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.

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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

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 pre-emptive salvage logging (Ellison et al., 2010). Two types of control plots include either mature hemlock with ⩾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

potential pitfall of the design, we feel that genuine patterns of ungulate foraging and use would likely still emerge and reflect the characteristics of the individual treatments rather than their spatial arrangements. Indeed, other studies have successfully examined ungulate activity in different canopy treatment plots that were close in proximity (Kuijper et al., 2009).

2.3. Woody regeneration and herbivory

In June–July of 2008, we assessed understory woody vegetation and browsing intensity in a 30 × 30 m (900 m^2) plot in the center of each 90 × 90 m treatment and control plot. In each plot, regenerating woody stems ⩾0.3 m and <3 – the approximate height range of stems available to deer and moose (Faison et al., 2010) – were recorded and identified in 56 4-m^2 (224-m^2 total) circular subplots arrayed in a systematic grid. Each stem was assessed for signs of past browsing; twigs were considered browsed if they had a torn, ragged appearance characteristic of ungulates (McInnes et al., 1992). In 2012, the subplots were resampled for woody regeneration and browsing in each treatment. Porcupine (*Erethizon dorsatum*) and lagomorph browsing were readily distinguishable from ungulate browsing by the neat 45° angle cut of the stems, and stems browsed by these smaller herbivores were excluded from analysis.

2.4. Ungulate activity indices

We sampled pellet groups for deer and moose for supporting evidence to assess relative abundance among our experimental stand types; we did not use it to estimate actual moose and deer densities (cf. Van Dyke and Darragh, 2007). We sampled pellet groups in each of the 56 4-m^2 (224-m^2) vegetation and browsing subplots in 2008. Pellet groups were defined as having at least 15 individual pellets (Eschtruth and Battles, 2008). Despite this relatively large sampling area (cf. Kuijper et al., 2009), we still obtained enough zero values (75% of the plots) that we decided to double the pellet group sampling area to 450 m^2 in 2012. A 15 × 30-m area was divided into five 3 × 30-m subplots that were systematically searched with two observers walking side by side. Pellet groups in the subplots were pooled for each plot and expressed as number ha^{-1} to standardize values between 2008 and 2012. Although size and shape of pellet group plots have been shown in some cases to bias pellet density estimates (McKelvey et al., 2002), the different sampling approaches likely provided an unbiased relative intensity of use by treatment for each sampling period, which was the more critical information for the questions that we asked in this study.

In December 2011, we installed a remote camera (Reconyx, Inc., Holmen, Wisconsin) on the edge of each plot in which pellet counts were sampled. The cameras were programmed to take repeated pictures of herbivore movement, which enabled us to document the total time spent by animals in each field of vision. Images were compiled from December 2011 to April 2013, and we calculated the total time spent by moose and deer in each treatment per week (seconds week^{-1}; Kuijper et al., 2009). The late installment of the cameras precluded comparison of visitation rates among treatments between 2008 and 2012 and limited our ability to detect differences in habitat use by ungulates in 2008 to pellet group counts.

2.5. Data analysis

We compared the three major functional responses of large herbivores to their food supply (Types I, II, and III; Sinclair et al., 2006) using Akaike's Information Criterion (AIC) model selection. We estimated a functional response across all four treatment types (logged, girdled, hemlock, and hardwood) of the experiment to enable sufficient replication and variation in browse density. It was not possible to calculate functional responses within each treatment type because of limited sample sizes ($N = 2$ for each treatment). Because moose and deer browsing are generally indistinguishable and overlap considerably in height, we examined the combined functional response of the animals in the study area, rather than attempting to separate them (cf. Soluk, 1993). We used the number of woody stems (0.3–3 m in height) in each plot as an estimator of forage density, and the total number of individual woody stems (0.3–3 m in height) browsed in each treatment plot as an estimator of browse consumption rate. Other studies have used similar estimates of browse removal in functional response studies (White et al., 2003).

The Type I functional response is a simple linear regression in which number of stems browsed increases directly with the number of stems available:

$$Y = f(x) = a + bx$$

where Y is the number of stems browsed, x = woody stem density, and a and b are intercept and slope parameters, respectively.

For the Type II response, we used a Michaelis–Menton function (Bolker, 2008):

$$f(x) = ax/b + x$$

Here, the fitted parameters x = woody stem density and a and b refer respectively to the browsing asymptote and the stem density at which browsing intensity reaches half its maximum.

For the Type III response, we used the sigmoidal function (Bolker, 2008):

$$f(x) = ax^2/b^2 + X^\wedge 2$$

Here, the parameters x = woody stem density and a and b refer respectively to the asymptote and the half maximum point (Bolker, 2008).

For each model, we estimated the parameters and then calculated an AICc value (Burnham and Anderson, 2004). Models with Δi values <2 apart are generally deemed to be similar, whereas those with Δi values ⩾4 are considered distinct (Bolker, 2008). Functional response models were analyzed and compared using nls2 (non-linear regression with brute force) and AICtab (package AICmodavg) in R (The R Foundation for Statistical Computing 2014; R version 2.15.2).

3. Results

In 2008, stem densities (0.3–3 m in height) ranged from 89 to 15,700 ha^{-1} across the eight treatment plots (Table 1). Mean woody stem densities were highest in logged plots and exceeded those in hemlock controls by a factor of 24. In 2012 stem densities were highest in girdled plots, exceeding densities in logged plots by a factor of three, hardwood plots by a factor of eight, and hemlock plots by over two orders of magnitude. Densities in logged plots were also higher than densities in hemlock plots by almost two orders of magnitude (Table 1).

Table 1
Mean woody stem densities (0.3–3 m in height) by canopy treatment in 2008 and 2012. $N = 2$.

Treatment	2008		2012	
	Stem density	SD	Stem density	SD
Girdled	9218	5082	62,079	23,569
Logged	14,129	2304	19,165	884
Hemlock	580	694	208	295
Hardwood	10,758	1831	7500	737

Moose and deer pellet groups were only detected in logged and girdled plots in both 2008 and 2012 (Fig. 1). Moose accounted for 80% of pellet groups sampled in 2008 and 73% of pellet groups in 2012. In 2008, moose and deer pellet group densities were highest in the logged ridge plot, corresponding with the highest stem density. In 2012, pellet group densities remained highest in logged plots, corresponding with intermediate stem densities (Fig 1b). Total deer time recorded by remote cameras was relatively high in logged (16.7 s week^{-1}, SD = 0.6), hemlock (19.0 s week^{-1}, SD = 22.8), and hardwood (13.7 s week^{-1}, SD = 15.4) plots and low in girdled plots (0.4 s per week^{-1}, SD = 0.06). Total moose time recorded by remote cameras was highest in logged plots (8.3 s wk^{-1}, SD = 0.50) and was low in hemlock control (1.0 s week^{-1}; SD = 0.27), hardwood control (0.03 s week^{-1}, SD = 0.05), and girdled plots (0.22 s week^{-1}, SD = 0.28).

Number of stems browsed ha^{-1} increased in 2008 with increasing stem densities, reaching 10,400 stems browsed ha^{-1} in the most densely vegetated logged ridge plot (15,800 stems ha^{-1}; (Fig. 2a). The linear (Type I) functional response model was the best fit for the 2008 data (w_i = 0.996; Table 2). The Type III functional response model was the best fit for the 2012 data (w_i = 0.86), although the Type II model had limited support (Δ_i = 3.7, Table 2). Browsing was absent or low in hemlock and hardwood controls, rose sharply with increasing stem densities

Fig. 2. Functional response models of combined moose and deer foraging in 2008 and 2012. In 2008 (A), the Type 1 (linear model) was the best fit. In 2012 (B), the Type III (sigmoidal) model was the best fit when compared with other functional response models with AIC (see Table 2). Each point in the figures reflects a single treatment plot. Woody stems included upright trees and shrubs between 0.3 and 3 m in height.

Table 2
Comparison of functional response models of combined moose and white-tailed deer foraging (number of stems browsed) in relation to woody stem food supply. The lowest AICc value (in bold) corresponds with the best model. Δ_i = the difference in AICc from the best model. w_i = AIC weights – the probability that a model was the best fit, given the data.

Functional response model	2008				2012			
	AICc[a]	Δ_i	df	w_i	AICc	Δ_i	df	w_i
Type I[b]	**155.1**	**0**	3	1	164.1	9.0	3	0.01
Type II[c]	167.1	12.0	3	0	158.8	3.7	3	0.13
Type III[d]	169.6	14.5	3	0	**155.1**	**0**	**3**	**0.86**

[a] Adjusted Akaike's Information Criterion recommended for small sample sizes.
[b] $f(x) = a + bx$.
[c] $f(x) = ax/b + x$.
[d] $f(x) = ax^2/b^2 + x^\wedge 2$.

Fig. 1. Ungulate pellet group densities by canopy treatment in 2008 (A) and 2012 (B). Bars represent mean ± SE. N = 2.

in logged plots to a peak at ~10,000 stems browsed ha^{-1} in the logged ridge plot, and then reached an asymptote with increasing stem densities in girdled plots (Fig. 2b). Browsing intensity (the proportion of stems browsed) generally increased with increasing stem densities across all treatments in 2008. In 2012, browsing intensity increased from low to moderate stem densities and then declined at moderate to high stem densities (Fig. 3).
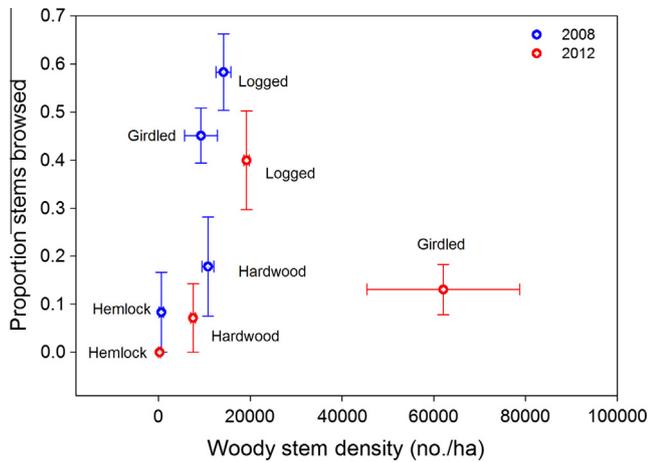
Fig. 3. Ungulate browsing intensity in 2008 and in 2012 presented as the proportion of stems browsed in relation to stem density. Woody stems included all upright trees and shrubs 0.3–3 m in height. Bars = mean ± SE. N = 2.

4. Discussion

Our results showed that eastern hemlock stands killed by simulated HWA attack diverged in woody plant regeneration over time from those that were logged or undisturbed, resulting in different relationships between large herbivores and their food supply at different stages of stand regeneration and across different stand structures. Consistent with our first prediction, the results showed greater top down control by ungulate browsers at lower stem densities in 2008 than at higher stem densities in 2012, with the 2008 data approximating a Type I (or the lower leg of a Type III) functional response. However, contrary to our second prediction, a Type II functional response did not emerge as the best model for ungulate browsing in 2012. Instead, consumption by ungulates increased between low density and intermediate food density sites before leveling off at high stem densities in 2012, consistent with a Type III functional response. Our results highlight the dynamic and context dependent nature of top down control by browsers, even at small spatial and temporal scales, in response to different disturbance regimes.

In this experiment, the hemlock canopy died gradually in the simulated HWA (girdled) plots relative to the logged plots. Lustenhouwer et al. (2012) and Orwig et al. (2013) revealed that this difference in timing of canopy death caused initially greater soil and air temperature and solar radiation levels in the logged plots and a lag in tree regeneration in the girdled plots. By 2008, three years post disturbance, woody stem densities (0.3–3 m in height) in the girdled plots had roughly equaled those in the hardwood control plots and were approaching densities in the logged plots (Table 1). Within the range of woody stem densities among treatments in 2008 (89–15,700 stems ha^{-1}), herbivores increased their consumption in sites with greater stem densities, revealing a Type I functional response (Fig. 2a). A Type I response likely emerged because of relatively low stem densities in the three year old disturbed stands that were still several years away from reaching peak browse production (cf. Renecker and Schwartz, 1997; Sinclair et al., 2006). Indeed, although the Type I functional model was by far the best fit, the increase in proportional browse consumption detected across all stem densities was more consistent with the lower leg of a Type III functional curve (Fig. 3; Sinclair et al., 2006). Density dependent browsing across all stem densities in 2008 was consistent with our prediction that top down control by ungulates would be strongest in 2008 when stem densities were relatively low (cf. Brandner et al., 1990; Thompson and Curran,

1993). Top down control weakened four years later when stem densities increased with forest succession.

By 2012, woody stem densities in the girdled plots increased substantially, far surpassing densities recorded in the logged plots and control treatments (Table 1), despite a convergence of soil moisture, available light, and soil and air temperature in the logged and girdled treatments (Lustenhouwer et al., 2012). Given the similar topography, soils, and environmental measurements between the two treatments, the discrepancy in tree regeneration may have resulted from greater soil disturbance and compaction from logging machines and a greater volume of coarse woody debris (CWD) that resulted in a physical barrier to regeneration in the logged plots (Bottero et al., 2013; Donato et al., 2006; Orwig et al., 2013). Within this broad range of stem densities that diverged sharply among canopy treatments in 2012, moose and deer foraging exhibited a sigmoidal (Type III) functional response in which foraging was density dependent from low to moderate stem densities and inverse density dependent at moderate to high stem densities (Fig. 3).

What accounts for the apparent Type III response in our study area when ungulates typically display a Type II response (Gross et al., 1993; Sinclair et al., 2006; White et al., 2003)? Our study area may have been unusual in that it included a relatively broad range of stem densities in the two types of control plots that were still below the threshold stem density at which the herbivores, particularly moose, found profitable to forage. Deer appeared to use the control plots relatively frequently (as detected by remote cameras), but apparently for other purposes besides browsing (e.g., perhaps thermal shelter, escape cover, and acorn foraging; Barrett and Schmitz, 2013; DeGraaf and Yamasaki, 2001), given the low browsing pressure in these plots. Hence there was a slow initial increase in browse consumption with increasing stem densities from the hemlock to the hardwood controls, consistent with the lower leg of a sigmoidal Type III curve (Sinclair et al., 2006). Moose activity (as determined by remote camera images and pellet groups) and proportional browse consumption then increased sharply at intermediate stem densities in the logged plots before declining in the highest stem density girdled plots. Regeneration was able to escape the "predator pit" (i.e., the sharply density dependent browsing between low and moderate forage densities of the control and logged plots) of a Type III response, presumably because the very high densities of regeneration in the girdled areas overwhelmed the relatively low density and browsing capacity of the herbivores (cf. McLaren and Peterson, 1994). Healy (1997) and Eschtruth and Battles (2008) reported increasing top down effects by white-tailed deer with disturbance in thinned and HWA-infested stands respectively, akin to the relationship we observed in the control and logged plots in our study area. Greater densities of ungulates (13–15 deer km^{-2} on average) combined with less intensively disturbed stands, which supported lower stem densities (Healy, 1997), may explain the difference between these authors' results and ours.

A contributing factor to the browsing asymptote and the Type III functional response in 2012 was that moose appeared to preferentially use the logged stands with intermediate stem densities. One possible explanation for this preference of the logged areas is that above a threshold forage density, other food related (e.g., stem palatability, energy intake) or non-food related (e.g., thermal environment, cover, and topography) factors became more important to ungulates than additional increases in stem density (cf. Hester et al., 2006; Thompson et al., 1989; Wilmshurst et al., 1995). With respect to food related factors, basal sprouting by hardwoods often leads to greater stem palatability, and sprouts on stumps and trees occurred more frequently in the logged plots than in the girdled and undisturbed plots (Ellison and Barker Plotkin, 2009; Moore and Johnson, 1967). Sprouts are often thicker in diameter, grow more vigorously, and have more extensive

branching than seed-origin stems (Bond and Midgley, 2001; Kauppi et al., 1990); these stem characteristics are particularly desirable to moose and other ungulates (Kuijper et al., 2009; Price, 1991; Rea and Gillingham, 2001). In addition, red maple, a preferred browse species of moose and white-tailed deer (Godin, 1977; Faison et al., 2010), was the most prolific sprouter in the logged plots (Ellison and Barker Plotkin, 2009).

4.1. Conclusions and management implications

Our results provide evidence that different relationships between large herbivores and their food supply (i.e., both density dependent and inverse density dependent) may develop over small spatial and temporal scales across forest stands of different disturbance histories, structures, and understory characteristics. Thus it is important for forest managers to be circumspect about applying broad and static generalizations about trophic cascades and tree recruitment failures to forestlands under their direction. Our study also suggests that preemptively salvage logging insect killed stands may result in significant reductions in tree regeneration densities 5–10 years post disturbance, relative to stands left unmanaged after severe insect infestations (cf. Belle-Isle and Kneeshaw, 2007; Payer and Harrison, 2000). Lower densities of tree regeneration combined with palatable stump sprouts in logged areas may lead to relatively high browsing intensities and top down control by ungulates. In contrast, greater tree regeneration and less palatable stems beneath stands completely killed by HWA may buffer the effects of browsing, particularly in areas with low ungulate densities.

If forest managers wish to promote tree regeneration that is more resistant to browsers, leaving hemlock stands infested with HWA uncut may be a better option than preemptively logging them. A non-management approach to mitigate subsequent browsing impacts would undoubtedly be more important in landscapes with greater ungulate densities. If, on the other hand, managers wish to reduce the density of regenerating stems, perhaps to avoid a pre-commercial thinning, than preemptive logging followed by increased ungulate activity and browsing intensity may be a desirable outcome (cf. Thompson and Curran, 1993).

Acknowledgments

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