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DEER HERBIVORY ALTERS FOREST RESPONSE TO CANOPY DECLINE CAUSED BY AN EXOTIC INSECT PEST

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Abstract. Hemlock woolly adelgid (HWA; *Adelges tsugae*) infestations have resulted in the continuing decline of eastern hemlock (*Tsuga canadensis*) throughout much of the eastern United States. While the initial impacts of HWA infestations have been documented, our understanding of forest response to this disturbance remains incomplete. HWA infestation is not occurring in isolation but within a complex ecological context. The role of potentially important interacting factors, such as elevated levels of white-tailed deer herbivory, is poorly understood. Despite the potential for herbivory to alter forest successional trajectories following a canopy disturbance, little is known about herbivory–disturbance interactions, and herbivory is rarely considered in assessing forest response to a co-occurring disturbance.

We used repeated censuses of deer exclosures and paired controls (400 paired plots) to quantify the impact of deer herbivory on tree seedling species abundance in 10 eastern hemlock ravines that span a gradient in HWA-induced canopy decline severity. Use of a maximum likelihood estimation framework and information theoretics allowed us to quantify the strength of evidence for alternative models developed to estimate the impacts of herbivory on tree seedling abundance as a function of varying herbivore density and canopy decline severity.

The exclusion of deer herbivory had marked impacts on the abundance of the studied seedling species: *Acer rubrum*, *Acer saccharum, Betula lenta*, *Nyssa sylvatica*, *Quercus montana*, and *Tsuga canadensis*. For all six species, the relationship between seedling abundance and deer density was either exponential or saturating. Although the functional form of the response varied among seedling species, the inclusion of both deer density and canopy decline severity measures consistently resulted in models with substantially greater support. Canopy decline resulted in higher proportional herbivory impacts and altered the ranking of herbivory impacts by seedling species. Our results suggest that, by changing species' competitive abilities, white-tailed deer herbivory alters the trajectory of forest response to this exotic insect pest and has the potential to shift future overstory composition.

Key words: canopy disturbance; forest dynamics; hemlock woolly adelgid; herbivory; maximum likelihood estimation; Odocoileus virginianus; Tsuga canadensis.

INTRODUCTION

Deer herbivory is recognized as an important regulator of forest ecosystem dynamics. Substantial evidence has shown impacts of browsing on the growth rate of seedlings and saplings (Tilghman 1989, Alverson and Waller 1997, Rooney et al. 2000, Tsujino and Yumoto 2004), plant reproductive fitness (Augustine and Frelich 1998, Ruhren and Handel 2003), forest structure (Anderson and Loucks 1979, Frelich and Lorimer 1985), successional patterns (Stromayer and Warren 1997), ecosystem processes (Huntly 1991, Hobbs 1996), and forest species composition (Anderson and Loucks 1979, Horsley et al. 2003, Potvin et al. 2003). These findings are particularly relevant given that deer populations have become uncoupled from their natural regulating factors, such as density-dependent predation and competition for resources, and have reached unprecedented levels in many ecosystems (Caughley 1981, Underwood and Porter 1997, Côté et al. 2004). The resulting intensive herbivory can function as a chronic disturbance in these systems with profound implications for forest integrity.

Chronic disturbances, such as elevated levels of deer herbivory, act on ecosystems for prolonged time periods and are therefore likely to occur simultaneously with other disturbance events (Frelich 2002). Disturbances such as pest and pathogen outbreaks, fire, timber harvesting, and drought typically occur at relatively more discrete intervals and interact with herbivory across multiple temporal and spatial scales (Wisdom et al. 2006). Several studies have shown herbivory impacts to be more intense following severe disturbances (i.e., those that result in high plant mortality) due to herbivore preference for early successional species and higher nitrogen availability (Cates and Orians 1975,

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Tripler et al. 2002, Spiller and Agrawal 2003). In addition, it is in the early recovery period following a canopy disturbance that herbivory may have the greatest potential to alter forest successional trajectories via selective browsing of tree seedlings (Hobbs 1996, Horsley et al. 2003, Tremblay et al. 2006). Despite these implications, little is known about herbivory–disturbance interactions and herbivory is rarely considered in assessing forest response to a co-occurring disturbance, even though improved understanding of these interactions is crucial to effective resource management (Wisdom et al. 2006).

In this study, we quantified the impact of white-tailed deer (*Odocoileus virginianus* Boddaert) herbivory on tree seedling abundance (measured as cover and height) in eastern hemlock (*Tsuga canadensis* (L.) Carr.) forests infested by an introduced insect pest, the hemlock woolly adelgid (HWA, *Adelges tsugae* Annand). Initial evidence indicates that HWA is causing meaningful changes in patterns of species abundance, stand structure, and ecosystem function (Orwig and Foster 1998, Jenkins et al. 1999, Eschtruth et al. 2006). However, hemlock decline is occurring at a time when many hemlock forests face a suite of novel stressors including elevated white-tailed deer populations, nitrogen deposition, and an abundant supply of exotic invasive plants (e.g., Liebhold et al. 1995, Alverson and Waller 1997, Vitousek et al. 1997). These compounded disturbances may have synergistic impacts and have the potential to fundamentally alter ecosystems (Castello et al. 1995, Hobbs 1996, Paine et al. 1998, Hall et al. 2002). Without accounting for these interactions, attempts to attribute changes in forest structure and function to a single disturbance may be unreliable and may result in poor management decisions (Liebhold et al. 1995, Paine et al. 1998, Foster 2000, Wisdom et al. 2006). Our understanding of forest response to HWA infestation remains incomplete without accounting for the role of elevated deer populations in influencing community and ecosystem response to hemlock mortality.

To test for disturbance interactions, we made use of natural variation in local deer densities to investigate and parameterize the relationships between deer density and impacts on tree seedlings along a disturbance severity gradient. We evaluated the role of deer density on seedling abundance across a gradient in hemlock canopy decline severity. Deer herbivory impacts on forest ecosystems depend primarily on the functional relationships between seedling abundance, the consumption rate as a function of seedling abundance, and deer density (Schmitz and Sinclair 1997). Despite the importance of these relationships and the obvious potential for management applications, there have been few attempts to determine the functional form of the relationship between deer density and herbivory impacts (Schmitz and Sinclair 1997, Hester et al. 2000, Côté et al. 2004). Most studies have examined the impact of herbivory with and without herbivores without quantifying the role of herbivore densities (e.g., Anderson and Loucks 1979, McInnes et al. 1992, Wardle et al. 2001). Consequently, deer impacts are typically estimated by assuming a directly proportional relationship to deer densities (Westoby et al. 1989, Russell et al. 2001). However, recent results suggest the potential for nonlinear functional responses (Augustine et al. 1998, Persson et al. 2005, Tremblay et al. 2006), which could significantly management targets for herbivore population levels (Hester et al. 2000).

We used maximum likelihood methods to choose among a set of competing mathematical models that predict the influence of deer density and canopy decline severity on the abundance of each seedling species. We determined the appropriate functional form and the relative importance of variables, then assessed model predictions and evaluated potential ecological mechanisms and consequences.

METHODS

Study sites

This research was conducted in the Delaware Water Gap National Recreation Area (DEWA), a 27 800-ha park located in northeastern Pennsylvania and western New Jersey, USA, along the Delaware River. We selected 10 eastern hemlock dominated forests that spanned a gradient in canopy decline severity caused by HWA: five in the Appalachian Plateaus physiographic province in Pike County, Pennsylvania and five in the Valley and Ridge physiographic province in Sussex and Warren Counties, New Jersey. All selected hemlock stands were located in stream ravines drained by either first- or second-order streams that flowed into the Delaware River. At the beginning of the study, hemlock accounted for greater than 50% of canopy basal area at each study site with other canopy constituents including *Acer saccharum* Marshall (sugar maple), *Quercus montana* Willd. (chestnut oak), *Acer rubrum* L. (red maple), *Betula lenta* L. (black birch), *Betula alleghaniensis* Britton (yellow birch), *Quercus alba* L. (white oak), and *Pinus strobus* L. (eastern white pine). The regional landscape is dominated by hardwood and hemlock forests but contains a mosaic of agricultural crops, pastures, and old fields (Myers and Irish 1981). The regional climate is humid continental with an annual mean monthly temperature of 9.7°C and mean summer (June, July, August) temperature of 20.8°C. Mean annual precipitation is 115.5 cm (NOAA 2002; Station 110). Elevation at these sites ranges from approximately 90 m to 420 m.

Many eastern hemlock forests are currently threatened by an introduced insect, the hemlock woolly adelgid (McClure 1991, Orwig and Foster 1998, Eschtruth et al. 2006). The adelgid feeds on hemlock ray parenchyma cells, causing needle loss and bud mortality (Young et al. 1995) and can result in complete mortality of infested stands (McClure 1991). HWA was

TABLE 1. Summary of site characteristics for 10 hemlock ravines in the Delaware Water Gap National Recreation Area (New Jersey and Pennsylvania, USA).

Site	Canopy basal area in 2003 (m^2/ha)	Hemlock relative basal area in 2003 (%)	Deer density (no./km^2)†	Slope (%)	Total transmitted radiation in 2003 (%)	Absolute change in total transmitted radiation, 2003 to 2006 (%)	Trees in severe decline or dead in 2003 (%)
Adams Creek	55.2 (20.5)	53.5	17 (6)	20 (15)	13.4 (6.0)	5.7	34
Buttermilk Falls	42.7 (20.9)	51.6	18 (11)	32 (21)	14.3 (4.2)	11.3	82
Conoshaugh	53.4 (36.4)	78.3	5 (2)	39 (23)	10.8 (5.2)	2.5	12
Donkeys Corner	53.1 (29.7)	61.1	15 (7)	14 (12)	9.7 (4.6)	7.2	52
Dry Brook	37.8 (21.4)	56.3	23 (13)	23 (19)	11.4 (4.5)	8.6	67
Fulmer Brook	46.6 (21.0)	65.9	22 (10)	19 (13)	6.7 (3.1)	4.4	17
Spackmans	45.6 (20.6)	82.0	8 (3)	24 (16)	8.1 (2.7)	2.2	6
Tumbling Water	59.1 (30.8)	83.9	13 (5)	16 (11)	5.9 (3.3)	1.8	1
Van Campens Brook	48.8 (24.0)	57.4	16 (10)	10 (8)	7.9 (3.9)	3.4	9
Warner Brook	32.6 (16.3)	73.2	11 (6)	41 (15)	15.7 (4.0)	12.5	71

Notes: Values reported are means (with SD in parentheses). Basal area, total transmitted radiation, and vigor values are based on measures recorded at permanent vegetation plots and at exclosure plots ($n = 58$ measurements). For slope, $n = 40$ per site, and for deer density, $n = 20$ per site.

† Average of summer and winter estimates from 2004, 2005, and 2006.

first reported in DEWA in 1989. However, the spread has been uneven presumably because the hemlock forests in the park occur in spatially disjunct, topographically isolated ravines. As a result, some hemlock ravines have severely deteriorated while others remain healthy (Evans 2004, Eschtruth et al. 2006). This differential rate of HWA impact provided a marked gradient of canopy decline across our 10 study sites (Table 1).

Deer densities are high in this region. Estimates from deer management zones range from 11 to 14 deer/km^2 (Pennsylvania Department of Conservation and Natural Resources 2003; Carole Kandoth, *personal communication*). These management zones contain areas outside DEWA boundaries and no park-specific deer density estimates are available. However, in the past, the New Jersey section of the Park was managed for 15.4 to 19.3 deer/km^2 (Larry Hilaire, *personal communication*). In this study, browse damage was assumed to be the result of white-tailed deer herbivory, as they are the primary woody seedling herbivores in hemlock forests in this region (Appendix A).

Hemlock decline gradient

Landsat Thematic Mapper satellite imagery was used to select sites along a gradient of hemlock canopy decline by calculating an index of hemlock stand condition as the difference between the percent of trees classified as healthy or in moderate decline and the percent of trees classified as dead or in severe decline (see Royle and Lathrop 2002, Evans 2004). The ranking of the 10 hemlock sites along the canopy decline gradient was confirmed in 2003 via field assessments of hemlock vigor to provide a more localized and timely (satellite imagery taken in 1998) estimate of current hemlock health (Table 1).

Permanent vegetation plots were established in 2003 (except at two sites, AC and VC, where plots were established in 1994 and resurveyed in 2003, see Eschtruth et al. [2006]) to monitor hemlock decline and the response of understory vegetation. At each site, random points were selected along the stream (>50 m apart) and six transects were established perpendicular to the stream with plots near the stream, at mid-slope, and at the edge of the hemlock dominated forest (18 plots per site). The location of all plots was recorded with a geographic positioning device and corners were marked with rebar to ensure precise relocation.

In 2003 and 2006, canopy tree species composition and density were quantified using the point quarter method (Engeman et al. 1994). To further quantify canopy composition and density, all trees within a 5 m radius of each permanent point were monitored. Species, crown class, dbh (diameter at breast height, 1.37 m), crown ratio, and vigor were recorded for each point quarter tree and all trees in the 5 m radius plot with a dbh ≥2 cm (nomenclature follows Rhoads and Block [2000]). In 2003 and 2006, each tree was assigned to one of the following vigor classes based on the amount of foliage retained: healthy (4, 76–100%), slight decline (3, 51–75%), moderate decline (2, 26–50%), severe decline (1, 1–25%), or dead (0; see Appendix B).

Understory light availability at each plot was characterized in 2003 and 2006 through use of hemispherical photographs. All photos were taken under diffuse light conditions using scientific grade photographic lenses (Nikkor 8 mm; Nikon Corporation, Tokyo, Japan). Distortions in the area projections (Herbert 1987) were corrected prior to analysis. We used the Gap Light Analyzer software to compute the fraction of total transmitted radiation reaching each photo point during the growing season (Canham 1988, Frazer et al. 1999). The above-canopy radiation model was based on long-term results from the nearest National Weather Service station (Scranton, Pennsylvania; Knapp et al. 1980). Precision error associated with photographic analyses was less than 5% relative root mean squared error (rRMSE).

Deer density

Deer density was estimated from fecal pellet group counts using the fecal accumulation rate (FAR) method (i.e., clearance plot [Neff 1968, Bailey and Putman 1981, Campbell et al. 2004]). Twenty circular pellet group plots (10 m radius) were established in each of the 10 study sites based on a stratified random design (200 total plots). These were placed at random distances (>15 m) and bearings from each of the 18 permanent vegetation plots such that pellet plots were separated by a minimum of 95 m. An additional pellet plot was placed for two randomly selected mid-slope plots at each site. Plot locations were recorded with a geographic positioning device and marked with metal stakes to ensure exact relocation.

Pellet groups containing 15 or more pellets were counted within each plot and cleared during each census (see Appendix A for standardization and error details). The 15 pellets per group minimum was chosen based on personal observations to avoid bias due to scattered pellet groups (Neff 1968). Deer density estimates were calculated as

$$D = \frac{p}{R \times \Delta t} \times A \tag{1}$$

where D is the deer density (deer/km^2), p is the number of pellet groups observed per plot census, Δt is the interval between each census or the fecal accumulation period (days), R is the defecation rate (assumed to be 12.7 pellet groups$\cdot$deer$^{-1}\cdot$d^{-1} for winter estimates [Eberhardt and Van Etten 1956] and 30.7 pellet groups$\cdot$deer$^{-1}\cdot$d^{-1} for summer estimates, average of summer estimates from Rogers [1987]), and A is the fixed multiplier to convert the plot area into square kilometers. Note that these measures of plot level deer abundance are reported as densities for ease of interpretation. A more typical measure of deer density would be an average of all plot values for a given site (as reported in Table 1). Therefore, our localized density estimates should be interpreted as a relative index of deer density or intensity of use at each plot and not as a measure of absolute regional deer abundance.

We conducted a total of five censuses: two winter use estimates and three summer use estimates. For winter estimates, we cleared pellet groups from all plots in September 2004 and 2005 and then counted and cleared pellet groups the following springs (8–19 April 2005 and 14–25 April 2006) for a winter accumulation period of 200 days. Summer deer use estimates were based on an accumulation period of $\sim$75 days. Plots were cleared during the first week of June and resurveyed in mid-August of 2004, 2005, and 2006 (see Appendix A, method rationale).

Deer exclosures

In 2003, 40 deer exclosures (1 m^2 at base and approximately 1.2 m high) were placed in a stratified random manner in each of the 10 hemlock ravine study sites (400 total exclosures). An uncaged control plot of the same size was randomly located between one and four meters of its' paired exclosure and marked with metal stakes. Exclosures were placed at random distances (10–30 m) and bearings from the established pellet plots: all pellet plots were used to position two exclosures. Plots were repositioned only if the exclosure or control contained no vegetation. The exclosures in each ravine were dispersed across a minimum area of approximately 10 ha. Plots were monitored annually (2003–2006) from mid-June to July.

The percent cover of each seedling species was measured annually in each exclosure and its paired control for a total of four years. Because loss of the terminal meristem via browsing can increase lateral branching at the expense of further terminal growth, total height (i.e., heights of tallest live branch of each seedling, summed by species) was also monitored. To assess error in percent cover and height measurements, 10% of exclosures at each site were resurveyed during each annual census (percent cover rRMSE = 2.7%, height rRMSE = 1.6%). In addition, for each exclosure and control plot pair, we measured the percent slope along the steepest grade and recorded the species, dbh (≥ 2 cm), and vigor of all trees ≥ 1 m tall within a 5 m radius.

Hemlock canopy decline

We used understory light levels to measure the timing and magnitude of the hemlock canopy decline at our study sites. While change in light is just one of several ecological consequences of HWA infestations, understory light availability is correlated with direct assessments of hemlock decline and HWA infestation severity (Eschtruth et al. 2006; Appendix B). Moreover, these light measurements could be taken at the same fine scale as our experimental exclosures. Thus the metrics used to assess both deer density and HWA induced changes were appropriately scaled to the vegetation response.

Understory light availability at each control plot was characterized in 2003 and 2006 through use of hemispherical photographs (as described in *Methods: Hemlock decline gradient*). We verified that these control plot estimates accurately reflected light availability for the paired exclosure plots by comparing instantaneous measures of photosynthetic photon flux density (PPFD) taken under isotropic sky conditions (Messier and Puttonen 1995; Appendix A).

Model development

We used likelihood-based methods (Buckland et al. 1997, Burnham and Anderson 2002) to quantify the strength of evidence for alternative models of the influence of deer density and canopy decline severity on tree seedling abundance. Each model (Table 2) represents a different hypothesis about the shape of the herbivory impact response curve as a function of deer density (D) and hemlock canopy decline (HCD).

TABLE 2. Summary of models.

Form	Name	Model
Linear		
Base	$\mathrm{Lin_B}$	$I = I_0 + b_D D$
Additive	$\mathrm{Lin_A.HCD_*}$	$I = I_0 + b_D D + \mathrm{HCD}_*$
Interacting	$\mathrm{Lin_I.HCD_*}$	$I = I_0 + b_D D \times \mathrm{HCD}_*$
Exponential		
Base	$\mathrm{Exp_B}$	$I = I_0 + m_1 e^{b_D D}$
Additive	$\mathrm{Exp_A.HCD_*}$	$I = I_0 + m_1 e^{b_D D} + m_2 e^{\mathrm{HCD}_*}$
Interacting	$\mathrm{Exp_I.HCD_*}$	$I = I_0 + m_1 e^{b_D D + \mathrm{HCD}_*}$
Saturating		
Base	$\mathrm{Sat_B}$	$I = a \times (1 - e^{b_D D})^c$
Additive	$\mathrm{Sat_A.HCD_*}$	$I = a \times \left[\frac{2 - (e^{b_D D} + e^{\mathrm{HCD}_*})}{2}\right]^c$
Interacting	$\mathrm{Sat_I.HCD_*}$	$I = a \times (1 - e^{b_D D + \mathrm{HCD}_*})^c$
Logistic		
Base	$\mathrm{Log_B}$	$I = \frac{e^{I_0 + b_D D}}{1 + e^{I_0 + b_D D}}$
Additive	$\mathrm{Log_A.HCD_*}$	$I = \frac{e^{I_0 + b_D D}}{1 + e^{I_0 + b_D D}} + \frac{e^{\mathrm{HCD}_*}}{1 + e^{\mathrm{HCD}_*}}$
Interacting	$\mathrm{Log_I.HCD_*}$	$I = \frac{e^{I_0 + b_D D + \mathrm{HCD}_*}}{1 + e^{I_0 + b_D D + \mathrm{HCD}_*}}$

Notes: For all models, I is the impact measure, D is the deer density estimate, and HCD_* is the index of hemlock canopy decline. The subscript asterisk in HCD_* refers to the number of the HCD index (see *Methods* for definitions). The parameters being estimated are represented by a, b, c, and m.

Hemlock canopy decline is quantified as an index based on the change in percentage total transmitted radiation from 2003 to 2006 (ΔL) and scaled by the initial percentage total transmitted radiation in 2003 (TL_0). To examine the role of initial light availability (2003) in potentially altering the herbivory impact due to a given level of canopy decline, we compared alternate models for each functional form in which HCD_* in the equations in Table 2 was replaced by one of the following functions:

$$\mathrm{HCD}_0 = b_{\Delta L}\Delta L \tag{2a}$$

$$\mathrm{HCD}_1 = b_{\Delta L}\Delta L + b_{\mathrm{TL}_0}\mathrm{TL}_0 \tag{2b}$$

$$\mathrm{HCD}_2 = b_{\Delta L}\Delta L \times \frac{b_{\mathrm{TL}_0}}{\mathrm{TL}_0} \tag{2c}$$

$$\mathrm{HCD}_3 = b_{\Delta L}\Delta L \times \mathrm{TL}_0^c. \tag{2d}$$

Models were fit to observations of herbivory impact (I), which was calculated as the difference between the change in seedling abundance (percent cover and total height) in the deer exclosure and the change in seedling abundance in its paired control plot from 2003 to 2006. We considered candidate models in four general functional forms (Table 2): linear models (herbivory impacts directly proportional to deer density), exponential models (impact per deer increases with deer density), saturating models (herbivory impact reaches a plateau at a certain deer density level), and logistic models (little effect up to a threshold level of deer density after which relatively small increases in deer density result in large increases in herbivory impact until a plateau is reached at some threshold level). The logistic model was modified to scale the data between 0 and 1. For each functional form, we compared models in which deer density and canopy decline had an additive effect on herbivory impact and models in which these parameters interacted (i.e., multiplicative effect, Table 2).

Six seedling species were sufficiently abundant for analysis: *Acer rubrum* ($n = 297$ trees), *Acer saccharum* ($n = 312$ trees), *Betula lenta* ($n = 354$ trees), *Nyssa sylvatica* Marshall ($n = 229$ trees, black gum), *Quercus montana* ($n = 270$ trees), and *Tsuga canadensis* ($n = 251$ trees). In our study sites, these six species comprised 78% of the total seedling density in 2003 (relative densities: 13% *Acer rubrum*, 19% *Acer saccharum*, 26% *Betula lenta,* 4% *Nyssa sylvatica,* 7% *Quercus montana*, and 9% *Tsuga canadensis*). These species differ in several life history traits, including shade tolerance and susceptibility to deer herbivory (Burns and Honkala 1990, Niinemets and Valladares 2006). We calculated the best model for each species individually. In addition, to compare herbivory impacts as a function of deer density and canopy decline at different severity levels, we performed separate model selection procedures for the five sites with the highest vigor and crown rating data measures (healthy stands) and the five sites with the lowest vigor and crown rating data measures (declining stands, Table 1).

Model selection

We solved for the maximum likelihood parameter estimates by entering the results from a global optimization procedure, simulated annealing, into a local optimization procedure, Nelder-Mead. We validated the assumption of normally distributed errors by examining model residuals. Statistical analyses and optimizations were conducted in S-Plus (Version 6.1, Insightful Corporation, Seattle, Washington, USA).

We compared alternate models using corrected Akaike's Information Criteria (AIC_c; Appendix A [Burnham and Anderson 2002]). AIC difference values (ΔAIC) provided a measure of the relative difference in the strength of evidence for each model. Akaike weights (w_i), which normalize the strength of evidence for a given model (AIC_i) relative to the best model (AIC_{min}), were interpreted as the weight of evidence that model i is the best Kullback-Leibler model for the data given the candidate set of R models (Burnham and Anderson 2002). In addition, we calculated evidence ratios to compare models including hemlock canopy decline indices to models of the same functional form without these indices. Specifically, we compared base models that included only deer density (D); ΔL models that included D and change in hemlock canopy decline from 2003 to 2006 (ΔL); and complete models that included D, ΔL, and initial light availability in 2003 (TL_0). For each species, the ΔL models include deer density and HCD_0 whereas the complete models include deer density and either HCD_1, HCD_2, or HCD_3. Evidence ratios were calculated as the ratio between Akaike weights and were used to assess the strength of evidence for a given model relative to a competing model. We considered evidence ratios greater than 10 as strong support for model improvement. Although the interpretation of evidence ratios is subjective, they provide an intuitive assessment of the strength of support for one model relative to another (Burnham and Anderson 2002).

We also calculated three metrics to evaluate model fits: overall goodness of fit was evaluated with R^2, prediction bias was assessed by fitting a linear regression (without intercept) to the observed vs. predicted data (a slope $\approx$1.0 indicates an unbiased model), and root mean squared error (RMSE) provided a measure of prediction error.

RESULTS

Summary of sites

The mean percent cover and height measured in 2003 varied greatly by species (Figs. 1 and 2). However, there were no significant differences between the 2003 percent cover and height measures in the exclosure plots and those in the control plots (OLS [ordinary least squares] bisector estimates and 95% confidence intervals, slope = 1.10 ± 0.23, intercept = 0.03 ± 0.16; see Isobe et al. [1990]). From 2003 to 2006, all seedling species declined in both percent cover and total height in the control plots relative to exclosures (Figs. 1 and 2). Although the relative difference varied by species, these impacts were consistently greater in plots with higher than average deer densities ($>$15.1 deer/km^2; t test, all $P < 0.01$; Figs. 1 and 2).

Hemlock canopy decline severity and deer density varied considerably within and among sites. The site-wide increase in percent total transmitted radiation ranged from 1.8% to 12.5% and the fraction of severely declining or dead trees varied between 1% and 82% (Table 1). The plot level index of deer density ranged from 0 to 38.9 deer/km^2 in summer surveys and 0.7 to 42.8 deer/km^2 in winter surveys. Site-wide deer density indices varied from 5 to 23 deer/km^2 and the overall mean plot level deer density index for all sites combined was 15.1 deer/km^2 (Table 1).

Evaluation of alternate functional forms

All models produced unbiased estimates of herbivory impact (regression slopes of $\approx$ 1.0 for predicted vs. observed) and symmetrically distributed residuals. The fraction of variation in herbivory impact explained by the best models for cover impact ranged from 0.52 for *Q. montana* to 0.85 for *T. canadensis* and for height impact ranged from 0.28 for *Q. montana* to 0.69 for *A. saccharum* (Table 3). Root mean squared errors were between 2% and 8% for the highest ranked models ($\Delta AIC_c < 4.0$).

The functional form of the selected best model varied among the six study species; however, the complete model form (including D, ΔL, and TL_0) was preferred for each species. Although the inclusion of both change in light availability (ΔL) and 2003 light availability (TL_0) consistently resulted in models with substantially greater support, there was no clear support for the HCD_1, HCD_2, or HCD_3 form (Tables 3 and 4). In fact, in most cases, the weight of evidence did not strongly support one of these HCD_* forms within species and the two or three models based on these forms were included in the selected model set ($\Delta AIC_c < 4.0$, Table 3). Therefore, to provide a weight of evidence for the selected functional form, the Akaike weights of the selected models in the same functional form as the top ranked model (i.e., models that differ only by HCD_*) were summed. This value is referred to as the total weight (Table 3).

For all six study species, the preferred model functional form was either exponential or saturating (Table 3). The exponential model was the most commonly selected for both percent cover and total height impacts. For all seedling species, except the *A. saccharum* height impact model, only one functional form was included in the selected model set. *Acer saccharum* height impact was also the only model to include both additive and interacting models in the selected model set. For all other species–impact type combinations there was clear support for either the interacting or additive form of the selected model (Table 3). *Nyssa sylvatica* was the only species for which the choice of functional form varied between percent cover impact and total height impact models (Table 3).

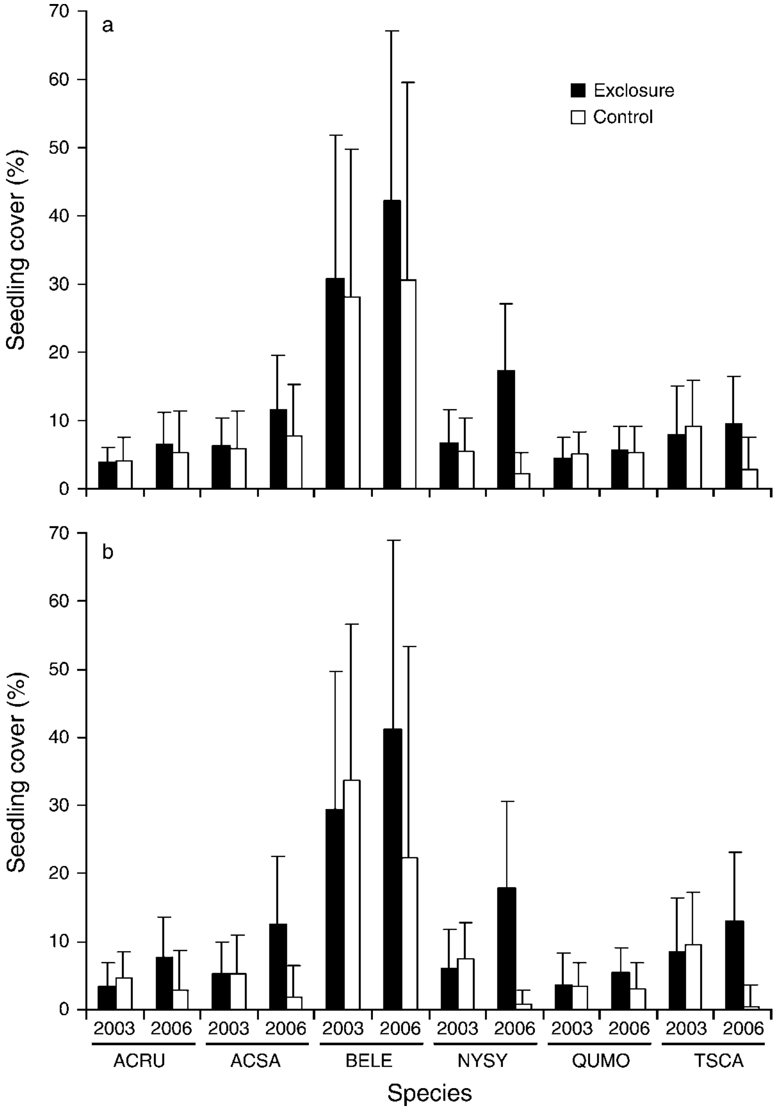

FIG. 1. Comparison of seedling percent cover (mean + SD) in exclosures and controls at (a) lower than average deer densities (<15.1 deer/km^2) and (b) higher than average deer densities (>15.1 deer/km^2) in 2003 and 2006. Seedling species codes: ACRU, red maple; ACSA, sugar maple; BELE, black birch; NYSY, black gum; QUMO, chestnut oak; and TSCA, hemlock.

Varying the deer density index estimate (summer or winter) did not alter the model rankings for any species and the resulting ΔAIC_c and w_i values varied only slightly. However, differences in goodness of fit occurred for all species (Table 3). The summer deer density data resulted in a higher percentage of variance explained in both cover and height impacts for *A. rubrum*, *A. saccharum, B. lenta*, and *N. sylvatica*. Whereas, the winter deer density data resulted in better fits for both cover and height impacts for *Q. montana* and *T. canadensis* (Table 3).

Effect of hemlock canopy decline

For all species, there was greater support for models that included the hemlock canopy decline parameters, canopy decline severity (change in light availability from 2003 to 2006, ΔL) and initial light availability in 2003 (TL_0). For all species, support for the complete model was overwhelming relative to the base model (Table 4). Support for the complete model relative to the ΔL model was also very strong in most cases. However, evidence ratios comparing the complete model and the ΔL model showed only marginal improvement in support for *T. canadensis* percent cover impacts (8.73) and low improvement in support for height impacts (4.85) with inclusion of canopy decline severity. Support for the complete model relative to the ΔL model was marginal for *N. sylvatica* (8.36) and *Q. montana* (11.78) height impacts (Table 4).

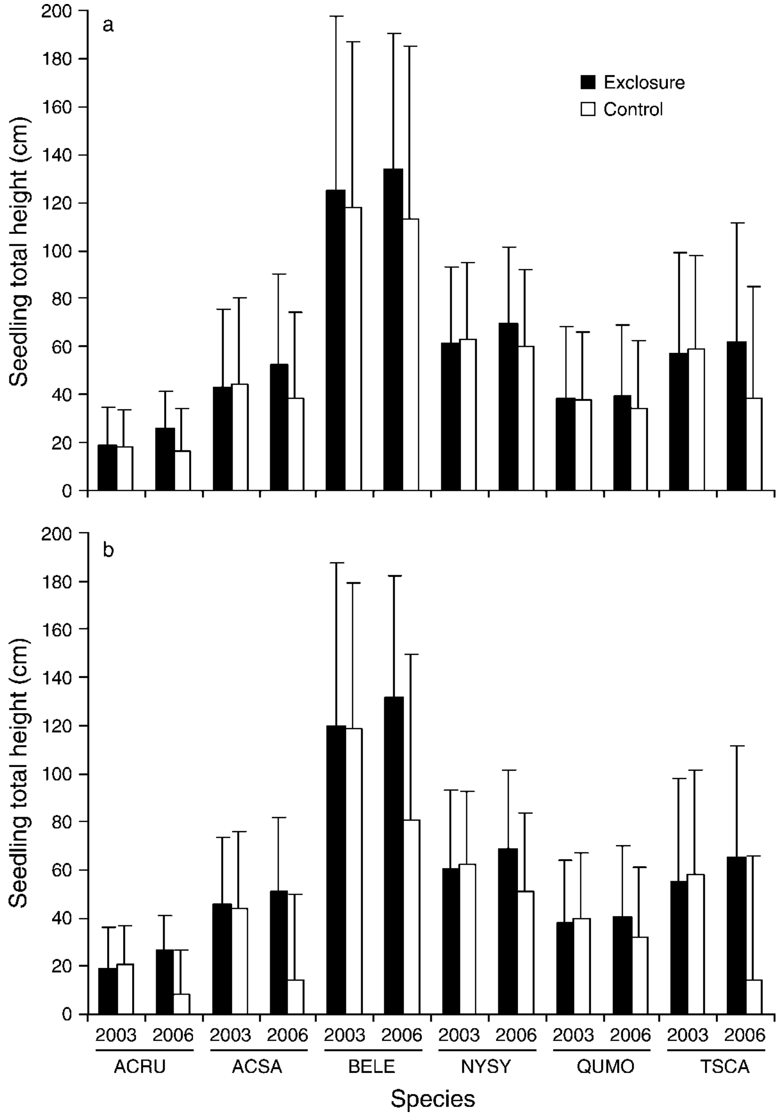

FIG. 2. Comparison of seedling total height (mean + SD) in exclosures and controls at (a) lower than average deer densities ($<$15.1 deer/km^2) and (b) higher than average deer densities ($>$15.1 deer/km^2) in 2003 and 2006. Seedling species codes: ACRU, red maple; ACSA, sugar maple; BELE, black birch; NYSY, black gum; QUMO, chestnut oak; and TSCA, hemlock.

Model predictions based on the selected best models showed marked variation among species in impacts across the observed range of deer densities and canopy decline severity (Figs. 3 and 4). Percent cover impacts at high deer densities were greatest for *B. lenta*. However, at lower deer densities, impacts to *B. lenta* percent cover were considerably less than those predicted for other species. *Quercus montana* had the smallest increase in percent cover impacts across the range of deer densities and ΔL (Figs. 3 and 4). Of the six study species, *B. lenta* and *A. rubrum* were most strongly impacted by ΔL (Figs. 3 and 4).

The species with the greatest total height impacts at high deer density varied with canopy decline severity. Although total height impacts were greatest for *A. saccharum* at low canopy decline severity, impacts at high canopy decline severity were far greater for *B. lenta* (Figs. 3 and 4). Predicted *B. lenta* height impacts at high deer density and low canopy decline severity were also lower than for *T. canadensis* and similar to *A. rubrum*. Total height impacts were low and similar for *N. sylvatica* and *Q. montana*, though *Q. montana* height responded more to ΔL (Figs. 3 and 4). We note that these representations are based on a fixed 2003 light availability (TL_0) and that species responses, to varying degrees, are altered by initial light availability (Table 4).

The comparison between healthy and declining sites clearly showed that deer had a greater proportional impact (herbivory impact per deer) on seedling cover and height in the declining sites (Fig. 5). This result was

TABLE 3. Model rankings and goodness of fit for models of percent cover impact and height impact.

Impact, by species	Model	$\Delta\mathrm{AIC_c}$†	w_i†	R^2 summer‡	R^2 winter‡	K§	Total weight¶
Percent cover							
Acer rubrum	$\mathrm{Exp_I.HCD_3}$	0	0.44	0.81	0.73	6	0.99
	$\mathrm{Exp_I.HCD_1}$	0.69	0.31	0.81	0.73	6	
	$\mathrm{Exp_I.HCD_2}$	1.15	0.24	0.80	0.73	6	
Acer saccharum	$\mathrm{Exp_A.HCD_1}$	0	0.72	0.83	0.74	7	0.72
Betula lenta	$\mathrm{Exp_I.HCD_3}$	0	0.50	0.72	0.56	7	0.93
	$\mathrm{Exp_I.HCD_2}$	0.26	0.43	0.72	0.56	7	
Nyssa sylvatica	$\mathrm{Sat_I.HCD_3}$	0	0.42	0.82	0.70	6	0.83
	$\mathrm{Sat_I.HCD_2}$	0.05	0.41	0.82	0.70	6	
Quercus montana	$\mathrm{Exp_A.HCD_3}$	0	0.40	0.52	0.61	7	0.89
	$\mathrm{Exp_A.HCD_2}$	0.82	0.27	0.52	0.61	7	
	$\mathrm{Exp_A.HCD_1}$	1.29	0.22	0.52	0.61	7	
Tsuga canadensis	$\mathrm{Sat_I.HCD_2}$	0	0.57	0.69	0.85	6	0.87
	$\mathrm{Sat_I.HCD_1}$	1.26	0.30	0.69	0.84	6	
Height							
Acer rubrum	$\mathrm{Exp_A.HCD_1}$	0	0.58	0.58	0.54	7	0.70
	$\mathrm{Exp_A.HCD_3}$	3.2	0.12	0.57	0.54	7	
Acer saccharum	$\mathrm{Exp_A.HCD_3}$	0	0.39	0.69	0.48	7	0.61
	$\mathrm{Exp_I.HCD_2}$	1.7	0.22	0.69	0.48	6	
	$\mathrm{Log_I.HCD_1}$	3.3	0.08	0.67	0.48	5	
Betula lenta	$\mathrm{Exp_I.HCD_3}$	0	0.43	0.38	0.31	6	0.99
	$\mathrm{Exp_I.HCD_2}$	0.60	0.32	0.38	0.31	6	
	$\mathrm{Exp_I.HCD_1}$	1.17	0.24	0.38	0.31	6	
Nyssa sylvatica	$\mathrm{Exp_A.HCD_2}$	0	0.44	0.56	0.43	7	0.71
	$\mathrm{Exp_A.HCD_3}$	1.01	0.27	0.56	0.43	7	
Quercus montana	$\mathrm{Exp_A.HCD_2}$	0	0.30	0.28	0.38	7	0.82
	$\mathrm{Exp_A.HCD_3}$	0.08	0.30	0.28	0.38	7	
	$\mathrm{Exp_A.HCD_1}$	0.60	0.22	0.28	0.38	7	
Tsuga canadensis	$\mathrm{Sat_I.HCD_1}$	0	0.54	0.59	0.66	6	0.97
	$\mathrm{Sat_I.HCD_2}$	1.05	0.32	0.59	0.66	6	
	$\mathrm{Sat_I.HCD_0}$	3.16	0.11	0.56	0.64	5	

Note: Results are presented by species for all models with a $\Delta\mathrm{AIC}$ value <4 (i.e., evidence ratio <7.5).

† The reported $\Delta\mathrm{AIC_c}$ and w_i are from the model run with summer deer density estimates. Model rankings did not vary between summer and winter deer densities. $\Delta\mathrm{AIC_c}$ and w_i varied slightly but did not impact model selection.

‡ R^2 summer is the goodness of fit for the model based on summer deer density estimates, and R^2 winter is the goodness of fit based on winter deer density estimates.

§ K is the total number of parameters (includes standard deviation of normal probability density function).

¶ Total model weight is the sum of the Akaike weights of the selected models in the same functional form as the top-ranked model (i.e., models that differ only by HCD_*).

consistent, to varying degrees, for all species (Fig. 5). For each species, the same model form was selected using the full data set and the data set divided into healthy and declining sites; however, the associated model predictions varied substantially.

DISCUSSION

This study demonstrates that white-tailed deer herbivory can alter tree seedling response to the canopy decline caused by an exotic insect pest. Canopy disturbance induced by HWA magnified the impact of herbivory for a given deer density and altered the ranking of impacts by seedling species. In addition, we found strong evidence of nonlinear relationships between deer density and the impact of herbivory on seedling abundance. Because the nature and magnitude of these nonlinearities vary among seedling species, deer herbivory may significantly alter forest successional trajectories following canopy disturbance. Therefore, where substantial herbivore populations are present, their role in forest response to disturbance must be considered.

Due to the spatially disjunct distribution of our study sites, HWA induced canopy decline severity and deer density varied considerably among sites and provided a model system in which to consider their interaction. In addition, there was little correlation between the estimates of deer density and the indicators of hemlock decline severity among sites (Table 1). This lack of correlation supports our assumption that deer densities at these sites were not controlled by canopy disturbance or by the availability of understory vegetation during the time frame of this study. Hunting, topography, and the availability of agricultural crops are likely the most significant factors in determining local variation in deer densities in this study area (McNulty et al. 1997, Kilpatrick et al. 2001).

Although deer impacts are often assumed to be directly proportional to their density, we found strong evidence of nonlinear relationships. Nonlinear relationships between herbivore densities and plant biomass have also been demonstrated for several understory forb species (Augustine et al. 1998, Tremblay et al. 2006), a rangeland shrub species (Hobbs et al. 1996), and for

TABLE 4. Model rankings and goodness of fit for the selected best model for each species (i.e., complete model) compared to the ΔL model (no initial light availability) and base model (deer density only) for the selected functional form.

Impact, by species	Model	$\Delta\mathrm{AIC_c}$†	w_i†	R^2†	Evidence ratio	K
Percent cover						
Acer rubrum	$\mathrm{Exp_I.HCD_3}$	0.00	0.44	0.81	1	6
	$\mathrm{Exp_I.HCD_0}$	9.82	0.00	0.78	135.45	5
	$\mathrm{Exp_B}$	215.69	0.00	0.61	6.87×10^{46}	4
Acer saccharum	$\mathrm{Exp_I.HCD_1}$	0.00	0.72	0.83	1	7
	$\mathrm{Exp_I.HCD_0}$	11.76	0.00	0.79	359.05	6
	$\mathrm{Exp_B}$	90.25	0.00	0.71	3.95×10^{19}	4
Betula lenta	$\mathrm{Exp_I.HCD_3}$	0.00	0.50	0.72	1	7
	$\mathrm{Exp_I.HCD_0}$	36.56	0.00	0.66	8.67×10^{7}	6
	$\mathrm{Exp_B}$	66.46	0.00	0.64	2.70×10^{14}	4
Nyssa sylvatica	$\mathrm{Sat_I.HCD_3}$	0.00	0.42	0.82	1	6
	$\mathrm{Sat_I.HCD_0}$	5.06	0.03	0.80	12.55	5
	$\mathrm{Sat_B}$	143.05	0.00	0.57	1.34×10^{31}	4
Quercus montana	$\mathrm{Exp_A.HCD_3}$	0.00	0.40	0.52	1	7
	$\mathrm{Exp_A.HCD_0}$	5.83	0.02	0.49	18.41	6
	$\mathrm{Exp_B}$	17.69	0.00	0.44	6946.04	4
Tsuga canadensis	$\mathrm{Sat_I.HCD_2}$	0.00	0.57	0.69	1	6
	$\mathrm{Sat_I.HCD_0}$	4.33	0.06	0.65	8.73	5
	$\mathrm{Sat_B}$	36.18	0.00	0.60	7.19×10^{7}	4
Height						
Acer rubrum	$\mathrm{Exp_A.HCD_1}$	0	0.58	0.58	1	7
	$\mathrm{Exp_A.HCD_0}$	31.50	0.00	0.46	6.93×10^{6}	6
	$\mathrm{Exp_B}$	83.22	0.00	0.44	1.88×10^{18}	4
Acer saccharum	$\mathrm{Exp_I.HCD_3}$	0	0.39	0.69	1	7
	$\mathrm{Exp_I.HCD_0}$	13.40	0.00	0.65	811.68	6
	$\mathrm{Exp_B}$	86.49	0.00	0.52	6.05×10^{18}	4
Betula lenta	$\mathrm{Exp_I.HCD_3}$	0	0.43	0.38	1	6
	$\mathrm{Exp_I.HCD_0}$	23.48	0.00	0.23	76 286.10	5
	$\mathrm{Exp_B}$	31.64	0.00	0.21	7.41×10^{6}	4
Nyssa sylvatica	$\mathrm{Exp_A.HCD_2}$	0	0.44	0.56	1	7
	$\mathrm{Exp_A.HCD_0}$	4.24	0.03	0.54	8.36	6
	$\mathrm{Exp_B}$	11.19	0.00	0.51	269.20	4
Quercus montana	$\mathrm{Exp_A.HCD_2}$	0	0.30	0.28	1	7
	$\mathrm{Exp_A.HCD_0}$	4.93	0.03	0.27	11.78	6
	$\mathrm{Exp_B}$	53.03	0.00	0.15	3.27×10^{11}	4
Tsuga canadensis	$\mathrm{Sat_I.HCD_1}$	0	0.54	0.59	1	6
	$\mathrm{Sat_I.HCD_0}$	3.16	0.11	0.56	4.85	5
	$\mathrm{Sat_B}$	12.26	0.00	0.52	460.83	4

† The reported $\Delta\mathrm{AIC_c}$, w_i, and R^2 are from the model run with summer deer density estimates. Model rankings did not vary between summer and winter deer densities. $\Delta\mathrm{AIC_c}$ and w_i varied slightly but did not impact model selection.

several woody seedling species (Tremblay et al. 2006). These nonlinearities may reflect the underlying relationship between deer and their food resources (Schmitz and Sinclair 1997, Palmer and Truscott 2003) or may result from herbivory induced changes in the competitive interactions among plant species (Rooney and Waller 2003, Tremblay et al. 2006).

The exponential form of the deer density–impact relationship was the highest ranked in all but three cases (*N. sylvatica* percent cover impacts and the *T. canadensis* percent cover and total height impacts), for which saturating models had greater support. An exponential relationship indicates that the herbivory impact per deer increases with deer density, whereas the saturating form suggests a more detrimental effect of herbivory per seedling. We observed particularly high mortality and significant loss of cover for browsed *T. canadensis* and *N. sylvatica* seedlings; this suggests that, for these species, the maximum herbivory impact occurs at the deer densities at which deer encounter all plots. The impact level may saturate because it is more dependent on deer finding the seedlings than on repeated browsing or percent of browse damage in each plot. Observed variation in impact likely reflects differences in plant response in the exclosure plots.

Tsuga canadensis is known to be preferred winter browse and, like many slow-growing evergreens, is highly susceptible to herbivory (Hough 1965, Rogers 1978, Alverson et al. 1988). *Nyssa sylvatica* is also reported to have moderate to high palatability (Della-Bianca and Johnson 1965, Harlow et al. 1975) although few studies have documented herbivory impacts for this species. *Nyssa sylvatica* was the only species for which the selected functional form varied between percent cover and total height impacts. Although herbivory to *N. sylvatica* often resulted in total removal of aboveground biomass, this species has a rapid sprouting response. These sprouts grow faster in height than in cover for several years and, therefore, herbivory may appear to have a greater impact on height than on

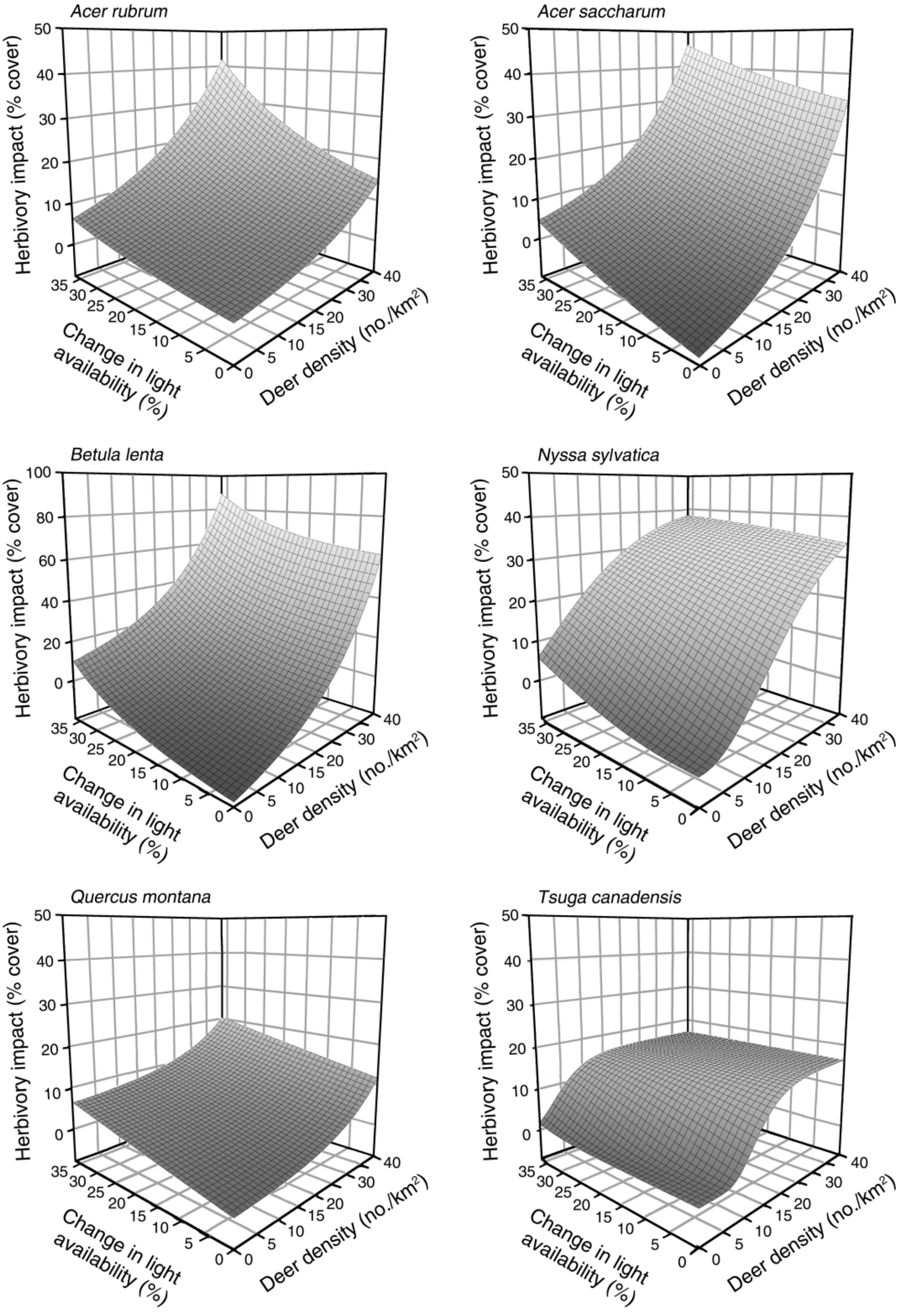

FIG. 3. Predicted herbivory impact on percent cover as a function of deer density and change in light availability from 2003 to 2006. Predictions for each species were generated from the top-ranked model shown in Table 3 for percent cover impacts. Initial light availability (2003) is held constant at the mean value (10.1%). Note that the *Betula lenta* graph is scaled differently than the graphs for the other five species.

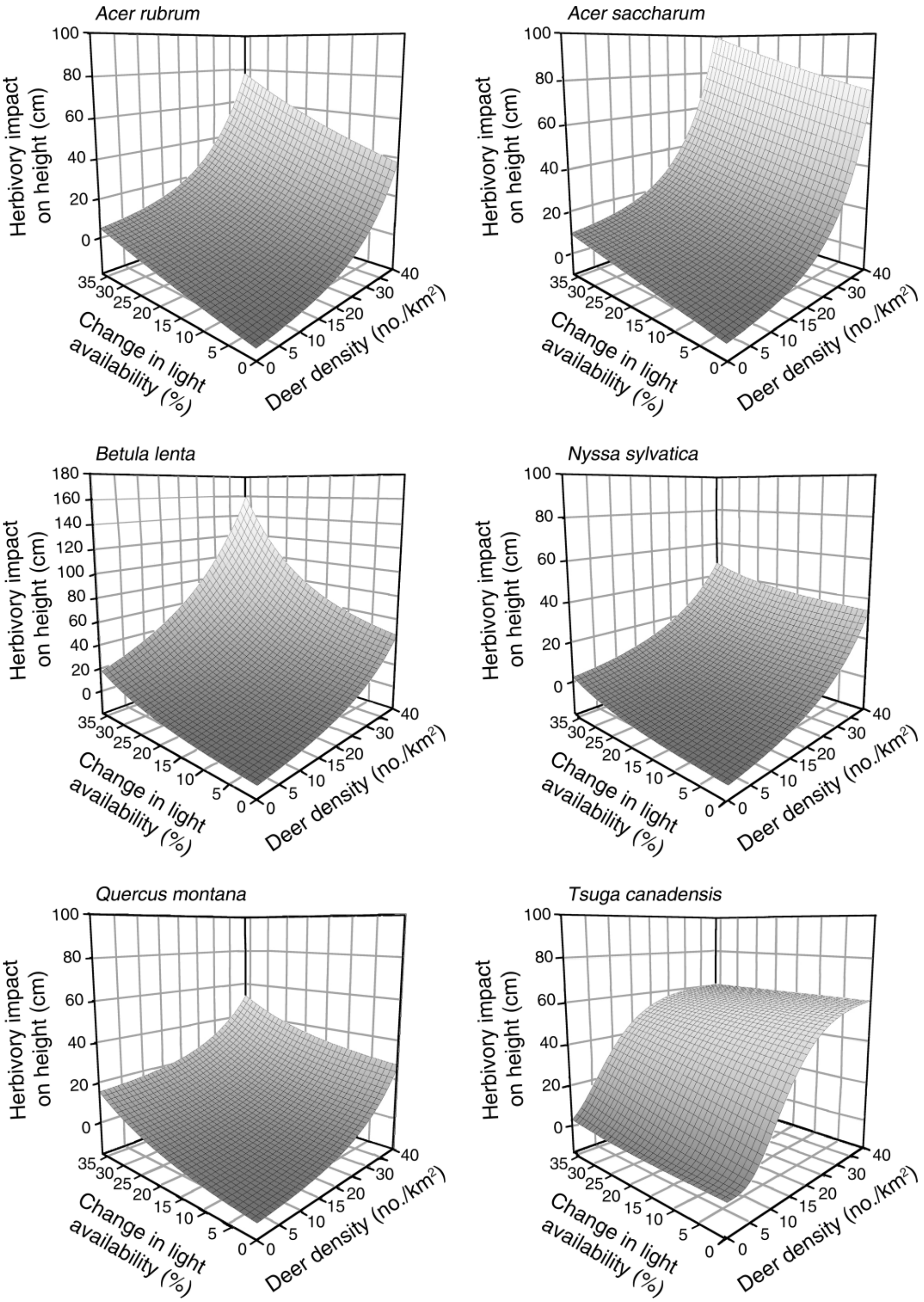

FIG. 4. Predicted herbivory impact on height as a function of deer density and change in light availability from 2003 to 2006. Predictions for each species were generated from the top-ranked model shown in Table 3 for height impacts. Initial light availability (2003) is held constant at the mean value (10.1%). Note that the *Betula lenta* graph is scaled differently than the graphs for the other five species.

cover. Thus *N. sylvatica* height response may be more dependent on repeated browsing and, therefore, the relationship was best described by an exponential model.

The measure of herbivory impact in our analyses (Figs. 3 and 4) reflects the actual change in seedling abundance as a function of deer density but does not illustrate community response to a given impact. For

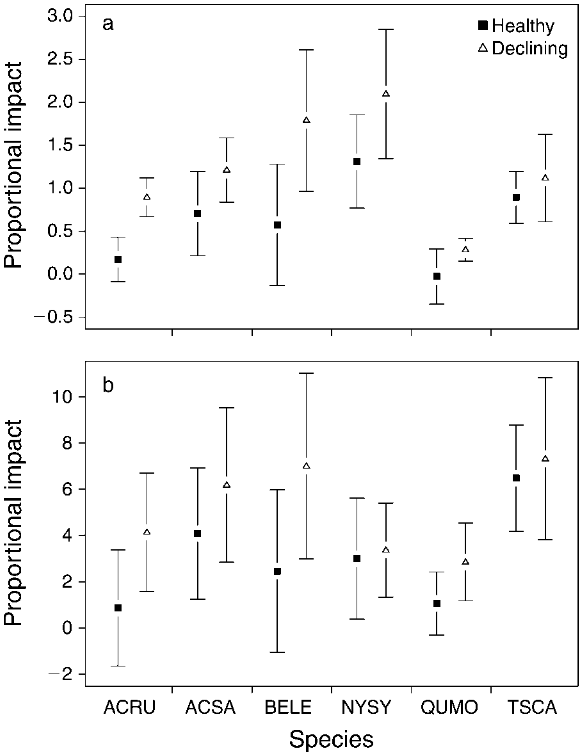

FIG. 5. Proportional impacts (herbivory impact/deer density) on each seedling species in the five healthy vs. the five declining hemlock stands for (a) percent cover impacts and (b) height impacts (mean ± SD). The deer density used to calculate proportional impact was an average of all winter and summer surveys. Seedling species codes: ACRU, red maple; ACSA, sugar maple; BELE, black birch; NYSY, black gum; QUMO, chestnut oak; and TSCA, hemlock.

instance, although the mean herbivory impact values were higher for *B. lenta* than for *N. sylvatica* (Figs. 3 and 4), the relative impacts were higher for *N. sylvatica* due to its lower abundance (Figs. 1, 2, and 5). Therefore, both values are needed to interpret the deer density-herbivory impact relationship and the community effects of a given deer density. *Nyssa sylvatica* and *T. canadensis* experienced the highest relative impacts of the studied seedling species. Both were reduced to very low cover and total height at relatively low deer densities (Figs. 1 and 2). It is also important to note that, because plots were not placed in areas with no seedlings, the percent cover and height values may be an overestimate of community wide seedling abundance.

The inclusion of both deer density and canopy decline severity measures consistently resulted in models with substantially greater support. However, model predictions and the relative importance of these factors varied considerably among species. For instance, though an exponential functional form was selected for both *A. saccharum* and *A. rubrum* percent cover and total height impacts, *A. saccharum* had higher impact for a given density and was less impacted by changes in light. Similarly, though both *N. sylvatica* and *T. canadensis* percent cover impact models saturate, model predictions vary greatly and suggest different implications for seedling response at varying deer densities. Percent cover impacts for *N. sylvatica* saturated at a higher deer density and a higher maximum impact value than was predicted for *T. canadensis*. The *Q. montana* model was unique in that, at low levels of canopy decline severity, negative impacts (i.e., increase in abundance in the control plot relative to the exclosure) were predicted up to a relatively high deer density. This suggests that *Q. montana* benefits from deer herbivory at low to intermediate deer densities; likely resulting from a competitive release via selective browsing. Selective browsing can reduce the abundance of preferred species and indirectly promote the abundance of low preference, browse resistant, or browse tolerant species (Horsley et al. 2003, Rooney et al. 2004).

Summer deer density estimates resulted in the best fits for all species except *T. canadensis* and *Q. montana*. It is not surprising that winter deer estimates resulted in better fits for *T. canadensis* and *Q. montana* as both are thought to be preferred winter foods (Hosley and Ziebarth 1935, Dahlberg and Guettinger 1956). However, this study provides some of the best quantitative evidence of this relationship and may challenge the conventional view that deer primarily browse woody seedlings during winter months. Alternatively, this result may reflect a higher impact of summer browsing on the growth and survival of some seedling species, as was demonstrated by Canham et al. (1994*b*). In general, the models of herbivory impact had high goodness of fit. However, for several species, the models did not perform well for projecting impacts at sites with both very low deer densities and high canopy decline values (positive impacts at 0 deer/km^2). While this result is likely due to the limited number of plots with less than 5 deer/km^2 and random variability in herbivory impacts at low densities, we did not force models through zero as these inconsistencies may reflect actual differences at low deer densities.

The comparison of proportional impacts in healthy and declining hemlock stands showed that, at the scale of an entire site, a given deer density results in a higher impact in declining sites (Fig. 5). The mechanism for this interaction may be the higher nitrogen availability in declining stands (Jenkins et al. 1999), which can increase herbivory rates (Mattson 1980, Tripler et al. 2002). The interaction between herbivory and canopy decline severity may also be explained by differences in patterns of carbohydrate storage in seedlings in high vs. low light environments. Canham et al. (1994*b*) proposed that the carbohydrate reserves of shaded seedlings are primarily stored in roots, whereas seedlings in higher light environments store more reserves in shoots. Therefore, seedlings in areas of higher canopy disturbance may be more vulnerable to loss of carbohydrates from browsing. In addition, canopy decline changed the ranking of herbivory impacts by seedling species (Fig. 5). For instance, among the percent cover impacts for the six studied seedling species, proportional impacts for *B. lenta* were the fourth highest in healthy stands but the second highest in declining stands. By altering the competitive hierarchy of tree seedlings, deer herbivory can alter the course and rate of community recovery following canopy disturbance.

Tree seedlings exhibit varied and complex growth responses to herbivory (Anderson and Loucks 1979, Canham et al. 1994*b*, Tremblay et al. 2006). We found species-specific variation in both the functional form of the deer density-impact relationship and in the predicted response. Therefore, it is difficult to extrapolate specific findings to other seedling species. However, given the diversity of the studied seedling species and the strength of support observed for the selected models, the findings of nonlinear functional responses and herbivory–disturbance interactions can likely be generalized to many other moderate to highly preferred browse species. The interaction of canopy disturbance and herbivory may be easier to observe or more important in systems, such as hemlock forests, in which the canopy exerts strong control over the availability of nitrogen and light in the understory (Canham et al. 1994*a*, Jenkins et al. 1999). In addition, seedlings in hemlock forest understories may be more impacted by herbivory due to the relatively low productivity.

Management implications

The sustainable management of forest systems with substantial deer populations will require improved methods for predicting forest ecosystem response to deer densities. Although the basic mechanisms by which deer modify forest ecosystems are well documented (e.g., Côté et al. 2004), our ability to predict forest response to deer management remains limited by a need for (1) scale-appropriate methods of measuring deer abundance, (2) improved understanding of the functional relationship between deer densities and their impacts, and (3) more information on factors, such as canopy disturbance, that may alter forest response to a given deer density (Healy et al. 1997). Our study contributes to these three management needs.

The spatial scales used to measure deer densities and impacts of herbivory on vegetation are typically incompatible. Estimates of deer density are usually performed over landscapes much larger than the units of vegetation monitoring or management (Healy et al. 1997). However, habitat selectivity by deer results in unequal use of habitat patches within landscapes (Bever 1955, Loft and Kie 1988, Healy et al. 1997). This selectivity can confound attempts to establish a relationship between landscape level deer density and vegetation impacts. In this study, we accounted for habitat selectivity by monitoring deer density and impacts on seedlings at the same local scale. Our model fits suggest that plot level deer density indices provided a good measure of relative habitat use. In addition, high variability in the localized estimates of deer density within and between sites provides evidence of the deer habitat selectivity that is not captured in most exclosure studies. Although time and labor intensive, this method does not rely on the assumption that deer use all microsites equally and, therefore, more accurately links deer density to the degree of impact on vegetation.

Despite the advantages gained with this novel approach, there remain complications with estimating deer density from pellet plots. Chief among these is the use of daily defecation rates to scale pellet group counts to estimates of deer density. We converted to density for ease of interpretation but caution that daily defecation rates are known to vary by sex, season, deer age, and food quality (Rogers et al. 1958, Neff 1968, Ryel 1971, Rogers 1987) and that white-tailed deer are believed to have highly variable defecation rates (Rollins et al 1984). While this does not affect the interpretation of these values as a relative index, it could alter estimates of absolute population size. For instance, the availability of high quality food from nearby agricultural fields could increase the daily defecation rate (Rogers et al. 1958, Ryel 1971).

An improved understanding of the relationship between deer densities and their impacts on forest regeneration is critical to the establishment of deer population goals that are compatible with forest management objectives. The existence of nonlinear deer density–impact relationships has significant implications for the maintenance and restoration of plant species and for forest succession. The most commonly selected model form, the exponential relationship, implies that herbivory impacts above a threshold deer density are greater than would be predicted by a linear model. Determination of these threshold levels could have important implications for the maintenance of biodiversity or a desired tree species. For example, our results suggest that above ~20 deer/km^2 the severity of impacts on *A. saccharum* height growth increase rapidly (Figs. 3 and 4). Management plans based on the assumption of a linear relationship between deer densities and their impacts may result in management decisions that fail to accomplish desired objectives.

Moreover, our results show that deer densities alone do not adequately reflect their potential to impact the community and that factors such as disturbance dynamics need to be considered in determining the appropriate deer density to meet management objectives. Our results demonstrate an interaction between herbivory and canopy disturbance that results in elevated per capita herbivory impacts at higher disturbance severities. Therefore, deer densities should be lower in declining hemlock stands than in healthy stands to achieve the same herbivory impact. Through altering the ranking of herbivory impacts by seedling species and the predicted outcomes for each species across the range of deer densities, the interaction of deer herbivory and canopy disturbance could result in long-term changes in the plant community that may be difficult to reverse. For instance, for *A. rubrum* and *N. sylvatica*, the difference in proportional cover impacts between healthy and declining sites was quite high relative to their absolute cover values which suggests that the interaction of canopy decline and deer herbivory could severely reduce the occurrence of these species in the forest understory.

Although disturbance is recognized as an important factor in determining forest ecosystem composition, structure, and function; few field studies have quantified the impacts of interacting disturbances. Given that the diversity, frequency, and intensity of forest disturbances have continued to increase throughout the past century, a fundamental understanding of disturbance interactions is becoming increasingly critical for the sustainable management of forest resources.

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Literature Cited

Alverson, W. S., and D. M. Waller. 1997. Deer populations and the widespread failure of hemlock regeneration in northern forests. Pages 280–297 *in* W. McShea and J. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. Conservation Biology 2:348–358.

Anderson, R. C., and O. L. Loucks. 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. Journal of Applied Ecology 16:855–861.

Augustine, D. J., and L. E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conservation Biology 12:995–1004.

Augustine, D. J., L. E. Frelich, and P. A. Jordan. 1998. Evidence for two alternate stable states in an ungulate grazing system. Ecological Applications 8:1260–1269.

Bailey, R. E., and R. J. Putman. 1981. Estimation of fallow deer (*Dama dama*) populations from faecal accumulation. Journal of Applied Ecology 18:697–702.

Bever, W. 1955. A study of deer pellet-groups as an index to population trend, true population and range use, 1953–1954. South Dakota Department Game, Fish and Parks Job Completion Report, Pierre, South Dakota, USA.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. Biometrics 53: 603–618.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America: 1 and 2. Agriculture Handbook 654. USDA, Forest Service, Washington, D.C., USA.

Campbell, D., G. M. Swanson, and J. Sales. 2004. Comparing the precision and cost-effectiveness of fecal pellet group count methods. Journal of Applied Ecology 41:1185–1196.

Canham, C. D. 1988. An index for understory light levels in and around canopy gaps. Ecology 69:1634–1638.

Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994*a*. Causes and consequences of resource heterogeneity in forests—interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research 24:337–349.

Canham, C. D., J. B. McAninch, and D. M. Wood. 1994*b*. Effects of frequency, timing and intensity of simulated browsing on growth and mortality of tree seedlings. Canadian Journal of Forest Research 24:817–825.

Castello, J. D., D. J. Leopold, and P. J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. BioScience 45:16–24.

Cates, R. G., and G. H. Orians. 1975. Successional status and palatability of plants to generalized herbivores. Ecology 56: 410–418.

Caughley, G. 1981. Overpopulation. Pages 7–9 *in* P. A. Jewell and S. Holt, editors. Problems of management of locally abundant wild mammals. Academic Press, New York, New York, USA.

Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147.

Dahlberg, B. L., and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin. Technical wildlife bulletin. Number 14. Game Management Division, Wisconsin Conservation Department. Madison, Wisconsin, USA.

Della-Bianca, L., and F. M. Johnson. 1965. Effect of an intensive cleaning on deer-browse production in the southern Appalachians. Journal of Wildlife Management 29:729–733.

Eberhardt, L., and R. C. Van Etten. 1956. Evaluation of the pellet group count as a deer census method. Journal of Wildlife Management 20:70–74.

Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Canadian Journal of Forest Research 36: 1435–1450.

Engeman, R. M., R. T. Sugihara, L. F. Prank, and W. E. Dusenberry. 1994. A comparison of plotless density estimators using Monte-Carlo simulation. Ecology 75(6):1769–1779.

Evans, R. A. 2004. Hemlock ecosystems and hemlock woolly adelgid at Delaware Water Gap National Recreation Area. Pages 1–22 *in* 2003 Annual Report of the Division of Research and Resource Planning. U.S. Department of the Interior, National Park Service, Bushkill, Pennsylvania, USA.

Foster, D. R. 2000. Hemlock's future in the context of its history: an ecological perspective. Pages 1–4 *in* K. A. McManus, K. S. Shields, and D. R. Souto, editors. Proceedings: symposium on sustainable management of hemlock ecosystems in Eastern North America. General technical report 267. USDA Forest Service, Newtown Square, Pennsylvania, USA.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap light analyzer (GLA). Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs. Simon Fraser University, Burnaby, British Columbia, Canada, and the Institute of Ecosystem Studies, Millbrook, New York, USA.

Frelich, L. E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, New York, New York, USA.

Frelich, L. E., and C. G. Lorimer. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biological Conservation 34:99–120.

Hall, B., G. Motzkin, D. R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography 29:1319–1335.

Harlow, R. F. S., A. Paul, and M. E. Seehorn. 1975. Deer browse resources of the Oconee National Forest. Research Paper SE-137. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina, USA.

Healy, W. M., D. S. deCalesta, and S. L. Stout. 1997. A research perspective on white-tailed deer overabundance in the northeastern United States. Wildlife Society Bulletin 25: 259–263.

Herbert, T. J. 1987. Area projections of fisheye photographic lenses. Agricultural and Forest Meteorology 39:215–263.

Hester, A. J., L. Edenius, R. M. Buttenschon, and A. T. Kuiters. 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry 73:381–391.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate grazing in sagebrush grassland: Mechanisms of resource competition. Ecological Applications 6:200–217.

Horsley, S. B., S. L. Stout, and D. S. deCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13:98–118.

Hosley, N. W., and R. K. Ziebarth. 1935. Some winter relations of the white-tailed deer to the forests in North Central Massachusetts. Ecology 16:535–553.

Hough, A. F. 1965. A 20-year record of understory vegetational change in a virgin Pennsylvania forest. Ecology 46:370–373.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics 22:477–503.

Isobe, T., E. D. Feigelson, M. G. Akritas, and G. J. Babu. 1990. Linear regression in astronomy I. The Astrophysical Journal 364:104–113.

Jenkins, J. C., J. D. Aber, and C. D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research 29:630–645.

Kilpatrick, H. J., S. M. Spohr, and K. K. Lima. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. Canadian Journal of Zoology 79:949–954.

Knapp, C. L., T. L. Stoffel, and S. D. Whittaker. 1980. Insolation data manual: long term monthly averages of solar radiation, temperature, degree-days, and global K_T for 248 National Weather Service stations. Solar Energy Research Institute, Washington, D.C., USA.

Liebhold, A. M., W. L. Macdonald, D. Bergdahl, and V. C. Maestro. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science 41:1–49.

Loft, E. R., and J. G. Kie. 1988. Comparison of pellet-group and radio triangulation methods for assessing deer habitat use. Journal of Wildlife Management 52:524–527.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

McClure, M. S. 1991. Density-dependent feedback and population-cycles in *Adelges tsugae* (*Homoptera, Adelgidae*) on *Tsuga canadensis*. Environmental Entomology 20:258–264.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan. Ecology 73:2059–2075.

McNulty, S. A., W. F. Porter, N. E. Mathews, and J. A. Hill. 1997. Localized management for reducing white-tailed deer populations. Wildlife Society Bulletin 25:265–271.

Messier, C., and P. Puttonen. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands—the basis for a quick and efficient method of characterizing light. Canadian Journal of Forest Research 25:343–354.

Myers, W. L., and R. R. Irish. 1981. Vegetation survey of Delaware Water Gap National Recreation Area. Final Report. U.S. Department of the Interior, National Park Service, Mid-Atlantic Region, University Park, Pennsylvania, USA.

Neff, D. J. 1968. Pellet group count technique for big game trend census and distribution: a review. Journal of Wildlife Management 32:597–614.

Niinemets, U., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76:521–547.

NOAA. 2002. Climatography of the United States no. 81. Monthly station normals of temperature, precipitation, and heating and cooling degree days. 1971–2000. National Oceanic and Atmospheric Administration, Washington, D.C., USA. ⟨http://lwf.ncdc.noaa.gov/oa/climate/normals/usnormalsprods.html⟩

Orwig, D. A., and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 125:60–73.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1:535–545.

Palmer, S. C. F., and A. M. Truscott. 2003. Browsing by deer on naturally regenerating Scots pine and its effects on sapling growth. Forest Ecology and Management 182:31–47.

Pennsylvania Department of Conservation and Natural Resources. 2003. Estimating County Deer Population Sizes and growth rates. Annual report of the Pennsylvania Bureau of Wildlife Management Research Division. Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA.

Persson, I. L., K. Danell, and R. Bergstrom. 2005. Different moose densities and accompanied changes in tree morphology and browse production. Ecological Applications 15: 1296–1305.

Potvin, F., P. Beaupre, and G. Laprise. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Quebec: a 150-year process. Ecoscience 10:487–495.

Rhoads, A., and T. A. Block. 2000. The plants of Pennsylvania: an illustrated manual. University of Pennsylvania Press, Philadelphia, Pennsylvania, USA.

Rogers, G., O. Julander, and W. L. Robinette. 1958. Pellet-group counts for deer census and range-use index. Journal of Wildlife Management 22:193–199.

Rogers, L. L. 1987. Seasonal changes in defecation rates of free-ranging white-tailed deer. Journal of Wildlife Management 51:330–333.

Rogers, R. S. 1978. Forests dominated by hemlock (*Tsuga canadensis*): distribution as related to site and postsettlement history. Canadian Journal of Botany 56:843–854.

Rollins, D., F. C. Bryant, and R. Montandon. 1984. Fecal pH and defecation rates of eight ruminants fed known diets. Journal of Wildlife Management 48:807–813.

Rooney, T. P., R. J. McCormick, S. L. Solheim, and D. M. Waller. 2000. Regional variation in recruitment of hemlock seedlings and saplings in the upper Great Lakes, USA. Ecological Applications 10:1119–1132.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165–176.

Rooney, T. P., S. M. Wiegmann, D. A. Rogers, and D. M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conservation Biology 18:787–798.

Royle, D., and R. Lathrop. 2002. Using Landsat imagery to quantify temporal and spatial patterns in hemlock decline. Pages 67–72 *in* B. Onken, R. Reardon, and J. Lashomb, editors. Proceedings: hemlock woolly adelgid in the eastern United States Symposium. New Jersey Agricultural Experiment Station, New Brunswick, New Jersey, USA.

Ruhren, S., and S. N. Handel. 2003. Herbivory constrains survival, reproduction and mutualisms when restoring nine temperate forest herbs. Journal of the Torrey Botanical Society 130:34–42.

Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer on plants, plant populations and communities: a review. American Midland Naturalist 146:1–26.

Ryel, L. A. 1971. Evaluation of pellet group surveys for estimating deer populations in Michigan. Research and Development Report 250. Michigan Department of Natural Resources, Ann Arbor, Michigan, USA.

Schmitz, O. J., and R. E. Sinclair. 1997. Rethinking the role of deer in forest ecosystem dynamics. Pages 201–223 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Spiller, D. A., and A. A. Agrawal. 2003. Intense disturbance enhances plant susceptibility to herbivory: natural and experimental evidence. Ecology 84:890–897.

Stromayer, K., and R. J. Warren. 1997. Are overabundant deer herds in the Eastern United States creating alternate stable states in forest plant communities? Wildlife Society Bulletin 25:227–234.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management 53:524–532.

Tremblay, J. P., J. Huot, and F. Potvin. 2006. Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. Oecologia 150:78–88.

Tripler, C. E., C. D. Canham, R. S. Inouye, and J. L. Schnurr. 2002. Soil nitrogen availability, plant luxury consumption, and herbivory by white-tailed deer. Oecologia 133:517–524.

Tsujino, R., and T. Yumoto. 2004. Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. Ecological Research 19:291–300.

Underwood, H. B., and W. F. Porter. 1997. Reconsidering paradigms of overpopulation in ungulates. *In* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press. 402 pp.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications 7:737–750.

Wardle, D. A., G. M. Barker, G. W. Yeates, K. I. Bonner, and A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71:587–614.

Westoby, M., B. Walker, and I. Noymeir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266–274.

Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. Wildlife Society Bulletin 34:283–292.

Young, R. F., K. S. Shields, and G. P. Berlyn. 1995. Hemlock woolly adelgid (*Homoptera*, *Adelgidae*): stylet bundle insertion and feeding sites. Annals of the Entomological Society of America 88:827–835.

APPENDIX A

Methodological details (*Ecological Archives* A018-010-A1).

APPENDIX B

Assessment of the relationship between hemlock crown health and understory light availability (*Ecological Archives* A018-010-A2).