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Introduced Invasive Mammals of Argentina

Mamíferos Introducidos Invasores de Argentina

Alejandro E. J. Valenzuela, **Christopher B. Anderson**, **Sebastián A. Ballari** and **Ricardo A. Ojeda**, Editors

The Argentine Society for the Study of Mammals (Sociedad Argentina para el Estudio de los Mamíferos – SAREM) was created in 1983, and currently has about 300 members from several countries. SAREM is an interdisciplinary society of natural sciences professionals whose main goals are the promotion of scientific and technical research, the consolidation of national collections and research centers, and the publication and diffusion of research on living and/or extinct mammals. SAREM has organized scientific meetings for mammal researchers since 1994, publishes the journals *Mastozoología Neotropical* and *Notas sobre Mamíferos Sudamericanos*, and has edited books on the systematics, distribution and conservation of the mammals of southern South America, including *Libro Rojo de los mamíferos amenazados de la Argentina* (first ed. 2000, second ed. 2012) and *Mamíferos de Argentina. Sistemática y distribución* (2006), as well as contributing to the *Libro Rojo de los mamíferos y aves amenazados de la Argentina* (currently out of print).

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Introduced invasive species are a major driver of local to global environmental change, including important negative impacts on biodiversity, ecosystem processes, economies, health and other social values. At the same time, however, different social actors can hold diverse representations of these species, particularly of introduced invasive mammals (IIMs). Such divergent values and perceptions can lead to conflicts regarding the management of IIMs, but also invite researchers and managers to be reflexive regarding their own work at a more fundamental level. Therefore, it is key that we advance towards a holistic understanding of IIMs and develop strategies to manage them based on solid technical information and plural perspectives regarding their multiple values. Despite a rich history of initiatives in Argentina to study and manage IIMs, until now there has not been an opportunity to assess the state-of-the-art knowledge in our country. This book seeks to provide rigorous, relevant and legitimate information to support research, policymaking and management decisions regarding IIMs in Argentina. With this objective in mind, the book presents a series of chapters selected to highlight priority topics concerning the conceptualization and implementation of IIM research and management. Then, fact sheets are provided for the different IIMs found in Argentina. Finally, beyond the realm of academic inquiry, the timing of this publication is ideal to re-enforce policy and decision-making, such as the recently approved National Invasive Exotic Species Strategy, which seeks to implement actions and enhance institutional capacities related to invasive species management in Argentina, and the Convention on Biological Diversity's new Global Biodiversity Framework, which also addresses biological invasions as part of broader efforts to attain the 2050 Vision for Living in Harmony with Nature.

Dr. Alejandro E.J. Valenzuela
Dr. Christopher B. Anderson
Editors, Vol. III SAREM Series A

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Foreword

Biological invasions by introduced species are one of the great changes rapidly transforming the globe today, with innumerable impacts on economics, human health, ecosystem services, and biodiversity. Mammals are among the most impactful of invasive species, transmitting diseases to humans, livestock, and native animals, trampling native grasslands, voraciously devouring vegetation from groundcover to saplings of forest trees, fouling water, causing erosion, and preying on and outcompeting native animals. They were among the first species humans introduced worldwide and in Argentina, both deliberately (*e.g.*, livestock) and inadvertently (*e.g.*, rats and mice). They have been introduced for sport (*e.g.*, deer, boar) and companionship (*e.g.*, cats, dogs), or simply as attractive ornamentals (*e.g.*, squirrels). Some that are meant to be kept in captivity, such as cats, dogs, and squirrels, escape and establish feral populations.

Argentina looms large in the history of biological invasions by introduced mammals. The earliest permanent European settlers of Buenos Aires in 1580 discovered huge herds of feral horses already on the pampas, and soon after, Vázquez de Espinoza described feral horses in Tucumán that were "in such numbers that they cover the face of the earth…". Many sheep were in Tucumán as well at that time, and of course later sheep were enormously numerous in Patagonia, effecting huge changes in the vegetation and driving land degradation and desertification to this day. When Charles Darwin visited the La Plata region in 1832 during the voyage of the Beagle, he reported that "…countless herds of horses, cattle, and sheep, not only have altered the whole aspect of the vegetation, but they have almost banished the guanaco, deer and ostrich. Numberless other changes must likewise have taken place; the wild pig in some parts probably replaces the peccari; packs of wild dogs may be heard howling on the wooded banks of the less-frequented streams; and the common cat, altered into a large and fierce animal, inhabits rocky hills."

Approximately 40 mammals have been introduced to South America, of which 25–30 have established populations; most of these are in the Southern Cone. In Argentina, I count 23 successfully introduced mammal species, including feral cats, dogs, and cows. Many, such as rats, rabbits, boar, and goats, are widely distributed around the world. By contrast, the hairy armadillo has been introduced nowhere else but from the mainland of Patagonia to Tierra del Fuego Island. Strikingly, except for the rats and house mouse, all these mammals were brought to Argentina deliberately; this is very different from, say, introduced insects. A few of these invasive mammals, like the squirrel, were not intended to be released, but I hesitate to term such invaders truly "accidental," because the people who brought them should have realized that escapes or later releases were almost inevitable. Of course, almost all of these mammals were introduced before the late twentieth century, which was when most scientists and the public began to recognize the extent and importance of impacts of introduced species. However, the squirrel and armadillo introductions were recent enough that potential impacts should have been foreseen. Things could be worse, of course—mammals deliberately brought to Argentina that either were released, but did not establish persistent populations or have not yet escaped from hunting preserves include reindeer, silver fox, mule deer, African buffalo, white-tailed deer, Père David's deer, thar, barbary sheep, wisent, mouflon, chamois, and ibex.

The technology of eradicating introduced invasive mammals has made enormous strides in the last thirty years—at least 31 mammal species have been eradicated from islands worldwide, including relatively large islands like South Georgia. Both Norway and ship rats have been eradicated hundreds of times, and house mice about 100 times. Most large mammals, such as deer and horses, are technologically easier eradication targets—many can simply be tracked and shot, for instance. However, mammals more than any other introduced species pose the complication that many people—especially hunters—simply do not want to eradicate them, and many animal welfare advocates, even those recognizing the damage some invaders cause, object to eradicating them by the only currently feasible means—killing them, humanely if possible. Even rat eradication has been impeded on animal rights/animal welfare grounds, and free-ranging dog and cat populations frequently are seen more as animal welfare issues than as conservation problems to broad sectors of some societies. In Argentina, the problem of implementing feasible eradication programs for invasive mammals is epitomized by the rather schizophrenic attitude taken by the National Parks Administration (Administración de Parques Nacionales – APN) towards red deer. The APN's conservation imperative is supported by the section of Law #22,351 that forbids propagating introduced animals, yet red deer, known to damage native species and ecosystems, are managed in Lanín National Park to foster ongoing hunting, and even to improve the size and quality of the deer for better hunting trophies. Additionally, there is often inconsistent and inadequate funding for managing and eradicating invasive mammals in protected areas, almost always constituting a supervening impediment even when a rational and effective goal is stated.

Argentine scientists have participated heavily in the rapid growth of modern invasion science since its inception in the 1980s, and they and overseas colleagues have conducted substantial research on the biology and impacts of many of the introduced invasive mammals in Argentina, as well as other invasive species. Some of the threats posed by these mammals have even become widely known to the general public in Argentina and beyond—the spread of the beaver from Tierra del Fuego to the mainland has been an international news story. *Introduced Invasive Mammals of Argentina* is therefore an exciting and timely addition to the literature on invasions in southern South America for both the Argentine public (and its political representatives and environmental managers) and scientists worldwide. The many authors assembled for this book explore how these biological invasions happened in the first place, how they spread, what they do to biodiversity, ecosystems, and human enterprises, what has been done about them so far, what can be done about them now, and what might be done with them in the future. The editors and authors are to be congratulated for an excellent exposition of the Argentine part of a growing global phenomenon.

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5 | IMPACT OF INTRODUCED INVASIVE HERBIVORES IN PATAGONIAN FORESTS

IMPACTO DE LOS HERBÍVOROS INTRODUCIDOS INVASORES EN BOSQUES DE LA PATAGONIA

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Abstract. There are 13 invasive mammalian herbivore species in Argentina, which were introduced in the 15th and 19th centuries principally for livestock and hunting purposes. Currently, many of these invasive herbivores (*e.g.*, cattle, *Bos primigenius taurus*; red deer, *Cervus elaphus*; wild boar, *Sus scrofa*; European hare, *Lepus europaeus*) have greatly expanded their distributions across Argentina, causing negative impacts to native biodiversity and ecosystem processes. Selective browsing or grazing by herbivores in Patagonian forests has been shown to decrease plant growth, increase mortality, and alter flowering season, seed set, and plant tissue chemistry of many herb, shrub and tree species. At the community level, invasive herbivores often heavily browse on just a few species, favoring browse-resistant plants and thereby altering the species composition of native plant communities. Additionally, invasive herbivores can directly impact native herbivores through competition for resources and habitat modifications. Competition for food, for example, is likely to affect native herbivores like the Patagonian huemul (*Hippocamelus bisulcus*), guanaco (*Lama guanicoe*), and southern pudu (*Pudu puda*), given their diet overlap. Additionally, several studies have shown that invasive herbivores can alter entire food webs by increasing food availability for native predators or by disrupting plant-animal mutualisms that lead to trophic cascades. Lastly, invasive herbivores can also cause ecosystem level impacts by altering nutrient cycling, hydrology, and disturbance regimes. Notably, wild boar rooting and North American beaver (*Castor canadensis*) dam construction can cause long-lasting impacts to native ecosystem structure and function. While there is a relatively good understanding of introduced invasive herbivore impacts in Patagonian forests, there is still a need for more study of their impacts in other biomes and in relation to co-occurring invasive species. There is also a particular need, as with most introduced invasive species, to focus greater attention on how to manage this socio-ecological problem.

Resumen. Dentro de los mamíferos, los herbívoros son las especies que más frecuentemente se han introducido en el mundo, ya que son fuente de alimento y transporte. En Argentina, la ganadería y la caza deportiva fueron los principales motivos de introducción de herbívoros originarios de Europa y Asia. Muchos de ellos, como la vaca (*Bos primigenius taurus*), el ciervo colorado (*Cervus elaphus*), el

jabalí (*Sus scrofa*) y la liebre europea (*Lepus europaeus*) se han vuelto invasores, expandiendo ampliamente su distribución desde los sitios de introducción hasta áreas remotas y protegidas.

Numerosos estudios en la Patagonia argentina han demostrado el impacto negativo de los herbívoros invasores en las comunidades vegetales y animales nativas, así como en diversos procesos ecosistémicos. A través del ramoneo y pastoreo selectivo los herbívoros invasores disminuyen el crecimiento de las plantas y alteran la composición de las comunidades vegetales nativas. Por ejemplo, se ha reportado que la vaca disminuye el crecimiento del coihue (*Nothofagus dombeyi*) y el ciprés (*Austrocedrus chilensis*), inhibiendo la recuperación de los bosques luego de disturbios como el fuego. También se ha observado que la herbivoría afecta el éxito reproductivo de numerosas especies vegetales como el romerillo (*Baccharis obovata*), el maitencillo (*Maytenus chubutensis*), la parrilla (*Ribes magellanicum*), el maqui (*Aristotelia chilensis*) y los *Nothofagus*, reduciendo el número de flores y semillas que producen. Además, se ha reportado que la herbivoría puede alterar los rasgos foliares como el tamaño de hoja, el contenido de agua y la dureza, así como también la calidad de los tejidos vegetales. A largo plazo, la herbivoría selectiva puede también alterar la composición del sotobosque favoreciendo las especies resistentes a la herbivoría, como los *Berberis* spp., y suprimiendo a las especies palatables. Por otra parte, los herbívoros introducidos pueden afectar a las comunidades animales nativas a través de la competencia por los recursos y la modificación del hábitat. Específicamente se ha propuesto que existe competencia por alimentos entre el ganado y el huemul (*Hippocamelus bisulcus*), el ganado y el guanaco (*Lama guanicoe*), la oveja (*Ovis orientalis aries*) y el guanaco, el ciervo colorado y el pudú (*Pudu puda*) la liebre europea y la mara (*Dolichotis patagonum*), y la liebre europea y el chinchillón (*Lagidium viscacia*), debido a una superposición de ítems dietarios que estas especies utilizan. También los herbívoros introducidos pueden afectar a las comunidades animales aumentando la disponibilidad de recursos para los depredadores nativos. Por ejemplo, se ha reportado que la liebre europea y el conejo (*Oryctolagus cuniculus*) son los principales ítems dietarios del puma (*Puma concolor*), zorro gris (*Lycalopex gymnocercus*), zorro colorado (*L. culpaeus*), y aves rapaces de la Patagonia. Los impactos de los herbívoros invasores pueden también perturbar mutualismos planta-animal provocando efectos en cascadas. Específicamente, se ha reportado que el ramoneo por vaca y ciervo colorado puede reducir la abundancia de maqui (*A. chilensis*), generando efectos indirectos en la interacción monito del monte (*Dromiciops gliroides*) – quintral (*Tristerix corymbosus*) – picaflor rubí (*Sephanoides sephaniodes*). Por último, los herbívoros invasores también pueden causar impactos a nivel de ecosistema alterando el ciclo de nutrientes, la hidrología y los regímenes de disturbios. En particular, el hozado del jabalí y la construcción de represas por el castor (*Castor canadensis*) pueden causar grandes impactos en la estructura y función del ecosistema nativo. Por ejemplo, la actividad de los castores inunda grandes superficies y crea ecosistemas similares a praderas con regeneración limitada de *Nothofagus*, facilitando la invasión de plantas herbáceas introducidas. Además, la construcción de represas aumenta la concentración de nitrógeno y fósforo, y la retención de material orgánico de las cuencas hidrográficas. Estos cambios en el flujo y la calidad del agua también alteran la composición de los macroinvertebrados acuáticos y la dinámica de la red alimentaria.

Si bien tenemos una buena comprensión del impacto de los herbívoros invasores en algunos ecosistemas nativos de Argentina, aún tenemos muy poca información sobre el impacto de los herbívoros invasores en otros ecosistemas fuera de los bosques patagónicos. Además, falta información sobre el impacto de las especies invasoras cuando co-ocurren en un mismo ambiente, y finalmente acerca de cómo el manejo de estas puede revertir sus efectos.

Introduction

Herbivores are among the world's most frequently introduced mammals, as they provide a source of food, animal husbandry, and transportation (Long, 2003). In Argentina, the two main causes of mammalian herbivore introductions were livestock and hunting (Novillo and Ojeda, 2008; Merino *et al.*, 2009; Ballari *et al.*, 2016; Ballari *et al.*, this volume). In the 15th century, Spanish explorers introduced the large herbivorous livestock like cattle (*Bos primigenius taurus*), sheep (*Ovis orientalis aries*), and goats (*Capra aegagrus hircus*) (Primo, 1992; Ballari *et al.*, 2016). More recent introductions during the late 19th and 20th centuries were mostly driven by hunting practices and include the European hare (*Lepus europaeus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) (Ballari *et al.*, 2016). Argentina currently hosts 23 introduced invasive mammal species, of which 56% are herbivores (Ballari *et al.*, 2016; SAyDS and SAREM, 2019; Valenzuela *et al.*, this volume) (Table 1). All of these invasive herbivores are native to Europe and Asia and have successfully established wild populations that have expanded at different rates (Novillo and Ojeda, 2008; Ballari *et al.*, 2016).

Table 1. List of introduced invasive mammalian herbivores found in Argentina's forested biomes.

Order	Scientific name	Common name
Cetartiodactyla	*Antilope cervicapra*	blackbuck, Indian antelope
	Axis axis	chital, axis deer, spotted deer
	Bos primigenius taurus	cattle
	Bubalus arnee bubalis	buffalo
	Capra aegagrus hircus	goat
	Cervus elaphus	red deer
	Dama dama	fallow deer
	Sus scrofa	wild boar, feral pig, swine
Lagomorpha	*Lepus europaeus*	European hare
	Oryctolagus cuniculus	European rabbit
Perissodactyla	*Equus africanus asinus*	donkey
	Equus ferus caballus	horse
Rodentia	*Castor canadensis*	North American beaver

Many of Argentina's introduced invasive herbivore species, including cattle, red deer, wild boar (*Sus scrofa*), and European hare, have naturally expanded their distributions from their introduction sites, thereby establishing wild populations in large areas (Novillo and Ojeda, 2008; Ballari *et al.*, 2016; Scorolli, 2018). As a consequence, the supposedly "remote" biomes of the Sub-Antarctic and Patagonian forests, which are otherwise classified as "wilderness areas" (Mittermeier *et al.*, 2003), are actually one of the most invaded ecoregions of the Southern Cone (Ballari *et al.*, 2016). Additionally, commercially valuable species have expanded throughout Argentina thanks not only to their own dispersal abilities, but also help from humans (Valenzuela *et al.*, 2014). These types of expansion have occurred by the transportation of animals for production and work, such as sheep, horses, and goats, or through escapes from game reserves or rearing facilities with poor biosecurity measures, such as the red deer. In contrast, some game species, like the fallow deer, have expanded their territory much less than others (Novillo and Ojeda, 2008; Barrios-García, this volume), while the chital (*Axis axis*) is still mostly restricted to game reserves in several provinces (Guichón *et al.*, 2016).

While among Argentina's invasive herbivore assemblage, only red deer and goats are listed among the world's 100 most harmful introduced invasive species (Lowe, 2000), many of these remaining species still are known to cause negative impacts on native biodiversity and ecosystem processes (Novillo and Ojeda, 2008; Merino *et al.*, 2009). For example, numerous authors have studied the direct and indirect impacts of invasive herbivores on plant and animal communities, as well as on ecosystem properties in Patagonian forests of Argentina, highlighting their role in altering plant species composition, decreasing forest regeneration, facilitating dispersal of introduced plants, competing with native herbivores for resources, and altering soil properties (Vázquez, 2002; Relva *et al.*, 2010; Vila and Borrelli, 2011; Barrios-García *et al.*, 2012). In the following sections of this chapter, we will discuss these impacts in more depth.

Impacts on plant communities

Selective browsing or grazing by large introduced herbivores has several direct individual-level effects by altering plant survival, growth, and fitness (Crawley, 1986; Augustine and McNaughton, 1998; Côté *et al.*, 2004; Graff *et al.*, 2007). Ultimately, these impacts can induce changes in plant traits (*e.g.*, nutritional quality and defenses) that might confer resistance or tolerance to subsequent herbivory (*e.g.*, Shimazaki and Miyashita, 2002; Rooke and Bergström, 2007; Bailey and Schweitzer, 2010), and at the same time alters plant communities by changing the richness, abundance, and composition of the native flora. Below, we will summarize the empirical data available from Argentina's Patagonian forests.

Large introduced mammalian herbivores have been reported to decrease tree seedling survival and growth, especially when natural or anthropogenic disturbances also increase the access of livestock to the forest floor. For example, following natural bamboo (*Chusquea culeou*) die-back in northern Patagonia, cattle were shown to cause more than double the seedling mortality for *Nothofagus dombeyi* and decrease seedling height more than 130% (Raffaele *et al.*, 2007). Similarly, cattle grazing in post-fire, subalpine *N. pumilio* forests decreased seedling survival ca. 30%, probably due to the combined effects of browsing and trampling and their indirect influence through the removal of potential nurse plants (Tercero-Bucardo *et al.*, 2007). In contrast, in post-fire lowland forests, seedling survival of *N. dombeyi* and *Austrocedrus chilensis* in unfenced plots tended to be higher, possibly due to lower livestock pressure and/or reduced competition from highly palatable shrub species (Tercero-Bucardo *et al.*, 2007). However, although early survival might be higher in the latter habitat, mean maximum height of all woody species and climbers, including dominant tree species, was >70% higher in the absence of cattle than in unfenced areas (Blackhall *et al.*, 2008). For this reason, it has been proposed that large introduced herbivores often inhibit forest recovery, especially following disturbances, and favor community transitions from tall forests to shrublands dominated by resprouting woody species (Raffaele *et al.*, 2011). Similar trends had been described for the role of introduced European rabbits (*Oryctolagus cuniculus*) (Vázquez, 2002) and North American beavers (*Castor canadensis*), where direct herbivory and dam construction shift *Nothofagus* forest to grasslands (Lizarralde *et al.*, 1996).

Resilient plant species that survive and sustain viable populations might still suffer from introduced mammalian herbivory, if vigor, productivity or reproduction is impaired. Few empirical studies have explored these consequences in temperate Argentine ecosystems and have reported evidence of both the benefits and costs of browsing. For example, in *Nothofagus* forests in northwestern Patagonia, while some understory species (*e.g.*, *Baccharis obovata*, *Rosa rubiginosa* and *Maytenus chubutensis*) did not produce flowers in the presence of cattle, for others reproductive tissue output showed the opposite tendencies, depending on the shrub's palatability (de Paz and Raffaele, 2013). Specifically, whereas palatable wild currant (*Ribes magellanicum*) shrubs showed 25× fewer flowers, 10× fewer fruits, and null seed viability under livestock pressure, the less palatable box-leaved barberry (*Berberis microphylla*) increased flowers by 4×, fruits by 2×, and seed production by 9× under the same conditions (de Paz and Raffaele, 2013). Also, it is key to note that all forest strata can be susceptible to large herbivores, as ungulates have been shown to reduce 1) the number of male flowers of canopy *Nothofagus* trees in silvopastoral systems in Tierra de Fuego (Martínez Pastur *et al.*, 2008; Soler *et al.*, 2012); 2) the density of understory fruiting plants by 3× in *Nothofagus* forests in Neuquén and Río Negro (Rodríguez-Cabal *et al.*, 2013); and 3) the fitness of a common herbaceous plant, *Alstroemeria aurea*, by directly reducing its population density and thus, hindering pollen deposition on stigmas in *N. pumilio* forests in Río Negro province (Vázquez and Simberloff, 2004).

Changes in plant traits following damage by introduced herbivores have the potential to modify plant quality to subsequent herbivores (*e.g.*, Shimazaki and Miyashita, 2002; Rooke and Bergström, 2007; Bailey and Schweitzer, 2010). Such less obvious effects are particularly relevant in the case of novel plant-animal interactions. Recently, several studies in South America's temperate forests have reported changes in leaf traits, growth rate, phenology, and induced chemical defenses of remaining vegetative and reproductive tissues under introduced herbivore pressure. For example, in terms of leaf traits, two studies have shown that some browse-susceptible plant species decreased leaf size, toughness, and water content (Blackhall *et al.*, 2012), as well as leaf and shoot production (Sasal, 2009) under livestock herbivory pressure. Furthermore, phenological changes in reproductive span were reported for several understory species, with some palatable species shortening their blooming periods (*e.g.*, *R. magellanicum*, *Schinus patagonicus*), while browse-resistant species have shown to lengthen their flowering periods (*e.g.*, *B. microphylla*), favoring reproductive success (de Paz and Raffaele, 2013). Induced chemical defenses post-browsing, which aim at reducing subsequent herbivore damage (Karban and Baldwin, 1997), have not been assessed for temperate forest species, but indirect evidence suggests changes in secondary chemistry due to livestock grazing. Studies of tissue flammability in *N. antartica* shrublands described patterns of decreased tissue ignitability at the community level (Blackhall *et al.*, 2017) and species-specific changes in foliar flammability (Blackhall *et al.*, 2012) due to cattle browsing, suggesting changes in plant allelochemical content as some secondary metabolites, such as terpenes, often correlate with tissue flammability (*e.g.*, Owens *et al.*, 1998; Ormeño *et al.*, 2009; Page *et al.*, 2012; Pausas *et al.*, 2016). Moreover, in the neighboring Patagonian steppe, Cavagnaro *et al.* (2003) showed that *Senecio filaginoides*, the least preferred shrub species grazed by sheep, employs both high concentrations of constitutive allelochemicals and induced resistance following damage, especially by increasing oil and hydrocarbon fractions.

Alternatively, browsed plants could compensate the removed tissue by enhancing growth and photosynthetic rates, activation of dormant meristems, changing biomass allocation, or increasing nutrient uptake. All of these responses increase tolerance capabilities by minimizing the negative effects of damage on plant fitness (Tiffin, 2000; Fornoni, 2011), but evidence of these strategies in native species in the face of biological invasions by herbivores in Argentina's temperate forests is still scarce. Increased growth rates following cattle browsing have been reported for *N. antarctica* in northwestern Chubut, with such a response being stronger in larger rather than smaller saplings (Echevarría *et al.*, 2014). In addition, tolerance might depend on browsing pressure, with *N. antarctica* saplings being able to rise compensatory regrowth only under low stocking rates, while heavy browsing pressure suppressed tree regeneration and led to shrubby architecture and lower growth rates (Echevarría *et al.*, 2014). Lastly, only one study to date has measured resource allocation post-damage by introduced ungulates. Six years after cattle exclusion in a post-fire subalpine *N. pumilio* forest, the browse-resistant shrub *B. microphylla* showed similar vegetative, reproductive and root biomass as browsed plants and even increased in size, suggesting compensatory growth. In contrast, the more palatable *R. magellanicum* was unable to compensate, showing decreased overall size and biomass of all vegetative and reproductive tissues, and low shoot : root ratios compared to undamaged individuals in the exclosures (de Paz and Raffaele, 2015).

Through differences in seedling establishment and survival, plus selective browsing of understory species, introduced herbivore mammals also substantially modified vegetation cover and species composition of native plant communities. For instance, in northwestern Patagonia, long-term livestock presence reduces plant species richness and cover of subcanopy trees, shrubs and bamboo up to 80%, while simultaneously increasing the relative cover of ground-layer herbs (Veblen *et al.*, 1989; Raffaele and Veblen, 2001; Raffaele *et al.*, 2007; Blackhall *et al.*, 2015; Piazza *et al.*, 2016; but see Blackhall *et al.*, 2008). Besides cattle, browsing by introduced deer species, such as red and fallow deer, also strongly inhibit growth of native tree saplings, decrease cover of native understory plants, and change understory species composition (Relva *et al.*, 2010; Barrios-García *et al.*, 2012; Rodríguez-Cabal *et al.*, 2013). Given their generalist diet, these large ungulates can exert damage on ca. 30 woody species and several forbs and grasses (Vila and Borelli, 2011; Barrios-García *et al.*, 2012; Soler *et al.*, 2012), but often heavily browse on just a few selected species (Relva *et al.*, 2010; Vila and Borelli, 2011; Barrios-García *et al.*, 2012), favoring browse-resistant over browse-sensitive species (Relva *et al.*, 2010; Blackhall *et al.*, 2015), and decreasing plant evenness and species turnover along environmental gradients (Piazza *et al.*, 2016). For example, it has been reported that *Berberis* spp. increases its abundance in heavily browsed sites (Relva and Veblen, 1998). Moreover, although introduced herbivores could aid to control introduced plant species (*e.g.*, Zamora Nasca *et al.*, 2018), preferences towards more palatable native species often actually favor the invasion of introduced tree species, such as pines (Nuñez *et al.*, 2008; Relva *et al.*, 2010), as has been seen in other ecosystems worldwide (Oduor *et al.*, 2010). Such preferences are likely driven by the tissue quality of native plants (*e.g.*, Forsyth *et al.*, 2002), but such assessments are still missing for Argentine ecosystems. Furthermore, not only large but also medium-sized introduced herbivores like the European hare have been shown to reduce woody native plant cover, while increasing the area occupied by introduced forbs (Raffaele *et al.*, 2011).

Besides cattle and deer, Barrios-García and Simberloff (2013) reported that wild boar rooting increases by as much as 2× the establishment and biomass of non-native seedlings, compared to unimpacted sites. Additionally, the same authors showed that soil disturbance by wild boar, rather than endozoochorous dispersal, facilitates plant invasions. Another well-known biological invasion by an introduced herbivore is the huge impact on native plant communities attributed to beavers. In the 1940s, 20 beavers were introduced to the Argentine portion of Tierra del Fuego in an attempt to help start a fur industry. Beavers have colonized nearly all streams in the Fuegian Archipelago and are found in many watersheds on the mainland south of Puerto Natales, Chile, reaching as many as 100,000 individuals (Anderson *et al.*, 2009). Introduced beavers can devastate *Nothofagus* forests by cutting and killing the dominant tree species (*N. pumilio*, *N. betuloides*), but can actually favor regeneration of *N. antarctica* and ultimately create resilient grasslands dominated by introduced herbaceous species (Martínez Pastur *et al.*, 2006; Wallem *et al.*, 2010; Henn *et al.*, 2014). However, the greatest impact on riparian communities comes from the flooding associated with dam construction (Lizarralde, 1993). Beaver dams can reach up to 100 meters in length and cause floods, which has serious impacts on the native vegetation. This introduced herbivore is also an invasive ecosystem engineer and has directly modified around 30,000 ha on the Argentine side of Tierra del Fuego's main island (Isla Grande), constituting the largest ecosystem alteration in this biome in the Holocene (Henn *et al.*, 2016; see Anderson and Roulier, this volume).

Impacts on animal communities

Besides their effects on plants, introduced herbivores can also directly impact native herbivores through competition for resources and habitat modifications (Vázquez, 2002; Valenzuela *et al.*, 2014). Large native mammalian herbivores in the Andean Patagonia region include the guanaco (*Lama guanicoe*) and two species of endangered deer: the Patagonian huemul (*Hippocamelus bisulcus*) and the southern pudu (*Pudu puda*) (Vázquez, 2002). Competition for food has been presumed to occur between cattle and huemul (Vila *et al.*, 2009; Briceño *et al.*; 2013, Díaz *et al.*, 2013), cattle and guanaco (Fernández Pepi *et al.*, 2015), sheep and guanaco (Soler *et al.*, 2012), as well as between red deer and pudu (Silva-Rodríguez *et al.*, 2016). However, the suggestion that introduced herbivores likely affect native herbivores through exploitation competition stemmed from studies that described patterns of resource use and partitioning among sympatric species; establishing the potential for competition, but rarely demonstrating its action or effect (Dolman and Wäber, 2008). Similarly, Bonino *et al.* (1997) found a 50% trophic overlap between the native mara (*Dolichotis patagonum*) and the introduced European hare; and Galende *et al.* (1998) and Galende and Raffaele (2013) showed diet and spatial overlap between the native southern mountain viscacha (*Lagidium viscacia*) and the introduced European hare.

Introduced mammalian herbivores may also affect animal communities by increasing food availability for predators. This process is known as "apparent competition" (Holt, 1977), and occurs when prey species, in this case introduced herbivores, elevates predator abundance above levels that would have been maintained by native prey, which then increases predation pressure on native prey assemblages. In the temperate forests of Patagonia, puma (*Puma concolor*) and foxes (*Lycalopex gymnocercus* and *L. culpaeus*) prey upon introduced herbivores, and sometimes these non-native species contribute most of their diets (Novaro *et al.*, 2000). Similarly, avian predators consume introduced herbivores. A study by Barbar *et al.* (2016) found that the composition of the Patagonian raptor community is altered as a consequence of the introduction of European hare and rabbit. These authors found that the relative abundances of large and medium-sized raptor species have increased, probably because these introduced lagomorphs represent a new food resource, thereby providing higher biomass than native prey species and favoring large and medium-sized raptors compared to other smaller species of the same trophic level.

In addition to the impacts on vertebrates, introduced mammalian herbivores affect native invertebrates in several ways, directly by trampling on its nests, or indirectly through their effects on the quantity and quality of food sources, or by changing the habitat. For example, cattle browsing in post-fire *Nothofagus* forests increased beetle richness 18% by altering environmental heterogeneity, but reduced pollinator visits by increasing flower production through a "resource dilution effect" (Sasal *et al.*, 2015, 2017). In contrast, browsing on *Aristotelia chilensis*, one of the most common understory plants in Patagonian temperate forests, by cattle and red deer reduced foliar arthropod species and individuals compared to un-browsed plants in un-invaded sites (Rodríguez-Cabal *et al.*, 2019).

Cascading impacts—disruption of plant-animal mutualisms

Mutualisms are essential interactions not only for the persistence of these beneficial relationships' partners, but also for the maintenance of biodiversity and the integrity of ecosystems (Janzen, 1980; Feinsinger, 1987; Bond, 1994; Levey and Benkman, 1999; Traveset, 1999; Herrera, 2002). Patagonian temperate forests present a high degree of endemism (Heywood and Watson, 1995), and a large portion of its flora depends on mutualistic partners (Aizen and Ezcurra, 1998). Introduced mammalian herbivores may indirectly impact native plant communities by disrupting such plant-animal mutualisms (Mack and

D'Antonio, 1998; Rodríguez-Cabal *et al.*, 2013), ultimately leading to consequences at multiple levels via trophic cascades.

In the northern portion of this temperate forest, we find a unique interaction, including the world's southern-most hummingbird (*Sephanoides sephaniodes*), a mistletoe (*Tristerix corymbosus*), the most common host of mistletoe and dominant understory shrub (*A. chilensis*), three seed dispersers—a marsupial (known as monito del monte, *Dromiciops gliroides*) and two birds (the white-crested elaenia, *Elaenia albiceps*, and the austral thrush, *Turdus falcklandii*). The nectar produced by the mistletoe is the primary food resource for the hummingbird during the winter (Aizen, 2003). During the austral spring, the hummingbird pollinates nearly 20% of the endemic woody genera in Patagonian forests (Aizen and Ezcurra, 1998). The marsupial disperses seeds of at least 25 fleshy-fruited species and is the only known disperser of the mistletoe, allowing its seed to establish by fecal deposition on *A. chilensis* branches (Amico and Aizen, 2000). The elaenia and the thrush are generalist seed dispersers and carry the seeds of more than 80 plant species in these forests (Amico and Aizen, 2005). When *A. chilensis*, which is preferred forage for cattle, red and fallow deer (Veblen *et al.*, 1992; Jaksic *et al.*, 2002), is browsed, the close interaction network between these native species can be disrupted. Indeed, Rodríguez-Cabal *et al.* (2013) demonstrated

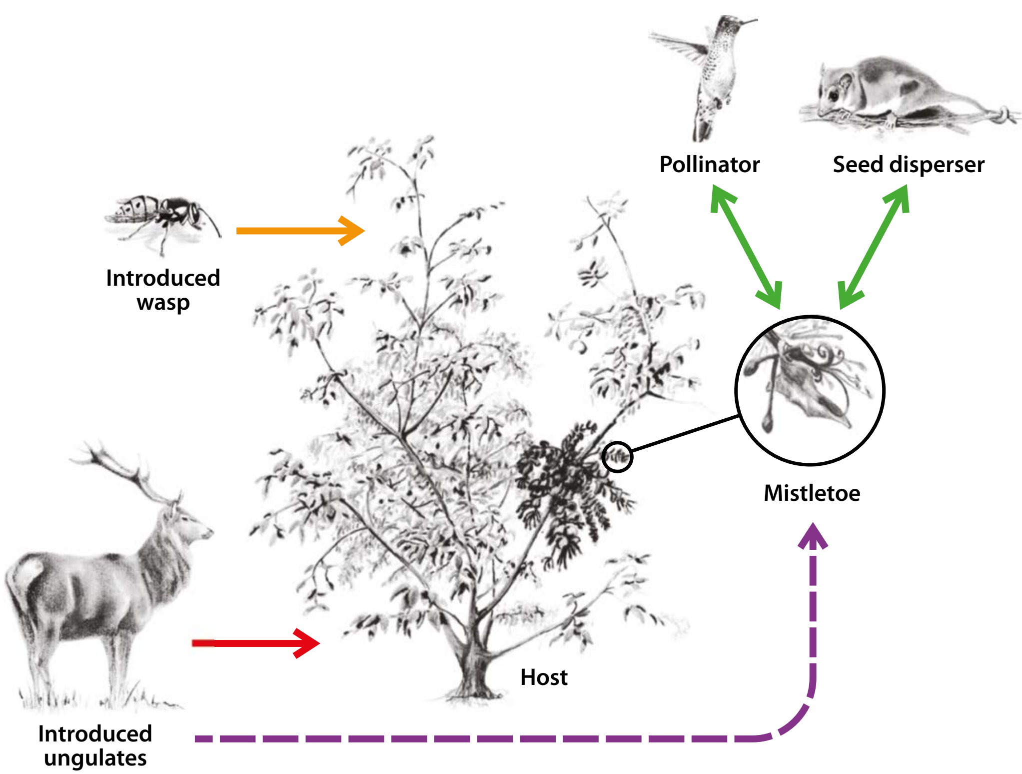

Figure 1. A keystone plant-animal mutualism in the northern portion of Patagonia's temperate forest biome. The red arrow indicates the direct negative effect of introduced ungulates on the most common host of the mistletoe, and the purple arrow indicates the indirect effect. The green arrows indicate native mutualistic interactions. Figure modified from Fig. 1 in Rodriguez-Cabal *et al.* (2013). (Drawings: Ezequiel Rodriguez-Cabal).

how the reduction of *A. chilensis* abundance by introduced ungulates caused indirect effects that lead to the disassembly of the entire web (Fig. 1). These authors showed a 16× reduction in the abundance of *A. chilensis* in sites invaded by introduced ungulates, compared to uninvaded sites (*i.e.*, intact sites). In turn, invasive herbivore browsing on *A. chilensis* indirectly reduced the abundance of the species in the keystone mutualistic interaction. Specifically, the abundance of mistletoe was 83× greater in intact compared to invaded sites, triggering the disassembly of this key mutualistic web. Another example of the negative effects of introduced ungulates on mutualisms comes from the study of Vázquez and Simberloff (2004), who showed that invasive ungulates indirectly alter the pollination and reproduction success of the herb *A. aurea* by decreasing population density via trampling. Also, pollination quantity (number of conspecific pollen grains) and quality (as determined by contamination with heterospecific pollen grains) were found to dramatically decrease at invaded sites, which in turn decreases reproductive performance of *A. aurea* at these invaded sites.

Another interesting effect of non-native herbivores was reported by Nuñez *et al.* (2013), who described facilitation among introduced species (pines, an ectomycorrhiza, and mammals) in northern Patagonian forests. Members of the family Pinaceae require an obligatory mutualism, an introduced ectomycorrhizal fungi, to thrive; however, both of them may disperse independently using different vectors. These authors found that introduced mammals, such as red and fallow deer and wild boar, disperse spores of ectomycorrhizal fungi in their feces via fungi consumption. Thus, introduced mammals may indirectly facilitate pine invasions via fungi dispersal in sites where they co-occur.

Ecosystem level impacts

While most studies of introduced species focus on the impact on native population and community properties, comparatively less is known about the role of biological invasions by mammalian herbivores on ecosystem-level properties. We know that invasive herbivores can change ecosystem structure and processes, such as productivity, nutrient cycling, hydrology, and disturbance regimes, thus altering fundamental rules of existence of all species living in the ecosystem (Vitousek, 1990; Ehrenfeld, 2010). In Argentina, very few studies have determined the consequences of invasive herbivores on native ecosystems and have mainly focused on the impacts of the beaver as an invasive ecosystem engineer. However, some effects by other introduced herbivores have been reported.

As described above, selective browsing by introduced herbivores can alter plant community composition and litter quality; these changes may, in turn, alter the rates of organic matter decomposition and/or nutrient cycles. For example, cattle grazing in grasslands in the wet Pampas biome (Buenos Aires province) reduces standing biomass by 65% relative to an exclosure, and total above-ground nutrient stocks decreased by half or less, compared to those in the ungrazed exclosure (Chaneton *et al.*, 1996). The same study showed that grazing increases N and P concentrations, and nutrient uptake by roots, enhancing mineralization rates. Similarly, rooting by introduced wild boar in the Monte desert biome (Mendoza province) results in decreased soil bulk density and soil respiration rates, but higher C:N (Cuevas *et al.*, 2012). In forested ecosystems, only two studies have looked at the impact of introduced deer and wild boar on soil properties after 6–7 years of exclusion and found mostly non-significant effects on soil N and C stocks and cycling, suggesting that forested ecosystems are either more resilient to disturbance or that longer-term studies are needed (Relva *et al.*, 2014; Barrios-García *et al.*, 2014).

The beaver again provides the most striking example of how an introduced species can alter ecosystems (Lizarralde *et al.*, 1996; Anderson *et al.*, 2009). As stated above, in the 1940s, 20 beavers were introduced in Tierra del Fuego, and since then the population has spread throughout the archipelago and onto the mainland (Valenzuela *et al.*, 2014). Beavers are semi-aquatic rodents that build dams with logs and branches to create a refuge from predators and a "garden" in the forest with patches containing more palatable forage. This activity modifies both riparian and stream ecosystems, creating meadow-like ecosystems with limited *Nothofagus* trees regeneration and facilitating the invasion of introduced herbaceous plants (Anderson *et al.*, 2006; Martínez Pastur *et al.*, 2006; Wallem *et al.*, 2010). Furthermore, dam construction increases the flow of terrestrial organic matter subsidies to in-stream systems (Anderson *et al.*, 2009). Specifically, dams increase nitrogen and phosphorus concentration (Lizarralde *et al.*, 1996), and enhance the retention of organic material and thereby carbon-standing stock by approximately 72% in watersheds (Anderson *et al.*, 2014). These changes in water flow and quality also alter the structure and function of the aquatic macroinvertebrate assemblage and food web dynamics (Anderson and Rosemond, 2007, 2010).

Conclusion

In this chapter, we have synthesized how invasive mammalian herbivores directly and indirectly alter biodiversity from the individual level to the ecosystem scale in the temperate forests of Argentine Patagonia. Furthermore, we have shown that invasive herbivores in Patagonian forests can have cascading effects on different trophic levels. While we now have some understanding of the distribution of introduced herbivores in Argentina and their consequences on some native species and ecosystems, there is still much to be studied. Particularly, we have very little information on ecosystem-level impacts in biomes outside of Patagonian forests. There is also a relative dearth of information on how invasive herbivores interact with other co-occurring invasive species or drivers of global change. Finally, as noted by Anderson and Valenzuela (2014), there is still a tremendous need to concentrate on applied research concerning how management can address or reverse these effects.

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INTRODUCED INVASIVE MAMMALS OF ARGENTINA

Introduced Invasive Mammals (IIMs) are a major driver of global and local environmental change, including negative impacts on biodiversity, ecosystem processes, economies, health and other social values. However, as complex social-ecological systems, invasive species cannot be conceived solely as "negative," nor merely as "biological" invasions. This book presents conceptual and practical perspectives from 49 authors with expertise in communication, ecology, education, genetics, history, philosophy, social sciences and veterinary medicine to better understand and manage IIMs in Argentina. It concludes by providing updated information on Argentina's IIM assemblage, which includes 23 species.

Alejandro E. J. Valenzuela, **Christopher B. Anderson**, **Sebastián A. Ballari** and **Ricardo A. Ojeda**, EDITORS

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