ORIGINAL PAPER

Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown

María Andrea Relva · Martin A. Nuñez ·
Daniel Simberloff

Abstract Invasive species are a major threat to native communities and ecosystems worldwide. One factor frequently invoked to explain the invasiveness of exotic species is their release in the new habitat from control by natural enemies (enemy-release hypothesis). More recently, interactions between exotic species have been proposed as a potential mechanism to facilitate invasions (invasional meltdown hypothesis). We studied the effects of introduced deer on native plant communities and exotic plant species on an island in Patagonia, Argentina using five 400 m^2 exclosures paired with control areas in an *Austrocedrus chilensis* native forest stand. We hypothesized that introduced deer modify native understory composition and abundance and facilitate invasion of introduced tree species that have been widely planted in the region. After 4 years of deer exclusion, native *Austrocedrus* and exotic *Pseudotsuga menziesii* tree sapling abundances are not different inside and outside exclosures. However, deer browsing has strongly inhibited growth of native tree saplings (relative height growth is 77% lower with deer present), while exotic tree sapling growth is less affected (relative height growth is 3.3% lower). Deer significantly change abundance and composition of native understory plants. Cover of native plants in exclosures increased while cover in controls remained constant. Understory composition in exclosures after only 4 years differs greatly from that in controls, mainly owing to the abundance of highly-browsed native species. This study shows that introduced deer can aid the invasion of non-native tree species through negatively affecting native plant species.

Electronic supplementary material The online version of this article (doi:10.1007/s10530-009-9623-0) contains supplementary material, which is available to authorized users.

M. A. Relva (✉)
Laboratorio Ecotono, Inibioma-Conicet, Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Río Negro, Argentina
e-mail: arelva@crub.uncoma.edu.ar;
andrearelva@gmail.com

M. A. Nuñez · D. Simberloff
Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

Introduction

Large herbivores can substantially affect forest communities from single plants to the landscape scale (Coté et al. 2004; Hobbs 1996; Russell and Fowler 2004; Skarpe and Hester 2008). Direct effects of herbivory by deer on vegetation are well-documented (Danell and Bergström 2002; Gill 1992),

while studies exploring subtler or indirect effects of deer are less common (Gill and Beardall 2001; Rooney and Waller 2003). In general, selective browsing by deer prevents natural tree regeneration by reducing seedling density and delaying sapling growth, and alters plant community composition, generally leading to dominance by less preferred and/or more browse-tolerant species (Augustine and McNaughton 1998; Gill and Beardall 2001). More recent studies have revealed that large herbivores may also play a role in spreading introduced invasive species and aiding them to establish (Kellogg and Bridgham 2004; Vavra et al. 2007). For example, deer and other ungulates can carry seeds from infested to uninfested areas (Malo et al. 2000). Also, disturbance often promotes invasion (Hobbs and Huenneke 1992), and trampling by large herbivores can favor exotic species that are well-adapted to disturbed sites (Hobbs and Huenneke 1992, Wiser and Allen 2006).

Invasive species threaten native communities and ecosystems worldwide (Vitousek et al. 1997), and much effort has been focused on understanding factors controlling alien plant invasions. This is the case for exotic conifers, many of which are highly invasive worldwide and threaten native communities in the southern hemisphere, especially in South America (Richardson et al. 2008). However, in some areas conifers seem unable to invade. For example, on an Argentinean island with plantations with many exotic tree species adjacent to native forest, only a few species have begun to invade and only in areas adjacent to plantations (Nuñez et al. 2008b; Simberloff et al. 2002). Simberloff et al. (2002, 2003) suggested that red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) introduced to this island could be retarding invasion by browsing selectively on introduced trees or otherwise damaging them.

Forests of northwestern Patagonia have undergone extensive grazing and browsing by domestic cattle and introduced deer since the beginning of twentieth century, and detrimental effects on native forest communities have been documented (Blackhall et al. 2008; Gallopin et al. 2005; Relva and Veblen 1998; Relva et al. 2009; Veblen et al. 1989, 1992). Results from a cafeteria experiment, in which native and exotic foliage was offered, have suggested that deer browse selectively on native trees, therefore promoting invasion by the non-natives

(Nuñez et al. 2008a). However, long-term deer effects can be more complex than those observed in a cafeteria experiment owing to factors such as trampling or how browsing is affected by the density or presence of other species.

To assess the net effect of introduced herbivores on a plant invasion, we must know their relative impact on native and introduced plants. If deer affect native plants more heavily and reduce their abundance, they would benefit exotic plant species by competitive release. This would be an example of invasional meltdown (Simberloff and Von Holle 1999), in which the success of an invasive species is facilitated by another non-native species. On the other hand, if deer preferentially browse exotic plants, they could prevent invasion, which would support the hypothesis that enemy release promotes invasion (Keane and Crawley 2002). However, an exotic species could be subjected simultaneously to control by a natural enemy and facilitation by other invaders.

In particular, for this study we hypothesized that exotic deer facilitate invasion by introduced trees by more heavily impacting native trees. We tested this hypothesis through a long-term field exclosure experiment.

We asked: (1) to what extent do deer affect establishment by native and introduced tree seedlings? (2) How much do deer influence native and introduced tree sapling growth? (3) Do exotic deer alter understory and groundcover composition? (4) Are exotic shrubs and herbs promoted by introduced deer?

Methods

Study system

The study was conducted in a forest dominated by the evergreen conifer *Austrocedrus chilensis* located on Isla Victoria, Nahuel Huapi National Park, Argentina (40°57′S; 71°33′W; Fig. 1). Isla Victoria, an island running NW to SE that comprises 3,710 ha, has a varied topography including flat, shallow valleys and elevations of up to 1,025 m above sea level. Mean annual rainfall is 1,700 mm (Barros et al. 1983), mostly occurring during winter (June to September). Soils are allophanic (derived from volcanic ash),

Fig. 1 Location of exclosures and control areas on Isla Victoria, Nahuel Huapi National Park, Argentina
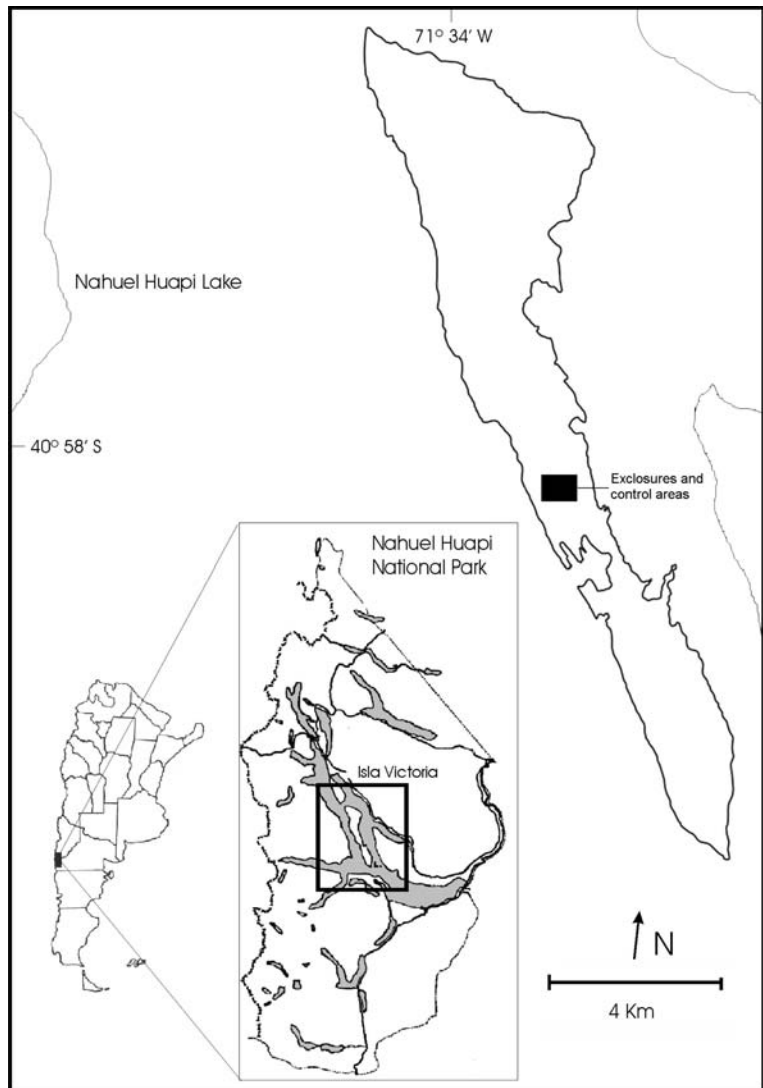
sandy, permeable, rich in organic matter, and acidic (Koutché 1942). Isla Victoria is covered mainly by forests dominated by southern beech (*Nothofagus dombeyi*) or *Austrocedrus chilensis (*hereafter *Austrocedrus*), or by mixed *N. dombeyi-Austrocedrus* forests, with several subdominant tree species and dense understory vegetation composed of shrubs, herbs and graminoids.

Beginning in 1910, trees of at least 108 non-indigenous species (62 conifers, 46 deciduous species) were planted in different areas of the island (Koutché 1942). Most plantings occurred between 1925 and 1939, when plantings ended in this region, mostly owing to the establishment of Nahuel Huapi National Park. Thus, many individuals of many

exotic species were planted, primarily at one site in the center of the island, and small subsets of these were planted at a few other locations (Fig. 1). Planting stopped 60 years ago, and few species have invaded the native forest (Simberloff et al. 2002; Simberloff et al. 2003).

Another important introduction consisted of Old World deer established in the region of Nahuel Huapi National Park between 1917 and 1922, and both red deer (*Cervus elaphu*s) and fallow deer *(Dama dama)* have long been on Isla Victoria (Relva and Caldiz 1998). Native deer *Pudu pudu* (pudu) and *Hippocamelus bisulcus* (huemul) have become very rare (pudu, believed to dwell only at the northern tip of the island) or extinct (huemul) on the island, but red

and fallow deer are abundant. Anziano (1962) estimated their population at ca. 1,500 (40 individuals/km^2), and more recently it was estimated at ca. 1,200 (32 individuals/km^2, Relva unpublished). In addition, ca. 1999 wild boar arrived on the island, apparently swimming the 0.5 km from the Huemul Peninsula, and they are reproducing and are frequently seen (Mujica, personal communication).

Experimental design

Five square exclosures were constructed in 2002 in a native *Austrocedrus* forest stand south of the Puerto Pampa plantation (Fig. 1). We delimited control treatments in areas adjacent to the exclosures where introduced deer browse freely. Exclosures are constructed of wire mesh and are 2 m tall and 20 m × 20 m. In the exclosures and the controls, we set up a grid with 20 2 m^2 circular plots evenly spaced with a distance of 2 m between plots, in which we measured various vegetation features. Every plot was marked with a permanent central stake and re-measured three times in March and April from 2002 to 2006. Vegetation attributes recorded for seedlings (individuals < 10 cm tall) and saplings (individuals > 10 cm tall, but smaller than 4 cm in diameter at breast height) were: (1) *Seedling density*: numbers of native and exotic tree seedlings were recorded annually on 20 1 m^2 circular plots located in the inner portion of the 2 m^2 plots; (2) *Sapling density and size*: number and height of native and exotic saplings were recorded in 20 2 m^2 circular plots. We focused on the exotic *Pseudotsuga menziesii* owing to our previous research, which showed that it is by far the most abundant exotic tree species and the only one substantially spreading on Isla Victoria (Simberloff et al. 2002). At the beginning of the study we observed some seedlings and saplings of this species in the experimental area; (3) *Understory cover*: cover of all vascular species was visually estimated in 20 2 m^2 circular plots using the Braun-Blanquet scale (Newton 2007). In addition, height of the tallest individual of each woody species was measured.

Statistical analyses

To examine whether exclosures and control plots differed in tree seedling and sapling abundances,

maximum height of *P. menziesii* and *Austrocedrus*, and total cover and species richness of understory vascular species, we used repeated-measures analyses of variance (ANOVAs). The effect of excluding deer was considered significant if there was a significant interaction term between time and treatment (von Ende 1993). The difference in plant species composition between exclosures and controls during the initial and final years was compared by Analyses of Similarity with the ANOSIM procedure in the statistical software Primer (Clarke and Warwick 2001). This procedure is a non-parametric permutation test applied to rank similarity matrices underlying sample ordinations (Parr et al. 2004). ANOSIM produces an *R*-statistic that measures relative distance between treatments (Parr et al. 2004). An *R*-value close to 1 indicates that all replicates within a treatment are more similar to each other than to any replicates from a different treatment, while a value close to 0 indicates replicates in different treatments cannot be differentiated. A *p*-value associated with this statistic quantifies the level of significance of the results. Data were fourth-root transformed before analyses to reduce the weight of common species (Clarke and Warwick 2001). We used non-metric multidimensional scaling (NMDS) to represent graphically the plant species composition of replicates before and after 4 years of herbivory by deer in the controls. NMDS is a robust ordination procedure that produces a plot in which different replicates are placed far apart in the ordination space, while similar replicates are placed close together (Gotelli and Ellison 2004). In addition, we used the SIMPER (similarity percentages) procedure in Primer to identify species responsible for determining the sample groupings in the NMDS analysis. All ordinations were run using 10,000 iterations. For this analysis we used data from 34 species and their average cover in each replicate.

Results

Abundance of native and exotic tree regeneration

Pseudotsuga menziesii was the most abundant exotic tree species in the studied plots. At the beginning of the study the total number of exotic seedlings was 79 *P. menziesii*, 3 *Pinus contorta* and 5 *Acer pseudo-*

Table 1 Mean density (and ±SE) of seedlings (individuals/20 m^2) and saplings (individuals/40 m^2) of native and exotic dominant tree species in exclosures and control areas from 2002 (year one) to 2006

	Austrocedrus (native)		*P. menziesii* (exotic)	
	Exclosures	Control	Exclosures	Control
Seedling density				
2002 (year one)	5.8 (2.2)	2.4 (1.5)	4.4 (1.2)	11.4 (4.5)
2005	2.6 (1.03)	0.4 (0.24)	1.4 (0.4)	5.2 (1.2)
2006	2.2 (1.07)	7.4 (4.72)	2.8 (1.3)	10 (6.1)
Sapling density				
2002 (year one)	12.6 (7.3)	8.2 (8.2)	7.8 (3.9)	15.4 (4.9)
2005	10.6 (6.9)	13.8 (13.8)	7.4 (3.4)	19.4 (5)
2006	11.8 (6.8)	14.4 (13.9)	7 (2.5)	22.6 (8.6)

Fig. 2 Mean maximum height (±SE) of native (*Austrocedrus chilensis*) and exotic (*Pseudotsuga menziesii*) tree saplings in the exclosures and control areas on Isla Victoria, Argentina

platanus, while the total number of exotic saplings was 116 *P. menziesii*, 6 *P. contorta* and 2 *A. pseudoplatanus*. The total numbers of seedlings and saplings of *Austrocedrus* at the beginning of the study were 41 and 104, respectively. A marginally significant difference in treatments (exclosures and controls) over time was found for densities of *Austrocedrus* seedlings ($F = 3.37$, $p = 0.06$, Table 1) but we found no differences in density of saplings of *Austrocedrus* ($F = 0.51$, $p = 0.60$) and of seedlings and saplings of *P. menziesii* ($F = 0.29$, $p = 0.74$ and $F = 1.53$, $p = 0.24$, respectively).

Growth responses to cessation of deer herbivory on native and exotic saplings

We detected differences over time in maximum height of saplings between exclosures and controls (year x treatment interaction) for both *Austrocedrus* and *P. menziesii* ($F = 6.25$, $p = 0.004$; and $F = 9.46$, $p = 0.0001$, respectively). At the end of the experiment, saplings of both species were taller inside the exclosures than in the controls (Fig. 2). Relative height growth ((initial height—final height)/initial height) was 77% lower for saplings of *Austrocedrus* growing in the controls than for those growing inside exclosures. By contrast, the relative height growth of *P. menziesii* growing outside exclosures was only 3.3% lower than for those growing inside exclosures.
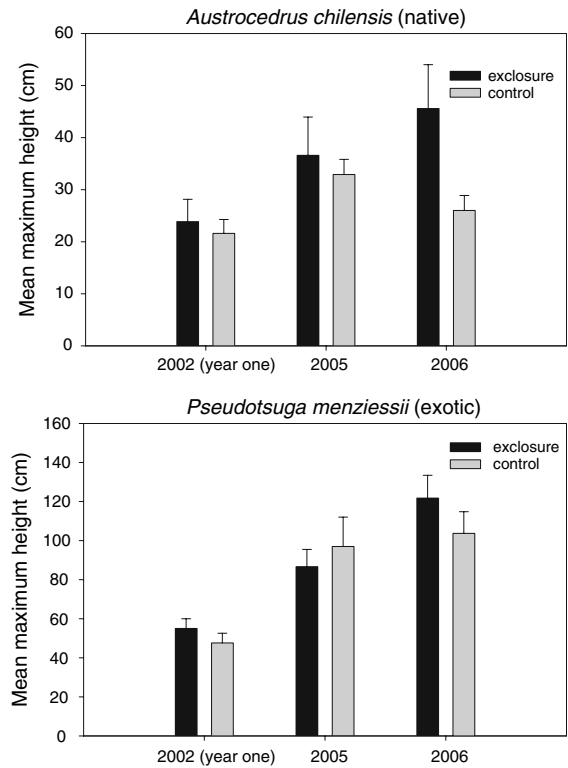
Abundance and understory composition responses to deer exclusion

We recorded 47 vascular plant species in the understory and ground cover during the study in both treatments: 18.4% were trees, 16.3% were shrubs, 44.9% were herbs, and 20.4% were graminoids (see Appendix). Introduced plant species constituted 32% of the total number of recorded species: 3 trees, 1 shrub, 8 herbs, and 3 graminoids. Repeated measures ANOVA revealed significant year-by-treatment interactions for total cover and richness of native plant species ($F = 8.22$, $p = 0.003$; and $F = 13.69$, $p = 0.0003$, respectively, Figs. 3, 4) owing to an increase in both variables in the exclosures compared to the adjacent control plots. By contrast, removal of deer for 4 years had no effect on total cover and richness of exotic plant species, as indicated by the treatment-by-year term ($F = 2.33$, $p = 0.13$ and $F = 0.06$, $p = 0.94$, Figs. 3, 4).
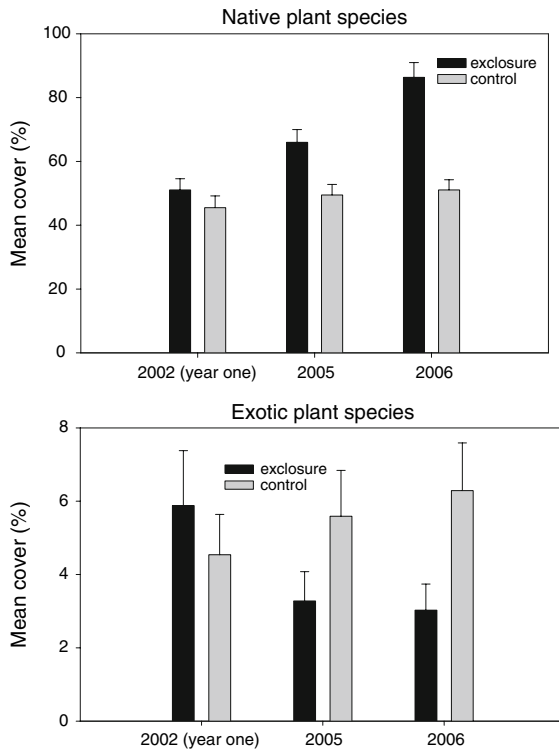
Fig. 3 Absolute cover (mean, ±1 SE) of native and exotic understory species in the exclosures and control areas on Isla Victoria, Argentina

An ANOSIM pairwise test showed no differences between treatments in plant species composition at the beginning of the experiment ($R = -0.14$, $p = 0.8$), while significant differences were detected in plant species composition between exclosure and control treatments after 4 years ($R = 0.7$, $p = 0.008$). NMDS sample ordinations clearly revealed that replicates with 4 years of cessation of herbivory by deer can be separated from control replicates based on plant species composition (Fig. 5). SIMPER analyses showed that native species recognized as highly-browsed such as *Aristotelia chilensis* and *Ribes magellanicum* (Barrios Garcia Moar 2005; Blackhall et al. 2008; Veblen et al. 1989) contributed most (dissimilarity contributions = 7.5 and 4.75%, respectively) to the mean difference in floristic composition between exclosures and controls after 4 years. At the beginning of the experiment the main species that contributed to within-group similarity were the same for exclosures and controls (*Schinus patagonica*, *Berberis darwinii* and *Uncinia* sp. cumulatively account for approximately 40%, Fig. 6).
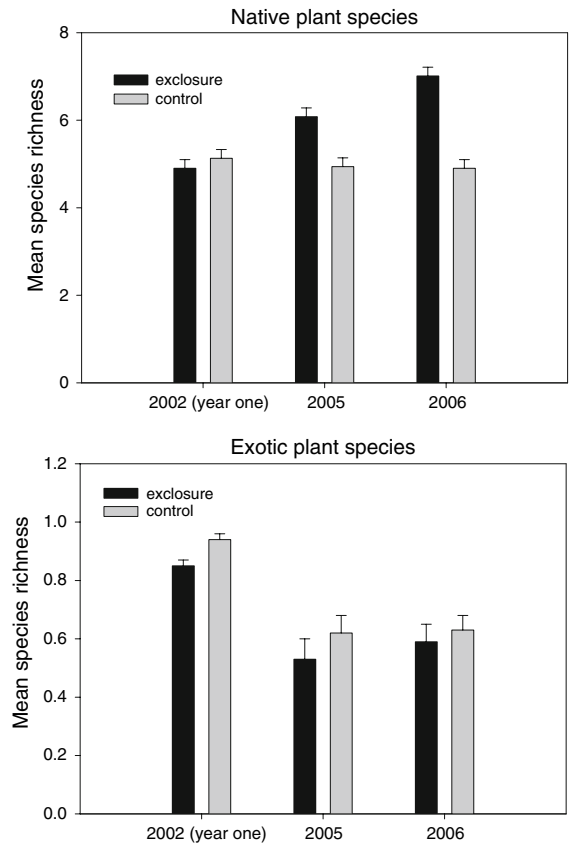

Fig. 4 Species richness (number of species per plot) for native and exotic plant species (mean ± 1SE) in exclosures and control areas on Isla Victoria, Argentina
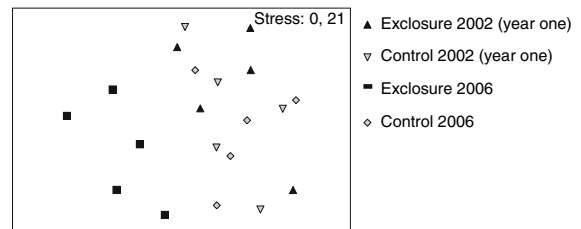

Fig. 5 NMDS (non-metric multidimensional scaling) ordination based on Bray-Curtis similarities using 34 plant species distributed across two treatments (exclosure and control) at the beginning (2002) and end (2006) of the experiment. Each point represents the species composition of a replicate

After 4 years of the experiment, the same species were the main contributors to similarity between control plots, while in exclosures highly-browsed *A. chilensis* and *R. magellanicum* were the main contributors (Fig. 6).

Fig. 6 Species contributing cumulatively to 50% to average similarity within exclosure and control plots. Species references are: ari chi (*Aristotelia chilensis*), rib mag (*Ribes magellanicum*), sch pat (*Schinus patagonicus*), ber dar (*Berberis* darwinii), unc sp (*Uncinia* sp), pse men (*Pseudotsuga menziesii*)
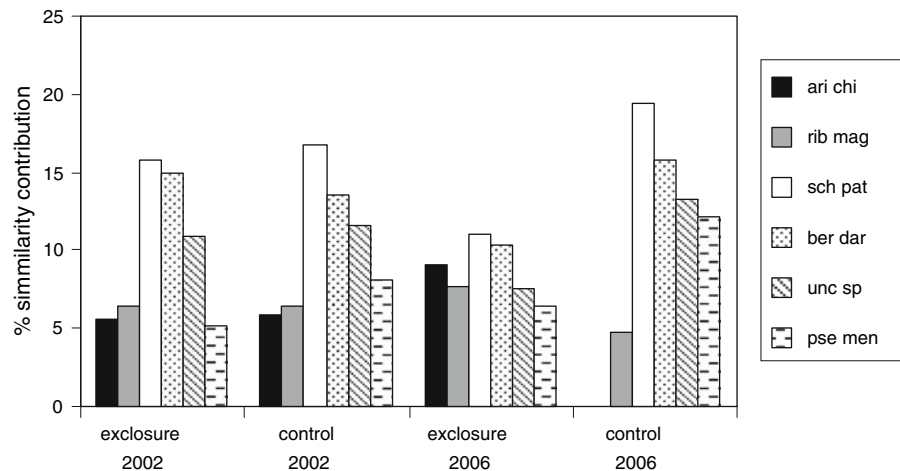
Discussion

After 4 years of exclusion our results show that introduced deer strongly affected the plant community, retarding height growth of the dominant native tree, reducing understory cover, and modifying understory composition. By contrast, the effects of introduced deer on abundances of seedlings and saplings of the native tree species and the preponderant exotic tree species are unclear. We observed much variation in seedling and sapling numbers between control and exclosures during the study. However, we found fewer *Austrocedrus* seedlings in exclosures compared to control plots at the end of the experiment, which could be due to darker conditions determined by greater understory cover in the absence of deer. For young seedlings factors other than browsing strongly influence survival, such as light regime, microtopography, and competition, so the true effect of browsing may be masked (Gill 1992; Gill and Beardall 2001; Rooney 2001; Russell et al. 2001). We therefore agree with assertions that it is important to distinguish natural processes from browsing impact to assess deer effects on vegetation (Bellingham and Lee 2006; Veblen and Stewart 1982). Future studies should assess deer impact on germination rate and early seedling survival through control of light levels or competition.

Introduced deer had an important negative effect on height growth of both the dominant native and the main exotic tree species. However, the impact is stronger for native *Austrocedrus* than for exotic *P. menziesii*. This observation aligns with our previous study showing that deer preferred native over exotic foliage (Nuñez et al. 2008a). Height growth inhibition is critical to trees because vertical growth is the main mechanism for escaping herbivory by ungulates (Brookshire et al. 2002). When ungulate populations decrease (intensive hunting, increased predation, or decreased available forage), a window of opportunity opens and trees can escape from browsing limits and renew height growth (Vila et al. 2003). Even though the mean height of native and exotic tree saplings in our study site is within the range of deer browse, it is much lower for *Austrocedrus* (26 cm, ±2.9) than for *P. menziesii* (103 cm, ±11.05). In light of the limited ability of *Austrocedrus* to compensate for loss of tissue (Relva and Sancholuz 2000), deer browsing can significantly lengthen the time required for this native species to reach a height threshold to escape from browsing. Our results may thus support the invasional meltdown hypothesis, as the net effect of exotic deer was more negative on native trees than on exotic trees, therefore facilitating the exotics.

Deer have been in the area for more than 80 years, and the quick response of the plant community to deer removal is remarkable. Vegetation cover showed a notable increase soon after deer exclusion, corresponding mainly to the positive responses of the preferred native shrubs *A. chilensis* and *R. magellanicum*. There is no statistical difference in the cover of exotic species after deer exclusion; however, there is a trend for a reduction in the cover of exotics and an increase in the cover of natives. Although 32% of recorded species were exotics, they are not as

important as natives in terms of abundance and richness. Thus, to date we have no direct evidence that deer promote exotic shrubs and herbs.

It is possible that exotic deer currently play the same ecological role that the now rare native ungulates (*Pudu pudu* and *Hippocamelus bisulcus*) once played. However, this is unlikely, because *H. bisulcus* usually dwells in open areas at the ecotone between the steppe and the forest or in elevated areas where forest is sparse (Diaz 1993; Povilitis 1998), and this type of ecosystem is uncommon on Isla Victoria. *Pudu pudu* inhabits dense forest, like the ones on the island, but they feed mostly on herbaceous vegetation, and they are much smaller than exotic deer, reaching only 42 cm shoulder height when adult (Redford and Eisenberg 1992). Owing to the differences in habit and habitat between exotic and native deer, it is likely that exotics can affect the forest in different ways than native deer (Parker et al. 2006). Exotic deer are clearly selecting against some species, presumably palatable or browse-sensitive (e.g. *A. chilensis* and *R. magellanicum*), in favor of browse-resistant or unpalatable species (e.g. *S. patagonicus*, *B. darwinii* and *Uncinia* sp.), and this selection is probably producing drastic changes in local ecosystem processes, though these are currently unstudied.

Finally, the fast positive response of native plant species and the insignificant response of exotic plant species to the lack of deer suggest that eradication of deer from Isla Victoria would aid conservation of native communities. Several eradication and control programs have failed and have had undesirable consequences owing to the isolated removal of one exotic species with no consideration of its interactions with other exotic and native species (Bergstrom et al. 2009; Zavaleta et al. 2001). However, our results suggest that this may not be the case for deer in the study system, because deer are detrimental to the native vegetation and have positive or neutral effects on exotic plants.

References

Anziano AF (1962) Acción de los animales sobre la flora. Anales de Parques Nacionales, p 107–112

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J Wildl Manage 62:1165–1183

Barrios Garcia Moar MN (2005) Patrones de daño, uso actual y tendencia histórica de la abundancia de ciervos introducidos en bosques nativos de Isla Victoria, Patagonia, Argentina. Universidad Nacional del Comahue

Barros VR, Cordon VH, Moyano C, Forquera JC, Pizzio O (1983) Carta de precipitación de la zona oeste de las provincias de Río Negro y Neuquén. Primera contribución (1972–1981). Facultad de Ciencias Agrarias, Cinco Saltos, Río Negro, p 28

Bellingham PJ, Lee WG (2006) Distinguishing natural processes from impacts of invasive mammalian herbivores. In: Allen RB, Lee WG (eds) Biological invasions in New Zealand. Springer, Berlin, pp 323–336

Bergstrom DM, Lucieer A, Kiefer K, Wasley J, Belbin L, Pedersen TK, Chown SL (2009) Indirect effects of invasive species removal devastate World Heritage Island. J Appl Ecol 46:73–81

Blackhall M, Raffaele E, Veblen TT (2008) Cattle affect early post-fire regeneration in a *Nothofagus dombeyi–Austrocedrus chilensis* mixed forest in northern Patagonia, Argentina. Biol Conserv 141:2251–2261

Brookshire J, Kauffman B, Lytjen D, Otting N (2002) Cumulative effects of wild ungulate and livestock herbivory on riparian willows. Oecologia 132:559–566

Clarke KR, Warwick RM (2001) Change in Marine communities: an approach to statistical analysis and interpretation. Primer E Ltd, Plymouth

Coté SD, Rooney P, Tremblay JP, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. Annu Rev Ecol Evol Syst 35:113–147

Danell K, Bergström R (2002) Mammalian herbivory in terrestrial environments. In: Herrera CM, Pellmyr O (eds) Plant—animal interactions: an evolutionary approach. Blackwell, England, pp 107–131

Diaz NI (1993) Changes in the range distribution of *Hippocamelus-bisulcus* in Patagonia. Zeitschrift Für Saugetierkunde-Int J Mamm Biol 58:344–351

Gallopin GC, Martín CE, Mermoz MA (2005) Impacto de la ganadería en la cuenca del río Manso Superior. Parte I: Bosque de Ñire con Laura. Editorial APN, Buenos Aires, p 119

Gill RMA (1992) A review of damage by mammals in north temperate forests: 3. Impact on trees and forest. Forestry 65:363–388

Gill RMA, Beardall V (2001) The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74:209–218

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer associates. INC, Sunderland

Hobbs NT (1996) Modification of ecosystems by ungulates. J Wildl Manage 60:695–713

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity and invasion: implications for conservation. Conserv Biol 6:324–337

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Kellogg CH, Bridgham SD (2004) Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. Biol Invasions 6:319–329

Koutché V (1942) Estación Forestal de Puerto Anchorena, Isla Victoria; su organización y trabajos., Ministerio de Agricultura. Dirección de Parques Nacionales, Buenos Aires

Malo JE, Jiménez B, Suarez F (2000) Herbivore dunging and endozoochorous seed deposition in a Mediterranean *dehesa*. J Range Manag 53:322–328

Newton AC (2007) Forest ecology and conservation. A handbook of techniques. Oxford University Press, UK

Nuñez MA, Relva MA, Simberloff D (2008a) Enemy release or invasional meltdown? Deer preference for exotic and native trees on Isla Victoria, Argentina. Austral Ecol 33:317–323

Nuñez MA, Simberloff D, Relva MA (2008b) Seed predation as a barrier to alien conifer invasions. Biol Invasions 10:1389–1398

Parker JD, Burkepile DE, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. Science 311:1459–1461

Parr CL, Robertson HG, Biggs HC, Chown SL (2004) Response of African savanna ants to long-term fire regimes. J Appl Ecol 41:630–642

Povilitis A (1998) Characteristics and conservation of a fragmented population of huemul *Hippocamelus bisulcus* in central Chile. Biol Conserv 86:97–104

Redford K, Eisenberg J (1992) Mammals of the neotropics. University of Chicago Press, Chicago

Relva MA, Caldiz MS (1998) Composición estacional de la dieta de ciervos exóticos en Isla Victoria, P.N. Nahuel Huapi, Argentina. Gayana Zoología 62:101–108

Relva MA, Sancholuz LA (2000) Effects of simulated browsing on the growth of *Austrocedrus chilensis* saplings. Plant Ecol 151(2):121–127

Relva MA, Veblen TT (1998) Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. For Ecol Manag 108:27–40

Relva MA, López Westerholm C, Kitzberger T (2009) Effects of introduced ungulates on forest understory communities in northern Patagonia are modified by timing and severity of stand mortality. Plant Ecol 201(1):11–22

Richardson DM, van Wilgen BW, Nuñez MA (2008) Alien conifer invasions in South America: short fuse burning? Biol Invasions 10:573–577

Rooney TP (2001) Deer impact on forest ecosystems: a North American perspective. Forestry 74:201–208

Rooney TP, Waller DM (2003) Direct and indirect effects of white-tailed deer in forest ecosystem. For Ecol Manag 181:165–176

Russell FL, Fowler NL (2004) Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of *Quercus buckleyi*. Plant Ecol 173:59–72

Russell FL, Zippin DB, Fowler NL (2001) Effects of White-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. Am Midl Nat 146:1–26

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Simberloff D, Relva MA, Nuñez M (2002) Gringos en el bosque: introduced tree invasion in a native *Nothofagus/Austrocedrus* forest. Biol Invasions 4:35–53

Simberloff D, Relva MA, Nuñez M (2003) Introduced species and management of a *Nothofagus/Austrocedrus* forest. Environ Manage 31:263–275

Skarpe C, Hester AJ (2008) Plant traits, browsing and grazing herbivores, and vegetation dynamics. In: Gordon IJ, Prins HT (eds) The ecology of browsing and grazing. Springer, Berlin, pp 217–261

Vavra M, Parks CG, Wisdom MJ (2007) Biodiversity, exotic plant species and herbivory: the good, the bad and the ungulate. For Ecol Manag 246(1):66–72

Veblen TT, Stewart GH (1982) The effects of introduced wild animals on New Zealand forests. Ann Assoc Am Geogr 72:372–397

Veblen TT, Mermoz M, Martin C, Ramilo E (1989) Effects of exotic deer on forest regeneration and composition in northern Patagonia. J Appl Ecol 26:711–724

Veblen T, Mermoz M, Martin C, Kitzberger T (1992) Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. Conserv Biol 6:71–83

Vila B, Torre F, Guibal F, Martin J-L (2003) Growth change of young *Picea sitchensis* in response to deer browsing. For Ecol Manag 180:413–424

Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. N Z J Ecol 21:1–16

von Ende CN (1993) Repeated-measures analysis: growth and other time-dependent measures. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Chapman & Hall, New York

Wiser SK, Allen RB (2006) What controls invasion of indigenous forests by alien plants? In: Allen RB, Lee WG (eds) Biological invasions in New Zealand. Springer, Berlin, pp 195–209

Zavaleta ES, Hobbs RJ, Money HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends Ecol Evol 16(8):454–459