Impacts of Garlic Mustard Invasion on a Forest Understory Community

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Abstract - To assess the community-level responses of a New England forest to invasion by the Eurasian biennial *Alliaria petiolata* (garlic mustard), we conducted a vegetation census at twenty-four plots ranging from low to high invasive cover, and experimentally removed 0, 50, or 100% of garlic mustard from adjacent highly invaded plots at the same study site. Species richness did not respond to natural or experimental levels of invasion, but the Shannon diversity and equitability indices declined with increasing *in situ* densities of garlic mustard, and increased in response to removal of garlic mustard at the experimental plots. Individual species demonstrated variable responses to high-, intermediate-, and low-level invasion. Of all plant functional groups, tree seedlings declined most notably with increasing *in situ* levels of invasion. This functional group, and seedlings of three key canopy tree species within the group, increased in response to partial, but not full eradication of garlic mustard. Our results demonstrate that the effectiveness of full or partial removal depends on management priorities for promoting overall diversity, species richness, native species composition, and/or individual species performance within native communities.

Introduction

Although it is often assumed that exotic plant species alter the structure and biodiversity of the resident communities they invade, we know surprisingly little about their effects on native flora (e.g., Alvarez and Cushman 2002). Relationships between native plant diversity and invasion have been well studied within the context of invasibility (Brown and Peet 2003, Davis et al. 2000, Dukes 2002, Kennedy et al. 2002, Knops et al. 1999, Levine 2000, Lyons and Schwartz 2001, Naeem et al. 2000, Prieur-Richard and Lavorel 2000a), drawing upon Elton's (1958) hypothesis that higher native species diversity confers greater community-level resistance to invasion. It is now well accepted that resource availability and disturbance regimes also determine resistance or invasibility of communities (Brooks 2003, Dukes and Mooney 1999, Gordon 1998, Vitousek 1986). Very few studies have focused on whether increasing levels of invasion have negative relationships with native community richness, diversity, and species composition (see Alvarez and Cushman 2002, Levine et al. 2003 and references therein, Vlok 1988). The majority of these use observational data to compare invaded

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communities to their uninvaded counterparts (Levine et al. 2003) and focus on heavily invaded versus uninvaded systems (D'Antonio and Kark 2002, Mooney and Drake 1986, Parker et al. 1999). Thus, there is a need for observational and experimental data on the effects of invasive plants on native communities across a range of infestation levels. Experiments that use both full and partial eradication methods can empirically answer fundamental ecological questions about how invasion levels affect native communities, while simultaneously demonstrating how well a given removal strategy can achieve specific management goals.

Here, we join two years of correlative data with experimental field manipulations to assess the effects of increasing levels of infestation by an exotic plant on a New England forest understory community. *Alliaria petiolata* Bieb., Cavara, and Grande (garlic mustard) is a Eurasian forb increasing in density within forest-edge and understory habitats throughout much of North America (Nuzzo 1993, Welk et al. 2002). Because invasion by exotic plants into intact communities, such as the forest understory, is less common than invasion into disturbed sites (Von Holle et al. 2003), garlic mustard's unusual capacity to enter and proliferate within the intact forest community has prompted research on its interaction with understory vegetation (McCarthy 1997, Meekins and McCarthy 2001, Nuzzo 2000). While it has been implicated as a cause of reduced native plant diversity and native plant performance (Anderson et al. 1996, McCarthy 1997, Nuzzo 1993, Welk et al. 2002), only one other study has directly tested this idea in the field (McCarthy 1997). A recent greenhouse study suggested that garlic mustard competes with seedlings of some but not other canopy tree seedlings in the midwestern United States (Meekins and McCarthy 1999). No data exist about this species' impact on forest communities in New England, where it ranges from low to very high densities in both disturbed and wooded areas throughout New York, Connecticut, Massachusetts, and Vermont (Nuzzo 2000). At a forested site in western Massachusetts, we tested: (1) whether different degrees of invasion by garlic mustard resulted in declines in indices of community-level diversity; (2) whether and how full and partial eradication of garlic mustard affected indices of diversity and community structure; and (3) whether native species, particularly tree seedlings, differed in their responses to garlic mustard.

Methods

Study species

Garlic mustard is an obligate biennial, sexually reproducing forb. Flowers are typically borne on one or more stalks (Nuzzo 2000). Plants breed primarily via self-pollination, but outcrossing via insect-pollination can also occur (Anderson et al. 1996). Seeds germinate in early spring, and seedlings progress to an evergreen rosette form during the first year of growth. Second year plants begin flowering in early summer, regardless of size, and subsequently die after seed production (Byers and Quinn 1998, Cavers et al.

1979). Seeds are borne in linear capsules (siliques), are dispersed by gravity, water, and soil disturbance, and require overwintering prior to germination (Cavers et al. 1979). Some flowering stalks can reach over 100 cm in height, and a single plant can produce hundreds of seeds. Garlic mustard was introduced into the northeastern United States from Europe in the mid-1800s (Nuzzo 1993), and its native habitat consists of hedges, semi-shaded floodplain, and forest-edge sites, preferring intermediate light and soil moisture levels to extremely shaded or dry sites (Dhillion and Anderson 1999, Meekins et al. 2001). In the last two decades, garlic mustard has undergone rapid population explosions throughout North America, and has become increasingly widespread in forest-edge, riparian, and forest habitats (Nuzzo 2000, Welk et al. 2002).

Study area

The Berkshire Taconic Landscape (BTL) is a 120,000-acre area located on the borders of Connecticut, Massachusetts, and New York, and is representative of mixed hardwood forests throughout the Lower New England-Northern Piedmont ecoregion. Our study site is situated in a largely unfragmented forest of about 36,000 acres at the heart of BTL, on a lower slope of the Taconic Mountains in rich maple woods (42°07'20"N, 73°42'38"W, approx 250 m elevation). The canopy is dominated by native species, primarily *Acer saccharum* Marsh. (sugar maple), with a mixture of *Fraxinus americana* L. (white ash), *Acer rubrum* L. (red maple), and *Prunus serotina* Ehrh. (black cherry). Soils generally consist of patchy quaternary sediments and glacial till with calcareous bedrock. Mean annual precipitation is 114 cm, mean monthly temperatures range from -6 °C (Jan) to 21 °C (July), with freezing temperatures between November and March and typical growing seasons from March–November (www.weather.com/weather/climatology/monthly/01257). Garlic mustard has begun to successfully invade both forest edges and woodland habitats in this area. At some local sites, it has attained between thirty and sixty percent cover in the understory (K. Stinson and S. Kaufman, pers. observ.).

Census plots

We implemented a stratified random sampling design to establish sixteen 4- x 4-m study plots throughout the study area, where our overall estimates of garlic mustard cover ranged from 0–35%. We established four strata consisting of areas with: high (over 30%), medium (10–30%), low (less than 10%), and uninvaded (0%) cover of garlic mustard. Within each of these areas, a random-number chart was used to determine the midpoint locations of four 4- x 4-m plots, for a total of 16 plots. We conducted vegetation censuses at each plot in June 2002, August 2002, and June 2003 for the following functional group categories: herbaceous plants, tree seedlings, and shrubs. Using a 1-m^2 grid for accuracy, we recorded percentage cover on a square-meter basis for each functional group and for garlic mustard. Percentage-cover levels were averaged across grids to generate plot-level percentage-cover means. The

plot-level percentage-cover levels of garlic mustard ranged from 0–37%. We identified to species all stems within the functional group categories mentioned above. We measured species abundance as the number of stems for each species in each 1-m^2 grid cell and tallied the cell counts to generate plot-level species abundance totals for each plot.

In order to segregate effects of physical environment from those of garlic mustard invasion on the native plant community, we collected environmental data at each census plot during midsummer 2002. We measured soil moisture at six locations per plot using a Delta-T type ML2x Theta Probe (Delta-T Devices Ltd, Burwell, Cambridge, UK) on a single, overcast day in July. On the same day, eight soil samples were taken from directly beneath the loose litter layer and then combined into one sample per plot and sent to the University of Massachusetts Soil and Plant Tissue Testing Laboratory in Amherst, MA for analysis. Soil nutrients were determined in ppm along with soil pH and cation exchange capacity (MEQ/100g). We measured average incident light intensity in volts at 100 cm from the forest floor at eight locations within each plot using a LI-COR 1600 photometer (LI-COR Inc., Lincoln, NE) on a single, overcast day in August. We also recorded slope and aspect for each plot, and measured litter depth at eight randomly selected points at each plot. Measurements for each plot were pooled into plot-level average values for analysis.

Experimental removals

To experimentally test the effects of varying degrees of garlic mustard invasion on the understory community, we imposed full and partial removal treatments in a heavily invaded forest understory area (30–35% garlic mustard cover levels). Within this area, twelve 4- x 4-m plots, consisting of nine 1-m^2 subplots and a 0.5-m wide buffer, were randomly selected as described above in June 2002. All plots were fenced so that potential herbivory by local deer populations would not disrupt the treatments. Four plots were each subjected to three treatments in 2002: full removal of garlic mustard, partial removal of garlic mustard, and no removal. Full removal was achieved by pulling all first- and second- year plants from each of the nine subplots. Partial removal was achieved by thinning subplots to 50% of original cover of garlic mustard. Additional garlic mustard plants were pulled in May 2003 to maintain the treatment levels. We conducted a diversity census in June 2003, in which we identified and counted all plants per plot, as described above. We calculated species richness, Shannon equitability index, and Shannon diversity index for each experimental and control plot. We compared diversity indices and environmental variables in the removal treatments to those within four unfenced, heavily-invaded plots and four unfenced, uninvaded plots in order to detect possible differences between sites with and without natural deer herbivory. The uninvaded plots also allowed us to assess similarities between our experimental removals and intact, non-manipulated sites and to evaluate management potential of our treatments.

Using the methods described above, we measured soil moisture and light during June and August 2003 within each 1-m^2 subplot of all fenced and unfenced study plots. To capture vertical light profiles along different strata of the understory vegetation, we measured incident light intensity at three heights in the forest understory (0, 50, and 100 cm). We also recorded daytime soil temperature using a Tenma dual-input thermometer with K-type thermocouples (MCM Electronics, Centerville, OH) at each point. From these data, we generated plot-level means for early and late summer conditions.

Data analysis

Plants were classified at the species level and by functional groups (tree seedlings, shrubs/vines, graminoids, and forbs) for analysis. Species richness (S), Shannon diversity (H') and Shannon equitability (J), of native species were calculated from vegetation census data at our observation and experimental plots as follows: S = the total number species per plot; $H' = -\sum_i P_i \ln P_i$, where P_i = # individuals per species/total number of individuals in the community; and J = H'/ln S.

We used stepwise regression methods (SAS REG procedure) to test for effects of environmental variables and garlic mustard presence on the density (# individuals per m^2), percent cover (% cover per m^2), relative abundance of species (# stems within single species/total # stems for all species), relative abundance of functional groups (% cover for a given functional group/total % cover for all functional groups), and diversity indices (S, H', and J) at our census observation plots. This approach allowed us to determine the effects of garlic mustard on community responses while accounting for environmental variation among our observation plots. We employed linear regression methods (SAS REG) to test for relationships between garlic mustard density and the abundances of tree seedlings, graminoids, forbs, and shrubs.

We tested for the effects of our removal treatments on native plant species diversity, species equitability, species richness, and abundances of functional groups and key species, as defined above, using an analysis of variance (ANOVA) model with treatment (full, partial, or no removal) as a fixed effect. We analyzed differences between treatments in the percent cover of garlic mustard at the time of the census. We tested for differences in environmental variables and community diversity (H', J, and S) between our experimental plots and those undergoing natural deer herbivory using a two-way ANOVA, with invasion level (high or low) and fencing (fenced or unfenced) as the main effects. By comparing relative abundances with and without garlic mustard, we separated the effects of our treatments on proportional changes in invader abundance from those on proportional changes in the native flora itself. Means for early (June) and late (August) summer environmental measurements (light, soil moisture, and soil temperature) were estimated separately on each date of observation for each plot. The effects of removal treatment and time on these non-independent observations were analyzed using repeated measures ANOVA with treatment as the fixed main effect. For light measurements, the effect of treatment was tested

against the height x treatment variance. The treatment x time interaction was tested against the height x treatment x time effect.

Results

Census plots

Overall species richness (S) did not change with respect to garlic mustard abundance (Fig. 1A). However, species diversity (H') and species equitability (J) declined with increasing garlic mustard abundance (Figs. 1B–C). The linear regressions between garlic mustard cover and species diversity were negative, as were those between garlic mustard density and the dependent variables species equitability, tree seedling relative abundance, and graminoid relative abundance (Table 1). The cover and density of graminoids were both negatively correlated with increasing light levels. Graminoid relative abundance was negatively correlated with soil K content. Percent cover of graminoids was positively correlated with soil moisture and Mg and was nonrandom with respect to aspect. The abundance, cover, and relative abundance of forbs were not affected by any of the variables measured. Due to very low numbers of individuals on the census plots, shrub and vine species were not included as a response variable in our analysis of functional group responses to increasing field densities of garlic mustard . In addition to native shrubs, we observed small numbers of the non-native shrubs *Berberis thunbergii* D.C.(Japanese barberry) and *Celastrus orbiculata* Thunb. (oriental bittersweet) at several plots, but their presence was not correlated with garlic mustard. All other species observed in our census were native species. Thus, after accounting for heterogeneity in the abiotic environment, we found evidence for negative effects of garlic mustard densities on graminoids and tree seedlings, but not on the herbaceous or shrub layers of the community.

Table 1. Stepwise linear regression results for effect of environmental variables and garlic mustard invasion on community measurements (species diversity, species richness, density, % cover, and relative abundance). Only those variables that contributed significantly to the model are shown. The parameter estimate indicates whether there was a positive or negative effect on the dependent variable. The model R^2 is the cumulative R^2 value for the model. * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$.

Dependent variable	Independent variable	Parameter estimate	Model R^2
Species diversity	Garlic mustard % cover	-0.252	0.64***
Species equitability	Garlic mustard density	-0.092	0.46**
	Mg	0.115	0.62*
Tree seedling relative abundance	Garlic mustard density	-0.434	0.75***
Graminoid density	Light	-0.219	0.49**
	North aspect	0.428	0.77***
	Soil moisture	3.19	0.94***
Graminoid % cover	Light	-1.696	0.61***
	North aspect	0.271	0.74*
	Mg	1.06	0.88**
Graminoid relative abundance	Garlic mustard density	-0.813	0.59**
	K	-0.035	0.75*

The change in absolute tree seedling abundance was negatively correlated with total garlic mustard density for four canopy tree species. Regression

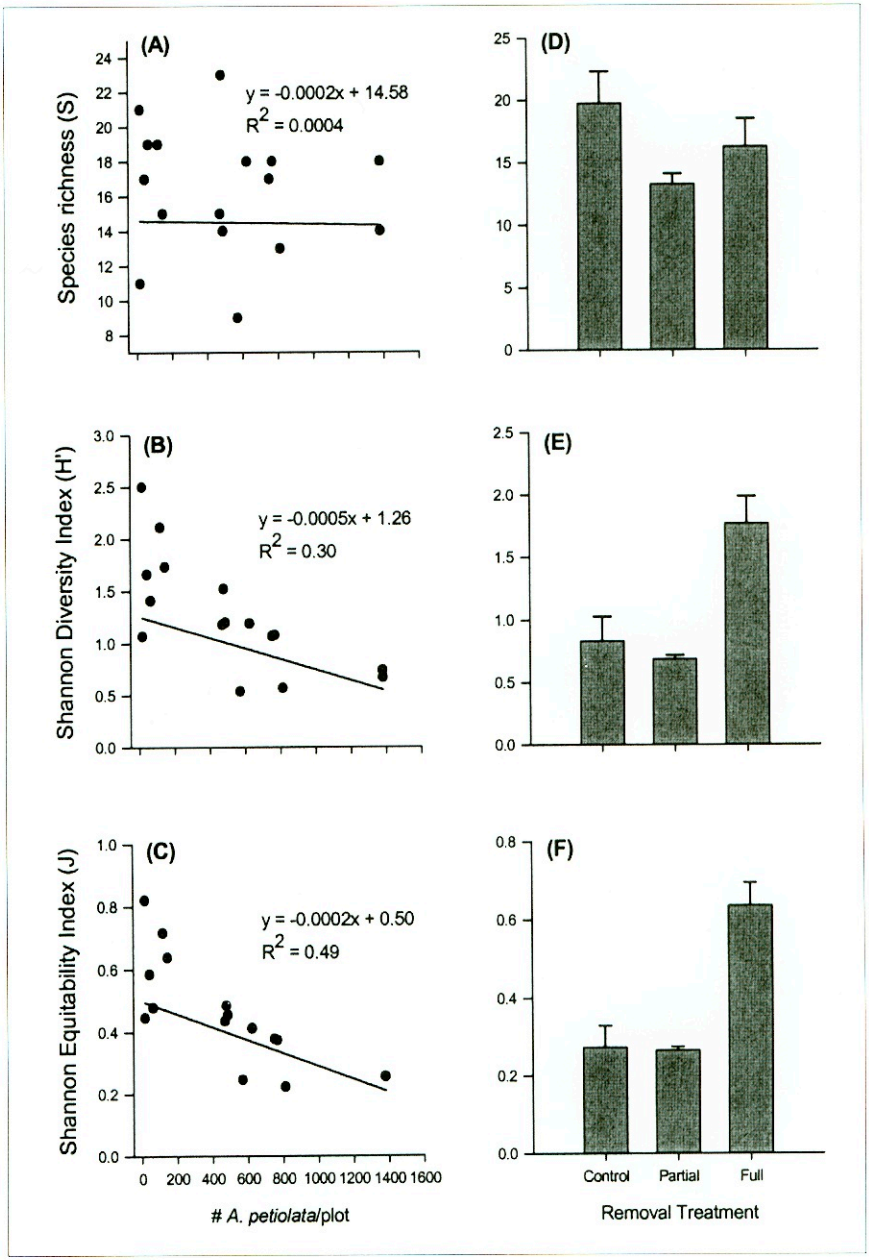

Figure 1. Species richness (S), Shannon diversity index (H'), and Shannon equitability index (J) as a function of: abundance of *Alliaria petiolata* (garlic mustard) at *in situ* observation plots (A–C), and response to experimental *A. petiolata* removal treatments (D–F). Error bars represent ± 1 std error of the mean.

equations demonstrated significantly more negative changes in abundance in sugar maple, white ash, and black cherry (Table 2). Negative changes in red maple abundance were also observed with increasing density of first year garlic mustard seedlings, but the correlation was not significant.

Experimental removals

The percent cover of garlic mustard was reduced by ≈ 57% on average in the partial-removal treatment and by ≈ 99% on average in the full-removal treatment (ANOVA for main effect of removal treatment: $F = 20.22$, $P < 0.001$), and the garlic mustard canopy ranged from 10 to 100 cm in height. Average plot-level light intensity from 0–100 cm was significantly lower in the highly invaded plots compared to the full- and partial-removal plots, indicating that both medium and high garlic mustard density decreased the amount of light available to surrounding forest vegetation ($F_{treatment} = 7.59$, $P < 0.001$). As expected, more light was available at higher understory strata than on the forest floor ($F_{height} = 7.41$, $P < 0.01$). In June, average light levels were highest in the full-removal treatment and lowest in the high-density control plots. In August, light levels were lowest in the partial-removal treatment ($F_{time \times treatment} = 5.02$, $P < 0.01$), most likely because leaf senescence of garlic mustard occurred later at these sites (K. Stinson, pers. observ.). Soil moisture did not differ among treatments, but was higher in August than in June (main effect in repeated measures ANOVAs: $F_{moisture} = 0.78$, $P = 0.46$; $F_{time} = 68.43$, $P < 0.001$). Mean soil temperature was higher in the high-density garlic mustard plots compared to those with full and partial removal, perhaps due to insulating effects of dense garlic mustard stands, but did not differ throughout the summer ($F_{temp} = 3.99$, $P = 0.02$; $F_{time} = 0.13$, $P = 0.72$).

Analysis of variance demonstrated that the total number of species (S) did not differ among removal treatments at the $P = 0.05$ level (Fig. 1D). In contrast, H' significantly increased in the full-removal treatment compared to the other two treatments (Fig. 1E), indicating that garlic mustard negatively affects diversity of native species in this community. The Shannon equitability index (J) was also greater in the full-removal plots than in the other treatments (Fig. 1F). Thus, a more even representation of species, rather than a higher total number of species, contributed to the short-term enhancement of diversity by removal of garlic mustard in our experimental plots.

We found no difference in H' between our full-removal plots and our uninvaded observation plots ($F = 0.2294$, $P = 0.6489$). Comparisons between our fenced treatment plots and unfenced controls demonstrated a significant

Table 2. Results from linear regression equations relating the change in absolute tree seedling abundance 2002–2003 to increasing total garlic mustard density at observation plots in the field. * = $P < 0.05$. NS = not significant.

Species	Beta	R^2
A. saccharum (sugar maple)	-23.49	0.42 *
F. americana (white ash)	-04.53	0.18 *
P. serotina (black cherry)	-57.88	0.45 *
A. rubrum (red maple)	NS	NS

effect of invader density on H', but there were no detectable effects of fencing on S (ANOVA: $F_{\text{fence trt}} = 2.46$, $P = 0.14$; $F_{\text{gm density}} = 0.67$, $P = 0.43$; $F_{\text{fence trt x density}} = 1.42$, $P = 0.26$) or H' (ANOVA: $F_{\text{fence trt}} = 0.003$, $P = 0.951$; $F_{\text{gm density}} = 28.881$, $P < 0.001$; $F_{\text{fence trt x density}} = 2.35$, $P = 0.15$). There were no differences in light ($F = 0.77$, $P = 0.38$), soil moisture ($F = 0.1.83$, $P = 0.18$), or soil temperature ($F = 0.46$, $P = 0.50$) between our full-removal plots and our uninvaded observation plots.

The relative abundance of the tree seedling functional group increased in response to partial, but not full removal of garlic mustard (Fig. 2A). The relative abundances of graminoids, shrubs, and forbs did not change in response to either treatment. When garlic mustard was included in the analysis, relative abundance of all native taxa increased in response to the full-removal treatment, but did not change in response to partial removal (Fig. 2B), indicating that the invader was dominant at both medium- and high-invasion levels. The native flora showed no differences in absolute abundances of individuals in the native functional groups. Thus, the major change in functional-group composition following removal of the invader was to release native plants from dominance by the invader.

The absolute abundances of individual native species varied with full or partial removal of garlic mustard (Fig. 3). In general, tree seedling abundances did not change in response to the removal treatments. Both ash and sugar maple showed slight declines in relative abundance in the full-removal plots, while increasing in the partial-removal plots, but the response was only significant (post hoc $P < 0.05$) for ash in the full-removal plots. Typical understory species—such as *Viola papilionacea* Pursh. (common violet), *Aster divaricatus* L. (white wood aster), and *Carex appalachica* J. Webber and S. Ball (Appalachian sedge)—increased in response to full removal, whereas others—such as *Prunus serotina* Ehrh. (black cherry), *Geum triflorum* Pursh. (old man's whiskers), and *Carex deweyana* Schwein (Dewey sedge)—become less abundant after partial and full removal of garlic mustard (post hoc tests between treatments for each species: $P < 0.05$). Thus, there were species-specific changes in abundance in response to the invader.

Discussion

Effects of invasion severity on native diversity

Most studies that examine relationships between native plant diversity and invasion focus on the invasibility of communities (Brown and Peet 2003, Davis et al. 2000, Dukes 2002, Elton 1958, Kennedy et al. 2002, Knops et al. 1999, Levine 2000, Lyons and Schwartz 2001, Naeem et al. 2000, Prieur-Richard and Lavorel 2000a), but effectively controlling invasions that have already occurred requires an understanding of their impacts. Here we present correlative and experimental evidence that increasing invasion by garlic mustard directly reduces native plant diversity as measured by the Shannon index (H'), providing critical data on the incremental impacts of sparse to severe invasions (cf. Manchester and Bullock 2000). Other studies have focused on species richness (S) as an indicator of community-level

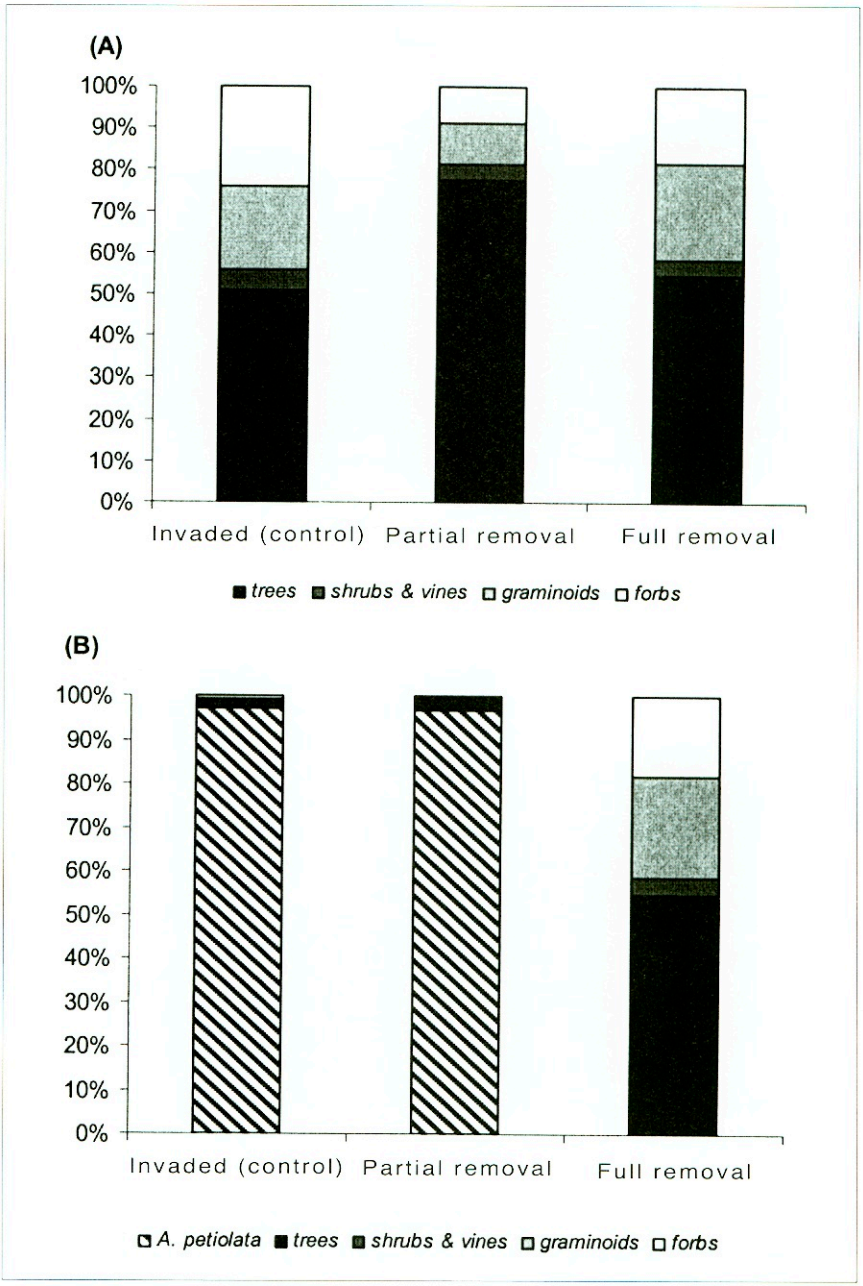

Figure 2. (A) Relative abundances of native functional groups (trees, shrubs, forbs, and graminoids) in response to control, partial-removal, and full-removal treatments (*A. petiolata* [garlic mustard] excluded). (B) Relative densities of *A. petiolata* with respect to native trees, shrubs, forbs, and graminoids in response to control, partial-removal, and full-removal plots. Bars represent proportional status of groups within each treatment.

response to invasion (Alvarez and Cushman 2002, Manchester and Bullock 2000, Meiners et al. 2002), and in some cases both, S and H' are negatively correlated with invader presence (Fairfax and Fensham 2000). Since we did not observe a corresponding decline in S, we conclude that garlic mustard does not reduce the number of native taxa in the understory as it increases in abundance, at least within the time frame of this study. Instead, the decline in H' was related to reduced overall species equitability (J), which indicates

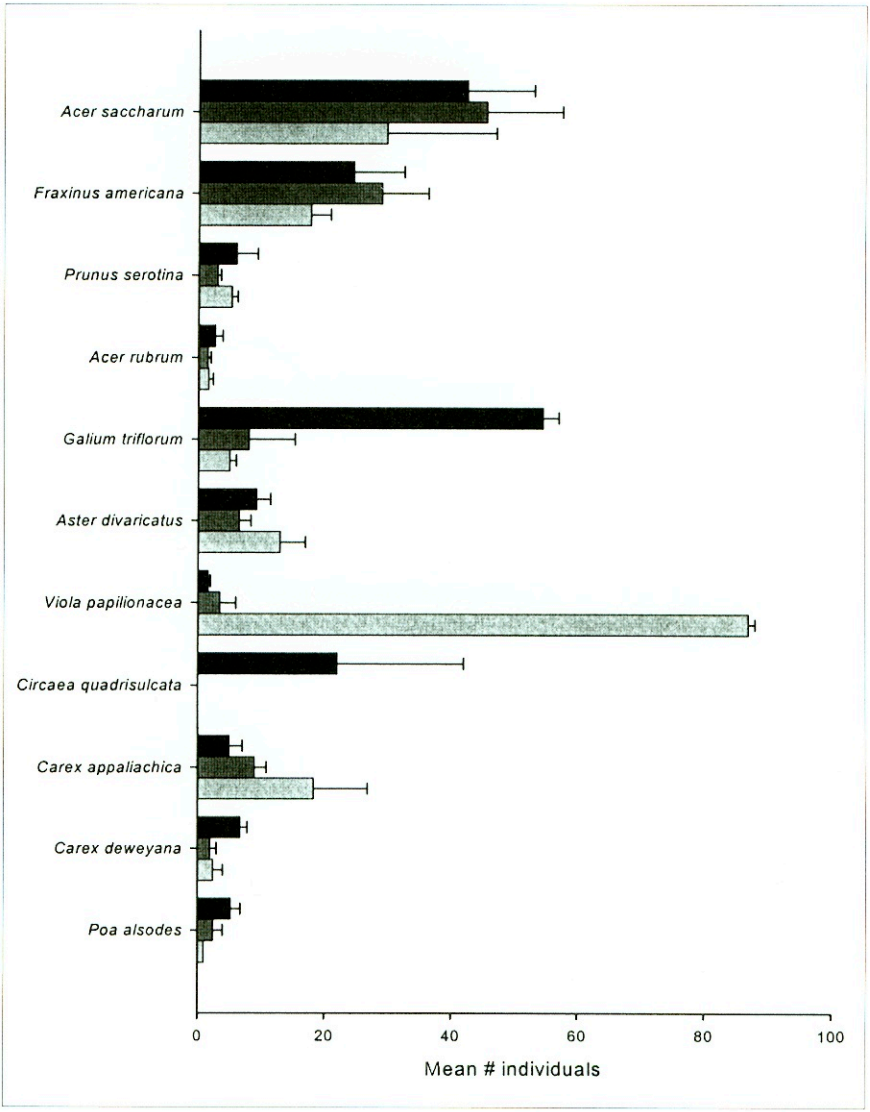

Figure 3. Mean number of individuals (mean absolute abundance) observed for the ten most common species in the experimental plots. Bars indicate control (darkest fill), partial removal (mid-tone fill), and full removal (light-gray fill) of *A. petiolata* (garlic mustard). Error bars indicate ± 1 standard error of the mean.

invasion-driven changes in the proportional representation of species. As discussed below, we also show that individual plant taxa respond differently to increasing invasion severity, leading to species compositional changes that are not reflected by measures of diversity or richness. Similarly, Nuzzo (1999) found a decline in the percent cover of perennial plants with increasing garlic mustard invasion over time, but no change in overall species richness at a long-term monitoring study in Illinois.

Because environmental variation was not generally associated with garlic mustard invasion levels at our sites, it is unlikely that abiotic factors control the negative relationship between invasion and native diversity. Also, since environmental variables, diversity, and species composition at our full-removal plots were similar to those at our uninvaded, unfenced observation plots, deer exclusion does not appear to influence our results, and the native community appears to "recover" to diversity levels that are similar to those at uninvaded locations within two growing seasons following full eradication. Based on our combined experimental and correlative data, we conclude that declines in native diversity with increasing garlic mustard densities reflect compositional responses of the native flora to increasingly severe invasion. Our combined field and experimental data further suggest that short-term community-level recovery of H' and J can be achieved by eradication methods.

Responses of native taxa to increasing severity of invasion

Other studies have suggested that garlic mustard invasion has negative impacts on native plant performance (McCarthy 1997, Meekins et al. 2001, Nuzzo 2000, Yost et al. 1991), but none have tested this idea in the field. Here we provide both correlative and experimental evidence that high levels of garlic mustard presence reduce native graminoid and tree seedling abundance. The significant decline in the percent cover of tree seedlings shown in Table 1 provides *in situ* evidence that increasing garlic mustard invasion may interfere with recruitment of this functional group. At the species level, the significantly more negative changes in the abundance of sugar maple, white ash, black cherry, and red maple seedlings at higher garlic mustard densities shown in Table 2 provide correlative evidence that seedlings of these key canopy trees favor less invaded areas. The distribution of graminoids, which was correlated with microsite factors as well as invasion levels, is probably due to environmental heterogeneity as well as the presence of garlic mustard.

The removal of garlic mustard has been indicated for short-term "release" periods to allow recovery of native species (McCarthy 1997). Despite natural declines with increasing invader presence at our observation plots, our experimental data show that removal of garlic mustard did not alter the abundance of native functional groups after two growing seasons. However, the relative abundance of native tree seedlings responded positively to partial but not full removal (Fig. 2A), suggesting that this functional group recovers quickly in dominance after moderate control measures to remove the dominant invader. To determine whether or not negative effects of the eradication treatment itself may in part explain the lack of native plant responses to full removal requires further investigation.

Variable responses of individual species were masked at the functional-group level, indicating the need for management plans that do not necessarily target a generalized component of native vegetation. Ash seedling abundance contributed most to the release of tree seedlings in response to partial removal, and sugar maple showed a similar trend, but the responses of the other tree seedlings were not as pronounced. It is important to note that the longer-term recovery of individual species of tree seedlings will be dependent on seedling dynamics, including seed crop and seed production, which can vary interannually within a given species. Forbs as a functional group did not respond to the treatments, but full removal of garlic mustard clearly releases the understory species *V. papilionacea* and *C. appalachica,* while reducing abundance of weedy species such as *G. triflorum* and *C. deweyana* (Uva et al. 1997). In herbaceous plants, much of the recovery we observed may have been due to short-term vegetative growth, while population increases resulting from sexual reproduction may take longer than the period of our experiment. As with tree seedlings, recovery times may differ across herbaceous species according to seedling demography, dispersal, and other factors affecting growth. One hypothesis that emerges from our observations is that species-specific responses to garlic mustard invasion are related to variation in dependence of native plants on mycorrhizal fungi at our study sites. Stinson et al. (2006) recently demonstrated that garlic mustard disrupts native plant-mycorrhizae mutualisms, having the strongest effect on highly dependent tree species, including those in the present study. Differential responses to shading may be another driver of species-specific responses to high and moderate invasion levels, as well as other environmental and demographic factors (Byers and Quinn 1998, Meekins and McCarthy 2000). In another experimental eradication study for this species, removal of garlic mustard from a wooded floodplain in western Maryland resulted in the release of different plant functional groups, and its effect on species diversity was not distinguishable from effects of environmental variability among heavily and sparsely invaded sites through time (McCarthy 1997). Similarly, in a potted competition experiment in Ohio, garlic mustard negatively affected the growth and survival of *Quercus prinus* L. (chsetnut oak) seedlings, but not *Acer negundo* L. (box elder) or the annual plant *Impatiens capensis* Meerb. (jewelweed) (Meekins and McCarthy 1999). Thus, garlic mustard invasion appears to impact native plants, including the recruitment of tree seedlings, via individualistic species-level responses at our experimental site and in other forests.

Management considerations

Short-term, individualistic species responses to high-, intermediate-, and low-level invasion contribute to variable effects of garlic mustard on native forest understory flora at our site in New England. Both full and partial removal of garlic mustard can rapidly increase diversity and species equitability in the forest understory, but neither affects native-species richness. The costs of full eradication may outweigh the benefits, since full removal does not appear to serve immediate goals for maintaining overall native-species richness or encouraging release of the overall native flora.

Seedlings of two important canopy tree species may, in fact, initially benefit more from partial than from full removal, although individual species losing dominance may become more vulnerable to other stochastic factors that could influence their abundance over time (Smith and Knapp 2003). Conversely, when conservation priorities emphasize species diversity and equitability, rather than overall richness or individual native taxa, then full-eradication efforts may be warranted even where garlic mustard abundance is currently moderate. Managers should also consider that re-colonization by garlic mustard may occur, in which case repeated eradications may be necessary. In practice, removal via herbicide may be necessary at many sites where manual removal is not viable, and the secondary effects of herbicide treatments on native species' responses to removal are not addressed here. We urge longer-term removal studies to assess community-level responses to this and other exotic species to help develop strategic control plans for specific management priorities.

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