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Exotic consumers interact with exotic plants to mediate native plant survival in a Midwestern forest herb layer

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Abstract Consumer-facilitated invasions have been proposed as an alternative mechanism to direct competitive exclusion to explain the replacement of native plants by exotics. In a factorial field experiment manipulating competition from the exotic plant *Alliaria petiolata* and herbivory by exotic mollusks, we documented that mollusk herbivory significantly reduced the survival of two species of native palatable plants, but found minimal direct herbivore effects on less palatable species, including the invasive *A. petiolata*. These effects were evident after one growing season on younger juvenile plants of *Aster cordifolius*, but only after two growing seasons on older transplants of the same species, suggesting a greater vulnerability of young plants. In contrast to our expectations, *A. petiolata* competition alone had no effect on any of the six native species we tested. However, competition from *A. petiolata* did affect the survival of the most palatable native plant when mollusks were also present. While not significant for any other single species, this same pattern was observed for three of the five remaining native species tested. The selective grazing on palatable plants that we document provides novel evidence contributing to our understanding of observed shifts in the forest herbaceous layer towards the dominance of exotic plants and unpalatable species. More broadly, our results highlight the importance of the interactive effect of consumers and inter-specific competition in forest understories via its contribution to differential survival among regenerating species.

Keywords *Alliaria petiolata* · Competition · Consumers · *Deroceras reticulatum* · Garlic mustard · Herbivory · Invasive species · Mollusk · Slug

Introduction

The negative impact of exotic species on ecosystem processes, biodiversity, and human economic systems are well documented, making invasive species control a top priority for ecologists and land managers (Mack et al. 2000). To date, the predominant strategy for invasive species management has been to target

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problematic species and prioritize their control (Byers et al. 2002), under the presumption that direct competitive exclusion is limiting native species success (Gurevitch and Padilla 2004; Didham et al. 2005). However, in many cases invasive plant removal efforts or herbicide applications result in only minimal to moderate recovery of the native flora (Hochstedler et al. 2007; Stinson et al. 2007), and can actually facilitate the establishment of other exotic species (Zavaleta et al. 2001). These results suggest that other factors, in addition to direct competition with invasive plants, can limit native plant abundance in many invaded habitats (Gurevitch and Padilla 2004; Didham et al. 2005).

Competition and predation are two of the main biotic forces shaping ecological communities (Chase et al. 2002), with both equally capable of either increasing or decreasing coexistence among species (Chesson and Kuang 2008). When intra-specific competition is greater than inter-specific competition, species are more likely to coexist. In contrast, when inter-specific competition is greater than intra-specific competition, subordinate species can be competitively excluded by community dominants (Wilsey et al. 2009). Efficient foraging and predation on competitively dominant species can promote coexistence by reducing the abundance of dominant species, thereby moderating their community-wide competitive impact (Chase et al. 2002; Hanley and Sykes 2009). Alternatively, if consumer pressure is selective towards subordinate species, predation can promote the abundance of less preferred species, irrespective of their competitive ability (Chase et al. 2002; Hanley and Sykes 2009). In the context of species invasions, herbivores that selectively consume exotic taxa provide biotic resistance to community invasion, while herbivores that selectively consume native plants can promote invasion and dominance by less preferred, exotic plants (Maron and Vilà 2001). Despite this well established theory, empirical work investigating the effects of herbivory on plant invasions has received less attention than the effects of competition (Gurevitch and Padilla 2004; Didham et al. 2005).

The invasive plant *Alliaria petiolata* (garlic mustard) is a biennial woodland herb introduced into North American in the mid-1800's and is considered a serious threat to the diverse, native forest herbaceous layer because of its pervasive spread throughout northeastern North America (Rodgers et al. 2008). *Alliaria petiolata*'s success has previously been attributed to its autogamous breeding habit, rapid growth, high seed production (Anderson et al. 1996), and production of allelopathic and secondary compounds (Rodgers et al. 2008). Recent experimental evidence shows that *A. petiolata* also avoids herbivory from white-tailed deer (*Odocoileus virginianus*) (Eschtruth and Battles 2009; Knight et al. 2009), and that the introduced herbivorous slug, *Deroceras reticulatum*, avoided consuming *A. petiolata* in both field and laboratory trials in Wisconsin, USA (Hahn et al. 2011). Herbivore avoidance by *A. petiolata* likely results from its high level of antiherbivore chemical defenses (Cipollini et al. 2005). These studies suggest that consumers may also play an important role in promoting *A. petiolata* success in North American forest herbaceous layers.

We have observed high densities of the exotic terrestrial mollusk *Deroceras reticulatum*, a generalist herbivore and globally important agricultural pest, in a forest invaded by *A. petiolata* in NE Wisconsin, USA, and have documented high levels of mollusk grazing on many native plants, but not on *A. petiolata* at this site (Hahn et al. 2011). The potential for mollusk grazing to alter plant communities through selective seedling predation is well documented in their native Europe (e.g. Hanley et al. 1995a; Buschmann et al. 2005), and the evidence for their impact in areas where they are introduced is accumulating from around the globe. Recent studies from New Zealand (Sessions and Kelly 2002), Australia (Holland et al. 2007), Hawaii (Joe and Daehler 2008), and California (Strauss et al. 2009; Motheral and Orrock 2010) all document impacts of introduced mollusks on the resident plant communities. Furthermore, the pervasiveness of introduced mollusks in other systems throughout North America (Robinson 1999; Moss and Hermanutz 2010; Ross et al. 2010) implicates introduced mollusks as important consumers in many systems, but their effects on North America forest herbaceous layers are not well documented. Furthermore, the combined effects of competition from the widespread forest herb layer invader *A. petiolata* and herbivory from exotic mollusks on native plant regeneration has yet to be examined. For these reasons, our site provides a unique opportunity to study multi-trophic community interactions in a novel ecosystem (i.e. a community composed of a unique mixture of native and exotic species at multiple tropic levels, sensu Hobbs et al. 2006). In this paper, we investigate the relative contribution of competition by *A. petiolata* and herbivory from *D. reticulatum*, two trophically distinct introduced species, on the success of restored native forest herbs in the understory of a NE Wisconsin, USA forest.

Methods

Study site and experimental design

We conducted two experiments to evaluate the relative role of exotic plant competition and exotic mollusk herbivory in regulating native plant success at the Bay Beach Wildlife Sanctuary in Green Bay, WI (44°31′ N, 87°56′ W), a secondary lowland deciduous forest dominated by *Populus deltoides*, *P. tremuloides*, *Acer negundo*, and *Fraxinus pennsylvanica*. The herbaceous layer is dominated by the exotic *Alliaria petiolata* (garlic mustard), with sparse native or naturalized plants. Soils are a Keowns silt loam, a coarse-loamy, Mollic Endoaquept. Mean annual temperature of the site is 6.9°C and it receives approximately 740 mm of annual precipitation.

Alliaria petiolata (garlic mustard) is a biennial forb introduced into North America in the mid 1800's that continues to invade and subsequently reach high abundance in North American woodlands (Nuzzo 1993; Rodgers et al. 2008). In the Midwest, *A. petiolata* germinates in early spring and forms rosettes which persist through the winter. In the second year it bolts, flowers, produces seed, and senesces by midsummer (Anderson et al. 1996). Mean *A. petiolata* rosette cover averaged 56.6% (±0.8 SE) across all experimental plots at our site prior to treatment establishment in June 2006.

Two species of introduced terrestrial mollusks (slugs) were also documented at our site, *Deroceras reticulatum* and *Arion cf. circumscriptus*, with the former approximately 5-times more abundant on an annual basis (PGH *unpublished data*). *Deroceras reticulatum* is a generalist herbivore native to Europe with an annual lifecycle (Chichester and Getz 1973). It was introduced into North America in the mid-1850's and is now common throughout most of the continent (Ross et al. 2010). Many terrestrial mollusk species, particularly *D. reticulatum* are known agricultural pests (South 1992) and significant plant damage has previously been attributed to *D. reticulatum* at our site (Hahn et al. 2011). Therefore, these experiments focus on the grazing effects of *D. reticulatum*.

In 2006, a randomized factorial split-plot experiment ($n = 4$ replicate blocks) was established to examine the effects of *Odocoileus virginianus* (white-tailed deer) grazing, *A. petiolata* presence, and native plant restoration on forest herbaceous diversity. Plots (3 × 3 m) were established within deer exclosure whole-plot treatments (open access or fenced), consisting of *A. petiolata* treatments (present or removed), and native plant restoration treatments (non-restored or restored) in a complete factorial design ($n = 8$ split-plots/block). In April, 2008 we expanded this experiment by establishing experimental mollusk reduction treatments within each of the plots restored with native species to examine the effects of *A. petiolata* removal and mollusk grazing on native plant success. Two 1-m^2 circular plots, one control and one mollusk reduction, were installed into each of the existing restoration treatment plots ($n = 16$ plots) in a complete factorial split–split-plot design. Because of an unintended effect of the mollusk exclosures (i.e. reduced deer browsing inside of the mollusk exclosures), we restricted our analyses to plots located inside the established deer exclosures ($n = 16$ mollusk treatment plots). This reduced experimental design resulted in a factorial split-plot experiment, which includes four blocks, an *A. petiolata* treatment (whole-plot), and a mollusk reduction treatment (split-plot).

Our mollusk reduction methods are similar to those of Joe and Daehler (2008) and Strauss et al. (2009). All 1-m^2 circular plots were surrounded by a 15-cm tall aluminum flashing barrier buried 5 cm into the soil. A 4-cm strip of copper tape was placed along the upper edge of the mollusk reduction treatments to deter mollusk movement, while 5-cm diameter holes were cut at 10-cm intervals at ground level in control plots to allow mollusk entry. Additional mollusk reduction was achieved through manual removal in both years, with beer traps in 2008, or by application of molluscicide bait (Ortho® Bug-Geta, Marysville, OH, USA) in 2009. Mollusk treatment flashing remained installed throughout both years, with additional mollusk removal methods occurring from May through September in both years.

Mollusk abundance

Mollusks were counted biweekly on 10-cm × 10-cm cardboard traps, with two traps present per split-plot, throughout the growing season in both 2008 ($n = 11$) and 2009 ($n = 11$). This provides a consistent survey method by which relative mollusk abundance could be estimated in a non-destructive manner through time (Hawkins et al. 1998).

Experiment 1

The objective of this experiment was to provide a general test of the susceptibility of six, two-month old native understory species to the interactive effects of competition from the dominant exotic understory plant, *Alliaria petiolata*, and grazing from exotic mollusks. In addition, we also evaluated the effect of exotic molluskan grazing on the exotic plant *Alliaria petiolata*. Each mollusk treatment split-plot received twelve transplanted juveniles, two individuals of each species of late summer forest herbs (*Aster cordifolius*, *Bidens frondosa*, *Cryptotaenia canadensis*, *Elymus virginicus*, *Eupitorium rugosum*, and *Solidago flexicaulus*). Species selection was based on their presence in similar habitats in Wisconsin (Curtis 1959), the availability of commercially available native seed, a desire to include a range of growth forms (rosette forbs, erect forbs, and a graminoid) and a range of palatabilities as documented by Hahn et al. (2011). Native seed (purchased from Prairie Moon Nursery, Winona, MN, USA) was cold-stratified for a minimum of 60 days, germinated in April 2008, and grown in potting soil in the University of Wisconsin-Green Bay greenhouse. Two-month old plants were transplanted into the 1-m^2 circular mollusk split-plots of the field experiment in mid-June, 2008, in a predetermined random order with approximately 20-cm spacing between plants. These plants are hereafter referred to as “two-month old plants.” At the start of experiment 1, *A. petiolata* plants were approximately two months old, thus closely matching the age of our other native transplants. We conducted monthly censuses (all censuses occurred at the end of each month) for two consecutive growing seasons, at which time we counted the number of leaves, recorded the length and width of three leaves per plant, and documented the number of surviving plants. For all species, survival was defined as those plants that were both green and physically present aboveground. The annual plant *Bidens frondosa* was censused four times (June–September) in 2008 before it died naturally. The biennial *Alliaria petiolata* was censused seven times over the two-year experiment, five times (June-October) in 2008 and twice (May and June) in 2009 before it set seed and died naturally in July, 2009. All other plants were perennial and were censused five times in 2008 (June-October) and five times in 2009 (May–September) before natural seasonal dormancy. Measurements were averaged for each mollusk split-plot treatment to avoid pseudoreplication.

Experiment 2

This experiment was conducted during the second growing season of our study to better evaluate the effect of mollusk herbivory and competition from *A. petiolata* on the mortality of smaller, establishing juvenile plants of a palatable species. Because mollusk grazing (Fenner 1987; Hanley et al. 1995b) and interspecific-plant competition (Martin and Wilsey 2006; Metz et al. 2010) most strongly affect the survival of small plants, we chose to use one-month old *Aster cordifolius* (hereafter *Aster*) plants, a species that we had previously found to be highly preferred by mollusks (Hahn et al. 2011). Plants were grown for one month in 2009 under conditions described above in Experiment 1. These juvenile plants are hereafter referred to as “one-month old plants.” On average these plants were roughly one-quarter the size of the two-month old *Aster cordifolius* plants used in experiment 1; the mean length of the longest leaf was 1.06 cm (± 0.05 SE, $n = 48$) for the one-month old plants used in experiment 2 and 4.76 cm (± 0.21 SE, $n = 32$) for the two-month old plants used in experiment 1. In mid-June 2009 each mollusk treatment split-plot ($n = 16$) received 10 transplanted one-month old juveniles, evenly spaced in a 30-cm diameter circle. The number of surviving individuals was tallied three times between June and mid-September 2009. Survival was defined in an identical manner as in experiment 1. In mid-September 2009, aboveground biomass of the surviving transplants was harvested, dried for 48 h at 65°C, dry mass was recorded, and then averaged for each mollusk treatment split-plot to avoid pseudoreplication.

Data analysis

Mollusk abundance was seasonally variable and mollusks were difficult to detect during dry periods because of reduced activity, so we analyzed the three periods of peak mollusk abundance for each year ($n = 6$ sample periods). The effects of *A. petiolata* presence, mollusk reduction, and time on mollusk abundance counts were analyzed using a generalized linear mixed model. The *A. petiolata* treatment, mollusk reduction treatment, and the interaction term were fixed effects. The block-by-*A. petiolata* treatment interaction term was a random effect used as the error term for the *A. petiolata* treatment (whole-plot) and time was modeled as a repeated (random) effect to account for multiple within-subject measures. A Poisson distribution, with a log link, was used to account for the discrete count data used as the response variable. An inverse link function was applied in order to report the estimated means on a linear scale.

For Experiment 1, the effects of *A. petiolata* competition, mollusk herbivory, time and the interactions on the mean proportion of two-month old transplants surviving per plot were determined using linear mixed model ANOVAs. *Alliaria petiolata*, mollusk herbivory, and the interaction were categorical fixed effects. The block-by-*A. petiolata* treatment interaction term was a random effect used as the error term for the *A. petiolata* treatment (whole-plot) effect and time was modeled as a repeated (random) effect to account for multiple within-subject measures. A binomial error structure was also tested, but the Gaussian models fit better based on fit statistics and visual assessment of the residuals. Separate ANOVAs were run for each species. These experiments focused on native plants, but we also analyzed the effects of mollusk grazing on *A. petiolata* for comparison. For Experiment 2, a mixed model ANOVA was used to determine the effects of time (three sampling periods, modeled with an autoregressive covariance structure), *A. petiolata* competition, mollusk herbivory and the interaction terms on the proportion of one-month *Aster* transplants surviving. *Alliaria petiolata*, mollusk herbivory, and their interaction were categorical fixed effects. The block-by *A. petiolata* treatment interaction term and the time term (repeated measures) were random effects.

For all analyses, the time effect was modeled using a first-order autoregressive covariance structure in order to account for within-subject correlations through time and denominator degrees of freedom were estimated using the Kenward-Rogers method (Littell et al. 2006). Residual plots were checked to ensure normality and homoscedacity of variance. All analyses were performed in PROC MIXED or PROC GLIMMIX in SAS 9.2 (SAS Institute Inc., Cary, NC, USA).

Results

Mollusk abundance

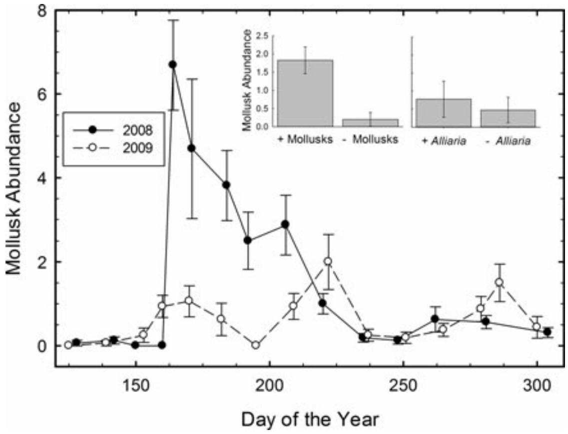

Fig. 1 Temporal trends of mollusk abundance measured over two years in a Midwestern forest. Data are means (±1 SE) of mollusks counted on 10 cm × 10 cm cardboard traps from all split-plots sampled on each date. Inset figures are pooled treatment means analyzed using a generalized linear mixed model for the three peak abundance dates for each year (see Methods)

In general, *Deroceras reticulatum* neonates emerged in early June, peaked in abundance during the summer before declining in the fall (Fig. 1). This general pattern was interrupted during periods of low rainfall, where mollusk activity declined (PGH *personal observation*). Over the course of the two-year experimental period, our reduction treatment significantly ($F = 5.51$, $P = 0.02$) decreased the number of individual mollusks (mean ± SE) counted in mollusk-reduction split-plots (0.20 ± 0.19), relative to mollusk-control (full-access) split-plots (1.83 ± 0.37). Thus, averaged across all survey dates, mollusk abundance in reduction split-plots was only 11% that observed in full-access split-plots. There was a temporal effect on mollusk abundance ($F = 2.68$, $P = 0.03$), but no significant interaction with mollusk control treatments ($P > 0.1$). We found no significant difference in mollusk abundance among *A. petiolata* removal or control treatments ($F = 0.25$, $P = 0.6$), but there was a slight trend toward lower mollusk abundance in *A. petiolata* removal plots (Fig. 1). In general, mollusk abundance in plots containing *A. petiolata* was approximately 60% greater than plots from which *A. petiolata* had been removed.

Experiment 1

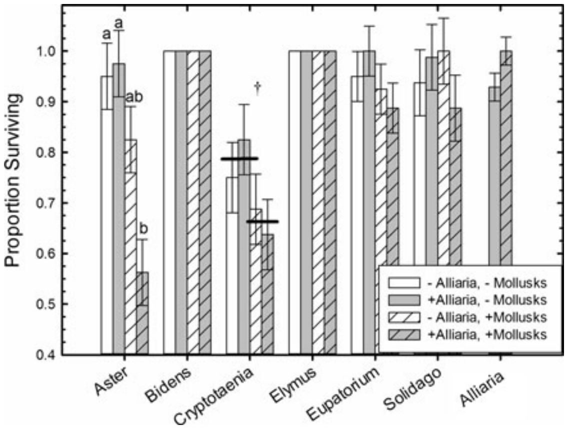

Fig. 2 Results of a two-year factorial experiment (Experiment 1) manipulating the effects of competition from *Alliaria petiolata* (garlic mustard) and molluskan herbivory on native plant survival and natural *A. petiolata* rosettes, averaged across two years. Mixed model ANOVAs for a split-plot repeated measures design were performed separately for each species. For *Alliaria*, only the effect of mollusk herbivory was analyzed. Treatments with different letters are significant different, applying the Tukey HSD correction for multiple comparisons. Thick bars indicate mollusk main effect treatment means for *Cryptotaenia canadensis* and the † indicates the marginally significant mollusk treatment effect. Variance estimates are ±1 standard error of the mean

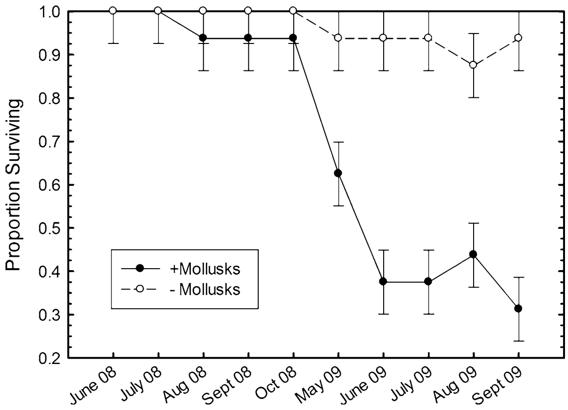

Fig. 3 Effect of mollusk herbivory on the survival of two-month old *Aster cordifolius* plants over the two year field experiment (Experiment 1). Note that increases in survival resulted from plants resprouting from belowground reserves after complete defoliation. Variance estimates are ±1 standard error of the mean

The interaction of competition from *A. petiolata* and herbivory from *D. reticulatum* significantly reduced the survival of two-month old *Aster cordifolius* transplants ($F = 4.82$, $P = 0.047$), averaged across both years (Fig. 2). Mollusk herbivory also reduced *A. cordifolius* survival through time ($F = 3.82$, $P = 0.0004$), although the trend was not significant until the second year (Fig. 3). Mollusk herbivory reduced survival of *Cryptotaenia canadensis*, averaged across both years, although the effect was only marginally significant ($F = 3.27$, $P = 0.087$). The temporal effect of mollusk herbivory on this species was similar to that of *A. cordifolius*, although the effect was again not quite significant ($F = 1.29$, $P = 0.25$). *A. petiolata* presence alone had no detectable effect on *C. canadensis* ($F = 0.02$, $P = 0.89$, Table 1). Survival of two-month old plants from the remaining four other native species, were also not significantly affected by either *A. petiolata* competition or by mollusk herbivory ($P > 0.1$, Fig. 2, Table 1). *Bidens frondosa*, an annual, had 100% survival through the 2008 growing season, and only one individual of the species *Elymus virginicus* died during the two year experiment. Therefore, these two species were not subjected to statistical analysis, but the data are presented in Fig. 2 for comparison. However, while not statistically significant, for the four native species examined, the combined effects of *A. petiolata* and mollusk herbivory resulted in lower survival than for treatments containing either of these two effects alone, and universally produced lowest observed transplant survival of all treatment combinations (Fig. 2). There was no effect of mollusk herbivory on the survival of *Alliaria petiolata* ($F = 2.07$, $P = 0.23$, Fig. 2, Table 1). The results of the

Table 1 ANOVA table from Experiment 1 showing the effects of competition from *Alliaria petiolata* (Comp), mollusk herbivory (Herb), and time (Time) on the survival of six forest herbs transplanted into the field at an age of two months, and naturally established *A. petiolata* plants

Species	Effect	Num *df*	Den *df*	*F*	*P*
Alliaria	Herb	1	3.48	2.07	0.2332
	Time	6	33	0.77	0.6003
	Time*Herb	6	33	0.77	0.6003
Aster	Comp	1	3.31	2.41	0.2099
	Herb	**1**	**12.8**	**16.83**	**0.0013**
	Comp*Herb	**1**	**12.8**	**4.82**	**0.0472**
	Time	**9**	**99.8**	**5.21**	**<0.0001**
	Time*Comp	9	99.8	0.99	0.4569
	Time*Herb	**9**	**99.8**	**3.82**	**0.0004**
	Time*Comp*Herb	9	99.8	1.19	0.3078
Bidens	–	–	–	–	–
Cryptotaenia	Comp	1	3.13	0.02	0.8931
	Herb	**1**	**18.2**	**3.27**	**0.087**
	Comp*Herb	1	18.2	0.82	0.3775
	Time	**9**	**97.2**	**5.09**	**<0.0001**
	Time*Comp	9	97.2	1.49	0.1608
	Time*Herb	9	97.2	1.29	0.2511
	Time*Comp*Herb	9	97.2	0.51	0.8642
Elymus	–	–	–	–	–
Eupitorium	Comp	1	3.82	0.03	0.8743
	Herb	1	13.7	1.61	0.2258
	Comp*Herb	1	13.7	0.65	0.4334
	Time	**9**	**99.3**	**1.79**	**0.0794**
	Time*Comp	9	99.3	0.94	0.4930
	Time*Herb	9	99.3	0.88	0.5483
	Time*Comp*Herb	9	99.3	0.65	0.7526
Solidago	Comp	1	4.15	0.45	0.536
	Herb	1	8.25	0.06	0.8061
	Comp*Herb	1	8.25	1.21	0.3031
	Time	9	100	1.52	0.1501
	Time*Comp	9	100	1.06	0.3954
	Time*Herb	9	100	0.62	0.7812
	Time*Comp*Herb	9	100	0.86	0.5667

This experiment lasted for two growing seasons in a NE Wisconsin, USA forest. All models were split-plot, repeated measures mixed models which included a random blocking term ($df = 3$). Dashes indicate the species was not subjected to statistical analysis because of high survival (see "Methods"). Significant ($\alpha = 0.05$) and marginal P values ($\alpha = 0.1$) are in bold

plant-size measurements were qualitatively similar to those of survival. Therefore, because plant mortality is a stronger indicator of how competition or herbivory will affect plant community composition, we only present survival data for succinctness.

Experiment 2

After one year, mollusk herbivory significantly reduced the survival of one-month old *Aster* plants by approximately 40%, relative to plants in mollusk reduction treatments ($F = 50.52$, $P < 0.0001$,

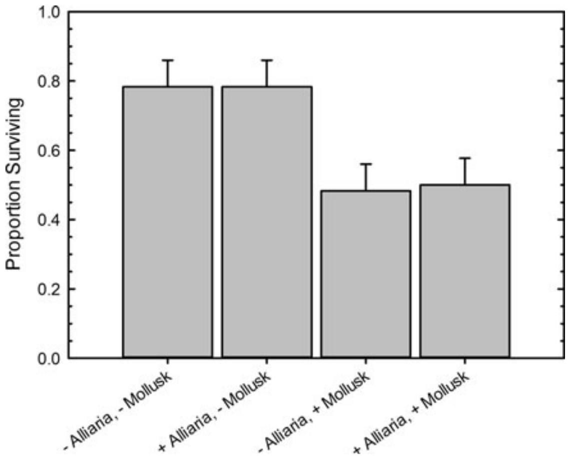

Fig. 4 Results of a one-year factorial experiment (Experiment 2) manipulating the effects of competition from *Alliaria petiolata* (garlic mustard) and molluskan herbivory on the survival of small (one-month old) *Aster cordifolius* juvenile plants, averaged over three sampling periods in 2009 (Experiment 2). Variance estimates are ±1 standard error of the mean

Table 2 ANOVA table from Experiment 2 showing the effects of competition from *Alliaria petiolata* (Comp), mollusk herbivory (Herb), and time (Time) on the survival of one-month old *Aster cordifolius* transplants

Effect	Num df	Den *df*	*F*	*P*
Comp	1	5.92	0.01	0.9368
Herb	**1**	**17.8**	**50.52**	**<0.0001**
Comp*Herb	1	17.8	0.04	0.8414
Time	**2**	**19.6**	**15.17**	**0.0001**
Time*Comp	2	19.6	0.24	0.7926
Time*Herb	2	19.6	1.4	0.2709
Time*Comp*Herb	2	19.6	0.14	0.8666

This experiment lasted for one growing seasons in a NE Wisconsin, USA regenerating forest. All models were split-plot repeated measures mixed models which included a random blocking term ($df = 3$). Significant P values ($\alpha = 0.05$) are in bold

Fig. 4). *Aster* survival also decreased through time ($F = 15.17$, $P = 0.0001$), but neither competition from *A. petiolata*, nor any of the interaction terms significantly affected this trend ($P > 0.1$, Table 2).

Discussion

Two years of cumulative herbivory from the introduced terrestrial mollusk *Deroceras reticulatum* reduced the survival of two species of native forest herbs established as two-month old plants. Mollusk herbivory alone had no detectable effect on similar-aged transplants from the four other native plant species we examined, or on the invasive plant *Alliaria petiolata*. Surprisingly, *Alliaria petiolata* presence alone did not affect the survival of any of the six native two-month old transplants. However, when mollusks were also present competition from *A. petiolata* did reduce the survival of the most palatable species (*Aster cordifolius; see* Hahn et al. 2011). This trend was also supported by three of the five other native species, although the effect was not statistically significant for any of them. In a second experiment, one year of cumulative mollusk herbivory reduced the survival of notably smaller, one-month old *A. cordifolius* juvenile transplants by 40%. However, as seen with the larger transplants, we again found no significant effect of *A. petiolata* competition alone on the survival of the smaller *A. cordifolius* individuals. Our results contradict the expectation that *A. petiolata* alone is responsible for the direct competitive exclusion of native plants, at least once seeds have germinated and plants have established, but rather support experimental results from other systems, where native plant mortality is more closely linked to consumer effects (Gonzales and Arcese 2008; Orrock and Witter 2009).

Consumer effects from white-tailed deer browsing have previously been shown to contribute to *A. petiolata* dominance in eastern North American forests (Eschtruth and Battles 2009; Knight et al. 2009), and at our site in NE Wisconsin (Dornbush and Hahn *in review*). Deer grazing is generally greatest on medium- or larger-sized understory plants and saplings (Rooney et al. 2000). The mollusk grazing effects on small regenerating juvenile plants that we documented, raises the potential that where deer and mollusks are both abundant, consumer effects may interact to alter understory composition; mollusks in the establishment phase and deer during the larger, adult phase. Unfortunately, the unintended effect that our mollusk exclosures had on deer grazing prevented us from adequately addressing this question. Nevertheless, it is of particular note that both white-tailed deer and terrestrial mollusks both appear to prefer similar food types (e.g. many non-graminoid forbs, see Wiegmann and Waller 2006; Hahn et al. 2011), suggesting that cryptic seedling herbivory by mollusks may be going unnoticed in systems where more conspicuous consumers (i.e. white-tailed deer) are abundant. This point is further bolstered by the general pervasiveness of introduced mollusks in natural areas across North America (Chichester and Getz 1973; Ross et al. 2010). Our results highlight the need for future studies evaluating the effects of interactions among multiple consumer guilds in shaping forest understory community composition.

Alliaria petiolata has a documented arsenal of allelopathic chemicals shown to disrupt mycorrhizal colonization and plant growth (Stinson et al. 2006; Burke 2008; Callaway et al. 2008; Wolfe et al. 2008; Lankau et al. 2009), findings which suggest that *A. petiolata* holds a competitive advantage over many native North American forest herbs and tree seedlings. In this study, we found that competition from *A. petiolata* only significantly affected survival of the most palatable species, *A. cordifolius*, and only when mollusks were also present. Several, non-mutually exclusive factors could have contributed to our findings of weaker than expected *A. petiolata* effects on native transplants. First, competition from *A. petiolata* may be weak relative to other factors regulating understory diversity, such as propogule limitation (Brudvig et al. 2011) or consumers (Wiegmann and Waller 2006). In support of this position, several previous studies have found that some native plants can outcompete *A. petiolata* (Meekins and McCarthy 1999; Murphy 2005), that native vegetation is often slow to return despite *A. petiolata* removal (McCarthy 1997; Hochstedler et al. 2007), and that consumers often reduce native plant success more than *A. petiolata* (Esctruth and Battles 2009; Knight et al. 2009). Second, the competitive ability of *A. petiolata*, via the release of allelopathic chemicals, may most affect tree seedling regeneration (Stinson et al. 2006; Wolfe et al. 2008; Lankau et al. 2009), a functional group we did not test in this experiment. Third, if *A. petiolata* alters plant community composition via effects on seed germination (Prati and Bossdorf 2004), or seedling establishment, our planting of juvenile plants would have explicitly excluded our ability to detect this effect, thereby causing us to underestimate the overall effects of *A. petiolata* presence in shaping community composition.

Although *A. petiolata* competition alone did not significantly affect transplant survival in this study, *A. petiolata* presence did interact with molluskan grazers to significantly increase the mortality of our most palatable transplant, and while not statistically significant, this general pattern was shared by the three remaining transplant species that showed even minimal, negative effects from mollusks. There are several potential explanations for this pattern. First, mollusk herbivory may be weakening native plants, thereby increasing their susceptibility to *A. petiolata* competition. This seems a reasonable explanation, as leaf loss or damage in the low-light understory have significant impacts on plant carbon balance (Neufeld and Young 2003), and could thereby affect interspecific competition. Clearly, the reciprocal is also possible, where *A. petiolata* presence weakens plant resistance to herbivory (Herms and Mattson 1992; Cipollini 2004). However, the generally stronger impact of mollusk herbivory than *A. petiolata* competition in this study suggests more support for the former relationship. The interactive effect of *A. petiolata* competition and mollusk herbivory may also result from more indirect interactions, such as refuge-mediated apparent competition (Orrock et al. 2010a, b). While not statistically significant, mollusk abundance was approximately 60% higher in plots with *A. petiolata* than in *A. petiolata* removal plots. These differences in slug abundance may contribute to the negative interactive effect observed between mollusks and *A. petiolata* on native plant survival. Irrespective of the exact mechanistic nature of this relationship, our study provides support for an interactive role of the exotic mollusk *D. reticulatum* and the exotic herb *A. petiolata* in affecting juvenile plant mortality at our site.

In contrast to competition based community assembly, our study is unique in demonstrating an example of a negative consumer mediated effect by the introduced mollusk *Deroceras reticulatum* on the survival of two native forest herbs, with potential indirect benefits for the invasive *A. petiolata* and other unpalatable native forest herbs via reduced competitor survival. Our results lend support to a growing body of evidence raising awareness of the role of exotic consumer-mediated effects in plant invasions (Nuñez et al. 2010). In a meta-analysis comparing exotic vertebrate and invertebrate consumers, Oduor et al. (2010) found that invertebrate herbivores were equally likely to consume both native and exotic plants, thus providing biotic resistance to invasion, while vertebrate consumers were more likely to consume native vegetation and thus facilitate invasional meltdowns. Other reports of molluskan consumers found that herbivorous introduced mollusks, like vertebrate consumers, preferred native plants, and thus facilitated exotic plant invasion (Sessions and Kelly 2002; Holland et al. 2007; Joe and Daehler 2008; Motheral and Orrock 2010). Our results are mixed, in that we found a pronounced effect of grazing by the exotic *D. reticulatum* on two native species, but no direct grazing effects on the exotic *A. petiolata* or four other small native transplants, suggesting that general palatability or plant growth form (Hahn et al. 2011) may be more important than native or exotic status in predicting plant susceptibility to mollusk grazing. Importantly, our results provide a striking example of the complex mechanisms by which new combinations of native and exotic producers and consumers are likely to assemble into novel communities (Hobbs et al. 2006). For example, despite the rather limited effects of *A. petiolata* competition on survival of our native transplants, and the fact that direct mollusk herbivory only significantly affected two of our six native species, the combined effect of mollusk and *A. petiolata* presence consistently resulted in the lowest survival of all treatment combinations for those species that suffered even limited mortality. Our work lends growing support for the need to evaluate the importance of consumers, in addition to interspecific competition, in shaping plant community composition and facilitating exotic invasions.

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