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Review

Large predators and trophic cascades in terrestrial ecosystems of the western United States

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ABSTRACT

Large predators potentially can help shape the structure and functioning of terrestrial ecosystems, yet strong evidence of top-down herbivore limitation has not been widely reported in the scientific literature. Herein we synthesize outcomes of recent tri-trophic cascades studies involving the presence and absence of large predators for five national parks in the western United States, including Olympic, Yosemite, Yellowstone, Zion, and Wind Cave. Historical observations by park biologists regarding woody browse species and recently compiled age structure data for deciduous trees indicate major impacts to woody plant communities by ungulates following the extirpation or displacement of large predators. Declines in long-term tree recruitment indexed additional effects to plant communities and ecological processes, as well as shifts towards alternative ecosystem states. The magnitude and consistency of vegetation impacts found within these five parks, in conjunction with other recent North American studies, indicate that broad changes to ecosystem processes and the lower trophic level may have occurred in other parts of the western United States where large predators have been extirpated or displaced. Thus, where ungulates have significantly altered native plant communities in the absence of large predators, restoration of native flora is urgently needed to recover former ecosystem services. Following the reintroduction of previously extirpated gray wolves *Canis lupus* into Yellowstone National Park, a spatially patchy recovery of woody browse species (e.g., aspen *Populus tremuloides*, willow *Salix* spp., cottonwood *Populus* spp.) has begun, indicating that large predator recovery may represent an important restoration strategy for ecosystems degraded by wild ungulates.

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1. Introduction

British ecologist Charles Elton began to recognize in the early 1900s that predators could exert important "top-down" controls on underlying animal populations (Elton, 1927). Later, based on a survey of deer ranges across the United States (US), Leopold et al. (1947) concluded the loss of large predators was a precursor to the irruption (i.e., a rapid increase in population) of wild ungulates and subsequent impacts to plant communities. Hairston et al. (1960) built upon the ideas of Elton, Leopold, and others with their Green World Hypothesis (GWH) and suggested that predators maintained global plant biomass at high levels by limiting herbivore densities. Paine (1980) first used the term "trophic cascade" to characterize a progression of direct and indirect effects of native predators across successively lower trophic levels. This concept

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was further refined by Pace et al. (1999) when they defined trophic cascades as "reciprocal predator–prey effects that alter the abundance, biomass, or productivity of a population community or trophic level across more than one link in the food web."

Ecologists who agree that trophic interactions between top predators (carnivores), herbivores (consumers), and plants (producers) are important in determining ecosystem structure and dynamics have often debated the relative effectiveness of top-down and bottom-up forces. Thus, there is an increasing need to better understand how and why various factors can affect the interactions and relative strengths of these contrasting forces (e.g., Schmitz et al., 2004; Borer et al., 2005). Although top-down influences upon community structure have typically been found in both terrestrial and aquatic ecosystems (e.g., Shurin et al., 2002; Schmitz et al., 2000), a particularly troubling aspect of trophic cascades research in terrestrial ecosystems is the paucity of studies involving large predators. This may be due, at least in part, to the difficulty of assessing their effects at long temporal and large spatial scales.

Across much of the globe, humans have reduced the range of large carnivores. In the US, widespread poisoning, trapping, and hunting in the 1800s and early 1900s by Euro-Americans and a concerted effort at predator eradication by federal agencies greatly reduced gray wolf *Canis lupus* and cougar *Puma concolor* ranges (Laliberte and Ripple, 2004). Ecologically effective populations of wolves were largely gone in the western US by the early 1900s and cougar ranges became fragmented. These human-caused reductions in large predator distributions beg several questions: Have significant ecosystem adjustments occurred following the loss of large predators? Are potential effects confined primarily to prey species, or are there broader consequences to the structure and functioning of ecosystems?

In the late-1800s and early 1900s, the US Congress began establishing national parks at various locations within the diverse landscape that comprised the American West. These parks generally afforded increased protection to wildlife but not always to predators. In retrospect, these parks created a series of natural experiments (Diamond, 1983) that could be useful for assessing the historical effects of large predator presence/absence upon lower trophic levels. National parks provided experimental design benefits for undertaking such assessments since (1) confounding effects of land uses such as forest harvesting, livestock grazing, and hunting were largely absent following park establishment, (2) individual parks comprised a large contiguous area, (3) parks were established in a variety of biomes, (4) riparian ecosystems within a park typically had free-flowing streams and rivers (i.e., uninfluenced by dams or diversions), and (5) spatial controls, such as areas with a continued presence of large predators, refugia from browsing, or ungulate exclosures, were variously present.

Of all the western parks, the effects of wild ungulates on ecosystems probably have been studied the most in Yellowstone National Park (NP). Following the extirpation of wolves from Yellowstone in the early 1900s, Aspen *Populus tremuloides* recruitment (i.e., growth of seedlings/root sprouts above the browse height of ungulates into tall samplings and trees) began to rapidly decline as a result of intensive elk *Cervus elaphus* browsing (Fig. 1a; NRC, 2002a). Today, numerous aspen stands across the elk winter ranges of northern Yellowstone reflect a history of reduced recruitment spanning multiple decades (Ripple and Larsen, 2000) and, for many of these stands, only large diameter trees remain (Fig. 1b). In contrast, aspen recruitment within fenced ungulate exclosures has been ongoing (Fig. 1c). As aspen stands declined in Yellowstone NP and the foraging effects of elk became a major scientific and public controversy (NRC, 2002a), ensuing debates failed to consider seriously the possible role of large predators.

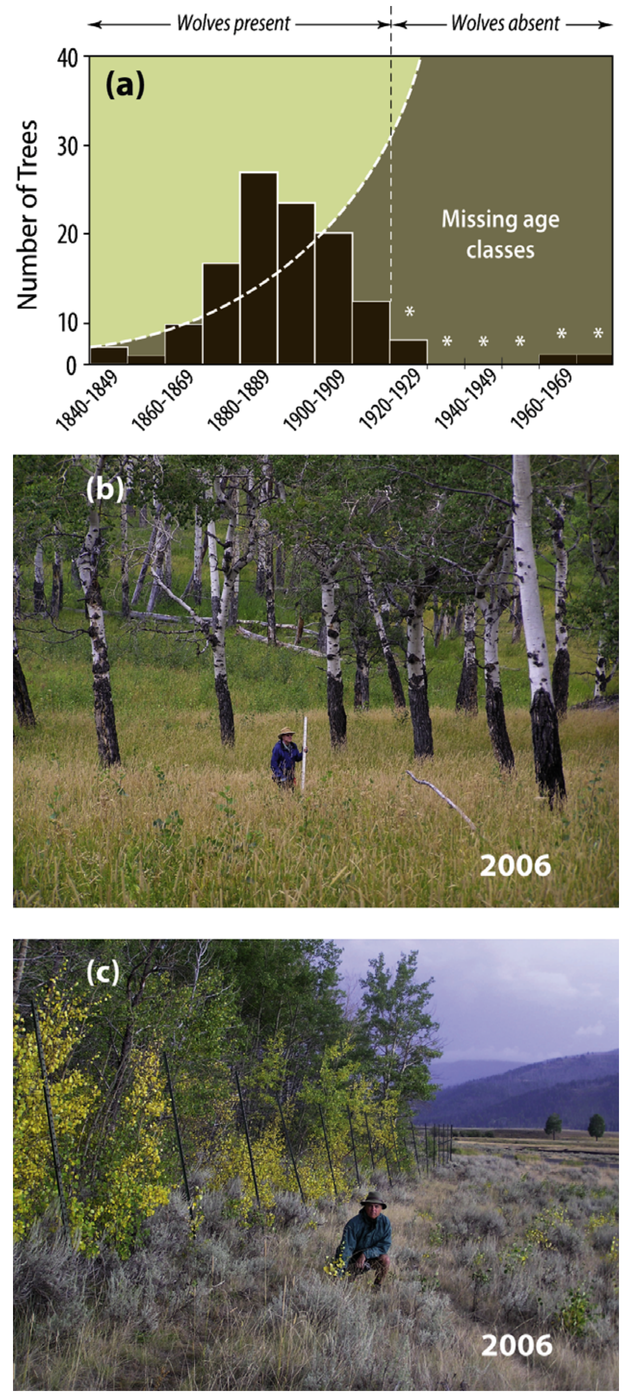

Fig. 1. (a) Aspen age structure from 1840 to 2000, (b) an aspen stand showing heavy bark damage from elk along the lower several meters of each tree and a long-term lack of recruitment (tall saplings and small diameter trees are missing), and (c) ongoing aspen recruitment within a fenced elk exclosure and an absence of recruitment outside the fence (even though root sprouts are present); all in the northern range of Yellowstone National Park. For the period following the extirpation of wolves in Yellowstone, significant decreases (95% lower CI) in aspen tree frequencies are indicated by "∗". *Source*: adapted from (a) Larsen and Ripple (2003).

Herein our objective was to compare the potential influence of large predator presence (top-down forces) and absence on plant communities over a period of more than one and one-half centuries in five western US national parks — Olympic, Yosemite, Yellowstone, Zion, and Wind Cave. Each park originally supported a large carnivore guild that was subsequently altered by the