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Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion

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Abstract. The current rate of invasive species introductions is unprecedented, and the dramatic impacts of exotic invasive plants on community and ecosystem properties have been well documented. Despite the pressing management implications, the mechanisms that control exotic plant invasion remain poorly understood. Several factors, such as disturbance, propagule pressure, species diversity, and herbivory, are widely believed to play a critical role in exotic plant invasions. However, few studies have examined the relative importance of these factors, and little is known about how propagule pressure interacts with various mechanisms of ecological resistance to determine invasion success.

We quantified the relative importance of canopy disturbance, propagule pressure, species diversity, and herbivory in determining exotic plant invasion in 10 eastern hemlock forests in Pennsylvania and New Jersey (USA). Use of a maximum-likelihood estimation framework and information theoretics allowed us to quantify the strength of evidence for alternative models of the influence of these factors on changes in exotic plant abundance. In addition, we developed models to determine the importance of interactions between ecosystem properties and propagule pressure. These analyses were conducted for three abundant, aggressive exotic species that represent a range of life histories: *Alliaria petiolata*, *Berberis thunbergii*, and *Microstegium vimineum*.

Of the four hypothesized determinants of exotic plant invasion considered in this study, canopy disturbance and propagule pressure appear to be the most important predictors of *A. petiolata*, *B. thunbergii*, and *M. vimineum* invasion. Herbivory was also found to be important in contributing to the invasion of some species. In addition, we found compelling evidence of an important interaction between propagule pressure and canopy disturbance. This is the first study to demonstrate the dominant role of the interaction between canopy disturbance and propagule pressure in determining forest invasibility relative to other potential controlling factors. The importance of the disturbance–propagule supply interaction, and its nonlinear functional form, has profound implications for the management of exotic plant species populations. Improving our ability to predict exotic plant invasions will require enhanced understanding of the interaction between propagule pressure and ecological resistance mechanisms.

Key words: Alliaria petiolata; Berberis thunbergii; *canopy disturbance; Delaware Water Gap National Recreation Area, USA; exotic plants; hemlock woolly adelgid; herbivory; invasibility; invasive plants;* Microstegium vimineum*; propagule pressure; relative variable importance.*

Introduction

The ecological threats posed by exotic invasive plant species have intensified the need to better understand the factors determining invasion success. The current rate of invasive species introductions is unprecedented, and the dramatic impacts of invasive plant species on community and ecosystem function have been well documented (Vitousek and Walker 1989, D'Antonio and Vitousek 1992, Gordon 1998, Mack et al. 2000). Despite the pressing management implications, ecologists do not fully understand the mechanisms that control exotic plant invasion, and general theories explaining community susceptibility to invasion remain elusive.

The extent of exotic plant invasion varies widely among ecosystems. However, it is unclear to what degree these differences result from properties of the invading species, the number and distribution of arriving propagules (i.e., propagule pressure), or the inherent susceptibility of an ecosystem to invasion (i.e., invasibility; Lonsdale 1999). Invasibility is defined as the probability of establishment and subsequent survival of individual plants per arriving propagule or the increase in biomass or percent cover of the plant species over a specified time at a given propagule pressure (Davis et al. 2000). Our ability to attribute exotic plant invasion to differences in ecosystem invasibility requires an improved understanding of the factors that control "ecological resistance," the community properties that

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negatively influence an environment's susceptibility to invasion, and insight into how these resistance factors interact with the supply of propagules to influence exotic plant invasions (Lonsdale 1999, D'Antonio et al. 2001). Many aspects of ecological resistance have been related to invasibility, foremost among these are the roles of disturbance (Crawley 1987), herbivory (Maron and Vila 2001, Keane and Crawley 2002, DeWalt et al. 2004), and species diversity (Elton 1958, Kennedy et al. 2002). However, few studies have examined the relative importance of these mechanisms. Exotic plant invasions are likely the result of many factors. Therefore, it is critical that we quantitatively assess the relative importance and potential interactions among these mechanisms under field conditions. In this study, we quantified the relative importance of three components of ecological resistance (disturbance, herbivory, and species diversity) and of propagule pressure in contributing to exotic plant invasion.

Disturbance is commonly implicated in exotic plant invasions (Elton 1958, Lodge 1993, Burke and Grime 1996). Although the mechanism by which disturbance facilitates invasion is rarely investigated, it may be due to reduced competition, higher resource availability, and/or increased propagule pressure (Hobbs 1989, Hobbs and Huenneke 1992, D'Antonio 1993, Davis et al. 2000). Furthermore, changes in the severity, frequency, and type of disturbance could alter community susceptibility to invasion (Hobbs and Huenneke 1992).

The successful invasion of exotic plants is often attributed to the absence of coevolved enemies in the introduced range (Darwin 1859, Elton 1958, Crawley 1987, DeWalt et al. 2004). 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 (Mack et al. 2000, Shea and Chesson 2002). The enemy release hypothesis predicts that, in the introduced range, both specialist and generalist enemies will have a greater impact on native plant species than on exotics. To date, most tests of the enemy release hypothesis have examined the role of plant release from specialist enemies (Maron and Vila 2001, Keane and Crawley 2002). However, Keane and Crawley (2002:164) note that "competitive release through greater generalist enemy impact on natives seems to be an important but understudied mechanism of enemy release."

The idea that species-rich communities are less susceptible to invasion by exotic plants has received considerable attention (Elton 1958, Levine and D'Antonio 1999, Kennedy et al. 2002). This theory contends that more diverse assemblages use available resources more completely and, therefore, exclude the establishment of additional species (MacArthur 1970). However, empirical tests of this theory have produced decidedly mixed results (Tilman 1997, Lonsdale 1999, Naeem et al. 2000, Stohlgren et al. 2002). This inconsistency may reflect environmental factors that covary with species diversity or the scale at which these studies were conducted (Levine and D'Antonio 1999, Stohlgren et al. 2003).

Gradients in propagule pressure are believed to be a major source of the variation in invasion between communities. Greater numbers of introductions and more propagules per introduction should result in increased invasion success (Simberloff 1989, Williamson and Fitter 1996, Green 1997). In the few studies that have considered the role of propagule pressure in invasion success, it was consistently found to be a prevailing factor (Tilman 1997, von Holle and Simberloff 2005, Colautti et al. 2006). While it is clear that differences in dispersal play an important role in invasion success, few studies have quantified the role of variation in propagule supply in determining invasion patterns across sites (Colautti et al. 2006). In addition, little is known about how propagule pressure interacts with the various mechanisms of ecological resistance to determine invasion success (D'Antonio et al. 2001).

In this study, we examined the relative importance of disturbance, herbivory, species diversity, and propagule pressure in the establishment and growth of three invasive plant species that represent a range of life-history strategies: an annual grass, Japanese stiltgrass (*Microstegium vimineum*); a biennial forb, garlic mustard (*Alliaria petiolata*); and a woody shrub, Japanese barberry (*Berberis thunbergii*). These were the most common exotic species in our study sites (Eschtruth et al. 2006) and are considered widespread, aggressive invaders (Ehrenfeld 1999, Nuzzo 1999, Gibson et al. 2002, USDA/NRCS 2007). The relative importance of the mechanisms governing invasion of these plant species was assessed in 10 eastern hemlock (*Tsuga canadensis*) forests that span a gradient in canopy decline severity resulting from the infestation of an introduced insect pest, the hemlock woolly adelgid (HWA; *Adelges tsugae*; Orwig and Foster 1998, Eschtruth et al. 2006). As resources previously controlled by the hemlock canopy become available to other plants, understory species composition is undergoing dramatic change and invasion by exotic plant species has increased (Orwig and Foster 1998, Eschtruth et al. 2006). Although the spread of exotic invasive plants in these forests has been attributed to hemlock canopy decline (e.g., Orwig and Foster 1998), the specific mechanisms controlling this invasion remain unclear. Additional factors such as white-tailed deer (*Odocoileus virginianus*) herbivory, which has been shown to accelerate exotic plant invasion (A. K. Eschtruth and J. J. Battles, *unpublished manuscript*), and increased propagule pressure may be more important in explaining exotic plant invasion.

Although many studies have examined the potential determinants of invasibility, few have simultaneously investigated the relative importance of multiple invasion mechanisms (von Holle and Simberloff 2005). Our main

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

Site	Canopy basal area in 2003 (m^2/ha)	Hemlock relative basal area in 2003 (%)	Deer density (deer/km^2)†	Total transmitted radiation in 2003 (%)	Absolute increase in total transmitted radiation 2003–2006 (%)	Vascular plant cover in 2003 (%)
Adams Creek	55.2 (20.5)	53.5	17 (6)	13.4 (6.0)	5.7	16.6 (24.2)
Buttermilk Falls	42.7 (20.9)	51.6	18 (11)	14.3 (4.2)	11.3	8.7 (6.6)
Conoshaugh	53.4 (36.4)	78.3	5 (2)	10.8 (5.2)	2.5	11.4 (10.5)
Donkeys Corner	53.1 (29.7)	61.1	15 (7)	9.7 (4.6)	7.2	9.2 (11.1)
Dry Brook	37.8 (21.4)	56.3	23 (13)	11.4 (4.5)	8.6	14.3 (17.9)
Fulmer Brook	46.6 (21.0)	65.9	22 (10)	6.7 (3.1)	4.4	4.0 (4.3)
Spackmans	45.6 (20.6)	82.0	8 (3)	8.1 (2.7)	2.2	6.1 (4.8)
Tumbling Water	59.1 (30.8)	83.9	13 (5)	5.9 (3.3)	1.8	2.1 (1.7)
Van Campens Brook	48.8 (24.0)	57.4	16 (10)	7.9 (3.9)	3.4	3.4 (3.9)
Warner Brook	32.6 (16.3)	73.2	11 (6)	15.7 (4.0)	12.5	19.8 (14.5)

Notes: Values reported are means with SD in parentheses. Basal area and total transmitted radiation are based on measures recorded at permanent vegetation plots and at exotic-plant-monitoring plots ($n = 58$ per site). Vascular plant cover is based on measures recorded at permanent vegetation plots ($n = 18$ per site). For deer density, $n = 20$ per site.

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

objective was to quantify the relative importance of canopy disturbance, herbivory, species diversity, and propagule pressure in determining exotic plant invasion in declining hemlock forests. In addition, we assessed the potential interactions between these factors. Due to the marked gradients in canopy disturbance, herbivory, species diversity, and propagule pressure, our study system provided an ideal opportunity to investigate the manner in which propagule pressure interacts with several mechanisms of ecological resistance to determine community susceptibility to invasion. We hypothesize that propagule pressure drives invasion but that its relative importance is reduced at high levels of deer herbivory or canopy disturbance.

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 forests dominated by eastern hemlock 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 flow into the Delaware River. At the beginning of the study, hemlock accounted for >50% of canopy basal area at each study site with other canopy constituents including *Acer saccharum* (sugar maple), *Quercus montana* (chestnut oak), *Acer rubrum* (red maple), *Betula lenta* (black birch), *Betula alleghaniensis* (yellow birch), *Quercus alba* (white oak), and *Pinus strobus* (eastern white pine; nomenclature follows Rhoads and Block 2000). 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 ~90 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). In 2003, when this study was initiated, a striking gradient in HWA-induced canopy decline was observed across our 10 study sites (Table 1; Eschtruth and Battles 2008). This gradient presumably resulted from a differential rate of HWA spread between the spatially disjunct, topographically isolated hemlock forests in the Park (Evans 2004, Eschtruth et al. 2006, Eschtruth and Battles 2008).

A distinct gradient in exotic plant propagule pressure occurred across the 10 study sites. The spread of exotic plants into these hemlock forests was a relatively recent occurrence. In fact, surveys of two of these study sites in 1994 found that, while *A. petiolata*, *B. thunbergii*, and *M. vimineum* were present along roadsides and in adjacent hardwood forests, these species did not occur in the studied hemlock forests (Eschtruth et al. 2006). However, in 2003, these exotic species were present, to varying degrees, in all of the study sites, and their patchy occurrence constituted an important propagule source within many of the studied forests (Table 2).

Habitat selectivity by deer results in unequal use of habitat patches within landscapes and, therefore, results in a wide range of deer densities within and between sites (Table 1; Loft and Kie 1988, Healy et al. 1997, Eschtruth

TABLE 2. Summary of exotic plant species density and indices of propagule pressure (PP_{SR} and PP_{SBG}) for the 10 studied hemlock sites in the Delaware Water Gap National Recreation Area in 2006.

Species	Plant density (no./m^2)	Mean distance (m)	Mean PP_{SR}	Mean PP_{SBG}
Alliaria petiolata	0.07 (0.21)	9.5 (10.4)	0.39 (0.31)	0.34 (0.28)
Berberis thunbergii	0.004 (0.02)	4.7 (4.6)	0.42 (0.28)	0.56 (0.25)
Microstegium vimineum	0.11 (0.25)	6.2 (5.9)	0.37 (0.32)	0.43 (0.33)

Notes: Values reported are means with SD in parentheses. Plant density values are reported as an average of all 30 m radius plots established around each of the exotic-species-monitoring plots ($n = 400$). The mean distance measures and indices of propagule pressure are based on $n = 181$ plots for *A. petiolata*, $n = 152$ plots for *B. thunbergii*, and $n = 129$ plots for *M. vimineum*. SR is seed rain; SBG is seed bank germination.

and Battles 2008). 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; C. Kandoth, *personal communication*). These management zones contain areas outside of 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 15–19 deer/km^2 (L. Hilaire, *personal communication*). At our research sites, there was no correlation between deer density and hemlock decline severity (Eschtruth and Battles 2008).

Plot design

In each of the 10 hemlock forests, permanent vegetation plots (5 m radius) were established in 2003 (except at two sites, 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 at the stream, mid-slope, and edge of hemlock-dominated forest (18 plots per site; Appendix A). The location of all plots was recorded with a geographic positioning device, and corners were marked with rebar to ensure precise relocation.

In 2003, 40 plots (1 m^2) were established in each study site (400 total plots) to monitor the spread of exotic plants. These exotic-species-monitoring plots were placed at random distances (10–30 m) and bearings from the deer density plots: all deer density plots were used to position two 1-m^2 plots. Plots were repositioned only if no vegetation was present. At each site, the monitoring plots were dispersed across a minimum area of ~10 ha.

In each of these 400 plots, the percent cover and density of all plant species was measured annually (2003–2006) from mid-June to July. To assess error in percent cover measurements, 10% of plots at each site were resurveyed during each annual census (percent cover rRMSE = 2.1%). In addition, for each exotic-species-monitoring plot, we recorded the species, diameter at breast height (dbh [measured at 1.37 m above the ground surface], ≥2 cm), and vigor of all trees ≥1 m tall within a 5-m radius.

Canopy disturbance

The change in total transmitted radiation from 2003 to 2006 was used as an index of hemlock canopy disturbance. While change in light is just one of several ecological consequences of HWA infestations, understory light availability is well correlated with direct assessments of hemlock decline and HWA infestation severity (Eschtruth et al. 2006, Eschtruth and Battles 2008). Understory light availability at each of the 400 monitoring plots was characterized in 2003 and 2006 through use of hemispherical photographs (Appendix A).

Herbivory

We used white-tailed deer density as an indicator of herbivory impact (Eschtruth and Battles 2008). Deer density was estimated from fecal pellet group counts using the fecal accumulation rate (FAR) method (i.e., clearance plot; Appendix A; Bailey and Putman 1981, Campbell et al. 2004). This is the preferred method for estimating deer density in forests, particularly evergreen forests, with high pellet group density and has been shown to accurately represent seasonal habitat use (Leopold et al. 1984, Loft and Kie 1988, Marques et al. 2001). Twenty circular pellet group plots (10-m radius) were established in each study site 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.

We calculated deer density as a function of defecation rate, length of census period, and the number of pellet groups counted (Appendix A). We conducted five censuses: two winter and three summer use estimates (Appendix A). We monitored deer density and impacts on vegetation at the same localized scale to account for the deer habitat selectivity that is not incorporated into standard measures of regional deer density (see Appen-

dix A, method rationale). These localized density estimates should be interpreted as a relative index of deer density or intensity of use and not as a measure of absolute regional deer abundance (Eschtruth and Battles 2008).

Species diversity

We used species richness (the total number of species within each 1-m^2 plot) as a metric of species diversity (sensu Levine 2000, Stohlgren et al. 2002, Brown and Peet 2003). The 1-m^2 plot data reflect the immediate competitive environment of arriving exotic species propagules and may help provide insight into the mechanistic relationship between species diversity and community invasibility (i.e., direct competitive effects or covarying environmental factors).

Propagule pressure

We developed two indices to estimate seed availability at the plot level: (1) a seed rain (SR) index based on the weighted distance to the nearest seed sources, seed dispersal distance, and estimates of seed production and (2) an effective seed bank germination (SBG) index based on the number of successful germinants obtained from soil samples in greenhouse seedbed germination studies.

Seed rain index.—A 30 m radius plot was established around each of the 400 monitoring plots. In each of these plots we conducted a detailed mapping of the distribution, cover, and density of all exotic plant species. For *A. petiolata*, the age class (i.e., first-year basal rosette or second-year plants with flower stalks) was noted. These surveys were completed in June of 2003, 2005, and 2006. Measures of cover and density were repeated in early August of 2003 and 2005 to account for seasonal variation. This information was combined into geographic information systems (GIS) maps and used to calculate an index of seed rain for each exotic-species-monitoring plot as

$$\mathrm{SR} = \sum_{n=1}^{N} \mathrm{fecundity} \times e^{(-b)\,\mathrm{distance}_n} \qquad (1)$$

where SR is the seed rain index, N is the total number of individuals of a given exotic species, fecundity is the number of seeds produced per plant, distance is the distance in meters to each individual within 30 m (n), and b is the dispersal coefficient for the negative exponential seed dispersal curve (see Appendix A for methodological details). For *A. petiolata*, we assessed the strength of support for an index of seed rain including only second-year reproducing plants and an index including all individuals. For each species, these plot-level estimates of seed rain (PP_{SR}) were normalized by the maximum observation to scale the values between 0 and 1.

The seed rain index provided an estimate of propagule availability based on local dispersal patterns; however, it did not account for long-distance dispersal events. Although dispersal agents and patterns of the studied species are not well known, the importance of long-distance dispersal has been suggested for each (Cavers et al. 1979, Ehrenfeld 1999, Nuzzo 1999, Silander and Klepeis 1999, Meekins and McCarthy 2001). Therefore, we conducted seed bank germination studies to provide an index of the number of propagules actually arriving at these plots.

Seed bank germination index.—Seed bank composition was assessed using direct germination methods (Gross 1990). Two soil samples were collected near each of the exotic-species-monitoring plots in May of 2003, 2005, and 2006 (800 total samples in each year; see Appendix A for methodological details). A metal cylinder with a 20-cm diameter was used to collect soil to a depth of 10 cm. Soil samples were divided into two depth classes: 0–5 cm and >5–10 cm. Within 24 h after collection, each sample was hand-mixed and spread to a depth of <2 cm over a base of sterile peat-based growth substrate (Sunshine germinating mix number 3; Sun Gro Horticulture Canada, Vancouver, British Columbia, Canada) in a labeled cell of a divided potting tray. All samples were exposed to natural lighting conditions in a temperature-controlled (minimum, 15°C; maximum, 30°C) glasshouse and watered as required to keep the soil moist. Each tray also contained two cells of sterile soil to check for greenhouse seed contamination. Trays were rotated periodically to account for heterogeneity in the glasshouse environment.

All seedlings that emerged were identified to species and removed (see Appendix A for methodological details). For each species, the index of seed bank germination was then calculated by summing the number of germinants observed in 2003, 2005, and 2006. For each species, these plot-level estimates of seed bank germination (PP_{SBG}) were normalized by the maximum observation to scale the values between 0 and 1.

Model development

We used maximum-likelihood estimation (Edwards 1992) and information theoretics (Buckland et al. 1997, Burnham and Anderson 2002) to quantify the strength of evidence for alternative models of the influence of HWA canopy disturbance (HWA), deer herbivory (DH), species diversity (SD), and propagule pressure (PP_{SR} and PP_{SBG}) on exotic plant abundance (i.e., density and cover). Each model represents a different hypothesis about the role of these factors in the change in exotic plant species abundance over the study period. Models were fit to observations of exotic plant invasion (I), which was calculated as the change in abundance (percent cover and density) of each exotic plant species from 2003 to 2006.

We initially considered candidate models in four general functional forms that represent common hypotheses suggested to explain the pattern of exotic plant

invasion: linear, exponential, saturating, and logistic. Likelihood values from a preliminary comparison of these functional forms demonstrated that only linear and exponential models warranted further investigation. Therefore we compared exponential and linear models in which the four invasion mechanisms (HWA, DH, SD, and PP) were considered alone and in combination. To investigate our hypothesis that the relative importance of propagule pressure in invasion is altered at high levels of canopy disturbance or deer herbivory, we compared candidate models that included the following interactions: canopy disturbance and propagule pressure, herbivory and propagule pressure, and a three-way interaction between canopy disturbance, deer herbivory, and propagule pressure. We also considered a canopy disturbance–herbivory interaction, as it was shown to be important in predicting the invasion of the studied species (A. K. Eschtruth and J. J. Battles, *unpublished manuscript*). In total we evaluated 47 models.

The three most abundant exotic plant species in these forests were selected for this analysis (97% of the relative exotic species frequency): *Microstegium vimineum* ($n = 129$), *Alliaria petiolata* ($n = 181$), and *Berberis thunbergii* ($n = 152$). To compare the impact of propagule pressure on invasion success (I) at high and low canopy disturbance severities, we calculated an invasibility index: mean increase in exotic plant species cover and density (2003 to 2006) at a given propagule pressure (i.e., invasion/propagule pressure). To make comparisons across species, changes in exotic species abundance (I) were normalized by the maximum change observed for each species. We compared results from the five sites with the highest vigor and crown rating measures (i.e., healthy stands) and the five sites with the lowest measures (i.e., declining stands; Eschtruth and Battles 2008).

Model selection

We solved for the parameter estimates that maximized the likelihood of the observed changes in exotic plant abundance by entering the results from an iterative global optimization procedure, simulated annealing, into a local optimization procedure, Nelder-Mead (Nelder and Mead 1965). We validated the assumption of normally distributed errors by examining 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; Burnham and Anderson 2002; Appendix A). The AIC difference values (ΔAIC), the difference between the AIC_c value of a given model (AIC_i) and the AIC_c value of the best model (AIC_{min}), 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).

To provide a relative ranking of variables in order of their importance for each species, we calculated the relative variable importance values for canopy disturbance, herbivory, species diversity, and propagule pressure. Relative variable importance is calculated for a given variable by summing the Akaike weights across all models in the candidate set in which the variable occurs (Burnham and Anderson 2002). Because we were interested in the relative importance of the individual variables, we excluded the models with interaction terms from the calculations of relative variable importance. When interactions between variables did occur in the selected model set, we assessed the strength of evidence for these interactions by calculating evidence ratios to compare the selected best model with and without interacting variables. Evidence ratios (ratio between Akaike weights) 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).

Although our analysis focused on the relative importance of variables rather than on model fitting, 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

From 2003 to 2006, the mean cover and density of *A. petiolata* (mean cover increase, 12.5%; mean density increase, 48.4 plants/m^2), *B. thunbergii* (mean cover increase, 6.4%; mean density increase, 2.7 plants/m^2), and *M. vimineum* (mean cover increase, 3.1%; mean density increase, 78.1 plants/m^2) increased in the studied plots (t test, all Bonferroni-adjusted $P < 0.01$; Appendix B). Although these species occurred in many study plots in 2003, over the study period 42% of plots were invaded by *A. petiolata*, 15% by *B. thunbergii*, and 23% by *M. vimineum*. In 2006, the exotic plant density and spatial distribution varied greatly among species (Table 2).

Hemlock canopy decline severity, deer density, plant species diversity, and propagule pressure varied considerably within and among sites (Tables 1 and 2). The mean plot level increase in understory light availability for the 400 exotic species plots was 11.6% $\pm$ 0.38% (mean $\pm$ SE). The index of deer density ranged from 0.4 to 40.9 deer/km^2 and averaged 15.1 deer/km^2. Species richness ranged from 1 to 21 species/plot with a mean of

TABLE 3. Model rankings and goodness of fit for models of the effects of canopy disturbance (HWA), herbivory (DH), species diversity (SD), and propagule pressure indices, seed rain (PP_{SR}) and seed bank germination (PP_{SBG}), on exotic species percent cover and density.

Model	ΔAIC_c	w_i	R^2	K
Percent cover				
Alliaria petiolata				
HWA × PP_{SR}.DH	0	0.39	0.58	6
HWA × PP_{SBG}.DH	0.45	0.31	0.55	6
Berberis thunbergii				
HWA × PP_{SBG}.DH	0	0.51	0.44	6
HWA × PP_{SBG} × DH	1.64	0.22	0.43	5
HWA × PP_{SBG}	2.80	0.12	0.38	4
Microstegium vimineum				
HWA.PP_{SR}	0	0.47	0.31	3
HWA.PP_{SBG}	1.18	0.25	0.28	3
HWA.PP_{SR}.DH	2.97	0.11	0.25	4
Population density				
Alliaria petiolata				
HWA × PP_{SR}.DH	0	0.49	0.47	6
HWA × DH.PP_{SR}	1.88	0.19	0.43	5
Berberis thunbergii				
HWA × PP_{SBG}	0	0.58	0.29	4
Microstegium vimineum				
HWA.PP_{SBG}	0	0.55	0.39	5
HWA.PP_{SR}	1.58	0.24	0.37	5
HWA.PP_{SBG}.SD	2.89	0.12	0.33	7

Notes: Results are presented by species for all models with an Akaike Information Criterion difference value (ΔAIC) <3. An "×" denotes a multiplicative interaction between variables, and "." indicates variable inclusion. K is the total number of parameters (includes standard deviation of normal probability density function); w_i is the Akaike weight. Both of the selected *M. vimineum* percent cover models were linear. All other models presented in this table were exponential.

5.8 ± 0.18 species/plot. Propagule pressure indices varied considerably among plots (Table 2) and among species (Appendix B). Seed rain varied twofold and seed bank germination varied 15-fold among species (Appendix B). Although there were no significant correlations between these predictor variables (all VIF < 2), species diversity had a weak, positive correlation with canopy disturbance (Pearson's product–moment correlation, $r = 0.21$).

Evaluation of model form

All models produced unbiased estimates of exotic plant invasion (regression slopes ~1.0 for predicted vs. observed) and symmetrically distributed residuals. The fraction of variation in invasion explained by the top-ranked models ranged from 0.29 to 0.58 (Table 3). The measure of abundance that resulted in the best model fit varied by species: percent cover for *A. petiolata* (0.58) and *B. thunbergii* (0.44) and population density for *M. vimineum* (0.39; Table 3). Root mean squared errors were between 1.8 and 5.7 for the highest ranked models ($\Delta AIC_c < 4.0$).

Varying the *A. petiolata* seed rain index (PP_{SR}; index based on second-year plants or including both age classes) did not alter the model rankings for either abundance measure, and the resulting ΔAIC_c and w_i values varied only slightly. However, inclusion of both age classes in the seed rain index improved model fits. Therefore, all reported *A. petiolata* results are based on the PP_{SR} calculated with both first- and second-year plants.

Within the candidate model set, the exponential model was the highest ranked for all species and abundance measures except *M. vimineum* percent cover, for which a linear model was selected (Table 3). The Akaike weights (w_i) of the top-ranked models varied between 0.39 and 0.51 for cover and between 0.49 and 0.58 for plant density.

Relative variable importance

For all species and abundance measures, canopy disturbance (HWA) and propagule pressure (i.e., total PP, the sum of both indices of propagule pressure) had the highest relative variable importance values (Table 4). Compared to the other species, propagule pressure had the lowest importance values for *B. thunbergii* and canopy disturbance had the lowest importance values for *M. vimineum*. Species diversity (SD) did not occur in the highest ranked model for any species and had the lowest overall importance values. For both abundance measures, deer herbivory (DH) was most important in models of *A. petiolata* invasion and least important in models of *M. vimineum* invasion. All candidate factors (HWA, DH, SD, PP) for which a relationship was observed had a positive impact on exotic plant invasion.

TABLE 4. Relative variable importance of canopy disturbance (HWA), herbivory (DH), species diversity (SD), and propagule pressure (PP) in models predicting exotic species percent cover and density.

Species	Canopy disturbance	Herbivory	Species diversity	Propagule pressure indices		
				PP_{SR}	PP_{SBG}	Total PP
Percent cover						
Alliaria petiolata	1.0	0.96	0.12	0.54	0.43	0.97
Berberis thunbergii	1.0	0.67	0.02	0.09	0.62	0.71
Microstegium vimineum	0.90	0.34	0.15	0.25	0.58	0.83
Population density						
Alliaria petiolata	0.93	0.61	0.09	0.59	0.41	1.0
Berberis thunbergii	1.0	0.24	0.00	0.05	0.84	0.89
Microstegium vimineum	0.81	0.04	0.32	0.33	0.67	1.0

Notes: Models with interaction terms were excluded from the calculations of relative variable importance. The indices of propagule pressure, PP_{SR} and PP_{SBG}, were substituted into all models and never occur in the same model. Therefore, this is a conservative estimate of their importance values because HWA, DH, and SD each occur in 24 models and PP_{SR} and PP_{SBG} occur in only 16 models. The sum of PP_{SR} and PP_{SBG} relative importance values provides a measure of the overall importance of propagule pressure. Because these indices were substituted in all models and never occur in the same model, the maximum value of the combined indices is 1.

The index of propagule pressure with the highest relative variable importance varied between species (note that the maximum value of the combined indices is 1). The relative variable importance of the seed bank germination index greatly exceeded that of the seed rain index for *B. thunbergii*. The relative importance values of the two propagule pressure indices were more similar for *A. petiolata* and *M. vimineum*, though PP_{SBG} had a higher importance value for both measures of *M. vimineum* abundance.

Interactions between variables

For *A. petiolata* and *B. thunbergii*, all models in the selected set included interactions between variables (Table 3) and support for the models including interaction terms was overwhelming (Table 5). For *A. petiolata*, the highest ranked models for both plant cover and density contained an interaction between canopy disturbance and propagule pressure (Tables 3 and 5). In addition, a model including an interaction between canopy disturbance and herbivory is in the selected model set for *A. petiolata* density (Table 3). The highest ranked models for *B. thunbergii* percent cover and density both included an interaction between canopy disturbance and propagule pressure (Tables 3 and 5). A model including an interaction between canopy disturbance, propagule pressure, and herbivory is in the selected set for *B. thunbergii* cover (Table 3). No interaction terms appeared in the selected model set for *M. vimineum*.

The magnitude of the influence of canopy disturbance and propagule pressure on changes (2003 to 2006) in invasive plant cover and density varied markedly among the three focal species (Figs. 1 and 2). For instance, canopy cover and its interaction with propagule pressure had a greater effect on *B. thunbergii* abundance, whereas *M. vimineum* abundance was driven more by propagule pressure. Model predictions also illustrate the different effects of canopy disturbance and propagule pressure between abundance measures for each species (Figs. 1 and 2). For example, changes in the cover of *A. petiolata* were more impacted by canopy disturbance than by propagule pressure, whereas *A. petiolata* density was more evenly dependent on both factors and their interaction (Figs. 1 and 2). Note that for species in which deer herbivory was also included in the highest

TABLE 5. Model rankings, goodness of fit, and evidence ratios comparing selected best models with and without interacting variables, including only species and abundance measures for which the selected best model contained an interaction term.

Model	ΔAIC_C	w_i	R^2	Evidence ratio	K
Percent cover					
Alliaria petiolata†					
HWA × PP_{SR}.DH	0	0.39	0.58	1	6
HWA.PP_{SR}.DH	6.03	0.02	0.49	20.47	7
HWA × PP_{SBG}.DH	0.45	0.31	0.55	1	6
HWA.PP_{SBG}.DH	6.72	0.02	0.46	23.13	7
Berberis thunbergii					
HWA × PP_{SBG}.DH	0	0.51	0.44	1	6
HWA.PP_{SBG}.DH	10.28	0.00	0.32	170.60	6
Population density					
Alliaria petiolata					
HWA × PP_{SR}.DH	0	0.49	0.47	1	6
HWA.PP_{SR}.DH	19.75	0.00	0.31	1.94×10^4	7
Berberis thunbergii					
HWA × PP_{SBG}	0	0.58	0.29	1	4
HWA.PP_{SBG}	11.6	0.00	0.20	323.52	5

Notes: An "×" denotes a multiplicative interaction between variables, and "." indicates variable inclusion. Abbreviations are: HWA, canopy disturbance; DH, herbivory; SD, species diversity; PP, propagule pressure; PP_{SR}, seed rain; PP_{SBG}, seed bank germination. ΔAIC_c is the Akaike Information Criterion difference value; w_i is the Akaike weight; K is the total number of parameters (includes standard deviation of normal probability density function).

† The two best models are presented for *A. petiolata* cover because they had nearly identical AIC weights (w_i).

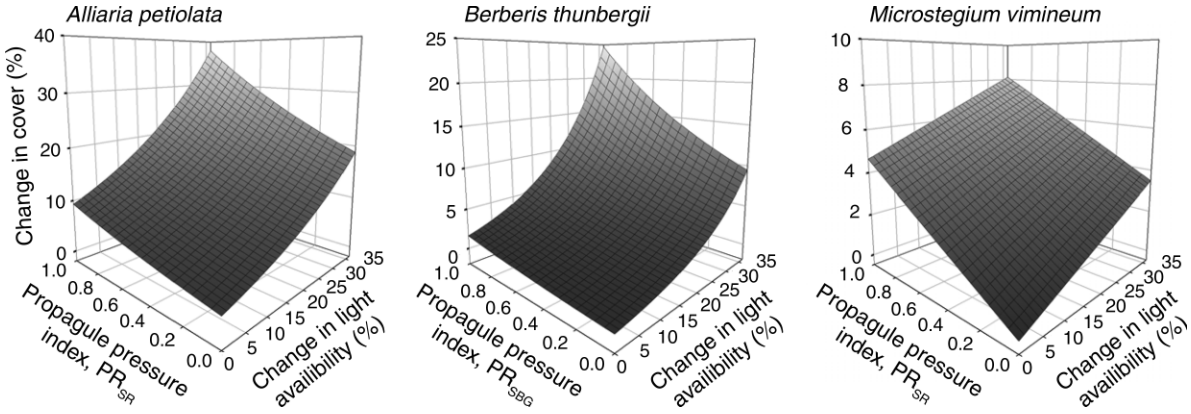

FIG. 1. Predicted change in exotic plant species percent cover as a function of canopy disturbance, i.e., change in light availability from 2003 to 2006, caused by the hemlock woolly adelgid (HWA), and propagule pressure (seed rain, PP_{SR}). Predictions for each species were generated from the top-ranked model shown in Table 3. For species in which deer herbivory was also included in the best model, it was held constant at the mean value (15.1 deer/km^2).

ranked model, these representations are based on a fixed deer density (Table 3). The comparison between healthy and declining sites clearly demonstrates that invasibility, the increase in exotic plant cover and density per propagule, is higher in the declining sites (Fig. 3). This result was consistent, to varying degrees, for all species and both measures of plant abundance. The invasibility index varied the least between healthy and declining sites for *M. vimineum* and the most for *A. petiolata*. For each species, most notably *B. thunbergii*, the difference in the invasibility index between healthy and declining stands was greater for plant density than for cover (Fig. 3).

DISCUSSION

The canopy disturbance caused by hemlock woolly adelgid infestation and propagule pressure were the most important predictors of *A. petiolata*, *B. thunbergii*, and *M. vimineum* invasion. Although the relative importance and degree of impact of these two factors varied, this finding was consistent for all three studied species despite their very different life histories. White-tailed deer herbivory proved to play an important role in contributing to the invasion of two of the three species, while plant species diversity had little influence for any of the studied species. These results demonstrate the importance of multiple mechanisms in exotic plant invasion. In addition, we found that these mechanisms can interact to produce nonlinear impacts on the invasion of exotic plant species.

Due to the marked gradients in canopy disturbance, deer herbivory, species diversity, and exotic plant propagule pressure, the hemlock communities at DEWA were ideal for investigating the relative roles of these factors and their interactions in contributing to community susceptibility to invasion. Further, by studying the invasion dynamics of three exotic species that represent a wide range of life histories, we gained insight into the existence of generalities among diverse plant

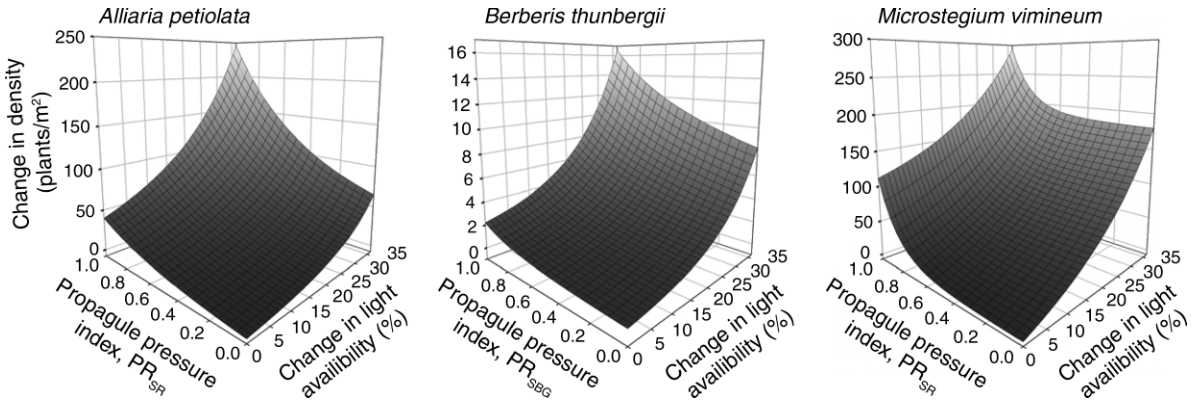

FIG. 2. Predicted change in exotic plant species density as a function of canopy disturbance, i.e., change in light availability from 2003 to 2006, caused by the hemlock woolly adelgid (HWA), and propagule pressure (seed rain, PP_{SR}). Predictions for each species were generated from the top-ranked model shown in Table 3. For species in which deer herbivory was also included in the best model, it was held constant at the mean value (15.1 deer/km^2).

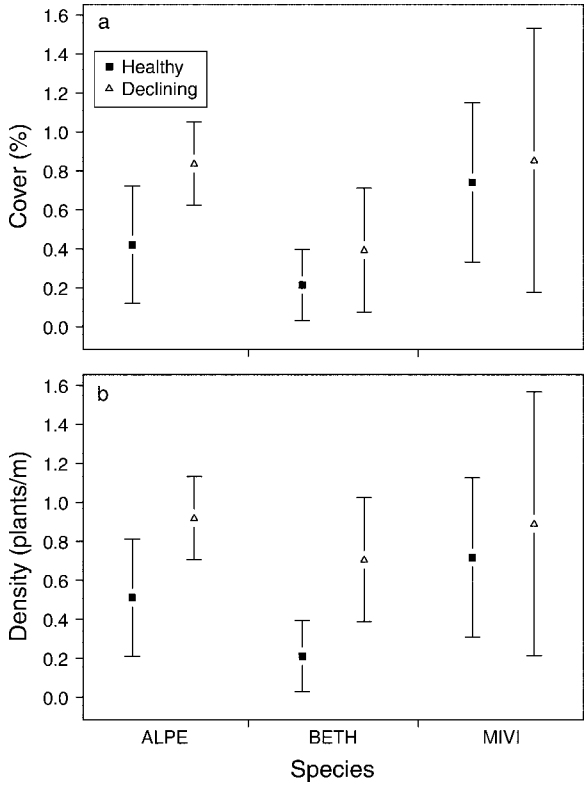

FIG. 3. Invasibility index or the mean increase in exotic plant species (a) percent cover and (b) density from 2003 to 2006 at a given propagule pressure (i.e., invasion/propagule pressure) for each species in the five healthiest vs. the five most declining hemlock stands (mean ± SD). For each species, the index of propagule pressure (seed rain, PP_{SR}, or seed bank germination, PP_{SBG}) with the highest relative variable importance (Table 4) was used to calculate invasibility. Species codes: ALPE, *A. petiolata*; BETH, *B. thunbergii*; and MIVI, *M. vimineum*. Note that changes in species abundance were normalized by the maximum change to scale values between 0 and 1.

species. The fact that these hemlock forests were in the early stages of exotic plant invasion provided an additional advantage, as it is difficult to identify the causal factors influencing community invasibility once an invasion is already widespread (Davis and Pelsor 2001). The strong support observed for the exponential impact of canopy disturbance, herbivory, and propagule pressure on the invasion of the studied exotic species may, in part, be a function of the current extent of invasion. The exponential relationship indicates that the invasion per unit change in understory light availability increases with canopy disturbance severity. However, over a longer time period these models may fit a logistic curve as the invasion must eventually reach saturation once suitable habitat is occupied (Shigesada et al. 1995). Further, the relative importance of canopy disturbance, herbivory, species diversity, and propagule pressure in predicting exotic plant invasion may vary temporally. For instance, the early stages of invasion are often more constrained by propagule availability (Rouget and Richardson 2003).

Our primary interest in this study was to quantify the relative importance of the four proposed determinants of exotic plant invasion. Nevertheless, it is interesting to note that models including only indices of propagule supply and disturbance were able to explain a substantial fraction of the variation in exotic plant invasion. However, the role of canopy disturbance in exotic plant invasion may be more important in ecosystems such as hemlock forests, in which the canopy exerts strong control over aspects of the understory environment, such as light and nitrogen availability (Canham et al. 1994, Jenkins et al. 1999). Inclusion of additional variables, such as soil and plant characteristics, would likely improve the overall model fits (Martin et al. 2008).

Canopy disturbance

Although disturbance is recognized as an important factor in exotic plant invasion (Hobbs and Huenneke 1992, Lodge 1993, Colautti et al. 2006), field studies designed to quantify the importance of disturbance relative to propagule pressure and alternative ecological resistance mechanisms are rare (Rouget and Richardson 2003, von Holle and Simberloff 2005). Our results show that HWA canopy disturbance plays an important role in the invasion of *A. petiolata*, *B. thunbergii*, and *M. vimineum*. However, model predictions and the relative importance of this factor varied among species (Table 4, Figs. 1 and 2). For instance, canopy disturbance was predicted to be the most important for the invasion of *B. thunbergii* (Tables 3 and 4). In addition, *B. thunbergii* cover and density did not increase substantially until relatively high canopy decline severities (Figs. 1 and 2). This threshold response suggests that some degree of disturbance is required for *B. thunbergii* establishment and growth. Although *B. thunbergii* persists under a broad range of light conditions, its biomass production and seedling establishment are limited by light availability (Silander and Klepeis 1999). Furthermore, change in light availability is just one of several ecological consequences of HWA infestation. For instance, the higher nitrogen availability in declining hemlock stands (Jenkins et al. 1999) may also explain the response of *B. thunbergii* to canopy disturbance severity.

Canopy disturbance had the lowest relative importance for *M. vimineum*. This result may reflect *M. vimineum*'s extremely plastic response to shade and its ability to invade relatively undisturbed, late-successional forests (Barden 1987, Claridge and Franklin 2002, Drake et al. 2003). Further, for *A. petiolata* and *M. vimineum*, the relative importance of canopy disturbance was higher in models predicting changes in percent cover than in models predicting changes in population density (Table 4, Figs. 1 and 2). This pattern suggests that canopy disturbance is more important in predicting

plant size than in determining the number of plants likely to establish.

Propagule pressure

Gradients in propagule pressure are believed to be a major source of the variation in the extent of invasion between communities (Simberloff 1989, Williamson and Fitter 1996, Green 1997, Colautti et al. 2006). However, few studies have quantified the role of variation in exotic plant propagule supply in determining invasion patterns across sites (D'Antonio et al. 2001, Colautti et al. 2006). We found that propagule pressure consistently ranked as one of the most important predictors of *A. petiolata*, *B. thunbergii*, and *M. vimineum* invasion. Of the three species, propagule pressure had the least impact on *B. thunbergii*. This may be a consequence of the high resistance to *B. thunbergii* invasion at low disturbance severities in these forests, which reduces the predictive power of propagule pressure over a wide range of disturbance severities.

D'Antonio et al. (2001) suggested that a large supply of propagules is needed for invasion to occur in systems in which environmental resistance (biotic or abiotic) is strong. Our results for *B. thunbergii* suggest a limited ability for high levels of propagule pressure to overcome abiotic resistance at these sites. At low canopy disturbance severities, only minimal *B. thunbergii* invasion occurs at the highest levels of propagule pressure ($PP_{SBG} > 0.8$; Figs. 1 and 2). In contrast, *M. vimineum* shows a strong ability to overcome suboptimal habitat conditions via a mass seed effect. In fact, the increase in *M. vimineum* density predicted at the highest propagule pressure levels and low canopy disturbance is similar to the extent of invasion predicted for the lowest propagule pressure index values and high disturbance severity (~30% absolute change in light availability; Fig. 2). Therefore, it appears that *M. vimineum* can invade to nearly equal extents given a high degree of canopy disturbance or a large supply of propagules, whereas the other studied species, particularly *B. thunbergii*, appear to be more dependent upon disturbance.

The relative importance of propagule pressure was higher in models of change in density than in models of change in cover (Table 4). This was particularly true for *B. thunbergii* and *M. vimineum*. This difference likely reflects the fact that *B. thunbergii* is a woody perennial, and first-year seedlings contribute little to total plant cover (Ehrenfeld 1999). For *M. vimineum*, the high variability in plant size in response to environmental conditions may explain the lower importance of propagule pressure in predicting plant cover (Claridge and Franklin 2002).

The relative importance of the seed rain index and the seed bank germination index varied between species. These differences provide insight into the significance of alternate modes of seed dispersal for these species. For example, the relative variable importance of the seed bank germination index greatly exceeded that of the seed rain index for *B. thunbergii* and *M. vimineum* (Table 4). This difference may indicate the importance of long-distance dispersal for these species. For both species, the fact that many plots with a predicted seed rain index of 0 (i.e., no local propagule source) were invaded during the study period further supports the significance of long-distance dispersal mechanisms in the invasion of these species. Although dispersal agents and patterns of the three study species are not well known, *B. thunbergii* seeds are believed to be dispersed by birds (Ehrenfeld 1999, Silander and Klepeis 1999). Several studies have proposed that the rate of spread exhibited by *M. vimineum* is higher than would be predicted by local dispersal patterns; however, the mechanisms for long-distance dispersal of this species have not been thoroughly documented (Mehrhoff 2000, Judge 2005). Further analysis of the spatial patterns of invasion at our study sites showed that plots with a predicted seed rain index of 0 (i.e., no local propagule source) in which *M. vimineum* invaded and increased in cover over the study period were nearly always located less than 15 m from a stream. This spatial pattern suggests the importance of flooding as a long-distance dispersal mechanism for *M. vimineum*. The importance of water dispersal has also been suggested for *A. petiolata* (Nuzzo 1999, Meekins and McCarthy 2001). However, the similarity between the relative importance values of the two propagule pressure indices for *A. petiolata* suggests that local dispersal dominates the spread of this species in our study sites.

The role of persistent seed banks may have altered the relative importance of the two indices of propagule pressure. For instance, it is possible that the invasion of *M. vimineum* in plots with no local propagule source (i.e., $PP_{SR} = 0$) may have been a result of a seed bank that is believed to persist for up to three years (Barden 1987). The importance of a persistent seed bank has been suggested for both *M. vimineum* and *A. petiolata* (Roberts and Boddrell 1983, Barden 1987, Baskin and Baskin 1992, Gibson et al. 2002). A persistent *A. petiolata* seed bank may also explain the higher explanatory power of a seed rain index based on the distribution of both first- and second-year plants. Finally, the fact that seeds of these species can remain viable in the seed bank for several years may contribute to the fact that several species models predict relatively high invasion at a propagule pressure index of 0.

Herbivory

Of the four factors considered in this study, the relative importance of herbivory varied the most among species. For models of both plant cover and density, deer herbivory was most important for *A. petiolata* invasion and least important for *M. vimineum* invasion. These relative rankings are consistent with findings from a previous study that showed *A. petiolata* was the most influenced and *M. vimineum* the least influenced by deer herbivory (A. K. Eschtruth and J. J. Battles, *unpublished*

manuscript). These results, which were based on exclosure studies, demonstrated that deer herbivory substantially accelerated the invasion of all three studied species, but suggested that *M. vimineum* was grazed to some extent.

We suggest that the positive relationship between deer density and the abundance of *A. petiolata* and *B. thunbergii* results from competitive release via selective browsing of more preferred native plant species (A. K. Eschtruth and J. J. Battles, *unpublished manuscript*). This result is consistent with the enemy release hypothesis prediction that generalist enemies have a greater impact on native plant species than on exotics (Keane and Crawley 2002). The role of selective deer browsing in indirectly promoting the abundance of low-preference, browse-resistant, or browse-tolerant native plant species has been demonstrated (Tilghman 1989, Horsley et al. 2003). Although the increased abundance of exotic plants due to a reduction in generalist enemy regulation is not well documented in forest systems, introduced generalist grazers have been shown to facilitate the invasion of some exotic grasses (Mack 1981, O'Connor 1991, Hobbs 2001, Parker et al. 2006). However, our results and the findings of others (e.g., Colautti et al. 2004, Levine et al. 2004, Liu and Stiling 2006) suggest that generalist enemy release is unlikely to be a primary mechanism of invasion for most exotic plant species. For instance, generalist mammalian herbivores have been shown to reduce the survival and reproduction of several nonnative plants (D'Antonio 1993, Rachich and Reader 1999, Cadenasso et al. 2002). Our results may, in part, reflect the fact that herbivore density was measured in this study. Variation in herbivore density has the potential to dramatically alter the measured effect size, and, therefore, failure to account for herbivore density may lead to flawed generalizations. We suggest that future studies of the impact of generalist herbivory in exotic plant invasion should directly account for herbivore density to control for the influence of this potentially confounding factor.

For each of the studied species, deer herbivory had a higher relative variable importance in models of change in plant cover than in models of change in density. Therefore, herbivory appears to be more important in influencing the size of individual plants than in determining the number of plants likely to establish. This differential impact on exotic plant cover may result from temporal patterns of deer herbivory. The fact that herbivory influences exotic plant density suggests that it provides a competitive release before or during the germination of these exotic species. However, deer herbivory can provide a release from competing plants and, therefore, increase exotic plant cover throughout the growing season. On a longer time scale the effects of deer herbivory on these abundance measures may converge, as an increase in plant cover will likely result in larger plants with greater reproductive capacity (e.g., Byers 1988).

Deer herbivory had the highest relative variable importance for *A. petiolata* invasion. This may reflect *A. petiolata*'s highly plastic reproductive response (Cavers et al. 1979, Byers 1988, Nuzzo 1999) or its ability to persist in a wide range of light levels and respond rapidly to release from competition (Dhillion and Anderson 1999, Meekins and McCarthy 2001). In addition, first-year *A. petiolata* rosettes continue to grow in winter and may be able to respond to resources made available by winter herbivory prior to the germination of most herbaceous species (Cavers et al. 1979, Anderson et al. 1996). These factors may contribute to a more rapid response of *A. petiolata* to the resources made available by deer herbivory. Alternatively, the high relative importance of herbivory in *A. petiolata* invasion may indicate that this species grows in more direct competition with other plants or occurs more often with species preferred by deer. In a study comparing the effects of insect herbivory on *A. petiolata* in the native and introduced ranges, Lewis et al. (2006) found that although insect herbivory was reduced in the introduced range, no increased plant growth was observed.

Species diversity

Our results did not support the theory that species-rich communities are less susceptible to invasion by exotic plants (e.g., Elton 1958, Lodge 1993, Naeem et al. 2000, Kennedy et al. 2002). Relative to the other factors examined in this study, species richness was the least important predictor of exotic plant invasion. Further, our results demonstrate a weak positive relationship between species diversity and the invasion of *A. petiolata* and *M. vimineum*. These findings support the conclusion of Stohlgren et al. (1999, 2003) and others (Levine and D'Antonio 1999, Lonsdale 1999) that species diversity has no direct causative effect on invasibility and that environmental factors that covary with species diversity may explain the positive relationship. The underlying mechanism influencing both species diversity and site invasibility may be resource availability (Davis et al. 2000, Wardle 2001). Alternatively, variation in the supply of both native and exotic species propagules may explain the positive relationship between diversity and exotic plant invasion (Levine and D'Antonio 1999). We found that exotic plant invasion, species diversity, and the supply of native and exotic propagules were higher in plots near hemlock forest edges (i.e., near more diverse hardwood forests). These relationships highlight the importance of quantifying propagule pressure in studies of ecosystem invasibility.

An alternative explanation for the inconsistencies observed in the relationship between species richness and exotic species abundance is the lack of studies that control for plant density or cover (Weltzin et al. 2003). Resident cover and biomass have been proposed as important determinants of community invasibility (Burke and Grime 1996, Crawley et al. 1999, Lavorel et al. 1999). As our goal was to assess the relative

importance of several potential determinants of invasion success, we did not include native species cover or density in our models, though it would likely improve model fits and may provide further insight into the diversity–invasibility relationship. Furthermore, although species richness varied widely in these hemlock forests, the total cover of understory vegetation was relatively low (Table 1). The role of biotic resistance factors, such as species diversity, may become more important as hemlock canopy decline progresses and competition intensity increases (e.g., Lonsdale 1999). Moreover, exotic plant invasion may be more influenced by abiotic factors in disturbed ecosystems (Hood and Naiman 2000).

Interactions between variables

Despite significant interest, little is known about how propagule pressure interacts with mechanisms of ecological resistance to determine invasion success (D'Antonio et al. 2001). For *A. petiolata* and *B. thunbergii*, we found compelling evidence of an important interaction between propagule pressure and canopy disturbance. The consequence of this interaction was that higher canopy disturbance severities magnified the extent of invasion that occurred at a given propagule pressure level or, conversely, higher levels of propagule pressure intensified the invasion that occurred at a given canopy disturbance severity. We propose that the increase in resource availability associated with disturbance severity resulted in a reduction in community resistance to these species. This result is consistent with the mechanistic models of the relationship between ecosystem resistance and propagule pressure that have been proposed by Davis et al. (2000) and D'Antonio et al. (2001). This was the first study to demonstrate the dominant role of the interaction between canopy disturbance and propagule pressure in determining forest invasibility in comparison with other potential controlling factors. The importance of the disturbance–propagule supply interaction and its nonlinear functional form have profound implications for the management of exotic plant species populations.

The comparison of invasibility indices in healthy and declining hemlock stands illustrates the impact of the interaction between canopy disturbance and propagule pressure. This comparison demonstrates that a given propagule pressure resulted in a greater increase in exotic plant abundance in declining hemlock forests and that the effects of this interaction were evident at the scale of an entire site (Fig. 3). In addition, Fig. 3 provides a simplified illustration of differences in the potential for *A. petiolata*, *B. thunbergii*, and *M. vimineum* invasion in healthy and declining hemlock forests. Again, the greatest differences in invasion success by disturbance severity occurred for changes in *A. petiolata* abundance and *B. thunbergii* density. *Microstegium vimineum* had the highest invasion per propagule level in the healthy sites and the smallest disparity in invasion success between healthy and declining forests.

Interestingly, although deer herbivory also resulted in an increase in resources available to exotic plant species, we found only modest support for an interaction between deer herbivory and propagule pressure. In contrast, deer exclosure studies in these forests demonstrated the important role of the herbivory–disturbance interaction in accelerating the rate of exotic plant invasion (A. K. Eschtruth and J. J. Battles, *unpublished manuscript*). This apparent inconsistency may reflect the difficulty in isolating this interaction without directly controlling for herbivory impacts using exclosures. Furthermore, it is possible that interactions between herbivory and disturbance and between herbivory and propagule pressure did occur but that their relative importance was small compared to the canopy disturbance–propagule pressure interaction.

Conclusions

Despite a prevalence of studies focused on the potential determinants of ecosystem invasibility, little is known about the relative importance of these factors. Results from this study highlight the dominant role of a canopy disturbance–propagule pressure interaction in exotic plant invasion. This interaction has important implications for ecosystem invasibility and suggests that understanding exotic plant invasion in response to canopy disturbance (i.e., ecological resistance mechanisms) or propagule supply alone will not adequately reflect its invasion potential. Therefore, single-factor studies of the influence of a given community property in determining invasion success are incomplete and more studies need to account for the role of naturally occurring levels of propagule pressure in exotic plant invasion. Further, results from this study demonstrate that exotic plant species vary in the relative importance of factors determining invasion success, in their ability to overcome ecological resistance via a mass seed effect, and in the relationship between canopy disturbance and propagule pressure. Consequently, more studies focused on the interaction of propagule supply with ecological resistance mechanisms are required to confirm the generality of these patterns and improve our ability to predict exotic plant invasions. Without careful experiments that isolate the impacts of ecological resistance mechanisms, propagule supply, and their interaction, explanations of the mechanisms controlling the invasion of exotic species may be unreliable.

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Literature Cited

Anderson, R. C., S. S. Dhillion, and T. M. Kelley. 1996. Aspects of the ecology of an invasive plant, garlic mustard (*Alliaria petiolata*), in central Illinois. Restoration Ecology 4: 181–191.

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.

Barden, L. S. 1987. Invasion of *Microstegium vimineum*, an exotic, annual, shade-tolerant, C-4 grass, into a North Carolina floodplain. American Midland Naturalist 118:40–45.

Baskin, J. M., and C. C. Baskin. 1992. Seed germination biology of the weedy biennial *Alliaria petiolata*. Natural Areas Journal 12:191–197.

Brown, R. L., and R. K. Peet. 2003. Diversity and invasibility of Southern Appalachian plant communities. Ecology 84:32–39.

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

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:776–790.

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

Byers, D. L. 1988. Life history variation of *Alliaria petiolata* in a range of habitats in New Jersey. Thesis. Rutgers University, New Brunswick, New Jersey, USA.

Cadenasso, M. L., S. T. A. Pickett, and P. J. Morin. 2002. Experimental test of the role of mammalian herbivores on old field succession: community structure and seedling survival. Journal of the Torrey Botanical Society 129:228–237.

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

Cavers, P. B., M. I. Heagy, and R. F. Kokron. 1979. Biology of Canadian Weeds. 35. *Alliaria petiolata* (M Bieb) Cavara and Grande. Canadian Journal of Plant Science 59:217–229.

Claridge, K., and S. B. Franklin. 2002. Compensation and plasticity in an invasive plant species. Biological Invasions 4: 339–347.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions 8:1023–1037.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7:721–733.

Crawley, M. J. 1987. What makes a community invasible? Pages 429–453 *in* S. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession, and stability. Blackwell Scientific, Oxford, UK.

Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion resistance in experimental grassland communities: Species richness or species identity? Ecology Letters 2: 140–148.

D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent. Ecology 74: 83–95.

D'Antonio, C. M., J. M. Levine, and M. Thomsen. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. Journal of Mediterranean Ecology 2:233–245.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Darwin, C. 1859. The origin of species by means of natural selection. Literary Classics, New York, New York, USA.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421–428.

DeWalt, S. J., J. S. Denslow, and K. Ickes. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85:471–483.

Dhillion, S. S., and R. C. Anderson. 1999. Growth and photosynthetic response of first-year garlic mustard (*Alliaria petiolata*) to varied irradiance. Journal of the Torrey Botanical Society 126:9–14.

Drake, S. J., J. F. Weltzin, and P. D. Parr. 2003. Assessment of non-native invasive plant species on the United States Department of Energy Oak Ridge National Environmental Research Park. Castanea 68:15–30.

Edwards, A. W. F. 1992. Likelihood. Johns Hopkins University Press, Baltimore, Maryland, USA.

Ehrenfeld, J. G. 1999. Structure and dynamics of populations of Japanese barberry (*Berberis thunbergii*) in deciduous forests of New Jersey. Biological Invasions 1:203–213.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.

Eschtruth, A. K., and J. J. Battles. 2008. Deer herbivory alters forest response to the canopy decline caused by an exotic insect pest. Ecological Applications 18:360–376.

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.

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.

Gibson, D. J., G. Spyreas, and J. Benedict. 2002. Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. Journal of the Torrey Botanical Society 129:207–219.

Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications 8:975–989.

Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. Journal of Animal Ecology 66:25–35.

Gross, K. L. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology 78:1079–1093.

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.

Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. Pages 389–405 *in* J. A. Drake, F. Di Castri, R. H. Groves, and F. J. Kruger, editors. Biological invasions: a global perspective. John Wiley and Sons, New York, New York, USA.

Hobbs, R. J. 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. Conservation Biology 15:1522–1528.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion—implications for conservations. Conservation Biology 6:324–337.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology 148:105–114.

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.

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.

Judge, C. A. 2005. Japanese stiltgrass (*Microstegium vimineum*): population dynamics and management for restoration of native plant communities. Dissertation. North Carolina State University, Raleigh, North Carolina, USA.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17:164–170.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636–638.

Lavorel, S., A.-H. Prieur-Richard, and K. Grigulis. 1999. Invasibility and diversity of plant communities: from pattern to processes. Diversity and Distributions 5:41–49.

Leopold, B. D., P. R. Krausman, and J. J. Hervert. 1984. Comment: the pellet-group census technique as an indicator of relative habitat use. Wildlife Society Bulletin 12:325–326.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7:975–989.

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26.

Lewis, K. C., F. A. Bazzaz, Q. Liao, and C. M. Orians. 2006. Geographic patterns of herbivory and resource allocation to defense, growth, and reproduction in an invasive biennial, *Alliaria petiolata*. Oecologia 148:384–395.

Liu, H., and P. Stiling. 2006. Testing the enemy release hypothesis: a review and meta-analysis. Biological Invasions 8:1535–1545.

Lodge, D. M. 1993. Biological invasions—lessons for ecology. Trends in Ecology and Evolution 8:133–137.

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

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536.

MacArthur, R. 1970. Species packing and competitive equilibrium for many species. Theoretical Population Biology 1:1–11.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L into western North America—an ecological chronicle. Agro-Ecosystems 7:145–165.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710.

Maron, J. L., and M. Vila. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95:361–373.

Marques, F. F. C., S. T. Buckland, D. Goffin, C. E. Dixon, D. L. Borchers, B. A. Mayle, and A. J. Peace. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. Journal of Applied Ecology 38:349–363.

Martin, P. H., C. D. Canham, and P. L. Marks. 2008. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers in Ecology and Environment. [doi: 20.1890/070096]

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

Meekins, J. F., and B. C. McCarthy. 2001. Effect of environmental variation on the invasive success of a nonindigenous forest herb. Ecological Applications 11:1336–1348.

Mehrhoff, L. J. 2000. Perennial *Microstegium vimineum* (Poaceae): An apparent misidentification? Journal of the Torrey Botanical Society 127:251–254.

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.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108.

Nelder, J. A., and R. Mead. 1965. A simplex method for function minimization. Computer Journal 7:308–313.

NOAA [National Oceanic and Atmospheric Administration]. 2002. Climatography of the United States. Number 81. Monthly station normals of temperature, precipitation, and heating and cooling degree days. 1971–2000. ⟨http://lwf.ncdc.noaa.gov/oa/climate/normals/usnormalsprods.html⟩

Nuzzo, V. 1999. Invasion patterns of the herb garlic mustard (*Alliaria petiolata*) in high quality forests. Biological Invasions 1:169–179.

O'Connor, T. G. 1991. Local extinction in perennial grasslands—a life-history approach. American Naturalist 137:753–773.

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.

Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. Science 311:1459–1461.

Pennsylvania Department of Conservation and Natural Resources. 2003. Estimating county deer population sizes and growth rates. Annual Report. Pennsylvania Bureau of Wildlife Management Research Division, Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA.

Rachich, J., and R. Reader. 1999. Interactive effects of herbivory and competition on blue vervain (*Verbena hastata* L.: Verbenaceae). Wetlands 19:156–161.

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

Roberts, H. A., and J. E. Boddrell. 1983. Seed survival and periodicity of seedling emergence in 8 species of Cruciferae. Annals of Applied Biology 103:301–304.

Rouget, M., and D. M. Richardson. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. American Naturalist 162:713–724.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17:170–176.

Shigesada, N., K. Kawasaki, and Y. Takeda. 1995. Modeling stratified diffusion in biological invasions. American Naturalist 146:229–251.

Silander, J. A., and D. M. Klepeis. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. Biological Invasions 1:189–201.

Simberloff, D. 1989. Which insect introductions succeed and which fail? Pages 39–61 *in* J. A. Drake, H. A. Mooney, F.

Di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. Frontiers in Ecology and the Environment 1:11–14.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25–46.

Stohlgren, T. J., G. W. Chong, L. D. Schell, K. A. Rimar, Y. Otsuki, M. Lee, M. A. Kalkhan, and C. A. Villa. 2002. Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. Environmental Management 29: 566–577.

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

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92.

USDA/NRCS [U.S. Department of Agriculture Natural Resources Conservation Service]. 2007. The PLANTS database. ⟨http://plants.usda.gov⟩

Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59:247–265.

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86:3212–3218.

Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility: Evidence of a biological mechanism or a consequence of sampling effect? Oikos 95: 161–170.

Weltzin, J. F., N. Z. Muth, B. Von Holle, and P. G. Cole. 2003. Genetic diversity and invasibility: a test using a model system with a novel experimental design. Oikos 103:505–518.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology 77:1661–1666.

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* M079-010-A1).

APPENDIX B

Summary of exotic plant species cover and density for the 1-m^2 monitoring plots of exotic species in 10 hemlock sites in the Delaware Water Gap National Recreation Area (New Jersey and Pennsylvania) in 2003 and 2006 (*Ecological Archives* M079-010-A2).

APPENDIX C

Propagule pressure indices (*Ecological Archives* M079-010-A3).