Enemy release or invasional meltdown? Deer preference for exotic and native trees on Isla Victoria, Argentina

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Abstract How interactions between exotic species affect invasion impact is a fundamental issue on both theoretical and applied grounds. Exotics can facilitate establishment and invasion of other exotics (invasional meltdown) or they can restrict them by re-establishing natural population control (as predicted by the enemy-release hypothesis). We studied forest invasion on an Argentinean island where 43 species of Pinaceae, including 60% of the world's recorded invasive Pinaceae, were introduced *c.* 1920 but where few species are colonizing pristine areas. In this area two species of Palearctic deer, natural enemies of most Pinaceae, were introduced 80 years ago. Expecting deer to help to control the exotics, we conducted a cafeteria experiment to assess deer preferences among the two dominant native species (a conifer, *Austrocedrus chilensis*, and a broadleaf, *Nothofagus dombeyi*) and two widely introduced exotic tree species (*Pseudotsuga menziesii* and *Pinus ponderosa*). Deer browsed much more intensively on native species than on exotic conifers, in terms of number of individuals attacked and degree of browsing. Deer preference for natives could potentially facilitate invasion by exotic pines. However, we hypothesize that the low rates of invasion currently observed can result at least partly from high densities of exotic deer, which, despite their preference for natives, can prevent establishment of both native and exotic trees. Other factors, not mutually exclusive, could produce the observed pattern. Our results underscore the difficulty of predicting how one introduced species will effect impact of another one.

Key words: biological invasion; facilitation; Patagonia; Pinaceae; pine invasion.

INTRODUCTION

Biological invasions can cause species extinction, habitat degradation, change in ecosystem function and facilitation of further invasions (D'Antonio *et al.* 2001). Interactions between introduced species and natives can greatly affect invasions (see Richardson *et al.* 2000). Two hypotheses that entail interactions between exotic species have recently been advanced to explain the invasiveness of some exotic species. These are the enemy release hypothesis and the invasional meltdown hypothesis. The enemy release hypothesis states that exotic species experience decreased regula-tion by natural enemies (e.g. herbivores), resulting in increased abundance and distribution (Williamson 1996; Keane & Crawley 2002; Colautti *et al.* 2004; Agrawal *et al.* 2005). In invasional meltdown, synergy between exotic species facilitates their invasion and/or increases their invasiveness and impact (Simberloff & Von Holle 1999; Simberloff 2006). Some exotic species could be subjected to both factors (released from enemies and facilitated by other invaders). Also,

it is possible that introduced herbivores can have either effect on invasive plant species (serving either as bio-control agents or as facilitators) depending on the details of the local ecosystem.

Herbivores influence diverse ecological processes, including biological invasion (Bellingham & Coomes 2003; Chauchard *et al.* 2006). In forest systems, wild ungulates such as deer damage trees by browsing, stripping bark and fraying (Gill 1992b). Browsing is the most important damage, affecting sapling growth and survival (Hester *et al.* 2000; Gill & Beardall 2001). Evidence for the mechanisms by which ungulates affect invasion by non-native plants is often inconclusive (Parks *et al.* 2003). Herbivory by mammals may con-tribute to the success or failure of plant invasion by selective attacks (Maron & Vila 2001; Parker *et al.* 2006). If they affect native plants more heavily and reduce their abundance, deer would benefit exotic plant species by competitive release – which can be seen as evidence for invasional meltdown. On the other hand, if deer preferentially browse exotic plants, they could prevent invasion, which would support the importance of enemy release in determining extent of an invasion.

On an Argentinean island with old plantations of many exotic tree species adjacent to native forest, only
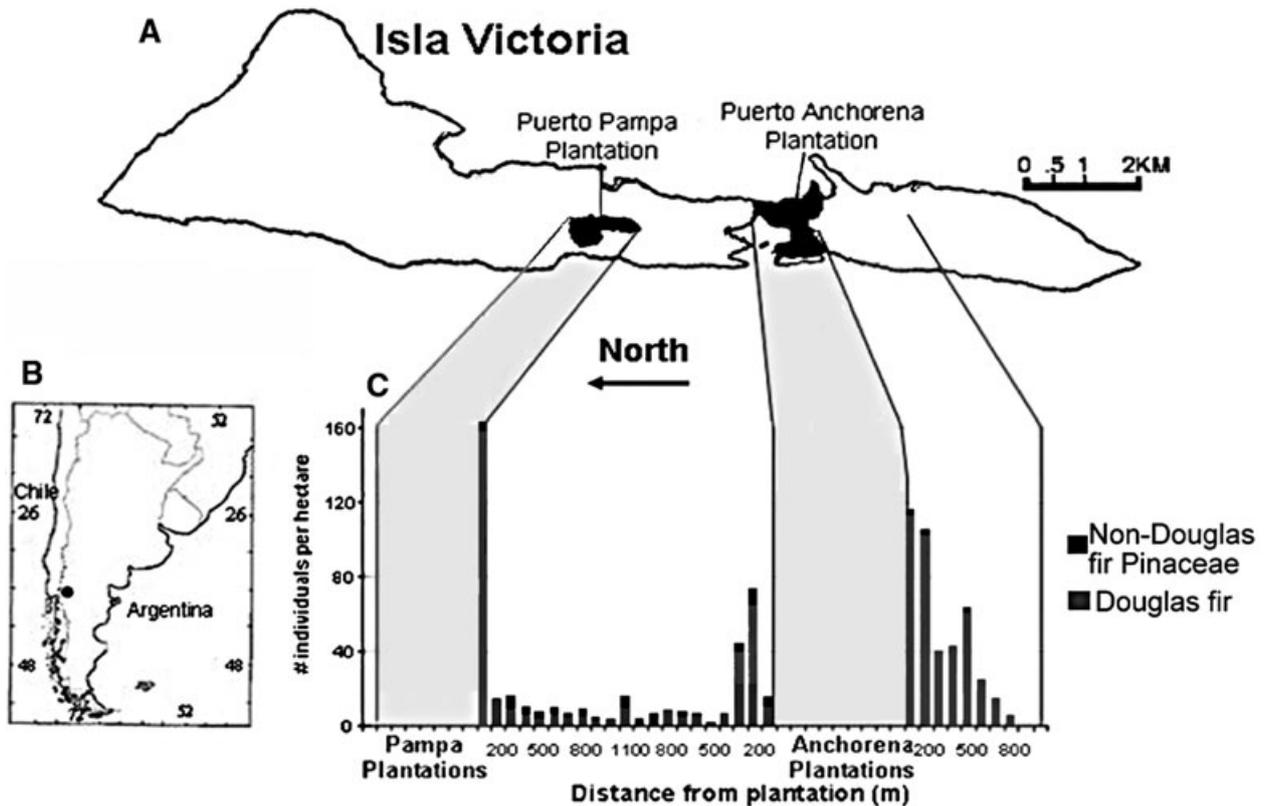
Fig. 1. Map of Isla Victoria with geographical location and abundance of exotic conifers outside plantations. (A) Map of Isla Victoria with plantations of exotic Pinaceae in black (Puerto Pampa and Puerto Anchorena plantations). (B) Geographic location of the study area (black dot). (C) Density of seedlings, saplings and adults of Douglas fir (*Pseudotsuga menziesii*, in grey) and other Pinaceae (in black) outside plantations from the Puerto Pampa plantations southward through the Puerto Anchorena plantations found after a detailed survey using 10 m wide transects distributed every 100 m, parallel to the plantations (see Simberloff *et al.* 2002 for a detailed description of the methods).

a few species have begun to invade (Simberloff *et al.* 2002). We sought to determine the effect of exotic herbivores, in this case Palearctic deer, on the invasion process. On the one hand, deer could be driving or contributing to the observed low invasion rates by Pinaceae on Isla Victoria if deer damage exotic conifers more than native species. However, if deer prefer native species over exotics, they could aid establishment of exotic seedlings, an impact that can be exacerbated by their disturbance of the soil. The relative impacts of deer on native and exotic tree species remain unexplored.

Simberloff *et al.* (2002, 2003), based on field observation of native and exotic trees in the area, suggested that deer could be halting invasion of exotic trees by selectively browsing on them. Such a hindrance to pine establishment has been observed in other areas where pines are introduced (Richardson *et al.* 1994) and where they are native (Rogers *et al.* 2006). Thus, our hypothesis is that exotic deer impede invasion by exotic trees by damaging them more than their native competitors.

METHODS

Study system

Isla Victoria, in Nahuel Huapi National Park, Argentina (Fig. 1), is 20 km long and 4 km across at its widest point. In 1902 the island began to suffer major damage from logging, cattle ranching and fires, which affected 50–60% of the island. With the establishment of the national park in 1934, such activities decreased. Today, most of the island is covered by either primary or substantial secondary forest dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis* trees, but several roads, trails, buildings and abandoned pastures remain.

In 1917, Palearctic deer were introduced: *Cervus elaphus* [elk or red deer], *Dama dama* [fallow deer] and *Axis axis* [axis deer]. In 1962, combined red and fallow deer density was estimated at 40 per square kilometre (Anziano 1962) and more recently at 26 per square kilometre (M. A. Relva, unpubl. data 2004); axis deer disappeared. These densities are very high compared

with normal densities in native areas, which range from six to 20 deer per square kilometre (Mayle *et al.* 2000; Scott *et al.* 2000) or compared with those in other areas were deer are exotic, such as New Zealand, where densities of 16 per square kilometre are considered high (Nugent *et al.* 2001). Native deer *Pudu pudu* and *Hippocamelus bisulcus* have become very rare in the region, probably because of human activities (Vazquez 2002).

In 1925, the Argentine government established a tree nursery on Isla Victoria. A few species introduced then had already been introduced beginning in 1910 (Koutché 1942; APNA 1988). The last plantings by the government were in 1939. At least 73 conifers – including 60% of the world's known invasive conifer species – and 62 broad-leaved species were planted, including species from every continent but Antarctica. Included were 43 species of Pinaceae, including 17 of the 28 species of Pinaceae that Richardson and Rejmánek (2004) cite as having invasive qualities. There has been no recent survey of which species remain on Isla Victoria, but at least 50 are apparent to casual observation (Simberloff *et al.* 2002), occupying an extensive area (Fig. 1). Of the 22 species of the genus *Pinus c.* 20 years after their introduction, 19 were well established and most were producing viable seeds (Barrett 1952). However, only a few species have dispersed beyond the plantations; most are present in very low densities if at all outside the plantations (Simberloff *et al.* 2002; Fig. 1). Among introduced Pinaceae, Douglas fir (*Pseudotsuga menziesii*) is by far the most widespread.

FIELD EXPERIMENT

Selective browsing by deer

We conducted an experiment to determine whether deer preferentially browse on native (*A. chilensis* and *N. dombeyi*) or introduced *(Pseudotsuga menziesii* and *Pinus ponderosa*) tree species. *Austrocedrus chilensis* and *N. dombeyi* are the only dominant trees in this region; the exotic *P. menziesii* reaches high densities near plantations but is rare far from them, and *P. ponderosa* is found outside plantations but is always rare (Simberloff *et al.* 2002). We collected saplings from five different locations on the island to offer an array of individuals with nutritional composition (Bergman *et al.* 2005) similar to what deer find in nature.

In late winter – early spring 2005 (31 August to 1 October), in 45 feeding stations we randomly placed one sapling, approximately 1 m tall, of each of the four tree species in each corner of a 1.5 × 1.5 m square. We distributed feeding stations from the Puerto Pampa plantations southward through the Puerto Anchorena

plantations in the same area where Simberloff *et al.* (2002) conducted their survey of exotic conifers (Fig. 1). We used saplings uneaten by deer, to avoid possible plant responses to herbivory that can affect deer preference. Immediately before the experiment, we transplanted the saplings into pots 40 cm in diameter and 50 cm high and planted them the same day, burying the pots. We measured deer preference every 2 weeks during the first 10 weeks after the experiment started. We observed no ill effects in most planted trees that were not browsed by deer, and at stations where at least one tree showed signs of stress (e.g. low turgor) we ceased measurement. We believe there was little effect on palatability or preference owing to experimental conditions. We used only the feeding stations that were not attacked by other animals or affected by human activities. At the end of the experiment, we were able to collect information from 38 of the initial 45 stations. No other animals on this island would browse on these saplings.

To quantify browsing preference, at each feeding station we recorded, for each sapling, the number of branches browsed divided by the total number of branches, and the type of deer damage (whether on lateral or apical shoots). We also recorded the number of saplings browsed and number of individuals with browsed apical shoots. Ten weeks after initiating the experiment we recorded the percentage of browsed branches per species to account for change in deer preference when the preferred species had been browsed.

Statistical analyses

We analysed the data using logistic regression (for binomial variables) and Poisson regression (for percentages and counts) with the GENMOD procedure of SAS 9.1 (SAS 2003). We used species as a fixed effect and the feeding stations as a random effect in our model. These assignments accurately model the correlation found within feeding stations. These models account for lack of independence between the different saplings in the feeding stations, a common problem in this type of experiment, although most similar studies do not use this type of model (Mangeaud & Videla 2005).

RESULTS

Deer browsed more heavily on the natives *A. chilensis* and *N. dombeyi* than on the exotic conifers *P. menziesii* and *P. ponderosa*. In terms of the number of individuals browsed on the first visit ($\chi^2 = 21.45$; $P < 0.001$; Fig. 2A), per cent of browsed branches ($\chi^2 = 21.45$; $P < 0.001$; Fig. 2B), number of individuals with browsed apical shoots ($\chi^2 = 24.02$; $P < 0.001$; Fig. 2C)
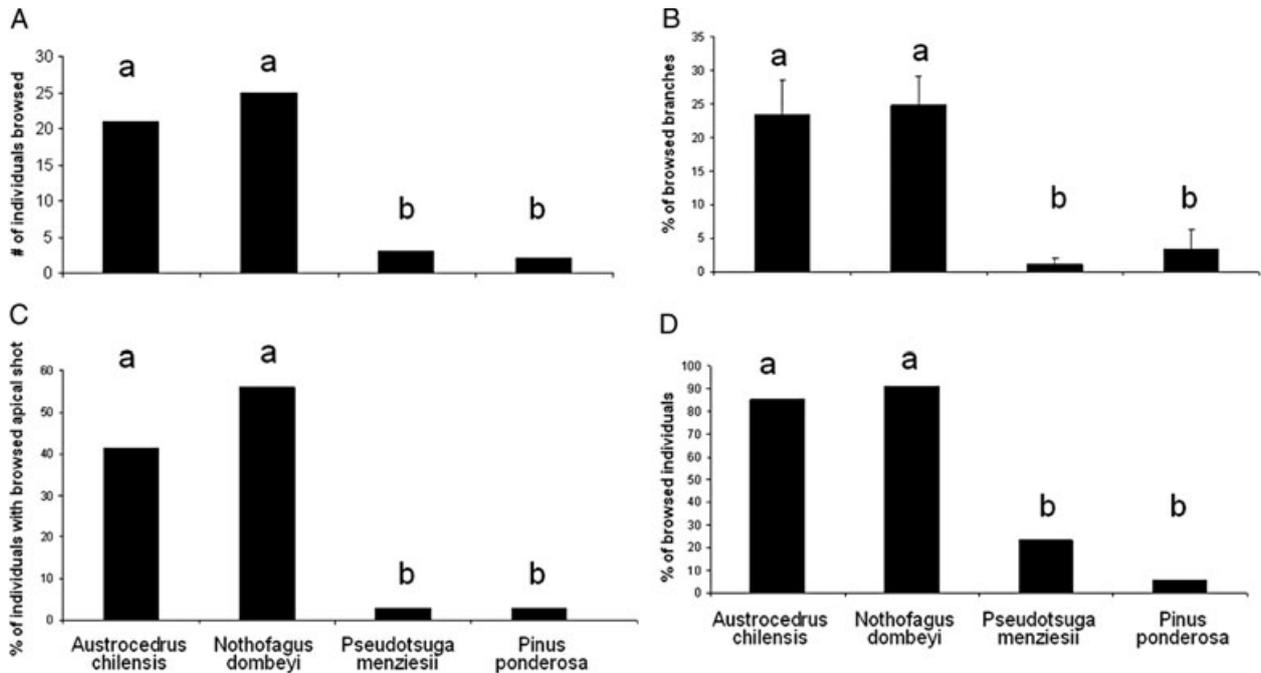
Fig. 2. Results of the cafeteria experiment for the two native (*A. chilensis* and *N. dombeyi*) and two exotic (*Pseudotsuga* and *Pinus*) tree species at the 38 stations attacked by deer. Different letters represent significant differences for an α of 5%. (A) Individuals browsed at the time of the first deer visit (first time when browsing was recorded in the different stations). (B) Per cent of browsed branches at the time of first deer visit. (C) Per cent of individuals with browsed apical shoot at the time of the first deer visit. (D) Per cent of individuals with browsed branches at the end of the experiment (10 weeks).

and per cent of individuals browsed at the end of the experiment ($\chi^2 = 28.58$; $P < 0.001$; Fig. 2D), both natives were preferred over both exotics. There were no significant differences between the two native trees or between the two exotics (in all cases $\chi^2 \leq 3.51$, $P > 0.05$).

DISCUSSION

Contrary to our hypothesis, we found that exotic deer preferentially browsed on native rather than exotic species, a preference that could potentially aid invasion by exotic pines, perhaps generating invasional meltdown. Despite the short-term nature of this study and the limited number of species studied, we observed that deer preference was much greater for native tree species than for exotic conifers in terms of the number of browsed individuals and intensity of browsing. Deer are known to influence survival and growth of plant species and can strongly alter dominance patterns through selective browsing (Pastor *et al.* 1993; Zimov *et al.* 1995; Gill & Beardall 2001), and deer herbivory can suppress tree growth, limit competitive abilities and affect tree survival rates (Gill 1992a; Ueda *et al.* 2003). Although browsing preference need not mean negative effects on tree growth, owing to the ability of some plants to compensate for lost tissues (McNaughton 1983), in our study areas, exotic deer have been shown to affect sapling growth and tree seedling density of natives (Veblen *et al.* 1989; Relva & Sancholuz 2000).

Differences in abundance between natives (abundant) and exotics (rare) could explain the observed patterns if deer foraging behaviour depends on the relative abundance of plants. However, we think this is not a determining factor in this study, given the strength of the observed pattern of preference and the fact that there is evidence for frequency-independent forage selection by deer (Chevallier-Redor *et al.* 2001).

In New Zealand, as on Isla Victoria, deer and Pinaceae are both introduced. Introduced deer in New Zealand have caused a rapid decline of palatable tree, herb and shrub species (Allen *et al.* 1984), but its effects are less clear on species that are avoided or at least not preferred, such as *Nothofagus* (Forsyth *et al.* 2002). Several researchers have found no evidence (Nugent 1990), or little evidence (Husheer & Frampton 2005) of negative effects of introduced deer on establishment and growth of *Nothofagus* seedlings, while others have found strong evidence (Allen & Allan 1997; Allan *et al.* 1997; Husheer *et al.* 2003; Husheer & Robertson 2005) of such effects.

Also in New Zealand, pine species constitute a small but noteworthy proportion of the diet of exotic deer (Nugent 1990; Nugent *et al.* 2001). The different

levels of tree invasion found in the two areas (Richardson & Higgins 1998; Simberloff *et al.* 2002; Buckley *et al.* 2005; Bustamante & Simonetti 2005; Williams & Wardle 2005) suggest that deer may play a similar role in pine invasions of Isla Victoria and New Zealand, but that factors impeding the invasion on Isla Victoria are not operating in New Zealand.

Deer can be important in regulating regeneration of native (Gill 1992a; Bellingham & Allan 2003) and exotic tree species (Richardson & Bond 1991). Because deer attain very high densities in our study area compared with those where it is native, the observed high intensity of browsing (Barrios-Garcia 2005) could limit both exotics and natives. If deer had achieved somewhat lower density, they might have promoted Pinaceae invasion because of the currently much higher abundance of native species. This idea is consistent with the hypothesis of Richardson *et al.* (1994) that low or high levels of herbivore pressure could control spread of introduced pines but intermediate levels could promote invasion.

Observational studies of deer browsing on Isla Victoria (Barrios-Garcia 2005) showed high preference for native *A. chilensis* saplings in relation to their availability relative to the preference for *N. dombeyi*. Barrios-Garcia surveyed saplings of different species in randomly selected plots. She found that 81% of individuals of *A. chilensis* were browsed *versus* 36% of individuals of *N. dombeyi*. Nevertheless, faecal composition analyses reveal that both *A. chilensis* and *N. dombeyi* constitute important food items during the year (32.3% of their total diet), and they are especially important during winter – 46.2% of their total diet (22.2% *A. chilensis* and 24% *N. dombeyi*) (Relva & Caldiz 1998). Unfortunately, no data are available on introduced tree species in deer diets on Isla Victoria. Barrios-Garcia also collected data on browsing on exotic conifers, finding that 48% of the individuals recorded were browsed by deer. Despite the large dissimilarities between the sample sizes of exotic and native tree species (27 and 2277, respectively) caused by the local rarity of the introduced conifers, these data support the idea that lower densities of deer could generate a release from herbivory for the exotic tree species.

The relative lack of tree invasion found on Isla Victoria cannot be explained entirely by herbivory by exotic deer. Deer might have been seen as an inadvertent case of biological control, but actually they are having the opposite impact through selective herbivory on natives and also perhaps by other types of disturbances such as ground alteration (Richardson *et al.* 1994). For example, trampling has been observed to favour establishment of exotic conifers at Isla Victoria (Simberloff *et al.* 2002) and elsewhere (Richardson & Bond 1991). Our results coupled with information from other studies suggest that deer could potentially aid invasion of exotic conifers and that this invasion may presently be halted by the high densities of deer found in the areas.

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