

Acceleration of Exotic Plant Invasion in a Forested Ecosystem by a Generalist Herbivore

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Abstract: *The successful invasion of exotic plants is often attributed to the absence of coevolved enemies in the introduced range (i.e., the enemy release hypothesis). Nevertheless, several components of this hypothesis, including the role of generalist herbivores, remain relatively unexplored. We used repeated censuses of exclosures and paired controls to investigate the role of a generalist herbivore, white-tailed deer (*Odocoileus virginianus*), in the invasion of 3 exotic plant species (*Microstegium vimineum*, *Alliaria petiolata*, and *Berberis thunbergii*) in eastern hemlock (*Tsuga canadensis*) forests in New Jersey and Pennsylvania (U.S.A.). This work was conducted in 10 eastern hemlock (*T. canadensis*) forests that spanned gradients in deer density and in the severity of canopy disturbance caused by an introduced insect pest, the hemlock woolly adelgid (*Adelges tsugae*). We used maximum likelihood estimation and information theoretics to quantify the strength of evidence for alternative models of the influence of deer density and its interaction with the severity of canopy disturbance on exotic plant abundance. Our results were consistent with the enemy release hypothesis in that exotic plants gained a competitive advantage in the presence of generalist herbivores in the introduced range. The abundance of all 3 exotic plants increased significantly more in the control plots than in the paired exclosures. For all species, the inclusion of canopy disturbance parameters resulted in models with substantially greater support than the deer density only models. Our results suggest that white-tailed deer herbivory can accelerate the invasion of exotic plants and that canopy disturbance can interact with herbivory to magnify the impact. In addition, our results provide compelling evidence of nonlinear relationships between deer density and the impact of herbivory on exotic species abundance. These findings highlight the important role of herbivore density in determining impacts on plant abundance and provide evidence of the operation of multiple mechanisms in exotic plant invasion.*

Keywords: canopy disturbance, enemy release hypothesis, hemlock woolly adelgid, herbivory, invasive plants, maximum likelihood estimation, *Odocoileus virginianus*

Aceleración de la Invasión de Plantas Exóticas en un Ecosistema Boscoso por un Herbívoro Generalista

Resumen: *La invasión exitosa de plantas exóticas a menudo es atribuida a la ausencia de enemigos coevolucionados en el área de introducción (i.e., la hipótesis de liberación de enemigo). Sin embargo, varios componentes de esta hipótesis, incluyendo el papel de los herbívoros generalistas, permanecen relativamente inexplorados. Utilizamos censos repetidos de exclusiones y controles pareados para investigar el papel de un herbívoro generalista, el venado cola blanca (*Odocoileus virginianus*), en la invasión de tres especies de plantas exóticas (*Microstegium vimineum*, *Alliaria petiolata* y *Berberis thunbergii*) en bosques de abeto (*Tsuga canadensis*) en Nueva Jersey y Pennsylvania (E.U.A.). Este trabajo se realizó en 10 bosques de abeto (*T. canadensis*) con gradientes de densidad de venado y de severidad de perturbación del dosel provocada por una especie introducida de insecto parásito (*Adelges tsugae*). Utilizamos la estimación de la máxima probabilidad y teoría de la información para cuantificar el poder de la evidencia para tres modelos alternativos de la influencia de la densidad de venados y su interacción con la severidad de la perturbación del dosel sobre la abundancia de plantas exóticas. Nuestros resultados fueron consistentes con la hipótesis de la liberación de enemigo ya*

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que las plantas exóticas ganaron una ventaja competitiva en la presencia de herbívoros generalistas en el área. La abundancia de las tres especies de plantas exóticas incrementó significativamente en las parcelas control que en las exclusiones pareadas. Para todas las especies, la inclusión de parámetros de perturbación del dosel resultó en modelos sustancialmente con mayor soporte que los modelos exclusivamente de densidad de venados. Nuestros resultados sugieren que la herbivoría de venado cola blanca puede acelerar la invasión de plantas exóticas y que la perturbación del dosel puede interactuar con la herbivoría para magnificar el impacto. Adicionalmente, nuestros resultados proporcionan evidencia convincente de las relaciones no lineales entre la densidad de venados y el impacto de la herbivoría sobre la abundancia de especies exóticas. Estos hallazgos resaltan la importancia del papel de la densidad de herbívoros en la determinación de impactos sobre la abundancia de plantas y proporcionan evidencia de la operación de múltiples mecanismos en la invasión de plantas exóticas.

Palabras Clave: *Adelges tsugae*, estimación de la máxima probabilidad, herbivoría, hipótesis de la liberación de enemigo, *Odocoileus virginianus*, perturbación del dosel, plantas invasoras

Introduction

The dramatic impacts of exotic plant invasions on community and ecosystem properties have been well documented (e.g., Vitousek et al. 1996; Mack et al. 2000). Despite the pressing management implications, many of the mechanisms that determine the success of exotic plant invasions remain poorly understood. A successful invasion is often attributed to the absence of coevolved enemies in the introduced range (Darwin 1859; Elton 1958; Crawley 1987). This idea, the enemy release hypothesis, maintains that plant species introduced into a new region experience a competitive advantage over native plant species due to a relative reduction in regulation by herbivores and other natural enemies. The enemy release hypothesis posits that this reduced enemy impact (relative to native plants) results in an increase in exotic plant distribution and abundance (Mack et al. 2000; Shea & Chesson 2002). Although the enemy release hypothesis is commonly accepted as an explanation for the increased success of plants outside their native range, little experimental work has been conducted that directly tests many of its assumptions (Maron & Vila 2001; Keane & Crawley 2002).

The enemy release hypothesis predicts that, in the introduced range, specialist and generalist enemies will have a greater impact on native plant species than on exotic species. To date, most tests of the enemy release hypothesis have examined the role of plant release from specialist enemies (e.g., Louda & Potvin 1995; Wise & Sacchi 1996), whereas the impact of generalist herbivores on exotic plants has received much less attention (Maron & Vila 2001; Keane & Crawley 2002). Keane and Crawley (2002) conclude, however, that “competitive release through greater generalist enemy impact on natives seems to be an important but understudied mechanism of enemy release” and that there is “a serious need for experiments involving exclusion of natural enemies in invaded plant communities.” In this context the key com-

petitive release is gained not via escape from generalist herbivores in the native range but through a reduction in the impact of generalist herbivores on exotic species relative to their native competitors (sensu Keane & Crawley 2002).

The role of generalist mammalian herbivores in exotic plant invasion may be particularly important given that populations of several herbivorous mammals have become uncoupled from their natural regulating factors, such as predation and resource competition, and have reached unprecedented levels in many ecosystems (Caughley 1981; Vare et al. 1996; Côté et al. 2004). These elevated populations of generalist mammalian herbivores can be important regulators of native plant populations (Tilghman 1989; McInnes et al. 1992). White-tailed deer (*Odocoileus virginianus*) in North America are a good example of this phenomenon because the geographic range and population density of this species have increased dramatically since European settlement (Rooney 2001). White-tailed deer herbivory is recognized as an important regulator of forest ecosystem dynamics (e.g., Frelich & Lorimer 1985; Rooney et al. 2000; Horsley et al. 2003). Furthermore, there is substantial evidence that selective deer herbivory can indirectly promote the abundance of low-preference, browse-resistant, or browse-tolerant species (Horsley et al. 2003; Rooney et al. 2004). Despite the implications of these findings for the invasion of exotic plants, few experimental studies have examined the role of native mammalian herbivores in exotic plant invasion in forests.

Studies of the impacts of mammalian herbivory must account for the role of potentially confounding factors such as herbivore densities and the influence of co-occurring disturbances. Although the intensity of herbivory is recognized as a critical determinant of plant response, few enclosure studies quantify the role of herbivore density. Failure to account for deer density could confound understanding of the impacts of herbivory on exotic plant abundance, particularly given the potential

for nonlinear functional responses (Augustine et al. 1998; Tremblay et al. 2006; Eschtruth & Battles 2008). Furthermore, the impact of herbivory can be altered by canopy disturbance (Spiller & Agrawal 2003; Eschtruth & Battles 2008). Given the ubiquity of canopy disturbance, it is critical to account for the potential effects of herbivory-disturbance interactions. Therefore, we examined the impact of a generalist herbivore on exotic plant invasion while simultaneously accounting for the role of herbivore density and the severity of canopy disturbance.

We experimentally examined the impact of white-tailed deer herbivory on the abundance (measured as density, cover, and height) of 3 exotic invasive plant species with diverse life-history strategies: an annual grass, *Microstegium vimineum* (Japanese stiltgrass); a biennial forb, *Alliaria petiolata* (garlic mustard); and a woody shrub, *Berberis thunbergii* (Japanese barberry). We assessed the role of deer herbivory in the invasion of these species in 10 eastern hemlock (*Tsuga canadensis*) forests. These forests spanned gradients in deer density and in the severity of canopy disturbance caused by the infestation of an introduced insect pest, the hemlock woolly adelgid (HWA; *Adelges tsugae*) (Orwig & Foster 1998; Eschtruth et al. 2006).

We used maximum likelihood estimation and information theoretics to choose among a set of competing models that predicted the influence of deer density and its interaction with canopy decline severity on exotic plant abundance. On the basis of the weight of evidence supporting the best models in our candidate set of models, we evaluated the enemy release hypothesis prediction that exotic plant species gain a competitive advantage in the presence of a generalist herbivore (Keane & Crawley 2002).

Methods

The Delaware Water Gap National Recreation Area (DEWA) is a 27,800-ha park in northeastern Pennsylvania and western New Jersey (U.S.A.). We selected 10 forests in DEWA that were dominated by eastern hemlock and spanned a gradient of severity of canopy decline caused by HWA (Table 1; Supporting Information). These forests also had high white-tailed deer densities (Supporting Information). No correlation between deer density and the severity of hemlock decline was found at these sites (Eschtruth & Battles 2008).

Deer Density

We used the fecal accumulation rate (i.e., clearance plot) method to estimate deer density (Supporting Information; Bailey & Putman 1981; Campbell et al. 2004). Twenty circular plots (hereafter pellet plots) (10-m radius) were established in each study site in a stratified random design (200 total plots). Plots were located at random distances (> 15 m) and bearings from each of the 18 permanent vegetation plots (Supporting Information) such that pellet plots were separated by a minimum of 95 m.

We calculated deer density as a function of defecation rate, length of census period, and the number of pellet groups (Supporting Information; Eschtruth & Battles 2008). We conducted 5 censuses—2 in winter and 3 in summer—to estimate localized deer densities (Supporting Information). We monitored the impacts of deer density and herbivory on vegetation at the same localized scale and thus accounted for deer habitat selectivity, which is not incorporated into standard measures of

Table 1. Summary of site characteristics for 10 hemlock forests in the Delaware Water Gap National Recreation Area (New Jersey and Pennsylvania).^a

Site	Canopy basal area in 2003 in 2003 (m ² /ha)	Hemlock relative basal area (%) in 2003	Deer density (deer/km ²) ^b	Slope (%)	Total transmitted radiation in 2003 (%)	Absolute increase 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

^aValues reported are means (SD). Basal area, total transmitted radiation, and vigor values were recorded at permanent vegetation plots and at exclosure plots (n = 58) for slope n = 40 per site and for deer density n = 20 per site.

^bAverage of summer and winter estimates from 2004, 2005, and 2006.

regional deer density. Our measures of plot-level deer abundance are reported as densities for ease of interpretation. A more typical estimate of deer density is the average of plot values of density for a site (as 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.

Deer Enclosures

In 2003, 40 deer enclosures (1 m² at base and approximately 1.2 m high) were placed in a stratified random manner in each of the 10 hemlock study sites (400 enclosures). An unenclosed control plot of the same size was randomly located between 1 and 4 m from each enclosure. Enclosures were placed at random distances (10–30 m) and bearings from each pellet plot. Enclosure and control plots were repositioned only if no vegetation was present. The enclosures in each study site were dispersed across a minimum area of 10 ha. Plots were monitored annually (2003–2006) from mid-June to July. We assumed browse damage was the result of deer herbivory and monitored the density of other herbivores (Supporting Information).

A visual estimate of percent cover for all plant species was recorded annually in each enclosure-control pair for 4 years. For the herbaceous exotic species, *A. petiolata* and *M. vimineum*, we also quantified the population density (number per square meter). The density of *B. thunbergii*, the only woody exotic, did not change over the study period and, therefore, was not included in the analysis. The total height of *B. thunbergii* (i.e., sum of the heights of the tallest live branch of each individual) was monitored (see Supporting Information for error estimates). We determined the statistical significance of herbivory impacts with *t* tests. All reported probabilities are Bonferroni adjusted to account for multiple comparisons.

Hemlock Canopy Decline

We used understory light levels to measure the timing and magnitude of the decline in the hemlock canopy because understory light availability is well correlated with direct assessments of hemlock decline and HWA infestation severity (Eschtruth et al. 2006; Eschtruth & Battles 2008). Moreover, these light measurements could be taken at the same fine scale as our experimental enclosures. Understory light availability at each plot was characterized in 2003 and 2006 with hemispherical photography (Supporting Information).

Model Development

We used maximum likelihood estimation (Edwards 1992) and information theoretics (Burnham & Anderson 2002) to quantify the strength of evidence for alternative models of the influence of deer density and the severity of

canopy decline on exotic plant abundance (i.e., density, cover, height). Each model (Supporting Information) represented a hypothesis about the shape of the herbivory-impact response curve as a function of deer density (*D*) and hemlock canopy decline (HCD). Hemlock canopy decline was quantified as an index based on the change in percent total transmitted radiation from 2003 to 2006 (ΔL) and scaled by the initial percent total transmitted radiation in 2003 (TL_0). To examine the effect of initial light availability (2003) on the impact of herbivory at a given level of canopy decline, we compared alternate models for each functional form in which canopy decline (Supporting Information) was replaced by one of the following functions:

$$HCD_0 = b_{\Delta L} \Delta L,$$

$$HCD_1 = b_{\Delta L} \Delta L + b_{TL_0} TL_0,$$

$$HCD_2 = b_{\Delta L} \Delta L * \frac{b_{TL_0}}{TL_0}, \text{ or}$$

$$HCD_3 = b_{\Delta L} \Delta L * TL_0^C,$$

where *b* is constant.

Models were fit to measurements of herbivory impact (*I*), which was calculated as the difference between the change in exotic species abundance (percent cover, population density, total height) in the control plot and the change in exotic species abundance in its paired enclosure plot from 2003 to 2006. A positive value of *I* indicated an increase in the exotic species in the control plot relative to the enclosure. We considered candidate models in 4 functional forms (Supporting Information): linear models (herbivory impacts directly proportional to deer density), exponential models (herbivory impact per deer increases with deer density), saturating models (herbivory impact plateaus at a certain deer density), and logistic models (little effect of herbivory 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). 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, Supporting Information).

Candidate models were compared for the 3 most abundant exotic plant species in these forests (97% of the relative exotic species frequency): *M. vimineum* (*n* = 129), *A. petiolata* (*n* = 181), and *B. thunbergii* (*n* = 152). These species are widespread, aggressive invaders; however, little is known about their susceptibility to deer herbivory (USDA/NRCS 2007).

Model Selection

We solved for the parameter estimates that maximize likelihood of the observed herbivory impacts by entering the results from an iterative global optimization procedure,

simulated annealing, into a local optimization procedure, Nelder-Mead. We validated the assumption of normally distributed errors by examining residuals. Statistical analyses and optimizations were conducted in S-Plus (Version 6.1, Insightful, Seattle, Washington).

We compared alternate models with corrected Akaike's information criteria (AIC_c ; Burnham & Anderson 2002). The AIC difference values (ΔAIC) provide 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 & Anderson 2002).

We calculated evidence ratios to compare models including indices of hemlock canopy decline 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 included deer density and HCD_0 , whereas the complete models included 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 (Burnham & Anderson 2002). We considered evidence ratios >10 as strong support for model improvement.

We also calculated 3 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 versus predicted data (a slope of approximately 1.0 indicated an unbiased model), and root mean squared error (RMSE) provided a measure of prediction error.

Results

From 2003 to 2006 the abundance of the 3 exotic plant species increased in the presence of deer herbivory, whereas abundance of the most common native plant species decreased (t test, all Bonferroni adjusted $p < 0.05$; Fig. 1). When averaged across all deer densities, the abundance of all 3 exotic species increased in the control plots relative to the paired exclosures ($p < 0.01$; Figs. 2–4). Although the relative difference in impact varied by species, exotic abundance consistently increased more in plots with higher than average deer densities (>15.1 deer/km²; $p < 0.003$; Figs. 2–4). All models produced unbiased estimates of herbivory impact (i.e., slope of regression of predicted versus observed of approximately 1.0) and symmetrically distributed residuals. The fraction

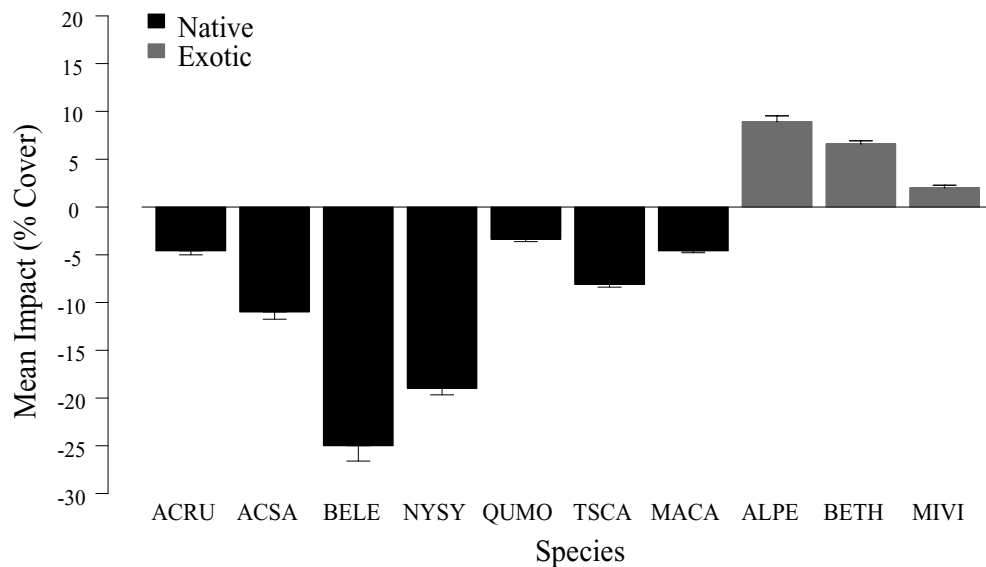


Figure 1. Mean impacts of deer herbivory on the percent cover of seedlings of the most common native tree species (ACRU, *Acer rubrum* [red maple]; ACSA, *A. saccharum* [sugar maple]; BELE, *Betula lenta* [black birch]; NYSY, *Nyssa sylvatica* [black gum]; QUMO, *Quercus montana* [chestnut oak]; TSCA, *Tsuga canadensis*; 78% relative seedling frequency); native herbaceous species (MACA, *Maianthemum canadense* [Canada mayflower]; 16% relative herb frequency); and exotic plant species (ALPE, *Alliaria petiolata*; BETH, *Berberis thunbergii*; and MIVI, *Microstegium vimineum*; 97% relative exotic plant frequency) from 2003 to 2006. A positive herbivory impact value indicates an increase in the exotic species in the control plot relative to the deer exclosure plot (error bars SE).

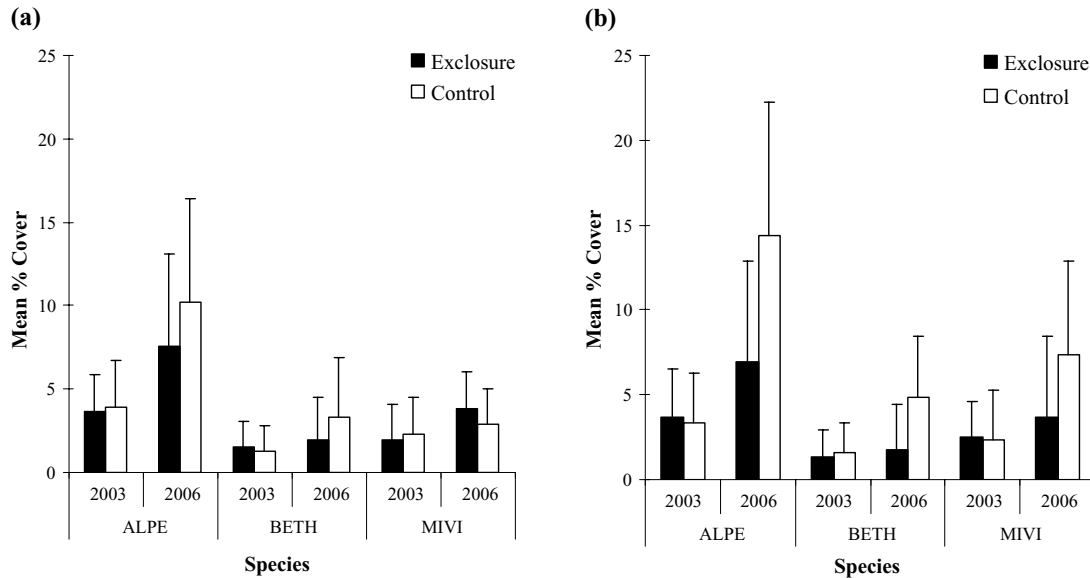


Figure 2. Comparison of mean percent cover of exotic plant species in deer exclosures and controls at (a) lower than average deer densities (<15.1 deer/ km^2) and (b) higher than average deer densities (>15.1 deer/ km^2) in 2003 and 2006 (ALPE, *Alliaria petiolata*; BETH, *Berberis thunbergii*; and MIVI, *Microstegium vimineum*; error bars SD).

of variation in herbivory impact explained by the best models ranged from 0.44 to 0.78 (Table 2). The measure of abundance that resulted in the best model fit varied by species: percent cover for *A. petiolata* (0.78), total height for *B. thunbergii* (0.73), and density for *M. vimineum* (0.63, Table 2). Root mean squared errors were between 1.71 and 5.56 for all highest ranked ($\Delta\text{AIC}_C < 4.0$) models.

For all species, the complete model form (i.e., model including D , ΔL , and TL_0) was the highest ranked model. 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 preference between species for the HCD_1 , HCD_2 , or HCD_3 form (Tables 2 & 3). In several cases no clear support emerged for one of these HCD_* .

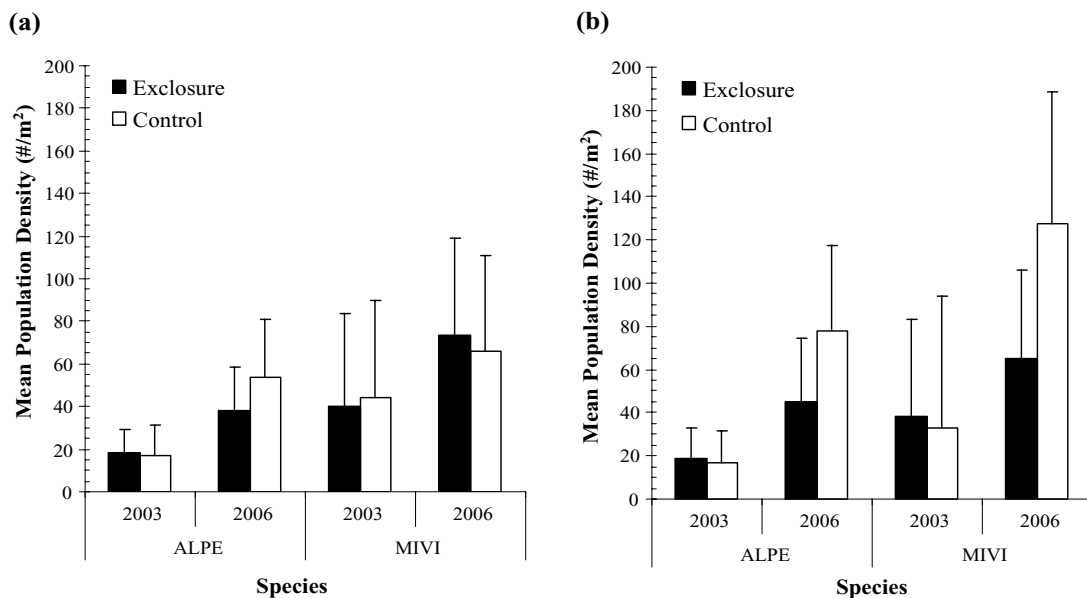


Figure 3. Comparison of exotic plant population density in deer exclosure and control plots at (a) lower than average deer densities (<15.1 deer/ km^2) and (b) higher than average deer densities (>15.1 deer/ km^2) in 2003 and 2006 (ALPE, *Alliaria petiolata* and MIVI, *Microstegium vimineum*; error bars SD).

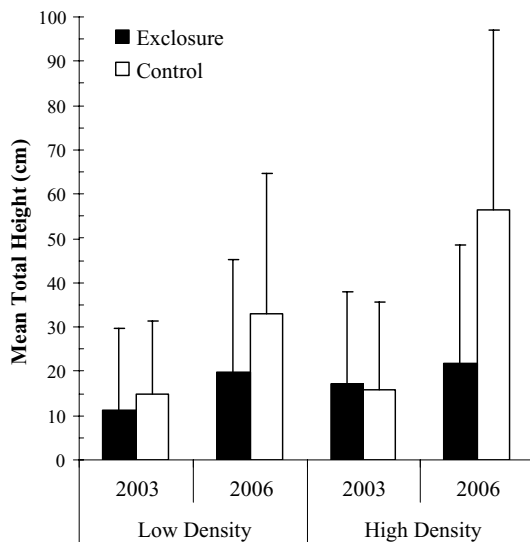


Figure 4. Comparison of *Berberis thunbergii* mean total height in deer exclosure and control plots at lower than average deer densities (<15.1 deer/km²) and at higher than average deer densities (>15.1 deer/km²) in 2003 and 2006 (error bars, SD).

forms within species, and the 2 or 3 models with these forms were included in the selected model set ($\Delta AIC_C < 4.0$; Table 2). 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 differed only by HCD_{*}) were summed. We refer to this value as the total weight (Table 2).

The exponential functional form had the greatest support for all species and abundance measures except *M. vimineum* percent cover, for which a linear model was selected (Table 2). Only for *M. vimineum*, percent cover was more than one functional form included in the selected model set. *M. vimineum* percent cover impact was also the only species-abundance measure combination that included both additive and interacting models in the selected model set. For all other selected models, there was clear support for either the interacting or additive form, although no overall trend was observed among the 3 species and abundance measures (Table 2).

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. Nevertheless, models run with the summer data resulted in a higher percentage of variance explained for all species-abundance measure combinations except for *B. thunbergii* (Table 2).

Model rankings for all species showed improved support for models including the canopy disturbance parameters—canopy decline severity (ΔL) and 2003 light availability (TL₀). The species base model, which included only estimates of deer density, was never in the

Table 2. Model rankings and goodness of fit for models of herbivory impacts on exotic species percent cover, count, and total height.

Data	Model ^a	ΔAIC_C ^b	w_i ^b	R ² summer ^c	R ² winter ^c	K ^d	Total weight ^e
Percent cover							
<i>Alliaria petiolata</i>	Exp _A .HCD ₁	0	0.35	0.78	0.69	7	0.96
	Exp _A .HCD ₃	0.13	0.33	0.78	0.69	7	
	Exp _A .HCD ₂	0.39	0.29	0.75	0.58	7	
<i>Berberis thunbergii</i>	Exp _I .HCD ₃	0	0.59	0.59	0.67	6	0.92
	Exp _I .HCD ₂	1.2	0.33	0.56	0.61	6	
<i>Microstegium vimineum</i>	Lin _A .HCD ₁	0	0.61	0.44	0.37	5	0.61
	Log _I .HCD ₁	3.43	0.11	0.36	0.29	5	
Population density							
<i>A. petiolata</i>	Exp _I .HCD ₁	0	0.78	0.70	0.65	6	0.90
	Exp _I .HCD ₂	3.69	0.12	0.65	0.64	6	
<i>M. vimineum</i>	Exp _I .HCD ₂	0	0.41	0.63	0.41	6	0.91
	Exp _I .HCD ₃	1.0	0.25	0.59	0.37	6	
	Exp _I .HCD ₁	1.0	0.25	0.59	0.37	6	
Total height							
<i>B. thunbergii</i>	Exp _A .HCD ₁	0	0.96	0.66	0.73	7	0.96

^a Results are presented by species for all models with a ΔAIC value <4 (i.e., evidence ratio <7.5). Model name indicates functional form (Exp, exponential function; Lin, linear function; Log, logistic function). The subscripts refer to the nature of the deer herbivory-hemlock canopy decline (HCD) interaction; A, additive model; I, interacting (i.e., multiplicative) model; B, base deer-density model. See Supporting Information for complete model forms.

^b The reported ΔAIC_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. The ΔAIC_C and w_i varied slightly but did not affect model selection.

^c The R² summer is the goodness of fit for the model with summer deer-density estimates, and R² winter is the goodness of fit for winter deer-density estimates.

^d Total number of parameters (includes SD of normal probability-density function).

^e 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_{*}).

Table 3. Model rankings and goodness of fit for the selected best model for each species (i.e., complete model) compared with the ΔL model (no initial light availability) and base model (deer density only) for the selected functional form.

Data	Model ^a	ΔAIC_C ^b	w_i ^b	R^{2b}	Evidence ratio	K		
Percent cover	<i>Alliaria petiolata</i>	Exp _A .HCD ₁	0.00	0.35	0.78	1	7	
		Exp _A .HCD ₀	51.37	0.00	0.75	1.43E+11	6	
		Exp _B	84.99	0.00	0.58	2.85E+18	4	
	<i>Berberis thunbergii</i>	Exp _I .HCD ₃	0.00	0.59	0.67	1	6	
		Exp _I .HCD ₀	8.13	0.01	0.56	58.31	5	
		Exp _B	42.52	0.00	0.53	1.71E+09	4	
	<i>Microstegium vimineum</i>	Lin _A .HCD ₁	0.00	0.61	0.44	1	5	
		Lin _A .HCD ₀	4.76	0.06	0.42	10.80	4	
		Lin _B	15.43	0.00	0.39	2241.05	3	
Population density	<i>A. petiolata</i>	Exp _I .HCD ₁	0	0.78	0.70	1	6	
		Exp _I .HCD ₀	11.77	0.02	0.69	358.91	5	
		Exp _B	23.16	0.00	0.62	1.07E+05	4	
	<i>M. vimineum</i>	Exp _I .HCD ₂	0.00	0.41	0.63	1	6	
		Exp _I .HCD ₀	4.38	0.05	0.60	8.95	5	
		Exp _B	11.71	0.00	0.56	349.10	4	
	Total height	<i>B. thunbergii</i>	Exp _A .HCD ₁	0.00	0.96	0.73	1	7
			Exp _A .HCD ₀	14.76	0.00	0.68	1602.50	6
			Exp _B	48.28	0.00	0.64	3.04E+10	4

^aModel name indicates functional form (Exp, exponential function; Lin, linear function; Log, logistic function). The subscripts refer to the nature of the deer herbivory–hemlock canopy decline (HCD) interaction; A, additive model; I, interacting (i.e., multiplicative) model; B, base deer-density model. See Supporting Information for complete model forms.

^bThe reported ΔAIC_C , w_i , and R^2 are from the model run with summer deer-density estimates for *A. petiolata* and *M. vimineum* and with winter deer-density estimates for *B. thunbergii*. Model rankings did not vary between summer and winter deer densities, and ΔAIC_C and w_i varied slightly but did not affect model selection.

set of selected best models (Table 3). For all species support for the complete model was overwhelming relative to the base model. Support for the complete model relative to the ΔL model was also very strong in most cases. Nevertheless, evidence ratios comparing the complete model and the ΔL model for *M. vimineum* showed only marginal improvement in support for inclusion of canopy-decline severity for impacts on percent cover (10.80) and density (8.95, Table 3).

Model predictions derived from the best models showed marked variation among species in the impacts occurring across the observed range of deer densities and the severity of canopy decline (Fig. 5). Cover impacts at high deer densities were predicted to be greatest for *A. petiolata* and lowest for *M. vimineum*. At low deer densities, *M. vimineum* cover and mean population density declined slightly from 2003 to 2006; however, at deer densities above approximately 12 deer/km², *M. vimineum* increased substantially in both measures in the control relative to the enclosure (Fig. 5).

Discussion

Our results suggest that a generalist herbivore, white-tailed deer, can accelerate the invasion of exotic plant species and that canopy disturbance has the potential to

interact with herbivory to magnify the observed impact. In addition, our results provide compelling evidence of nonlinear relationships between deer density and the impact of herbivory on exotic species abundance.

Herbivory and Exotic Plant Invasion

Our results are consistent with the enemy release hypothesis prediction that generalist enemies have a greater impact on native plant species relative to exotics (Fig. 1; Keane & Crawley 2002). It appears that *A. petiolata*, *B. thunbergii*, and *M. vimineum* experienced varying degrees of generalist enemy release (relative to competing native species) in these study sites. Nevertheless, we did not test the specific mechanisms accounting for the release. Our experimental approach only manipulated deer density (via exclosures) and our inferences are drawn from comparisons of the relative impact of deer density on plant cover. We suggest that the positive relationship between deer density and exotic plant abundance results from competitive release due to selective browsing of more preferred native plants. Although our results demonstrate that white-tailed deer are accelerating the invasion of exotic plants in these hemlock forests, we have no direct evidence that white-tailed deer preferred native plants to exotic plants. The role of selective deer browsing in indirectly promoting the abundance of low-preference, browse-resistant, or browse-tolerant native

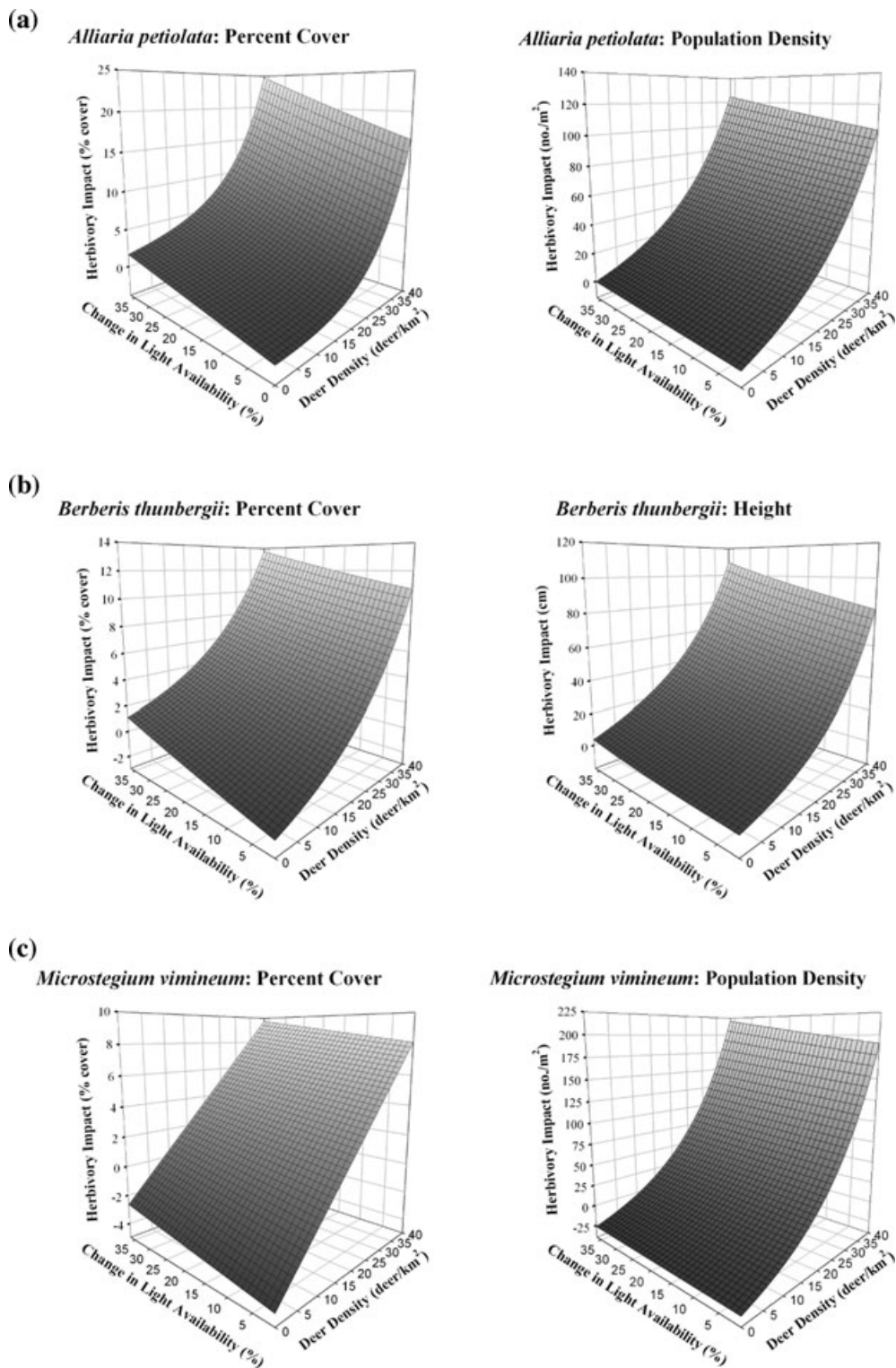


Figure 5. Predicted herbivory impact as a function of deer density and change in light availability from 2003 to 2006. Predictions for each species were generated from the top-ranked model shown in Table 2 for impacts on (a) percent cover and population density for *Alliaria petiolata*, (b) percent cover and total height for *Berberis thunbergii*, and (c) percent cover and population density for *Microstegium vimineum*. Initial light availability (2003) is held constant at the mean value (10.1%).

species has been demonstrated (Tilghman 1989; Horsley et al. 2003; Eschtruth & Battles 2008).

Our results provide convincing evidence of a link between a greater impact of white-tailed deer herbivory on native plants and improved exotic species performance (Fig. 1). An increase in plant species growth or abundance on release from specialist herbivores has been well documented (e.g., Louda & Potvin 1995; Wise & Sacchi 1996). In addition, recent work has provided evidence of lower herbivory of exotic plants relative to native plants (Carpenter & Cappuccino 2005). Few researchers, however, have directly assessed the relationship between generalist herbivore density and exotic species performance. Although the increased abundance of exotic plants due to a reduction in generalist enemy regulation is not well documented in forest ecosystems, introduced generalist grazers have been shown to facilitate the invasion of some exotic grasses (e.g., Mack 1981; O'Connor 1991).

Although *A. petiolata*, *B. thunbergii*, and *M. vimineum* are commonly believed to be avoided by white-tailed deer (e.g., Nuzzo 2000; Tu 2000), we found no published studies in which the impacts of deer herbivory on these species was investigated. Our results suggest that both *A. petiolata* and *B. thunbergii* are avoided by white-tailed deer across the range of deer densities occurring at our study sites. *M. vimineum* cover and population-density models, however, predicted negative impacts up to a relatively high deer density (approximately 12 deer/km²; Fig. 5). This suggests that *M. vimineum* abundance is reduced by deer herbivory at low to intermediate deer densities, likely resulting from direct consumption. At higher deer densities, the effect of this consumption appears to be overwhelmed by competitive release due to higher consumption of more preferred species.

Functional Form of Herbivory–Impact Relationship

Although deer impacts are typically estimated by assuming a directly proportional relationship to deer densities (e.g., Russell et al. 2001), our results provide strong evidence of nonlinear relationships. The existence of nonlinearities between deer densities and their impacts could have profound management implications. The most common native tree species at these sites experienced an exponential decline in seedling abundance with increasing deer density (Eschtruth & Battles 2008). We suggest the exponential increase in exotic species abundance with increasing deer density may be explained by the competitive release resulting from selective consumption of native species.

The exponential form of the deer-density–impact relationship was selected for all species models except the *M. vimineum* cover impacts (Table 2). *M. vimineum* cover responded linearly to deer density and canopy disturbance. This variation in model form between

M. vimineum abundance measures indicates that the number of individuals had a greater response than cover to competitive release at high deer densities. Because *M. vimineum* is an annual plant with a persistent seed bank, seedlings killed in late spring or early summer are often replaced by further germination (Barden 1987; Gibson et al. 2002). Competition at higher plant densities, however, may limit the size of individuals (i.e., cover; Leicht et al. 2005). Therefore, herbivory may reduce the size of individual plants more than the number of individuals.

Interaction between Canopy Disturbance and Herbivory

Our results demonstrate an interaction between herbivory and canopy disturbance that results in higher proportional herbivory impacts for higher canopy disturbance severities. Previous work at these sites supports an herbivory–disturbance interaction in which higher disturbance severity resulted in a greater reduction in the abundance of dominant native tree seedling (Eschtruth & Battles 2008) and herbaceous species (A.K.E., unpublished data) for a given deer density. We propose that more severe canopy disturbance resulted in increased exotic species abundance at a given deer density due to the competitive release resulting from the observed decrease in the abundance of many native species at higher levels of canopy disturbance.

The inclusion of both deer density and canopy-decline-severity measures consistently resulted in models with substantially greater support. Among the 3 species, *A. petiolata* was most affected by interaction between herbivory and change in light availability. This pattern reflects *A. petiolata*'s ability to persist in a wide range of light levels and to respond rapidly to release from competition (Dhillon & Anderson 1999; Meekins & McCarthy 2002). Although the predicted percent cover impacts for *A. petiolata* and *B. thunbergii* were similar up to nearly 20 deer/km², the response of *A. petiolata* increased much more rapidly at higher deer densities.

Although we suggest that competitive release through greater herbivory of native plants is the most likely explanation for the observed increase in *A. petiolata*, *B. thunbergii*, and *M. vimineum* abundance at higher deer densities, we cannot rule out the role of indirect deer impacts, such as soil disturbance and nutrient deposition. These indirect effects can alter patterns of carbon and nitrogen mineralization and provide establishment opportunities (Pastor et al. 1993; Wardle et al. 2001).

Implications and Conclusions

Our results provide compelling evidence of a competitive advantage for *A. petiolata*, *B. thunbergii*, and *M. vimineum* due to the greater impact of a generalist enemy on native plant species. Despite the diversity of the studied species and the strength of support observed for the selected models, we do not suggest that generalist

enemy release is a primary mechanism of invasion for all exotic plant species. Generalist mammalian herbivores can reduce the survival and reproduction of several non-native plants (D'Antonio 1993; Rachich & Reader 1999; Cadenasso et al. 2002). In particular, release from herbivores may not be an important mechanism of invasion for plants with close relatives in the recipient flora. For instance, in a phylogenetically controlled experiment, Agrawal and Kotanen (2003) found equal or greater levels of insect herbivore damage on exotic species relative to native species. Although this mechanism may not generalize to all exotic species, our results demonstrate that deer herbivory can facilitate the invasion of 3 important understory invaders, *A. petiolata*, *B. thunbergii*, and *M. vimineum* and, therefore, has important implications for the management of these species.

Our results highlight the important role of herbivore density in determining herbivory impacts on plant abundance. For instance, *M. vimineum* abundance declined at low deer densities and increased at high deer densities. Failure to account for the role of herbivore densities may dramatically alter the measured effect size and lead to flawed generalizations. Herbivore density may be an important confounding factor in studies that report the impacts of generalist herbivores without directly accounting for herbivore density. For example, in a recent meta-analysis, Parker et al. (2006) concluded that native herbivores are more likely to suppress exotic plants, whereas exotic herbivores are more likely to facilitate exotic plant invasion. Nevertheless, given the marked variation in herbivore densities, disparities in impacts by plant species at a given herbivore density, and the fact that the abundance of exotic herbivores is often elevated, herbivore density is likely a confounding factor in this type of analysis.

Our results demonstrate that white-tailed deer are accelerating the invasion of 3 common exotic plants in the studied hemlock forests. We also found, however, that multiple factors influenced the success of plant invasions. For example, although there was a clear relationship between exotic abundance and deer density, each of the studied species also increased in abundance in the absence of herbivory (Figs. 2–4). Thus, generalist herbivory only partially explained the proliferation of these exotic species. The ecology of exotic plant invasions in these ecosystems is a complex process, and the role of additional mechanisms, such as canopy disturbance and propagule pressure, should also be investigated. Disturbance, which is commonly considered a dominant mechanism for exotic plant invasion, is thought to facilitate plant invasion via direct impacts on resource availability (Hobbs & Huenneke 1992; Davis et al. 2000). Nevertheless, by providing evidence of an interaction between disturbance and herbivory, our results highlight the potential importance of indirect disturbance effects on exotic species invasion.

An understanding of the diverse mechanisms by which exotic species invade forests is critical to the develop-

ment of appropriate management strategies. As resources previously controlled by the hemlock canopy become available, understory species composition is undergoing dramatic changes and invasion by exotic plants has increased (Orwig & Foster 1998; Eschtruth et al. 2006). Without accounting for the role of white-tailed deer herbivory, the increased abundance of *A. petiolata*, *B. thunbergii*, and *M. vimineum* would likely be attributed solely to the effects of canopy disturbance. Nevertheless, our results suggest that high densities of white-tailed deer are increasing the opportunity for invasion of these exotic species.

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Supporting Information

Methodological details for measuring the hemlock-decline gradient and estimating deer densities (Appendix S1) and a summary of model forms are available as part of the on-line article (Appendix S2). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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