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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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Keywords: Disturbance; Competition; Grazing; Exotic plants; Biological diversity; Ungulates; Herbivory

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