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Review

Herbivory, hunting, and long-term vegetation change in degraded savanna

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ABSTRACT

Large ungulate populations are associated with the degradation of many forest plant communities, but it is unclear if these population sizes are strictly a contemporary phenomenon. Human exploitation models predict they are not, with ungulate numbers varying with long-term fluctuations in hunting pressure. Alternatively, human disturbance models predict that abiotic limitations normally restrict herbivores, with contemporary increases reflecting increased productivity associated with agriculture and forestry. Both can explain ungulate abundance, but may have different implications for plant conservation because they predict different levels of prior evolutionary exposure to herbivory. Here, I review historical records and stand structure studies from degraded oak savanna of western North America to examine whether current ungulate levels are strictly a contemporary phenomenon. Although it was impossible to quantify pre-European herd sizes, all evidence indicates a strong relationship between hunting pressure and ungulate abundance. Historical accounts repeatedly describe large herds of deer and elk at first European contact, followed by sharp declines immediately after colonization, and then rapid recovery beginning in the early 1900s as subsistence hunting waned. Stand structure data for oak woodland appear to support this model. Present-day oak woodlands mostly derive from mass recruitment from 1850 to 1910, coinciding with the near elimination of ungulates by hunting. Although these results suggest that large ungulate herds are not strictly a contemporary phenomenon, browsing intensity appears to be unprecedented given limited hunting, predator extirpation, and savanna fragmentation within productive pasture and early successional forest. Hunting pressure thus continues to be important, in that it is now largely absent.

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1. Introduction

Herbivore effects on vegetation are ubiquitous to most grass-dominated ecosystems, and the transformation of these effects has been associated with the loss of structure, function, and diversity in grasslands worldwide (Fleischner, 1994; Cote et al., 2004; Maron et al., 2006; Parker et al., 2006). Transformations include herbivore expansion following hunting reductions or predator loss, herbivore collapse after predator introduction, or the replacement of native grazers with exotic livestock. Two primary challenges for quantifying herbivore effects on grasslands are that detailed descriptions of herbivore dynamics prior to European settlement are lacking or vague, and that they can co-occur with other changes (e.g., plant invasion, habitat loss, fire suppression). From a conservation perspective, both obscure appropriate management practices including restoration targets.

In systems undergoing substantial herbivore expansion, as is the case in many regions of North America (e.g., *Odocoileus* spp.), the degree of impact on grassland plants may depend on whether these increases are strictly a contemporary phenomenon (Mack and Thompson, 1982; Daubenmire, 1985; Martin and Szuter, 1999). Models emphasizing the importance of hunting pressure predict wide fluctuations in ungulate populations in the past, depending on variation in human population sizes (Martin and Szuter, 1999). Models emphasizing the importance of contemporary human land use practices predict that abiotic limitations previously restricted herbivores, with contemporary increases reflecting increased productivity associated with agriculture and forestry (Daubenmire, 1985; Van Vuren, 1987; Lyman and Wolverton, 2002). Although both can explain present-day ungulate abundance, they can have different management implications for plants. Because hunting models imply that ungulate numbers have been high previously, resident plants could be less sensitive to browsing compared to other changes (e.g., invasion, fire suppression). Management actions targeting browsers could have limited effect on plant recovery if these other factors are more limiting. Human disturbance models, in contrast, predict that ungulate populations may never have been larger, implying that plants may be less likely to tolerate intensive browsing and, thus, rapidly decline in its presence (Rooney, 2001; Rooney and Waller, 2003). Because we often lack information on long-term population trends for ungulates, the relative importance of these models for regulating browser populations, and their affect on plants, remains debated.

Here, I examine evidence of former herbivore levels in coastal oak savanna of the Pacific Northwest of North America, using historical records and current vegetation structure as an indication of past events. Determining regulatory mechanisms for ungulates in northwestern grasslands has been especially problematic. As is typical of degraded grasslands, there has been invasion, species loss, and altered function (e.g., nutrient cycling). However, the role of herbivory in these changes is unclear. Some historical evidence suggests that ungulate herds were largely absent in the northwest prior to European settlement (Burroughs, 1961). As a result, Mack and Thompson (1982) hypothesized that extensive plant invasion derived from the arrival of grazers into a plant community lacking evolutionary exposure to intense herbivory. Alternatively, other records reported large but localized ungulate populations in some areas, especially towards the coast (e.g., Menzies, 1923; Ludrin, 1928; Lamb, 1984; Brown, 1989; Gough, 1992; Rollins, 1995). There could be a number of explanations for these discrepancies in the historical literature, ranging from differences in the timing and location of the observations, to different socio-cultural histories (e.g., some observations may have been preceded by disease epidemics, which reduced hunting pressure). I focus this investigation mostly on southeastern Vancouver Island (Fig. 1), British Columbia. Because European colonization occurred there relatively recently (mid-1800s), there are extensive records of

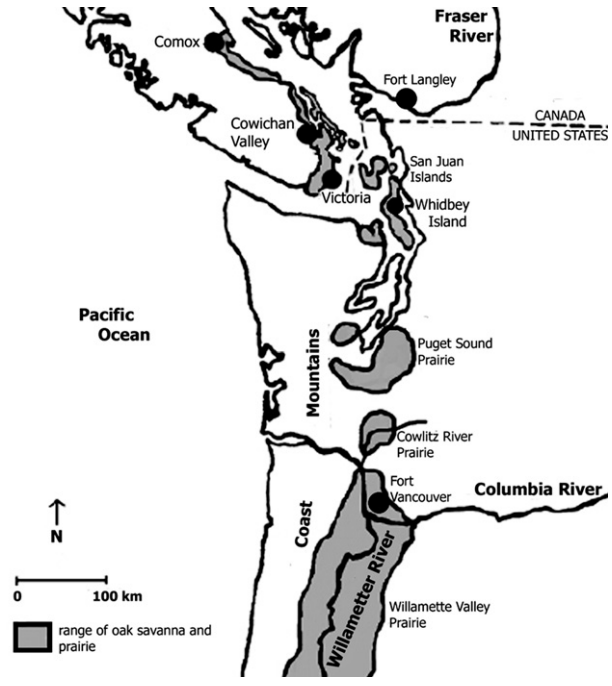

Fig. 1 – Distribution of oak savanna in northwestern North America, with locations of place names referenced in the text. Historical reports on ungulate abundances came mostly from areas within and around the major settlements (Victoria, Cowichan Valley, Comox). Modified from MacDougall et al. (2004).