studied except for seeds of *Nothofagus*, which were the least preferred. In areas far from plantations we

obtained photographs of 14 different individuals consuming seeds (nine rodents and five birds); in areas adjacent to plantations we obtained photographs of seven individuals (three rodents and four birds).

Discussion

Seed predation has been suggested as an important control of exotic plants, especially when these plants are not superabundant (Maron and Vilá 2001). Our data suggest that seed predators limit the establishment of exotic conifers and retard invasion in our study system. Predation was more intense in

uninvaded areas than in areas with high densities of exotic conifers, pointing to a mechanism for the current lack of invasion.

Plantations are not well suited for native animals in this region, and local animals are rare inside plantations. In the region of our research, studies have shown a pattern of low number of individuals in plantations for rodents (Muñoz and Murúa 1989, 1990) and birds (Schlatter and Murúa 1992), especially granivorous birds (Estades 1994). This habitat difference may cause the pattern of less predation in areas near plantations. If plantations had not lessened the presence of seed predators, we would have expected many seeds to have been consumed there as a consequence of a numerical response by local rodents and birds to the abundant exotic seeds.

Rejmánek and Richardson (1996) found that seed size contributed to invasiveness for pine trees. They suggested that species with smaller seeds could be more invasive because they produce more seeds and have higher initial germinability, shorter periods of chilling to overcome dormancy, and higher relative growth. In a subsequent study of conifers, Richardson and Rejmánek (2004) also suggested that species with very large seeds can be invasive only if they find a local vector to disperse their seeds, which is an uncommon event. Our study suggests that seed size can also be related to chances of seed predation, because seed size is known to affect preference by seed predators (Reader 1993; but see Moles et al. 2003, Moles and Westoby 2003). Despite the fact that seed predation was related to seed mass, other seed characteristics such as protective tissue or chemical defenses could be playing an important role.

Species characteristics, such as their dispersal abilities, are a key part of the invasion process. Colonization can be dispersal-limited at relatively small scales (Cadenasso and Pickett 2001; Pauchard and Alaback 2004). Seed dispersal is well-studied in pines (Lanner 1998). A very small percentage of seeds is known to disperse more than 100 m, but such relatively rare events of long-distance dispersal are extremely important for pine invasion (Higgins and Richardson 1999). Our results show that seed dispersal may play an important role, given that a small but noteworthy number of seedlings were able to emerge far from plantations (Fig. 3). However, conifer invasion in our system seems not to be limited only by dispersal, given the different levels of seed

predation and seedling emergence at different distances from seed sources.

More seedlings emerged close to plantations than far from them in caged treatments. This result could be due to differences in abiotic characteristics of the different areas, soil characteristics, and/or characteristics of the soil biota that could affect germination rates or early survival. For example, we know that pines need ectomycorrhizal fungi to survive, and when ectomycorrhizal plants are established, the primary inoculation source is thought to be existing hyphal networks associated with established plants (Newman 1988). Establishment of exotic Pinaceae around plantations is then limited to the root zone of the plantation trees, where seedlings can tap the mycelial network. Establishment beyond the root zone of trees is then limited by the presence of spore inoculum, but there is evidence of poor dispersal ability of fungal species outside Pinaceae plantations (Davis et al. 1996; Lamb 1979; Mikola 1953). Plantations can modify soil properties like pH and water content (Jackson et al. 2005) that could facilitate seedling establishment near plantations. These findings are evidence of the complexities of the invasion process, which is probably in most cases affected by multiple factors.

Seedling herbivory has been proposed as an important factor limiting pine establishment and invasion (Fuentes and Etchegaray 1983; Kruger et al. 1989; Richardson et al. 1994). Seedling herbivory could have affected our results, as seedlings in exclosures were less likely to be attacked than seedlings outside them. However, because we took measurements frequently, it is unlikely that herbivory on seedlings could have produced a strong difference. Also, results from a companion study on Isla Victoria on the role of seedling herbivory on pine invasion show relatively low rates of seedling herbivory. Only 8% of individuals of *Pinus ponderosa* and *Pseudotsuga menziesii* were attacked by herbivores during seven months starting in late winter (when seedling emergence is highest) in areas adjacent to and far from plantations (M. A. Nuñez unpublished data).

Abiotic factors such as climate can play an important role in controlling invasion of exotic conifers (Richardson and Bond 1991). However, the large number of species introduced, many of them from areas with similar climates to that of Isla Victoria (Critchfield and Little 1966) or that are successfully invading areas similar to Isla Victoria (Richardson and

Rejmánek 2004), suggests that these abiotic factors cannot fully explain the observed invasion pattern. Also the fact that many of these species are well-adapted to the area and attain remarkable growth rates in silviculture in the region (Schlichter and Laclau 1998) supports the idea that abiotic factors cannot completely explain invasion patterns on Isla Victoria.

It is important to note the limitations of this study. Seed predation and production show marked inter-annual fluctuations (Schnurr et al. 2004; Wilson et al. 2007). Therefore, our results, obtained in a single year, can yield limited information, since we cannot assess how this pattern would change between years. However, we can say, based on the data collected, that seed predation has probably affected invasions by our study species in this area, especially in areas distant from plantations, therefore acting as a barrier for conifer invasion.

Most studies on biological invasions are conducted on species that are already invading some area. By contrast, this study focused on species that one might have expected to invade—given their traits and the area characteristics—but that have not yet spread far from the point of introduction. This kind of system, in which species are not yet invading, can yield valuable information about what factors are limiting invasions rather than what factors are promoting them, and this information can aid land managers. This study suggests seed predation—a factor often proposed as important to plant invasion but one seldom tested—can be an important factor producing biological resistance and retarding plant invasion.

Acknowledgments We thank N. Sanders, A. Classen, D. Vazquez, F. Caccia, D. Richardson, and Y. Sasal for their comments on this manuscript. We are very grateful to field assistants J. Karlanian, F. Ginnani, R. Dimarco, M. Nuñez, and E. Bargas. A. Reed provided fundamental insight into the statistical analysis. The Administración de Parques Nacionales, the Delegación Técnica, and especially Tata Mujica provided essential logistic support and feedback for this project. MN was supported by a summer research grant from the Department of Ecology and Evolutionary Biology at the University of Tennessee.

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