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Review

Multiple effects of introduced mammalian herbivores in a temperate forest

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Abstract

Introduced mammalian herbivores can significantly affect ecosystems. Here, I review evidence on effects of introduced mammalian herbivores in the temperate forest of the southern Andes. Available data suggest that introduced herbivores decrease the abundance of seedlings and saplings of dominant tree species in some forest types, which could impair forest regeneration. They also affect understory species composition. The mechanisms of the effects of introduced herbivores are complex, and include direct effects of browsing or trampling and more complex interactions such as indirect effects through other species. Some native mammalian and avian predators may benefit from increased food availability resulting from high densities of some introduced mammalian herbivores. In turn, enhanced populations of predators may have resulted in increased predation on native prey. Competition for resources and disease transmission have also been proposed as possible negative effects of introduced herbivores on native herbivores, but little evidence supports this claim. Little is known about effects on invertebrates.

Introduction

Biological invasions are one of the most serious threats to biodiversity. They are the main cause of recent extinctions (i.e. since the year 1600), and one of the main causes of current endangerment of species, second only to habitat destruction (Vitousek et al. 1997; Brown and Lomolino 1998). Many invasions have led to fundamental changes in species composition, habitat structure, and ecosystem processes (Elton 1958; Simberloff 1991; Williamson 1996). Many introduced mammalian herbivores generate the latter effect (de Vos et al. 1956; Ebenhard 1988).

Introduced mammalian herbivores affect ecosystems in several ways. Through browsing, grazing, and trampling, they cause the population decline of individual plant species by decreasing survival, growth, or fitness (Crawley 1986; Ebenhard 1988). Some such effects are quite dramatic. For example, goats introduced to Santa Catalina Island off the coast of California drove the local population of *Artemisia californica* to extinction (Coblentz 1978). Of course, effects on multiple plant species can also lead to drastic changes in the diversity and species composition of the entire plant community. For example, intense herbivory on competitively dominant plant species can result in increased abundance of less palatable, competitively inferior species (Huntly 1991). In English chalk grasslands, rabbit grazing maintains plant diversity and prevents colonization by a few dominant woody species (Tansley and Adamson 1925; Hope-Simpson 1940). In many forest ecosystems, high densities of introduced mammalian herbivores can sometimes impair forest regeneration, modifying the entire forest habitat (Ebenhard 1988; Gill 1992). Furthermore, altered community structure resulting from introduced mammalian herbivores is in some cases accompanied by increased richness of exotic plant species (Mack 1989; Hobbs and Huenneke 1992; Hobbs 2001; Chaneton et al. 2002).

Besides the effects on the plant community, introduced herbivores sometimes directly or indirectly affect other components of the ecosystem. Introduced herbivores can affect native herbivores through competition. For example, the introduced North American gray squirrel (*Sciurus carolinensis*) is believed to outcompete the native red squirrel (*S. vulgaris*) in England (Williamson 1996), and the North American beaver (*Castor canadensis*) is believed to displace the native European beaver (*C. fiber*) in Finland (Nummi 1996). Other animal species that use plants as resources can also be affected, such as pollinators and frugivores. Sheep grazing in California is believed to affect native pollinators of *Astragalus monoensis* through food removal (Sudgen 1985).

Alternatively, by enhancing predator populations, introduced herbivores can indirectly affect native prey species (i.e. apparent competition; Holt 1977). For example, introduced rabbit populations on many oceanic islands affect native birds indirectly by enhancing predator populations (Courchamp et al. 2000). A similar indirect effect of introduced mammalian herbivores on native animals, especially closely related species, can occur through disease transmission (Combes 2001). Many animal species can also be affected by habitat modifications induced by introduced herbivores (Simberloff 1991). In New Zealand forests, trampling by introduced deer and goats affects the composition of litter-dwelling mesofauna and macrofauna (Wardle 2001).

Finally, sometimes introduced mammalian herbivores affect fundamental ecosystem-level processes, such as nutrient cycles, primary production, and disturbance regimes (Williamson 1996; Mack and D'Antonio 1998). A good example is feral pigs (*Sus scrofa*), which have modified entire communities and ecosystems around the world through their digging and rooting activities (Mack and D'Antonio 1998). Introduced goats have contributed to soil disturbance and erosion in many island ecosystems (Coblentz 1978), and introduced ungulates can reduce above-ground biomass production, thus altering fire-regimes in fire-prone ecosystems (Mack and D'Antonio 1998).

An important point to consider when analyzing effects of introduced herbivores is the evolutionary history of herbivory in the invaded system. Systems that evolved in the absence of mammalian herbivores are expected to be more susceptible to introduced herbivores than systems with a long evolutionary history of mammalian herbivory (Milchunas et al. 1988). However, Hobbs and Huenneke (1992) argue that it is not only the absence of native herbivores that determines the potential effect of introduced herbivores, but also the imposition of a new type or level of herbivory. Thus, introduced herbivores are likely to affect the invaded ecosystem if they are functionally different from, or if they can attain higher densities than, native herbivores.

In this paper, I review the ecological effects of introduced mammalian herbivores in the temperate forest of the southern Andes (TFSA). I discuss effects on forest regeneration, plant community diversity and composition, vertebrate and invertebrate species, and ecosystem processes. Although little is known, available data suggest that introduced herbivores have important impacts on many components of the forest ecosystem.

Natural history of the temperate forest of the southern Andes

The system

The TFSA lies on the southwestern fringe of South America, between 39° and 55° S. The biota of the TFSA evolved under a warm climate in the former continental land mass formed by South America, Antarctica, and Australia (Arroyo et al. 1996). The later separation from Antarctica, the rise of the Andes, and the resulting rearrangement of the regional wind circulation patterns resulted in the development of the arid climates to the east and north, isolating the southern Andean forest from other moist forest regions (Arroyo et al. 1996; Aizen and Ezcurra 1998). This unique biogeographical history resulted in a species-rich biota with many tropical elements and high endemism. For example, 34% of its woody plant genera and three complete plant families are endemic (Arroyo et al. 1996), as well as all amphibian species (Duellman 1999). High endemism is also found in many other groups, such as bees (Michener 1979), weevils (Morrone and Roig-Juñent 1995), and birds (Stattersfield et al. 1998). Lawford et al. (1996) and Armesto et al. (1995) provide good general accounts of the natural history of the TFSA.

The natives

Native mammalian herbivores in Andean Patagonia include the guanaco (*Lama guanicoe*) and two species of deer, the huemul (*Hippocamelus bisulcus*) and the pudu (*Pudu pudu*) (Olrog and Lucero 1980; Redford and Eisenberg 1992). The guanaco uses mainly open dry areas throughout its range, although it does get into the TFSA in some areas. In Tierra del Fuego, guanacos feed on dominant *Nothofagus* trees (Bonino and Pelliza-Sbriller 1991); however, in Torres del Paine National Park, Chile, guanacos rarely use available forest habitats (Ortega and Franklin 1988). Although available data suggest that they impede forest regeneration, this effect is apparently restricted to steppe-forest ecotones (Rebertus et al. 1997; Martínez-Pastur et al. 1999).

The huemul was widespread in the southern Andes of Chile and Argentina before European colonization, occupying open areas above and below the tree line (Díaz 1993; Smith-Flueck and Flueck 1995; Povilitis 1998). Its distribution has been drastically reduced, and it is currently rare and geographically restricted (Díaz 1993; Povilitis 1998).

The pudu is found in a wide variety of habitats but typically occurs in thick forests from sea level to 1000 m (Redford and Eisenberg 1992). Pudu populations are believed to have declined due to human activities (Redford and Eisenberg 1992).

Thus, it is possible that the impact of guanacos and huemul on forest ecosystem has always been limited to ecotones. In contrast, pudus may have had greater effects in the past, when population densities were higher.

The invaders

Twelve herbivorous mammals have been successfully introduced to the TFSA. I include both domestic and wild introduced mammalian herbivores found in natural forest areas but exclude failed introductions (e.g. reindeer, *Rangifer tarandus*) and species mainly restricted to human dwellings (Norway and black rats [*Rattus norvegicus* and *R. rattus*], and house mouse [*Mus musculus*]), because their potential effects on the forest ecosystem are limited. General overviews of the history of the introduction and current distribution of these species are in Daciuk (1978), Navas (1987), Bonino (1995), Jaksic (1998), and Jaksic et al. (2002).

- Domestic cattle (*Bos taurus*) and horses (*Equus caballus*) were probably the first introduced herbivores in the TFSA. They escaped from ranches on the Chilean Pacific coast or the Argentinean pampas, spreading to the TFSA (see Veblen et al. 1996). For example, cattle and horses were present in the Nahuel Huapi area in Argentina in the early eighteenth century (Biedma 1997). Cattle occupy many natural areas, including 56% of the land area in Nahuel Huapi National Park in Argentina (Lauría Sorge and Romero 1999).
- Sheep (*Ovis aries*) and goats (*Capra hircus*) are mainly restricted to dry grasslands, although they do occur in some forest areas, especially in the dry eastern forest types (Relva and Veblen 1998; Lauría Sorge and Romero 1999).
- Red deer (*Cervus elaphus*) were originally introduced to central Argentina around 1904 and were later introduced to several areas in Chile and Argentina in the TFSA (Jaksic et al. 2002). They are currently the most widespread exotic deer in the region, ranging from Neuquén to Chubut Provinces in Argentina (Bonino 1995) and between regions VII and XI in Chile (Jaksic 1998; Jaksic et al. 2002).
- Fallow deer (*Dama dama*) and axis deer (*Axis axis*) were introduced in the 1930s in Nahuel Huapi National Park in Argentina (Navas 1987; Bonino 1995). Fallow deer are now apparently restricted to Isla Victoria, in Nahuel Huapi Lake (Navas 1987) and are not found in the wild in Chile (Jaksic 1998); axis deer were always restricted to Isla Victoria, and are presumed extinct (Navas 1987).
- Wild boar (*Sus scrofa*) were introduced into central Argentina around 1906 and were translocated to Neuquén between 1917 and 1922 (Daciuk 1978), spreading south and west. They are currently found in a large area of the TFSA, between Neuquén and northern Santa Cruz Provinces in Argentina (Daciuk 1978; Navas 1987) and in regions X and XI in Chile (Jaksic 1998; Jaksic et al. 2002).
- The European hare (*Lepus capensis*) was first introduced in Cañada de Gómez, Santa Fe, Argentina, in 1888 and was later introduced in southern Chilean Patagonia in 1896 (Grigera and Rapoport 1983). It is currently common and widespread, occupying most of Argentina, Chile, Paraguay, Uruguay, and southern Brazil and Bolivia (Grigera and Rapoport 1983; Jaksic et al. 2002).
- The European rabbit (*Oryctolagus cuniculus*) was introduced in two separate locations in Chile: in Tierra del Fuego around 1880, and in central Chile in 1884; from there it later expanded to Neuquén Province, Argentina (Jaksic and Yáñez 1983; Bonino and Amaya 1985; Bonino and Gader 1987; Jaksic et al. 2002). The northern population is spreading south in Neuquén, but it apparently has

not reached the TFSA region (Bonino and Gader 1987; Jaksic et al. 2002). The southern population is widespread in Tierra del Fuego, occupying a large area of the TFSA (Bonino and Amaya 1985; Jaksic et al. 2002).

- The Canadian beaver (*Castor canadensis*) was introduced to Tierra del Fuego in 1946. It has spread to most streams in Argentine Tierra del Fuego and is currently spreading to Chilean Tierra del Fuego; it is also found on several islands of the Magellanic Archipelago (Lizarralde 1993; Jaksic et al. 2002).
- The muskrat (*Ondatra zibethicus*) was introduced to Argentine Tierra del Fuego in 1948 and is now widespread throughout a large part of the island (Jaksic et al. 2002).

Effects of introduced mammalian herbivores in the TFSA

Effects on forest regeneration

The effects of introduced mammalian herbivores on forest regeneration have been quantitatively analyzed in four published studies (Ramírez et al. 1981; Veblen et al. 1989, 1992b; Relva and Veblen 1998), all of which dealt with introduced ungulates (cattle and deer). Results from these four studies are summarized in Table 1. Although the magnitude of the effect varies, in most cases introduced ungulates decrease the abundance and height of seedlings and saplings of dominant canopy trees.

Veblen and colleagues (Veblen et al. 1989, 1992b) suggest that introduced ungulates can decrease seedling and sapling abundance and height of coihue, *Nothofagus dombeyi* (Table 1). Notice, however, that seedlings (5–200 cm tall) of coihue, *N. dombeyi*, were more abundant in the grazed than in the ungrazed site in forest gaps in Veblen et al.'s (1989) study, although these authors mention that saplings (i.e. >200 cm tall) were absent from canopy gaps in the grazed site but present in the ungrazed site. Furthermore, it is also noteworthy that the magnitude of the effect is higher for seedling height than for seedling abundance (Table 1). Thus, even though shorter size classes are more abundant in grazed gaps, it appears that they do not reach taller size classes.

De Pietri (1992b) argues that the combined effect of fire and heavy grazing by cattle can transform *N. dombeyi* forest into grasslands. However, in many post-fire *N. dombeyi* forests in northern Argentine Patagonia established during the 1930s and 1940s (when livestock pressure was highest), even the heaviest grazing seems to have failed to impede regeneration of *N. dombeyi* forests (Veblen et al. 1992a). Thus, although introduced ungulates appear to decrease abundance and growth of *N. dombeyi* seedlings and saplings, it is unclear whether this effect can inhibit forest regeneration.

Seedling abundance of the Patagonian cypress, *Austrocedrus chilensis*, was higher in the grazed than in the ungrazed site in Veblen et al.'s (1992b) study. In contrast, the well-replicated study by Relva and Veblen (1998) shows that abundance of seedlings/saplings of *A. chilensis* is lower in grazed than in ungrazed sites (Table 1). The apparent contradiction between these two studies could be due to the fact that the former included only seedlings (i.e. 5–200 cm tall), whereas the latter included both seedlings and saplings (i.e. >5 cm tall and <4 cm dbh). Furthermore, both in Veblen et al.'s (1992b) and in Relva and Veblen's (1998) studies, seedling/sapling height is lower in grazed than in ungrazed sites; as for *N. dombeyi*, the magnitude of this effect is higher than for seedling/sapling abundance (Table 1). This evidence agrees with experimental results showing that even low levels of browsing can inhibit the growth of this species (Relva and Sancholuz 2000) and strongly suggests that regeneration of *A. chilensis* forest can be inhibited by introduced ungulates. In fact, retrospective studies of forest dynamics indicate that introduced ungulates appear to have inhibited post-fire regeneration of *A. chilensis* forest in the past (Veblen et al. 1992a).

The only published study addressing the effect of ungulates on the regeneration of ñire, *Nothofagus antarctica*, suggests that regeneration of this species can also be inhibited by introduced ungulates: both seedling abundance and height were lower in the grazed than in the ungrazed sites in Veblen et al.'s (1992b) study. As for *N. dombeyi* and *A. chilensis*, the magnitude of the effect on seedling height is higher than on seedling abundance (Table 1).

Finally, Ramírez et al.'s (1981) study shows that the abundance of seedlings and saplings of three dominant tree species was higher with early grazing (i.e. two years after deer introduction to Islote Rupanco) than with late grazing (i.e. six years after deer introduction; Table 1). This result holds for all seedling/sapling height classes except the shortest (0–20 cm), which had higher abundance after deer introduction for two of the tree species (Table 1).

Table 1. Summary of results of studies of the effects of introduced ungulates on forest regeneration. Studies compared sites with contrasting levels of ungulate browsing and grazing, except study (4), where the comparison was made between two and six years after deer introduction at the same island site (Islote Rupanco, Osorno, Chile). For each comparison, the mean effect in grazed and ungrazed sites, the number of statistical replicates (n), and the effect size (lr) are given. lr, the log response ratio statistic, is a conventional measure of effect size in meta-analysis (Gurevitch and Hedges 2001). The response ratio is calculated for study i as $lr_i = \ln(\overline{X}_i^G / \overline{X}_i^U)$, where $\overline{X}_i^G$ is the mean effect in the experimental (i.e. grazed) sites, and $\overline{X}_i^U$ is the mean effect in control (i.e. ungrazed) sites.

Canopy species	Variable	Stand age	Grazed		Ungrazed		*lr*	Source
			Mean	*n**	Mean	*n**		
Nothofagus dombeyi	Seedling % freq. in quadrats (50-200 cm tier)	Young (80–100 yr)	32.7	1	61.2	1	−0.63	(2)
		Young (80–100 yr)	30.6	1	32.7	1	−0.07	(1)
		Mature (∼200 yr)	18.4	(2)	24.5	1	−0.29	(1)
		Forest gap	62.7	(10)	15.6	(6)	1.39	(1)
	Seedling mean max. height (cm)	Young (80–100 yr)	10.7	1	56.0	1	−1.66	(2)
		Forest gap	28.0	(10)	117.0	(6)	−1.43	(1)
Austrocedrus chilensis	Seedling % freq. in quadrats (5–200 cm tier)	Young (80–100 yr)	20.4	1	0.0	1	7.62	(2)
		Young (80–100 yr)	2.0	1	6.1	1	−1.12	(1)
		Mature (∼200 yr)	1.0	(2)	14.3	1	−2.66	(1)
		Forest gap	1.3	1	2.2	1	−0.53	(1)
	Seedling-sapling abundance per ha	—$^{(a)}$	3250.0	14	6320.5	13	−0.67	(3)
	Seedling mean max. height (cm)	—$^{(a)}$	10.3	1	101.0	1	−2.28	(1)
Nothofagus antarctica	Seedling % freq. in quadrats (5–200 cm tier)	>80 yr	14.3	1	16.3	1	−0.13	(2)
	Seedling mean max. height (cm)	>80 yr	19.4	1	97.9	1	−1.62	(2)
Aexotoxicon punctatum	Number of individuals per ha	—$^{(a)}$	1485$^{(b)}$	1	1409$^{(b)}$	1	0.05	(4)
	Number of individuals per ha (>20 cm tier)	—$^{(a)}$	1121$^{(b)}$	1	1727$^{(b)}$	1	−0.43	(4)
Laurelia philippiana	Number of individuals per ha (0–20 cm tier)	—$^{(a)}$	2226$^{(b)}$	1	1829$^{(b)}$	1	0.20	(4)
	Number of individuals per ha (>20 cm tier)	—$^{(a)}$	7012$^{(b)}$	1	8963$^{(b)}$	1	−0.25	(4)
Eucrypia cordifolia	Number of individuals per ha (0–20 cm tier)	—$^{(a)}$	177$^{(b)}$	1	289$^{(b)}$	1	−0.49	(4)
	Number of individuals per ha (>20 cm tier)	—$^{(a)}$	506$^{(b)}$	1	715$^{(b)}$	1	−0.35	(4)

(a) Not specified in the original study.

(b) Approximate estimates obtained from Figure 7 in study (4).

Sources: (1) Veblen et al. (1989); (2) Veblen et al. (1992b); (3) Relva and Veblen (1998); (4) Ramírez et al. (1981).

*Numbers between brackets indicate replicates included in the study that cannot be considered true statistical replicates due to lack of spatial interspersion (see Hurlbert 1984).

Little evidence is available on the effects of introduced herbivorous mammals on the regeneration of other forest types besides those discussed above. Roig et al. (1985) noted that cattle do not forage in the forest interior of deciduous forest dominated by lenga, *Nothofagus pumilio*, but that they do use forest gaps, where they browse on *N. pumilio* seedlings and saplings. Since regeneration of *N. pumilio* is gap-dependent (see Rebertus and Veblen 1993), Roig et al. (1985) suggest that cattle can impede forest regeneration. Bava and Rechene (1998) note that *N. pumilio* saplings of approximately 30 years of age growing inside exclosures or among fallen trees typically reach 7–10 m height, whereas saplings of the same age exposed to continuous guanaco or cattle browsing do not grow above 30 cm. To my knowledge, there has been no quantitative evaluation of the impact of ungulate grazing on this species.

I know of no quantitative studies in this region addressing impacts of introduced mammalian herbivores other than ungulates on forest regeneration. Rebertus and Veblen (1993) studied forest regeneration in treefall gaps in Tierra del Fuego, in six sites with different compositions of dominant trees, of which one was dominated by *N. pumilio*. They observed that current sapling abundance was lower than in other forest types. They also observed some rabbit browsing on saplings. Based on this observation, they suggest that rabbits prevent regeneration of *N. pumilio*. However, it is important to consider other possible causes for this pattern, such as differences among sites not related to rabbit browsing.

Introduced beavers devastate *Nothofagus* forests in Tierra del Fuego. They cut and kill the dominant tree species – *N. pumilio*, *N. betuloides*, *N. antarctica* and *Drymis winteri* – for dam construction. However, the flooding associated with the dams probably causes the greatest damage (Daciuk 1978; Lizarralde 1993). In Argentine Tierra del Fuego, beavers have apparently colonized all streams in the Andean and extra-Andean areas on the island, and about 91% of all streams if adjacent islands of the Magellanic Archipelago are included. They cause complete destruction of the flooded forest and clear surrounding areas for dam construction (Lizarralde 1993).

In conclusion, available evidence suggests that introduced herbivorous mammals can negatively affect the establishment and growth of seedlings and saplings of several dominant canopy trees. Effects are apparently stronger on seedling/sapling growth than on their abundance.

Effect on understory species richness and invasion by exotic plants

A few studies have analyzed the effect of introduced herbivores on species richness of understory plants (summarized in Table 2). As for forest regeneration, all these studies dealt with introduced ungulates. Grazing by introduced ungulates seems to result in increased species richness in some cases, while the opposite effect is observed in other instances. In the only published study in which experimental exclosures have been used to study the effect of introduced herbivores in the TFSA, Raffaele and Veblen (2001) reported increased richness in ungrazed (fenced) plots in a post-fire mixed *Austrocedrus chilensis–Maytenus boaria* matorral, compared with control (unfenced) plots with low levels of cattle grazing. Similarly, Veblen et al. (1989) reported that ungrazed young and mature *N. dombeyi* forest sites had higher understory species richness compared with grazed sites of similar ages, and Veblen et al. (1992b) found a similar pattern in another pair of grazed and ungrazed young *N. dombeyi* forest sites (Table 2). On Islote Rupanco, Ramírez et al. (1981) also found higher species richness in 1977 (2 years after deer introduction) compared with 1981 (6 years after introduction). In all these cases, all species were native except in the grazed, mature forest of Veblen et al. (1989), where foxglove (*Digitalis purpurea*) was recorded. Thus, decreased plant species richness in grazed sites in these studies is due to a reduction in the richness of native species.

Conversely, Veblen et al. (1989) reported higher richness in grazed forest gaps in *N. dombeyi* forest on Isla Victoria compared with ungrazed gaps on the Quetrihué Peninsula. Likewise, Veblen et al. (1992b) reported higher richness in a grazed *N. antarctica* forest site compared with an ungrazed site of the same forest type. In both cases, increased total richness was partly due to increased richness of herbaceous exotic species (Table 2).

It is noteworthy that in Veblen et al.'s (1989, 1992b) studies the only cases where substantial invasion by

Table 2. Summary of results of effects of grazing by introduced ungulates on species richness of understory plants. Studies compared sites with contrasting levels of ungulate browsing and grazing, except study (4), where the comparison was made between two and six years after deer introduction at the same island site (Islote Rupanco, Osorno, Chile). For each comparison, the mean effect in grazed and ungrazed sites, the number of statistical replicates (*n*), and the effect size on mean richness (*lr*) are given. (See Table 1 for details on the calculation of *lr*).

Canopy species	Forest characteristic	Grazed			Ungrazed			*lr*	Source
		Mean richness	% exotic	*n**	Mean richness	% exotic	*n**		
Nothofagus dombeyi	Forest gap	44	11.4	(10)	21	0.0	(6)	0.74	(1)
	Young stand (80–100 yr)	12	0.0	1	17	0.0	1	−0.35	(1)
	Young stand (80–100 yr)	9	0.0	1	10	0.0	1	−0.11	(2)
	Mature stand (∼200 yr)	22	2.9	(2)	24	0.0	1	−0.09	(1)
Austrocedrus chilensis	Post-fire matorral	5.6	0.0	5	8.5	0.0	5	−0.42	(3)
Nothofagus antarctica	>80 yr	17	29.4	1	12	0.0	1	0.35	(2)
Aexotoxicon punctatum	Not specified	47	?	1	52	?	1	−0.10	(4)

Sources: (1) Veblen et al. (1989); (2) Veblen et al. (1992b); (3) Raffaele and Veblen (2001); (4) Ramírez et al. (1981).

*Numbers between brackets indicate replicates included in the study that cannot be considered true statistical replicates due to lack of spatial interspersion (see Hurlbert 1984).

exotic plants occurred were in an open forest type (*N. antarctica*) and in gaps in a closed-canopy forest type (*N. dombeyi–Austrocedrus chilensis*). This fact suggests an interaction between forest cover and grazing, so that introduced mammalian herbivores favor invasion by exotic plants only when canopy cover is low. Below, I discuss additional evidence that can help to answer this question.

Simberloff et al. (2002) studied invasion by exotic woody plants on Isla Victoria, in Nahuel Huapi National Park. Over 100 introduced woody species were planted between 1910 and 1940 as part of an experimental plantation near the center of the island. Two species of introduced deer (*Cervus elaphus* and *Dama dama*) have heavily impacted the understory of *Nothofagus dombeyi–Austrocedrus chilensis* forest. Yet very little invasion by exotic species into the forest has occurred. Invasion by woody plants does occur on the island (particularly by highly invasive shrubs *Rosa eglanteria* and *Cytisus scoparius*, and a few tree species, mainly conifers), but it is largely restricted to areas cleared for use as cattle pastures.

In *N. dombeyi–Austrocedrus chilensis* forests in and near Los Alerces National Park, De Pietri (1992a) found livestock burden and soil compaction positively correlated with relative cover of exotic plant species. However, in De Pietri's study, designed for identifying ecological indicators of cattle ranching, it is not possible to separate the effect of introduced herbivores *per se* from the effect of associated ranching activities – such as forest clearing or burning – used to create pastures. Therefore, the increased cover of exotic plant species cannot be solely attributed to livestock. A more plausible explanation of De Pietri's finding is that both livestock and the reduction of forest cover favor invasion by introduced plants.

In conclusion, available data suggest that, when introduced ungulates lead to decreased plant species richness, this is because of a loss of native species in grazed sites, whereas increased plant species richness with grazing results, at least in part, from increased richness of exotic species. However, the latter effect might be possible only when canopy cover is low.

Effect on understory plant composition: patterns and mechanisms

Browsing by introduced herbivores can decrease abundance of palatable, browsing-susceptible understory trees, shrubs and herbs. Probably the best-documented case is that of maqui, *Aristotelia chilensis*, a small tree that dominates the understory of ungrazed *N. dombeyi* forests but almost disappears from grazed forests (Dimitri 1962; Veblen et al. 1989, 1992b; Vázquez and Simberloff 2002).

Interestingly, a similar pattern is observed for *Aristotelia serrata* in New Zealand, where it is affected by introduced red and sika deer (Allen et al. 1984). Other understory species that tend to decrease with grazing in *N. dombeyi–Austrocedrus chilensis* forests are the herb *Alstroemeria aurea*, the shrub *Ribes magellanicum*, the milkweed vine *Cynanchum diemii*, the mistletoe *Tristerix corymbosus*, and the bamboo *Chusquea culeou* (Veblen et al. 1989, 1992b; Vázquez and Simberloff 2002).

Likewise, several palatable shrub and vine species become less abundant with grazing in post-fire *Austrocedrus chilensis–Maytenus boaria* matorrals (Raffaele and Veblen 2001).

Although all these species show a similar response to grazing by introduced herbivores, the underlying mechanism probably differs among species. For some species, the direct effect of browsing is the most likely explanation. For example, *Aristotelia chilensis*, *Ribes magellanicum*, and *Chusquea culeou* are preferred food items for both cattle and deer and are highly susceptible to ungulate browsing (Dimitri 1962; Veblen et al. 1989, 1992b; Relva and Caldiz 1998). Thus, it seems likely that the decline of these species in areas with introduced herbivores is due to the direct, negative effect of browsing.

The mechanisms underlying the observed effect of introduced herbivores on other understory species are probably more complex and may involve indirect effects through one or more other species. An indirect effect occurs when one species affects another through a third species (Strauss 1991; Wooton 1994). In part because the possibilities for indirect effects are probably unlimited, their documentation is usually difficult. Below, I discuss a few examples for which evidence suggests that indirect effects could be occurring.

Besides the direct effect on individual plant survivorship, herbivores can affect plant fitness, both directly by consuming flowers or seeds (Louda 1982; Herrera 1993, 2000; Gómez and Zamora 2000) and indirectly by affecting the interaction with pollinators through a modification of floral traits (Strauss et al. 1996; Strauss 1997; Mothershead and Marquis 2000).

The amancay, *Alstroemeria aurea*, is an abundant insect-pollinated herb flowering during the summer in the TFSA. Vázquez (2002) recently found that the decreased abundance of *A. aurea* resulting from cattle trampling alters the interaction between this species and its pollinators, which in turn results in lower reproductive performance. Although lower population density of *A. aurea* does not necessarily mean lower visitation frequency by its main pollinators (*Bombus* bumblebees, Aizen 2001; Aizen et al. 2002), pollination quantity (number of conspecific pollen grains) and quality (as determined by contamination with heterospecific pollen grains) dramatically decrease with grazing; decreased pollination performance in turn results in lower reproductive performance.

Another possible indirect effect is on the mistletoe *Tristerix corymbosus*. The main host of this parasitic shrub in *Nothofagus dombeyi* forests is *Aristotelia chilensis*; and although *T. corymbosus* does grow occasionally on other host species in *N. dombeyi* forests (such as *Azara* sp. and *Maytenus boaria*), no individual of *T. corymbosus* growing on other species besides *Aristotelia chilensis* was recorded by Vázquez and Simberloff (2002) in their study sites in Nahuel Huapi. As I mentioned above, *Aristotelia* drastically decreases in abundance in grazed sites. Abundance of *T. corymbosus* also decreases in grazed sites (Vázquez and Simberloff 2002). Thus, the decreased abundance of *T. corymbosus* is better explained by a decreased availability of its host plant than by a direct effect from cattle.

It has been suggested that grazing by introduced ungulates results in an overall increase in the abundance of spiny shrubs (e.g. De Pietri 1992b; Veblen and Alaback 1996). *Berberis buxifolia* is probably the most conspicuous example in the TFSA. Several studies have documented increased abundance of this species with ungulate grazing, despite heavy browsing pressure by ungulates (Veblen et al. 1989, 1992b; De Pietri 1992b; Relva and Veblen 1998; Vázquez and Simberloff 2002). However, Raffaele and Veblen (2001) found, in a post-fire *Austrocedrus chilensis–Maytenus boaria* matorral, that *B. buxifolia* was less abundant in grazed than in ungrazed plots. Another *Berberis* species, *B. darwinii*, has also been cited as increasing with introduced herbivores (Ramírez et al. 1981; Veblen et al. 1989, 1992b), although Vázquez (2002) failed to find such an increase. Thus, although introduced mammalian herbivores may in some cases increase the abundance of some spiny shrubs, that effect is not universal. Furthermore, it is important to bear in mind that many areas subject to grazing (especially by domestic animals) have partially or totally lost forest cover, a loss that cannot always be attributed to grazing; other anthropogenic disturbances, such as fire or logging, may be causal. In such cases, the increased abundance of spiny shrubs cannot be unambiguously attributed to the presence of introduced herbivores.

Could the increased abundance of browse-resistant, shade-intolerant shrubs influence forest dynamics and forest regeneration? Several studies show that grazing-resistant shrubs can have nurse effects on seedlings of many plant species (De Pietri 1992a; Raffaele and Veblen 1998; Kitzberger et al. 2000). Raffaele and Veblen (2001) suggested that nurse plants could play a double facilitative role: protection from moisture stress and from large herbivores. Along the same lines, De Pietri (1992a) suggested that bushes of the exotic eglantine rose, *Rosa eglanteria*, could help the regeneration of the forest under heavy grazing conditions.

In conclusion, introduced mammalian herbivores are able to affect understory community structure and composition strongly through a variety of mechanisms, involving both direct effects of browsing and trampling and several kinds of indirect effects.

Effects on vertebrates

One way in which introduced mammalian herbivores could affect native vertebrate herbivores is through competition for resources and habitat modification. The recent abrupt decline in the distribution of huemul (Díaz 1993; Povilitis 1998) has been attributed partly to competition for resources and habitat modification caused by exotic herbivorous mammals (Flueck et al. 1995; Smith-Flueck and Flueck 1995; Povilitis 1998). Many areas formerly occupied by huemul have now been colonized by red deer (Flueck et al. 1995). Similarly, Lever (1985) argues that red deer could be competing with pudu populations in Neuquén, Argentina. Competition for food has also been presumed to occur between sheep and guanacos in Torres del Paine National Park, Chile (Sarno and Franklin 1999), and dietary overlap between red deer and guanacos was reported in Neuquén, Argentina (Bahamonde et al. 1986). However, diet overlap does not necessarily imply competition. Thus, although it is possible that introduced herbivores are indeed negatively affecting native species through competition for food or habitat modification, no hard evidence exists demonstrating such effect.

Exotic herbivores may benefit native predators by increased food availability. There is ample evidence that native predators feed on exotic prey. Pumas (*Felis concolor*) and gray and culpeo foxes (*Pseudalopex griseus* and *P. culpaeus*) are the main large mammalian predators throughout Andean Patagonia. They are feeding generalists; their feeding habits usually reflect the availability of prey. They have been repeatedly reported to prey on exotic herbivores in areas where the latter are abundant; in many cases, exotic prey comprise the bulk of the predator's diet (pumas, Courtin et al. 1980; Yáñez et al. 1986; Iriarte et al. 1991; Rau et al. 1991; Franklin et al. 1999; Novaro et al. 2000; foxes, Jaksic et al. 1983; Novaro et al. 2000). Avian predators also prey on introduced herbivores. European hare and rabbit account for 55% of the prey biomass of great horned owl (*Bubo virginianus*), and 58% of frequency of the diet of gray buzzard-eagle (*Geranoaetus melanoleucus*) in arid Patagonia in Neuquén (Hiraldo et al. 1995; Donázar et al. 1997). In the same region, six species of avian scavengers feed on carcases of European hare (Travaini et al. 1997). Although these studies on the feeding habits of avian predators and scavengers were conducted in the Patagonian steppe, similar effects could occur in the temperate forest. On Isla Victoria (Nahuel Huapi, Argentina), black vultures (*Coragyps atratus*) feed on carcasses of introduced red deer (D.P. Vázquez, personal observation), which might explain their high local density.

Enhanced predator abundances could be detrimental to native prey. One way exotic herbivores could affect native animals is through 'apparent competition' (Holt 1977). Apparent competition occurs when 'the presence of multiple noncompeting prey species elevates predator abundance above levels maintained by single prey species, which increases predation pressure on multiprey assemblages' (Morin 1999). Predation by native predators on native prey is well documented (Courtin et al. 1980; Jaksic et al. 1983; Yáñez et al. 1986; Iriarte et al. 1991; Rau et al. 1991; Hiraldo et al. 1995; Smith-Flueck and Flueck 1995; Donázar et al. 1997; Franklin et al. 1999; Novaro et al. 2000). Populations of introduced herbivores are known to fluctuate (Novaro 1997), and in some areas current densities of native predators are probably higher than in the past (Crespo 1975). This fact could result in increased predation on native prey species during periods of low abundance of introduced herbivores (Novaro et al. 2000).

Another way in which introduced herbivores could affect native mammals indirectly is through parasites, in many cases also introduced. For example, parasites have the potential to affect the competitive relationships among species, so that competitively superior species become weaker competitors when parasitized (Combes 2001). Huemul are known to be susceptible to several parasitic diseases carried by livestock or introduced deer (see Smith-Flueck and Flueck 1995; Povilitis 1998). However, it is not known how much these diseases affect populations of huemul in the wild, and whether disease played a role in the distributional reduction of the species.

The decreased abundance of some plant species resulting from introduced herbivores could in turn be affecting pollinators and seed dispersers. The decreased abundance of the mistletoe *Tristerix corymbosus* with grazing described above could affect two vertebrate species. *T. corymbosus* is the only ornithophilous plant flowering in the winter in many areas and is the only food source for the hummingbird *Sephanoides sephaniodes* during this period (Fraga et al. 1997). Its fruits are also the main food source for the endemic marsupial *Dromiciops gliroides* (Amico and Aizen 2000). It is possible that the decreased abundance of *T. corymbosus* resulting from grazing also indirectly affects the hummingbird and the marsupial. Thus, introduced herbivores could affect these vertebrate species through a doubly-indirect effect (introduced ungulates → *Aristotelia chilensis* → *Tristerix corymbosus* → *Sephanoides* and *Dromiciops*).

Effects on invertebrates

Large introduced herbivores have the potential to affect invertebrates in several ways. They could affect them directly through trampling on nests or indirectly through their effects on habitat characteristics or on food sources (Siemann et al. 1998; Rambo and Faeth 1999). If introduced herbivores affect invertebrates through their food sources, species that depend on fewer food resource types (i.e. specialists) could be more affected by introduced herbivores than species that depend on many resource types (i.e. generalists). Vázquez and Simberloff (2002) tested this hypothesis using data on plant pollinator interactions in four pairs of grazed and ungrazed sites in *N. dombeyi* forest. They found no relationship between the degree of pollinator feeding specialization on flowers and their response to cattle grazing. Although the reasons for this lack of relationship between specialization and response to cattle disturbance are unclear, one possible explanation is that the direct effect of cattle on the pollinators (e.g. trampling on nests) is strong enough to override any indirect effect through resource availability. On the other hand, the fact that the response of pollinators to cattle is not related to their degree of specialization on floral resources need not mean there is no response. Some insect pollinator species tend to become rarer in the presence of cattle, whereas others tend to increase. A conspicuous 'decreaser' in the study of Vázquez and Simberloff (2002) is the bumblebee *Bombus dahlbomii*, a pollinator of many plant species in the TFSA (Aizen et al. 2002). Conspicuous 'increasers' are the syrphid flies *Allograpta hortensis* and *Toxomerus vertebratus* and the bees *Colletes seminitidus* and *Heterosarus* sp.

Another interesting question is whether the species diversity of entire invertebrate guilds is affected by introduced herbivores. Here, I analyze part of the Vázquez and Simberloff (2002) data discussed above to address this question. As I mentioned above, *Alstroemeria aurea* is an herbaceous plant flowering in the summer in the forest understory. In *Nothofagus dombeyi* forests, it is virtually the only insect-pollinated plant flowering during the summer, and it receives visits from a broad assemblage of flower visitors – twice as many as any other insect-pollinated plant in this forest type (Aizen et al. 2002; Vázquez and Simberloff 2002). Because abundance of *A. aurea* decreases with grazing (see above), one could hypothesize that this will in turn affect flower visitors.

Total species richness of flower visitors to *A. aurea* was lower in grazed than in ungrazed sites in three of the four pairs of sites studied by Vázquez and Simberloff (2002) and slightly higher in the remaining pair (Figure 1). However, in comparisons of species richness, it is important to account for differences in the number of individuals in the different samples. Due to random sampling, a sample of, say, 100 individuals is likely to contain more species than a sample of 10 individuals. Rarefaction (Simberloff 1978; Gotelli and Graves 1996) can account for this effect. After rarefaction, species richness of flower visitors of *A. aurea* in grazed and ungrazed sites are virtually identical in three of the four pairs of sites (Figure 1a, c and d) and slightly higher in the grazed site of the remaining pair (Figure 1b). Therefore, no effect of grazing on the diversity of insects visiting flowers of *A. aurea* is detected after adjusting for differences in total abundance of flower visitors.

Effects on ecosystem processes

Mammalian herbivores are known to have important effects on ecosystem processes in many biomes, including temperate forests. For example, ungulates can influence the nitrogen cycle by changing litter quality (and thus affect conditions for nitrogen mineralization), and by adding readily available nitrogen to upper levels of the soil through urine and feces, which can result in drastic changes in plant community composition (Hobbs 1996).

Not much is known about nutrient cycling in Patagonian forest ecosystems in general (Mazzarino et al. 1998), much less about how it is affected by introduced herbivores. Deforestation by beaver in Tierra del Fuego leads to increased erosion and increased accumulation of organic material in water courses, which can in turn affect nutrient cycling, altering the biochemical composition of waters, sediments, soils, and adjacent riparian areas (Lizarralde 1993; Lizarralde et al. 1996). Decreased plant cover and trampling resulting from ungulate activity can significantly affect soil properties, including litter quality and mineralization processes, and can lead to soil erosion (De Pietri 1992b).

Discussion and conclusions

It appears that introduced mammalian herbivores have multiple ecological effects on the TFSA. Evidence at hand suggests they can affect forest regeneration, understory plant community structure and composition, vertebrate and invertebrate species, and ecosystem processes. The mechanisms generating these impacts are complex and apparently involve many simultaneous direct and indirect effects.

Not all canopy tree species seem equally susceptible to introduced mammalian herbivores. In particular, even though juveniles of *N. dombeyi* are less abundant and attain lower heights in grazed than in ungrazed sites, this species appears to have been able to regenerate under heavy grazing in post-fire stands (Veblen et al. 1992a). In contrast, regeneration of *Austrocedrus chilensis* seems more susceptible to

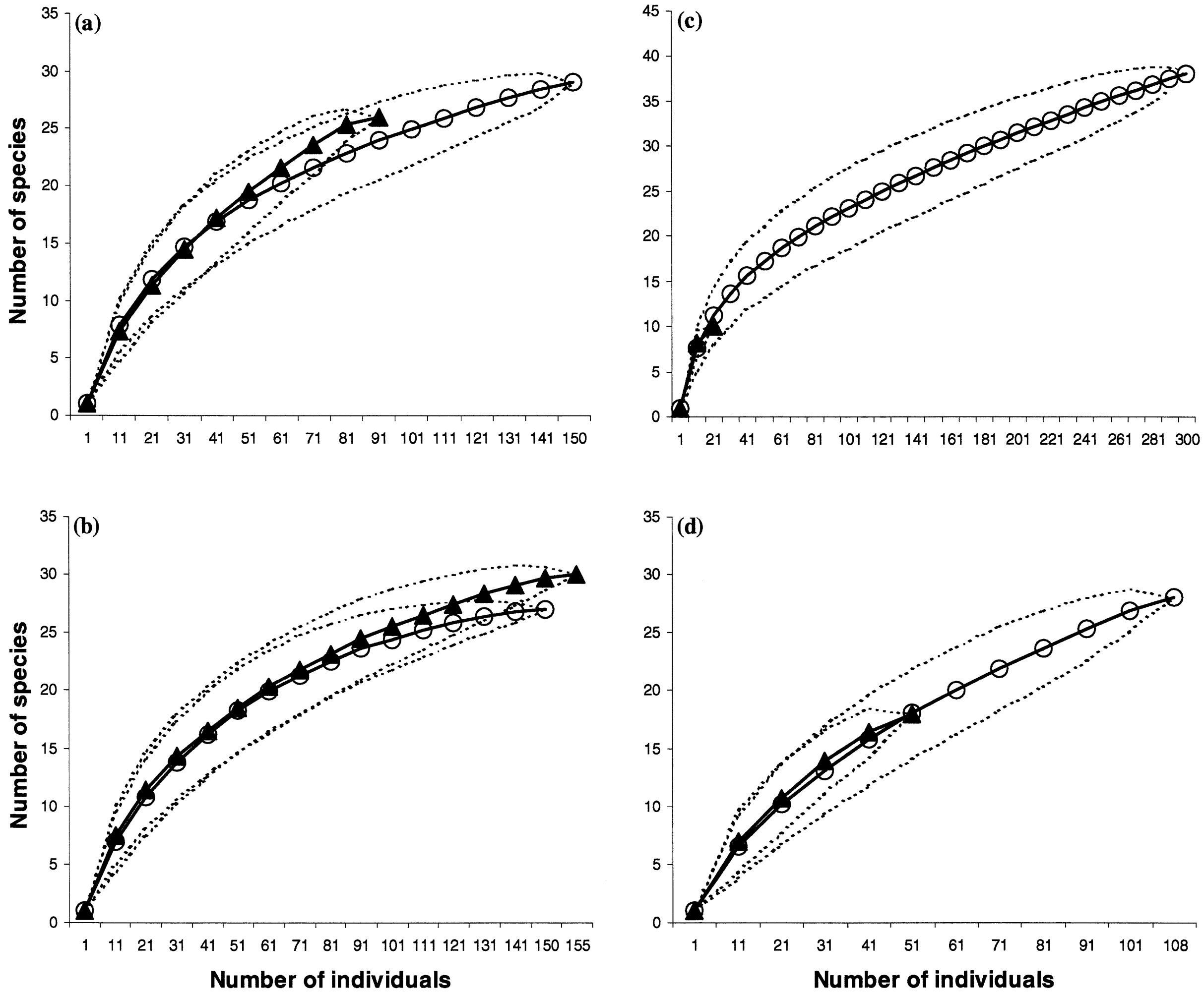

Figure 1. Rarefaction curves for the species richness of insects recorded visiting flowers of *Alstroemeria aurea* by Vázquez and Simberloff (2002). The rarefaction calculations were performed using EcoSim software (Gotelli and Entsminger 2000). The continuous lines indicate expected values of rarefaction curves; dashed lines above and below the expected values are 95% confidence limits calculated over 1000 iterations of the simulation. ▲: grazed sites; ○: ungrazed sites. Actual species richness corresponds to the upper-right end of the lines. Rarefaction curves given separately for each of four pairs of sites. Paired sites are: (a) Llao Llao (UG), Cerro López (G); (b) Safariland (UG), Arroyo Goye (G); (c) Mascardi (UG and G); (d) Quetrihué (UG and G) (UG, ungrazed site; G, grazed site).

introduced herbivores. This differential susceptibility has been attributed to the life history traits of these species. *Nothofagus dombeyi* can establish at higher densities and grow at faster rates than *A. chilensis*, making the former less susceptible to browsing by introduced ungulates than the latter (Veblen et al. 1992a).

The observed effects of introduced mammalian herbivores on forest regeneration in the TFSA are consistent with what has been observed in other regions. In New Zealand, deer do not seem to impede regeneration of *Nothofagus* species, and a long-term effect on forest regeneration seems unlikely (Veblen and Stewart 1982; Nugent et al. 2001). However, deer do impede the regeneration of several tree species accompanying *Nothofagus* (Allen et al. 1984), which could result in a switch in tree species relative abundances, favoring the most browse-resistant species (Nugent et al. 2001). In Australia, rabbits prevent the regeneration of trees and shrubs, especially *Acacia* sp. (Myers et al. 1994), and in continental Europe, high densities of introduced deer impede the regeneration of several dominant tree species (Ebenhard 1988; Gill 1992).

Available data also suggest that, when introduced ungulates lead to decreased plant species richness, this decrease is due to a loss of native species in grazed sites, whereas increased plant species richness with grazing results, at least in part, from increased richness of exotic species. Similar effects have been observed in North American temperate forests, where livestock grazing increases the richness of native and exotic ruderal species and causes a loss of woodland-restricted native species (Dennis 1997). Likewise, in many grassland ecosystems, grazing by introduced ungulates results in increased plant species richness, which is frequently accompanied by an increased proportion of unpalatable, exotic species (Mack 1989; Hobbs and Huenneke 1992; Hobbs 2001; Chaneton et al. 2002). However, it seems that low canopy cover could be a necessary condition for introduced herbivores to favor invasion by exotic plants, a situation that can happen both naturally (e.g. in some open forest types or in treefall gaps) and anthropogenically (e.g. through forest logging or burning). An interaction between canopy cover and plant invasions has been observed in many forest ecosystems worldwide, so that exotic plant richness increases with decreasing canopy cover (B. Von Holle, H. Delcourt and D. Simberloff, manuscript submitted). Thus, it is possible that an interaction between grazing and decreased forest cover, rather than grazing alone, favors invasion by exotic plants.

Although the mechanisms responsible for the effects of introduced mammalian herbivores on some plant species can be accounted for by the direct effects of trampling and browsing, several kinds of indirect effects are also possible. For example, introduced ungulates appear to affect the reproductive success of *Alstroemeria aurea*, and decreased abundance of the mistletoe *Tristerix corymbosus* is apparently caused by lower availability of its main host, *Aristotelia chilensis*. Likewise, increased abundance of browsing-resistant species in sites with introduced ungulates (including some spiny shrubs and herbaceous exotic species) may be attributed to an indirect effect of lowered light competition from palatable, shade-tolerant species. Although indirect effects are usually weaker in communities than direct effects, they are usually strong enough to make their study worthwhile (Schoener 1993; Menge 1995; Abrams et al. 1996).

Introduced mammalian herbivores may be affecting native animals through a variety of mechanisms, although little evidence currently exists. Competition with introduced ungulates has been suggested as a possible cause of the decline of the huemul and the pudu. Similar effects of introduced herbivorous mammals have been suggested in other regions, but in very few cases have those effects been demonstrated (see Introduction, and Ebenhard 1988). Disease transmission from introduced herbivores has also been invoked as a possible cause of the decline of huemul, although, again, no hard evidence exists. There are several well-documented cases of indirect effects between mammalian herbivores through disease transmission. In North America, white-tailed deer (*Odocoileus virginianus*) exclude moose (*Alces alces*) through their common parasite, the meningeal worm (*Parelaphostrongylus tenuis*) (Schmitz and Nudds 1994). Meningeal worm infection is clinically benign in white-tailed deer but almost always fatal in moose (Anderson 1972). Introduced herbivores could also be affecting native herbivores by enhancing predator populations. Other effects are likely (such as a doubly indirect effects of herbivores on a hummingbird and an endemic marsupial), although, again, no hard evidence exists.

Virtually no data are available about the effects of introduced mammalian herbivores on invertebrates. The only available study suggests that some functionally important insect pollinators could be negatively affected by cattle grazing; however, the mechanism accounting for this effect is not known. In other regions, there are several documented cases of negative effects of introduced mammalian herbivores on invertebrates. Sheep negatively affect the abundance and biomass of most invertebrate groups in New South Wales, Australia (Hutchinson and King 1980). And there are several documented cases of pollinator declines caused by grazing by domestic animals (Kearns 1997); for example, sheep grazing in California is believed to affect native pollinators of *Astragalus monoensis* through trampling and food removal (Sudgen 1985).

Little is known about effects on ecosystem processes. Beavers in Tierra del Fuego can affect nutrient cycling, and ungulates may affect soil properties and increase erosion processes. Effects of introduced mammalian herbivores on ecosystem processes have been observed in other systems. Feral pigs (*Sus scrofa*) have modified entire communities and ecosystems through their digging and ‘rooting’ activities. In the Great Smoky Mountains National Park in the southeastern United States, feral pigs have greatly modified soil characteristics by thinning the forest litter, mixing organic and mineral layers, and creating bare ground. These effects have in turn led to increased concentrations of nitrogen and potassium in soil solution and accelerated leaching of many minerals from the soil and litter (Singer et al. 1984). Similar effects of feral pigs have been observed in many other regions (Mack and D'Antonio 1998). Introduced goats have contributed to soil disturbance and loss in many island ecosystems (Coblentz 1978). And introduced ungulates can cause a decline in above-ground biomass production, altering fire-regimes in fire-prone ecosystems (Mack and D'Antonio 1998).

Evidence of the effects of introduced mammalian herbivores comes from a few studies, most of which are observational and with low replication. The importance of manipulation and appropriate replication in ecological studies cannot be overemphasized. The establishment of a network of well-planned, long-term exclosures stands out as a research priority in the TFSA. Similar systems of exclosures have proven extremely useful to understanding the ecological impacts of introduced mammalian herbivores in North America (Dennis 1997; Milchunas et al. 1998; Proulx 1998), New Zealand (Fitzgerald and Gibb 2001; Wardle 2001), and Europe (Hester et al. 2000). Furthermore, this kind of manipulative approach is necessary to understand the effects of introduced herbivores on relevant spatial and temporal scales. However, many ecological processes operate on broad spatial and temporal scales, and experimental removals or introductions of large herbivores at such scales are not feasible in many situations. In those cases, the comparison of areas where introduced herbivores were already present or absent is a more feasible option. And in some cases, it may simply be too late to document some effects. For example, although it is possible to hypothesize about the possible causes of the decline of the huemul throughout its range, it is probably not possible to test whether that decline was caused by introduced ungulates through some of the mechanisms discussed above.

I have not stressed the different ways in which different introduced mammalian herbivores can affect the invaded ecosystems. Obvious differences exist between species that differ greatly in their ecologies, such as beaver and deer. Beaver affect the invaded ecosystems through browsing on leaves for feeding, by deforestation resulting from dam construction, and by the flooding of large tracts of forest. Deer, on the other hand, can exert their effects through browsing, trampling and rubbing or 'horning'. But even species that are more ecologically similar, such as deer and cattle, may differ in their effects, sometimes in subtle ways. Deer are more selective than cattle in their feeding preferences (Veblen et al. 1992b); because other kinds of interactions besides herbivory are probably involved, such as competitive interactions among plants, differences in feeding preferences can result in very different effects of species of introduced herbivores on plant community structure and dynamics (Ebenhard 1988; Huntly 1991). The scarce, available information on the impacts of different herbivorous species does not allow a comparison of their impacts. Furthermore, most of the studies of the effects of introduced herbivores come from a few locations and forest types. Although it is tempting to extrapolate these effects to the entire TFSA and to other forest types, it would be risky to do so. Clearly, more research is needed.

More than anything, this review will contribute to the realization of how little we know about how introduced mammalian herbivores are affecting the biota of the TFSA. Virtually all aspects of the ecological impacts of introduced mammalian herbivores reviewed here need further research. Several research needs stand out as especially important. First, we need data on the effects of introduced mammalian herbivores on the regeneration of forest types not included in previous studies. Furthermore, even those forest types included in previous studies need further research, with higher replication and on broader spatial and temporal scales. Second, it is important to understand the effects on plant community structure and composition, including effects on rare and endemic plants, effects on exotic plant invasions, how these effects vary across space and time, and what mechanisms cause these effects. Third, the interaction between effects of introduced mammalian herbivores and other anthropogenic changes (especially fire and logging) needs to be understood. Fourth, it is important to understand the effects of introduced mammalian herbivores on other biotic components of the ecosystem besides plants. We know very little about the potential effects of introduced herbivores on other vertebrates, virtually nothing about the potential effects on insects, and absolutely nothing about effects on other organisms (e.g. other invertebrates, fungi). Given the drastic habitat changes introduced mammalian herbivores can induce, an equally drastic effect on the organisms using that habitat can be expected. Fifth, it is important to understand how habitat changes induced by introduced herbivores affect ecosystem processes. Finally, the effects of introduced herbivores must be understood in the context of climatic variability. A sound scientific understanding of the multiple effects of introduced mammalian herbivores is crucial for the long-term conservation of the unique biota of the TFSA.

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