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Functional response of ungulate browsers in disturbed eastern hemlock forests

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ABSTRACT

Ungulate browsing in predator depleted North American landscapes is believed to be causing widespread tree recruitment failures. However, canopy disturbances and variations in ungulate densities are sources of heterogeneity that can buffer ecosystems against herbivory. Relatively little is known about the functional response (the rate of consumption in relation to food availability) of ungulates in eastern temperate forests, and therefore how "top down" control of vegetation may vary with disturbance type, intensity, and timing. This knowledge gap is relevant in the Northeastern United States today with the recent arrival of hemlock woolly adelgid (HWA; *Adelges tsugae*) that is killing eastern hemlocks (*Tsuga canadensis*) and initiating salvage logging as a management response. We used an existing experiment in central New England begun in 2005, which simulated severe adelgid infestation and intensive logging of intact hemlock forest, to examine the functional response of combined moose (*Alces americanus*) and white-tailed deer (*Odocoileus virginianus*) foraging in two different time periods after disturbance (3 and 7 years). We predicted that browsing impacts would be linear or accelerating (Type I or Type III response) in year 3 when regenerating stem densities were relatively low and decelerating (Type II response) in year 7 when stem densities increased. We sampled and compared woody regeneration and browsing among logged and simulated insect attack treatments and two intact controls (hemlock and hardwood forest) in 2008 and again in 2012. We then used AIC model selection to compare the three major functional response models (Types I, II, and III) of ungulate browsing in relation to forage density. We also examined relative use of the different stand types by comparing pellet group density and remote camera images. In 2008, total and proportional browse consumption increased with stem density, and peaked in logged plots, revealing a Type I response. In 2012, stem densities were greatest in girdled plots, but proportional browse consumption was highest at intermediate stem densities in logged plots, exhibiting a Type III (rather than a Type II) functional response. Our results revealed shifting top–down control by herbivores at different stages of stand recovery after disturbance and in different understory conditions resulting from logging vs. simulated adelgid attack. If forest managers wish to promote tree regeneration in hemlock stands that is more resistant to ungulate browsers, leaving HWA-infested stands unmanaged may be a better option than preemptively logging them.

1. Introduction

Trophic cascades (i.e., severe herbivore consumption) in predator depleted North American forests are hypothesized to be a dominant ecological force leading to tree recruitment failures by unregulated ungulates (Estes et al., 2011; Schmitz and Sinclair, 1997). On the other hand, system heterogeneity tends to buffer terrestrial ecosystems against severe trophic cascades (Strong, 1992), particularly at larger spatial scales (Mladenoff and Stearns, 1993; Stohlgren et al., 1999). Canopy disturbances (e.g., logging, insect outbreaks, windstorms, and fire) represent a key source of spatial and temporal heterogeneity in temperate forest ecosystems (Oliver and Larson, 1996), which in turn play a critical role in determining density and distribution of ungulates and their impacts on vegetation (Eschtruth and Battles, 2008; Geist, 1998; Kuijper et al., 2009). It follows that the extent to which regenerating vegetation is controlled from the top down (by consumers such

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as ungulates) should vary and depend on the timing and intensity of disturbance (McLaren and Peterson, 1994).

Despite the inherent complexities of large herbivore control of vegetation in forest ecosystems, limited attention has been paid to the functional response (the rate of consumption in relation to food availability) of ungulate browsers across different forest stand and disturbance conditions (Schmitz and Sinclair, 1997). Because the control of tree recruitment by herbivores is directly related to the functional response of the animals, a closer examination of the functional response is warranted. Predation theory identifies three major functional response models: Types I, II, and III (Sinclair et al., 2006). A Type I response involves a linear increase in consumption rate with increasing forage density. A Type II response involves decelerating consumption as forage densities increase and a consumption asymptote at high forage densities resulting from satiation and limitations of handling time (i.e., searching, pursuing, and consuming; Sinclair et al., 2006). A Type II response therefore shows inverse density dependence of forage to consumption with increasing forage densities (Sinclair et al., 2006). A Type III response occurs when browsers avoid forage at low densities, consume forage at a greater than linear rate at intermediate food densities, and reach a plateau of consumption akin to the Type II response at high forage densities (Sinclair et al., 2006). This model shows initial density dependence control by browsers followed by inverse density dependent browsing at higher forage densities (Sinclair and Krebs, 2002).

In northeastern temperate forests, an exotic forest insect, the hemlock woolly adelgid (*Adelges tsugae*; HWA), is causing significant mortality to eastern hemlock (*Tsuga canadensis*), resulting in stands of young deciduous trees regenerating beneath the dying hemlocks (Orwig and Foster, 1998; Orwig et al., 2012). White-tailed deer (*Odocoileus virginianus*) occurring at high densities (~15 km^{-2}) increased their proportional impact on tree regeneration in stands partially killed by HWA (Eschtruth and Battles, 2008). In some areas landowners have responded to HWA infestations by cutting their forests, either pre-emptively or as the trees die (Orwig et al., 2012). The extent to which this management action influences subsequent browsing impacts by ungulates, relative to stands left dead standing, is unknown. If preemptive salvage logging results in tree regeneration densities that differ from those in unmanaged insect-killed stands (cf. Payer and Harrison, 2000), and ungulate browsers preferentially forage in one disturbance type over another, then top down control of the vegetation by browsers could be affected by whether hemlock stands exposed to HWA are managed or not.

We took advantage of an existing hemlock canopy removal experiment in Central New England that simulated severe HWA attack and salvage logging in a controlled setting to address this knowledge gap. Specifically we examined the three major functional response models of ungulate browsing in two different time periods of regeneration (3 and 7 years) across a range of understory conditions associated with the two disturbances. Moose (0.2 km^{-2}) and white-tailed deer (4.2–5.7 km^{-2}) both occur at low densities in this sub-region (Adams et al., 2009; McDonald et al., 2007). Given that moose are reported to have greater browsing effects in areas of low stem densities (Brandner et al., 1990; Thompson and Curran, 1993), we predicted that top down control by browsers would be more important in the early stages of regeneration (year 3), when stem densities were relatively low across all treatments, than in later stages of regeneration (year 7) when stem densities increased. Hence, we predicted that ungulate browsers would exhibit either a linear or accelerating (Type I or Type III) foraging response in year 3 followed by a decelerating Type II foraging response in year 7. Type II foraging responses are common for ungulate browsers (cf. Gross et al., 1993; Sinclair et al., 2006).

2. Materials and methods

2.1. Study area

The study was conducted at the Harvard Forest in north-central Massachusetts, (42.478 to 42.488 N, 72.218 to 72.228 W, 215–300 m.a.s.l.) in the white pine (*Pinus strobus*)-hemlock-hardwoods forest region at the transition between maple-birch-beech (*Fagus grandifolia*) forests to the north and oak (*Quercus* spp.)-red maple (*Acer rubrum*)-white pine forests to the south (Thompson et al., 2013). Exotic forest insects and pathogens including HWA, beech bark disease (*Cryptococcus fagisuga* and *Nectria* spp.), chestnut blight (*Cryphonectria parasitica*), and gypsy moths (*Lymantria dispar*), timber harvesting, and meteorological events (ice and windstorms) are the prevalent disturbances in the region (Foster et al., 2004). Central Massachusetts is close to the southern range limit for moose in eastern North America; moose range as far south as the mixed coniferous and deciduous forests of the elevated plateaus of northern Connecticut (Wattles and DeStefano, 2011). In central Massachusetts, moose densities are estimated to be about 0.2 km^{-2} and white-tailed deer densities about 4–6 km^{-2} (McDonald et al., 2007; USGS Massachusetts Cooperative Research Unit, unpublished data).

2.2. Experimental design

The Harvard Forest Hemlock Removal Experiment (HF-HeRE) includes two canopy manipulations that simulate structural changes caused either by severe HWA infestation or by preemptive salvage logging (Ellison et al., 2010). Two types of control plots include either mature hemlock with $\geqslant$70% hemlock basal area or younger (~50 year old) mixed hardwood with small hemlocks (Ellison et al., 2010). One block of HF-HeRE occurs on sloping lowland and the other on a north–south trending ridge; one set of the two treatments and two control plots are sited within each block. Within each block, the treatment and control plots have similar topography and aspect, and occur on the same soil types (Ellison et al., 2010).

Each canopy manipulation replicate was applied in a 90 × 90 m (0.81 ha) forest plot with at least 70% basal area hemlock. In the simulated HWA treatment, all hemlock trees, from small seedlings to mature trees, were girdled using knives or chainsaws in early May 2005 (Ellison et al., 2010). The girdled trees died over the course of the next two and a half years, a rate similar to hemlock mortality from HWA attack in the southern Appalachians, but more rapid than mortality rates from HWA infestations in the Northeast (Orwig et al., 2013). Most of the girdled overstory hemlocks remained standing 8 years later, resulting in structural and environmental (temperature, moisture) changes similar to that from HWA invasion (Orwig and Foster, 1998; Lustenhouwer et al., 2012). In the logged treatment, all hemlocks >20 cm in diameter were cut in February–April 2005 and removed along with merchantable white pine and hardwoods such as red oak (*Quercus rubra*) in a fashion similar to hemlock harvests observed in the region (Ellison et al., 2010). Approximately 60–70% of the basal area was removed in each logging plot (Ellison et al., 2010).

Because the logged, girdled, and hemlock control treatments were separated by a relatively small buffer within each block, and were not originally established with an ungulate foraging study in mind, one of the potential drawbacks of incorporating a study of wide ranging large mammals into the design is non-independence among treatments (cf. Gotelli and Ellison, 2013). It is possible that ungulate activity in a particular treatment plot could reflect, in part, animals passing through that treatment plot on their way to accessing another treatment plot. Despite this