

Biodiversity, exotic plant species, and herbivory: The good, the bad, and the ungulate

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Abstract

Invasion of natural ecosystems by exotic plant species is a major threat to biodiversity. Disturbance to native plant communities, whether natural or management induced, is a primary factor contributing to successful invasion by exotic plant species. Herbivory by both wild and domestic ungulates exerts considerable impact on structure and composition of native plant communities. Intensive herbivory by ungulates can enhance exotic plant invasion, establishment, and spread for three reasons: (1) many exotic plants are adapted to ground disturbances such as those caused by ungulate feeding, trampling, and movements; (2) many exotic plants are adapted for easy transport from one area to another by ungulates via endozoochory and epizoochory; (3) many exotic plants are not palatable or are of low palatability to ungulates, and consequently, their survival is favored as ungulates reduce or eliminate palatable, native plants. Ungulate herbivory is a chronic, landscape-scale disturbance capable of influencing plant communities as much as episodic events such as fire. Consequently, ungulate herbivory has the potential to facilitate the invasion and establishment of exotic plants in the interior Pacific Northwest where ungulates occupy nearly every ecosystem. Moreover, ungulate herbivory has intensified in many ecosystems, owing to the addition of domestic ungulates with that of existing, wild ungulates, coupled with the reduction or elimination of migratory movements and predators that previously regulated wild ungulate populations and influenced their distributions. Despite the observational evidence for ungulate herbivory as a strong facilitator of exotic plant invasion and establishment, current knowledge of cause–effect relations is severely limited by a lack of manipulative experiments. Most studies have been observational, unreplicated, and lack the experimental controls needed to eliminate or account for confounding sources of variation. Heightened attention to conservation of biodiversity will increase the importance of managing ungulates in balance with the plant communities that support them.

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1. Introduction

Invasion of natural ecosystems by exotic plant species is recognized as a major threat to biodiversity. The conifer-dominated forest communities of the interior Pacific Northwest (described in detail by Franklin and Dyrness, 1973) differ in their relative susceptibility to exotic plant invasion with respect to landscape ecology and land uses (Parks et al., 2005). The lower and mid-elevation communities of the ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) zones (Franklin and Dyrness, 1973) are the most impacted because of human induced (grazing, logging) disturbance. Disturbance of interior Pacific Northwest forest communities, whether natural or management induced, is

often considered a contributing factor to successful invasion by exotic plant species and to a concomitant decline in biodiversity (Parks et al., 2005).

Ungulate herbivory exerts considerable impact on structure and composition of native plant communities (Hobbs, 1996). Livestock particularly have been recognized as agents of detrimental change in the composition, structure, and development of plant communities (Fleischner, 1994). Herbivory by wild ungulates was once considered to have no impact, but now is recognized by scientists as an ecological force in ecosystems (Augustine and McNaughton, 1998; Riggs et al., 2000; Kie and Lehmkuhl, 2001).

One subtle aspect of ungulate herbivory is its potential role in the spread and establishment of non-native invasive plants. At least 17 million acres of western Federal lands were reportedly infested by invasive plants in 1996, more than quadrupling their range between 1985 and 1995 (Westbrooks, 1998). Effects of chronic herbivory, especially coupled with

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episodic disturbances such as wildfire and how together they influence exotic plant invasions, is an increasingly urgent issue for land managers in the interior Pacific Northwest where ungulates occupy most wildland landscapes.

In the Western United States (US) outside of national parks the ecological effects of foraging by native ungulates has not been recognized as evidenced by the lack of its mention in land management policies and plans (Wisdom et al., 2006). Also, Aber et al. (2000) made no reference to ungulate herbivory, either wild or domestic, in their publication “Applying ecological principles to management of US National Forests.”

Not only can the direct effects of herbivory increase the potential for exotic plant invasion, the associated affects of animal presence contribute to establishment of seedbeds and transportation of seeds. Hoof action disrupts the soil surface, providing a potential seedbed for exotic plants, many of which are well adapted to establishment on disturbed sites. Moreover, endozoochory and epizoochory provide the transportation pathway for seeds from infested to non-infested areas. Current knowledge of ungulate herbivory as a contributor to the invasion, establishment, and spread of non-native plants is severely limited by a lack of manipulative experiments. Most studies have been observational, unreplicated, and lacking the experimental controls needed to eliminate or account for confounding sources of variation. Ungulate herbivory is difficult to generalize as impacts from various species can be quite different dependent on body size, browser or grazer, and domestic or wild. However, physiological impact to individual plants and soil disturbance due to trafficking are the key issues related to the spread of invasive plants. Therefore, in our paper we considered all ungulates, wild and domestic, large and small, grazers or browsers. In our paper, we describe the potential role of ungulate herbivory as a threat to biodiversity through its influence on the establishment and spread of non-native invasive plants in interior Pacific Northwest forest ecosystems. Our paper is not meant to be an extensive review of the literature on herbivory (see Wisdom et al., 2006) but meant to point out the potential role of herbivory in facilitating the invasion of exotic plants.

2. Herbivory

Huntly (1991) identified the impact of herbivores on plant regeneration as a powerful, yet little studied influence on vegetation diversity. She noted that herbivores influence growth, recruitment, and mortality rates of plants and do so in ways correlated with plant density, frequency, or with other neighborhood traits, or through competitive abilities. Hobbs (1996) explained that herbivores are important agents of change in ecosystems, acting to create spatial heterogeneity, modifying succession, and controlling the switching of ecosystems between alternative states. Augustine and McNaughton (1998) reviewed studies of ungulate effects to gain insights about potential mechanisms of ungulate-induced changes in plant community composition and ecosystem processes. Despite this emerging evidence, Wisdom et al. (2006) could not substantiate the recognition of herbivory as an ecological

force in current policies of forest management in North America (Nevill et al., 1995; Aber et al., 2000; Cote et al., 2004; Riggs et al., 2005).

Competition theory suggests that ungulates feed selectively on palatable plant species, reducing their fitness relative to neighbors of lower palatability (Augustine and McNaughton, 1998). As a result, unpalatable plants replace palatable ones thereby reducing ungulate carrying capacity (Schreiner et al., 1996). Hanley and Tabor (1980) reported results similar to Schreiner et al. (1996) and attributed plant community responses to differing plant species’ tolerances to trampling and herbivory by ungulates. Horsley et al. (2003) reported a decrease in species richness with increasing deer density. The net result of increased deer impact was altered trajectory of secondary succession dominated by species avoided by deer or resilient to browsing. Hobbs (1996) focused on the importance of herbivory following ecosystem disturbance, e.g., fire. Herbivory immediately following episodic disturbance can determine the trajectory of the system among alternative states (Hobbs, 1996), and should be considered an agent of chronic disturbance equal in effect to the episodic disturbance (Riggs et al., 2000).

Studies of selective foraging by ungulates have shown that secondary compounds (e.g., phenolics and tannins) and structural compounds (e.g., lignins and cellulose) reduce plant palatability, thus conferring competitive advantage to plants that contain these compounds as a defense against herbivory (Augustine and McNaughton, 1998). Many invasive plant species employ such defenses, and thus are unpalatable to herbivores, or only palatable during short phenological periods (Kelsey and Locken, 1987; Sheley and Petroff, 1999). As a consequence, less intensive grazing of the invasive plants provides competitive advantage to these species over more palatable native plants, allowing the former to effectively invade, establish and disperse (Kimball and Schiffman, 2003). Carpenter and Cappuccino (2005) agreed that successful, highly aggressive exotic plant invaders often exhibit resistance to herbivory, which may indicate that such plants contain potent defense chemicals novel to North America. These effects of ungulate herbivory in facilitating exotic plant invasions agrees with the “enemy release hypothesis,” which postulates that because exotic plants have no natural enemies, they experience a rapid increase in distribution and abundance upon introduction to a new area (Keane and Crawley, 2002).

Despite the competitive advantages that ungulate herbivory may confer to invasive plants, the impact of grazing animals can vary greatly among ecosystems (Augustine and McNaughton, 1998). Ecosystem tolerance to herbivory is conferred by physiological and morphological traits and further affected by characteristics of a given ecosystem such as environmental conditions during periods of regrowth, and the intensity and frequency of tissue removal (Augustine and McNaughton, 1998). Tolerance to herbivory is illustrated well by Milchunas and Lauenroth (1993) in their comparison of ecosystems with long and short evolutionary histories of grazing under semiarid and subhumid environmental conditions. Ecosystems with short grazing histories exhibited a more rapid decline in species

diversity as grazing intensity increased than did ecosystems with long evolutionary histories of grazing. Stolgren et al. (1999) evaluated 26 long-term livestock grazing exclosures east of the Rocky Mountains where there is a long evolutionary history of grazing. They found little evidence to suggest that grazing has an effect on native species richness or on accelerated spread of most invasive plant species at landscape scales. Northwest landscapes may be more susceptible to invasion because of a short history of grazing and limiting precipitation (Milchunas and Lauenroth, 1993). Bakker et al. (2006) demonstrated that large herbivores caused a decline in plant species richness in grassland communities of lower productivity and precipitation, but increased richness in grasslands of higher productivity and precipitation. These results for grasslands are congruent with the idea that herbivory effects on plant species richness in forests, and in turn, on exotic plant establishment in forests, may vary strongly with site productivity. Livestock grazing in particular has been implicated as a contributor to weed invasions (Belsky and Gelbard, 2000) and ecosystem degradation in general (Fleischner, 1994). In many cases, however, these studies may be flawed or biased (Knopf, 1996; but see Olson et al., 1997). Brown and McDonald (1995) illustrate the flaws with Fleischner (1994) such as biased referencing of the literature. Sheley et al. (1997) reported that plots clipped to simulate intensive livestock grazing enhanced the establishment of diffuse knapweed (*Centaurea diffusa* Lam) but moderate defoliation had no effect. By contrast, Parker et al. (2006) summarized results from 63 manipulative studies of exotic plant invasions as affected by a wide spectrum of ungulate and non-ungulate herbivores. These authors concluded that herbivory by non-native herbivores facilitated exotic plant invasions, while feeding by native herbivores facilitated resistance to such invasions. Parker et al. (2006), however, did not separate results for ungulates from other herbivores, and thus the strength of native versus non-native ungulate effects on this pattern was not clear.

Both intensity and timing of herbivory can greatly affect plant productivity and vigor (Holechek et al., 1998). In the western US, growing seasons are limited by precipitation. Excessive herbivory during the plant growth cycle, particularly during the latter half when plants are completing reproduction and storing carbohydrates, can be especially damaging (Holechek et al., 1998). A key issue then is utilization or defoliation, considering both its timing and extent. An additional possibility is that intact plant communities may respond very differently to both wild and domestic ungulate herbivory than do those that have exotic plants as part of the species pool. "Natural levels" of herbivory may have novel effects on plant community development where an exotic species component is present. New standards for sustainable utilization may have to be developed. Acceptable utilization for intact systems depends on degree of aridity and evolutionary history of grazing (Milchunas and Lauenroth, 1993; Bakker et al., 2006). Acceptable levels vary from 25–35% for salt desert shrublands with a short history of grazing to 40–50% for shortgrass prairie with a long history of grazing (Holechek et al., 1998). For

forested ecosystems of the interior Pacific Northwest, utilization rates of 30–40% have been recommended (Skovlin et al., 1976). Timing can mitigate these suggested levels in that grazing during the dormant season is much less physiologically damaging to the plant. Considerations to utilization at that time are acceptable amounts of remaining litter and soil disturbance (Holechek et al., 1998). Grazing systems incorporating rest or deferment during the growing season are only effective if stocking rate in the pastures used during plant growth remains moderate.

The influence of herbivory by wild ungulates is strongly influenced by anthropogenic effects. Before European settlement, wild ungulate grazing was characterized by extensive migrations that probably exerted less long-term influence on the plant communities. Currently, migrations by wild ungulates and their effects on native plant communities are influenced by management. Controlling ungulate density through hunting seasons is a traditional tool of wildlife managers, but managing game animal numbers alone may not alter the relative grazing pressure on plant communities. Interior Pacific Northwestern plant habitats are now patchy and fragmented (Vavra and Sheehy, 1996; Wisdom and Thomas, 1996). Consequently, wild ungulates may concentrate their use on much smaller habitats, increasing the deleterious effects and potential invasibility of such habitats.

It seems possible that a herbivore's specific food habits might provide an advantage to a given class of invasive plants through selective foraging and a consequent shift in competitive advantage (interpreted from Severson and Urness, 1994). Smith (1949) (cited in Severson and Urness, 1994) observed differences in species composition in pastures utilized in winter by mule deer or in summer by cattle. The pasture browsed during winter by deer contained abundant and vigorous grasses and forbs but the shrub component was weakened or died as a result of heavy browsing. Conversely, the pasture grazed by cattle during summer supported abundant and vigorous shrubs but a paucity of perennial herbaceous plants. The potential invasibility facilitated by cattle grazing in this instance is obvious and direct. The lack of a herbaceous understory provides an empty niche easily filled by unpalatable invasive plants. In the case of deer browsing, the effect may be more subtle. A decline in the shrub component might be particularly important following disturbance like wildfire when secondary succession is initiated and the shrubs are nitrogen fixers that may play a long-term role in nitrogen self-sufficiency (Tiedemann and Berndt, 1972; Riggs et al., 2000). A nitrogen-limited environment may be more hospitable to invasive plants. Hobbs (1996) stated that moose browsing at moderate intensity stabilized plant community composition but destabilized it at high intensity browsing. These browser/grazer relationships to invasibility are not well defined beyond the point of massive overgrazing leading to a barren landscape open to invasion.

Compounding the issue of intensive ungulate herbivory and its potential to confer competitive advantage to exotic plants is the reduced role of ungulate predators in many ecosystems today. In many areas of western North America, for example,

wolves (*Canis lupus*) are absent but historically were common. Their effect on ungulate herbivory was demonstrated by their reintroduction to Yellowstone National Park in the 1990s, after an absence of over 50 years. Following wolf reintroduction, the distributions of elk (*Cervus elaphus*) were significantly altered (Fortin et al., 2005), resulting in substantially less herbivory by elk in riparian areas, which allowed widespread recruitment of cottonwood along stream courses for the first time in over 50 years (Beschta, 2005). This case example clearly demonstrates the role of predators in mediating the effects of wild ungulate herbivory, and in turn, mediating the potential facilitation of exotic plant invasions.

3. Associated herbivory effects

Associated with herbivory effects is the movement of animals that results in trampling effects and solifluction. Trampling is the damage caused by direct hoof impact. Trampling by grazing animals may increase runoff and erosion by reducing plant cover, by compacting or detaching soil surfaces, by redistributing litter, and enlarging bare openings (Meeuwig and Packer, 1975). Packer (1963) concluded that on an elk winter range the amount of eroded soil increased rapidly as the ground cover density decreased below 70% and the bulk density of the soil increased above 1.04 g/cm³. On steeper slopes in early spring when soils are supersaturated, soil displaced by herbivores may move downhill through plastic flow (solifluction) (Meeuwig and Packer, 1975). Trampling and solifluction together or separately create areas of disturbance which provide sites of high invasibility potential (Lonsdale, 1999).

Ungulates influence the nitrogen cycle by changing litter quality and by adding readily available nitrogen to the upper levels of soil through urine and feces deposition (Hobbs, 1996). In turn, the composition and productivity of plant communities can be stabilized or destabilized (Hobbs, 1996). This can be extremely important in ecosystems like the forests of the interior Northwest where nitrogen is significantly limiting to understory vegetation (Riegel et al., 1991). Moreover, invasive plants may immobilize disproportionately more nutrients; thereby limiting opportunities for native plants to establish and thrive (Olson, 1999) further compounding herbivory effects. Some studies show that increased nitrogen availability through the deposition of animal dung and urine encourages community dominance by invasive plant species (Harris, 1967; Hobbs, 1989). Greenhouse and garden experiments have shown that high nutrient or water availability can increase the ability of non-native plants to compete with natives (Wedin and Tilman, 1993; Nernberg and Dale, 1997; Claassen and Marler, 1998). A recent greenhouse study, however, evaluated five levels of nitrogen availability on the comparative growth of native and four invasive plant species and found the invasive plants did not display a more positive response to nitrogen fertility (Lowe et al., 2002). There were no differences between the exotic and native species at any level of nitrogen availability in root:shoot ratios, total biomass, or percent leaf tissue nitrogen, but the native species as a group gained more height than the exotics at

every level of nitrogen availability. Lowe et al. (2002) report no general relations between exotic or native plant groups and growth response to nitrogen were found in their study.

Ungulates can also have major effects on the belowground decomposer subsystem which, in turn, may influence above-ground biota by altering the supply of available nutrients from the soil (Wardle and Bardgett, 2004). Modified soil properties (i.e., pH) and nutrient availability (i.e., nitrogen and phosphorous) can also favor exotic invasive species with growth requirements better matched to such changed conditions than native species (Greenberg et al., 1997; Harris, 1967; Hobbs, 1989).

4. Prescribed livestock grazing

Numerous studies have tested the utility of “prescribed livestock grazing,” particularly with sheep and goats, to reduce biomass and composition of invasive plants. Olson et al. (1997) grazed sheep intermittently for 3 consecutive years on range infested by spotted knapweed. They found that knapweed density and seed viability were lower on grazed treatments versus ungrazed treatments. Other studies report some level of invasive plant reduction with controlled levels of grazing, selective timing of grazing, or multiple species of herbivores (Lacey and Sheley, 1996; Sheley and Petroff, 1999). Cattle appear less effective at reducing invasive plants than sheep or goats (Vallentine and Stevens, 1994; Lawrence et al., 1995). Most studies that used livestock to counter invasive plants have not been conducted in forested environments but rather in grassland settings using small enclosures.

5. Endozoochory and epizoochory

Animal-mediated spread of invasive plants is a common, worldwide phenomenon (Schiffman, 1997). Fruits and seeds are readily eaten by large herbivores intentionally or inadvertently in the course of general grazing, and may form a substantial part of their diet (Gill and Beardall, 2001). By moving seeds away from parent plants, which are usually competitively superior, animal dispersers are likely to increase the probability of seedling survivorship (Howe and Smallwood, 1982). Native ungulates and livestock have predictable patterns of habitat selection; hence, animal-dispersed seeds are likely to be spread among environmentally similar sites. Consequently, invasive plants are often deposited in conditions similar to sites where such plants have already become established (Howe and Smallwood, 1982). This role of ungulates to deposit seeds in environments where establishment can be successful can be particularly important for colonization of invasive plants in fragmented landscapes (Schiffman, 1997).

Invasive species with thick seed coats dispersed by endozoochory, in addition to benefiting from transport, may have enhanced germination as a result of scarification in the gut (Schiffman, 1997). Invasive plant seeds have been recovered from feces and found viable in numerous studies (Thill et al., 1986; Wallander et al., 1995; Malo et al., 2000; Olson and Wallander, 2002). Malo et al. (2000) concluded that the effect

of seed input to the seed bank from ungulate transport may be low at large and medium-sized spatial scales, but very important at small scales and for colonization processes. Nonetheless, it is not certain how important endozoochory is in initiating or increasing invasive plant infestations in natural systems (Gill and Beardall, 2001). Velland et al. (2003) noted that deer transported ingested *Trillium grandiflorum* seeds several hundred meters, and occasionally >3 km suggesting that endozoochory could be a significant dispersal agent.

Whereas endozoochory may be important at small scales, it is likely that epizoochory transport is an important mode of introduction and spread of invasive plants at several landscape scales. The fleece of a single sheep can carry as many as 8500 seeds of 85 vascular plant species (Fischer et al., 1996) and therefore, livestock can be effective long-distance dispersers of invasive plant seeds in rangelands (De Clerck-Floate, 1997; Olson et al., 1997).

Endozoochory and epizoochory are evolutionary adaptations that facilitated the dispersal of plant species as well as reseeding areas of intense herbivory (Howe and Smallwood, 1982). These were positive mechanisms. With human-caused transcontinental migration of plant species to exotic habitats these dispersal mechanisms are now considered potentially detrimental.

6. Knowledge gaps and research needs

Current knowledge of ungulate herbivory as a contributor to the loss of biodiversity, particularly from exotic plant invasions, is severely limited by a lack of manipulative experiments. Most studies have been observational, unreplicated, or lacking the experimental controls needed to eliminate or account for confounding sources of variation (Wisdom et al., 2006). For example, most studies have examined ungulate effects on composition or succession of plant communities by comparing only extant herbivory with total ungulate exclusion or evaluate the effects of only one ungulate species even though two or more species were typically present in the areas under study. Only a few studies have evaluated multiple densities of ungulates. Inferring cause–effect relations from such studies is questionable. Importantly, we are unaware of any herbivory studies designed to make inferences across large landscapes typically of interest to resource managers. In addition, studies like those of Bakker et al. (2006), using experimental controls and treatments, as applied across a broad spectrum of ecosystems, are needed to strengthen the geographic inference space regarding herbivory effects.

While landscape and broad scale ungulate herbivory information is lacking to inform managers, more data on how specific ungulates affect particular ecosystems is needed at all scales. In this paper, we have largely treated “ungulate herbivory” as a single general factor, yet ungulate species vary greatly in their diet selection, spatial use, and behavior, hence in their ecosystem effects. Future research synthesis may benefit from a simple division of ungulate effects on biodiversity that distinguishes “grazers”, i.e., ungulates that feed predominately on grass and herbage such as cattle or elk, and “browsers”, i.e.,

ungulates that primarily consume tender shoots and stems of shrubs and trees as food, such as deer and goats, or based on body size (used as an index to grazers versus browsers), such as done by Bakker et al. (2006). It would be valuable to predict which plants are likely to invade interior Pacific Northwest forests under different ungulate grazing regimes. For example, high foraging pressure by grazers may facilitate invasion by non-native woody shrubs whereas high foraging pressure from ungulate browsers may alter long-term forest gap dynamics and perhaps encourage non-native tree species that are better adapted to the changed conditions.

Heightened attention to conservation of biodiversity in Pacific Northwest forests will increase the importance of efforts to manage ungulates in balance with the ecosystems that support them. Tools that evaluate potential ecosystem effects of management scenarios are needed. For example, the regulated harvest of wild ungulates in hunting seasons is a traditional wildlife management tool to control future ungulate population sizes, but a population-based approach that does not consider feedbacks between ungulate herbivory and vegetation, or how different densities of wild ungulates influence specific ecosystems may not be an effective tool to protect biological diversity. Furthermore, the coexistence of wild ungulates with large populations of livestock complicates the issue and requires methodology to consider the effects of all herbivores on the ecosystem, rather than those of just one species at a time (Weisberg et al., 2002).

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