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Demographic hallmarks of an overbrowsed population state in American ginseng

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ABSTRACT

Effects of high deer herbivory in North America on populations of favored plant browse species have been well-documented, however since less palatable plants now dominate the understory, we asked whether these species could be vulnerable as well, and if so, what symptoms might signal that this was occurring? Using American ginseng (*Panax quinquefolius*L.) as our representative less palatable understory plant, we compared two subpopulations within a single natural population that were differentially exposed to browse; one isolated from deer by growing atop a large, flat-topped boulder, and a browse-exposed subpopulation in the surrounding low-lying area. We tested the hypothesis that deer effects would be manifested in all parts of the life history; through reduced growth, survival and reproduction. In turn, we hypothesized that browse would reduce population growth rates, and that differences in stage structure of the population would be produced. Taking advantage of a 20 year record of formal demographic censusing, we showed that browse effects were manifested primarily in reduced size-specific growth, while size-specific fertility and survival were relatively unaffected by exposure to browse. Demographically, these differences in growth were sufficient to drive population size reductions of 4.5%/y in the off rock subpopulation while the on rock plants slowly increased in number. High browse off the rock resulted in high proportions of plants in a stunted juvenile state in the off rock population relative to the on rock plants. A high proportion of juveniles is therefore a clear symptom of an understory subjected to chronic overbrowsing, providing land managers a rapid way to assess whether deer could be impacting understory biodiversity. The sharp demographic contrasts we observed between browsed and unbrowsed subpopulations also implies that promotion of refugia within managed lands will likely become increasingly important management tools for biodiversity preservation as long as unchecked deer populations persist.

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1. Introduction

“Since then I have lived to see state after state extirpate its wolves. I have watched the face of many a newly wolfless mountain, and seen the south-facing slopes wrinkle with a maze of new deer trails. I have seen every edible bush and seedling browsed, first to anemic desuetude, and then to death.”

—Aldo Leopold, from ‘Thinking Like a Mountain’, Sand County Almanac, 1949

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Since publication of Leopold's iconic Sand County Almanac, numerous studies have demonstrated the cascading effects of predator removal and predator re-introduction in a diverse array of biological communities (Pace et al., 1999). While many of the classic cases of trophic cascades were described in aquatic systems (Paine, 1966), profound impacts of top predator abundance have been demonstrated repeatedly in terrestrial communities as well (Schmitz et al., 2000; Terborgh et al., 2001; Rooney and Waller, 2003; Beschta and Ripple, 2009). In systems where herbivore abundance strongly affects vegetation, the loss of keystone predators can be particularly impactful (Côté et al., 2004). Overabundant herbivores can then shape the vegetation over time by profoundly altering recruitment patterns of overstory trees and reducing both abundance and diversity of the understory (Waller and Alverson, 1997; Russell et al., 2001; Côté et al., 2004; Habeck and Schultz, 2015).

In the eastern deciduous forest of the U. S., two top predators have been functionally extinct for more than a century. Eastern cougars (*Puma concolor*) were officially declared extinct in 2011, but this reflected a condition that had existed for approximately 8 decades (U. S. Fish and Wildlife Service, 2011), and they were uncommon to rare for several decades prior to that. The other top predator in eastern forests, the gray wolf (*Canis lupus*), had a similar history of being functionally extinct in most of its former eastern range by 1900 (Carson et al., 2014). Hunting by humans also kept white-tailed deer populations (*Odocoileus virginianus*) low, along with their predators. Over the past several decades, management by state wildlife agencies on behalf of human hunters successfully resurrected large deer herds, ultimately resulting in densities that have far exceeded those found in pre-settlement forests in most regions (Waller and Alverson, 1997; Russell et al., 2001; Côté et al., 2004; Habeck and Schultz, 2015). The subsequent widespread overbrowsing of understory tree seedlings, shrubs, and herbaceous understory plants is well-documented (Rooney and Waller, 2003; Côté et al., 2004). Indeed, it has been argued that the absence of keystone predators along with mismanagement of their populations resulted in white-tailed deer being recognized as keystone species in its own right (Waller and Alverson, 1997) due to their broad-ranging impacts on the entire ecosystem.

Frequently, ecologists have been concerned that common understory plant species may be gradually going extinct due to overbrowsing (Carson et al., 2014). Particular attention has been paid to browsing of seedlings and saplings of commercially valuable tree species that appear to be favored foods of deer (Côté et al., 2004; Bradshaw and Waller, 2016). However, since overstory trees persist for decades to centuries, future overstory species composition, not outright extinction, has been the primary immediate concern with trees. Somewhat less attention has been paid to effects of overbrowsing on forest understory herbaceous plants, probably because many have little direct economic value. In addition, due to the longevity of most understory herbs and the existence of perennating structures underground, the long-term effects of herbivory are difficult to observe over short time spans. Yet it would be valuable to identify populations in this stage of 'anemic desuetude' as a precursor to extinction in order to enable conservation action prior to critical endangerment.

Among understory species that have been studied with respect to deer herbivory, *Trillium*, a showy and palatable understory wildflower species, has provided an excellent model species (Anderson, 1994; Augustine and Frelich, 1998; Rooney and Gross, 2003; Jenkins et al., 2007; Knight et al., 2009; Kalisz et al., 2014). Anderson (1994) showed that mean height of *Trillium* plants was a strong indicator of deer browse intensity. Beauvais et al. (2017) even showed that reduced plant sizes in deer-browsed sites were reflected in the record of herbarium specimens. Rooney and Gross (2003) demonstrated population declines of 3.5% per year, even with relatively low browse rates. Jenkins et al. (2007) demonstrated the effect of herbivory in truncating the age-structure of natural populations in Great Smokey Mountain National Park, TN, U.S.A. Using matrix models for 12 Pennsylvania populations, Knight et al. (2009) demonstrated that a browse rate of only 15% was sufficient to threaten *Trillium*'s long-term persistence.

Several approaches have been employed to evaluate deer browse effects, each with its own advantages and disadvantages. Some studies have compared dynamics of different populations that naturally experience contrasting browse rates (e.g., Knight et al., 2009); this has the advantage of examining realistic rates in the current environment, but may not include populations at 'natural' pre-settlement rates, or browse rates that would be 'desirable' from a conservation standpoint. In addition, the reasons for the differences in browse rates (e.g., proximity to edge habitat) may be correlated with other factors (e.g., light) that also influence plant population dynamics. Others have modeled deer browse effects by removing or including browsed plants from the data set in the calculation of vital rates (e.g., Rooney and Gross, 2003; McGraw and Furedi, 2005); this allows for easy manipulation of browse rates and allows a nice dissection of affected model parameters, though it assumes browse effects on an individual are confined to a particular year. Others have taken an experimental approach, fencing areas to remove deer and observing the response over time (e.g., Augustine and Frelich, 1998; Heckel et al., 2010; Kalisz et al., 2014; Sabo et al., 2017; Wilbur et al., 2017). Exclusion experiments permit a rigorous, spatially controlled test of browse effects and result in an entire community response; therefore they are well-suited to examining rates of recovery following release from high browsing rates. However, unless such experiments are very long-term, allowing re-colonization by a full complement of understory plants, this approach primarily captures the initial recovery period, rather than a continuous condition of low browse rates. Finally, a few studies have used naturally-occurring refugia within populations exposed to browsing (Rooney, 1997; Carson et al., 2005); if the refugia have been in existence for a long time, then plant demography in the refugium presumably reflects performance, including the whole-community effects such as increased competition, that may counter some positive effects of no browsing. However, in extreme refugia, browse rates may be zero, which could be unrealistically low relative to a desirable, or generally achievable, rate.

In long-term demographic studies of the widespread medicinal plant, American ginseng, early work focused on human harvest, but deer browsing occurs at much higher rates than harvest (Furedi, 2004; McGraw and Furedi, 2005). Unlike *Trillium*, ginseng is not a 'preferred' food plant for deer, an idea supported by detailed analyses of interactions between deer

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