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ORIGINAL PAPER

Consumers and establishment limitations contribute more than competitive interactions in sustaining dominance of the exotic herb garlic mustard in a Wisconsin, USA forest

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Abstract The understory is a diverse component of temperate forest ecosystems, contributing significantly to forest ecosystem services. Despite their importance, many native understories face stresses from current and past land use, habitat fragmentation, invasive species, and overabundant herbivores. We established a four block, three factor experiment to evaluate the relative contribution of native plant establishment, competitive effects from the invasive herb garlic mustard (*Alliaria petiolata*), and herbivory from white-tailed deer (*Odocoileus virginianus*) to better understand the mechanisms promoting low native plant richness and cover and understory dominance by the biennial exotic herb garlic mustard in a NE Wisconsin, USA forest. Four years of garlic mustard removal failed to increase native plant richness or cover in non-restored plots. However, deer access and the introduction of native plants (restoration treatment) both significantly enhanced native plant cover and richness, with restored species cover in fenced plots approximately 216 % that of open-access plots, and the majority of these species flowered at significantly higher proportions inside of fenced areas. In contrast, deer access did not significantly alter the cover, or seed production of garlic mustard. We also found no significant effect of garlic mustard presence on the cover or flowering of restored native species. We conclude that multiple factors, including limited natural establishment by native species and selective herbivory drove low native, high exotic dominance at our site, suggesting that a shift in focus from invasive plant removal to combined native plant restoration and herbivore control is needed to maximize the recovery of this degraded forest understory.

Keywords *Alliaria petiolata* · Invasive species control · Lowland deciduous forest · Propagule limitation · Restoration ecology · Selective browsing

Introduction

Temperate deciduous forests provide diverse ecological and economic services to human society (Pearce 2001; Gilliam 2007). However, a majority of temperate forests are recovering from historic large-scale human disturbances (Flinn and Vellend 2005; Rhemtulla et al. 2009), while simultaneously facing a suite of current stressors (Likens and Franklin 2009),

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including invasion by exotic species (Ehrenfeld et al. 2001; Martin et al. 2009), spatial isolation from extensive mature forests (McLachlan and Bazely 2001; Vellend 2003), and over-browsing by white-tailed deer (Horsley et al. 2003; Wiegmann and Waller 2006). The understory contributes most of the species diversity to temperate forest plant communities (Gilliam 2007) and significantly affects forest processes such as tree regeneration, seasonal nutrient-cycling, and the physical location of NPP available to herbivores (Gilliam 2007), yet understories often appear most affected by past disturbances and current ecosystem stressors (Rodgers et al. 2008; Rogers et al. 2009). It follows that the slow rate by which the understory rebounds from perturbations (Singleton et al. 2001; Flinn and Vellend 2005) may reduce the quality and extent of the ecological services provided by many temperate forests.

Forests harboring invasive species are often associated with reduced native diversity and dominance (Rooney et al. 2004; Rogers et al. 2008), with implications beyond biodiversity preservation, as altered local plant community composition and species dominance directly influence the ecosystem services provided to humans (Ehrenfeld et al. 2001; Pejchar and Mooney 2009). Although few experiments have directly tested the causal relationship between exotic invasion and native plant abundance (Davis 2003; Gurevitch and Padilla 2004), the well documented correlation between low native diversity and invasive plant dominance is widely attributed to a superior competitive advantage by invaders (Wilcove et al. 1998; Mack et al. 2000; Rodgers et al. 2008). In response, large sums of money are expended annually in an attempt to manage these species and mitigate their undesired effects on communities and ecosystems (Pimental et al. 2005; Xu et al. 2006). Despite widespread acceptance of the economic and social costs of invasive species (MEA 2005), the mechanistic basis for their success remains poorly understood (e.g. MacDougall and Turkington 2005; Bradely et al. 2010; Lankau 2012), and forests have received less attention from researchers than many other ecosystems (Martin et al. 2009).

Past land use histories and the fragmented nature of many eastern North American forests provides an additional, non-competition based perspective through which one can view the low native diversity of forests harboring high exotic abundance. For example, younger, succeeding forests generally support native plant communities with a different composition and richness than those of more mature, less disturbed forests (Bellemare et al. 2002; Flinn and Vellend 2005). These differences result in part from the direct effects of past land use, such as agriculture, intensive browsing, or forestry (Dupouey et al. 2002, Fraterrigo et al. 2006), but are also the result of forest fragmentation at the landscape scale (Vellend 2003; Verheyen et al. 2003) coupled with the poor dispersal abilities of many native understory plants (Mabry 2004; Flinn and Vellend 2005). At the same time, past human land use, habitat fragmentation, and human activity are themselves positively associated with exotic species abundance (Lonsdale 1999; Ross et al. 2002; Lilley and Vellend 2009). Thus, following this model, low native diversity and high exotic abundance in forests may also result from larger scale processes, not solely as a result of competitive interactions at the local level.

Deer (Family Cervidae) browsing represents another important factor structuring many forest communities, with increasing evidence of the unintended ecological impacts of their growing populations in temperate forests (Côté et al. 2004). Forests supporting high deer densities are associated with lower native diversity (Horsley et al. 2003; Rooney et al. 2004) and decreased reproductive success for browsing sensitive species (Anderson 1994; Rooney and Gross 2003). Collectively, intensive browsing promotes well defended, annual, or fast growing plant species (Augustine and McNaughton 1998; Horsley et al. 2003), and has recently been show to promote exotic species (Gozales and Arcese 2008; Eschtruth and Battles 2008). For example, both Eschtruth and Battles (2008) and Knight et al. (2009) documented significant increases in the exotic understory plant *Alliaria petiolata* (garlic mustard) in response to increasing white-tailed deer activity in temperate North American forests, likely resulting from garlic mustard's anti-herbivore, chemical defenses (Cipollini 2002; Cipollini et al. 2005). Thus, following this line of evidence, wide-scale browsing pressures from white-tailed deer may be selectively shifting forest understories toward lower native diversity and greater exotic abundance, if deer selectively feed on native species, while avoiding exotics (Maron and Vilà 2001).

Our objective was to improve understory restoration strategies for degraded forests by evaluating the relative influence of interspecific competition, contemporary native plant communities, and white-tailed deer browsing in explaining current understory dominance by the biennial exotic herb *A. petiolata* (garlic mustard) in a suburban Midwestern USA forest preserve. We suggested, first, that land use legacies and the limited dispersal ability of many native woodland species, coupled with the fragmented Midwestern landscape may limit the presence of native plant competitors at our site. As such, we hypothesized (*sub-hypothesis 1*) that garlic mustard removal alone would not be sufficient to increase the richness or cover of native species at our study area, due to overriding establishment limitations for native species. Second, high abundance of white-tailed deer (*Odocoileus virginianus*) commonly shifts plant community composition toward unpalatable or non-preferred species, often resulting in greater exotic dominance. As stated above, deer avoidance of garlic mustard has been documented previously (Eschtruth and Battles 2008; Knight et al. 2009), and herbivore exclosures in garlic mustard invaded areas have significantly increased native plant cover (Knight et al. 2009). Furthermore, herbivory can interact with competition from garlic mustard to reduce survival of restored native plants (Hahn and Dornbush 2012). In agreement, we hypothesized (*sub-hypothesis 2*) that both competition from garlic mustard and selective herbivory by white-tailed deer would be important in controlling the cover and composition of native species introduced into our plots (restored natives). In contrast, we hypothesized that white-tailed deer activity would have no detectable negative impact upon garlic mustard cover, suggesting that competition from other plants, or other non-deer browsing factors, would most control garlic mustard cover. We additionally expected (*sub-hypothesis 3*) that competition from garlic mustard and selective herbivory by white-tailed deer would notably reduce the flowering of native plants, but the reciprocal effects of competition from native plants and white-tailed deer activity would have a notably muted response on garlic mustard silique and seed production. The combined effect of our three principle factors of interest, competitive interactions with garlic mustard, the need to actively restore native plants, and herbivore pressures from white-tailed deer, provided the basis for our overriding expectation (*integrated hypothesis*) that native plant richness and cover would be greatest in fenced, restored plots with garlic mustard removed. The relative magnitude of differences among these treatments is of principle interest for both understanding the factors maintaining garlic mustard dominance in invaded forests, and for the development of effective management strategies, as garlic mustard is regarded as one of the most widespread, and problematic invasive species in eastern North American forests (Rodgers et al. 2008; Lankau et al. 2009).

Methods

Our experiment was located in a suburban forest preserve (44° 31′N, 87° 56′W) in Green Bay, WI, USA within a secondary forest situated approximately 400-m from the Bay of Green Bay. The forest canopy consisted of *Acer negundo* (box elder), *Fraxinus pennsylvanica* (green ash), *Populus deltoides* (eastern cottonwood), and *Populus tremuloides* (quaking aspen) (*unpublished data*). The understory flora was dominated by *A. petiolata* (garlic mustard), with only sparse native or naturalized vegetation; approximately 5.8 ± 0.8 (mean ± SE) native species per 9 m^2 (*unpublished data*). The earliest voucher records for garlic mustard in the Green Bay, WI area were collected in 1992 by G. Fewless (University of Wisconsin-Green Bay Herbarium), suggesting our garlic mustard study population was approximately 15 years old at the start of our study. Initial garlic mustard rosette cover in June 2006 was 56.6 % ± 0.8 (SE). No public hunting is allowed within the preserve, although occasional deer culling by park administration does occur. Martinez and Dornbush (2013) utilized bi-weekly fecal group counts to estimate growing season (May to September) white-tailed deer density at the study site in 2010 and 2011 at 9.4 ± 1.3 deer km^{-2}. All experimental blocks were located on slightly elevated ridges, with soils mapped as Keowns silt loams, a coarse-loamy, Mollic Endoaquept (http://websoilsurvey.nrcs.usda.gov/). The study site had a mean annual temperature of 6.9 °C and received approximately 7,400 mm of precipitation annually (http://mcc.sws.uiuc.edu/).

In spring of 2006 we established a three-factor, split-plot experiment consisting of four replicated 10- by 17-m blocks, each containing eight 3- by 3-m treatment plots. The whole-plot treatment is a herbivore exclosure treatment running lengthwise within each block, surrounding four of the eight plots; the remaining plots were left open to herbivores. Exclosure fencing was constructed from 1.8-m tall polypropylene mesh fencing (holes 4.5-cm by 5.0-cm) manufactured to exclude white-tailed deer (*Odocoileus virginianus*) (Tenax Corp., Baltimore, MD, USA). The remaining two randomly applied split-plot treatments consisted of an *A. petiolata* (garlic mustard) removal or control application, and a native plant introduction (restoration) or non-restored control treatment. Garlic mustard was removed by hand from removal plots in July of 2006, then annually in May or early June thereafter. Averaged across the five sample dates when garlic mustard was in an actively growing life stage, the removal treatment reduced garlic mustard cover by approximately 93 %. The native plant restoration treatment was applied in three phases and utilized multiple means of establishing native species; our intent was not to test specific establishment methods, but rather to assure that native plant propagules were present and to limit the influence of uncontrollable climatic conditions on our restoration treatment results. Seedlings from nine different species were first planted at a density of 100 seedlings per 9 m^2 plot in August 2006, with an addition of 250 seeds m^{-2} from the same species pool added in December 2007. Our initial planting was enhanced in June of 2008 with the planting of an additional 102 individuals from 16 species, which included six species from the first planting and 10 new species. Both plantings occurred when garlic mustard was in its rosette growth form. All seedlings were germinated from seed in the University of Wisconsin-Green Bay greenhouse, and transplanted as seedlings into native plant restoration plots. Planted species lists and restoration details are presented in the Table 6 in Appendix. Native seeds used for both direct seeding and transplanted seedlings came from Prairie Moon Nursery, Winona, MN, USA.

Understory ($\leq$1-m tall) community composition was measured using the point-intercept method (Jonasson 1988) in August 2006, and in June and August of 2007, 2008, and 2009 following Ristau et al. (2001). Each 9-m^2 plot was divided into nine, 1-m^2 subplots, from which six subplots were randomly selected for sampling, producing a total of 150 vertical point drops per 9-m^2 plot. For each pin drop, species were recorded as present (hit) or absent (no hit), and garlic mustard hits were further recorded as either rosettes, adults, or both. A species list was also compiled for each plot at each sample date to assure that species missed by the point intercept method were captured; these species were credited with 0.5 hits. Point intercept data were used to calculate areal cover (%) of garlic mustard, and all restored and naturally occurring native and exotic understory species for each plot. To provide a surrogate measure of plant reproductive potential during the 2009 growing season we recorded the total number of individuals (i.e. stem counts) and the number of flowering individuals for the restored perennial species *Ageratina altissima*, *Bidens frondosa*, *Cryptotaenia canadensis*, *Desmodium glutinosum*, *Elymus virginicus*, and *Scutellaria lateriflora*. We selected these restored native species based on their relatively high abundance within native plant restoration plots, their presence within both deer treatments (many deer access plots lacked other species to support statistical comparisons), and the presence of reproductive structures from mid-to-late summer 2009. For the exotic garlic mustard, we recorded total silique and seed production (number m^{-2}) in July 2009, just prior to seed set and prior to plant senescence.

Changes in plant cover and richness were analyzed using mixed-model, split-plot ANOVAs in the proc mixed procedure of SAS 9.2 (SAS, Inc., Cary, NC, USA). We tested our *integrated hypothesis* examining the effects of deer access, native plant restoration, and garlic mustard removal ($n = 32$ plots) on total native plant richness and percent cover (restored plus naturally occurring natives) with a model that included a block effect, a deer exclosure whole-plot effect, a native plant restoration split-plot treatment, a garlic mustard removal split-plot treatment, a repeated measures time effect ($n = 7$), and all possible interactions among the treatments. We tested *sub-hypothesis 1* examining the effect of garlic mustard removal on naturally occurring native species cover and richness using the same model, but limited our analysis only to non-restored plots ($n = 16$), thereby eliminating the native plant restoration term from our model. *Sub-hypothesis 2* evaluating the effect of white-tailed deer access and garlic mustard presence on the cover of restored native species was tested using the same method, but was limited to plots restored with native species ($n = 16$). The reciprocal effect of white-tailed deer access and native plant restoration on garlic mustard cover was analyzed identically, but limited to plots in which garlic mustard was not removed ($n = 16$). We used a permutational multivariate analysis of variance (perMANOVA) to test the effects of deer access and garlic mustard treatments within restored plots on patterns of community composition for restored species by averaging relative abundances for June and August 2009. perMANOVA is a semi-parametric multivariate analysis of variance that allows testing of factorial experimental designs on multivariate responses and is appropriate for most ecological community data (Anderson 2001). We treated deer access, garlic mustard removal, and their interaction as fixed effects, with block as a random effect, using 1,000 permutations in the vegan package in R (Oksanen et al. 2012). These data were also ordinated using non-metric multidimensional scaling (NMDS). The NMDS was performed with a maximum of 250 iterations, 50 runs with real data, 50 runs with randomized data, and a stability criterion of 0.00001. We used Bray-Curtis distances for both analyses in PC-ORD v6 (MjM Software Design, Gleneden Beach, OR, USA). The effects of native plant restoration and deer access on garlic mustard silique and seed production (*sub-hypothesis 3*) were evaluated for plots in which garlic mustard was not removed ($n = 16$) using a model that included a block effect ($n = 4$), a deer exclosure whole-plot effect ($n = 2$), a native plant restoration split-plot treatment ($n = 2$), and a deer-by-restoration interaction effect. The effect of deer access and garlic mustard removal on the proportion of restored native species flowering within restoration-treatment plots ($n = 16$) were evaluated individually using Pearson Chi squared tests calculated manually (Ramsey and Schafer 1997). *Bidens frondosa* and *D. glutinosum* lacked sufficient numbers of flowering individuals for statistical analyses, so were not included in this formal analysis. In all univariate analyses, all treatments, including blocks, were treated as fixed effects, with fixed-effects denominator degrees of freedom determined using the Kenward-Roger method. Dependent variables were transformed as needed to meet equal variance assumptions and to improve heteroscedasticity of model residuals. All repeated-measures models included an autoregressive covariance structure to account for correlation among measurements through time (Little et al. 1996).

Results

Integrated hypothesis Native plant richness and cover would be greatest in fenced, restored plots with garlic mustard removed.

In partial agreement with our expectations, deer access and native plant restoration significantly (Deer Access-*by*-Native Restoration: $P < 0.03$) affected native plant richness (Table 1), with native richness notably enhanced in all treatment combinations that included the restoration treatment (Fig. 1a–c). However, the magnitude of the native plant restoration effect was not independent of deer access (Table 1), with higher native richness in fenced restored plots, than in open-access restored plots (Fig. 1a). This trend was opposite in non-restored plots, where deer access seemed to slightly enhance native richness (Fig. 1a). In contrast to our expectations, garlic mustard removal had little to no effect on native plant richness ($P > 0.4$; Fig. 1b–c). In absolute terms, restored plots with garlic mustard averaged (±SE) 15.4 (±0.91) native species, while restored plots from which garlic mustard was removed averaged 17.3 (±0.91) native species. The presence or absence of deer did not significantly alter the benefit, or the lack thereof, of garlic mustard removal (Deer Access-*by*-*A. petiolata* Presence: $P > 0.9$) on native plant richness (Table 1; Fig. 1b).

Native plant restoration ($P < 0.003$) and the deer-by-restoration interaction term also significantly ($P < 0.03$) affected native plant cover (Table 1), which notably increased through time in fenced, but not open-access plots (Fig. 1d–e). The importance of combining native plant restoration with fencing was clear; native cover reached 44.5 % (±3.8) in restored fenced plots, but only 10.6 % (±3.8) in restored open-access plots (Fig. 1d). In contrast, garlic mustard removal did not significantly affect ($P > 0.9$) native plant cover (Table 1), with native plant cover nearly identical in garlic mustard removal and control plots throughout the duration of the experiment (Fig. 1f).

Sub-hypothesis 1 Garlic mustard removal alone would not be sufficient to increase the richness or cover of native species, due to overriding establishment limitations for native species.

In agreement with our hypothesis, garlic mustard removal did not significantly affect the richness ($P > 0.9$; Fig. 2b) or cover ($P > 0.6$; Fig. 2d) of naturally occurring native plants in non-restored plots (Table 2). Naturally established native plant richness trended higher in plots open to white-tailed deer, with larger differences evident in June 2007 and August 2008 (Fig. 2a), potentially accounting for the significant ($P < 0.03$) time-by-deer interaction term

Table 1 ANOVA results evaluating (*integrated hypothesis)* the effect of *Odocoileus virginianus* (white-tailed deer) access, *Alliaria petiolata* (garlic mustard) presence, and native plant restoration on native plant richness and cover (%) in a northeastern Wisconsin forest, USA

Source of variation	Native species richness			Native species cover (%)		
	F	*df*	*P*	*F*	*df*	*P*
Block	**9.31**	**3, 3**	**<0.05**	6.20	3, 3.0	>0.08
Deer access	1.69	1, 4.1	>0.2	5.62	1, 3.6	>0.08
A. petiolata presence	0.61	1, 19.8	>0.4	0.01	1, 20.9	>0.9
Native restoration	**106.51**	**1, 19.8**	**<0.0001**	**11.79**	**1, 20.9**	**<0.003**
Time	**94.63**	**6, 141**	**<0.0001**	**18.52**	**6, 139**	**<0.0001**
Deer access-*by*-*A. petiolata* presence	0.01	1, 19.8	>0.9	1.84	1, 20.9	>0.1
Deer access-*by*-native restoration	**5.58**	**1, 19.8**	**<0.03**	**5.47**	**1, 20.9**	**<0.03**
A. petiolata presence-*by*-native restoration	1.44	1, 19.8	>0.2	0.89	1, 20.9	>0.3
Time-*by*-Deer access	**3.50**	**6, 141**	**0.003**	**3.14**	**6, 139**	**<0.007**
Time-*by*-*A. petiolata* presence	**4.48**	**6, 141**	**0.0003**	1.62	6, 139	>0.1
Time-*by*-native restoration	**61.23**	**6, 141**	**<0.0001**	**6.08**	**6, 139**	**<0.0001**
Deer access-*by*-*A. petiolata* presence-*by*-native restoration	0.38	1, 19.8	>0.5	0.50	1, 20.9	>0.4
Time-*by*-Deer access-*by*-*A. petiolata* presence	1.03	6, 141	>0.4	0.39	6, 139	>0.8
Time-*by*-Deer access-*by*-native restoration	1.56	6, 141	>0.1	1.16	6, 139	>0.3
Time-by-A. petiolata presence-by-native restoration	0.50	6, 141	>0.8	0.90	6, 139	>0.4
Time-*by*-Deer access-*by*-*A. petiolata* presence-*by*-native restoration	0.55	6, 141	>0.7	0.44	6, 139	>0.8

Native species cover was arc-sine square root transformed to meet model assumptions of normality and equal variance

Statistically significant differences ($\alpha = 0.05$) are indicated in bold

(Table 2). Averaged across all sample dates, open access plots averaged 6.9 (±0.6) naturally occurring native species per 9 m^2 plot, while fenced plots averaged only 5.4 (±0.6) (Fig. 2a). The time-by-garlic mustard removal ($P < 0.004$) interaction term was also significant (Table 2), with naturally occurring native plant richness in plots with garlic mustard actually appearing slightly higher in August 2006 and August 2009, and slightly lower in June 2007, relative to otherwise similar treatment means (Fig. 2b). Native plant cover (%) did not differ significantly among any treatment combinations, or through time (Table 2; Fig. 2c–d). Averaged across all dates, naturally occurring native plant cover in non-restored treatment plots averaged only 8.0 % (±0.7), highlighting that our non-restored plots supported limited naturally occurring native plants during this 4 year study, irrespective of garlic mustard management.

Sub-hypothesis 2 Both competition from garlic mustard and selective herbivory by white-tailed deer would be important in controlling the cover and composition of restored native species, while garlic mustard cover would be significantly affected by competition from restored native plants, or other non-deer browsing factors, but not by white-tailed deer activity.

In contrast to our expectations, neither white-tailed deer access ($P > 0.1$; Fig. 3a) nor garlic mustard presence ($P > 0.1$; Fig. 3b) significantly affected the richness of restored species (Table 3). However, as expected, white-tailed deer significantly ($P < 0.05$), and negatively affected the cover of restored native plants (Table 3). Averaged across all sample dates, restored-species cover within fenced plots was approximately 216 % that of open-access plots exposed to deer activity, with differences growing notably larger through time (Fig. 3c). By the end of the experiment restored-species cover within fenced plots was almost four times higher than in open-access plots (Fig. 3c). As observed for restored species richness, we found that four consecutive years of garlic mustard removal had no significant effect ($P > 0.3$) on the cover of restored native species (Table 3), suggesting that competition from garlic mustard did not determine the success of our restorations (Fig. 3b, d). Restored species cover in plots cleared of garlic mustard was only 2 % higher than in plots containing

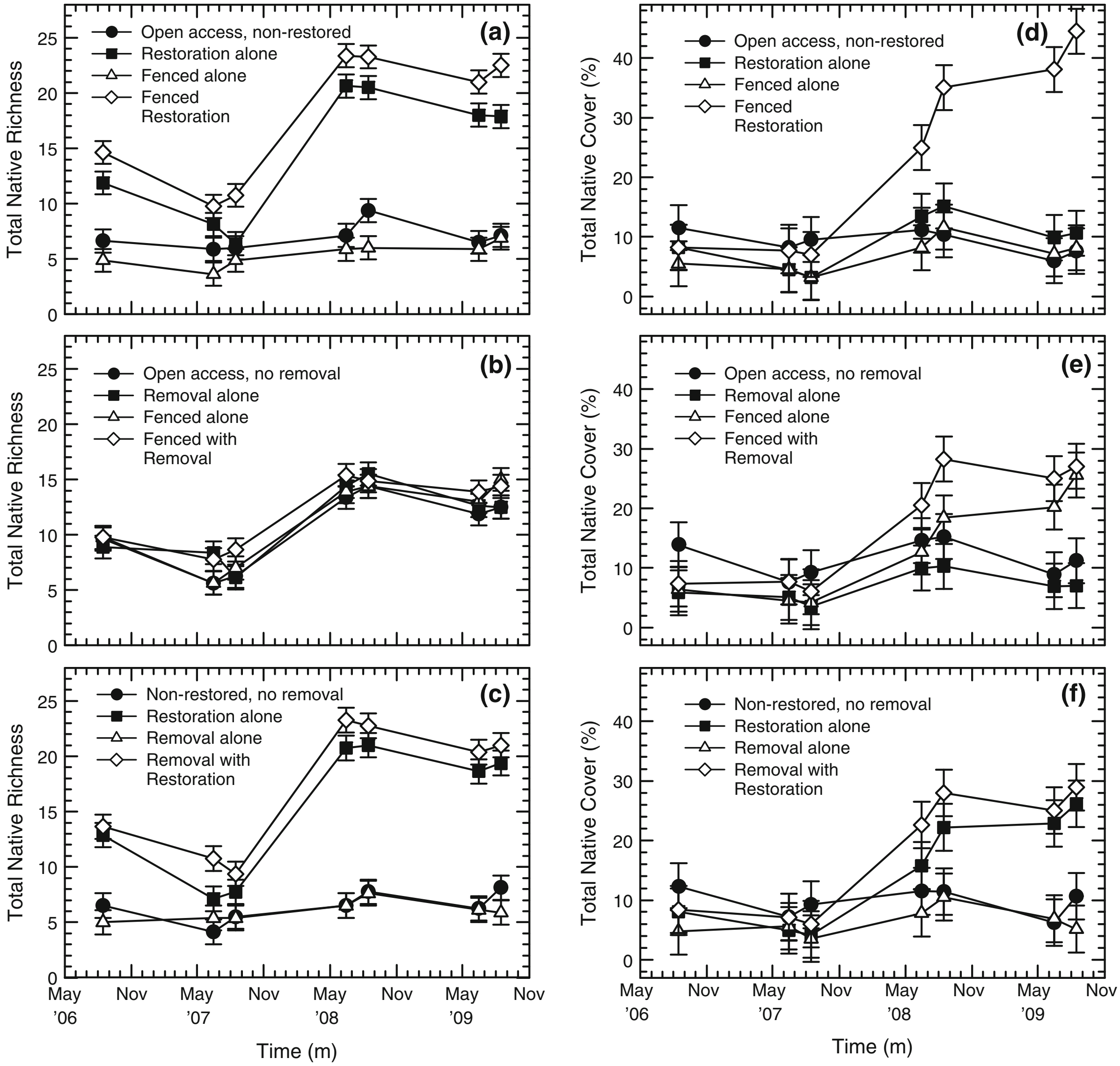

Fig. 1 Temporal pattern of total native richness (**a**–**c**) and cover (%) (**d**–**f**) in the understory of (**a** and **d**) the four possible combinations of native plant restoration and *Odocoileus virginianus* (white-tailed deer) access, (**b** and **e**) the four possible combinations of *Alliaria petiolata* (garlic mustard) removal and white-tailed deer access, and (**c** and **f**) the four possible combinations of native plant restoration and garlic mustard removal. All plots are 9 m^2; values represent treatment means ±1 standard error

garlic mustard (Fig. 3d), despite reducing average garlic mustard cover from 53.2 % in control plots to 3.8 % in removal plots across the five sample dates with actively growing garlic mustard (garlic mustard is biennial).

Treatment effects on restored species cover were further corroborated by the community composition analysis, which found significant differences in restored species composition between deer treatments (perMANOVA: $F_{1,12} = 11.4$; $P = 0.001$), but not between garlic mustard treatments ($F_{1,12} = 0.55$; $P = 0.68$), or among the deer-by-garlic mustard removal interactions ($F_{1,12} = 1.07$; $P = 0.35$). The NMDS ordination was rotated to maximize the variance explained by deer access, and highlights the separation between deer access plots (final STRESS = 5.66, Fig. 4). The first dimension was highly negatively correlated with erect forbs (Pearson

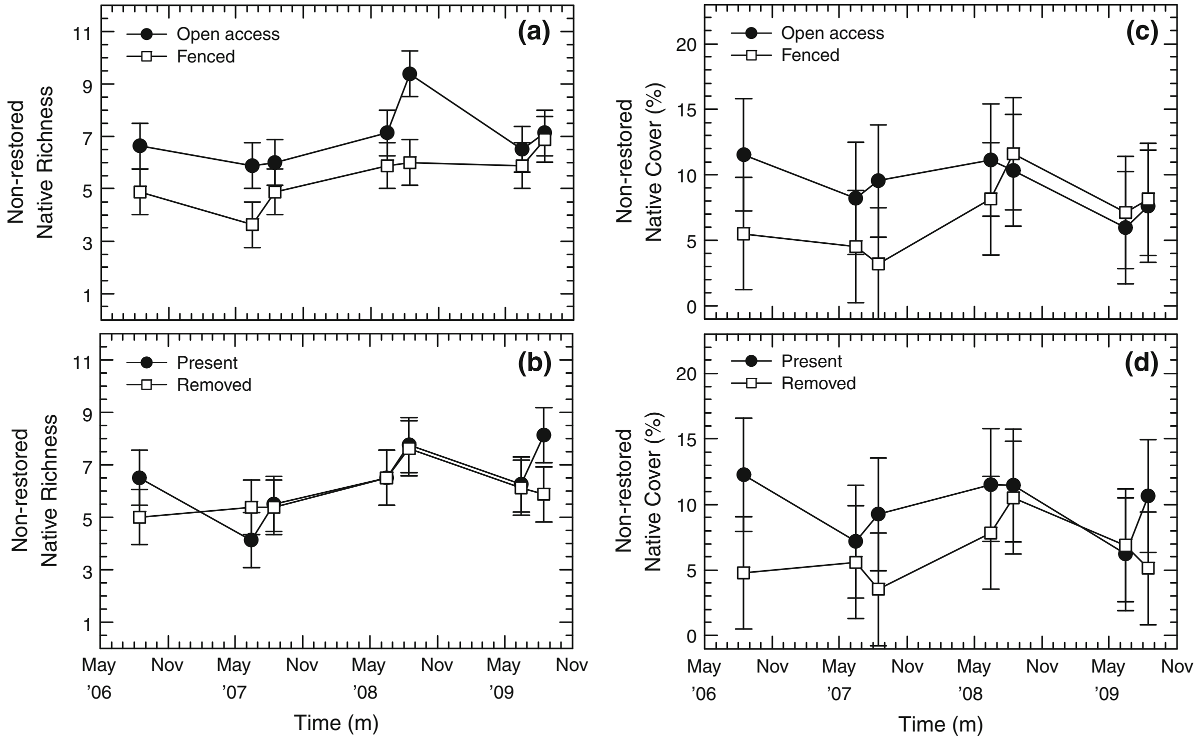

Fig. 2 Temporal pattern of naturally occurring native plant richness (**a** and **b**) and cover (%) (**c** and **d**) in the understory of (**a** and **c**) non-restored experimental plots that are either accessible to or fenced from *Odocoileus virginianus* (white-tailed deer) and in (**b** and **d**) non-restored plots in which *Alliaria petiolata* (garlic mustard) was either removed or left in situ. All plots are 9 m^2; values represent treatment means ±1 standard error

Table 2 ANOVA results evaluating (*sub-hypothesis 1*) the effect of *Odocoileus virginianus* (white-tailed deer) access and *Alliaria petiolata* (garlic mustard) presence on naturally occurring native plant richness and cover (%) in non-restored treatment plots (n = 16) in a northeastern Wisconsin forest, USA

Source of variation	Naturally occurring Native species richness			Naturally occurring Native species cover (%)		
	F	*df*	*P*	*F*	*df*	*P*
Block	8.04	3, 3.0	0.06	4.20	3, 3.0	>0.1
Deer access	3.94	1, 4.3	>0.1	0.06	1, 3.4	>0.8
A. petiolata presence	0.01	1, 7.0	>0.9	0.29	1, 8.1	>0.6
Time	**5.69**	**6, 69.5**	**<0.0001**	2.02	6, 68.5	>0.07
Deer Access-*by-A. petiolata* presence	0.05	1, 7.0	>0.8	1.69	1, 8.1	>0.2
Time-*by*-Deer access	**2.70**	**6, 69.5**	**<0.03**	0.41	6, 68.5	>0.8
Time-*by-A. petiolata* presence	**3.55**	**6, 69.5**	**0.004**	1.45	6, 68.5	>0.2
Time-*by*-Deer access-*by-A. petiolata* presence	0.27	6, 69.5	>0.9	0.10	6, 68.5	>0.9

Naturally occurring native species richness was natural log transformed, while naturally occurring native species cover was arc-sine square root transformed to meet model assumptions of normality and equal variance

Statistically significant differences ($\alpha = 0.05$) are indicated in bold

correlation coefficients: *Ageratina altissima,* r = −0.92; *Solidago flexicaulis*, r = −0.85; *Thalictrum dioicum*, r = −0.81), but not grasses or shorter statured plants (Pearson correlation coefficients: *Elymus virginicus*, r = −0.05; *Prenanthes alba*, r = −0.08; *Onoclea sensibilis*, r = −0.12).

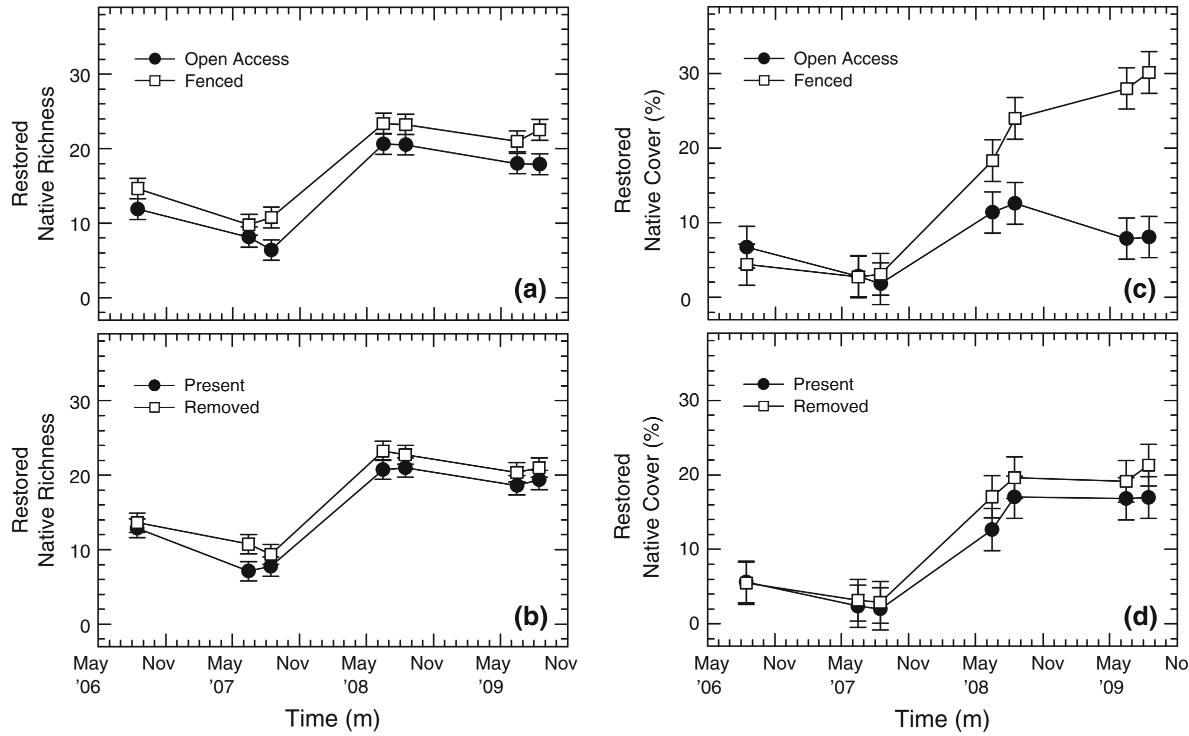

Fig. 3 Total richness (**a** and **b**) and cover (%) (**c** and **d**) of restored native understory species in experimental plots that differ in (**a** and **c**) access to *Odocoileus virginianus* (white-tailed deer) and (**b** and **d**) in *Alliaria petiolata* (garlic mustard) presence or absence. All plots are 9 m^2; values are means ±1 standard error

Table 3 ANOVA results evaluating (*sub-hypothesis 2*) the effect of *Odocoileus virginianus* (white-tailed deer) access and *Alliaraia petiolata* (garlic mustard) presence on restored native species richness and cover (%) in a northeastern Wisconsin forest, USA

Source of variation	Restored Native species richness			Restored Native species cover (%)		
	F	*df*	*P*	*F*	*df*	*P*
Block	0.91	3, 3	>0.5	0.86	3, 3	>0.5
Deer access	3.42	1, 3.3	>0.1	**9.98**	**1, 3.2**	**<0.05**
A. petiolata presence	2.00	1, 7.2	>0.1	1.18	1, 7.9	>0.3
Time	**124.76**	**6, 68.9**	**<0.0001**	**31.64**	**6, 66.9**	**<0.0001**
Deer access-*by-A. petiolata* presence	0.14	1, 7.2	>0.7	0.47	1, 7.9	>0.5
Time-*By*-Deer access	2.13	6, 68.9	>0.06	**5.89**	**6, 66.9**	**<0.0001**
Time-*by-A. petiolata* presence	2.01	6, 68.9	>0.07	0.61	6, 66.9	>0.7
Time-*by*-Deer access-*by-A. petiolata* presence	0.98	6, 68.9	>0.4	0.97	6, 66.9	>0.4

Restored native species cover was arc-sine square root transformed to meet model assumptions of normality and equal variance

Statistically significant differences (α = 0.05) are indicated in bold

Neither white-tailed deer access ($P > 0.4$; Fig. 5a), nor native-plant restoration ($P > 0.2$; Fig. 5b) significantly affected garlic mustard cover (Table 4). This conclusion was not altered when we restricted our analysis to only those dates when the biennial garlic mustard was actively growing (n = 5; *data not presented*). Based on this more conservative, restricted dataset, garlic mustard cover averaged 54.7 % (±3.5) in restored and 50.0 % (±3.5) in non-restored plots; garlic mustard cover averaged 49.7 % (±4.5) in plots accessible to deer and 54.9 % (±4.5) in fenced plots.

Sub-hypothesis 3 Competition from garlic mustard and selective herbivory by white-tailed deer would notably reduce the flowering of native plants, but the reciprocal effects of competition from native plants and white-tailed deer activity would have a notably muted response on garlic mustard silique and seed production.

The proportion of restored native plants that flowered differed significantly between open access and fenced plots for three of the four species evaluated. Specifically, *Cryptotaenia canadensis* ($\chi^2 = 4.32$; $P < 0.05$), *Ageratina altissima* ($\chi^2 = 14.02$; $P < 0.0005$), and *Scutellaria lateriflora* ($\chi^2 = 34.74$; $P < 0.0005$) all flowered at higher proportions within fenced than open-access plots (Fig. 6a). Because *A. altissima* regeneration was particularly high in one fenced treatment plot, holding approximately 20-times more individuals than in other comparable plots, we reran our *A. altissima* analysis omitting both this plot and the complementary, open-access treatment plot from the same block. However, omission of these two plots did not alter our statistical conclusion ($\chi^2 = 28.17$; $P < 0.0005$). Only the perennial grass *Elymus virginicus* flowered in equal proportions irrespective of deer access ($\chi^2 = 0.03$; $P > 0.3$). In agreement with results observed for native cover, garlic mustard removal did not significantly affect the proportion of native plants that flowered (Fig. 6b). Specifically, *C. canadensis* ($\chi^2 = 0.00$; $P > 0.3$), *S. lateriflora* ($\chi^2 = 0.06$; $P > 0.3$), and *E. virginicus* ($\chi^2 = 0.64$; $P > 0.3$) all flowered in equal proportions, irrespective of garlic mustard presence or absence. When all plots were included in our analysis, *A. altissima* plants appeared to flower in significantly higher proportions in plots containing garlic mustard ($\chi^2 = 89.62$; $P < 0.0005$), than in garlic mustard removal plots. However, this conclusion was driven entirely by a single high regeneration plot, and the omission of this and its paired, open-access plot eliminated the statistically significant difference ($\chi^2 = 0.17$; $P > 0.3$). There was no significant difference in the number of siliques produced by garlic mustard (Table 5) as a result of either deer access ($F = 0.53$, $P > 0.5$) or native plant restoration ($F = 1.19$, $P > 0.3$), nor did we find a significant difference in the number of seeds produced by garlic mustard (Table 5) in response to either deer access ($F = 0.01$, $P > 0.9$) or native plant restoration ($F = 1.18$, $P > 0.3$). Garlic mustard silique and seed production in native-plant restoration plots were 74 and 69 % that observed in non-restored plots, respectively (Table 5).

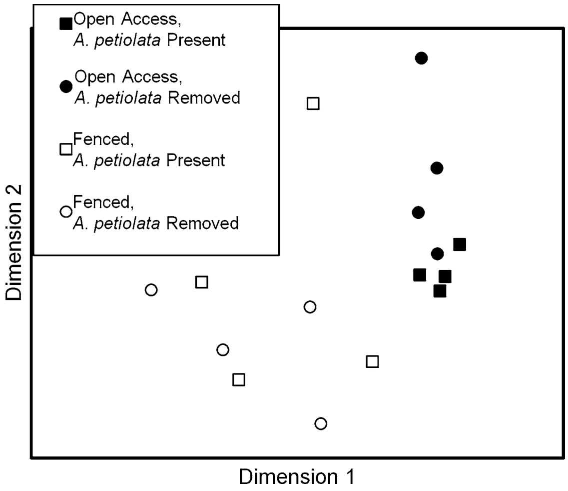

Fig. 4 Nonmetric multidimensional scaling (NMDS) ordination of restored understory communities based on the relative abundance of restored species averaged across June and August 2009 for the four combinations of *Alliaria petiolata* (garlic mustard) removal by *Odocoileus virginianus* (white-tailed deer) access treatments. The ordination was rotated to maximize the variance explained by deer access. The final 2-dimensional STRESS was 5.66

Discussion

Native plant richness and cover were both significantly enhanced by the active restoration of native herbs and the exclusion of white-tailed deer. The benefits of deer exclusion were notably greater on native plant cover, than on native plant richness. However, we detected no significant benefits of garlic mustard removal on either native plant richness or cover. For plots not receiving native restoration, the richness and cover of naturally establishing, non-restored native species remained quite low, and neither response was significantly affected by garlic mustard removal or deer access during our 4 year study. These results emphasize that the observed low native plant richness and cover in control plots resulted in large part from poor unassisted native plant establishment, irrespective of the relative strength of factors driving native species loss. For those plots receiving native restorations, herbivory from white-tailed deer significantly reduced the cover and altered the composition

Table 4 ANOVA results evaluating (*sub-hypothesis 2*) the effect of *Odocoileus virginianus* (white-tailed deer) access and native plant restoration on *Alliaria petiolata* (garlic mustard) cover (%) in garlic mustard-removal control plots (n = 16) in a northeastern Wisconsin forest, USA

Source of variation	*A. petiolata* cover (%)		
	F	*df*	*P*
Block	0.79	3, 2.9	>0.5
Deer Access	0.77	1, 2.9	>0.4
Native restoration	1.20	1, 19	>0.2
Time	**179.68**	**6, 61.1**	**<0.0001**
Deer access-*by*-native restoration	0.39	1, 19	>0.5
Time-*by*-Deer access	0.91	6, 61.1	>0.4
Time-*by*-native restoration	0.76	6, 61.1	>0.6
Time-*by*-Deer access-*by*-native restoration	0.30	6, 61.1	>0.9

Alliaria petiolata cover was arc-sine square root transformed to meet model assumptions of normality and equal variance

Statistically significant differences (α = 0.05) are indicated in bold

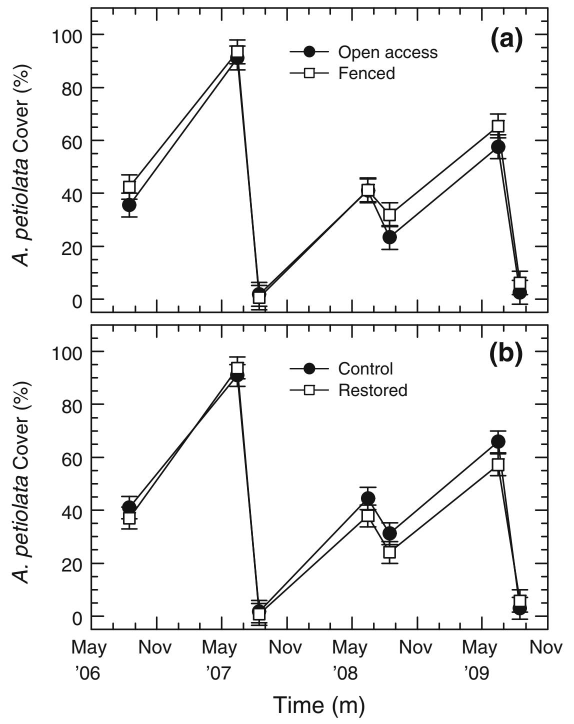

Fig. 5 Total cover (%) of *Alliaria petiolata* (garlic mustard) in experimental plots that are either (**a**) accessible to or fenced from *Odocoileus virginianus* (white-tailed deer), and in (**b**) plots to which native understory species were either restored, or left to natural colonization. Values are means ±1 standard error

of restored herbs, but had no detectable effect upon garlic mustard cover. In addition, deer herbivory significantly, and negatively affected flower production by three of the four restored native species examined, but had no apparent effect upon either garlic mustard silique production or seed output. In contrast, neither native plant restoration nor garlic mustard presence significantly affected the cover, or flowering, of garlic mustard or restored natives, respectively. Thus native cover was strongly influenced by deer browsing and establishment potential, but was independent of garlic mustard presence. Contemporary community dominance (high relative abundance) by garlic mustard also appeared maintained via non-competitive interactions, including lower herbivore pressure relative to native plants, and a high seed output that likely promoted colonization and reestablishment.

Our finding of poor native plant establishment, with subsequent limitations to native diversity, is well supported in many ecosystems (Turnbull et al. 2000; MacDougall and Turkington 2005), but may be particularly characteristic of recovering forest understories (Ehrlén and Eriksson 2000; Flinn and Vellend 2005). Reflecting our results, Hochstedler et al. (2007) found that 5 years of dormant season garlic mustard spraying in both old growth and secondary growth forests in Ohio, USA produced no significant change in species richness, Shannon-Wiener diversity, or species composition, despite significant declines in the cover of adult garlic mustard. In a similar study, Pavlovic et al. (2009) found that 3 years of removal of the exotic mustard *Hesperis matronalis* (dame's rocket) in an Indiana, USA forest also failed to increase native plant richness or diversity. Brudvig et al. (2011) found that seed addition, not the reduction

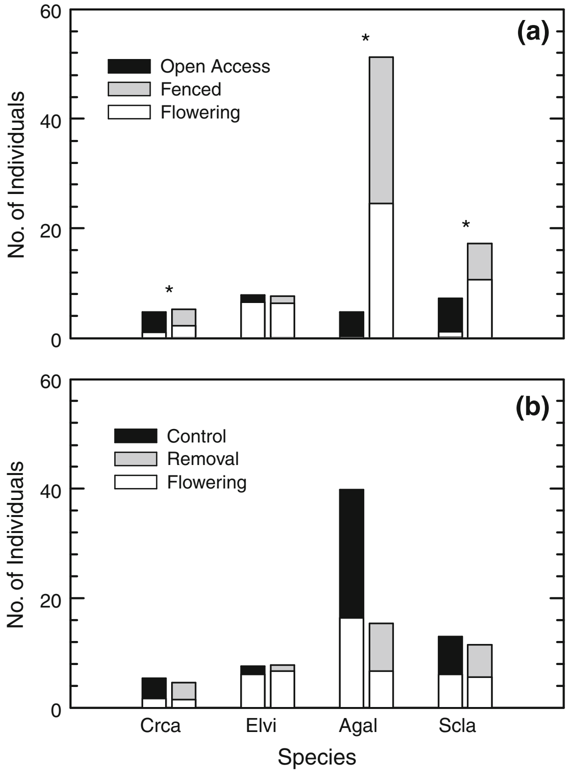

Fig. 6 Total number of individuals and the number of individuals flowering for the restored native understory species *Cryptotaenia canadensis* (Crca), *Elymus virginicus* (Elvi), *Ageratina altissima* (Agal), and *Scutellaria lateriflora* (Scla) recorded during the 2009 growing season in experimental plots that are either (**a**) accessible to or fenced from *Odocoileus virginianus* (white-tailed deer), and in (**b**) non-restored plots in which *Alliaria petiolata* (garlic mustard) was either removed or left in situ. All plots are 9 m^2; values represent treatment means; asterisks represent significant differences within a species at $P < 0.05$)

Table 5 Effect of (*sub-hypothesis 3*) *Odocoileus virginianus* (white-tailed deer) access and native plant restoration on silique and seed production by *Alliaria petiolata* (garlic mustard) in 3 × 3 m plots in a northeastern Wisconsin woodland, USA

Treatment	Siliques (no. m^{-2})	Seeds (no. m^{-2})
Deer exclosure		
Open access	1,670 (220)	28,470 (5,630)
Fenced	1,900 (220)	29,270 (5,630)
Restoration		
Control	2,050 (290)	34,130 (6,270)
Restored	1,520 (290)	23,600 (6,270)

None of the means differ significantly (α = 0.05). Values represent ANOVA least square means (±SE)

of interspecific competition, most increased woodland understory diversity in recovering forests in the Midwest, USA, concluding that the herbaceous communities they studied were relatively open to seedling establishment when seed rain was experimentally provided. Mabry (2004) found that the frequency of understory species in fragmented woodlands across Iowa, USA was negatively related to seed size and positively related to seed production, emphasizing the role of dispersal in structuring fragmented forest understories. Modeling and supporting field surveys by Vellend (2003) found that the limited dispersal ability of many understory species is likely to significantly delay, or virtually prevent their establishment in heavily fragmented landscapes. The strength of this effect declined as a species' dispersal ability increased (Vellend 2003), suggesting a predictable species composition in fragmented forests favoring species with high seed production and effective dispersal. The high seed output of garlic mustard (Cavers et al. 1979; Anderson et al. 1996; this study), coupled with the low native plant colonization rates we observed appears to support these predictions. Our results, and those of these complementary studies, support the position that forest understory composition in fragmented, disturbed forest landscapes is strongly controlled by plant establishment. We conclude that at our study site contemporary garlic mustard dominance was in part indirect, driven by the fact that garlic mustard naturally established while native species did not.

In contrast to our expectations, we found no evidence that garlic mustard presence significantly altered restored species richness or composition, or reduced native species cover or flower production. Significant evidence exists, mainly from greenhouse experiments, that garlic mustard-produced allelopathic chemicals disrupt mycorhizal colonization, resulting in reduced plant performance by North American woodland plants (Stinson et al. 2006; Wolfe et al. 2008). However, competitive effects of garlic mustard on native plants are often not detected in the field. For example, in a previous study at our site we found that garlic mustard presence had no significant direct effect on the survival of six species of native 2 month old planted seedlings, or on notably smaller 1 month old planted *Aster cordifolius* seedlings (Hahn and Dornbush 2012). Murphy (2005) found that transplanted *Sanguinaria canadensis* (blood root) ramets competed successfully with garlic mustard when grown together in the field, and Meekins and McCarthy (1999) reported that two of the three native species they tested were as, or more, aggressive than garlic mustard in controlled competition experiments. Our results contribute to a growing body of evidence that the competitive strength of garlic mustard in its invasive North American range is either less than previously reported, or more context dependent than generally emphasized (but see Lankau et al. 2009; Lankau 2012).

Several recent papers appear to both partially explain and justify a more nuanced approach to evaluating the interspecific competitive effects of garlic mustard in its invasive North American range. For instance, Lankau et al. (2009) found that when garlic mustard occurred in monocultures, as was the case at our field site, garlic mustard genotypes that produce lower amounts of allelopathic chemicals were favored, thereby reducing the population's interspecific competitive ability. Likewise, Lankau (2012) found that tolerance of the North American understory herb *Pilea pumila* to interspecific competition with garlic mustard depended upon its previous exposure to garlic mustard in the field. *Pilea pumila* individuals originating from areas supporting highly competitive garlic mustard populations were most able to grow and maintain arbuscular mycorrhizal relationships when competing with garlic mustard under experimental conditions. As such, our findings, and those from previous studies (Meekins and McCarthy 1999; Murphy 2005) reporting limited competitive strength of garlic mustard in its introduced North American range may be best placed within the context of garlic mustard invasion status.

Our study also focused on the influence of white-tailed deer, as their role in shaping forest understories is well documented (e.g. Horsley et al. 2003; Rooney et al. 2004), and more broadly, generalist herbivores are widely recognized for promoting invasive species (Keane and Crawley 2002). As expected, access by white-tailed deer significantly reduced restored plant cover, altered species composition, and reduced the proportion of restored individuals flowering. In fact, by the end of the experiment, restored species cover was approximately four-times higher in fenced plots than open access plots, suggesting that deer activity imposed a strong and biologically meaningful effect on the herbaceous plant community. Apart from direct mortality, intense browsing reduces plant size, which is often positively related to plant reproductive potential (Anderson 1994). In agreement, three of the four restored species we examined specifically for reproduction flowered at significantly higher frequencies within, than outside of, deer exclosures. An additional two other restored species, *Bidens frondosa* and *Desmodium glutinosum*, only flowered inside fenced areas (*unpublished data*). In contrast, deer-access had no effect on the proportion of the browse-tolerant grass *E. virginicus* that flowered. These results agree with patterns reported by Rooney et al. (2004), who found a notable decline in animal pollinated and dispersed understory species in northern Wisconsin forests. Wiegmann and Waller (2006) also noted increases in grasses, grass-like and browse-tolerant species and decreases in broad-leaved forbs over the last 50 years in Midwest, USA forests. In agreement with the results of our study, both of these studies identified white-tailed deer as a primary factor shaping forest understory compositions.

In contrast to the negative effect of deer-browsing on most non-graminoid restored natives, we found no effect of deer access on garlic mustard cover, silique production, or seed output. In agreement, Knight et al. (2009) documented higher abundance of garlic mustard, and lower abundance and flowering of native herbaceous plants in plots accessible to white-tailed deer than in plots protected from deer in a Pennsylvania, USA forest. Eschtruth and Battles (2008) documented a positive, exponential relationship between the abundance of white-tailed deer and garlic mustard in eastern USA hemlock forests. Lewis et al. (2006) found no significant differences in garlic mustard size or reproductive output between caged plants and plants accessible to herbivores in several populations in the northeast, USA. Furthermore, the exotic slug *Deroceras reticulatum* has also been shown to avoid feeding on garlic mustard (Hahn et al. 2011; Hahn and Dornbush 2012), suggesting that our results may also apply more broadly to generalist herbivores. These findings are consistent with an emerging literature documenting that selective herbivory plays an important role in promoting the high abundance of exotic (Gonzales and Arcese 2008; Eschtruth and Battles 2008), unpalatable, or browse tolerant (Wiegmann and Waller 2006) understory species in many North American forests.

The objective of this study was to improve our understanding of the mechanisms maintaining high relative abundance of exotic garlic mustard and low native richness and cover in a North American forest understory, with an expectation that our results would benefit the development of restoration strategies aimed at enhancing native diversity in similar, degraded forest understories. We conclude that no single factor adequately explained contemporary community composition at our site. Rather, active restoration of native species was required to increase native plant richness, and reducing herbivore pressure increased this effect. Both restoration and reducing herbivore pressure were essential to increase native plant cover and flowering. Notably, our results provided little to no support that the removal of garlic mustard had any impact on the recovery of the native understory. We stress that our study reflects only one point in the invasion process; approximately 15 years post invasion based on local herbarium records. Our results contribute to an emerging picture that, at least for garlic mustard, factors driving biodiversity decline during invasion, may not be the principle factors preventing diversity recovery at a later date. There exist numerous low diversity forest understories with well-established garlic mustard populations in North America (e.g. Rodgers et al. 2008), and our study provides strong evidence that they may be amenable to restoration. In this regard, our results provide a clear lesson for land managers; understory quality at our site, as defined by native cover and richness, appeared more dependent on the control of herbivores and the establishment of desired species than on the direct elimination of the dominant exotic.

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Appendix

See Table 6.

Table 6 Details for August 2006 and June 2008 native-species plantings and December 2006 native-plant seeding for the restoration treatment at the Bay Beach Wildlife Sanctuary, Green Bay, WI, USA

Species	Planting years	Density (#/9 m^2)	Height (cm)	Leaves (#/plant)	Seeding (seeds/9 m^2)
Ageratina altissima	2006/2008	27/8	7.2 (0.6)/15.1 (0.8)	6.6 (0.3)/7.5 (0.5)	608
Asarum canadense	2008	–/8	–/–	–/–	–
Aster cordifolius	2008	–/8	–/–	–/3.5 (0.7)	–
Bidens frondosa	2008	–/8	–/25.1 (0.8)	–/7.1 (0.3)	–
Cryptotaenia canadensis	2006/2008	7/8	–/–	3.6 (0.2)/2.9 (0.1)	158
Desmonium glutinosum	2006/2008	7/4	–/–	4.2 (0.2)/3.6 (0.2)	23
Elymus virginicus	2008	–/8	–/–	–/4.7 (0.5)	–
Geranium maculatum	2008	–/4	–/–	–/2.2 (0.2)	–
Hydrophyllum virginiatum	2008	–/8	–/–	–/–	–
Mertensia virginica	2006	2/–	–/–	2.2 (0.2)/–	45
Onoclea sensibilis	2008	–/3	–/–	–/–	–
Phlox divaricata	2006	1/–	4.1 (0.3)/–	9.9 (0.8)/–	23
Polemonium reptans	2006/2008	1/3	–/–	3.7 (0.2)/2.9 (0.3)	158
Prenanthes alba	2008	–/8	–/–	–/2.9 (0.2)	–
Rudbeckia laciniata	2008	–/8	–/–	–/2.1 (0.2)	–
Scutellaria lateriflora	2008	–/4	–/4.7 (0.2)	–/5.8 (0.3)	–
Solidago flexicaulis	2006/2008	27/8	–/–	5.9 (0.3)/4.3 (0.3)	608

Table 6 continued

Species	Planting years	Density (#/9 m^2)	Height (cm)	Leaves (#/plant)	Seeding (seeds/9 m^2)
Solidago ulmifolia	2006	26/–	–/–	6.0 (0.3)/–	585
Thalictrum dioicum	2006/2008	2/4	–/–	2.9 (0.2)/1.8 (0.1)	45

Asarum canadense, *Hydrophyllum virginiatum*, and *Onoclea sensibilis* were planted from root stocks, all other species were germinated from seed and transplanted as seedlings in the 2006 and 2008 plantings. Numbers under the planting density, height, and leaves columns are mean (±SE) for 2006/2008 plantings, respectively. Height to apical meristem is presented only for plants expressing clear stem growth as young seedlings, and for *Elymus virginicus* the number of leaves per plant is actually the number of culms per plant

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