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TRAIT VARIATION AND LONG-TERM POPULATION DYANMICS OF THE INVASIVE *ALLIARIA PETIOLATA* (GARLIC MUSTARD) ACROSS THREE MICROHABITATS IN ITS INVADED RANGE

A Thesis Presented

by

LAURA M. S. HANCOCK

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

February 2021

Organismic and Evolutionary Biology

TRAIT VARIATION AND LONG-TERM POPULATION DYANMICS OF THE INVASIVE *ALLIARIA PETIOLATA* (GARLIC MUSTARD) ACROSS THREE MICROHABITATS IN ITS INVADED RANGE

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ABSTRACT

TRAIT VARIATION AND LONG-TERM POPULATION DYANMICS OF THE INVASIVE *ALLIARIA PETIOLATA* (GARLIC MUSTARD) ACROSS THREE MICROHABITATS IN ITS INVADED RANGE

FEBRUARY 2021

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Long-term population dynamics across heterogeneous environments can be a major factor in determining species' ability to expand their ranges and persist in novel environments. Whether and how the relative performance of populations in different microsites over time impacts invasion into new microsites is poorly understood. Though largely restricted to disturbed semi-shaded microhabitats in its home range, the invasive herb *Alliaria petiolata* (garlic mustard) successfully invades intact forest understories – a novel microhabitat – in its introduced range, where it is known to impact above and below ground community composition. To test the hypothesis that source-sink metapopulation dynamics may be promoting *A. petiolata*'s incursion into the forest understory, I utilized two multi-season field surveys – approximately a decade apart – to evaluate trait variation, biomass allocation, and long-term population demographics of *A. petiolata* growing at the forest edge, within the intact forest understory, and in the intermediate transition zone between the two. My results show that adult plants in the edge were taller and branchier, produced more fruits, and had higher total and reproductive biomass than plants in the intermediate and forest microhabitats. Over time,

seedling density remained highest in the edge microhabitat compared to the forest and intermediate microhabitats, which had similar densities. Reproductive adult densities were similar among all microhabitats at the beginning of the study, but a decade later, all microhabitats exhibited a decline in the number of adult plants they supported. Populations in the intermediate microhabitat displayed the steepest decline in reproductive adults between sampling periods but still supported more adult plants than the forest microhabitat. Populations in all microhabitats were predicted to grow ($\lambda>1$) at the onset of the study. A decade later, declines in population size were only predicted in the forest understory ($\lambda<1$), with the edge and intermediate populations still growing ($\lambda>1$). Since edge and intermediate patches had higher densities of adult plants which produced the most fruit and had larger reproductive biomass, it appears that the edge populations, and possibly the intermediate populations, have sustained the low-density forest populations through source-sink dynamics at my study sites.

Keywords: Alliaria petiolata; demography; forest; invasion; population dynamics; microhabitat; range expansion; source-sink dynamics

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CHAPTER 1

TRAIT VARIATION AND LONG-TERM POPULATION DYANMICS OF THE INVASIVE *ALLIARIA PETIOLATA* (GARLIC MUSTARD) ACROSS THREE MICROHABITATS IN ITS INVADED RANGE

1.1 Introduction

Understanding changes in the dynamic connections between the core and marginal habitats of a species' range, as well as between habitats of differing suitability over time at the local scale is critical to predicting establishment and population growth in new habitat types (Holt and Barfield 2011; Kawecki 2008). Large, high-quality habitats can support source populations which produce high propagule numbers that then disperse into adjacent lower quality environments (Hodgson et al. 2011). Thus, these larger areas of high-quality habitat can be key determinants of whether species can shift and expand their geographic ranges outside of core habitat (Hodgson et al. 2011). Small-scale environmental and ecological variability is also a critical component of the rates and patterns of species' range expansion (Baack et al. 2006; Bell and Lechowicz 1991; Bennie et al. 2013; Stratton 1994).

Temporal patterns of source-sink dynamics, metapopulation structure, and dispersal of propagules from patches of varying qualities are important, but relatively unstudied, topics in relation to range expansion of invasive species (Koehncke et al. 2013; Thomson 2007; Wallace and Prather 2013). Invasive species tend to establish at sites of disturbance, such as roadsides, where soil is disturbed and there is high anthropogenic activity (Burke and Grime 1996; Christen and Matlack 2006; Mortenson et al. 2009). However, geographic expansion outside of the core range of a species, such as sites of disturbance for invasive species, can lead to establishment within novel, peripheral habitats and possibly larger-scale range expansion over time (Kirkpatrick and Barton

1997). Improved understanding of how species-specific population dynamics affect range expansion into novel habitat types will have important implications for understanding future range shifts and developing the most effective long-term strategies for the management of invasive species (Biswas and Wagner 2015; Merow et al. 2017).

Alliaria petiolata (garlic mustard (Bieb.) Cavara & Grande) is a biennial Eurasian forb that is currently invading both forest edge and intact forest understory microhabitats across North America. In its native range, *A. petiolata* usually occupies disturbed semi-shaded forest edge microhabitats (Grime et al. 1988). In North America, *A. petiolata* readily invades disturbed areas with high to low shade conditions (Cavers et al. 1979) and has been increasingly invading intact woodland ecosystems – a novel microhabitat for this species (Nuzzo 1999, 2000). What determines whether and how forest understory colonization is successful for *A. petiolata* is not well understood (Rodgers et al. 2008; Stinson and Seidler 2014), and few other studies have captured more than a short snapshot of the invasion process for this species.

Given that higher-quality wooded understories have different environmental conditions than those at forest edges where *A. petiolata* originated, how do temporal patterns of microhabitat patch dynamics influence this species' invasion into and persistence in a novel microhabitat type? My study examines the role of trait variation and long-term population dynamics in relation to expansion into novel microhabitats, and more broadly, the potential for species to establish in novel microhabitat types of varying quality. Long-term monitoring of invasions is rare, but can provide vital insight into the invasion process, impacts on ecosystem processes, and community structure (Blossey 1999). To my knowledge, no other studies have investigated long-term changes in closely

associated populations of *A. petiolata* across multiple growth microhabitats: the forest edge, forest understory, and the transition zone between the two. In this study, I investigate: 1) if growth microhabitat type significantly affects reproductive capacity, growth, and biomass allocation in *A. petiolata*, 2) if there are demographic differences among populations of *A. petiolata* growing in three distinct microhabitat types over a decadal time scale, and 3) which life-stage transitions are most important for sustained population growth within each microhabitat. I hypothesized that varying environmental conditions, namely light availability, across the three microhabitat types contribute to variable plant traits and patch dynamics that influence population growth rates and stability over time (Smith and Reynolds 2014; Stinson and Seidler 2014). Specifically, I predicted that population densities, biomass, and reproductive capacity of *A. petiolata* would be highest in the disturbed, semi-shaded edge sites but depressed in the intact forest understories.

1.2 Materials and Methods

1.2.1 *Study species*

Alliaria petiolata was first documented in the United States on Long Island in 1868 (Nuzzo 2000), though this species has likely been introduced to the U.S. multiple times (Durka et al. 2005). Since its initial introduction in the 19th century, *A. petiolata* has become established across North America with large populations in the Northeast, Midwest, and Northwest United States, and sporadic populations established elsewhere (Nuzzo 2000). A member of the Brassicaceae, *A. petiolata* is non-mycorrhizal and produces multiple phytotoxic secondary compounds (Renwick 2002) that have been shown to disrupt North American plant-arbuscular mycorrhizal fungi (AMF) associations

even in low concentrations (Callaway et al. 2008; Cantor et al. 2011). Along with producing novel phytotoxic chemicals (Barto et al. 2010), *A. petiolata* is highly invasive due to such attributes as early spring phenology (Engelhardt and Anderson 2011), high propagule pressure (Eschtruth and Battles 2009), and release from herbivores in its invaded range (Rodgers et al. 2008).

Alliaria petiolata has a biennial life-cycle. Seedlings emerge in the spring and then develop into basal rosettes over the first growing season. Basal rosettes overwinter and in the second growing season, adult plants form stalks which support the maturation of reproductive organs (flowers, fruits) before subsequently dying. Flowers are primarily self-pollinated, though cross pollination has been documented (Cruden et al. 1996; Durka et al 2005). Seed production per plant can vary due to factors such as environmental conditions and population density, but individual plants have been shown to produce up to approximately 8000 seeds under robust conditions (Nuzzo 2000). The majority of seeds (95%) disperse only short distances (1.14 m or less) from the maternal plant, though it is possible for seeds to be dispersed longer distances through epizoochory (Loebach and Anderson 2018), anthropogenic activities, flooding, or other mechanisms (Nuzzo 2000).

1.2.2 *Study site and experimental design*

To investigate *A. petiolata* growth, performance, reproduction, and long-term population dynamics across different microhabitats, I conducted a long-term observational study at three locations within the Harvard Forest Long-Term Ecological Research (LTER) site in Petersham, Massachusetts, USA (42.5°N Latitude; 72°W Longitude). Along with my advisor, I established three sets of observational plots (n=3)

and conducted two multi-year population samplings (2003-2006 and 2015-2016) to monitor demographic and individual plant performance of *A. petiolata* populations which have been present at the Harvard Forest since at least 1979 (Jenkins et al. 2008). The forest canopy at this site is dominated by species such as red maple (*Acer rubrum*), red oak (*Quercus rubra*), birch (*Betula sp.*), American beech (*Fagus grandifolia*), and white pine (*Pinus strobus*) (Jenkins et al. 2008). Mean annual air temperature at the Harvard Forest is 7°C, with temperatures ranging between 32°C in the summer to -25°C in the winter. Total annual mean precipitation, including the water equivalent of snow, is 110 cm (Contosta et al. 2011).

I established my study populations at three replicate sites located within the continuous forest at the Harvard Forest. Each of the three sites contained three adjacent microhabitat types where *A. petiolata* was growing: disturbed forest edge microhabitat near trails, roadsides, and houses (hereafter: edge), the understory of a mature mixed-deciduous forest (hereafter: forest understory), and the transition zone between the forest edge and understory microhabitat which had signs of semi-recent disturbance (hereafter: intermediate). Within a replicate site, the size of each microhabitat patch varied by the area of *A. petiolata* invasion. If the area of *A. petiolata* invasion exceeded 20 x 20 m in each microhabitat patch a 20 x 20 m area was marked, and I established five equally spaced transects across the entire length of the patch for sampling. In 2004, we used a random number generator to determine placement of two 1-m^2 quadrats on each transect for a total of ten quadrats per microhabitat patch per site (N=30 per microhabitat). In 2015, I re-established the transects and quadrats at the same sites using the same methods. I also established an additional site in 2015 only containing forest edge and

forest understory microhabitat types, with 3 transects (six quadrats) in each microhabitat. Microhabitat patches at a single site were within approximately 55 m from each other and all sites were within approximately 275 m of each other.

1.2.3 *Microhabitat environmental variation*

To characterize environmental variation within the microhabitats, I compiled or periodically collected data (described below) on light availability, canopy cover, soil moisture, soil temperature, and nutrient availability between June 2003 and July 2016. Consistent methods were used for each respective type of data throughout the study period.

Light availability and canopy cover – I compiled photosynthetically active radiation (PAR) data collected on two days in June 2003, once in June 2004, and once in July 2004 at a height of 100 cm above the ground in the middle of each quadrat using a LI-COR 185A photometer (LI-COR Inc., Lincoln, Nebraska, USA). We captured hemispherical canopy cover photos on a single day in July 2005 and two days in July 2016 after canopy leaf out using a Nikon CoolPix 5000 camera with a Nikon FC-E8 fisheye lens converter (Nikon, Inc., Melville, New York, USA). I determined percent canopy openness from the hemispherical canopy photos using the "Sky" package (Bachelot 2016) in R version 3.4.1 (R Core Team 2017).

Soil moisture, temperature, and nutrient availability – We measured soil moisture on single days in each month of the following years: 2003 (June), 2004 (June and July), 2005 (April, May, and June), 2015 (September), and 2016 (July) using a ThetaProbe ML2x Soil Moisture Sensor (Delta-T Devices Ltd, Houston, Texas, USA) and soil temperature on single days in each month of the following years: 2003 (June), 2004

(July), 2005 (April and May), 2015 (September), and 2016 (May and July) using a Weber Probe instant-read digital thermometer (Weber-Stephen Products LLC, Palatine, Illinois, USA). We recorded soil temperature and soil moisture at a point nearest to the middle of every quadrat at all sites. Temperature measurements were taken at a depth of approximately 3.5 cm.

In order to characterize possible differences in nutrient availability between microhabitats, I collected two 10 cm deep soil cores at opposite ends of each of the microhabitat patches in July 2016. I dried the soil cores in a laboratory drying oven at 105 °C for a minimum of 72 hours. I then sieved a random subsample of each replicate to remove large debris and ground it to a fine powder using a Spex Sample Prep Grinder (SPEX SamplePrep, New Jersey, USA). I analyzed the subsamples for percent soil carbon (C), percent soil nitrogen (N), and soil C:N ratio with an Elemental Analyzer vario Micro Cube (Elementar Analysensysteme GmbH, Germany).

1.2.4 *Individual plant trait measurements*

I randomly selected five adult plants closest to each transect in every microhabitat patch for individual plant performance data. If there were fewer than twenty-five plants within a microhabitat patch (e.g. 5 plants × 5 transects), all identified adult plants within the microhabitat patch were included in data collection. I recorded the following traits in 2003, 2004, 2005, and 2016: 1) height to tip of plant from root collar, 2) number of branches per plant, and 3) number of siliques (fruits) per plant. Functional and fitness trait data were recorded for each plant when biomass was harvested at the point of reproductive maturity (between late June and late August) prior to fruit dehiscence and

senescence. I then divided individuals into root, shoot, and reproductive organs, dried tissues at 60 °C for 10 days in a drying oven and measured dry biomass for each plant.

I estimated the number of seeds produced per plant for the 2004 and 2016 seasons by obtaining the total weight of all seeds produced per plant and then dividing by the average weight of a single seed for that plant. Average seed weight was calculated by weighing 10 randomly selected seeds and dividing by 10. If a plant produced fewer than ten seeds, I counted the exact number of seeds produced.

1.2.5 *Population demography surveys*

In each quadrat, I recorded the number of individuals in each life stage: seedlings, first-year rosettes, second-year rosettes, and reproductive adults. Surveys occurred twice per year, once during the spring (April to early May) and once in the summer (late June to late July) of every study year. The specific survey periods varied from year to year because of differences in phenology timing. Spring surveys occurred at the approximate peak of seedling germination in the spring and summer surveys occurred before any considerable adult plant senescence. Sampling period 1 (hereafter: sampling 1) was in 2003, 2004, and 2005 and sampling period 2 (hereafter: sampling 2) was in 2015 and 2016.

1.2.6 *Statistical analyses*

For all responses, I constructed linear or generalized linear mixed models using the 'lme4' package in R version 3.4.1 (R Core Team 2017). All models included microhabitat as a fixed factor and replicate site as a random factor. For all environmental and plant performance (trait and biomass) data that was collected in multiple years, year was also included in the model as a random factor. For demographic data, sampling

period and the interaction between microhabitat and sampling period were also included in the models to test for an effect of time on invasion and any differential effects between microhabitats. For all environmental responses, Gaussian error structures were used. In Table 1.1, I report all other model error structures and responses. All models with a Gamma error structure used a log link. When I detected significant fixed effects from Analysis of Variance or Likelihood Ratio Tests (Whitlock and Schluter 2014), I used Tukey's HSD post hoc test to determine pairwise comparisons between categories using the 'glht' function in R.

I checked for outliers in the models using Cook's Distance plots. Two models (total biomass and elasticity of growth life stages) each had a single extreme data point (Cook's distance > 1), and thus those data points were removed prior to final analysis. For total reproductive biomass and the ratio of reproductive biomass to vegetative biomass (non-reproductive root and shoot tissues), 11 of 784 observations were zero. Since Gamma error structures cannot include zeros, a miniscule number equal to one one-hundredth of the next smallest observation for reproductive biomass (.0005) and the ratio of reproductive to vegetative biomass (.019443) was added to the zero observations.

I determined the population growth rates (lambda; λ) for each of the microhabitat patches using life stage structured population matrix models following Caswell (2001). I constructed projection matrices for each of the microhabitat patches for the 2003-2004, 2004-2005, and 2015-2016 growing seasons in R version 3.2.3 (R Core Team 2015). The matrices consisted of transitions between the following life stages: seed to seedling, seedling to second-year rosette, second-year rosette to fruiting adult, and fruiting adult to seed (Figure 1.1). I also included a seed to seed transition (i.e. ungerminated seeds that

remained in the seed bank). Germination rates and seed to seed transitions rates were calculated from a previous germination experiment conducted at the same study sites at the Harvard Forest (Stinson et al. 2019). We were not able to collect fecundity data in 2005. In order to estimate seed production for plants growing during the 2004-05 cycle, I averaged the mean number of seeds produced per plant in each microhabitat using 2004 and 2016 data. From 29 matrices (3 or 4 sites × 3 microhabitats × 3 life cycles), I obtained values for λ, transition sensitivities, and transition elasticities using the 'popbio' package (Stubben and Milligan 2007) in R version 3.2.3 (R Core Team 2015). Due to the linear life-stage transitions of *A. petiolata*, the elasticity values that I calculated represent two "loops". The first loop consists of growth stage transitions from seed to seedling; seedling to rosette; and rosette to reproductive adult. The second loop consists of a single transition from seed back into the seed bank (e.g. seed to seed). I prioritize the sensitivity results in this thesis (e.g., Kalisz et al. 2014, Stinson et al. 2019), but also report the elasticity values for comparison.

1.3 Results

1.3.1 *Environmental variation across microhabitats*

The growth microhabitats differed in light availability, canopy cover, soil moisture, and soil temperature ($P<0.05$; Tables 1.2, 1.3). Soil C, N, and C:N were not affected by microhabitat ($P>0.05$; Tables 1.2, 1.3). As expected, the edge microhabitats had higher photosynthetically active radiation (PAR) and canopy openness than both the intermediate and forest microhabitats, which were statistically similar to each other. In the spring, soil in the intermediate and edge microhabitats was warmest and soil in the forest was coolest. During the summer, soil was warmest in the edge and coolest in the

forest, with all microhabitats different from each other (Table 1.3; Figure 1.2). Unlike other environmental characteristics, soil moisture did not show any directional gradient from forest edge to forest interior. During both the spring and summer, the intermediate microhabitat was the wettest and the edge microhabitat was the driest. Later in the growing season, soil moisture in the forest was similar to both the edge and intermediate soil moisture, though the edge soil was significantly drier compared to the intermediate soil (Tables 1.2, 1.3; Figure 1.2).

1.3.2 *Trait and biomass variation across microhabitats*

Adult *A. petiolata* plants differed significantly in their height, number of branches, number of fruits, total biomass, reproductive biomass, and reproductive:vegetative tissue ratio across the microhabitats ($P<0.05$; Table 1.4; Figures 1.3, 1.4). Surprisingly, the only non-significant difference in biomass allocation was for root:shoot ratio, which was similar for plants growing in all three microhabitats ($P>0.05$; Table 1.4). Plants growing in the edge microhabitat were taller, produced more branches and fruits, and had more total and reproductive biomass compared to plants in the intermediate and forest microhabitats (Figures 1.3, 1.4). Plants growing in the edge and intermediate microhabitats had similar reproductive:vegetative tissue ratios, which were significantly higher than for plants in the forest (Figure 1.3). Plants growing in the forest produced fewer branches and fruits and had less total and reproductive biomass compared to both the edge and intermediate plants (Figures 1.3, 1.4). However, the intermediate and forest microhabitats supported plants of similar height (Figure 1.4). Plants growing in the edge produced more and heavier seeds than plants growing in the intermediate or forest microhabitats (Table 1.5; Figure 1.5). While there was no interactive effect of year and

microhabitat (P>0.05), there was a significant effect of year on both seed weight and number, with all microhabitats showing a decline in both seed number and seed weight between 2004 and 2016 (Table 1.5; Figure 1.5).

1.3.3 *Long-term population dynamics across microhabitats*

I constructed demographic models to assess variation in the density of three life stages, population growth, and the contribution of each life stage to population growth, depending on microhabitat, sampling period, and the growth microhabitat × sampling period interaction.

Microhabitat, sampling period, and their interaction affected all life stage densities and λ ($P_{\text{microhabitat}}$<0.05, $P_{\text{sampling period}}$<0.05, and $P_{\text{microhabitat × sampling period}}$<0.05; Tables 1.5, 1.6). The sensitivity of two life stage transitions (rosette to adult and adult to seed transitions) was affected by microhabitat ($P_{\text{microhabitat}}$<0.05; Table 1.6). Additionally, the adult to seed transition sensitivity was also affected by sampling period (Table 1.6). Sampling period only significantly affected transition elasticities during growth stages, i.e. the second "loop" (Table 1.6). None of the transition sensitivities or elasticities had a microhabitat × sampling period interaction (Table 1.6).

The edge consistently supported higher densities (plants per m^2) of seedlings and 1st year rosettes (Figure 1.6). Early life stage densities (seedlings and 1st year rosettes) have remained stable over time within the edge and intermediates habitats, while the forest populations have shown declines (Figure 1.6). Fruiting adult densities (plants per m^2) have declined in all microhabitats between the two sampling periods, with the forest microhabitat consistently supporting the lowest number adult plants (Figure 1.6).

Population growth was consistent across time and slightly above 1 (i.e. stable individual rate of replacement) within the intermediate microhabitat (Figure 1.7). The population growth rates within the edge and forest microhabitats declined over time, with the forest populations sharply declining to a population growth rate below 1 in sampling period 2 (Figure 1.7). There was also a significant effect of microhabitat on the contributions of different life stages to λ (Tables 1.6, 1.7). Microhabitat significantly affected the contribution of the rosette to adult transition and the adult to seed transition to λ. Edge populations showed higher sensitivity of λ to the rosette to adult transition than the intermediate and forest populations, while the forest populations had the strongest sensitivity to reproduction (adult to seed). Within each growth microhabitat, the importance of each transition to population growth was consistent, with the germinant to rosette transition sensitivity being highest for all three microhabitats. While there was no significant effect of microhabitat on transition elasticity, populations in the intermediate microhabitat had higher elasticity for the seed to seed transition, while the edge and forest populations had higher elasticity for the growth stage transitions (Table 1.7).

1.4 Discussion

I used *in situ* monitoring data of *A. petiolata* in 2003-06 and again a decade later in 2015-16 across three growth microhabitats to investigate plant performance and the long-term population dynamics contributing to this species' invasion into the intact forest understory in its introduced range. Since *A. petiolata* shows suppressed growth and reproductive output in reduced light environments and little evidence for genetic divergence across habitats (Meekins and McCarthy 2000; Meekins and McCarthy 2001; Myers et al. 2005; Stinson and Seidler 2014), I hypothesized that plants from the edge

microhabitats would produce the most robust plants (tallest, branchiest, most fruits and seeds) in the highest densities and that this pattern would persist over time. I found that plants performed best and had the most reproductive output in the highest light edge microhabitats and plants in the forest understory performed the worst. Further, *A. petiolata* demographic performance (density and rate of replacement) was also best in the edge microhabitat and worst in the forest understory– and this trend was consistent over a decadal time scale. Together, this data supports the hypothesis that populations growing at the forest edge may be supporting forest understory invasion through source-sink metapopulation dynamics.

Over the past several decades, *A. petiolata*'s range has expanded drastically not only in disturbed habitats, but also within intact, low disturbance woodland ecosystems (Nuzzo 1999, 2000) and is one of only a few successful invaders of forest understories across North America (Nuzzo 2000). However, the mechanisms behind the success of *A. petiolata*'s invasion into North American woodland understories is not clear (Stinson and Seidler 2014). Because *A. petiolata* grows within multiple microhabitats in its invaded range, it is important to understand how population dynamics contribute to invasion and microhabitat expansion of this species over time (e.g., Thomson 2007; Wallace and Prather 2013). At the study location, *A. petiolata* has been present in various microhabitats since at least the late 1970s, but is most commonly found in anthropogenically disturbed areas along roads, trails, and houses at the edge of the forest (Jenkins et al. 2008; Stinson et al. 2019). The forest populations in my study showed the lowest plant and population performance, confirming my prediction that forest understory is the lowest quality microhabitat. While intermediate microhabitats supported slower

plant growth and rates of replacement compared to the edge microhabitats, the intermediate sites showed consistent and sufficient reproductive capacity and population growth, indicating that these populations were not self-limiting (Figures 1.3-1.7). The edge populations showed significantly higher and better provisioned reproductive output and may be sourcing propagules into the low reproductive capacity forests where there was high sensitivity to perturbations in adult fecundity (Table 1.7; Figures 1.3-1.5, 1.7). Since high propagule pressure can be a driving factor in the ability of exotic species to invade novel habitats (Colautti et al. 2006; Warren et al. 2012), my results indicate that edge sites may be important long-term drivers of forest invasion.

Despite spatially close proximity to one another, I found that environmental characteristics, *A. petiolata* population attributes, and individual plant traits within each of the microhabitats do not strictly follow a directional gradient from forest edge to understory. Surprisingly, the three microhabitats did not represent a clear light, soil temperature, and soil moisture gradient, but rather a complex suite of environmental variables throughout the season (Table 1.3; Figure 1.1), which may inhibit genetic divergence across microhabitats. Consistent with my hypothesis, the findings supported that the edge microhabitat maintained the most robust plants and population densities and forest populations were the most suppressed. Elsewhere, light availability has been shown to be one of the most important factors in the growth and reproduction of *A. petiolata*, with plants having suppressed growth and reproductive output in reduced light environments (Meekins and McCarthy 2000; Meekins and McCarthy 2001; Myers et al. 2005; Stinson and Seidler 2014). However, light availability alone did not appear to be the most significant environmental factor driving the results in the present study (Tables

1.3-1.5; Figures 1.2-1.7). Periodic disturbance within the intermediate microhabitats may explain in part why the intermediate sites are outperforming the forest sites (Figures 1.3-1.7), even though they have similar low-light conditions (Table 1.3; Eschtruth and Battles 2009; Nuzzo 1999). Another possibility is that leaf litter accumulation or composition in the forest understory could be restricting seedling recruitment and reducing population density, impeding invasion (Bartuszevige et al. 2007, Taylor et al. 2015). Moist soils, however, may be signs of frequent seed washout leading to early life stage limitations on population size (Table 1.7; Figures 1.2, 1.6). Thus, moist soil in conjunction with warm soil during the spring in the intermediate sites (Table 1.3; Figure 1.2) may also lead to increased risk of disease compared to the edge sites (Ciola and Cipollini 2011; Cipollini and Enright 2009), preventing intermediate populations from edge population equivalent performance.

As expected, biomass was highest for plants in the edge microhabitat, which had the most available light (Table 1.3; Figures 1.3, 1.5; Stinson and Seidler 2014). Unexpectedly, root:shoot ratios did not differ among the microhabitats, and reproductive:vegetative ratios were similar for plants in the edge and intermediate microhabitats but were significantly lower for forest plants (Table 1.4; Figure 1.3). Significantly cooler soil temperatures in the spring and summer in addition to reduced light in the forest understory (Table 1.3), could create inhospitable growth conditions. Another possibility is that the environmental conditions cause a delay in phenology, ultimately reducing *A. petiolata*'s phenological niche separation with native species, which could reduce overall reproductive output and growth (Engelhardt and Anderson 2011; Meekins and McCarthy 2000). Meekins and McCarthy (2000) showed that nutrient

addition to areas of low-density invasion increased population growth; however since the sites did not differ in nutrient availability (C, N, C:N), I speculate that factors such as nutrient composition are affected by larger spatial-scale processes and do not play a significant role in *A. petiolata* invasion into the forest understory on this smaller spatial scale (Table 1.2).

Long-term monitoring of invasive species across heterogeneous growth microhabitats is logistically difficult and rarely accomplished in ecological studies, but characterizing invasion over relevant spatial and temporal contexts is vital for understanding invasion processes, impacts on native ecosystems, population dynamics, and best management strategies (Blossey 1999; Evans et al. 2012; Evans et al. 2012; Menges 2000). Structured life stages and density dependence on short-term time scales likely contribute to complex factors in *A. petiolata* populations which could confound long-term dynamics and management, though this effect may differ based on habitat quality (Evans et al. 2016; Pardini et al. 2009; Smith et al. 2003). In my study, early life stage (seedling, rosette) densities were relatively stable over decadal time-scales in intermediate and edge microhabitats, but declined in the forest microhabitat. I observed a decline in the number of mature reproductive adults across all microhabitat types, but populations were not impacted equally, such that densities were more depressed in the intermediate microhabitat (Table 1.5; Figure 1.6). In addition to a decline in the number of reproductive plants, both the number of seeds produced and provisioning to individual seeds declined over time across all microhabitats (Table 1.5; Figure 1.5). This supports the hypothesis that *A. petiolata* invasions may become less aggressive over time due to

evolutionary constraints (Lankau et al. 2009), but I found that overall long-term plant performance varied considerably by microhabitat.

At the beginning of the study all three microhabitats supported populations which were self-sustaining and indicated future growth. At the end of the study, two of the growth microhabitats had populations (edge and intermediate) which were still predicted to grow ($\lambda>1$). However, both the edge and forest populations showed declines in λ at the end of the study, with the forest populations predicted to decline over time ($\lambda<1$). Since the edge and forest λ declines closely track, it is likely that the forest populations depend heavily on propagules from the edge. Specifically, *A. petiolata* populations have been present at the Harvard Forest for several decades, so I did not expect - nor did I see - low densities and high λ at the beginning of the study with reversed patterns at the end of the study, as would have been expected under newly founded populations (Evans et al. 2016). It is possible that the decrease in λ between sampling periods within the edge microhabitat may be due to harsh, transient environmental conditions such as low rainfall in 2016, which were asymmetrically impacting the plants in the highest light microhabitat (Table 1.3; Figure 1.7), especially since I was not able to calculate multiple years of life-cycle transitions during sampling 2.

Overall, my results show that population performances have remained fairly stable, with significant decreases only in the forest populations. While I do not report yearly variation or dynamics here, my results do not suggest future population declines of mature *A. petiolata* populations on a decadal time scale within 2 of the 3 microhabitats (Figure 7; Nuzzo 1999). In fact, λ may be underestimated due to the contributions of ungerminated seeds in the seed bank to local population growth rates. Although the seeds

in the seed bank were not accounted for in my population growth rate matrices, the majority of ungerminated *A. petiolata* seeds (>80%) in the seed bank can remain viable for several years (Redwood et al. 2018) and are an important factor in *A. petiolata*'s ability to invade and persist in an area (Eschtruth and Battles 2009). Since this study was conducted *in situ* without manipulation, I did not control propagule spread between microhabitats, which could impact λ. Further, since germination rates were only calculated once at the beginning of the study, it is possible that long-term germination dynamics within and among microhabitats could affect population growth.

Unmeasured abiotic factors may also have affected *A. petiolata* population dynamics. For example, reduced precipitation and winter snowfall trends documented in New England in the last half of the 1900s (Huntington et al. 2004) could be causing overwintering *A. petiolata* rosettes to have increased sun exposure during over-wintering. Increased sun exposure has been shown to cause irradiation damage and increased mortality, thereby reducing adult plant densities (Figure 1.6; Smith and Reynolds 2014). It is also possible that these environmental trends could increase herbivory during the winter and early spring (e.g., Yates and Murphy 2008), leading to declines in overall plant survival and densities in some microhabitats, but not others.

Biotic factors such as presence of earthworms and/or ungulates were not measured in this study but have been shown to impact *A. petiolata* growth and abundance (e.g. Dávalos et al. 2015; Kalisz et al. 2014; Knight et al. 2009). Whether and how these effects impact *A. petiolata* populations across all microhabitats is unclear and could be a fruitful avenue of research to help determine underlying abiotic drivers of invasion across heterogeneous conditions. Further, the population dynamics, growth, and ability for *A.*

petiolata to invade forests is likely dependent on other variables which occur at different spatial scales and/or are regionally dependent (Burls and McClaugherty 2008; Urbanowicz et al. 2018). Land use history, disturbance frequency, and physical landscape characteristics, such as elevation, would likely affect invasion success and population dynamics within and across regions.

While I did not explicitly ask questions related to management strategies, understanding population dynamics related to density-dependence and population growth can contribute to successful mitigation of *A. petiolata* (Pardini et al. 2009; Evans et al. 2016). Designing effective management strategies is especially important since *A. petiolata* disrupts vital associations between native woodland species and AMF thereby decreasing native species' growth and fitness (Callaway et al. 2008; Cantor et al. 2011; Stinson et al. 2006). Without active and tailored management strategies, *A. petiolata* can alter above and below-ground biodiversity and ecosystem function (Anthony et al. 2017, Meekins and McCarthy 1999, Stinson et al. 2006; Stinson et al. 2007), likely for years (Lankau 2011; Lankau et al. 2014). However, if populations show signs of long-term decline or are not self-sustaining, eradication may not be the best strategy in light of limited resources available to most land managers (Lankau et al. 2009). In my study, plants were densest and had the highest reproductive capacity in the edge and intermediate populations (Figures 1.3-1.6) and two of the three microhabitats had populations which did not show signs of future self-limitation (Figure 1.7). Mitigation and eradication efforts focused on the edge and intermediate populations would therefore likely lead to reduced propagule pressure on not only those populations, but existing and new forest populations, since the edge and possibly intermediate populations may be

acting as propagule sources for incursion into the forest understory (Figures 1.5, 1.7). In addition, focusing mitigation efforts on the edge populations may have the most impact on reducing defensive phytochemical impacts on native biota (Smith 2015). My results have important broad implications for management, but future studies directly assessing the multi-year response of *A. petiolata* to mitigation would provide more clarity on the direct impacts of this species source-sink dynamics to management efforts.

1.5 Conclusion

My results show that edge, forest, and intermediate microhabitats support plants with differential trait expression, biomass allocation, and population demographics. Over a decadal time scale, populations in the forest edge and intermediate microhabitats did not show signs of future population declines ($\lambda>1$). Population growth rate declines in the forest populations could indicate environmental conditions that are not suitable for supporting self-sustaining populations, though light availability alone did not appear be the most important environmental indicator of robust populations. The edge and intermediate microhabitats likely sustain source populations that provide propagules into the forest microhabitat, since the edge and intermediate populations consistently showed population growth ($\lambda>1$) across time and had plants with higher total reproductive biomass and fruit number. My results suggest that management strategies in areas where *A. petiolata* is growing in heterogeneous environments should be carefully tailored to mitigate understory incursion, perhaps through focused eradications of source populations in edge microhabitat.

Table 1.1. Model error distributions for *A. petiolata* functional traits, biomass allocation, and demography responses.

Response Category	Response	Model Error Structure
Functional traits	Plant height (cm)	Gaussian
	Siliques per plant	Negative binomial
	Number of branches per plant	Poisson
	Number of seeds per plant	Negative binomial
	Individual seed weight (g)	Gaussian
Biomass allocation	Total plant biomass (g)	Gamma
	Total reproductive biomass (g)	Gamma
	Root:shoot ratio	Gamma
	Reproductive:vegetative ratio	Gamma
Demography	Density of seedlings per m^2	Negative binomial
	Density of 1^{st} year rosettes per m^2	Negative binomial
	Density of fruiting adults per m^2	Negative binomial
	Population growth rate (λ)	Gaussian
	Transition sensitivities	Gaussian
	Transition elasticities	Gaussian

Table 1.2. Statistical responses from Analysis of Variance tests for environmental variables across three growth microhabitats. *P* values are bolded when significant ($P<0.05$) and rounded to the third decimal place.

	Effect of microhabitat		
Response	*F*	df (num, den)	*P*
Soil carbon (%)	0.471	2, 16.381	0.633
Soil nitrogen (%)	1.044	2, 16.275	0.374
Soil C:N ratio	1.307	2, 19	0.294
Soil temperature (°C; spring)	27.446	2, 1457.8	**<0.001**
Soil temperature (°C; summer)	55.815	2, 554.78	**<0.001**
Volumetric soil moisture (spring)	39.71	2,1075	**<0.001**
Volumetric soil moisture (summer)	3.673	2, 1103.1	**0.026**
Light availability (PAR)	94.805	2, 355.96	**<0.001**
Canopy openness (%)	13.208	2, 27.634	**<0.001**

Table 1.3. Environmental variation in the three growth microhabitats. Data were collected in 2016 (soil carbon; soil nitrogen; soil C:N), 2003-05 & 2015-16 (soil temperature), 2003-05 & 2015-16 (soil moisture), 2003-04 (PAR), and 2005 & 2016 (canopy openness). Means and standard error of the mean (SEM) are shown rounded to the second or third decimal place. Within rows, means that do not share the same letter are significantly different, determined by a Tukey HSD post-hoc test ($P < 0.05$).

Environmental variable	**Month(s) data collected**	**N**	**Mean ± SEM**		
			Edge	Intermediate	Forest
Soil carbon (%)	July	8 (edge=6)	7.555 ± 1.848	7.802 ± 0.644	6.856 ± 0.673
Soil nitrogen (%)	July	8 (edge=6)	0.510 ± 0.101	0.510 ± 0.050	0.437 ± 0.046
Soil C:N ratio	July	8 (edge=6)	14.311 ± 0.736	15.560 ± 0.388	15.993 ± 0.934
Soil temperature (°C)	April-May (Spring)	486 (edge=492)	6.57 ± 0.097^{A}	6.80 ± 0.095^{A}	6.08 ± 0.10^{B}
Soil temperature (°C)	June-July, September (Summer)	192 (edge=178)	14.93 ± 0.25^{A}	14.35 ± 0.20^{B}	13.00 ± 0.20^{C}
Volumetric soil moisture	April-May (Spring)	357 (edge=366)	0.190 ± 0.005^{A}	0.296 ± 0.016^{B}	0.256 ± 0.005^{C}
Volumetric soil moisture	June-July, September (Summer)	371 (edge=369)	0.244 ± 0.008^{A}	0.263 ± 0.011^{B}	0.259 ± 0.009^{A,B}
Light availability (PAR)	June-July	120	440.68 ± 48.23^{A}	28.75 ± 5.74^{B}	10.80 ± 3.36^{B}
Canopy openness (%)	July	11 (edge=10)	21.49 ± 2.39^{A}	12.03 ± 0.93^{B}	12.54 ± 0.80^{B}

Table 1.4. Statistical responses from Analysis of Variance or Likelihood Ratio Tests for plant growth and fitness variables across three growth microhabitats. *P* values are bolded when significant ($P<0.05$) and rounded to the third decimal place.

	Effect of microhabitat		
Response	df	χ^2	*P*
Adult biomass	6	462.86	**<0.001**
Reproductive biomass	6	547.88	**<0.001**
Reproductive:vegetative tissue	6	24.8	**<0.001**
Adult root:shoot	6	0.678	0.713
Total number of branches	5	440.64	**<0.001**
Total number of fruits	6	469.14	**<0.001**
	df (num, den)	*F*	*P*
Adult height	2, 793.4	145.36	**<0.001**

Table 1.5. Statistical responses from Analysis of Variance or Likelihood Ratio Tests for population demography and plant reproductive capacity variables across three growth microhabitats. *P* values are bolded when significant ($P<0.05$) and rounded to the third decimal place.

	Microhabitat			**Year/ Sampling Period**			**Microhabitat x Year/ Sampling Period**		
Response	*F*	df (num,den)	*P*	*F*	df (num,den)	*P*	*F*	df (num,den)	*P*
Individual seed weight (g)	10.612	2, 369.88	**<0.001**	102.647	1, 351.02	**<0.001**	1.567	2, 370.83	0.210
	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
Number of seeds per plant	195.89	4	**<0.001**	21.963	3	**<0.001**	3.1673	2	0.205
Seedling density (plants/m^2)	127.4	4	**<0.001**	62.495	3	**<0.001**	11.888	2	**0.003**
First-year rosette density (plants/m^2)	55.798	4	**<0.001**	12.255	3	**0.007**	7.552	2	**0.023**
Fruiting adult density (plants/m^2)	27.676	4	**<0.001**	90.491	3	**<0.001**	13.954	2	**0.001**

Table 1.6. Statistical responses from an Analysis of Variance for demographic variables across three growth microhabitats. *P* values are bolded when significant (*P*<0.05) and rounded to the third decimal place.

	Microhabitat			**Sampling Period**			**Microhabitat x Sampling Period**		
Response	*F*	df (num, den)	*P*	*F*	df (num, den)	*P*	*F*	df (num, den)	*P*
Lambda (λ)	12.145	2,23	**<0.001**	19.728	1, 23	**<0.001**	5.682	2, 23	**0.001**
Sensitivity of λ									
Seed to seed	1.621	2, 18.557	0.224	0.142	1, 18.578	0.711	0.329	2, 18.557	0.724
Seed to germinant	1.101	2, 18.686	0.353	1.156	1, 18.871	0.296	0.270	2,18.686	0.766
Germinant to rosette	0.576	2, 20	0.571	0.077	1, 20	0.785	0.122	2, 20	0.886
Rosette to adult	9.838	2, 20	**0.001**	0.328	1, 20	0.574	0.193	2, 20	0.826
Adult to seed	18.360	2, 20.068	**<0.001**	5.287	1, 20.068	**0.032**	1.568	2, 20.068	0.233
Elasticity of λ									
Seed to seed	1.622	2, 18.557	0.224	0.142	1, 18.578	0.711	0.329	2, 18.557	0.724
Growth stage transitions	2.152	2, 17.373	0.146	4.980	1, 17.491	**0.039**	0.384	2, 17.296	0.687

Table 1.7. Summary of transition sensitivities and elasticities for *A. petiolata* across three growth microhabitats. Means are reported ± standard error of the mean (SEM). Largest sensitivity and elasticity within each microhabitat are italicized. Within rows, means that do not share the same letter are significantly different, determined by a Tukey HSD post-hoc test ($P < 0.05$). All values are rounded to the third decimal place.

Transition	**Microhabitat**		
	Edge	Intermediate	Forest
	Sensitivity		
Seed to seed	0.309 ± 0.007	0.415 ± 0.059	0.318 ± 0.018
Seed to germinant	0.826 ± 0.085	0.752 ± 0.220	0.479 ± 0.063
Germinant to rosette	*6.689 ± 1.836*	*4.891 ± 1.290*	*3.402 ± 1.400*
Rosette to adult	1.202 ± 0.181^{B}	0.453 ± 0.831^{A}	0.490 ± 0.065^{A}
Adult to seed	0.001 ± 0.000^{A}	0.005 ± 0.001^{A}	0.009 ± 0.002^{B}
	Elasticity		
Seed to seed	0.079 ± 0.009	*0.220 ± 0.079*	0.090 ± 0.024
All others	*0.230 ± 0.002*	0.195 ± 0.020	*0.227 ± 0.006*

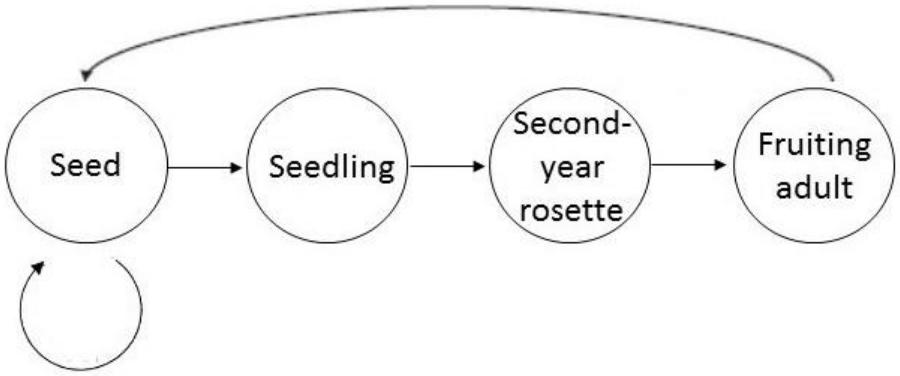

Figure 1.1. Life cycle schematic depicting possible transitions between seed, seedling, second-year rosette, and fruiting adult life stages for an *A. petiolata* individual. Each arrow represents a life stage transition.

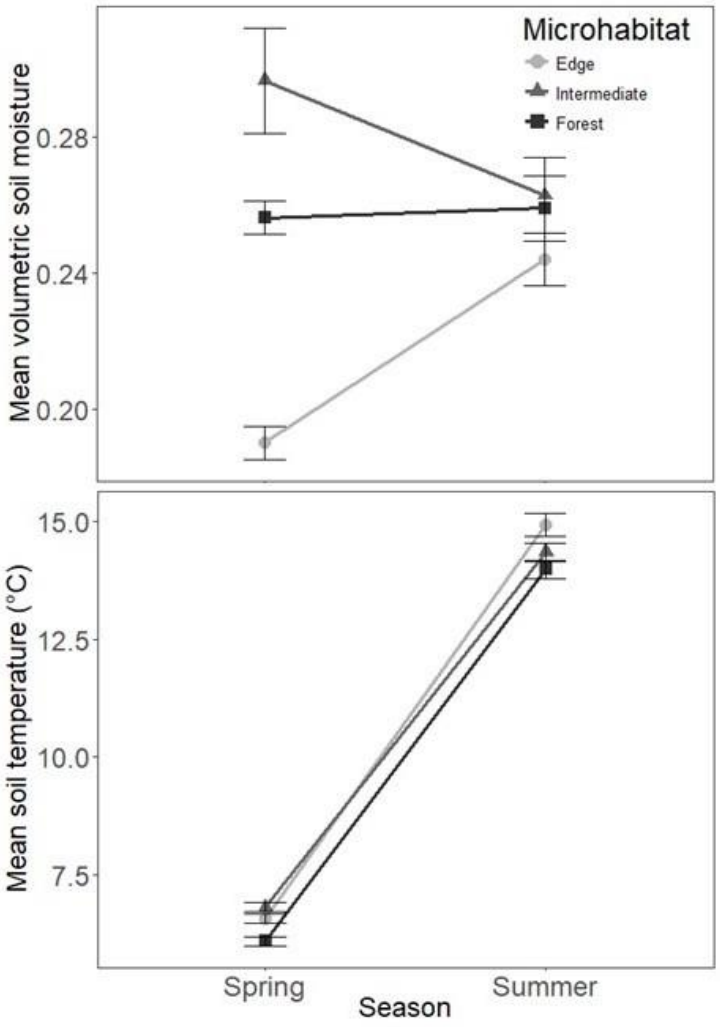

Figure 1.2. Mean soil moisture (% volume; top panel) and soil temperature (°C; bottom panel) in the three growth microhabitats in spring (April-May) of 2005 and summer (June-September) of 2003-05 and 2015-16. Means and standard error of the mean (SEM) are shown for each microhabitat.

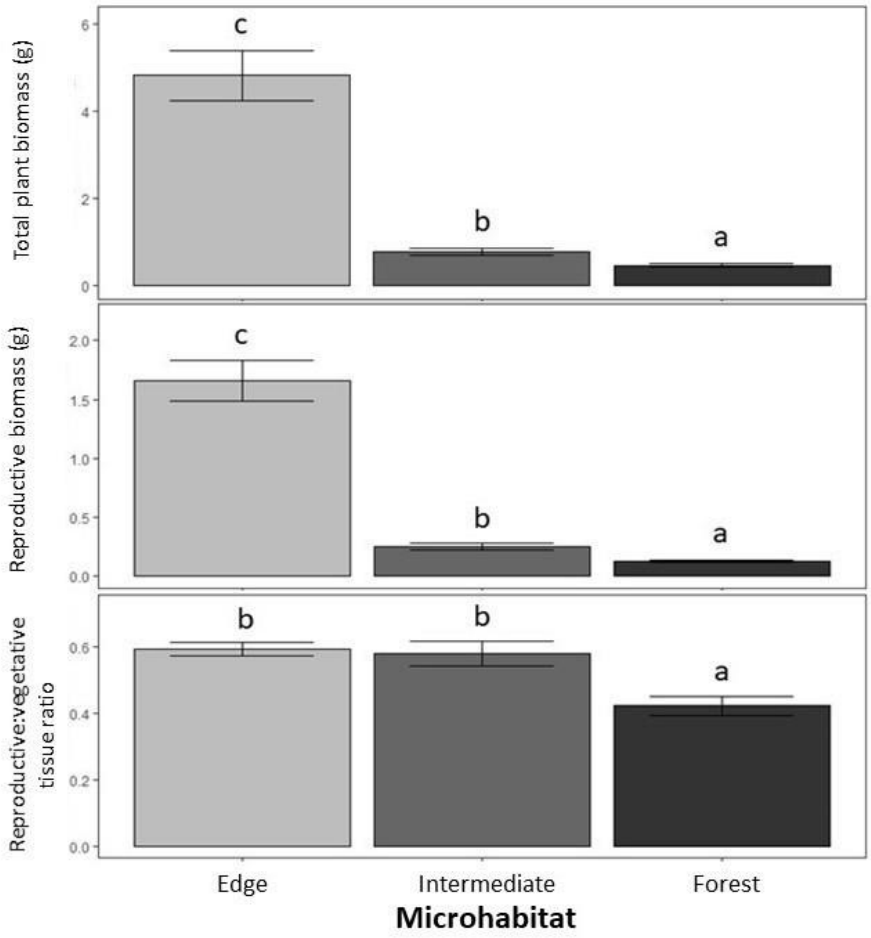

Figure 1.3. *Alliaria petiolata* (garlic mustard) biomass allocation of adult plants: mean total biomass (g; top panel), mean total reproductive biomass (g; middle panel), and the mean reproductive:vegetative tissue ratio (bottom panel) in three growth microhabitat types (edge, intermediate, and forest). Data were collected in 2003, 2004, 2006, and 2016 and averaged across years. The error bars represent standard error of the mean (SEM). Non-matching letters indicate significant differences between categories

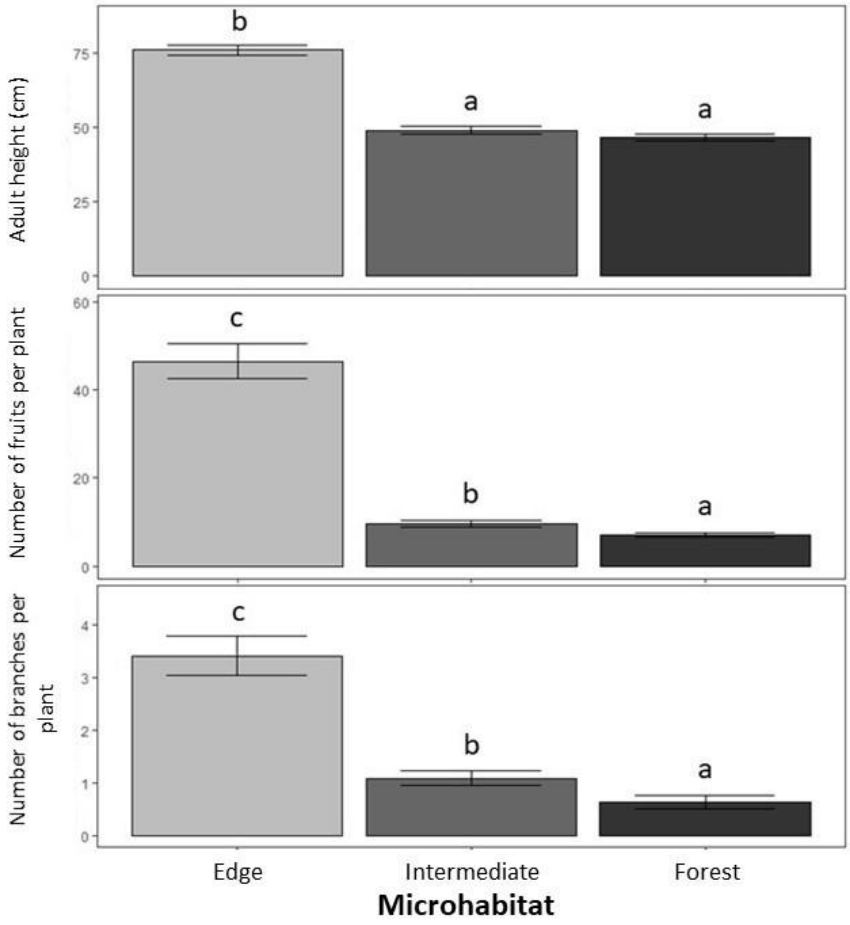

Figure 1.4. *Alliaria petiolata* functional and fitness traits of 2nd year plants: mean plant height (cm; top panel), mean number of fruits (middle panel), and mean number of branches (bottom panel) in three growth microhabitat types (edge, intermediate, and forest). Data were collected in 2003, 2004, 2006, and 2016 (height and fruit number) and 2003, 2006, and 2016 (branch number) and averaged across years for each response. The error bars represent standard error of the mean (SEM). Non-matching letters indicate significant differences between categories

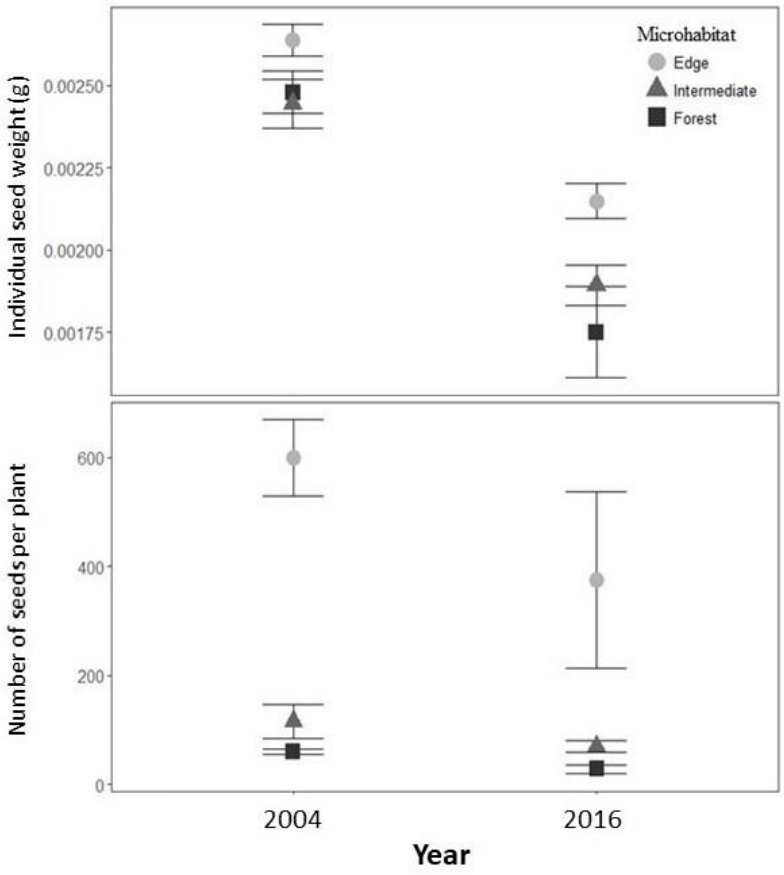

Figure 1.5. *Alliaria petiolata* mean seed weight (g; top panel) and mean number of seeds per plant (bottom panel) in 2004 and 2016 in three growth microhabitats (edge, intermediate, and forest understory). The error bars represent standard error of the mean (SEM)

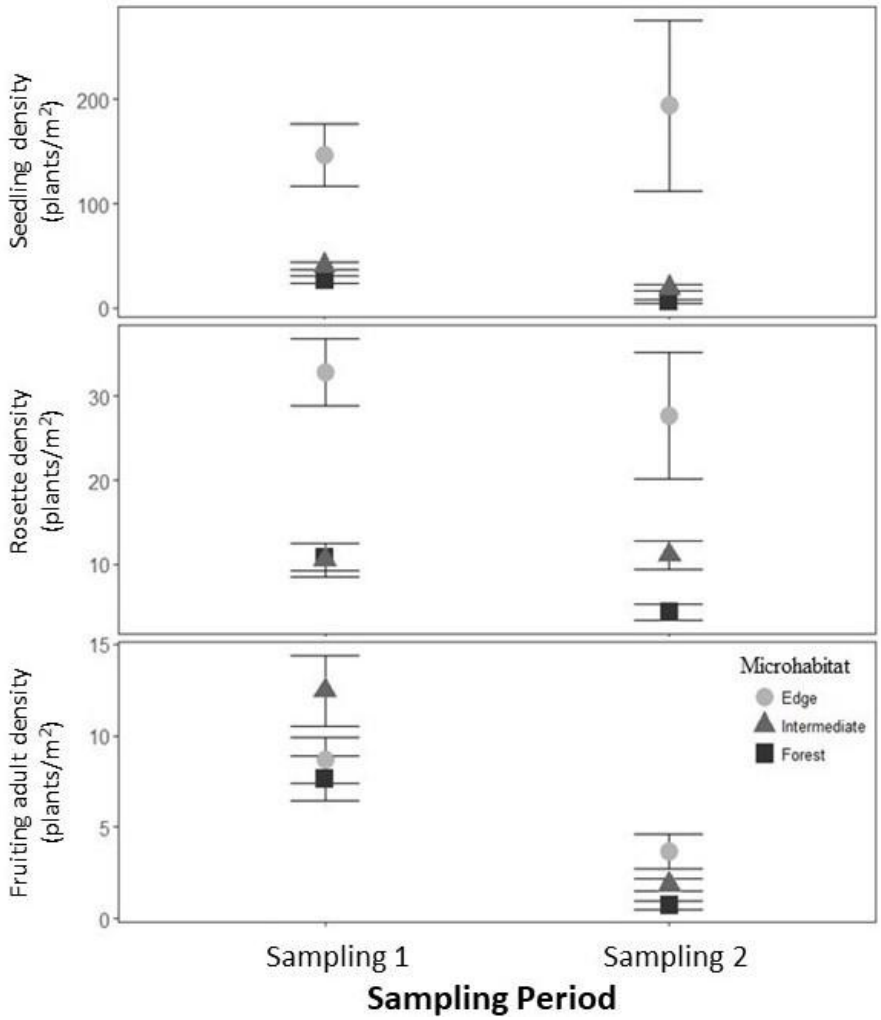

Figure 1.6. *Alliaria petiolata* life stage density (plants/m^2): mean number of seedlings (top panel), mean number of 1st year rosettes (middle panel), and the mean number of fruiting adults (bottom panel) in three growth microhabitats (edge, intermediate, and forest understory) in two sampling periods. Data were collected in spring 2003, 2004, and 2005 (sampling 1) and 2016 (sampling 2) for seedling density; summer 2003, 2004, and 2005 (sampling 1) and 2015 and 2016 (sampling 2) for 1st year rosettes and fruiting adults. The error bars represent standard error of the mean (SEM).

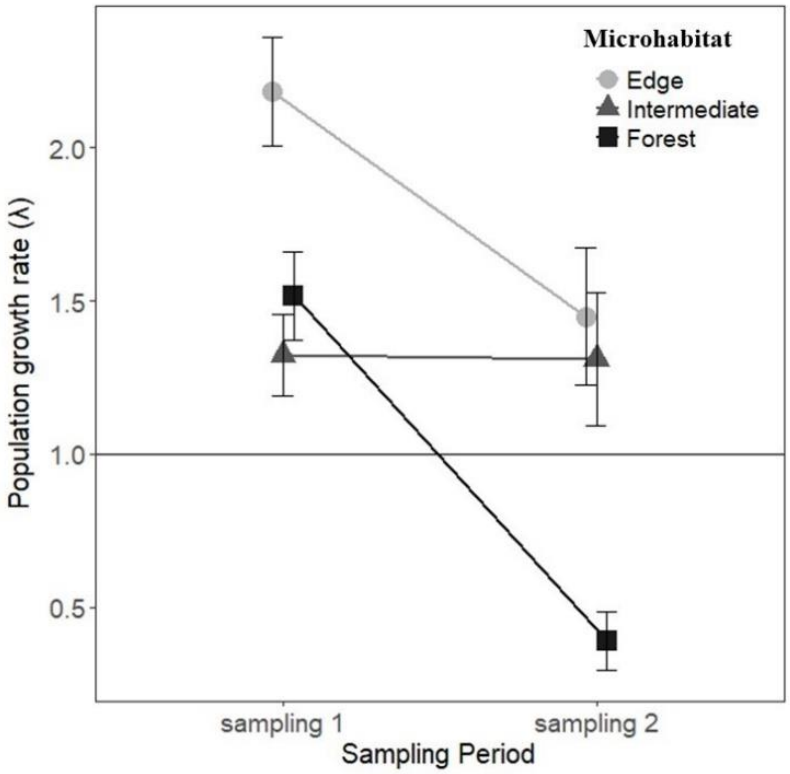

Figure 1.7. Mean population growth rates (λ) for *Alliaria petiolata* across three microhabitats (edge, intermediate, and forest understory) and time. Lambda was calculated for each microhabitat during 6 growing seasons (i.e. three life cycles) in 2003-2004 and 2004-2005 (sampling 1) and 2015-2016 (sampling 2). The grey horizontal line represents stable population size (λ = 1). Error bars represent standard error of the mean (SEM).

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