

# Population, community and ecosystem effects of exotic herbivores: A growing global concern

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**Abstract** Exotic herbivores represent a serious threat to native biodiversity, producing large scale changes in native communities and altering ecosystem processes. In this special issue, we present a series of case studies and reviews from different areas of the world that highlight (1) the consequences of herbivore introductions are a global problem; (2) they can result in wholesale shifts in the distribution of dominant plants on the landscape and; (3) the effects of herbivore introductions extend from the population to the community and ecosystem level. These studies suggest that introduced herbivores often retard ecosystem recovery after disturbance, facilitate invasion of plant species and can act as selective agents on native plant communities. These studies also suggest that several topics, including facilitation between exotic herbivores and exotic plants and animals (i.e., invasional meltdown) and the effect of exotic herbivores on ecosystem processes, require more research attention. Overall the papers in this special feature suggest that introduced herbivores are a global problem with wide-ranging ecological and evolutionary effects.

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## Introduction

Species introductions represent one of the three greatest threats to biodiversity globally; alongside climatic change and habitat loss. Exotic invasive species have been reported to greatly alter native diversity, transforming native ecosystems as well as contributing to the extinction of endangered species, creating important management challenges (Mack et al. 2000). For example, on Macquarie Island, Australia the removal of feral cats led to a trophic cascade in which the abundance of previously introduced rabbits drastically increased after cat removal. These increases in rabbit numbers resulted in wholesale shifts to plant communities at the local and landscape level (Bergstrom et al. 2009). While there is variation in the ecological and evolutionary effects of exotic species, some groups of exotic species are perceived as more or less detrimental than others (Duncan et al. 2003) and there is a growing interest in the effects of introduced herbivores on biodiversity and ecosystem function. It is this concern that led to this special feature.

With contributions from researchers around the world, this special feature utilizes specific case studies from natural ecosystems and reviews, that:

(1) demonstrates the consequences of herbivore introductions are a global problem; (2) introduced herbivores can result in wholesale shifts in the distribution of dominant plants on the landscape; and (3) the effects of herbivore introductions extend from the population to the community and ecosystem level. Based on the contributions to this special feature, it is clear that exotic herbivores can play a fundamental role in re-structuring communities and drastically altering native ecosystems. The impact that herbivores have on native ecosystems has been detected on every continent where it has been studied and has been shown to have, in some cases, severe consequences (Table 1; Fig. 1). For example, Relva et al. (in press) studied the effect of exotic deer on native and exotic vegetation in Patagonia. They found that introduced deer have strong detrimental effects on several abundant native plants, and that deer are promoting the invasion of non-native conifers. Stritar et al. (in press) studied the effect of exotic elk on soil processes after fire by analyzing a number of deer exclosures along an 18 year chronosequence. They found important differences in soil carbon and nitrogen dynamics due to the presence of elk and found that the exotic herbivore severely retards the recovery of the native ecosystem after fire. Wallem et al. (in press) studied the effect of introduced beaver on native plant communities. They analyzed the resilience of the native community to these ecosystem engineers, finding that the community is not resilient to this type of novel disturbance that is occurring in Tierra del Fuego. Bailey and Schweitzer

(in press) compared a native and exotic herbivore, finding that plant resistance and tolerance traits can mediate the effects of herbivory on associated species. Their results suggest that in the absence of specific evolutionary history between plants and herbivores (as is usually the case with exotic species), the effects of herbivory are more likely to reduce genetic variation and to homogenize habitats, thus severely affecting associated species. Martin et al. (in press) reviewed the top-down and bottom-up consequences of exotic ungulates on plant and animal diversity in temperate forests in the Canadian archipelago of Haida Gwaii, finding notable detrimental effects on communities due to the deer. O'Reilly-Wapstra and Cowan (in press) reviewed the effect of an exotic marsupial, the brushtail possum (*Trichosurus vulpecula*), in its native (Australia) and exotic environment (New Zealand). They synthesized the well-studied plant-herbivore interactions of the possum in its native range and discuss the success of this species in New Zealand in light of its interactions with novel resources. They focused on the role of plant secondary metabolites in browsing resistance to this herbivore and the role of this marsupial as a selective agent on secondary metabolites.

This special issue also includes more general reviews of the literature. Gandhi and Herms (in press) reviewed the direct and indirect effects of exotic and invasive herbivorous insects on forests of eastern North America. They reported that invasive insects have promoted forest disturbance by inducing decline and mortality of several tree species in North

**Table 1** Examples of exotic herbivores with documented high ecological impacts around the world (from the Current issue)

Species/taxa	Location of introduction	Main effects	Reference
<i>Castor canadensis</i>	Tierra del Fuego, Chile, Argentina	Shifts in plant communities, Facilitation of plant invasion	Wallem et al. (in press)
<i>Cervus elaphus</i>	Argentina, New Zealand, Australia, Islands in Canada	Facilitation of plant invasion, Shifts in soil properties	Relva et al., (in press) Martin et al. (in press) Stritar et al. (in press)
<i>Bos</i> spp. (Cattle)	Worldwide	Shifts in plant communities	Odour et al. (in press)
<i>Equus</i> spp.	Western USA, worldwide	Facilitation of plant invasion	Odour et al. (in press)
Lagomorpha	Chile, Mexico, Worldwide	Facilitation of plant invasion	Odour et al. (in press)
Insects	Worldwide	Shifts in plant communities	Gandhi and Herms (in press) Odour et al. (in press)

The species of herbivore, location of introduction, main ecological effects of the herbivory and references are cited (for further references see the articles published in this issue)

**Fig. 1** Map of case studies from this special feature in which exotic herbivores have been shown to have large ecological effects



America. This has triggered major shifts in forest composition, function and structure. Lastly, Odour et al. ([in press](#)) conducted a meta-analysis to compare the effects of introduced vertebrate and invertebrate herbivores on the performances of native and exotic plants. They found that the exotic vertebrates preferred to feed on native plants relative to exotic plant species, while the invertebrates preferred the exotic plants. They propose that introduced vertebrate herbivores may contribute to the invasiveness of exotic plants, in agreement with the invasional meltdown hypothesis, but that this effect is not as clear in invertebrate herbivores.

### Future directions and frontiers

The current literature on the topic of introduced herbivores, including several articles in this issue, have identified clear trends and research needs in the study of exotic herbivores. For example, the role of facilitation of exotic herbivores to other exotic plants and/or animals (i.e., invasional meltdown; Simberloff 2006) seems to be a subject with clear opportunities to explore. How common or rare is the facilitation of one exotic species on another and how important exotic herbivores are to other species are not yet resolved. Other important gaps in knowledge of exotic herbivores that still need to be resolved are if exotic herbivores produce the same effects on communities and ecosystems as native herbivores (i.e., the density

dependence of interactions as well as the characteristics of the native community). Hierro et al. (2005, 2009) have called for a biogeographical approach to understand the effect of exotics (studying them in the native range as well as in the exotic range) that can be relevant to the study of exotic herbivores. It may be especially important to examine how herbivore feeding behavior, foraging patterns and plant choice may vary between the native and exotic location as behavior may influence their effects on the landscape (Forsyth et al. 2002). Similarly, a number of articles in this issue have documented the drastic effects of exotic herbivores on modifying entire native communities (e.g. Gandhi and Herms [in press](#); Martin et al. [in press](#); Relva et al. [in press](#)), but it is not yet clear if some ecosystems are more prone to community shifts than others. For example, of the five case studies reviewing empirical data in this feature, that show pronounced shifts in community composition with the introduction of exotic herbivores, four of them take place in conifer/evergreen-dominated locations with mesic conditions and acidic soils (Relva et al. [in press](#); Martin et al. [in press](#); Wallem et al. [in press](#); O'Reilly-Wapstra and Cowan [in press](#)). Much more work is required to better understand if exotic herbivores can have equally as important effects on plant community structure in deciduous or boreal forests as well as grasslands and if ecosystems with more arid environments and loamy soils have equally large effects when herbivores are introduced. Lastly, geographically, research to date on introduced herbivores has focused

on the Americas and Australia/New Zealand (Fig. 1) with much more research attention required in Africa and Asia.

Another critical gap in the knowledge on the effects of introduced vertebrate herbivores in wild systems, as demonstrated with the papers in this special feature, is the lack of information on the ecosystem consequences of introduction, such as net primary productivity or nutrient cycling in soils. The anecdotal evidence from Stritar et al. (in press) suggests that exotic herbivores may have very different effects on local plant communities and subsequent soil processes than native herbivores, although the lack of studies on this topic suggests much more work is required to understand these interactions. Where much study has been undertaken to understand the consequences of exotic herbivores and ecosystem processes is with the introduction of livestock around the world. Reviews on this topic suggest that population density, season, vegetation type and feeding behavior of the herbivore all determine the strength of the effect of the herbivore on ecosystem processes, making conclusions very context specific (Shariff et al. 1994; Sarr 2002; Wheeler et al. 2002; Vavra et al. 2007). Across habitat types and climates there is evidence that indicates that livestock greatly reduce the cover and sometimes composition of plant communities, compact soils reducing water infiltration rates, reduce the accumulation of organic matter, enhance erosion all of which sometimes has profound consequences for soil processes and overall ecosystem productivity (Kauffman and Pyke 2001). The relative differences between the direct effects of removing plant biomass, compacting soils and introduction of wastes vs. the indirect effects of altering the cover and composition of plant communities are relatively unknown when herbivores are introduced but their cumulative effects are likely to be large. Therefore, if the effects of non-domestic introduced herbivores on wild systems are just as pronounced as domestic herbivores, the consequences of introduction of exotic herbivores to wild systems may be strong.

In conclusion, the papers included in this special issue provide clear evidence of how exotic herbivores have consistent, detrimental effects on the ecosystems in which they are introduced. While much remains to be investigated, the data to date suggest that exotic herbivores can cause wide-ranging

changes to the communities in which they are embedded, from retarding ecosystem recovery after disturbance to facilitation of exotic plant species as well as acting as selective agents on native plant (and animal and microbial) communities. It is likely the union of ecological and evolutionary approaches that may provide new insights into the range of causes and consequences of introduced herbivores on both ecological and evolutionary processes (Parker et al. 2006).

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