

Ephemeral disturbances have long-lasting impacts on forest invasion dynamics

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Abstract. Ephemeral disturbances are common in many systems. Often, these brief events are assumed to be a nuisance with little long-term ecological impact. We quantified the impact of the ephemeral forest disturbance caused by gypsy moth canopy defoliation on exotic plant invasion in eight hardwood forests in the Delaware Water Gap National Recreation Area, USA. Six years following the gypsy moth disturbance, we were able to predict 59% of the increase in *Alliaria petiolata* abundance and 42% of the increase in *Microstegium vimineum* abundance with models incorporating an interaction between disturbance severity and propagule pressure. In addition, we found that the disturbance timing had substantial impacts on the invasion dynamics of *Alliaria petiolata*. Our results suggest that ephemeral disturbances can have important and long-lasting impacts on plant communities, and highlight the need to account for variations in disturbance characteristics and the role of propagule pressure in determining the disturbance–invasion relationship.

Key words: *Alliaria petiolata*; disturbance regime; ephemeral disturbance; exotic plants; gypsy moth; *Microstegium vimineum*; plant invasions; propagule pressure; vulnerability to invasion.

INTRODUCTION

The potential to generate “big effects from small causes” (Ricker 1963) is a fundamental aspect of population, community, and ecosystem ecology (Ricker 1963, Holling 1973, Patten and Odum 1981). Often in these instances, it is the timing and the context of the small cause that leads to the magnification of its effect. The challenge is to detect and understand these cryptic but influential phenomena (Carpenter 2001).

Ephemeral disturbances may be small causes with big effects. In forests, these perturbations are defined as nonlethal events that damage forest canopies, with recovery times that vary from months to years (McNeil et al. 2007). These brief perturbations, including some insect defoliation, windstorm damage, and drought stress, are common in forest systems (Krasny and DiGregorio 2001, McNeil et al. 2007, Mitchell 2013). However, the impacts of ephemeral disturbances often go undocumented due to their brief duration and the high degree of temporal and spatial heterogeneity in their impacts.

Although forests appear to recover quickly after ephemeral disturbances, these perturbations may have long-term impacts (de Beurs and Townsend 2008). For instance, disturbance is commonly implicated in the invasion of exotic plant species (Hobbs and Huenneke 1992, Lodge 1993, D’Antonio et al. 1999). Much

empirical support suggests that by providing growing space, decreasing competition from native plants, and releasing a pulse of resources, disturbance promotes the invasion of exotic plants (Davis et al. 2000). Some evidence suggests that even short-lived disturbances may facilitate plant invasions. For instance, Davis and Pelsor (2001) found that short-duration increases in resource availability had large impacts on plant invasion success. However, most studies of the disturbance–invasion relationship quantify disturbance as either present or absent without accounting for variation in disturbance severity, duration, timing, or the interaction between these disturbance characteristics and propagule pressure (Moles et al. 2012). Therefore, we have very little information about how ephemeral disturbances might impact invasion dynamics.

The role of disturbance in the invasion of exotic plants is a complex process. Simple approaches that overlook the role of disturbance regime characteristics, the life histories of individual plants, and the importance of propagule pressure, likely contribute to the history of inconsistent evidence observed in studies of the disturbance–invasion relationship. A more holistic understanding of the interplay among these factors could yield important insights into the impacts of disturbance on exotic plant invasion and ecosystem invasibility (Davis et al. 2000, Levine et al. 2003, Eschtruth and Battles 2011).

In this study, we quantified the impact of the ephemeral forest disturbance caused by gypsy moth (*Lymantria dispar*) canopy defoliation on exotic plant invasion in eight hardwood forests in the Delaware

Manuscript received 22 October 2013; revised 10 December 2013; accepted 23 December 2013. Corresponding Editor: P. B. Adler.

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Water Gap National Recreation Area (New Jersey and Pennsylvania, USA). These forests were severely defoliated by a gypsy moth outbreak in 2006. The gypsy moth is an exotic insect pest, accidentally introduced into eastern Massachusetts, USA from Europe in 1869, and is currently considered the most significant defoliator of hardwood trees in the northeastern United States (Williams et al. 1985, Liebhold and Elkinton 1989, Liebhold et al. 1992). Populations have continued to spread, and it is widely believed that gypsy moth will soon occupy most of the hardwood forests in the eastern United States and Canada. Gypsy moth populations undergo outbreaks that result in the defoliation of more than 300 tree and shrub species (Herrick and Gansner 1987). However, the canopy defoliation caused by gypsy moth is short-lived, with many forests experiencing complete refoilation within weeks (Hurley et al. 2004).

Due to the ephemeral nature of gypsy moth disturbance, it is commonly viewed as a nuisance event with little long-term ecological impact (Lovett et al. 2006). In addition, though the area impacted by gypsy moth outbreak in a given year can be vast, defoliation is often markedly heterogeneous and tends to occur in a mosaic pattern across the landscape (Campbell 1979, Houston 1981). Therefore, we quantified the impact of both the timing and the severity of gypsy moth disturbance on exotic plant invasion. Our analysis focused on the invasion of *Alliaria petiolata* (garlic mustard), a biennial forb, and *Microstegium vimineum* (Japanese stiltgrass), an annual grass. These species are widespread, aggressive invaders (Nuzzo 1999, Gibson et al. 2002, data available online)² and are the most common exotic plant species at our study site (78% of the relative exotic species frequency in 2003). Further, these species are commonly cited as examples of exotic species that are invading in undisturbed forests (e.g., Nuzzo 1999, Cole and Weltzin 2005, Martin et al. 2009).

Our main objectives were to (1) determine if an ephemeral disturbance can have measurable impacts on the dynamics of plant invasion in forests, (2) examine the impact of disturbance regime characteristics, such as disturbance severity and timing, on the disturbance–invasion relationship, and (3) investigate the role of propagule pressure in the relationship between disturbance and invasion.

METHODS

Site description

This study was conducted in eight forests in the Delaware Water Gap National Recreation Area (DEWA), in northeastern Pennsylvania and western New Jersey. These spatially disjunct, topographically isolated forests are dominated by hardwood tree species including *Acer saccharum* (sugar maple), *Quercus montana* (chestnut oak), *Q. rubra* (northern red oak),

A. rubrum (red maple), *Betula lenta* (black birch), and *Q. alba* (white oak; nomenclature follows Rhoads and Block [2000]; see Appendix A for site details).

Plot design

In 2003, a total of 576 plots were established to monitor long-term changes in exotic plant invasion in these forests (72 plots per site). At each of the eight sites, random points were selected along the stream (>50 m apart) and transects were established perpendicular to the stream with 2 × 4 m plots set parallel to the streambed at the stream, mid-slope, and upper slope of the forested ravine. The location of all plots was recorded with a geographic positioning device and corners were marked with rebar to ensure precise relocation. At each site, the monitoring plots were dispersed across a minimum area of 19 ha.

In each of these 576 plots, the percent cover of each species and the density (i.e., abundance of each exotic plant species, plants/m²) were recorded annually from 2003 to 2008, and in 2010 and 2012 (except at two sites for which the first measurements were recorded in 2004). For the biennial *A. petiolata*, the age class (i.e., first-year basal rosette or second-year plants with flower stalks) was noted. In addition, in each study year, canopy tree composition and density were quantified at each plot using the point quarter method (Engeman et al. 1994) and the species, diameter at breast height (dbh; ≥2 cm), and vigor of all trees ≥1 m tall within a 5-m radius of each plot were recorded (see Appendix A for methodological details).

Canopy disturbance

These forests experienced a severe gypsy moth outbreak in 2006. Prior to the 2006 defoliation, the last significant outbreak at these sites occurred in 1990 (map available online).³

Understory light availability at each plot was characterized through use of hemispherical photographs (see Appendix A for methodological details). Hemispherical photographs were taken annually from 2003 to 2008, and then again in 2012. During the gypsy moth outbreak in 2006, hemispherical photographs were repeated at approximately two-week intervals throughout the canopy defoliation period (late May through mid-August) in order to assess the severity and timing of gypsy moth disturbance at each plot. Photos were repeated at each plot until the canopy was completely refoiliated. The change in total transmitted radiation was used as an index of gypsy moth defoliation severity and, for each plot, was calculated as the difference between the 2003, 2004, and 2005 combined mean values and the peak 2006 total transmitted radiation value. We combined the pre-disturbance measures (2003–2005) in order to provide the most reliable canopy reference condition.

² <http://plants.usda.gov>

³ <http://www.fs.fed.us/ne/morgantown/4557/gmoth/defoliation/>

In addition, to consider the potential impact of the timing of canopy defoliation on exotic plant invasion, we conducted separate model comparison analyses for the plots with an early peak defoliation period (mid-June) and for the plots with a late peak defoliation period (mid-July). For this purpose, the peak defoliation period was defined as the highest recorded understory light availability (reported as percentage of total transmitted radiation) in 2006.

Propagule pressure

We developed two indices to estimate propagule pressure at the plot level: an effective seed bank index based on direct germination methods and a seed rain index determined by a spatial model of seed dispersal.

Seed bank composition was assessed using direct germination methods (Gross 1990) in 2003, 2004, 2005, 2006, and 2007. To estimate propagule availability at the plot level using direct germination methods (Gross 1990), two soil samples were collected near each plot (1152 total samples in each year; see Appendix A for methodological details [Eschtruth and Battles 2009]). A metal cylinder with a 20 cm diameter was used to collect soil to a depth of 10 cm. 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. All seedlings that emerged were identified to species and removed (see Appendix A). For each exotic species, the index of propagule pressure was calculated for each plot as the number of germinants observed in each year. For each species, these plot-level estimates of seed bank germination were normalized by the maximum observation to scale the values between 0 and 1.

The seed rain index was determined based on the weighted distance to seed sources, seed dispersal distance, and estimates of seed production (see Appendix A; Eschtruth and Battles 2009). We collected data to determine the seed rain index in all study years (i.e., 2003–2008, 2010, and 2012). In June of each year we conducted a detailed mapping of the distribution of all exotic plants within a 30-m radius of each plot. This information was combined into geographic information systems maps and used to calculate a plot-level seed rain index (see Appendix A).

For both species, we found a significant linear relationship between estimates of propagule pressure based on seed bank germination and the seed rain model (for *A. petiolata*, $r = 0.87$, $t = 61.8$, $P < 0.001$, and for *M. vimineum*, $r = 0.83$, $t = 22.0$, $P < 0.0001$; see Fig. B1 in Appendix B [Eschtruth and Battles 2011]).

Invasibility

A community's invasibility (probability of establishment of individual plants per arriving propagule) to a particular species for a specified time period can be quantified as the mean invasibility over that time period (Davis et al. 2000). For each plot in which propagules

were recorded, invasibility was calculated annually for *A. petiolata* ($n = 286$ plots) and *M. vimineum* ($n = 197$ plots) as the number of new plants to establish divided by the plot-specific index of propagule pressure for that year. Thus the index of invasibility varied from 0 to 1, with a value of 0 indicating that no arriving propagules established and a value of 1 signifying that every arriving propagule established. To provide consistency across all study years, we used the seed rain data to determine the annual invasibility index for each plot. Our measure of establishment varied among the studied species to reflect their individual life histories. For *M. vimineum*, an annual plant, our measure of establishment was the number of individual plants measured each year. For *A. petiolata*, annual establishment was defined as the number of first-year basal rosettes. Since our measure of invasibility was based on establishment, we also monitored the survival of *A. petiolata* and the population persistence of *M. vimineum*. For *A. petiolata*, we recorded the number of plants that survived each year by recording the number of first-year basal rosettes that survived to the second-year reproductive stage. For *M. vimineum*, an annual plant, our measure of establishment was equivalent to survival.

Statistical analysis

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 gypsy moth defoliation severity (GM) and propagule pressure (PP; 2006 seed bank germination index values) on exotic plant abundance. 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, which was calculated as the change in abundance of each exotic plant species from 2006 to 2012.

We 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. We compared models in which gypsy moth disturbance severity and propagule pressure were considered alone and in combination (Appendix B: Table B1). We compared alternate models using Akaike's information criterion (AIC) because it provides a means of balancing goodness of fit and model complexity (Burnham and Anderson 2002). AIC difference values (ΔAIC) are provided as a measure of the relative difference in the strength of evidence for each model. Akaike weights (w_i) were calculated to normalize the strength of evidence for a given model (AIC_i) relative to the best model (AIC_{\min} ; Burnham and Anderson 2002). In addition, we calculated evidence ratios for both species to compare the gypsy moth disturbance-only models to the model incorporating both gypsy moth disturbance severity

and propagule pressure. Evidence ratios are calculated as the ratio between Akaike weights, and are used to assess the strength of evidence for a given model relative to a competing model. Although the interpretation of evidence ratios is subjective, they provide an intuitive assessment of the strength of support for one model relative to another (Burnham and Anderson 2002).

We 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.

We also calculated 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 ≈ 1.0 indicates an unbiased model), and root mean squared error (RMSE) provided a measure of prediction error. Statistical analyses and optimizations were conducted in R (v. 2.15.0; R Development Core Team 2012).

RESULTS

The gypsy moth outbreak in 2006 resulted in a striking gradient in the severity of canopy defoliation across and within our eight study sites (Table 1). Within each site, plot-level defoliation estimates ranged from little impact (absolute increase of 0–5% total transmitted radiation) to severe defoliation (absolute increase of 60–80% total transmitted radiation). In addition, significant temporal variation in the timing of peak canopy defoliation at the plot level was observed, with the earliest peak defoliation occurring in mid-June and the latest peak defoliation occurring in mid-July. The forest canopy recovered rapidly following gypsy moth defoliation; all plots experienced nearly complete refoliation within two to four weeks of peak defoliation. All sites were refoliated (i.e., within 5% of 2003–2005 mean total transmitted radiation levels) by early August. We found no evidence of increased tree mortality in the years following the gypsy moth outbreak.

From 2003 to 2012, the density of *A. petiolata* and *M. vimineum* increased in the studied plots (Table 1, Fig. 1). Although these species were present in 2003, more than 76% of plots that contained *A. petiolata* or *M. vimineum* in 2012 were first invaded during the study period. In all study years, the density of and invasibility to *A. petiolata* and *M. vimineum* varied markedly among plots (Table 1). Propagule pressure varied greatly among and within the studied forests. While many plots had no recorded *A. petiolata* or *M. vimineum* propagules throughout the study period, in plots with the highest levels of propagule pressure, we recorded over 600 *M. vimineum* seeds in a given year and a high of 169 *A. petiolata* seeds. Results from the seed rain model provided strong

support for the seed bank germination index of propagule pressure (see Appendix B: Fig. B1).

The canopy disturbance caused by gypsy moth in 2006 increased the invasibility (i.e., number of plants to establish per arriving propagule) of these sites to *A. petiolata* by 63% and to *M. vimineum* by 54% (Fig. 1, Table 1). Invasibility levels for both species returned to values similar to pre-defoliation levels by the following growing season and remained fairly consistent in all other study years. The trend is similar for both species, though the relative invasibility increase in 2006 was higher for *A. petiolata*, which increased from 0.41 in 2005 to 0.58 in 2006.

While the invasibility peaked in 2006 and returned to pre-defoliation levels by 2007, exotic plant density increased in 2006, but had even larger annual increases in 2007 and later years (Fig. 2). For *A. petiolata*, the annual change in density doubled in 2006 relative to the mean increases in 2004 and 2005. However, in 2007 the annual change in density was 5.1 times greater than the 2006 increase (the annual change increased from 0.7 plants/m² to 3.6 plants/m²). Though the highest increase in the annual change in exotic plant density was observed in 2007, the density continued to increase throughout the study period, and the annual increase in numbers of *A. petiolata* plants remained higher than the 2003–2006 rates of increase (Fig. 2). We observed a similar pattern for *M. vimineum*. There was a significant increase in the density of *M. vimineum* in 2006 relative to the mean increases in 2004 and 2005, the annual increase in density was highest in 2007 (mean increase of 14.2 *M. vimineum* plants/m²), and from 2008 to 2012 *M. vimineum* density remained higher than the 2003–2006 levels (Fig. 2).

Our model comparison analysis showed strong support for models of the change in exotic plant density that included an interaction between gypsy moth defoliation severity and propagule pressure. For *A. petiolata* and *M. vimineum*, all top-ranked models included a multiplicative interaction between canopy disturbance and propagule pressure ($D \times PP$; Table 2, Fig. 3). Evidence ratios comparing the selected interaction model to the disturbance-only model in the same functional form showed overwhelming support for models including the canopy disturbance–propagule-pressure interaction term (Table 2, Fig. 3). 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 the change in invasion explained by the top-ranked complete data models was 0.59 for *A. petiolata* and 0.42 for *M. vimineum* (Table 2).

Within the candidate model set, the exponential model form was the highest ranked for both species (Table 2). The Akaike weights (w_i) of the top-ranked models were 0.79 for *A. petiolata* and 0.88 for *M. vimineum* (Table 2). The linear interaction model also

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

Site	Canopy basal area in 2003 (m ² /ha)	Total transmitted radiation (%)		Total ALPE density (plants/m ²) 2003
		Baseline	Peak during 2006 defoliation	
Denmark Creek	34.4 (18.6)	11.6 (4.9)	59.7 (15.4)	3.4 (11.6)
Flatbrook	27.5 (17.3)	17.1 (7.0)	43.9 (18.2)	2.9 (15.3)
Front Pond	44.6 (21.7)	11.4 (6.5)	67.3 (15.7)	4.5 (17.9)
Merchants Creek	32.7 (15.9)	9.4 (4.3)	62.9 (13.6)	2.6 (9.8)
Silver Spray Brook	40.1 (22.4)	15.6 (4.4)	36.3 (13.3)	3.5 (12.7)
Shimers Creek	25.8 (12.5)	18.2 (6.8)	61.2 (14.8)	5.9 (16.8)
Tumbling Water	29.9 (14.0)	12.3 (5.2)	52.8 (17.9)	4.7 (19.2)
VanCampens Brook	39.6 (24.2)	12.7 (4.3)	56.1 (16.2)	3.6 (11.9)

Notes: Values reported are means with SD in parentheses. Basal area and total transmitted radiation are based on measures recorded at permanent vegetation plots ($n = 72$ measurements; one measurement at each of the 72 permanent vegetation plots). Plant density is reported as the number of individuals of *Alliaria petiolata* (ALPE) and *Microstegium vimineum* (MIVI) per m² in all plots in each of the studied forests in order to allow 2003 to 2012 comparisons. Values reported for invasibility (i.e. probability of establishment of individual plants per arriving propagule) are based on $n = 72$ plots for each site. Baseline total transmitted radiation is an average of total transmitted radiation (%) indices from 2003, 2004, and 2005.

received substantial support for models of the change in *A. petiolata* invasion ($w_i = 0.20$, Table 2).

The magnitude of the influence of gypsy moth defoliation severity and propagule pressure on changes in invasive plant density from 2006 to 2012 varied between the studied species (Fig. 3). For instance, the disturbance–propagule–pressure interaction ($D \times PP$) had a greater effect on *M. vimineum* abundance (Fig. 3). For both species, there was a significant relationship between the change in plant density from 2006 to 2012 and the index of propagule pressure in 2006 (*A.*

petiolata; $R^2 = 0.18$, $F_{1,284} = 597.4$, $P < 0.00001$; *M. vimineum*; $R^2 = 0.22$, $F_{1,195} = 523.0$, $P < 0.00001$). However, evidence ratios comparing the best selected models to the propagule pressure-only model in the same functional form showed overwhelming support for model improvement by including the disturbance–propagule–pressure interaction term (*A. petiolata* evidence ratio = 1.3×10^{68} ; *M. vimineum* evidence ratio = 3.4×10^{26}).

The timing of peak canopy defoliation had a substantial impact on *A. petiolata* invasion. The model

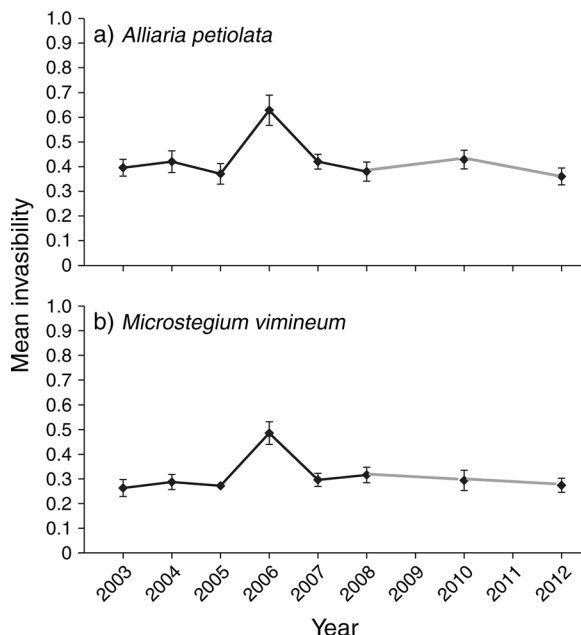


FIG. 1. Invasibility index (defined as the increase in the number of exotic plants divided by the index of propagule pressure) from 2003 to 2012 for (a) *Alliaria petiolata* and (b) *Microstegium vimineum* (mean \pm SE). Gray lines indicate the absence of 2009 and 2011 data.

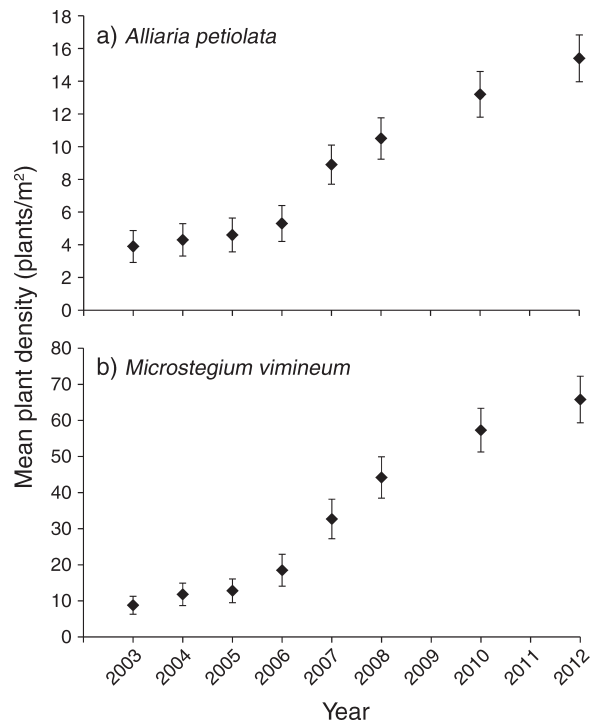


FIG. 2. Plant density (plants/m²) from 2003 to 2012 for (a) *Alliaria petiolata* and (b) *Microstegium vimineum* (mean \pm SE).

TABLE 1. Extended.

Total ALPE density (plants/m ²)	Total MIVI density (plants/m ²)		Invasibility index ALPE, 2006	Invasibility index MIVI, 2006
2012	2003	2012		
15.6 (20.5)	11.2 (32.8)	56.9 (84.1)	0.62 (0.18)	0.49 (0.14)
11.3 (25.7)	6.4 (41.9)	21.7 (93.2)	0.51 (0.24)	0.56 (0.21)
16.2 (32.2)	9.8 (31.5)	94.8 (72.0)	0.68 (0.14)	0.45 (0.17)
12.5 (17.4)	5.1 (33.8)	83.2 (67.4)	0.7 (0.16)	0.44 (0.12)
9.3 (24.5)	6.3 (41.1)	17.5 (98.3)	0.49 (0.12)	0.41 (0.19)
26.2 (29.1)	14.3 (26.9)	112.4 (105.1)	0.74 (0.24)	0.59 (0.22)
15.9 (30.9)	7.3 (52.7)	77.2 (112.6)	0.63 (0.15)	0.48 (0.16)
16.1 (22.0)	9.7 (48.0)	62.3 (89.0)	0.59 (0.13)	0.46 (0.20)

comparison analyses of plots with an early peak defoliation period (mid-June) and plots with a late peak defoliation period (mid-July) showed that, while both models suggest the same general response and the importance of the disturbance–propagule–pressure interaction, the earlier defoliation was a much better predictor of changes in *A. petiolata* abundance from 2006 to 2012 (Table 2, Fig. 3). Models of the plots with early peak defoliation had a higher weight of evidence and better fits (Table 2). In addition, the plots with an earlier peak defoliation period had a greater overall increase in *A. petiolata* density and the disturbance–propagule–pressure interaction had a greater impact (Table 2, Fig. 3). We observed no difference in the severity or duration of peak defoliation between the early and late defoliation periods. The timing of peak canopy defoliation had little impact on *M. vimineum* invasion, with only a slight improvement in the weight of evidence and fit in the later defoliation period (Table 2).

DISCUSSION

Our results demonstrate that ephemeral disturbances can have important and long-lasting impacts on exotic

plant invasion dynamics in forests. Although the forest canopy recovered rapidly following gypsy moth defoliation and the invasibility of the forests returned to previous levels by the following growing season, the impact of the gypsy moth canopy defoliation was clearly evident in the abundance of exotic plants six years after the defoliation event. The ephemeral canopy disturbance caused by gypsy moth resulted in a substantial but short-lived increase in invasibility during the 2006 growing season. Despite the ephemeral nature of this disturbance, the increased supply of propagules created during the temporary high-resource conditions in 2006 resulted in sustained increases in the extent of exotic plant invasion.

There is growing awareness that the current approach to studies of the role of disturbance in invasion is overly simplistic and that variation in key disturbance characteristics can alter the outcome and confound predictions. For instance, studies have begun to document the important impacts of varying disturbance severity and frequency on the invasion of exotic plant species (e.g., Bradford and Lauenroth 2006, Eschtruth and Battles 2009). However, few studies have assessed the role of

TABLE 2. Model rankings and goodness of fit for models of the effects of gypsy-moth-induced canopy disturbance (2006) and the index of propagule pressure on exotic species density from 2006 to 2012.

Data	Model	ΔAIC	w_i	R^2	K	Evidence ratio
<i>Alliaria petiolata</i>						
All plots	Exp _I D × PP	0	0.79	0.59	5	1.6×10^{95}
	Lin _I D × PP	2.7	0.20	0.54	4	1.8×10^{93}
Early defoliation period	Exp _I D × PP	0	0.89	0.66	5	1.7×10^{188}
Late defoliation period	Exp _I D × PP	0	0.65	0.44	5	2.4×10^{34}
	Exp _A D.PP†	2.2	0.26	0.35	4	8.5×10^{20}
<i>Microstegium vimineum</i>						
All plots	Exp _I D × PP	0	0.88	0.42	5	3.9×10^{25}
Early defoliation period	Exp _I D × PP	0	0.85	0.40	5	2.3×10^{24}
Late defoliation period	Exp _I D × PP	0	0.89	0.43	5	1.7×10^{28}

Notes: Exp denotes exponential models and Lin denotes linear models. D stands for canopy disturbance and PP stands for propagule pressure; the subscript I stands for interacting and the subscript A stands for additive. The × represents a multiplicative interaction between variables. Results are presented by species for all models with a ΔAIC (change in the Akaike information criterion) value less than 4. The reported evidence ratio compares the selected best model with the base model (i.e., disturbance only model) in the same functional form. K is the total number of parameters (includes standard deviation of normal probability density function); w_i is the Akaike weight.

† The period indicates variables included in an additive relationship.

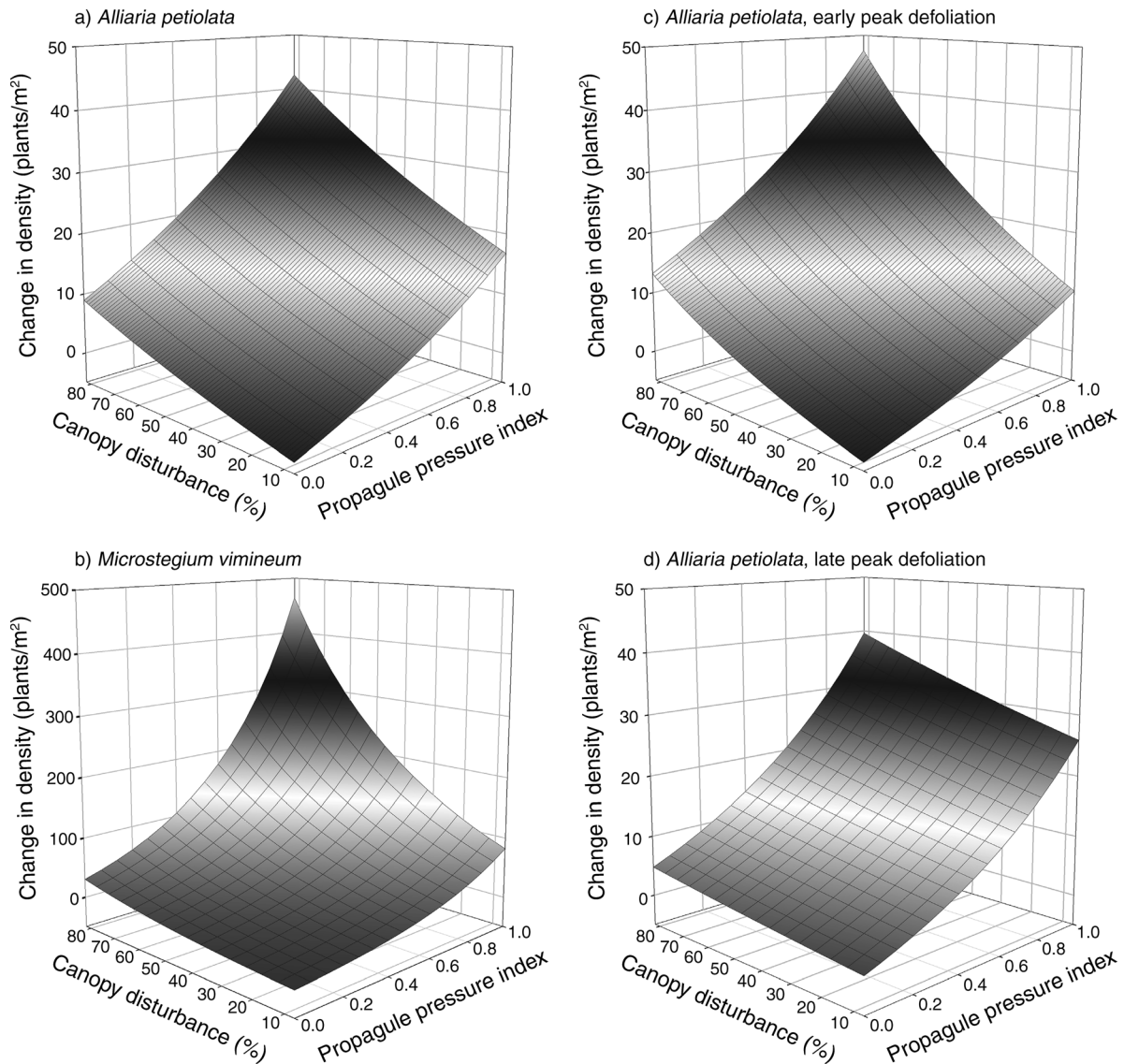


FIG. 3. Predicted change in exotic plant species density (plants/m²) as a function of gypsy-moth-induced canopy disturbance (i.e., percent change in light availability in 2006) and propagule pressure for (a) *Alliaria petiolata* (all plots), (b) *Microstegium vimineum* (all plots), (c) *Alliaria petiolata* in plots with an early peak defoliation period, and (d) *Alliaria petiolata* in plots with a late peak defoliation period. Predictions for each species were generated from the top-ranked model shown in Table 2.

disturbance duration or timing in determining community invasibility and exotic plant abundance. Despite experimental evidence provided by Davis and Pelsor (2001) showing that short-duration increases in water availability had important impacts on plant invasion success, few studies have attempted to examine the importance of naturally occurring ephemeral changes in resource availability in impacting plant invasion. Our results illustrate the important impacts of both disturbance severity and timing in influencing exotic plant invasion dynamics and document the importance of a short-duration disturbance in plant invasion.

One of the most significant challenges to the study of the relationship between disturbance and invasion is the

degree of temporal variability inherent both within and among individual perturbation events (Pickett and White 1985, White and Jentsch 2001). Our results show that the timing of peak gypsy moth defoliation, which typically occurs from June to mid-July, had important ramifications for the invasion of some exotic plant species. In fact, by incorporating a very basic measure of the temporal heterogeneity in peak defoliation, the disturbance–invasion relationship became strikingly more apparent for *A. petiolata*. This relationship is especially interesting because peak defoliation only varied over an approximately six-week period.

Plots with an earlier peak defoliation period had a greater overall increase in *A. petiolata* density, and the

disturbance–propagule–pressure interaction had a greater impact. This importance of the timing of canopy defoliation on *A. petiolata* invasion may be due to the phenology of *A. petiolata* flowering and seed production. Second-year *A. petiolata* plants produce flowers in the spring or early summer. These plants develop seeds and begin to senesce by late June (Anderson et al. 1996). The earlier defoliation period may have a greater impact on *A. petiolata* density because it is more likely to overlap with the timing of seed development. By the later peak defoliation period in July, nearly all the second-year plants have completely senesced (Anderson et al. 1996). It is also possible that the more open forest environment resulting from the gypsy moth defoliation temporarily increased the probability of cross-pollination. Pollinator visitation rates may be higher in open habitats in part due to the higher thermoregulatory capacity of insects in open habitats relative to shaded habitats (Larson and Barrett 2000). *A. petiolata* can be self-pollinated or cross-pollinated by small solitary bees, syrphid flies, and rarely honey bees or bumble bees (Cruden et al. 1996). The cross-pollinated seeds have been shown to be significantly more vigorous than those produced by self-pollinated plants (Cavers et al. 1978). The timing of peak defoliation had little impact on *M. vimineum* invasion success, perhaps due to the timing of *M. vimineum* flowering and senescence, which both occur in the fall.

In addition to the timing of peak defoliation, our results reflect another temporal pattern with important implications for incorporating timing into disturbance–invasion studies. We observed a lag effect in the exotic plant density response, such that the impact of gypsy moth defoliation is much more evident in the exotic plant response in the years after the disturbance occurred. Our results show much lower strength of evidence for models of the impact of gypsy moth defoliation severity on exotic plant density during the 2006 defoliation period relative to later study years. The ephemeral canopy disturbance that occurred in 2006 resulted in a short-lived increase in invasibility during the 2006 growing season. The fact that this short-lived increase in invasibility resulted in a long-term impact on exotic plant density, which largely occurred after invasibility returned to pre-disturbance levels, suggests that this response is the result of the increased supply of propagules created during the temporary high-resource conditions. The importance of propagule pressure in the observed lag effect is supported by the annual plot-level measures of propagule pressure.

The key role of propagule pressure may also explain, in part, the lack of a similar response in the native plant ground cover. By far the most common native understory plants in the studied plots were tree seedlings (e.g., *Acer saccharum*, *A. rubrum*, *Betula lenta*, *Carya glabra*, *C. ovata*, *Fraxinus americana*, *Prunus serotina*, *Quercus alba*, *Q. montana*, and *Q. rubra*; in all study years tree seedlings occurred in more than 82% of the studied

plots). Woody shrubs such as *Vaccinium* spp. and *Viburnum acerifolium* were also relatively abundant in these plots. While some of these species may have experienced increased change in cover in 2006 due to the canopy defoliation, the density of these species was not impacted in the time frame of this study. Unlike the studied exotic plants, which are an annual and a biennial, the temporary increase in resources did not result in an increase in native tree seedling species density during the studied time period, as these seedlings were not reproductively mature individuals. The propagule supply for the tree seedling and woody shrub species may actually be reduced for many years following defoliation, due to the impact of the defoliation on carbon allocation in the reproductively mature trees and shrubs (McConnell 1988). Further, in plots severely defoliated by the gypsy moth outbreak, even smaller woody seedling and shrub species were defoliated, and therefore could not benefit from the resource pulse. In addition to the native tree seedling and shrub species, the species diversity in the ground cover of these plots was quite high. While it is likely that some of the native species did benefit from the gypsy moth canopy defoliation, these species did not occur often enough in these plots to demonstrate this relationship. When examined as a group, we found no significant change in the cover of native herbaceous species following the gypsy moth canopy defoliation.

Models of the role of disturbance severity in determining changes in exotic plant density were not well supported for either species. However, the interactions between disturbance severity and propagule pressure consistently resulted in highly supported models for *A. petiolata* and *M. vimineum*. While propagule pressure-only models better predicted invasion patterns than the disturbance-only models, the interaction of these variables resulted in models with far greater support and significantly higher fits. A study of this disturbance that did not quantify the disturbance–propagule–pressure interaction would have erroneously concluded that gypsy moth defoliation did not have a measurable impact on the studied exotic plant species. Furthermore, the severity of disturbance needed to be included in order to fully explain the interaction with propagule pressure (e.g., Eschstruth and Battles 2009, Warren et al. 2012). Quantification of the influence of varying disturbance characteristics is essential to attain a mechanistic understanding of the role of disturbance in plant invasion.

The role of increased resource availability in promoting invasion by exotic plants is well supported (Huenneke et al. 1990, Burke and Grime 1996, Davis et al. 2000). However, in an attempt to search for generalities in the disturbance–invasion relationship, studies often overlook the fact that the relative importance of increased resource supply is likely to vary among invaders. In addition, invasive plant species will likely respond differently to changes in diverse resources. For instance, while we used

the increase in light availability as our metric of gypsy moth canopy defoliation severity, this disturbance also likely contributes to changes in nitrogen availability (McNeil et al. 2007). While our results show similar trends for both studied species, we did observe important differences between *A. petiolata* and *M. vimineum*. For instance, the relative mean invasibility increase in 2006 was higher for *A. petiolata*, perhaps reflecting that this species is more disturbance dependent. In addition, our results show that the timing of peak canopy disturbance was an important predictor of changes in plant abundance for only *A. petiolata*. These differences highlight the need to consider species life histories in studies of the role of disturbance in exotic plant invasion. Understanding mechanisms by which different invasive species respond to increased resource supply will help to target the most important species to control during ephemeral or long-lasting disturbances.

Studies of the disturbance–invasion relationship have been plagued by a history of idiosyncratic findings. As a consequence, the broader question of whether disturbance directly increases invasibility and the extent of exotic plant invasion remains unresolved (e.g., Moles et al. 2012). The results of this study strongly suggest the importance of disturbance in invasion and, perhaps more importantly, these results illustrate that the role of disturbance in the invasion of exotic plants is a complex process. Far too many studies view disturbance as a present–absent dichotomy and, without incorporating any interaction with propagule pressure or disturbance characteristics, conclude that disturbance does not play an important role in plant invasion dynamics (e.g., Moles et al. 2012). Simplistic approaches that overlook the role of disturbance regime characteristics, the life histories of individual plants, and especially the importance of propagule pressure, have likely contributed to the history of inconsistent evidence observed in studies of the disturbance–invasion relationship. A more holistic understanding of the interplay among these factors could yield important insights into the impacts of disturbance on exotic plant invasion and ecosystem invasibility (Davis et al. 2000, Levine et al. 2003).

Reports that many undisturbed or intact forests are, in some cases, highly invaded have further contributed to the confusion regarding the relationship between disturbance and the invasion of exotic plants in forest systems (e.g., Martin et al. 2009). However, our results suggest that these claims require further scrutiny. Many forests that appear to be relatively undisturbed are frequently subject to varying levels of ephemeral disturbances that go undocumented due to their brief duration (de Beurs and Townsend 2008). While some exotic plant species may be able to invade undisturbed forests due to their life-history characteristics (Martin et al. 2009), our results suggest that it is difficult to rule out the role of ephemeral disturbance in many instances, given the failure to account for the complete disturbance regime as well as the role of propagule pressure. Given

that ephemeral disturbances often go undocumented, the impacts of stochastic, ephemeral disturbance events that temporarily increase ecosystem invasibility may make it difficult or impossible to determine retrospectively the factors that contributed to current invasion patterns.

The gypsy moth is one of the most widespread and persistent exotic pests in North America (Liebhold et al. 1992). Although the short-term impacts of gypsy moth defoliation are the most obvious, our results suggest that the long-term impacts may be more pernicious. Our results illustrate the importance of accounting for the complexities of the disturbance–invasion relationship and demonstrate the potential for ephemeral disturbances to have important and long-lasting effects.

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SUPPLEMENTAL MATERIAL

Appendix A

Methodological details: site description, vegetation measurements, hemispherical photography, invasibility, and propagule pressure indices ([Ecological Archives E095-156-A1](#)).

Appendix B

Propagule pressure results ([Ecological Archives E095-156-A2](#)).