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RESEARCH ARTICLE

# Effects of maternal source and progeny microhabitat on natural selection and population dynamics in *Alliaria petiolata*

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**PREMISE**: The success or failure of propagules in contrasting microhabitats may play a role in biological invasion. We tested for variation in demographic performance and phenotypic trait expression during invasion by *Alliaria petiolata* in different microhabitats.

**METHODS**: We performed a reciprocal transplant experiment with *Alliaria petiolata* from edge, intermediate, and forest understory microhabitats to determine the roles of the environment and maternal source on traits, fecundity, population growth rates (λ), and selection.

**RESULTS**: Observations of *in situ* populations show that edge populations had the highest density and reproductive output, and forest populations had the lowest. In experimental populations, population growth rates and reproductive output were highest in the edge, and the intermediate habitat had the lowest germination and juvenile survival. Traits exhibited phenotypic plasticity in response to microhabitat, but that plasticity was not adaptive. There were few effects of maternal source location on fitness components or traits.

**CONCLUSIONS**: *Alliaria petiolata* appears to be viable, or nearly so, in all three microhabitat types, with edge populations likely providing seed to the other microhabitats. The intermediate microhabitat may filter propagules at the seed stage, but discrepancies between *in situ* observations and experimental transplants preclude clear conclusions about the role of each microhabitat in niche expansion. However, edge microhabitats show the highest seed output in both analyses, suggesting that managing edge habitats might reduce spread to the forest understory.

**KEY WORDS** *Alliaria petiolata*; Brassicaceae; garlic mustard; invasion; maternal effects; plasticity; source-sink dynamics.

During the process of biological invasion, many introduced plant species first establish in areas of disturbance and subsequently colonize other habitats as they spread across a new range (e.g., Crawley, 1987; Burke and Grime, 1996). The processes underlying the shift from one to many habitats during invasion is not well-understood (Sajna, 2017) and may involve a number of interacting processes that affect population growth, including phenotypic plasticity, maternal effects, gene flow, and natural selection (see e.g., Crispo, 2008). For example, adaptive phenotypic plasticity can allow a genotype to perform well across a range of microhabitats and hence contribute to niche expansion into new microsites across a heterogenous landscape (e.g., Donohue et al., 2001; Sultan, 2001; reviewed in Sexton et al., 2009). Alternatively, niche expansion could occur through divergent adaptation, even at the microsite scale (Antonovics, 1968, 1976; Williams and Guries, 1994; Stanton and Galen, 1997; Morrison and Molofsky, 1998; Lyons et al., 2010; Rice et al., 2013). Another possibility is asymmetric dispersal from high-quality source populations into adjacent low-quality habitats, which may be demographic sinks (Holt and Gaines, 1992; Kawecki, 2000; Sultan and Spencer, 2002). Experimental work testing the fate of propagules across a range of contrasting microhabitats during biological invasion is scarce but important for understanding the processes that affect geographic spread (Thomson, 2007).

Invasion into one or more novel microhabitats may further depend on which life-stage transitions are most important in different microsites. For instance, seeds originating in a given environment may outperform those from other microhabitats during the establishment phase, regardless of their later fecundity in subsequent adult phases. Stage-specific adaptation may also affect the contribution of a given life-stage transition to population viability (e.g., Stanton and Galen, 1997). Comparing the performance of different life stages as they expand into new microhabitat types can help to identify the life stages at which demographic bottlenecks occur during invasion or range expansion (Woodruff and Gall, 1992; Ellstrand and Schienrenbeck, 2000; Tsutsui et al., 2000; Ronce et al., 2005). Data comparing vital rates and selection estimates in different microhabitats are uncommon but may help explain why some populations go through "lag phases" followed by rapid proliferation and range expansion (e.g., Ellstrand and Schierenbeck, 2000) while others fail to invade (Kowarik, 1995), thereby improving predictions of future invasion and management plans for invasive plants (Coulatti and Lau, 2015).

Here we experimentally tested for fine-scaled variation in both demographic performance and trait expression during invasion by the Eurasian biennial plant *Alliaria petiolata* (Bieb.) Cavara & Grande (garlic mustard, Brassicaceae). In the home range, garlic mustard primarily occupies fields, hedges, and paths, where light levels are intermediate to high and moisture levels are moderate (Grime, 1985). In contrast, this species has become increasingly abundant in many shaded mesic forests in its introduced range in North America, where it negatively affects native forest understory species (e.g., Rogers et al., 2008; Hale et al., 2016). In other areas, garlic mustard invades the forest edge with minimal encroachment into the forest itself (Rogers et al., 2008; Stinson and Seidler, 2014). What determines the failure or success of understory colonization in this species' non-native range is not well understood. To test how microhabitat variation affects the invasion process, we conducted a reciprocal transplant experiment in a region where garlic mustard has been present for decades in full sun at the forest edge but shows relatively low incursion into shaded intermediate and forest understory microhabitats. Specifically, we asked four questions: (1) Do maternal source and progeny microhabitat influence population growth rates, and which life-stage transitions affect population dynamics most strongly in different microhabitats? (2) Do maternal source and progeny microhabitats interact to influence the expression of phenotypes and fitness? (3) Is there evidence for local adaptation such that progeny have highest fitness when grown in the source environment? and (4) How might variable natural selection affect establishment and persistence in different microhabitats?

We predicted a progressive decline in population growth from edge to intermediate to forest microhabitats (e.g., Stinson and Seidler, 2014), such that edge and intermediate populations may be the primary donors of dispersing propagules for forest incursion. We further hypothesized that size and stage-specific fitness components would decline from edge to forest microhabitats (Anderson et al., 1996; Byers and Quinn, 1998; Myers and Anderson, 2003;) but that natural selection on phenotypes could contribute to expansion into forest microhabitats via plasticity and/or local adaptation. Finally, we predicted that the source microhabitat may affect phenotypes and fitness, with progeny from some sources faring better than others across microhabitats (Warren et al., 2011; Stinson and Seidler, 2014).

## MATERIALS AND METHODS

### Study populations

*Alliaria petoliata*, or garlic mustard, is a biennial forb that produces siliques containing five to more than 100 seeds that are passively dispersed (Anderson et al., 1996) and/or can sometimes be transported on animal fur, with 95% of seeds estimated to be dispersed within 1.14 m of the maternal plant (Loebach and Anderson, 2018). The present study populations are located at a ~1200-hectare tract at the Harvard Forest Long Term Ecological Research Site (latitude: 42.531612, longitude −72.189963) in Petersham, Massachusetts, USA, dominated by a canopy of mature *Acer saccharum* Marshall, *Acer rubrum* L., *Quercus rubra* L., *Pinus strobus* L., and *Fraxinus americana* L. trees. The understory consists of seedlings of these same species, shrubs such as *Vaccinium spp*. and *Viburnum acerifolium* L., and by low densities of common forest understory plants such as *Maianthemum canadense* Desf., *Aster divaricatus* L., and *Aralia nudicaulis* L. (Jenkins et al., 2008). Our study populations have been present at the Harvard Forest since the 1980s and have been followed by our research team since the late 1990s. At this location, garlic mustard is largely restricted to edge microhabitats, with population densities highest along roadsides and trails, and some encroachment into disturbed sites that create an intermediate transition microhabitat (i.e., forest gaps and patches of early successional forest due to fragmentation), and into the forest interior itself.

We selected three study sites in forested areas approximately 500 m apart from each other with garlic mustard present in three adjacent microhabitats: (1) along trails and roadsides (edge); (2) transition zones of ~20–50 m between edge and forest (intermediate), with signs of recent disturbance and a canopy of shrubs and small trees; and (3) forest interiors (forest). To characterize standing levels of invasion in each microhabitat, we estimated seedling density, adult density, and reproductive output in naturally occurring garlic mustard populations. We established five observational transects across the entire length of the invading garlic mustard population and used a random number generator to place two 1 m$^2$ quadrats along each transect, for a total of ten quadrats per microhabitat per site ($N$ = 30 per microhabitat). We counted and recorded the number of seedlings and reproductive adult plants within each quadrat on a single date in July. We then selected ten adult individuals nearest to the transect line and harvested each plant when the majority of existing siliques were mature. We separated the seeds from their siliques in the laboratory and recorded the total seed weight for each plant in each microhabitat to acquire estimates of reproductive output of those individuals that survived to reproduce.

### Reciprocal transplant experiment

We conducted a reciprocal transplant experiment to test for variation among populations of *Alliaria petiolata* in the three distinct microhabitats (edge, intermediate, and forest), focusing on the effects of the maternal and progeny microhabitats on progeny traits, demographic performance, and natural selection. We established an experimental garden in each of the three microhabitats at each of the three study sites described above, using small hand trowels to sink 75 square 6 × 6 × 6 cm peat pots to soil level in a 5 × 15 pot grid within a natural matrix of existing vegetation. We filled each pot with microhabitat- and site-specific soil, which we autoclaved to remove the viable seed bank to prevent emergence of non-experimental seedlings in the pots.

We randomly selected 25 maternal plants per microhabitat per site from those harvested from natural populations to use in the experiment. In October, approximately six weeks after seed collection, we filled 25 pots per garden with seeds from each of the three microhabitats, yielding 75 pots per microhabitat in each site ($N$ = 225 pots per site; 675 pots total). We sowed ten seeds from a single maternal plant into each pot, such that each maternal family was represented in each microhabitat within a site. To prevent loss or accidental movement of seeds between pots, we covered each pot with a 10-cm$^2$ piece of fine metal screen and an open metal Mason jar ring, secured to the ground by fabric staples. The pots overwintered *in situ* until March.

We also measured environmental variables at each of six randomly selected points per experimental garden on two dates during the growing season (mid-June and mid-July). In the first year of the experiment we measured soil temperature (Weber Probe instant-read digital thermometer, Weber-Stephen Products LLC, Palatine, Illinois, USA), soil moisture (ThetaProbe ML2x Soil Moisture Sensor, Delta-T Devices Ltd., Houston, Texas, USA), and photosynthetically active radiation (PAR) at 100 cm above the ground (LI-COR 185A photometer, LI-COR Inc., Lincoln, Nebraska, USA). In the second year, we measured soil moisture and soil temperature approximately every four days from early April through mid-July. We assessed light levels in year two from two hemispherical photos per site, taken on a single day in May and on a single day in July (Nikon CoolPix 5000 camera with a Nikon FC-E8 fisheye lens converter, Nikon, Inc., Melville, New York, USA). We analyzed the photos for canopy openness with a digital image analyzer (WinSCANOPY, Regent Instruments Inc., Québec, Quebec, Canada).

### Experimental plant measurements

We monitored the gardens throughout the winter and began collecting data immediately following snowmelt the following spring. We recorded new germinants and the total number of seedlings per pot on a weekly basis from March 1 to late April, or until a pot reached 90–100% germination. The overall germination proportion in each pot was calculated by dividing the number of seedlings by the number of seeds planted. When all remaining seedlings had two true leaves (~April 20), we selected the individual closest to the center of the pot as a target plant to follow for the duration of the study and removed all other seedlings with forceps. We then monitored the pots weekly to record survival of each target individual and its developmental stage (seedling or first year rosette in year one; second year rosette or reproductive adult in year two). We also measured the height and number of leaves of each surviving experimental plant on July 9 during the first growing season. In the second growing season, we conducted an initial census of overwinter survival in March, then recorded time of initial fruit set on all surviving target plants during weekly visits thereafter. We harvested plants in July at the point of individual reproductive maturity, i.e., when the majority of a plant's siliques were ripe, but prior to dehiscence and senescence. We divided individuals into root, shoot, and reproductive organs, dried tissues to final weight in a 50°C drying oven and measured dry biomass for each organ of each individual plant. We thus obtained data for the following traits for juvenile plants: germination proportion, number of leaves, height, and survival; and for second-year, adult plants: height, number of leaves, timing of reproduction, root:shoot biomass, fecundity, and survival.

### Statistical analyses

We compared the *in situ* density (seedlings and adults) and reproductive output of natural populations, as well as environmental conditions at our sites, using restricted maximum likelihood (REML) linear mixed models in JMP Pro 13.0 (SAS Institute Inc., 1989–2019). These models specified a fixed effect of microhabitat and random effect of site.

To test for demographic variation among microhabitats in the experimental populations, we constructed life-stage structured population matrix models in R using the popbio package (Stubben and Milligan, 2007), following methods in Caswell (2001). We calculated transition rates between the following four life stages: (1) seed to seedling; (2) seedling to second-year rosette; (3) second-year rosette to fruiting adult; and (4) fruiting adult to seed. We also included a seed to seed transition representing ungerminated seeds remaining in the seed bank. We calculated values for population growth rate (λ) and the sensitivity and elasticity of λ to each transition for each combination of maternal source and microhabitats, with three replicates per microhabitat (one per site). We constructed linear mixed models in R version 3.4.3 (R Core Team, 2015) using the lme4 package (Bates et al., 2015) to test for effects of maternal microhabitat, progeny microhabitat, and the maternal × progeny microhabitat interaction on λ, sensitivity, and elasticity values for each life stage. Garden site was included as a random factor in each model. Due to the biennial life cycle of garlic mustard, the elasticity values that we calculated represent two "loops". The first includes transitions from seed to seedling, then seedling to rosette, and then rosette to reproductive adult. The second loop includes a single transition from seed bank to back into the seed bank. We prioritize the sensitivity results in this paper (e.g., Kalisz et al., 2014), but report the elasticity values for comparison between these two "loops" in Appendix S1.

We used REML linear mixed models to test for the effects of maternal microhabitat, progeny microhabitat, and the maternal × progeny microhabitat interaction on juvenile morphological traits, adult morphological traits, and time of initial fruiting of experimental plants. Garden site was included as a random effect in each model. We used Tukey HSD post-hoc tests to determine differences among categories as needed.

For metrics of germination success and survival, we fit linear mixed-effects logistic regressions using the function *lmer* (juvenile survival proportion) and generalized linear mixed-effects logistic regressions using the function *glmer* (adult survival proportion) with a logit link function in the package lme4 version 1.1-15 (Bates et al., 2015) in R version 3.4.3 (R Core Team, 2015). Binomial survival was modeled as a function of maternal microhabitat, progeny microhabitat, and the maternal × progeny microhabitat interaction, with garden site included as a random effect. The significance of fixed effects in logistic regressions was determined using likelihood ratio tests (Whitlock and Schluter, 2014). Comparisons of total silique mass per adult plant were conducted with a REML linear mixed model, as described above.

Because seeds used in this experiment were collected directly from the field, the effect of maternal source microhabitat includes effects of both maternal microenvironment (maternal effects) and maternal genotype. The response of seeds of a given sibship to progeny microhabitat effects indicates evidence for plasticity in response to the progeny's microenvironment. We plotted norms of reaction for plant traits from each maternal source microhabitat as a function of the microhabitat where the progeny were grown to evaluate plasticity to progeny microhabitat.

We performed phenotypic selection analyses (Lande and Arnold, 1983) within each progeny microhabitat by regressing relative fitness against standardized phenotypic values of the following four traits: (1) height; (2) number of leaves; (3) root:shoot ratio; and (4) fruiting date. While we collected data on other phenotypes, we only performed selection analyses on variables that were not significantly correlated with one another (Pearson correlations; $P > 0.05$). Relative fitness was calculated as an individual's total reproductive biomass (including zero values of individuals that did not survive to reproduce) divided by the population mean reproductive biomass within a given progeny microhabitat. To standardize phenotypic traits, we subtracted the population mean trait value from the individual values in that microhabitat and divided that value by the standard deviation of the trait. For each trait, we calculated the selection gradient (direct selection, $\beta$), as the partial regression coefficient linking each predictor trait to relative fitness in a multivariate model. We also calculated the selection differentials, or total selection on each trait, as measured by regression coefficients in univariate regressions.

To test for differences in the direction and magnitude of selection gradients across progeny microhabitats, we constructed a multivariate model with total reproductive biomass (relativized within each progeny microhabitat) as the dependent variable, and all phenotypic traits as fixed factors. We included all individual trait × progeny microhabitat and trait × progeny microhabitat × maternal microhabitat interaction effects, as well as the random effect of site. Significant interactions between traits and progeny microhabitat would indicate that selection on the traits differed across the three distinct progeny microhabitats. Likewise, significant interactions between traits and maternal microhabitat would indicate that selection on the traits differed according to maternal source microhabitat. We constructed these selection models in JMP Pro 13.0 (SAS Institute Inc., 1989–2019).

## RESULTS

### Natural variation across growth microhabitats: standing populations and environmental factors

Adult garlic mustard densities at our sites varied significantly across microhabitats, ranging from 26.52 reproductive individuals per square meter in edge to 16.3 in the transition microhabitat (intermediate) and 11.06 in forest understory (Appendix S2). Garlic mustard seedling densities followed a similar pattern, decreasing significantly from edge to interior. Ratios of adults to seedlings were lowest in the edge and highest in the intermediate microhabitats, suggesting self-thinning in the edge, possibly due to negative density-dependence. Adult plants in the edge microhabitat also had markedly higher reproductive output, producing nearly seven times more seed biomass per adult plant than populations in intermediate microhabitats, and more than thirteen times more than populations in forest habitats (Appendix S2). The ratio of total reproductive output per quadrat to total number of seedlings per quadrat gives a rough estimate of reproductive output per seedling; edge populations had the highest ratio (0.80) and forest populations had the lowest (0.11), with intermediate microhabitats having intermediate values (0.29). In sum, edge populations had the highest density and highest total and per-seedling reproductive output, while forest populations had the lowest.

The microhabitats also differed significantly in light availability, soil moisture, and soil temperature. As expected, the edge microhabitats received more light, with significantly greater photosynthetically active radiation (PAR) and canopy openness than in the intermediate and forest microhabitats (Appendix S3). However, the intermediate and forest microhabitats had similarly low-light conditions, rather than forming a directional gradient from sun to shade. Likewise, variation in soil composition did not follow directional gradients from edge to understory. The intermediate microhabitat was the wettest, with significantly higher soil moisture than edge and forest microhabitats in both years of the experiment (Appendix S4). In April, soil in the intermediate microhabitats was ~2°C warmer than that in edge and forest microhabitats, but higher temperature at intermediate sites was not consistent throughout the season (Appendix S5).

### Demographic variability

Our demographic model was designed to assess variation in overall population growth as well as the contribution of each life stage to population growth, depending on maternal source microhabitat, progeny microhabitat, and their interaction. Maternal microhabitat did not affect either population growth (λ) or the sensitivity of λ to any life-stage transition (LRT, $N = 27$; $P_{\text{maternal microhabitat}} > 0.05$ and $P_{\text{maternal} \times \text{growth}} > 0.05$ for λ and all sensitivities and elasticities). Progeny microhabitat, however, had a significant effect on population growth rate (λ) (Table 1). Populations were stable or slightly declining within the intermediate microhabitat ($\lambda < \approx 1$), while populations were predicted to rapidly increase in both the edge and forest microhabitats ($\lambda > 1$) (Fig. 1).

The contributions of different life-stage transitions to λ also differed among progeny microhabitats (Table 1). Progeny microhabitat significantly affected the contribution of seed dormancy (seed → seed transition), early life survival (germinant → rosette transition), and reproduction (adult → seed transition) to λ. For these vital rates that varied across progeny microhabitats, populations in the intermediate microhabitat showed higher sensitivity of λ to seed germination and lower sensitivity of λ to early life survival than the other microhabitats; populations in forest microhabitats had the strongest sensitivity to reproduction (adult → seed), and populations in edge microhabitats had the lowest. Within each microhabitat, the relative importance of each transition to population growth also varied; in the edge and forest microhabitats, λ was most sensitive to adult survival, but in the intermediate microhabitat λ was most sensitive to germination and secondarily to rosette survival to reproduction. Elasticity analyses also showed that proportional changes in seed dormancy or seed mortality contributed most to proportional changes in population size in the intermediate microhabitat, whereas changes in aboveground growth, survival, and reproduction had greater proportional effects on population growth in the edge and forest microhabitats (Appendix S1).

### Plasticity and maternal effects on trait expression

Juvenile traits were affected by both the maternal source and progeny microhabitats (Table 2). Juvenile plant growth was

**TABLE 1.** Summary of demographic variation (λ and transition sensitivities) across the three growth microhabitat types. Least-squared means and standard errors (SE) for each microhabitat were calculated in models that tested for the fixed effects of maternal source, microhabitat, and maternal source × microhabitat, with a random effect of site. Significant variation across growth microhabitats ($P < 0.05$) is indicated in bold. Within a row, means not connected with matching letters are significantly different.

| | Microhabitat | | | Model effect of growth microhabitat | | |
|---|---|---|---|---|---|---|
| Vital rate | Edge | Intermediate | Forest | df (num, den) | *F* | *P* |
| *Population growth rate (λ)* | $1.895 \pm 0.352^{A}$ | $0.933 \pm 0.352^{B}$ | $1.878 \pm 0.352^{A}$ | 2, 16 | 3.658 | **0.049** |
| | | Sensitivity of λ | | | | |
| *Seed to seed* | $0.284 \pm 0.039^{a}$ | $0.435 \pm 0.040^{b}$ | $0.315 \pm 0.037^{a}$ | 2, 11.431 | 10.853 | **0.002** |
| *Seed to germinant* | 0.915 ± 0.276 | 1.206 ± 0.289 | 0.740 ± 0.256 | 2, 11.417 | 1.561 | 0.252 |
| *Germinant to rosette* | $0.834 \pm 0.138^{a}$ | $0.378 \pm 0.146^{b}$ | $0.679 \pm 0.127^{ab}$ | 2, 11.434 | 4.391 | **0.038** |
| *Rosette to adult* | 1.648 ± 0.232 | 1.062 ± 0.246 | 0.868 ± 0.201 | 2, 13.00 | 3.355 | 0.067 |
| *Adult to seed* | $0.006 \pm 0.004^{b}$ | $0.009 \pm 0.004^{ab}$ | $0.014 \pm 0.004^{a}$ | 2, 11.203 | 4.828 | **0.031** |

*Notes:* Capital letters in superscripts: Student's t-test, $P < 0.05$; lower case: Tukey HSD, $P < 0.05$.

suppressed in intermediate microhabitats, with progeny grown there showing reduced height and fewer leaves (Fig. 2, Appendix S6). Juvenile leaf number also varied in response to the maternal microhabitat, with plants whose seeds were sourced from the edge microhabitat producing slightly more leaves. The contribution of maternal source microhabitat to juvenile trait variation was additive, as there was no significant interaction between maternal source and progeny microhabitat for either height or leaf number.

By the second year of growth, maternal source no longer affected variation in any of the plant traits measured, but there was evidence of plasticity of adult traits in response to progeny microhabitat (Table 2, Fig. 3). Adult plants were larger when grown in the edge microhabitat (Fig. 3A-B, Appendix S6), and fruiting was delayed in the intermediate microhabitat (Fig. 3C, Appendix S6). There was no difference in the number of leaves or root:shoot ratio among maternal source or progeny microhabitats (Table 2).

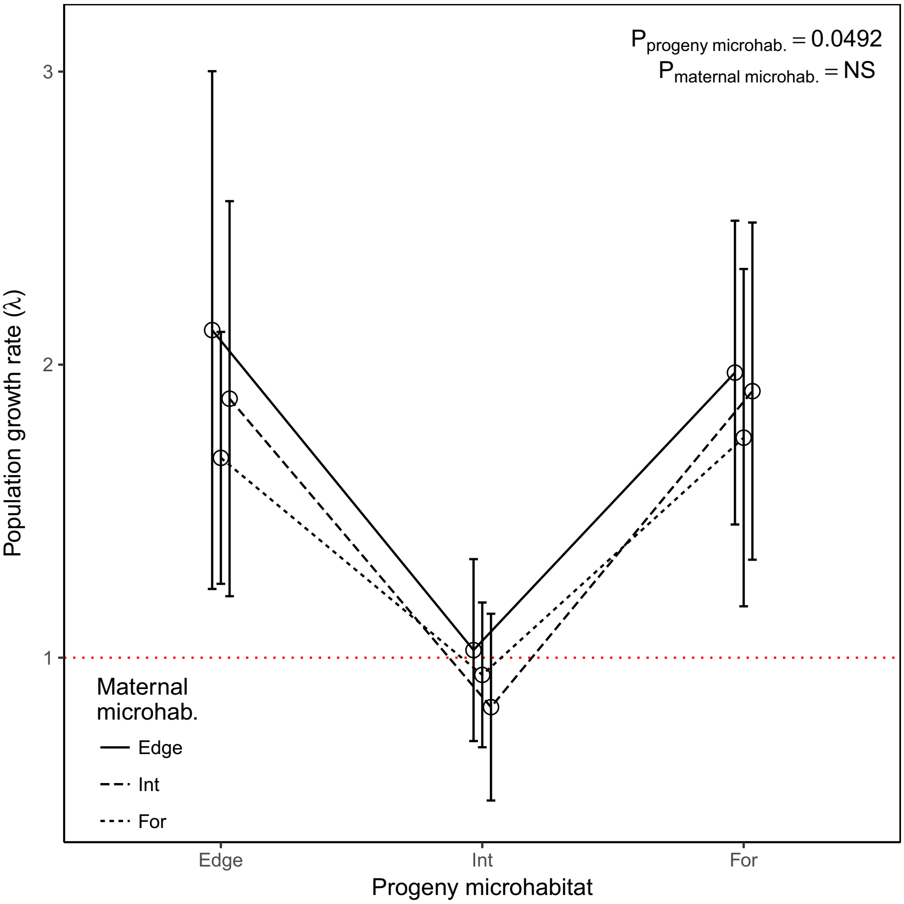

**FIGURE 1.** Population growth rate in each combination of maternal and progeny microhabitat. Red horizontal line represents stable population growth (λ = 1). Values shown are the least-squared mean across three sites ± 1 standard error, calculated from models that include fixed effects of maternal and progeny microhabitat, and maternal × progeny microhabitat interaction, and a random effect of site.

### Fitness components

Juvenile and adult fitness components differed across progeny microhabitats (Table 2, Appendix S6), and were generally lowest in the intermediate microhabitat (Fig. 4). Germination proportion varied in response to both maternal source and progeny microhabitat; seeds sourced from the edge had significantly lower germination than seeds from the other two sources, and seeds sowed into the intermediate growth microhabitat had the lowest germination overall (Fig. 4A, Appendix S6). Juvenile survival was also lowest in the intermediate progeny microhabitat compared to the others. Across all microhabitats, juvenile survival was marginally lower for seedlings sourced from intermediate maternal microhabitats than for forest- and edge-derived seedlings (Fig. 4B, Appendix S6). Adult survival and reproduction did not differ among maternal sources, but plants grown in the forest microhabitat had the highest survival compared to the other microhabitats (Fig. 4C, Appendix S6). Fecundity was marginally higher in the edge microhabitat (Fig. 4D, Table 2, Appendix S6) and was not influenced by the maternal environment (Table 2).

**TABLE 2.** Results of mixed models to test effects of maternal and progeny microhabitat and their interaction on: (A) phenotypic traits fitted with linear regression; and (B) survival of juveniles and adults fitted with a logistic regression (see Methods for model details). All models include random effect of experimental site. Significant predictors ($P < 0.05$) are indicated in bold.

| | | | **Model effect** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | **Growth microhabitat** | | | **Maternal microhabitat** | | | **Maternal × growth microhabitat** | | |
| **Trait (response)** | **N** | **Figure** | **df (num, den)** | ***F*** | ***P*** | **df (num, den)** | ***F*** | ***P*** | **df (num, den)** | ***F*** | ***P*** |
| (A) | | | | | | | | | | | |
| *Germination proportion* | 664 | 4A | 2, 653 | 11.1 | < **.0001** | 2, 653 | 3.4 | **0.0329** | 4, 653 | 1.8 | 0.1234 |
| *Juvenile height* | 664 | 2A | 2, 653 | 35.5 | < **.0001** | 2, 653 | 1.1 | 0.3411 | 4, 653 | 0.8 | 0.5180 |
| *Juvenile leaf number* | 664 | 2B | 2, 653 | 15.9 | < **.0001** | 2, 653 | 3.1 | **0.0468** | 4, 653 | 0.9 | 0.4948 |
| *Adult height* | 145 | 3A | 2, 135.9 | 9.5 | **0.0001** | 2, 134.2 | 1.0 | 0.3590 | 4, 134.2 | 0.7 | 0.5587 |
| *Adult leaf number* | 140 | - | 2, 130.5 | 1.9 | 0.1487 | 2, 129.2 | 0.5 | 0.6303 | 4, 129.2 | 0.9 | 0.4799 |
| *Adult root:shoot ratio* | 144 | - | 2, 38.69 | 2.2 | 0.1258 | 2, 134.5 | 0.9 | 0.4115 | 4, 134 | 0.7 | 0.5727 |
| *Fruiting date* | 141 | 3C | 2, 131.2 | 13.7 | < **.0001** | 2, 130 | 0.4 | 0.6550 | 4, 130.1 | 0.8 | 0.5077 |
| *Silique mass* | 138 | 4D | 2, 125.4 | 2.7 | 0.0742 | 2, 127.3 | 1.4 | 0.2610 | 4, 127.6 | 0.9 | 0.4767 |
| | | | **df** | **$\chi^2$** | ***P*** | **df** | **$\chi^2$** | ***P*** | **df** | **$\chi^2$** | ***P*** |
| (B) | | | | | | | | | | | |
| *Juvenile survival* | 675 | 4B | 2 | 43.3 | **< .0001** | 2 | 5.86 | 0.0535 | 4 | 4.9 | 0.3003 |
| *Adult survival* | 579 | 4C | 2 | 50.6 | **< .0001** | 2 | 2.39 | 0.3034 | 4 | 1.7 | 0.7978 |

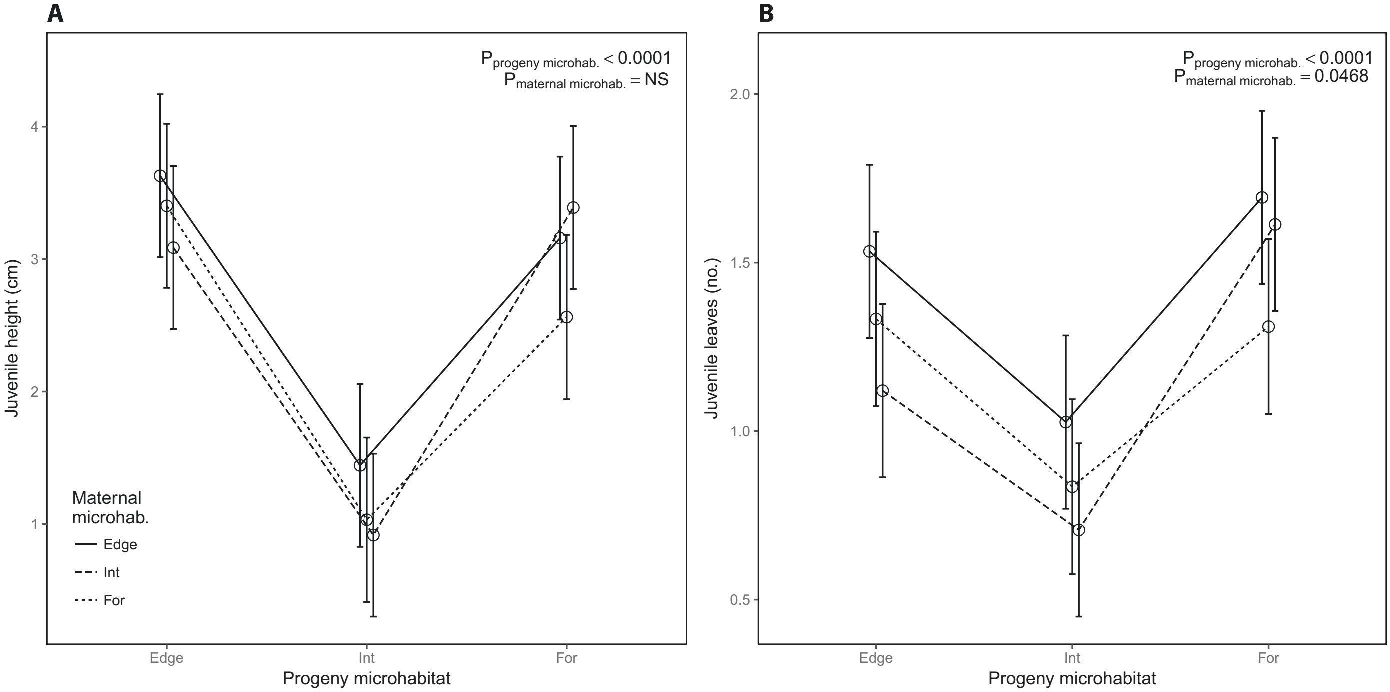

**FIGURE 2.** Variation in juvenile trait expression. (A) Height. (B) Total number of leaves per plant. Least-squared mean values ± 1 standard error are shown, calculated from models that include fixed effects of maternal and progeny microhabitat, and maternal × progeny microhabitat interaction, and a random effect of site.

## Phenotypic selection

We detected direct selection on adult height and leaf number, but not on time of reproduction or allocation to roots versus shoots (Table 3, Appendix S7). Selection on adult height varied across progeny microsites, such that taller plants had higher fitness in the forest microhabitat, while selection was relaxed in the edge and intermediate microhabitats. Plants with more leaves were favored across all microhabitats, but the strength of selection was marginally higher in intermediate microhabitats. Correlations among traits ranged from −0.76 to 0.88 (Appendix S8); these correlations were accounted for in the multivariate selection models. In addition, we used separate univariate models to measure total selection on the number of leaves, fruiting date, height, and root:shoot ratio (Appendix S9). These univariate analyses showed similar patterns,

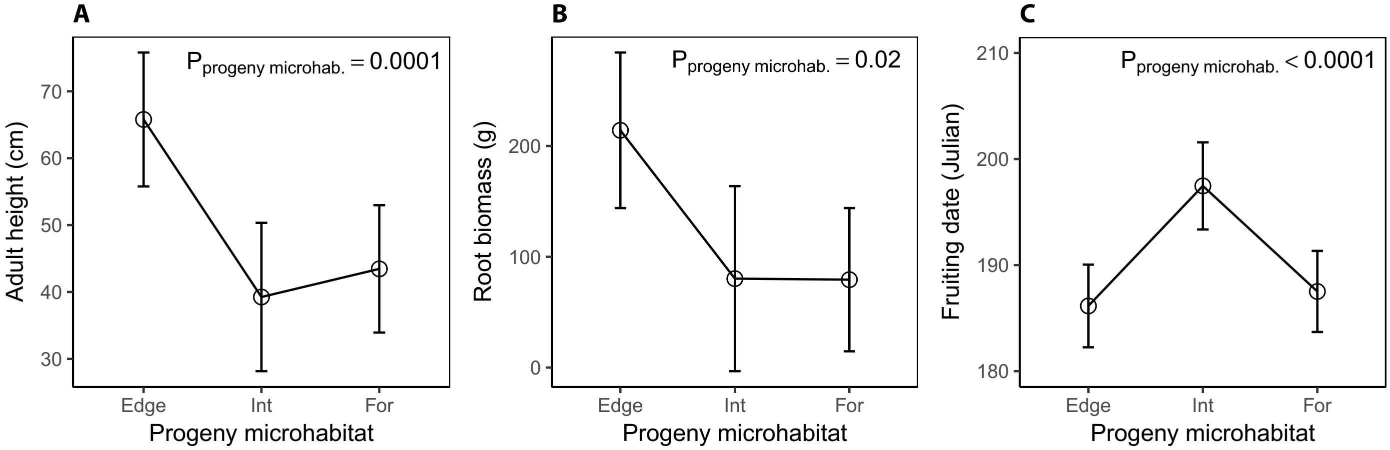

**FIGURE 3.** Variation in adult trait expression. (A) Adult height. (B) Root biomass. (C) Fruiting date. Values shown are least squared means ± 1 standard error, calculated in a REML model with main effects of maternal microhabitat, maternal × progeny microhabitat interaction, and a random effect of site. Maternal source had no significant effect on any traits, so only variation across microhabitats is shown.

revealing evidence for total selection on height and total number of leaves, and variation in selection on these traits among microhabitats (Appendix S9).

These selection analyses also revealed that plastic variation in trait expression was not in the adaptive direction. Selection favored taller plants, especially in the forest microhabitat (Table 3), but plants grown in the forest had reduced height (Fig. 3A). Selection for more leaves was especially strong in intermediate microhabitats (Tables 3, Appendix S9), but adult leaf number was not plastic across growth microhabitats (Table 2).

## DISCUSSION

Niche expansion into undisturbed sites may involve differential performance of invading populations across heterogenous landscapes (e.g., Crawley, 1987; Kowarik, 1995; Christen and Matlack, 2006; Thomson, 2007). We tested this by comparing the fate and phenotypic expression of garlic mustard reciprocally transplanted into adjacent edge, intermediate, and intact forest microhabitats. Standing density was highest in edge populations, and reproduction was also highest there, both *in situ* and within our experimental transplants, indicating that edge populations are likely to be the largest source of dispersing propagules in the landscape. While seeds from edge populations had slightly lower germination success, the microhabitat origin of seeds had little effect on other aspects of performance, suggesting that propagules can perform comparably, regardless of where they originated. Although adaptive plasticity, maternal effects, and genetic adaptation have been shown to facilitate niche expansion in other systems (e.g., Holt and Gaines, 1992; Eriksson, 1996; Kanda et al., 2009; Boulangeat et al., 2012), they did not appear to play a significant role in performance across microhabitats in our study populations. In our experimental populations, the intermediate microhabitat had the lowest seed and juvenile performance, resulting in the lowest projected population growth rate, suggesting that transitional microhabitats between edge and forest do not promote incursion but may actually impede it, at least at the seed stage. As such, our findings generally suggest that management of edge populations could be effective at minimizing spread to other microhabitats.

### Demographic performance in different microhabitats

In North America, garlic mustard readily establishes in disturbed sites, but shows variable success invading forest understory across its new range (Rodgers et al., 2008; Stinson and Seidler, 2014). In the location of our study, garlic mustard is commonly found in edge microhabitats exposed to high light levels, but it is not abundant in the forest understory. We predicted that garlic mustard might therefore exhibit source-sink dynamics, such that edge microhabitats could be the primary donors of dispersing propagules, and that forest populations are dependent on edge or intermediate populations to maintain them. Consistent with this prediction, natural populations in edge microhabitats persist at much higher densities, surviving adults have higher reproductive output there, and total reproductive output per area (quadrat) is higher there, suggesting more dispersing propagules originate at the edge than elsewhere (Appendix S1; Fig. 4D). Moreover, *in situ* observations suggest a gradient in microhabitat quality from edge (best) to forest interior (worst), based on standing density and estimated reproductive output per seedling.

In our experimental populations, the lowest population growth, lowest germination, and lowest survival were within the intermediate microhabitat, suggesting a depletion of propagules in intermediate sites at the seed stage. It should be noted that the *in situ* observations, which showed higher performance of intermediate than forest populations, did not provide estimates of germination or seed to seedling survival. Therefore, low germination success and/or early seedling mortality could contribute to the lower projected population growth rate in intermediate compared to forest experimental populations. Low performance in intermediate microhabitats coincided with wetter soils and warmer temperatures (Fig. 4B, Appendices S4 and S5), which may be linked to higher abundances of pathogens (e.g., Cipollini and Enright, 2009), saturation, hypoxia, or more frequent washout of seeds or small seedlings (Baskin and Baskin, 1998).

Unexpectedly, the experimental populations showed high rates of increase in both edge and forest microsites (λ ~ 1.85; Fig. 1), a finding that is inconsistent with *in situ* field observations of low densities and low per-seedling reproduction in the forest. A number of factors may have contributed to this discrepancy between

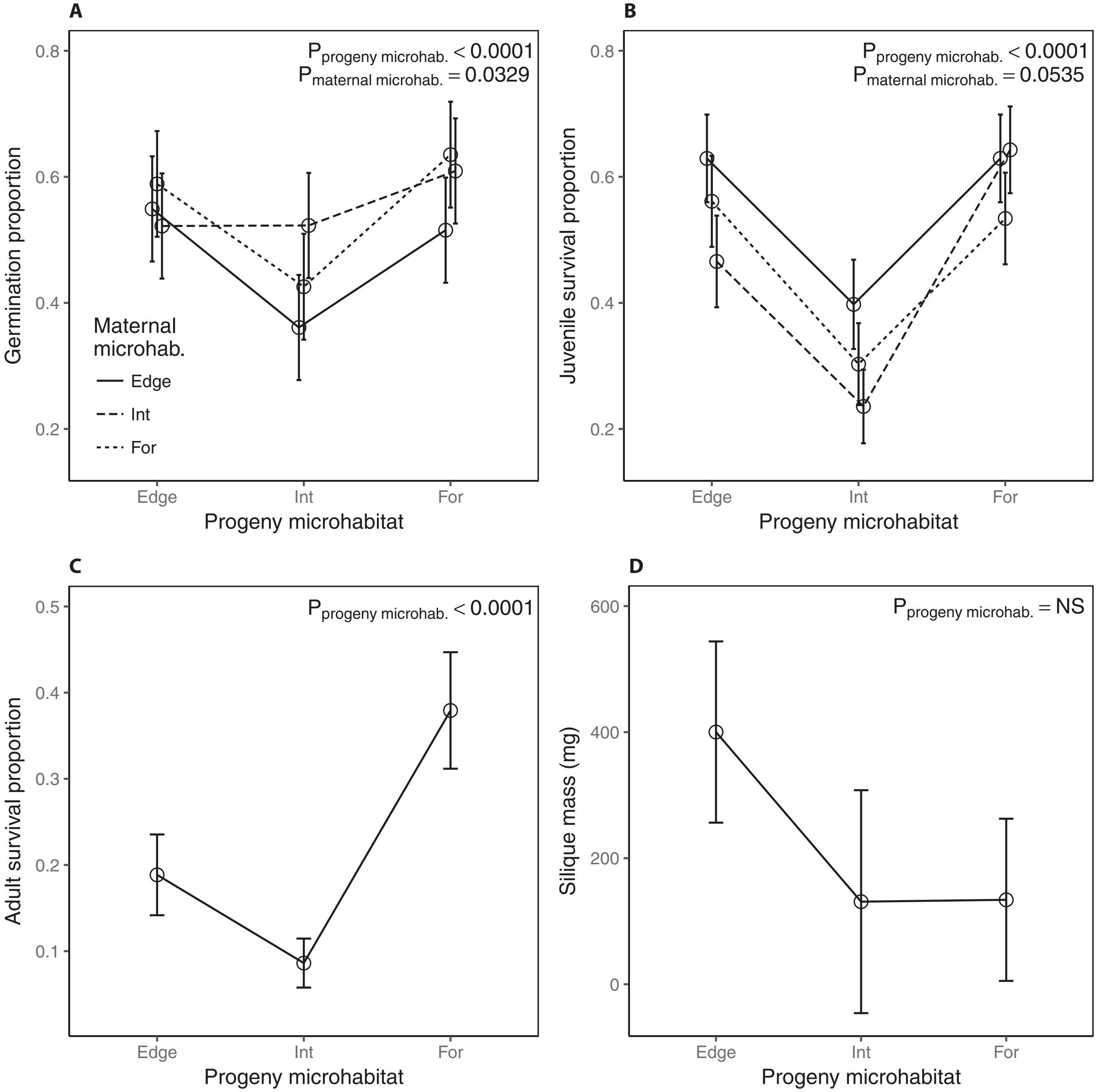

**FIGURE 4.** Variation in fitness components. (A) Germination proportion. (B) Juvenile survival. (C) Adult survival. (D) Silique biomass. Maternal source is indicated by line dashing in (A); there were no significant effects of maternal source on other fitness components. Least-squared means ± 1 standard error are shown for each trait, calculated with mixed models including fixed effects of maternal, progeny, and maternal × progeny microhabitat interaction, and a random effect of site.

*in situ* and experimental populations, including experimental conditions that do not accurately reflect natural conditions. For example, we excluded seed predation in the experiments, and it is possible that seed predators are denser and/or more active in forest microhabitats than in edge and intermediate microsites, leading to overestimates of seed survival in the forest. Additionally, we may have altered litter quality and quantity in the process of transplanting; if litter impedes survival in the forest more than in the edge (which is likely, given that litter is more abundant in the forest), survival in the forest could have been over-estimated. Our experimental populations also did not experience density-dependent dynamics. If neighbors have more intense adverse effects in the forest than in the edge, then our removal of neighbors could have enhanced performance in the forest more than in the edge (Meekins and

**TABLE 3.** Estimates of the strength of direct selection ($\beta$) on standardized phenotypic traits, and model results testing for differences in selection across progeny microhabitats (see Methods). Selection gradients that were significant in the multivariate model are marked in bold; significant trait × progeny microhabitat interactions, indicating variation in selection across microhabitats, are marked with an asterisk.

| | β within progeny microhabitat | | | Trait × progeny microhabitat model effect | | |
|---|---|---|---|---|---|---|
| **Trait** | **Edge** | **Intermediate** | **Forest** | **df (num, den)** | ***F*** | ***P*** |
| *Height* | 1.910 | −1.288 | **4.170** | 2, 108.1 | 3.96 | 0.02* |
| *Total leaves*[a] | **0.121** | **0.451** | 0.174 | 2, 117.6 | 2.49 | 0.87 |
| *Fruiting date* | −0.134 | −1.453 | 0.458 | 2, 117.3 | 1.22 | 0.79 |
| *Root:Shoot ratio* | −0.012 | −0.002 | −0.007 | 2, 116.5 | 0.24 | 0.79 |

*Notes:* [a]While selection on most traits was not influenced by maternal microhabitat, there was a leaf number × maternal microhabitat effect in the full multivariate selection model. Specifically, more leaves conferred higher fitness in plants sourced from the edge maternal microhabitat, possibly because of higher phenotypic variation, and therefore opportunity for selection, in the edge habitat (SD height in edge, 0.51) than the others (SD height in intermediate, 0.44; SD height in forest, 0.46). Full model results are presented in Appendix S7.

McCarthy, 1999, 2000). However, greater density-dependence in the forest seems unlikely, since density itself was much higher in the edge populations, which showed some evidence of self-thinning. If performance was over-estimated in the forest for these reasons, it is also possible performance is lower in the forest, even compared to the intermediate microhabitat. We thus note that the experimental manipulations themselves may have altered demographic performance, and that *in situ* density dynamics, unmeasured factors that interact with microsite variation, and interannual variation in environmental conditions were not fully captured by the experiment, thereby preventing clear conclusions about the relative contribution of microsite variation to demographic performance.

### Plasticity, selection, and adaptation across environments

In addition to demographic dynamics, niche expansion across heterogenous landscapes can involve both phenotypic plasticity and differentiation among populations, which together can influence species distributions and spread (e.g., Holt and Gaines, 1992; Eriksson, 1996; Kanda et al., 2009; Boulangeat et al., 2012). In situations where environmental change is rapid or connectivity is high among divergent microhabitat patches, adaptive plasticity may aid in the establishment and persistence of populations even when adaptive evolution lags behind or fails to occur (Dyer et al., 2010; Fenesi et al., 2014). Surprisingly, we did not find evidence that adaptive plasticity, maternal effects, or genetic adaptation influence population success in any microhabitat, but observed instead that garlic mustard is capable of establishing and persisting in a variety of microhabitat types (e.g., Byers and Quinn, 1998).

Plasticity has been implicated in contributing to the invasive ability of some plants (Anderson et al., 1996; Byers and Quinn, 1998; Myers and Anderson, 2003; Stinson and Seidler, 2014). We found no evidence that plasticity in the traits that we measured enhanced fitness. Although progeny growth microhabitat largely determined trait expression, fitness, and population growth rates in this study, we found that some traits exhibited plasticity even when selection on them did not vary across microhabitats; moreover, when selection did vary, patterns of plasticity in the progeny microhabitat did not match patterns of selection. One explanation for this mismatch could be that plastic trait variation was not adaptive due to physiological constraints (Stinson and Seidler, 2014); i.e., plants in the intermediate and forest environments altered their phenotypes simply because they experienced poorer growing conditions compared to those of the forest edge, and were therefore limited in the number of leaves and height they could attain. These data suggest that phenotypic plasticity contributes to population growth but may not be sufficient to enhance fitness across all microhabitats.

Local adaptation to new environments has also been shown to contribute to invasion success, with and without inputs from nearby seed sources from different microhabitats. Net dispersal into less favorable microhabitats can facilitate adaptation to increasingly novel conditions, as has been demonstrated for incursion by the non-native graminoid *Microstegium vimineum* (Trin.) A. Camus (Warren et al., 2011), and the forb, *Prunella vulgaris* L. [Lamiaceae], into shaded forest understory habitats from high light conditions at the forest edge (Godoy et al., 2011). Similarly, Blossey et al. (2017) found evidence for rapid evolutionary changes among garlic mustard populations across North America. Thomson (2007) demonstrated that the invasive grass *Aegilops triuncialis* L. can successfully spread into extreme serpentine habitats even without sustained input of seed from nearby populations, possibly through divergence into serpentine-tolerant ecotypes after introduction from non-serpentine locations (Lyons et al., 2010). In contrast to these examples, adaptive divergence seems unlikely to have occurred yet for these populations of *Alliaria petiolata*, as we did not find strong evidence of local adaptation to forest interior or intermediate microhabitats. Specifically, progeny microhabitat effects were stronger than maternal source effects for most traits, and those that did vary in response to maternal source did not show "home-site advantage" in the intermediate and forest microhabitats (Figs. 1A–B, 2A–B). In contrast to prior work suggesting local adaptation as a major driver of invasion (Thomson, 2007; Dyer et al., 2010; Fenesi et al., 2014; Blossey et al., 2017), our results do not provide compelling evidence that local adaptation facilitates garlic mustard invasion into either intermediate sites or the forest understory. Rather, maternal effects on juvenile size (Fig. 2) suggest that larger plants produced by edge-derived seeds have early life-stage fitness advantages over those originating in other microhabitats. Moreover, while seeds produced in the intermediate microhabitat had higher germination there than seeds produced elsewhere, the resulting seedlings had the lowest survival (Fig. 4A–B). In particular, edge-derived seedlings had a slight survival advantage in the intermediate microhabitat compared to those from the intermediate microhabitat (Fig. 4B). These results suggest that maternal effects do not increase the fitness of seeds dispersed locally within intermediate microhabitats, but instead that propagules from the edge generally perform better in the intermediate and forest microhabitats than do locally produced seeds (e.g., Stanton and Galen, 1997; Kawecki, 2000).

Given that we detected some variation in selective regimes across microhabitats, why there is no signal of adaptive evolution or adaptive plasticity remains unclear. It is possible that there is insufficient genetic variation for populations to respond to selection, that the relatively recent expansion of these populations into forest understories through the intermediate patches simply has not provided sufficient time for detectable responses to selection to occur (Holt and Gaines, 1992; Kowarik, 1995), or that trait covariances (Appendix S6) constrain adaptation of optimal phenotype combinations that are favored in these newer microhabitat patches.

### Incursion into forest habitat

Several prior studies point to increasing shade as the most limiting factor for performance in garlic mustard (Dhillion and Anderson, 1999; Meekins and McCarthy, 2000, 2001; Smith, 2015), and in other invasive plants (Godoy et al., 2011; Warren et al., 2011). Indeed, the higher *in situ* densities and reproductive output of garlic mustard in the forest edge microhabitat suggest that edge populations may be a primary source of propagules into the other microhabitats. However, $\lambda$ in the forest was greater than 1, and survival was comparable (juvenile) or higher (adult) in the forest compared to the edge, indicating that understory microhabitats can support garlic mustard populations under some conditions, such as those created in our experimental populations. That this occurs despite plants being smaller while under selection for greater size in the forest habitat points to potential physiological limitations under which understory populations may not have sufficient resources to produce more or larger leaves (e.g., Stinson and Seidler, 2014).

Why the forest understory populations have not expanded further during the time that garlic mustard has been present in this landscape, especially given high estimates of $\lambda$ in the demographic models, remains unclear. As discussed above, one possibility is that our experiment artificially inflated fitness, recruitment, and survival in forest habitats by eliminating seed predation, inhibition by litter, or by inadvertently altering other unmeasured factors, leading to overestimates of population performance in the forest. In fact, the natural, *in situ* density and reproductive output of forest populations were low, suggesting at least some metrics of performance could have been overestimated in the experimental populations.

Another contribution to the low incursion into the forest could be low performance in the intermediate microhabitat. In the experimental populations, projected population growth rates were significantly lower there than elsewhere, in large part due to low germination and/or early seedling mortality. Although reproductive output per seedling was intermediate between edge and forest populations in the field, those estimates did not include germination success or early seedling mortality. Therefore, intermediate microhabitats may impede population growth by depletion at the seed stage. Because the intermediate habitat also produced significantly less reproductive biomass than edge populations (based on both *in situ* and experimental populations), it is possible that a forest landscape with an abundance of intermediate habitat may reduce seed rain into the forest compared to a landscape in which forest and edge are immediately adjacent. This interpretation is consistent the observation that incursion of garlic mustard into the forest understory was more common in less-fragmented forests (62% of sites) than in the more heavily disturbed forests (16%) around our study sites (Urbanowicz et al., 2018), based on presence/absence surveys across >100 randomly selected locations. A direct comparison of incursion in patchy versus intact forest would be necessary to test the hypothesis that disturbance, such as that present in intermediate microhabitats in our study sites, may actually impede understory invasion, rather than facilitate it, as commonly assumed.

### Future research needs

It is important to note that we did not measure certain other factors that could affect our findings, including the degree of genetic variation in source populations, which may or may not vary across microhabitats (Stanton and Galen, 1997; Colautti and Lau, 2015). In addition, direct and indirect interactions with other organisms such as large herbivores and earthworms (Kalisz et al., 2014; Davalos et al., 2015; Nuzzo et al., 2017) and plant competitors (e.g., Meekins and McCarthy, 2000; Davalos et al., 2015) are known to affect garlic mustard and may influence population dynamics and trait expression. Although we controlled for some biotic interactions by planting gardens within a natural matrix of co-occurring plants and excluding seed predation with screening over the winter, we did not experimentally evaluate the effects of other biotic factors on performance. Unmeasured abiotic factors including variation in land use history, and current disturbance frequency (e.g., Lundgren et al., 2004; Burls and McClaugherty, 2008) could also affect performance of seedlings and adults in the different microsites. Thus, the relative roles of genetics and other aspects of the environment, especially biotic interactions, in influencing the patterns we observed here warrant further study.

### Management considerations

Efforts to eradicate garlic mustard populations in forest ecosystems are common and time-consuming but may not be warranted if populations are self-limiting or declining (Rogers et al., 2008; Lankau et al., 2009). Our results suggest that populations in edge microhabitats most warrant removal efforts if eradication of invasive plants is a management priority, as both reproductive output and population growth are likely to be high there. At the same time, differential selection in the forest raises the possibility that eventual local adaptation may increase performance of forest populations (Thomson, 2007; Colautti and Lau, 2015). Thus, managers may wish to monitor forest populations to ensure that subsequent adaptation does not lead to further population growth there over time. Lower population growth in the intermediate microhabitat due to higher mortality of seeds and juveniles in that microhabitat than elsewhere may make populations near a transition zone between edge and understory a lower management priority. Significant variation in the sensitivity of $\lambda$ to different life stages suggests targeted removal of flowering adults in summer may be most effective in edge and forest microhabitats, while removal of overwintered rosettes in early spring may be most effective at limiting population growth in intermediate sites. While these are intriguing avenues for further investigation of invasion dynamics, we caution against over-interpretation of these conclusions as they may reflect transient conditions and/or some degree of experimental artifact related to the potting of experimental plants. Future studies comparing metapopulation dynamics and seed dispersal patterns in response to density manipulation and/or or removal in different microhabitats would link our experimental findings more explicitly to management recommendations.

## CONCLUSIONS

Spatial patterns of environmental heterogeneity can influence the incursion of invasive species into new habitats through demographic as well as microevolutionary processes. We found that garlic mustard is expanding in both the forest understory and the forest edge, with similar rates of population increase in these contrasting microhabitats despite higher *in situ* densities and reproductive output at the forest edge. While high rates of adult survival contribute to expansion in forest and edge microhabitats, expansion into intermediate microhabitats may be slowed by conditions that affect population growth via early life stages. Moreover, adaptive plasticity, maternal effects, and genetic adaptation do not appear to play a role in performance across microhabitats. Rather, a complex matrix of micro-environmental conditions may impede forest incursion in these populations, making management a higher priority in edge microhabitats. To fully understand the potential for populations to establish in new locations, critical features of this species' seed dispersal still need to be explored (e.g., Loebach and Anderson, 2018), especially as they relate to dispersal and gene flow within versus across microhabitat types. This would improve our ability to assess populations' potential for local adaptation to different microhabitats, which is necessary to ultimately predict the spread of this invasive species across heterogeneous landscapes. Most interestingly, the degree to which transitional microhabitats differ in quality from adjacent microhabitats could provide valuable information on the conditions in which habitat fragmentation might affect rates of invasion.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**APPENDIX S1.** Summary of transition elasticities across the three growth microhabitat types.

**APPENDIX S2.** Effect of microhabitat on seedling and adult densities, and reproductive biomass of garlic mustard, as observed in natural populations surveyed in the three growth microhabitats across all sites.

**APPENDIX S3.** Light variation (PAR and canopy openness) across the three progeny growth microhabitats.

**APPENDIX S4.** Volumetric soil moisture and soil temperature (°C) in the three growth microhabitats for years 1 and 2.

**APPENDIX S5.** Mean soil temperature (°C) from 810 measurements over time in the second year of the study, averaged within each growth microhabitat.

**APPENDIX S6.** Least-square mean values (± SE) for traits across progeny microhabitats (a) and maternal habitats (b) when those effects were significant predictors of trait variation.

**APPENDIX S7.** Results of multiple mixed-effects regression testing for variation in direct selection ($\beta$) on phenotypic traits depending on maternal and progeny microhabitat type.

**APPENDIX S8.** Pairwise Pearson correlations ($r$) among standardized phenotypic traits, shown separately within each progeny growth microhabitat: (a) edge, (b) intermediate, and (c) forest.

**APPENDIX S9.** Estimates of total selection ($S$) and results of linear mixed models to test for variation in total selection on phenotypic traits depending on maternal and growth microhabitat type.

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