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Exotic Slugs Pose a Previously Unrecognized Threat to the Herbaceous Layer in a Midwestern Woodland

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Abstract

Developing effective restoration strategies requires first identifying the underlying factors limiting native plant recovery. The slug *Deroceras reticulatum* is an important herbivore in Europe, a global agricultural pest, and is introduced and abundant throughout eastern North America, but little information is available on the effect of this exotic herbivore on the forest herbaceous layer. Here, we test the palatability of 12 forest herbs to the introduced slug *D. reticulatum* and use field surveys to determine the degree to which slugs are damaging plants in the field. In laboratory feeding trials, slugs readily consumed most plants, but avoided the grass *Elymus virginicus*, the invasive forb *Alliaria petiolata* (garlic mustard), and thicker leaved plants. In the field, we documented significant slug damage, with close to 50% or more of plant leaves damaged by slugs on five of the six native species tested. Slug damage in the field was predicted by laboratory-determined acceptability, but was significantly greater on short-statured rosette species than on erect plants for a given acceptability value. Our results identify introduced slugs as an important, but overlooked obstacle to forest herb restoration and potential drivers of larger scale understory compositional change. The relaxed herbivore pressure on *A. petiolata*, relative to native competitors, suggests that invasive plant removal alone may not result in the recovery of native flora. Rather, restoration of unpalatable native species should accompany invasive plant control in slug invaded areas. Erect forbs, thick-leaved plants, and graminoids should have the greatest success where introduced slugs are abundant.

Key words: ***Deroceras reticulatum*, exotic plants, forest restoration, garlic mustard, herbivory, invasive species, slugs, woodland understory.**

Introduction

Temperate deciduous forests offer society rich ecological and economic services (Costanza et al. 1997; Pearce 2001). The forest herbaceous layer, although only a small fraction of total biomass, contributes significantly to forest biodiversity and ecosystem processes (Muller & Bormann 1976; Muller 2003; Whigham 2004; Gilliam 2006). Unfortunately, many forested natural areas in eastern North America have a history of disturbance (Keddy & Drummond 1996), are overgrazed by white-tailed deer (Côté et al. 2004), are experiencing exotic species invasions (Wilcove et al. 1998; Mack et al. 2000), and are fragmented from larger contiguous forest tracts (Flinn & Vellend 2005). In general, these impacts appear to significantly and negatively affect the herbaceous layer (Rodgers et al. 2009), and it appears that the slow rate by which forest herb diversity returns following disturbances (McLachlan & Bazely 2001; Vellend 2003; Flinn & Vellend 2005) may limit the potential ecological and economic benefits of aggrading forests. For these reasons, restoration of the native herbaceous layer is critically important for improving habitat conditions and ecosystem processes in eastern North American forests (Jolls 2003; Whigham 2004; Vidra et al. 2007). However, the development of robust restoration strategies relies upon our ability to first identify the factors limiting the recovery of native plant diversity (Mack et al. 2000; Hobbs & Harris 2001).

A growing body of research identifies introduced mollusks as potential threats to native flora and restoration efforts. Slugs have long been identified as global agricultural pests (South 1992), but only recently have studies investigated the effects of introduced slugs on native plants. Slugs have reduced native plant success and facilitated the invasion of an exotic grass in New Zealand (Sessions & Kelly 2002). Introduced slugs in California are part of a complex community directing the natural selection of chemical defenses in *Brassica nigra* (Lankau & Strauss 2008) and are shaping local plant distributions (Strauss et al. 2009). In Hawaii, exotic slugs preferentially graze on selective native seedlings, potentially threatening rare plant restoration (Joe & Daehler 2008). Collectively, this evidence suggests that introduced slugs are important, but underappreciated, generalist herbivores shaping many native plant communities.

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Introduced slugs are found at high densities in disturbed ecosystems throughout eastern North America (Chichester & Getz 1973; McCracken & Selander 1980; Robinson 1999). To date, the role of slug herbivory in forested ecosystems has largely been ignored, possibly because forests have historically been considered less disturbed than roadsides or waste areas (McCracken & Selander 1980) or because many slugs found in forests are mycophagous or omnivorous (Chichester & Getz 1973; Jennings & Barkham 1975; Speiser 2001). Although the Great Lakes region supports high terrestrial snail diversity (Nekola 2003), native snails tend to be predominantly microphagous, feeding on the microorganisms associated with soil detritus and vegetation (Speiser 2001). *Deroceras laeve* Muller (Limacidae) is the most abundant native slug in eastern North America (Chichester & Getz 1973), is predominantly herbivorous, and has been documented to co-occur with introduced slugs (Getz 1959). Herbivorous exotic slugs, such as *D. reticulatum* Muller, consume a variety of eastern North American forest herbs (Rathcke 1985) and appear to be both common and widely distributed in eastern North American forests (Chichester & Getz 1973; Rathcke 1985). Unfortunately, for most ecosystems little comparable information is available on pre-invasion native mollusk communities, the impact of native mollusks on native plant communities, the effect of introduced slugs on native plants, or the reciprocal effects of native and introduced slugs on each other (Robinson 1999).

In their native Europe, where slugs are perhaps best studied, herbivorous slugs tend to avoid grasses and chemically well-defended plants, with preference for thin-leaved herbaceous dicotyledon seedlings that lack strong chemical defenses (Briner & Frank 1998; Dirzo 1980; Dirzo & Harper 1980; Hanley et al. 1995*a*; Fenner et al. 1999; Hanley 2004). In addition, slug grazing is not life stage or growth-form neutral, but rather most affects seedlings (Harper 1977; Hanley et al. 1995*a*, 1995*b*; Fenner et al. 1999; Ehrlén 2003; Hitchmough 2003) and short-statured plants (Rathcke 1985, Albrectsen et al. 2004). The combined effects of selective grazing by slugs significantly affect plant regeneration, resulting in measureable effects to plant species abundances and distributions in Europe (Cottam 1986; Bruelheide & Scheidel 1999; Buschmann et al. 2005). We predict that introduced slugs are having a similar effect in eastern North American forests, promoting a shift in dominance toward species whose seedlings are less palatable to slugs. To our knowledge, no study has yet evaluated the effects of slug herbivory within the context of woodland understory restoration, and in fact we know of only one previous study (Rathcke 1985) that has even evaluated the effect of slug herbivory on the forest herbaceous layer in North America. An improved understanding of the potential impact that introduced slugs have on native forest herbs is needed to guide effective conservation and restoration of this diverse community.

To determine the potential effects of slug grazing on eastern North American forest herbs, we took a combined approach that included a controlled laboratory feeding experiment and an experimental field restoration to quantify seedling palatability of several common native and exotic herbaceous species to the introduced slug *D. reticulatum*. We hypothesized that slugs would exhibit strong preference for certain plant species, while avoiding others. Specifically, we hypothesized that thin-leaved plants would be more vulnerable to slug grazing than thicker leaved plants. Finally, we predicted that species' palatability in laboratory feeding trials would correlate positively with observed slug damage in the field, but that the strength of this relationship may vary based on growth form (rosette vs. erect growth forms). Understanding the similarities and differences between results obtained from the field and controlled feeding trials expands the generality of our results beyond those species we directly tested, and thus aids in the development of effective restoration strategies at larger scales.

Methods

Slug Biology

Deroceras reticulatum was introduced to North America in the mid-1850s and is now abundant throughout most of the continent (Chichester & Getz 1973; McCracken & Selander 1980). In the Midwest, *D. reticulatum* has a predominantly annual lifecycle, with most adults dying in the fall after laying eggs, although a few may die over winter. Eggs hatch in the spring, and adult size and sexual maturity are reached in late summer (Getz 1959, Chichester & Getz 1973). Adults are hermaphroditic, but are not self-fertile (McCracken & Selander 1980). *Deroceras reticulatum* is the most abundant slug species found at our northeastern Wisconsin woodland restoration. We have documented only one other species of introduced slug (*Arion* cf. *circumscriptus*) and at least one unidentified snail species, but these mollusks were rare relative to *D. reticulatum* (P. G. Hahn, personal observation).

Laboratory Feeding Trial

We tested the acceptability of 11 late-summer native forest herbs and the invasive biennial forb *Alliaria petiolata* (garlic mustard) to *D. reticulatum* (Table 1). These plant species varied in growth form, leaf morphology, and phylogenetic associations, and they were common within our experimental woodland restoration in northeastern Wisconsin. Most plants were purchased as seed (Prairie Moon Nursery, Winona, MN, U.S.A.), cold stratified at 6°C, and then germinated and grown in potting soil in the University of Wisconsin-Green Bay greenhouse. *Urtica dioticum* was germinated from field soil collected from an area adjacent to our experimental restoration (Green Bay, WI, U.S.A.) and then transplanted into potting soil. *Alliaria petiolata* seeds were collected from the same location, cold stratified at 6°C for approximately 80 days, germinated, and then transplanted into potting soil. Feeding trials were conducted in 2008 for all species, except *A. petiolata* and *Desmodium glutinosum*, which were tested in 2009. At the time of testing, subsamples of at least five leaves from each species were dried to determine specific leaf mass (SLM; mg DW/cm^2), a measure of leaf thickness.

In accordance with previous feeding trials, we used lettuce leaves (*Lactuca sativa*) as a control species (Dirzo 1980;

Table 1. Characteristics of plants used in laboratory feeding trials to the exotic slug *Deroceras reticulatum*.

Species[a]	*Family*	*Age*[b] *(days)*	*n*	*Growth Form*[c]	*Leaf Texture*[d]	*Species Code*
Alliaria petiolata[e]	Brassicaceae	62	15	Rosette	Alveolate	Alpe
Aster cordifolius[e]	Asteraceae	59	9	Rosette	Glaucous	Asco
Aster lateriflorus	Asteraceae	52	10	Rosette	Glaucous	Asla
Bidens frondosa[e]	Asteraceae	22	19	Erect	Glabrous	Brfr
Cryptotaenia canadensis[e]	Apiaceae	55	16	Rosette	Glabrous	Crca
Desmodium glutinosum	Fabaceae	72	15	Erect	Glaucous to Scabrous	Degl
Elymus virginicus[e]	Poaceae	50	19	Erect	Scabrous	Elvi
Eupatorium rugosum[e]	Asteraceae	45	17	Erect	Glabrous	Euru
Prenathes alba	Asteraceae	64	9	Rosette	Glabrous	Pral
Scutellaria lateriflora	Lamiaceae	62	15	Erect	Glabrous	Scla
Solidago flexicalus[e]	Asteraceae	27	8	Rosette	Scabrous	Sofl
Urtica diodica	Urticaceae	52	12	Erect	Pubescent	Urdi

[a] Species names and family follow Gleason and Cronquist (1991).
[b] Age is the time from planting seed in potting soil to the time of testing in the laboratory feeding trial.
[c] Growth form is personal observation from our field site (P.G.H.).
[d] Leaf texture is described in Harris and Harris (2001).
[e] Indicates that the species were tested in the field experiment.

Buschmann et al. 2005). To determine the appropriate quantity of leaf material present in slug feeding trials, we offered to a random subset of slugs ($n = 7$) five lettuce discs (2.08 cm^2 ± 0.006 SE per disc, total area 10.4 cm^2) and recorded the foliar area consumed after a 12-hour feeding period. Slugs consumed a mean area of 4.96 cm^2 (±0.75 SE), or about 2.4 discs, during each 12-hour feeding trial, so we offered each slug two leaf discs, one lettuce and one test species, in all feeding trials. This leaf amount is approximately 83% of the leaf area eaten in the pre-trials, ensuring that slugs could not satiate their hunger during paired feeding trials (Dirzo 1980). Leaf discs were cut from live plants with a metal ring to ensure consistency and were used within 1 hour of cutting.

All slugs used in the laboratory feeding experiment were collected in September 2008 ($n = 22$) or August 2009 ($n = 16$), adjacent to our native-plant restoration experiment. Feeding trials were conducted from September to November 2008 and from August to September 2009 in 15 × 15 × 5–cm tall vented, frosted Rubbermaid (Rubbermaid, Inc., Huntersville, NC, U.S.A.) containers. Slugs were allowed to acclimate for at least 1 week before feeding experiments began and at least 36 hours between trials, during which time they fed normally on lettuce and carrots (*Daucus carota*). Slugs were not starved prior to each feeding trial to maintain discrimination in plant preference (Briner & Frank 1998). Before each trial, containers were cleaned and a fresh sheet of moist paper towel was placed at the bottom of the container. For each feeding trial, two leaf discs (one control lettuce and one test species) were assigned to a randomly selected slug and placed on either side of the test animal. Lettuce was also tested against itself in a lettuce–lettuce feeding trial. Each feeding trial ran for 12 hours in the dark at 17°C within a climate-controlled growth chamber. The leaf area remaining after each trial was measured using a LICOR LI-3000A Portable Area Meter (Licor, Inc., Lincoln, NE, U.S.A.). To quantify the relative palatability of each plant species, we calculated an acceptability index (AI) by dividing the area of the test species consumed by the area of control lettuce consumed (Dirzo 1980). We used the AI, which measures the area of plant material consumed, because our focus was to determine relative plant acceptability to slugs and quantify plant damage (i.e. photosynthetic area removed by slug grazing).

We used only one test plant species on each feeding trial date to ensure that the maturity of each plant species was identical when tested. Because of species-specific differences in plant growth rates, leaves were harvested and tested at approximately the same size, not age, but all species were tested within about 2 months of germination (Table 1). The number of replicates for each feeding trial varied from 8 to 19 (Table 1), depending upon the amount of leaf material available for testing. Trials in which only a small amount of lettuce was consumed (<0.5 cm^2) were discarded, because low amounts of lettuce consumption do not likely reflect a full feeding session and can severely inflate the AI (Dirzo 1980). Overall, only 5.5% of the feeding trials were omitted for this reason.

Field Experiment

Our restoration experiment is located at the Bay Beach Wildlife Sanctuary, Green Bay, WI, U.S.A. (44°31′N, 87°56′W), in a disturbed lowland deciduous forest dominated by eastern cottonwoods (*Populus deltoides*), quaking aspen (*P. tremuloides*), box-elder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*). The herbaceous layer is dominated by garlic mustard (*A. petiolata*), with approximately 5.5 ± 0.6 (SE) native species per 9 m^2 plot at the start of the restoration experiment in 2006. Experimental restorations are located on slightly elevated ridges scattered throughout this lacustrine forest, on a Keowns silt loam, a coarse-loamy, Mollic Endoaquept (http://websoilsurvey.nrcs.usda.gov/). The mean annual temperature of the study site is 6.9°C, with approximately 740 mm of annual precipitation (http://mcc.sws.uiuc.edu/).

The full-field experiment consists of four 10×17–m blocks, with eight 9-m^2 plots per block. Treatments consist of a deer exclosure split-plot treatment ($n = 2$ levels), a native-plant restoration treatment ($n = 2$ levels), and a garlic mustard removal treatment ($n = 2$ levels) present in a factorial design. In addition, we have also established a slug reduction treatment ($n = 2$ levels) nested within all native-plant restoration treatment plots ($n = 16$). To avoid the confounding factors of deer browsing and experimental slug reduction, here we only report data from plots with full access to slugs located within deer exclosures ($n = 8$ plots). Half of these plots had *A. petiolata* experimentally removed. Results of the full-field experiment will be reported elsewhere.

Seven of the plant species tested in the laboratory feeding experiment were also monitored within the restoration field experiment (Table 1). Six of these plants were germinated from seed in April 2008 and transplanted into the field in June 2008, whereas existing *A. petiolata* plants were randomly selected and marked in the field. Within each of the eight plots with full access to slugs and located within deer exclosures, we planted two individuals of each of the six native species. In addition, we randomly selected and marked four existing *A. petiolata* rosettes in the four plots within which *A. petiolata* was not removed. This resulted in 16 plants per species. The presence of *A. petiolata* within plots did not affect the amount of slug damage measured on test species ($p > 0.1$), so *A. petiolata* treatments (present or absent) were pooled together in all statistical analyses. Slug damage was quantified on each plant by recording the proportion of leaves damaged by slugs in late July, during peak slug activity. We considered all leaves that exhibited distinctive grazing patterns in the center of the leaf or leaves that were completely severed at the petiole as being damaged by slug herbivory (Dirzo & Harper 1980; Hanley et al. 1995b). Damage patterns observed in the field were consistent with slug grazing documented in controlled laboratory trials (P. G. Hahn, personal observation; Fig. 1). We used the mean proportion of leaves damaged by slugs, averaged across all plots, for analyses.

Data Analysis

To ensure consistency of slug feeding during the 3-month experiment in 2008 and between the 2 years, we offered five lettuce discs each to a random subset of slugs at the beginning of the 2008 feeding experiment ($n = 7$), at the end of the 2008 feeding experiment ($n = 4$), and again at the beginning of the 2009 feeding experiment ($n = 8$). We found no significant difference in the amount of lettuce consumed among the tested dates (analysis of variance [ANOVA]: $F_{[2,16]} = 1.32$, $p = 0.29$), so both feeding experiments were combined into one analysis.

We used a mixed model ANOVA to detect differences in AI among plant species with Tukey–Kramer adjusted p-values of the least square (LS) means. Plant species was a categorical fixed effect with AI as the response variable. To account for the repeated use of slugs in multiple feeding trials, we also included slug identity as a random effect (Littell et al. 2006). Simple linear regression was used to determine the effect of SLM (mg DW/cm^2) on the LS-mean AIs calculated previously from our mixed model ANOVA. Finally, the effects of plant growth form (rosette vs. erect growth forms) and the LS-mean AI for each plant species on observed slug herbivory in the field were determined using an analysis of covariance. This linear model included plant growth form as a categorical variable, LS-mean AI as a continuous variable, and the plant growth form by LS-mean AI interaction term to predict the mean proportion of damaged leaves observed on plant species in the field. All values were log transformed as needed, and residual plots were examined to ensure that normality and equal variance assumptions were met. Nonsignificant interaction terms ($p > 0.1$) were pooled into the residual error. Data analyses were conducted in SAS 9.2 (SAS Institute, Inc. Cary, NC, U.S.A.).

Results

Laboratory Feeding Trials

In agreement with our first hypothesis, AI (log + 1 transformed) values differed significantly among tested plant species ($F_{[12,136]} = 16.37$, $p < 0.0001$). AI values ranged from lows not significantly different than zero for *Alliaria petiolata*, *Desmodium glutinosum*, *Elymus virginicus*, *Scutellaria lateriflorus*, and *Solidago flexicaulis* to highs of around 1 for *Aster cordifolius*, *Lactuca sativa* (lettuce), and *Prenanthes alba* (Fig. 2). AI values close to zero reflect species nearly completely rejected by slugs, whereas AI values near 1 reflect species consumed at near-identical quantities to that of the control lettuce (Fig. 2). About half (5 of 11) of the native species were readily consumed by *D. reticulatum*, with AI values not significantly different than that of lettuce (Tukey HSD, $\alpha = 0.05$; Fig. 2). Specifically, *As. cordifolius*, *As. lateriflorus*, *Bidens frondosa*, *Cryptotaenia canadensis*, and *P. alba* were

Figure 1. Slug damage on an *Aster cordifolius* rosette at an experimental woodland restoration site in northeastern Wisconsin.

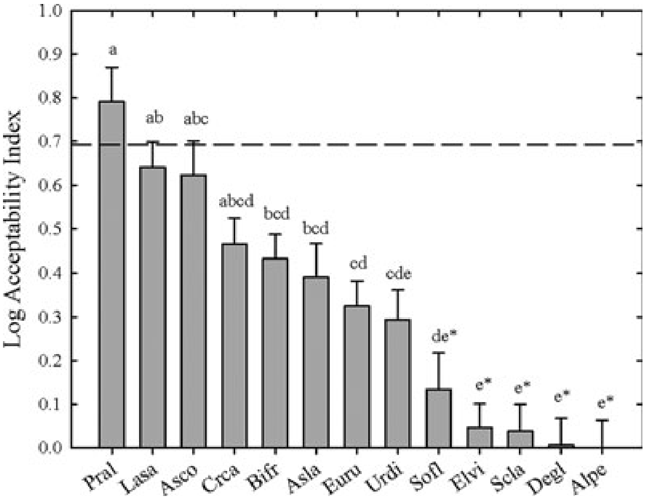

Figure 2. LS-mean AI (log + 1 transformed) for all plant species tested in the 12-hour laboratory feeding trials using the slug *Deroceras reticulatum*. Reference line represents an AI equivalent to 1 (log 1 + 1) and indicates that equal parts of lettuce and test material were consumed. Species labels are the first two letters of the genus and specific epithet and are described in Table 1, except Lasa = *Lactuca sativa* (lettuce). Species sharing the same letter are not significantly different ($\alpha = 0.05$) using the Tukey–Kramer adjustment for multiple comparisons. *indicates that the species AI is not significantly different than zero.

equally acceptable to *D. reticulatum* as lettuce. In partial agreement with our second hypothesis, species-specific differences in plant palatability (LS-mean AI) were negatively related to a species' SLM (mg DW/cm^2), although the trend was not quite significant ($r^2 = 0.23$, $F_{[1,11]} = 3.38$, $p = 0.09$; Fig. 3). AI values decreased at a rate of −0.31 (95% CI: −0.68 to 0.06) per 1 mg DW/cm^2 increase in SLM (both variables log transformed).

Field Data

As predicted, laboratory-defined LS-mean AI ($F_{[1,4]} = 104.92$, $p = 0.0005$) and plant growth form ($F_{[1,4]} = 16.59$, $p = 0.015$) were significant predictors of slug damage on plants in our field restoration ($r^2 = 0.97$). However, the interaction between AI and growth form was not significant ($p = 0.34$), and slug damage increased equally with increasing AI for both growth forms (slope = 1.18, 95% CI: 0.86–1.50; Fig. 4). The adjusted (LS) mean for damaged leaf rosettes (LS mean = 0.58, ±0.03 SE) was nearly twice that of erect growth forms (LS mean = 0.38, ±0.04 SE). Because our sample size for rosettes ($n = 4$) and erect species ($n = 3$) was small, we pooled growth forms and used AI to predict slug damage in the field ($n = 7$). Averaged across rosette and erect growth forms, AI remained a significant, positive predictor of slug damage in our restoration ($r^2 = 0.85$, $F_{[1,5]} = 27.46$, $p = 0.003$). In contrast to our laboratory feeding results, SLM alone could not predict slug damage to plants in the field ($r^2 = 0.28$, $F_{[1,5]} = 1.92$, $p = 0.2$).

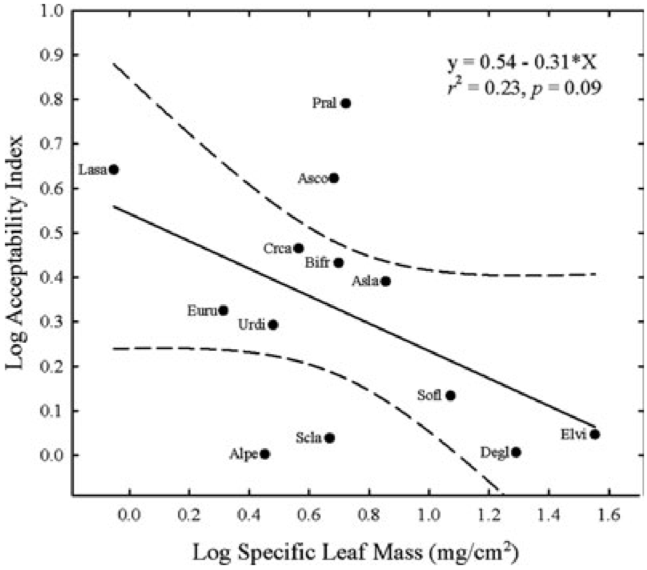

Figure 3. Relationship of dry weight SLM (log transformed) and LS-mean AI (log + 1 transformed) calculated from laboratory feeding trials using the slug *Deroceras reticulatum*. Species labels are the first two letters of the genus and specific epithet and are described in Table 1, except Lasa = *Lactuca sativa* (lettuce). Dashed lines indicate the 95% CI.

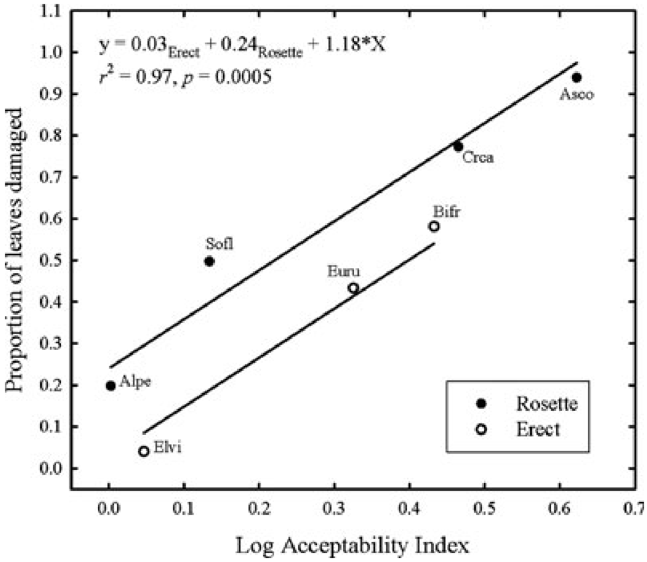

Figure 4. Effects of LS-mean AI (log + 1 transformed) calculated from laboratory feeding trials and plant growth form on the slug damage observed in the field. Species labels are the first two letters of the genus and specific epithet and are described in Table 1.

Discussion

Effective restoration strategies are needed to recover herbaceous layer diversity in many temperate forests (Hobbs & Harris 2001). Our research identifies introduced slugs as one previously unrecognized agent likely limiting the natural or directed recovery of understory native woodland plant communities. We used laboratory feeding trials to demonstrate the general acceptability of native forest herbs as a food source for the introduced slug *Deroceras reticulatum*. In agreement with our expectations, plant palatability varied among tested species and *D. reticulatum* consumption generally increased with decreasing SLM. Interestingly, SLM alone could not predict grazing damage observed in the field, but we found a significant positive relationship between plant acceptability (AI) determined in laboratory trials and grazing damage observed in the field. Grazing damage was severe in the field, with nearly 50% or more of the leaves damaged on most native species. Damage on all rosettes (including the invasive *Alliaria petiolata*) was roughly twice that observed on erect species, suggesting a degree of predictability concerning which growth forms are most likely to succeed, or fail, to recover where *D. reticulatum* is abundant. Furthermore, the relaxed herbivore pressure on *A. petiolata* provides a potential mechanism for its success as an invader. Collectively, our results suggest that active restoration of unpalatable forest herbs should accompany invasive plant removal to promote the recovery of the native herbaceous layer where herbivorous slugs are abundant.

In agreement with our results, Pallant (1969) identified many broad-leaved forbs in the guts and fecal samples of *D. reticulatum* (then called *Agriolimax reticulatus*) collected from European woodlands. Jennings and Barkham (1975) found a variety of European forest herbs in the fecal waste of eight slug species, concluding that many herbs and woody plants are quite palatable to most herbivorous slugs, including *D. reticulatum*. Similarly, Rathcke (1985) found that many North American forest herbs were palatable to three slug species from the genus *Arion* and *D. reticulatum*. In agreement with our study, *Urtica dioica* has previously been reported as palatable to *D. reticulatum* and other herbivorous slugs (Pallant 1969; Jennings & Barkham 1975; Rathcke 1985; Briner & Frank 1998) and *A. petiolata* has previously been reported as unpalatable to two slugs in the genus *Arion* (Briner & Frank 1998). Thus, while the palatability of most of the plant species we used in this study has not previously been tested, our finding of general acceptability of forest herbs to slugs and our results for those plant species that have previously been tested are consistent with previous findings. Furthermore, the noted similarities in food selection between *D. reticulatum* and facultatively herbivorous slugs in the genus *Arion* suggest that our results may be broadly applicable for herbivorous slugs in general. We acknowledge that this conclusion requires future direct confirmation.

A broader literature on slug feeding habits, mainly from European grasslands, connects slug feeding preference with specific plant traits. These studies suggest that slugs generally prefer softer, thinner leaves that posses fewer chemical defenses over plants with thicker leaves or prevalent chemical components (Dirzo 1980; Dirzo & Harper 1982; Fenner et al. 1999). Although surface hairiness does not seem to affect acceptability to slugs, increasing surface roughness appears to reduce slug grazing (Dirzo 1980; Scheidel & Bruelheide 1999). The high silica content of grasses is also frequently cited as decreasing leaf palatability to slugs (Cates & Orians 1975; Dirzo 1980; Hanley 2004). The results from our laboratory feeding trials support these previously reported patterns of slug feeding preference. For example, *U. dioica* seedlings, which have soft pubescent leaves, and all species with glabrous or glacous leaves (e.g. *Aster* spp., *Crytotaenia canadensis*, *Eupatorium rugosum*) were as acceptable, or nearly as acceptable, to *D. reticulatum* as lettuce. *Solidago flexicaulis* seedlings, which have rougher, scabrous leaves, and seedlings of the grass *Elymus virginicus* were not acceptable to slugs. *Alliaria petiolata* seedlings, which are chemically well defended (Cipollini 2002; Cipollini et al. 2005; Cipollini & Gruner 2007), were also largely avoided by *D. reticulatum* in our feeding trials. Irrespective of these more specific differences, plant acceptability was negatively related to a species' SLM in laboratory feeding trials.

In contrast to the general trend of increasing plant acceptability to slugs with decreasing SLM observed in the laboratory, we found no clear relationship between SLM and slug grazing damage in our field plots. One potential explanation for this difference may relate to the fact that plant growth form significantly affected the amount of slug damage observed in the field. Rosette plants were particularly vulnerable to slug grazing in the field, receiving on average twice the damage as all the other species tested. The higher susceptibility of rosette plants may result from their placement of leaves near the soil surface, where slugs are most active, whereas plants with erect growth forms elevate their leaves above the leaf litter (Cates & Orians 1975; Fenner 1987; Briner & Frank 1998). Rathcke (1985) demonstrated that the erect plants *Caulophyllum thalictroides* and *Trillium grandiflorum* were rarely grazed on by slugs, but when the stems were bent so that the leaves were lying on the ground, the plants appeared to be more damaged than nearby unbent plants. Similarly, the difference we found between laboratory and field results is exemplified by *S. flexicaulis*, which spends most of the growing season as a rosette. *S. flexicaulis* was unpalatable in laboratory feeding trials, but was intensively grazed in the field. In contrast, *A. petiolata* provides the only clear exception for slug grazing preference for rosette plants in the field, as *A. petiolata* was unacceptable to slugs both in laboratory feeding trials and in the field. *A. petiolata* has a known arsenal of anti-herbivory chemical defenses (Cipollini et al. 2005; Cipollini & Gruner 2007), which has been proposed as a potential mechanism for *A. petiolata*'s success as an invader (Blossey et al. 2001; Bossdorf et al. 2004; Cipollini 2002; Cipollini et al. 2005). Our findings, although not a direct test, support that *A. petiolata* may be successful in part because of relaxed herbivore pressures. The presence of chemical defenses provides a second explanation as to why SLM alone could not predict damage observed in the field and why *A. petiolata* was consumed less than predicted from its SLM in our laboratory feeding trial. However, species-specific acceptability values were a significant predictor of field damage. Clearly, acceptability values incorporate more information about a species' susceptibility to grazing than SLM, and we suggest that laboratory-determined acceptability values will likely serve as an effective predictor of a plant's ability to thrive in *D. reticulatum* invaded areas, particularly when combined with plant growth form. Future work needs to directly evaluate the mechanistic basis for slug feeding behavior in the field with respect to leaf texture, chemical defenses, and growth form.

The forest herbs we tested are primarily classified as late-summer species (Givnish 1987), with some considered disturbance-adapted early successional woodland species (e.g. *Bidens frondosus*, *Cryptotaenia canadensis*, and *Eupatorium rugosum*). Our use of these species deserves several additional considerations relative to general slug grazing effects. First, early and late-summer understory species may be particularly vulnerable to slug grazing, because they are physically present aboveground when *D. reticulatum* is most active at our study site (mid to late summer; Rathcke 1985; P. G. Hahn, personal observation). This is in direct contrast to spring ephemerals, which emerge, reproduce, and senesce before *D. reticulatum* reaches peak activity. Second, early successional plants generally have rapid growth, and rapidly growing plants are usually palatable to herbivores (Price 1991), including slugs (Cates & Orians 1975). Early and late-summer forest herbs also tend to have broader and thinner leaves, whereas spring ephemerals and many late-successional species have smaller, thicker leaves (Givnish 1987), which may make them more resistant to slug grazing. Rathcke (1985) found no difference in the acceptability of early and late-successional woodland herbs to slugs in laboratory feeding trials, but did not directly test differences in the field or species-specific traits that may make plants more or less vulnerable to slug grazing (e.g. growth form). Functional group-specific susceptibility to slug grazing in the field deserves further evaluation, as functional groups may differ in both their susceptibility to slug herbivory and their potential for long-term success where *D. reticulatum* is abundant.

To our knowledge, this study provides the first experimental documentation that exotic slug herbivory may be impacting understory diversity and restoration success in eastern North American forests. Our findings agree with general trends reporting the community level effects of mollusk herbivory from numerous other ecosystems. For example, introduced slugs have been identified as one potentially critical factor limiting rare plant restoration in Hawaii (Joe & Daehler 2008). Strauss et al. (2009) showed that cryptic nocturnal seedling herbivory by *D. reticulatum* significantly reduced seedling emergence in California old fields. Without intensive monitoring, these observations may have been attributed simply to poor seedling germination (Strauss et al. 2009). In addition to causing direct mortality to small seedlings, sublethal slug grazing can also reduce plant growth and fitness. Introduced apple snails have been identified as a serious threat to native wetland plant communities and their restoration efforts in southeastern United States (Rawlings et al. 2007; Burlakova et al. 2009). Hanley and May (2006) showed that cotyledon damage, which is typical of slug herbivory, reduced establishment, growth, and flower production of several herbaceous plants. Ehrlén (1995*a*, 1995*b*, 2003) found that meristem grazing by mollusks reduced growth, fitness, and flower production in the perennial herb *Lathyrus vernus*. In our study, the carbon costs associated with leaf loss from late-summer forest herbs may be particularly significant. These plants grow under light-limited conditions, thereby restricting plant carbon gain (Neufeld & Young 2003). Defoliation of light-limited herbs is known to affect leaf production, plant survival, and plant reproduction (reviewed by Whigham 2004). Collectively, this work highlights the importance of accounting for slug grazing in woodland restorations, a factor that has probably been overlooked as a result of the cryptic nature of nocturnal slug grazing on small seedlings.

In a broader sense, the results of our acceptability trials are in general agreement with recent declines in forest herbs from Midwestern forests. Wiegmann and Waller (2006) identify many grass-like and browse-tolerant species as "winners" and many broad-leaved forbs as "losers" over the last 50 years in Wisconsin forests. Slugs are associated with human development, are widespread throughout eastern North America (Chichester & Getz 1973), and are likely widespread throughout Wisconsin (Nekola 2003). If slugs are limiting natural recovery or restoration success, as they appear to be at our field site, and they are widespread in forests, then it is reasonable to hypothesize that slugs may be a previously unrecognized factor contributing to the documented decline of woodland understories. The generality and pervasiveness of exotic slug effects on North American plant communities is an avenue of research deserving greater attention.

Implications for Practice

- Many native forest herbs are palatable to exotic slugs, particularly thin-leaved plants and rosette species (*Aster cordifolius*, *Cryptotaenia canadensis*). Less palatable native species (*Desmonium glutinosum*), grasses (*Elymus virginicus*), erect forbs (*Eupatorium rugosum*, *Scutellaria laterfloria*), and plant species whose growth phenologies differ from that of slugs may have the greatest potential for effective woodland restorations where slugs are abundant.
- Slugs avoided the invasive plant *Alliaria petiolata* (garlic mustard) in both laboratory feeding trials and the field. *Alliaria petiolata* may be successful as an invader because of relaxed herbivore pressures relative to its native competitors, suggesting that removal efforts alone may not promote the recovery of native plants. Exotic plant management strategies should go beyond simple control efforts and incorporate restoration of unpalatable native competitors in areas invaded by *D. reticulatum*.

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