INVASIVE GARLIC MUSTARD IN A DECIDUOUS NEW ENGLAND FOREST: INSIGHTS FROM A 22-YEAR FIELD STUDY

by

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A thesis submitted in partial fulfillment
of the requirements for the
Degree of Bachelor of Arts with Honors
in Environmental Studies

WILLIAMS COLLEGE

Williamstown, Massachusetts

2021-05-17

Acknowledgements

First, of course, I'd like to extend my unspeakably deep gratitude to my advisors, Joan Edwards and Sonya Auer, for offering their encouragement, expertise, and assistance at every stage of this project. Their instruction and mentorship has been critical to my scientific development since before I even considered attempting a thesis, whether they were offering me my first proper fieldwork job or assigning dozens of primary research papers until I developed a vague understanding of how to engage with scientific literature.

I also owe many thanks to Professor Ron Bassar for his frequent assistance with computational methods, and for introducing me to ecology. This thesis could not have reached its final scope without his help. I'm grateful to Profs. Manuel Morales and David Smith for additional statistical insights, and to Prof. Smith once again for his lovely photography and deadpan humor. I'm also grateful to Professor Hank Art for changing my life by exposing me to the field of botany, and to all the teachers of various kinds who have contributed to my love and knowledge of plants and ecosystems.

I couldn't have made it through this thesis, or this degree, without the love and kindness of the family, friends, and acquaintances who listened patiently to my complaints and helped me take breaks when I got done complaining. There are far too many of you to name here, but if you ever read this for some reason please know that you (yes, *you*!) have brightened my life.

I'm grateful to both my parents for their constant support and advice, and to mom especially for patiently teaching me (among other things) how to make sentences work. And, finally, I want to thank my father for introducing me to the woods. You've done more than anyone, I think, to send me down the path that's led to this thesis project.

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Abstract

Biological invasions represent one of the most pressing environmental issues of the present day. Better understanding of invasive species' population dynamics and environmental preferences can offer critical insights on how the threats they pose vary in space and time. The invasive biennial herb garlic mustard (*Alliaria petiolata*) is of particular concern because it produces allelopathic compounds that negatively affect native plants, fungi, and insects. We report on a 22-year record of garlic mustard population dynamics in three deciduous forest stands in New England and examine how their demographics correlate with conspecific density, environmental conditions, and study site. All three populations showed sustained, unexpected declines in population density after 2016. Prior to this (1998-2015), population densities followed gradually declining trends marked by biphasic population cycles (alternation between high rosette density and high adult density from year to year).

Garlic mustard population growth was negatively density-dependent, but density dependence likely only affected seeds and seedlings. Population growth rate was positively correlated with summer and winter temperature but negatively correlated with spring temperature, supporting laboratory evidence that germination requires intermediate temperatures in late winter/early spring. Our models suggested that both presence and increased depth of snow cover promoted population growth by moderating temperatures, though snow depth's inverse relationship with winter temperature indicates their combined effects on garlic mustard are complex and deserve more study. Growth rate was positively related to both summer and fall precipitation, suggesting water-limitation of plants and possible promotion of seed dispersal by rainfall. Survival to adulthood's relationships with environmental conditions unexpectedly contradicted those for population growth, suggesting that environmental preferences of rosettes

require more study. Mean seed production per plant was not correlated with environmental variables. Comparisons among the three sites indicate that the mid-successional site was most resistant to invasion, the younger Norway maple site the least resistant, and the late-successional beech-maple site intermediate. Future work will be necessary to explore the factors that may have led to their differing invasibility.

The demographics of all three populations confirm that invasions of garlic mustard into deciduous forest eventually decline to low levels, indicating that controlling new invasions by removing adults prior to seed set may be more productive than managing established populations. Our uniquely long-term record confirms that population success is dependent on conspecific density and environmental conditions. Populations benefited from warm winters but also from deeper snow layers and cooler springs, indicating complex relationships which require more study in the field and may affect its invasiveness under future climate warming.

Introduction

Biological invasions represent one of the most pressing environmental issues of the present day. Invasions occur when species arrive in new habitats, often through human activity, and proceed to develop self-sustaining populations that cause significant damage to ecosystems, economies, or human health (Beck *et al.* 2008; Iannone *et al.* 2020). As a result of factors like uncontrolled growth, ability to outcompete native species, and toxic byproducts, invasive species pose serious threats to native biodiversity (Wilcove *et al.* 1998). They can incur extremely high economic costs by destroying biotic natural resources, reducing agricultural yields, and requiring expensive control efforts (Pimentel, Zuniga, and Morrison 2005).

One key question in invasion biology is that of what factors influence species' success in their invasive ranges. Better understanding of environmental preferences, for example, can improve predictions of which habitats are most susceptible to invasion as well as how the species' invasiveness might be affected by future global change. Understanding invasive species' general population dynamics also offers important insight on the threats they pose, as well as effective techniques for control.

We used twenty-two years of data on invasive garlic mustard populations at three deciduous forest sites in Hopkins Memorial Research Forest (Williamstown, MA), along with daily measurements of weather and other environmental conditions, to explore how the species' populations varied over time, between sites, with their own density, and with the abiotic environment. While other garlic mustard populations have received careful study, few authors have reported on long-term field data such as ours. Environmental factors on garlic mustard success such as temperature and snow depth, meanwhile, have primarily been studied in laboratory conditions if at all.

Our data included detailed records of population density for both first-year rosettes and second-year adult plants as well as seed production by the latter. These observations of distinct life stages allowed analysis of how population density and environmental factors affected the species at different points in its life history. The combination of long-term data for both garlic mustard populations and local weather at Hopkins Forest offered a unique opportunity to assess garlic mustard's population dynamics and environmental sensitivity by comparing population growth to environmental conditions over time. We examined these data with the following goals:

1. Characterize general population trends over the course of the study and consider differences between study sites.
2. Explore relationships between garlic mustard population success and factors like population density and interannual variation in environmental conditions.
3. Identify areas for future research in our study system based on findings from (1) and (2).

Garlic mustard (*Alliaria petiolata* (Bieb.) Cavara & Grande) has proved a particularly problematic invader in the northern United States (Nuzzo 1993a; McCarthy 1997; Stinson *et al.* 2006). As an herbaceous biennial, an individual seed will germinate into a low-growing "basal rosette" of leaves in its first year, remain green through the winter, and then sprout a central stem that grows 1-1.25 m tall and produces up to a thousand seeds before the plant dies in its second autumn (Cavers, Heagy, and Kokron 1979; Figure 1). Native to Eurasia, garlic mustard was first recorded in the USA in 1868 on Long Island, NY (Nuzzo 1993a). In the second half of the 20th century, it spread rapidly through much of the Northeast, northern Midwest, and southern Canada (Nuzzo 1993a; EDDMapS 2020). Its spread was likely encouraged by rising populations of white-tailed deer (*Odocoileus virginiana*), which avoid browsing garlic mustard in favor of native species and might make habitat more invasible by disturbing soil and vegetation with their hooves (Eschtruth and Battles 2009; Knight *et al.* 2009). Deer and other mammals may also help disperse garlic mustard seeds long distances through epizoochory (transport on the exterior of an animal) (Loebach and Anderson 2018).

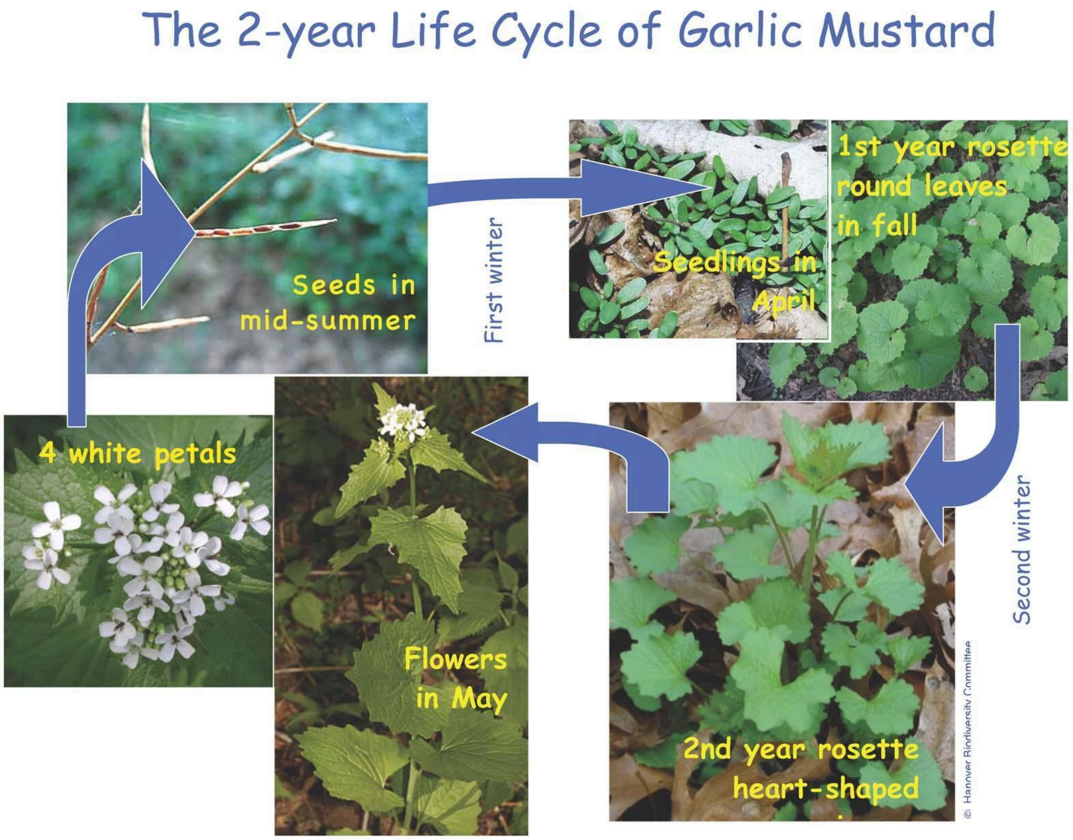

Figure 1: *Garlic mustard follows a strict biennial life cycle, in which plants spend their first year as a small, evergreen "basal rosette" before growing a tall stem, reproducing, and dying in their second year. © Hanover Biodiversity Committee. retrieved from: Upper Valley Land Trust, 2015. "Girls Get Tough on Garlic Mustard." Published 14 May. https://uvlt.org/2015/05/girls-get-tough-on-garlic-mustard/.*

Garlic mustard is of particular concern due to its ability to invade mature forest ecosystems, which are typically more resistant to non-native plants (McCarthy 1997). Invaded forests may have lower density and diversity of understory plants (McCarthy 1997). The species is also allelopathic, secreting compounds that can harm nearby organisms (Cipollini and Cipollini 2016). Garlic mustard's negative effects on native plants are greater in individuals with higher concentrations of its primary class of toxins, glucosinolates (Lankau *et al.* 2009; Smith and Reynolds 2014). The species is also notable for its allelopathic suppression of mycorrhizal fungi that support growth of native plants (Stinson *et al.* 2006; Cipollini and Cipollini 2016); this effect is expected to worsen with future climate warming (Anthony *et al.* 2020). It poses an additional threat to the native "West Virginia white" butterfly (*Pieris virginiensis*) through toxic effects on larvae that attempt to feed on it (Davis *et al.* 2015; Augustine and Kingsolver 2018). Garlic mustard is also a major pest in lawns and gardens, where it can require intensive removal efforts and encourage use of potentially harmful pesticides.

Invasive garlic mustard populations have shown negative density dependence, in which population growth decreases with increasing density of individuals (Pardini *et al.* 2009; Phillips-Mao *et al.* 2014; Stinson *et al.* 2019). Negative density dependence may help check garlic mustard populations, but also suggests that removal of immature garlic mustard plants can be counterproductive (Pardini *et al.* 2009). Our data can be used to support previous research by testing for density dependence over multiple decades. Environmental factors likely to affect garlic mustard populations include temperature, snow depth, precipitation, and irradiance. To date, these factors' effects on garlic mustard have typically been studied in laboratories (ex: Lhotská 1975; Baskin and Baskin 1992) or across field sites with numerous habitat differences whose effects can prove difficult to distinguish (ex: Meekins and McCarthy 2001; Stinson *et al.* 2019). The long-term nature of our data offers a novel opportunity to expand knowledge of garlic mustard's environmental preferences by studying population responses to environmental variation within individual field sites.

Features of garlic mustard's life history may make it particularly sensitive to variation in temperature. The fact that rosettes remain green through the winter leaves them susceptible to frost damage in particularly cold weather (Anderson, Dhillion, and Kelley 1996). Rosettes have shown quite high mortality of up to 79% during the winter months (Nuzzo 1993b), presumably for this reason. Conversely, rosettes have been observed to photosynthesize and increase biomass during warm winters (Anderson *et al.* 1996), which could increase fitness of individuals and promote population growth. There is also strong evidence that garlic mustard seeds require several weeks of "stratification" under near-freezing winter and spring temperatures for optimal germination. Laboratory experiments show optimal stratification temperatures ranging from 1-6° C, with either warmer temperatures or soil freezing causing reduced germination (Lhotská 1975; Baskin and Baskin 1992; Blossey, Nuzzo, and Dávalos 2017). Germination in an outdoor garden had negative associations with both higher temperatures *and* more frequent freezing (Blossey *et al.* 2017), further suggesting that garlic mustard seeds are vulnerable to temperature extremes in winter and spring. In the warmer months, deviation from typical temperatures can reduce plants' physiological efficiency and therefore their fitness (Sanders-DeMott *et al.* 2018; Carter *et al.* 2020), meaning that garlic mustard might be sensitive to summer and fall temperatures as well. Garlic mustard's temperature-sensitivity has rarely been directly studied in the field, however. Footitt *et al.* (2018) found decreased germination with artificial warming at field sites, but temperature-sensitivity of later life stages in particular has rarely been observed except as incidental components of other research projects.

Winter snow cover is another key environmental variable that is inextricably related to temperature. On the one hand, snow can have an insulating effect that might be expected to maintain rosettes and seeds at more stable, favorable temperatures through the winter (Ge and Gong 2010; Templer *et al.* 2017). On the other, a thicker snow layer might reduce rosette survival or reproductive output by blocking light and limiting potential for winter photosynthesis

(Curl, Hardy, and Ellermeier 1972). Garlic mustard receives notable snow cover through much of its North American range, yet its relationship with this component of the abiotic environment has not been studied.

As with temperature and snow depth, effects of precipitation and water availability on garlic mustard success have rarely been studied directly. There is some evidence to support the hypothesis that garlic mustard populations will be more successful with greater rainfall, however. Studies have noted that moister sites tend to support more garlic mustard (Meekins and McCarthy 2001; Stinson et al. 2019), though such findings are difficult to separate from other differences between sites. Seed dispersal may also be affected by precipitation, as flood events can promote dispersal to more distant locations (Meekins and McCarthy 2001) and seeds have been found to cling to mammal pelts more effectively when the fur is wet (Loebach and Anderson 2018).

Light availability is generally of critical importance to plant success. Previous studies of garlic mustard light preferences indicate that garlic mustard prefers intermediate levels of solar irradiance. An experiment with potted plants under artificial shade treatments found that the species grew best when exposed to seasonal shading simulating forest canopy cover (Smith and Reynolds 2014). Phillips-Mao *et al.* (2014) found that increased light levels could suppress seedling establishment, while others found evidence that garlic mustard may be limited by competition in high-light environments (Dhillion and Anderson 1999; Stinson et al. 2019). A more recent study failed to find a significant relationship between garlic mustard success and light level, but identified south-facing slopes (which tend to have high light exposure in the Northern Hemisphere) as particularly favorable habitat (Anderson *et al.*, 2019).

We hypothesized that overall growth, rosette survival, and reproductive output of the local garlic mustard populations would vary in association with environmental variables such as temperature, winter snow depth, precipitation, and solar irradiance. In particular, we predicted that warmer winters would be associated with higher rosette survival and reproductive output but might have variable effects on overall population growth due to the temperature-sensitivity of germination. We expected all demographic rates to improve with higher precipitation and solar irradiance, since our sites only received moderate amounts of each. We also expected population growth, rosette survival, and reproductive output to all decrease in denser populations due to negative density dependence. In general, however, we predicted increasing garlic mustard population densities over the course of the study given the species' invasiveness. By applying a uniquely long-term data set to comprehensive analysis of garlic mustard environmental preferences and population dynamics over time, our tests of these predictions aim to expand knowledge of factors that might influence garlic mustard invasion across habitats and future global change.

Materials and Methods

Sampling Garlic Mustard

To characterize garlic mustard population dynamics over time, we surveyed its population density at three sites in Williams College's Hopkins Memorial Research Forest (HMF, 42°43'25" N × 73°13'29" W). The sites were chosen to represent a range of local forest communities and successional stages. In 1998, we established between 15 and 44 0.25 m^2 permanent quadrats at random locations in each site (Table 1). The quadrats were each marked with a "permquad" made of four soldered stainless steel rods, which was secured at ground level with steel stakes (Figure 2). We placed a numbered flag in the corner of each permquad for ease of identification. Flags and permquads were relocated/replaced as necessary over the sampling period, using their relative positions as guides.

Figure 2: *A 0.25 m^2 "permquad" at the late site, marked with flags. No garlic mustard can be seen.*

Each summer from 1998-2019, typically in early-mid July, we counted the numbers of garlic mustard rosettes and adult plants rooted in each 0.25 m^2 permquad. At this time, adults were mostly developing fruit and had not yet senesced. Starting in 2000, we also assessed reproductive output by counting the total number of seeds on the adult plants in each permquad. Seeds were totaled by counting bulges on the exterior of their siliques (seedpods). In some cases, siliques had already split and the number of seeds was counted based on number of empty chambers in the remaining husk. Growth of the native herb Jack-in-the-pulpit (*Arisaema triphyllum*) was also studied in the area surrounding each permquad, but those data are not reported here.

Name	Elevation (m)	Successional Stage	Number of Quadrats
Early site	269	early	15
Mid site	299	intermediate	44
Late site	398	late	17
Main station	279	mown field	N/A
Sugarbush station	271	intermediate (managed sugarbush)	
Snow depth station	300	mown field	

Table 1: *We sampled garlic mustard populations at three field sites representing different stages of hardwood forest succession. Population trends were compared to environmental data obtained from three nearby weather stations (Figure 3). This table reports approximate elevation and successional stage of the vegetation community for each field site and weather station, as well as the number of quadrats in each site.*

Interannual Environmental Variation

To gain insight into the relationships between garlic mustard population success and environmental conditions, we calculated mean seasonal values for several environmental variables in Hopkins Memorial Forest (HMF) over the years of garlic mustard surveys (Table 2). Environmental variables were obtained as daily means (or daily totals, in the case of precipitation) from the HMF weather archive (Dethier and Racela 2021a). All variables except solar irradiance and snow depth were measured at the main HMF weather station, which is located in an open field roughly between the early and mid garlic mustard sites (Figure 3). Solar irradiance was measured at an auxiliary weather station in a nearby sugar maple sugarbush (“sugarbush station”) to approximate light levels available below the forest canopy. Snow depth was measured between 4 and 5pm each day at the main weather station or on a nearby private property (Dethier and Racela 2021b).

We used the daily means of weather measurements to calculate means for each season during the years 1997-2019. Seasons were delineated based on observations of approximate garlic mustard phenology in Williamstown and Petersham, MA (Table 3; Edwards pers. obs.; Newell pers. obs.; Stinson pers. comm.).

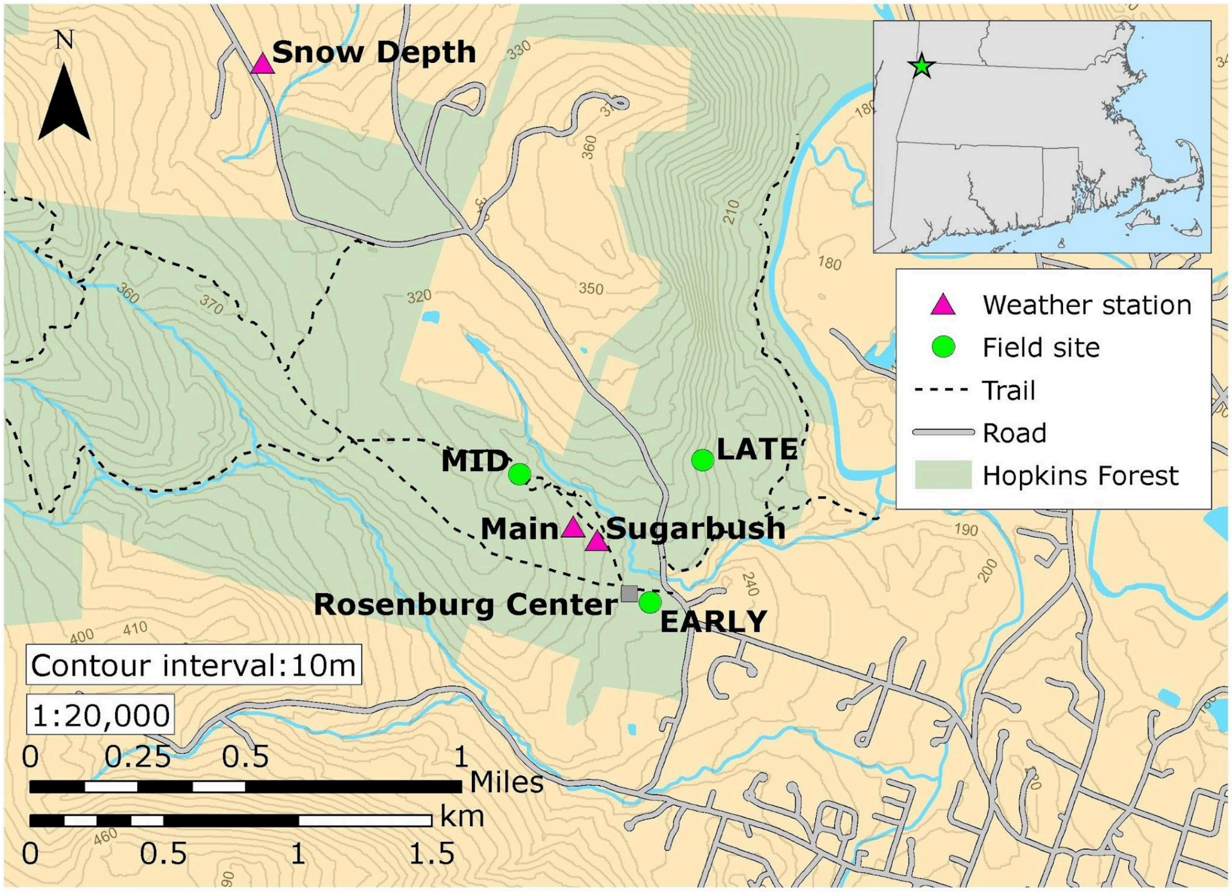

Figure 3: *Garlic mustard field sites and the main/sugarbush HMF weather stations were all located within a mile of the Hopkins Forest visitor center ("Rosenburg Center"), excepting the secondary snow depth station ("Snow Depth"). Hopkins Forest is located on the boundaries of Massachusetts, New York, and Vermont, USA.*

Environmental Variable	Source	Years Available
Mean air temperature (°C) Total precipitation (cm)	Main HMF weather station	1997-2019
Afternoon snow depth (cm)	Main weather station or nearby property	1997-2019
Mean solar irradiance (W/m^2)	Sugarbush weather station	2000-2019

Table 2: *We obtained records of mean daily environmental conditions in HMF to explore the relationships between environment and garlic mustard population growth. This table lists the variables considered and the sites and years for which each was measured.*

Season	Months	Data year(s) relative to year of subsequent garlic mustard survey	Garlic mustard life history events (approximate)

Fall	August-October	Previous year	Continued seed dispersal, adults senesce
Winter	November-March	Previous year, same year	Seeds and rosettes overwinter
Spring	April-May	Same year	Seeds germinate, rosettes “bolt” into adult plants and flower
Summer	June-July	Same year	Fruits develop, seeds disperse.

Table 3: *Months were sorted into four "seasons" based on approximate timing of garlic mustard life history. Each season was paired with the subsequent garlic mustard survey in July for purposes of modeling population dynamics. Fall and early winter data was thus associated with the following year's survey (ex: mean environmental data for fall 1997 was paired with garlic mustard data from 1998).*

Characterizing Sites

All three survey sites can be generally described as mesic northern hardwood forest, but each was selected to represent a different stage of forest development. They include one “early-succession” site (early site), an older “mid-succession” site (mid site), and one “late-succession” site believed to have experienced relatively minimal disturbance since European colonization (late site; Collier 1993). In fall 2020 and winter 2021, we characterized differences between sites by recording qualitative observations of their most dominant plant species as well as measurements of fall leaf litter depth and winter snow depth. Depths were recorded for 6-11 quadrats per site by inserting a ruler into the relevant layer at five random locations in each quadrat until it met resistance.

We also measured temperatures at ground level in each site in fall and winter of 2020-21, with the aim of identifying any systematic differences among them or between the sites and the weather stations at which environmental data was obtained. Hourly temperatures were recorded using portable Thermochron iButton® sensors (OnSolution Pty Ltd, Baulkham Hills, Australia), which were placed in small watertight bottles for protection and tied to six randomly selected permquads in each site. The iButton data was used to calculate mean daily ground-level temperatures for the three sites spanning from September 21, 2020 to March 18, 2021.

Modeling Winter Temperature

We compared ground-level temperatures recorded in the garlic mustard sites in 2020-21 to air temperatures from the HMF weather station to get a sense of how well the weather station data approximated conditions experienced by garlic mustard populations. We found that site and weather station mean daily temperatures were highly correlated in the fall, but that their relationship was weaker for low winter temperatures (Figure 4). This weakened relationship appeared to be related to snow cover, suggesting that snow had an insulating effect on the ground-level site temperatures.

To obtain more accurate predictions of winter temperatures experienced by overwintering garlic mustard, we developed a linear model of ground-level winter site temperatures using data from November 1, 2020-March 18, 2021. We modeled site temperatures using air temperature and 5cm-depth soil temperature from the HMF main weather station along with snow presence/absence. This model was considerably more effective than using air temperature alone (nested F test, $p<2.2\times10^{-16}$), and was thus used to generate estimates of mean ground-level temperature for each winter day from 2004-2019. Soil temperature data were unavailable prior to September 2004, so the number of days since November 1 was used as a proxy for it when predicting temperatures for 1997-2004 (Table 4). These daily predictions were averaged to calculate estimated mean ground-level temperature for each winter of data collection.

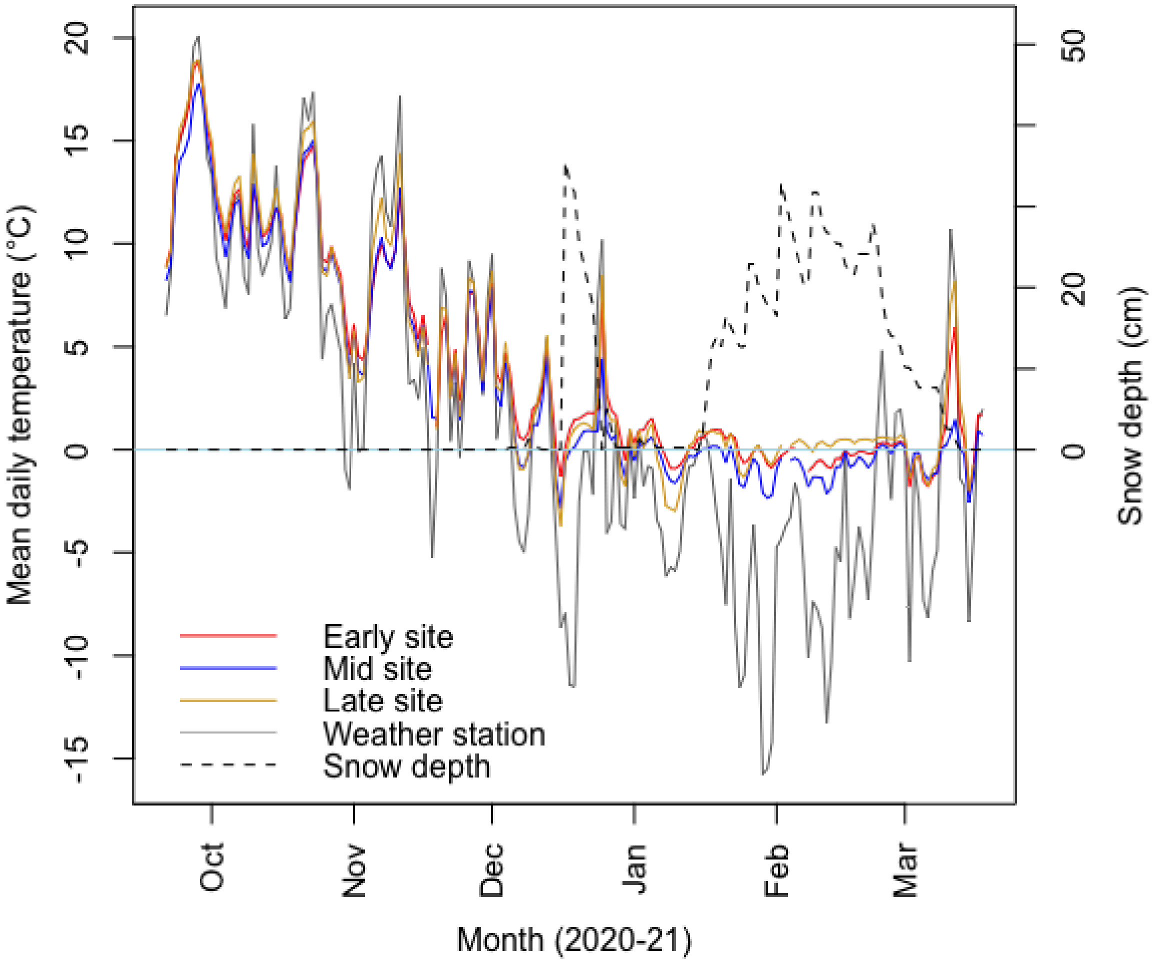

Figure 4: *In fall 2020, ground-level temperatures in the garlic mustard sites (colored lines) were closely related to air temperatures at the main HMF weather station (gray line). In winter 2020-21, the presence of snow (dashed line, righthand axis) had an apparent insulating effect, reducing variation in ground-level temperatures even as the air temperature continued to drop below 0° C. Breaks in the site data represent necessary pauses in collection to reset the iButton sensors.*

Term	Model with day of winter (1997-2004)	Model with soil temperature (2004-2019)
Intercept	**2.90****	**-0.572****
Air temperature	**0.562****	**0.440****
Snow presence (binary)	**-0.968****	0.00294
Air temperature * snow presence	**-0.394****	**-0.288****
Days since November 1	**-0.0133****	
Soil temperature (5cm depth)		**0.556****
R^2	**0.895****	**0.932****

Table 4: *Both models used to predict ground-level winter temperature were significantly more effective than a model using air temperature alone (nested F test, $p<2.2\times10^{-16}$ in both cases). Days since November 1 was used in the model at left due to a lack of soil temperature data. Model coefficients and R^2 values are shown here. '**' and bolding denote significant coefficients with $p<0.01$ (Welch's t-test).*

Modeling Population Success

To gain a broad understanding of environmental factors that might influence garlic mustard population success, we used ordinary linear models to assess the relationship between our three populations' intrinsic growth rates (r) and seasonal averages of various environmental variables. We further explored the relationship between environment and specific vital rates influencing population growth using quasibinomial models of survival from the rosette stage to adulthood and ordinary linear models of the mean number of seeds produced per adult plant. All models used data from the years 2001-2019, as some variables were unavailable for prior years.

Environmental variables/seasons hypothesized to be most relevant as predictors were identified based on primary research on garlic mustard, our own observations of the species, and general knowledge of plant physiology. While environmental variables were obtained from the HMF weather stations in most cases, we used predicted ground-level winter temperature instead of weather station winter air temperature in order to more accurately approximate conditions beneath the snow layer. Density of garlic mustard individuals was also considered when modeling all three dependent variables based on previous evidence for negative density dependence of garlic mustard population growth (Pardini *et al.* 2009; Phillips-Mao *et al.* 2014; Stinson *et al.* 2019). We included garlic mustard site as a categorical predictor to account for differences between the three study sites. We considered all identified variables in our models of intrinsic growth rate, while smaller subsets of environmental variables were used to model the more specific vital rates (Table 6).

Value	Usage	Formula

intrinsic growth rate (r)	dependent variable	ln $ln\,(\frac{total\ individuals,\ year\ t}{total\ individuals,\ year\ t-1})$
survival	dependent variable	$\frac{adult\ plants,\ year\ t}{rosettes,\ year\ t-1}$
mean seeds/plant	dependent variable	$\frac{total\ seeds\ per\ quadrat,\ year\ t}{adult\ plants,\ year\ t}$
quadrat density	independent variable	$total\ individuals,\ year\ t-1$
standardized variable	scales variables to allow comparison of model slopes	$standardized\ value\ = \frac{(\ value)-(mean\ of\ all\ values)}{(standard\ deviation\ of\ all\ values)}$

***Table 5:** Formulas used in calculating variables for the models of intrinsic growth rate, survival to adulthood, and mean seeds/plant. The formulas shown for dependent and independent variables would calculate the value for a given year t. Standardized values of independent variables were calculated by subtracting the variable's mean from each unstandardized value and dividing by the variable's standard deviation. The standardized values of independent variables were used in our models to give each variable equal variance and enable comparison of their slopes.*

For each year, we calculated the three dependent variables and the density per quadrat for each quadrat (Table 5). We then averaged these variables within sites, including only quadrats with >0 individuals of the relevant life stage(s) when calculating dependent variables and mean densities for each model (Table 6). Mean seeds/plant was natural-log-transformed before modeling to improve normality of model residuals, while mean quadrat density was natural-log-transformed in all models to make its relationship with the dependent variables more linear. In order to allow comparisons of magnitude between each model's slopes, predictors were standardized by mean and standard deviation (Table 5).

	Intrinsic growth rate	Survival from rosette to adult	Mean seeds per adult plant
Abbreviation	r	survival	mean seeds/plant
Regression type	ordinary least squares	quasibinomial	ordinary least squares
Observations included	quadrats with >0 individuals in current *or* previous year	quadrats with >0 rosettes in previous year	quadrats with >0 adults in current year
Dependent variable	r	survival	ln(mean seeds/plant)

Independent variables	ln(density)	ln(density)	ln(density)
	site	site	site
	spring air temperature summer air temperature		spring air temperature summer air temperature
	predicted ground-level winter temperature	predicted ground-level winter temperature	predicted ground-level winter temperature
	winter snow depth	winter snow depth	
	spring precipitation summer precipitation fall precipitation	summer precipitation fall precipitation	spring precipitation summer precipitation
	fall/winter solar irradiance spring/summer solar irradiance	spring/summer solar irradiance	fall/winter solar irradiance

Table 6: *Type of regression, subset of observations, and variables used in each set of models. Environmental predictors are grouped by variable being measured.*

We found that mean quadrat density was correlated with study site, while predicted ground-level temperature was correlated with snow depth. While low model VIFs suggested that these correlations were of little concern, for each pair we explored the effects the variables had on one another's slopes by removing them from our models one at a time. Mean solar irradiances for different seasons were also highly correlated with each other, so they were averaged to create two predictors: mean fall/winter irradiance and mean spring/summer irradiance.

We evaluated the explanatory power of each model using R^2 values and F tests (variance-function-based pseudo-R^2 and likelihood ratio tests for quasibinomial models of survival). The significance of individual terms was tested using Welch's t-test, with all models and slopes with p-values <0.05 considered significant. We visualized approximate relationships between the dependent variables and unstandardized significant independent variables using partial residual plots. All statistical analyses were performed in R 3.6.3 (R Core Team 2020).

Results

Differences in Site Conditions

The early site is near the main entrance to the forest and is dominated by disturbance-adapted species, with almost all tree cover provided by Norway maple (*Acer platanoides*; Table 7). Frequent tree and limb falls have created gaps in the canopy, allowing dense growth of shrubs and perennial herbs. This site has the most dense understory vegetation and the highest proportion of exotic plants. The early site is also the flattest of the three. The mid site was predominantly shaded by red oak (*Quercus rubra*) when established in 1998 (Edwards pers. obs.), but in 2020 almost all large trees were American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) (Newell pers. obs.). The late site is predominantly forested with sugar maple (*Acer saccharum*). It is located in Hopkins Forest's Beinecke stand, a section of forest that was not cleared for agriculture due to its steep terrain and is believed not to have experienced anthropogenic disturbance beyond possible minimal logging activity (Collier 1993). Both the mid and late sites are near the base of steep east-facing slopes and show evidence of soil and litter deposition (or sometimes erosion) following heavy rain events.

Evidence of white-tailed deer (*Odocoileus virginianus*) activity was observed in both the early and late sites, with copious feces found throughout the year and tracks visible in the snow during winter 2020-2021 (Newell pers. obs.). The mid site, by contrast, showed little evidence of deer visits. The only other mammals observed to visit the sites were chipmunks (*Tamius striatus*), which were seen at all three. No systematic effort was made to study animal visits, however, so other species were likely present despite being unobserved.

	Tree	Shrub	Herb
Early	_Acer platanoides_* _Fraxinus americana_ (one only)†	_Berberis thunbergii_* _Lonicera sp._* _Parthenocissus quinquefolia_† _Rhamnus cathartica_* _Rosa multiflora_* _Rubus occidentalis_† _Vitis sp._†	_Ageratina altissima_† _Arisaema triphyllum_† _Dryopteris carthusiana_† _Galium sp._ _Glechoma hederacea_* _Matteuccia struthiopteris_† _Poaceae_ (_Dichanthelium clandenstinum_?) _Onoclea sensibilis_† _Solidago sp._ _Viola sp._†
Mid	_Fagus grandifolia_† _Acer saccharum_† _Quercus rubra_† _Acer pensylvanicum_†		_Arisaema triphyllum_† _Cardamine diphylla_† _Dicentra canadensis_† _Dryopteris carthusiana_† _Erythronium americanum_† _Galium sp._ _Polystichum acrostichoides_† _Trillium erectum_† _Viola sp._
Late	_Acer saccharum_† _Fraxinus americana_† _Fagus grandifolia_† _Tilia americana_†	_Berberis thunbergii_* _Rosa multiflora_* _Rubus sp._ _Vitis sp._†	_Ageratina altissima_† _Allium tricoccum_† _Arisaema triphyllum_† _Aster sp._ _Cardamine diphylla_† _Carex sp._ _Caulophyllum thalictroides_† _Dicentra sp._† _Dryopteris carthusiana_† _Laportea canadensis_† _Phryma leptostachya_† _Pilea pumila_† _Polystichum acrostichoides_† _Trillium erectum_† _Viola sp._

Table 7: _Plant communities differed considerably between the three study sites, with the early site hosting particular richness and abundance of non-native species. This table reports plant species observed in notable abundance at the three study sites, by growth form. Species known to be native are marked with ‘†’, while those confirmed to be non-native are marked with ‘*’. Observations were made in 2019-2021._

Mean litter depths differed significantly between all sites whether or not variation between individual quadrats and sampling days was accounted for (Bonferroni-corrected multiple comparison, $p<0.05$; Figure 5; Appendix A). The mid site had the deepest leaf litter (mean depth 9.4 cm), while the late site had the thinnest litter layer (mean depth 5.8 cm). The early site had litter depths close to the mid site (mean depth 7.8 cm). Litter layers also differed in density and species-of-origin between sites. The mid site had denser litter than the other two (Newell pers. obs.), while early-site litter was particularly low-density due to numerous downed branches that helped elevate fallen leaves above the ground. It is unclear to what extent the less dense litter in the early site was an anomaly of fall 2020, when several large tree limbs fell across the site. Early-site litter was made up almost exclusively of Norway maple leaves, while mid-site litter was dominated by American beech and red oak and late-site by sugar maple.

We found that the late site had slightly less deep snow on average than the other sites across two days of sampling, both before and after accounting for variation between sampling days and quadrats (Bonferroni-corrected multiple comparison, $p<0.05$; Appendix A). It had a significantly thinner snow layer than either of the other sites on February 3, 2021, but only differed significantly with the mid site on February 6 (Figure 6). The mid site had more snow than the early site on February 3, but the reverse was true after three days of thaw. Differences between early and mid were not significant on either day. The mid site showed the least snow loss between sampling dates; this slower thaw is in line with observations that the mid site was last to lose snow cover in late winter 2021 (Newell pers. obs.). The early site showed the most variation in snow depth, as the many fallen tree limbs there created uneven snow drifts.

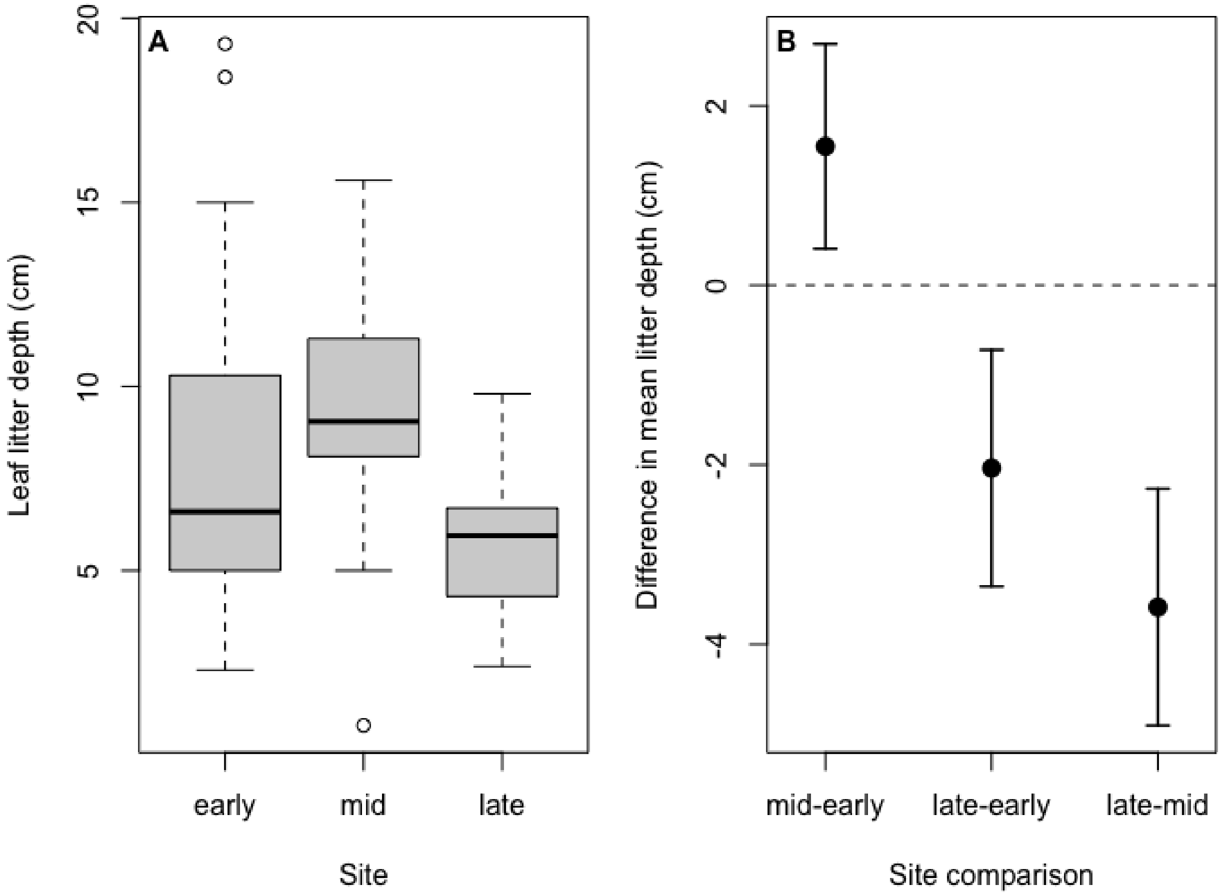

Figure 5: *The mid site had the thickest litter layer and the late site the thinnest, with mean litter depth at all sites differing significantly from one another. Box-and-whisker plots show differences in center and spread of litter measurements at the three sites (A). The boxes give the range of the middle 50% of data (25th-75th percentile), with the median shown as a bold central line. Thinner "whiskers" show the extent of the remaining data, with outlying points shown as open circles. Post hoc multiple comparisons of means showed significant differences between all three sites, even after differences between quadrats and sampling days were accounted for (B). In (B), points represent differences between the mean litter depth of two sites, while error bars give 95% confidence intervals for those differences. No confidence intervals include zero, indicating all differences are significant with* $p<0.05$.

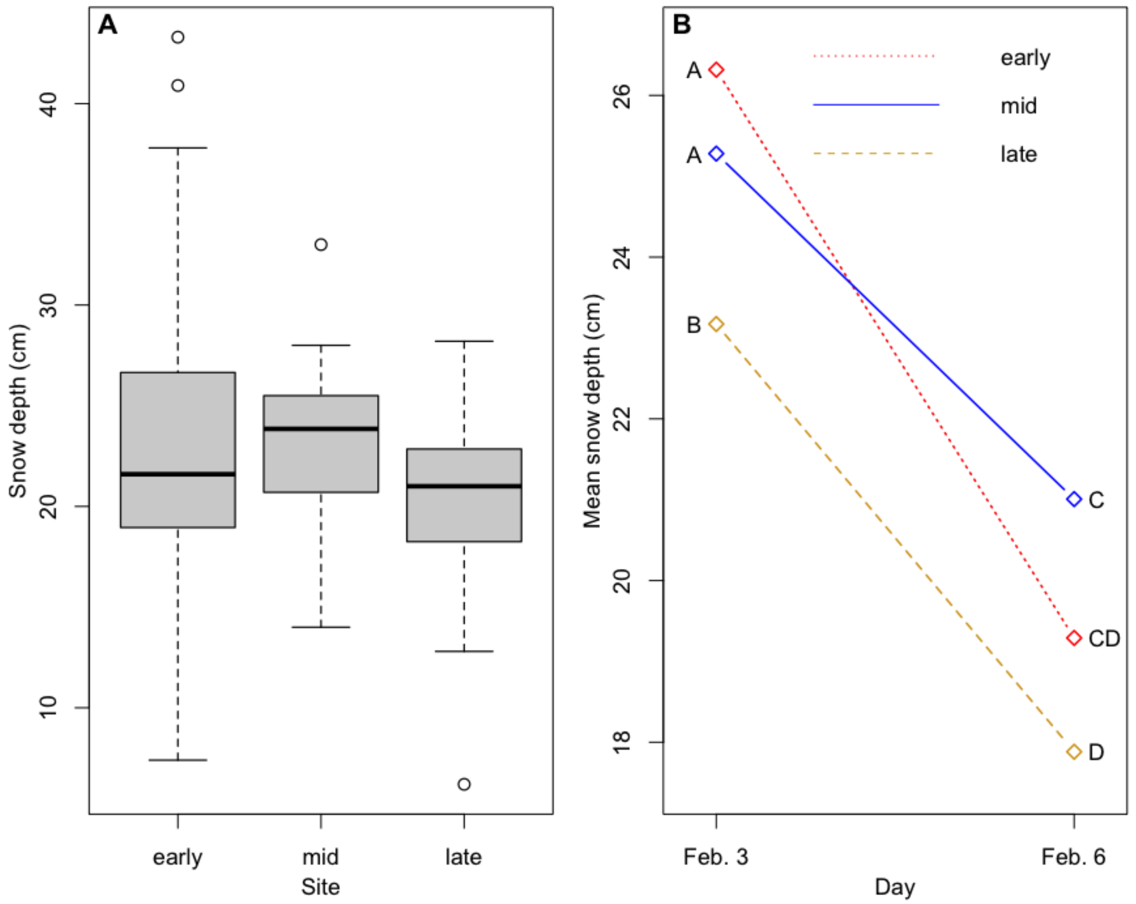

Figure 6: *The late site had significantly thinner snow layers on average than either the early or mid sites. Box-and-whisker plots show differences in center and spread of litter measurements at the three sites, without accounting for sampling day (A). Plotting mean depths for each site within each sampling day shows more rapid snow loss in the early site and slower loss in the mid site over three days of thaw (B). Means without any shared letters in their labels differed significantly (p<0.05) after accounting for variation among quadrats.*

Density of Rosettes and Adult Plants

Densities of second-year, reproductive plants (adults) were generally considerably lower than those of first-year rosettes, reflecting the species' high mortality rates in its first year of growth. The mean adult density per quadrat, across all sites and years, was only 7.64% of mean rosette density. This disparity was most extreme in the early site, where mean adult density was 5.8% of rosette density. The mid and late sites' adult densities averaged 13.1 and 10.2% of their rosette densities, respectively (Table 8).

	Early	Mid	Late	All
Mean rosettes per quadrat	52.73	2.97	17.20	15.96
Mean adults per quadrat	3.07	0.39	1.76	1.22
$\frac{Mean\ adults}{Mean\ rosettes}$ (%)	5.83%	13.14%	10.24%	7.64%

Table 8: *On average, densities of adult plants were considerably lower than those of rosettes. Grand means of rosettes and adults per quadrat (across all years) are shown here, along with the ratio of mean adults to mean rosettes*

The early site typically had the highest densities of garlic mustard. Its annual average rosette counts ranged between 7 and 162 per quadrat and an inter-year grand mean of 53 rosettes/quadrat, while average adult counts ranged from 0 to 11 per quadrat with a grand mean of 3.1 (Table 8; Figure 7). The Mid site tended to have the lowest densities, with average rosette counts per quadrat between 0 and 12 (grand mean 3.0) in any given year and adult counts between 0 and 3 (grand mean 0.39). The late site had intermediate densities, with rosette counts ranging from 0 to 66 rosettes/quadrat (grand mean 17) while adult counts ranged from 0 to 15 adults/quadrat (grand mean 1.8).

All three sites experienced “biphasic” or “two-point” population cycles for certain portions of the period 1998-2015 (Table 9; Figure 7). These cycles were marked by alternation between years in which rosette densities increased while adult densities decreased and years in which this pattern was reversed (with the rosette population falling while adults became more abundant). Biphasic cycling is noticeable as a “saw-tooth” pattern when rosette and adult averages are standardized by mean and standard deviation and plotted over one another (Figure 7). It is most evident from 1998-2003 and 2006-2011 in the early site and 2003-2010 in the mid site, and is also seen to some extent in the late site (Table 9). Biphasic cycles were synchronous across all three sites in certain years, especially from 2004-2009, with all sites having the same dominant life stage in a given year (Table 9).

Populations at all sites showed gradual declines in population density over the course of the study, though this trend was broken by large spikes in the mid and late-site populations during the late 2000s (Figure 7). All sites' populations had stabilized at low densities by 2016, with each site's average per-quadrat densities of both rosettes and adults consistently below their overall grand means. Populations showed little interannual variation from 2016-2019, with no evidence for biphasic cycling. This stabilization at low density first began in the mid site around 2013, but soon appeared in the late and early sites as well (2015 and 2016, respectively).

Year	**Dominant Life Stage (Increased Density from Previous Year)**			**Synchrony**
	Early	**Mid**	**Late**	
1998	Rosette	Adult	N/A	None
1999	Adult	Rosette	Rosette	M/L
2000	Rosette	Adult	Adult	M/L
2001	Adult	Rosette (unclear)	Rosette	M/L
2002	Rosette	Rosette (unclear)	Adult	E/M
2003	Adult	Adult	Rosette (less clear)	E/M
2004	Rosette (less clear)	Rosette	Rosette (less clear)	All
2005	Adult (less clear)	Adult	Adult	All
2006	Rosette	Rosette	Rosette (less clear)	All
2007	Adult	Adult	Adult	All
2008	Rosette	Rosette	Rosette	All
2009	Adult	Adult	Adult	All
2010	Rosette	Rosette	Neither (less clear)	E/M
2011	Adult	Adult (less clear)	Rosette (unclear)	E/M
2012	Neither (less clear)	Rosette	Rosette (less clear)	M/L
2013	Adult	Adult	Adult	All
2014	Rosette	Rosette (unclear)	Rosette	All
2015	Adult	Unclear	Adult (unclear)	None
2016	Neither (less clear)	Unclear	Rosette (unclear)	None
2017	Both (less clear)	Unclear	Unclear	None
2018	Both (less clear)	Unclear	Unclear	None
2019	Neither (less clear)	Rosette (unclear)	Rosette (unclear)	M/L

Table 9: *Biphasic population cycles with alternating increases in rosette and adult life stages occurred at all three sites from 1998-2015. All populations cycled synchronously during a high-population-density period in 2004-2009, with the same dominant life stage across the three sites in each of those years. The table reports "dominant life stage" at each site, for each year, based on whether rosettes or adults increased in density from the previous year (see Figure 7). Years with unclear dominance patterns are flagged in parentheses. The periods of time in which biphasic population cycles were readily apparent are shown in green. The righthand column indicates which sites shared the same dominant life stage in a given year, with years where all three populations were synchronous highlighted in blue.*

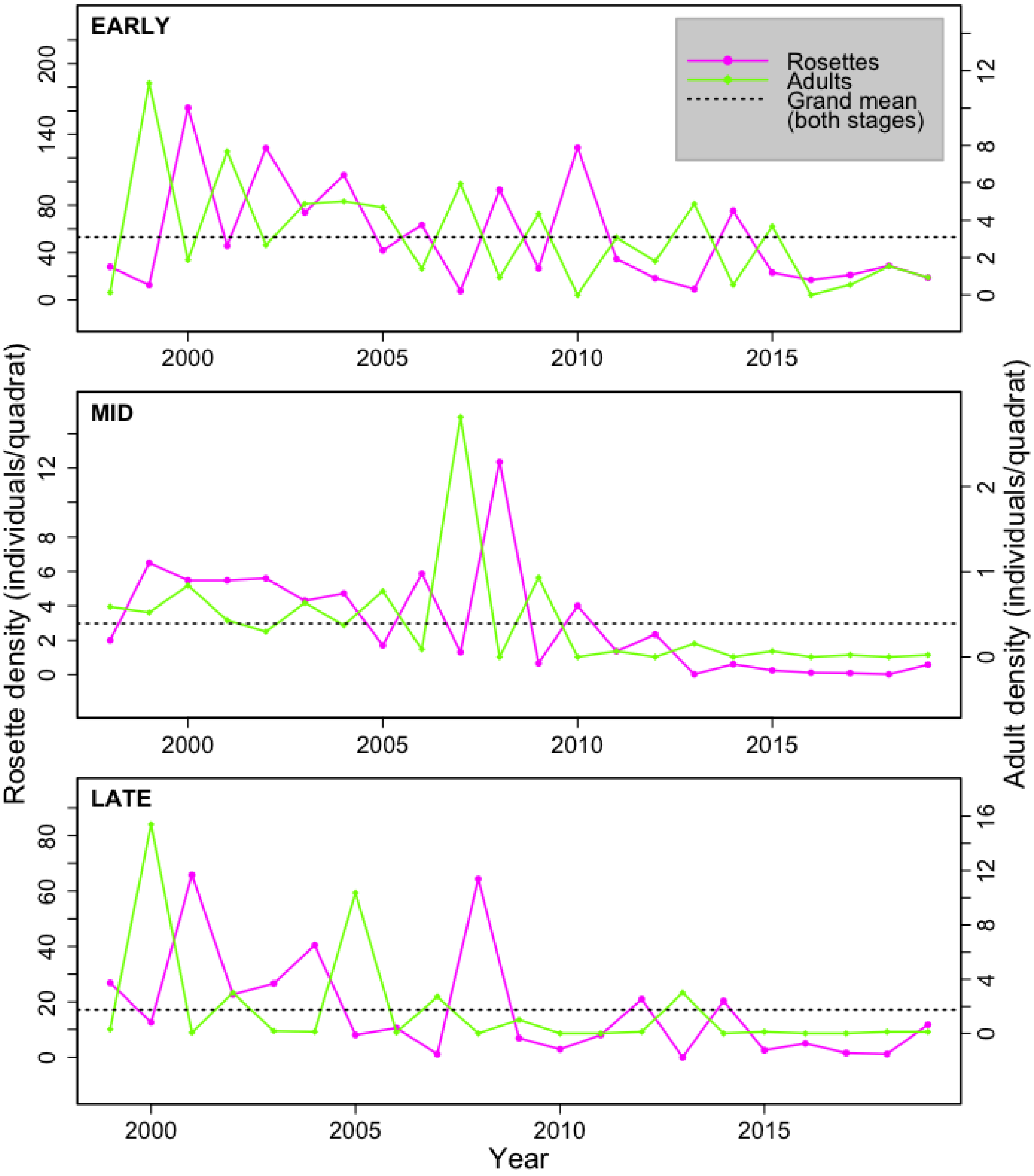

Figure 7: *Populations at all three sites showed sustained declines in density from 2016 onwards. From 1998-2015 all populations showed at least some degree of biphasic cycling, with a given life stage increasing while the other decreased before reversing the pattern in the following year. Plots show mean density of individuals per quadrat by year for each site. Rosette (pink) and adult (green) life stages are plotted separately. Annual mean densities of rosettes and adults were converted to standardized values to equalize their variance and allow plotting in the same figure (see Table 5). Rosette and adult densities are reported as unscaled units (individuals per 0.25 m^2 quadrat) on the left and right axes of each graph. Interannual grand means (z-score = 0) are plotted as dashed lines.*

Models of Intrinsic Growth Rate (r)

Garlic mustard population growth tended to be lower in denser populations, with the intrinsic growth rate of the garlic mustard populations significantly negatively associated with the natural-log mean density of garlic mustard individuals per quadrat (Welch's t-test, for full model: $t=-6.30$, $p=1.6\times10^{-7}$). This relationship was robust, holding across four of the models (Table 10) and for the populations at all three study sites (Figure 8). Population growth also varied between the three sites when density was accounted for, with both the mid and late sites showing lower growth rates on average despite their lower densities (Table 10; Figure 8).

	Density-Only	Site-Only	No Snow Depth	No Winter Temperature	Full Model
Intercept	-0.072	-0.139	**0.714***	**0.871****	**1.07****
ln(Mean density per quadrat)	**-0.655****		**-1.04****	**-1.23****	**-1.48****
Mid site (vs. Early)		0.0971	**-1.57****	**-1.88****	**-2.27****
Late site (vs. Early)		0.102	**-0.790***	**-0.955***	**-1.17****
Spring temperature	-0.193	-0.0135	-0.144	-0.202	**-0.417***
Summer temperature	0.253	0.141	0.110	0.221	**0.393***
Ground-level winter temperature	0.140	-0.214	-0.0435		**0.584***
Snow depth	0.228	-0.259		0.353	**0.837****
Spring precipitation	-0.151	-0.188	-0.123	-0.0834	-0.105
Summer precipitation	0.284	0.0382	0.204	0.240	**0.592***
Fall precipitation	0.355	0.239	0.329	**0.384***	**0.502****
Spring/summer irradiance	-0.166	-0.223	-0.136	-0.0974	-0.0945
Fall/winter irradiance	0.0210	-0.0336	0.0226	0.0487	0.0894
Model R^2	**0.332***	0.133	**0.463****	**0.508****	**0.560****

Table 10: *Intrinsic growth rate (r) showed strong negative density dependence. It also varied significantly with spring, summer, and winter temperatures, snow depth, and both summer and fall precipitation when all predictors were accounted for. This table reports coefficients and R^2 values for all models of intrinsic growth rate. All predictors are standardized by mean and standard deviation, so coefficients represent the average change in growth rate associated with a one standard deviation increase in predictor value. Coefficients that are significantly different from zero (Welch's t-test for predictor slopes, F-test for R^2) are bolded and labeled with asterisks (*: $p<0.05$, **: $p<0.01$).*

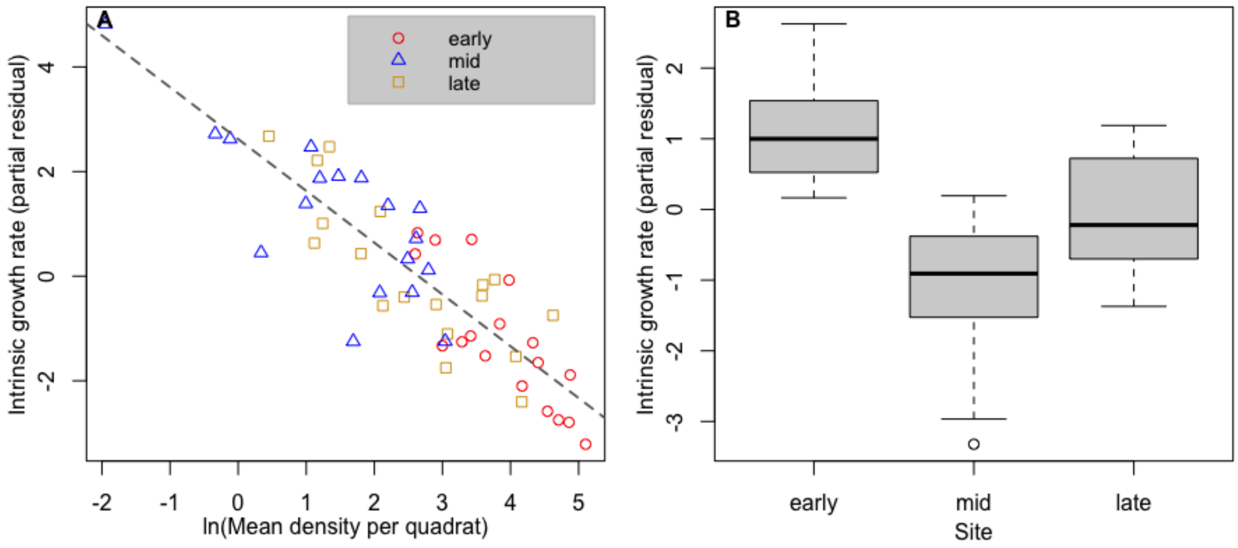

Figure 8: *Garlic mustard density and study site were both significantly associated with the intrinsic population growth rate (r) of garlic mustard populations. Population growth had a strong negative association with the natural-log density of garlic mustard individuals in the full model (A). It was also significantly lower in both the mid and late sites when compared to the early-successional site, though this was only apparent when density was also accounted for, as in the full model (B). Partial residual plots show the approximate relationship between growth rate and a given predictor when accounting for all other predictors in the model. Partial residuals are calculated as the sum of model residuals and the term for the predictor of interest. Points are differentiated by study site to allow comparisons among sites. In (B), the boxes encompass the middle 50% of partial residuals for each site (25th-75th percentiles), with the bolded line showing the median. "Whiskers" show the spread of remaining partial residuals, with outliers plotted as open circles.*

Population growth rate had a significant negative relationship with spring temperature but positive ones with summer and ground-level winter temperatures in the full model, suggesting that populations were more successful on average in colder springs but in warmer winters and summers (Table 10; Figures 9-10). These relationships were highly conditional on inclusion of other predictors, however, as they were only significant in the full model (Table 10).

Growth rate was also significantly positively associated with snow depth (Table 10; Figure 10). Snow depth was somewhat correlated with our estimates of ground-level winter temperatures, however (Pearson's r=-0.52), and neither of these two predictors were significant when the other was omitted. Thus, while population growth rate was positively associated with thicker snow layers, thicker snow layers were also associated with cold winters that appeared to offset snow depth's positive effects on garlic mustard populations.

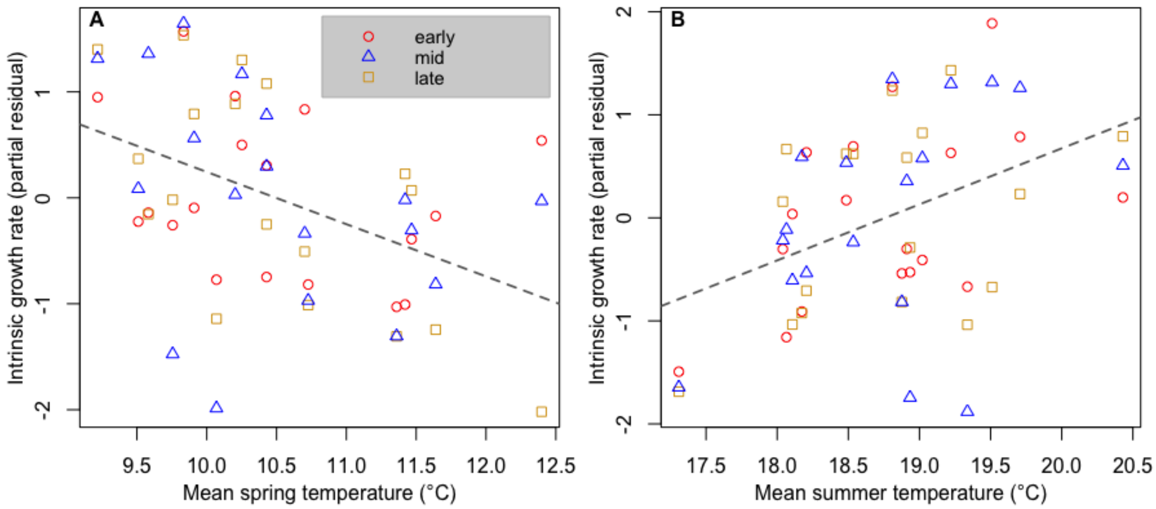

Figure 9: *Intrinsic population growth (r) showed significant but opposite relationships with spring and summer temperature, with higher spring temperatures associated with population decline (A) while higher summer temperatures were associated with growth (B). Partial residual plots approximate the shape of these predictors' relationships with intrinsic growth rate after accounting for all other predictors.*

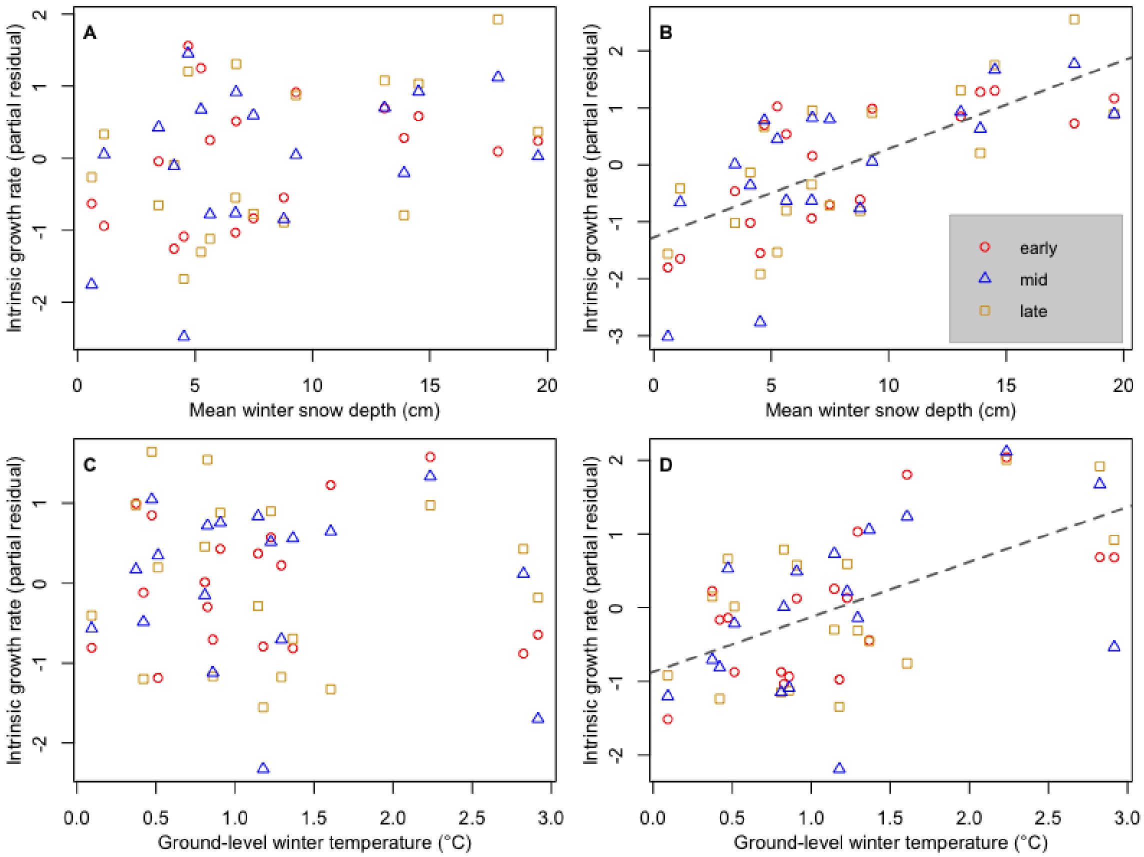

Figure 10: *Intrinsic growth rate showed significant relationships with neither mean winter snow depth nor estimated ground-level winter temperature when only one of the two was accounted for (A, C), but both relationships were significantly positive in the full model (B, D). These negatively correlated predictors' effects on growth rate thus seem to offset one another. Partial residual plots approximate the shape of the predictors relationships with the intrinsic growth rate after accounting for all other predictors in the model.*

Intrinsic growth rate also had significantly positive relationships with both summer and fall precipitation in the full model (Table 10; Figure 11), with wetter growing seasons associated with greater population growth. The slopes of these two terms are similar in the full model, suggesting that the variation in precipitation for each of these seasons is associated with similar amounts of variation in population growth. The relationship between growth rate and fall precipitation was significant for two models (no winter temperature and full models), indicating some robustness to variation in model structure, whereas spring precipitation was only significant for the full model (Table 10).

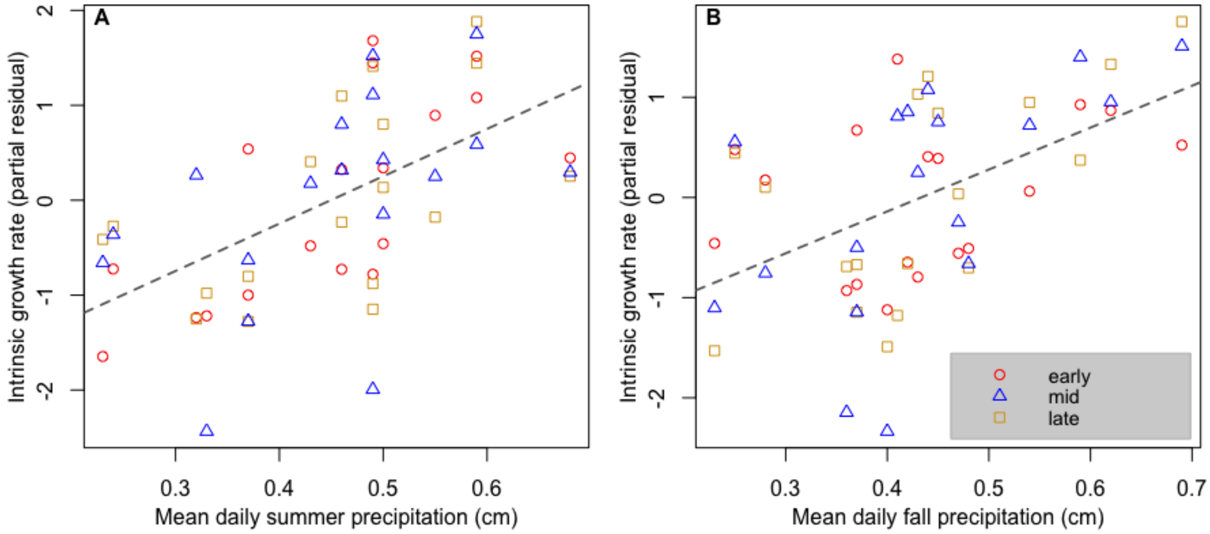

Figure 11: *Garlic mustard population growth had significant positive relationships with both summer and fall precipitation in the full model. Partial residual plots approximate the shape of their relationships with intrinsic growth rate after accounting for all other predictors.*

Models of Survival to Adulthood

Survival from the rosette life stage to adulthood had no clear association with population density, in contrast to the strong density dependence of overall population growth (Table 11). The mid-successional site had higher survival rates on average than the early site, but this difference was only significant when density was not accounted for (Figure 12). It was thus not possible to determine to what extent differences in the sites' qualities influenced survival to adulthood beyond their different population densities.

	Density-Only	Site-Only	No Snow Depth	No Winter Temperature	Full Model
Intercept	**-2.55****	**-2.94****	**-2.80****	**-2.97****	**-3.01****
ln(Mean density per quadrat)	-0.296		-0.223	0.0678	0.0642
Mid site (vs. Early)		**0.828***	0.497	0.874	0.918
Late site (vs. Early)		0.219	0.180	0.176	0.244
Ground-level winter temperature	**-0.457***	**-0.457***	-0.306		**-0.454***
Snow depth	-0.293	**-0.382***		0.197	**-0.399***
Summer precipitation	**-0.260***	**-0.290***	-0.198	-0.152	**-0.295***
Fall precipitation	-0.158	-0.171	-0.100	-0.0828	-0.172
Fall/winter irradiance	**0.272***	0.231	**0.293***	0.206	0.228
Model Pseudo-R^2	**0.284***	**0.342****	0.238	0.209	**0.343***

Table 11: *Survival to adulthood did not show density dependence but had unexpected negative relationships with winter temperature, snow depth, and summer precipitation. Here we give coefficients and variance-function-based pseudo-R^2 values for all models of survival to adulthood. Pseudo-R^2 is not directly comparable to traditional R^2 for ordinary least squares regression, but it allows comparison of explanatory power between the models of survival. All predictors are standardized by mean and standard deviation, so coefficients represent the average change in survival associated with a one standard deviation increase in predictor value. Coefficients that are significantly different from zero (Welch's t-test for predictor slopes, likelihood ratio test for pseduo-R^2) are bolded and labeled with asterisks (*: $p<0.05$, **: $p<0.01$).*

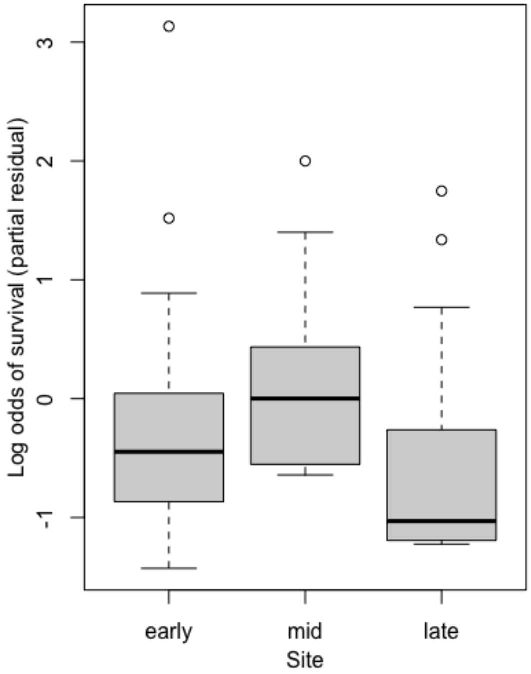

Figure 12: *Survival rates differed significantly between the early and mid sites, but these differences lost statistical significance when density was also accounted for. A partial residual plot based on the full model*

approximates differences in log odds of survival to adulthood, $\ln ln \left(\frac{s}{1-s}\right)$ *, between study sites after accounting for all other predictors.*

Survival to adulthood had significantly negative relationships with both estimated ground-level winter temperature and snow depth in the full model (Table 11). These predictors were only significant when both of them were included, however (Figure 13), suggesting that they may offset one another's effects on survival in the field. That is, while warmer temperatures were associated with lower survival they were also associated with thinner snow layers, which may have improved survival rates. Mean summer precipitation also showed a negative association with survival in the full model (Table 11; Figure 14), so that rosettes experiencing wetter summers tended to have lower chances of surviving to adulthood.

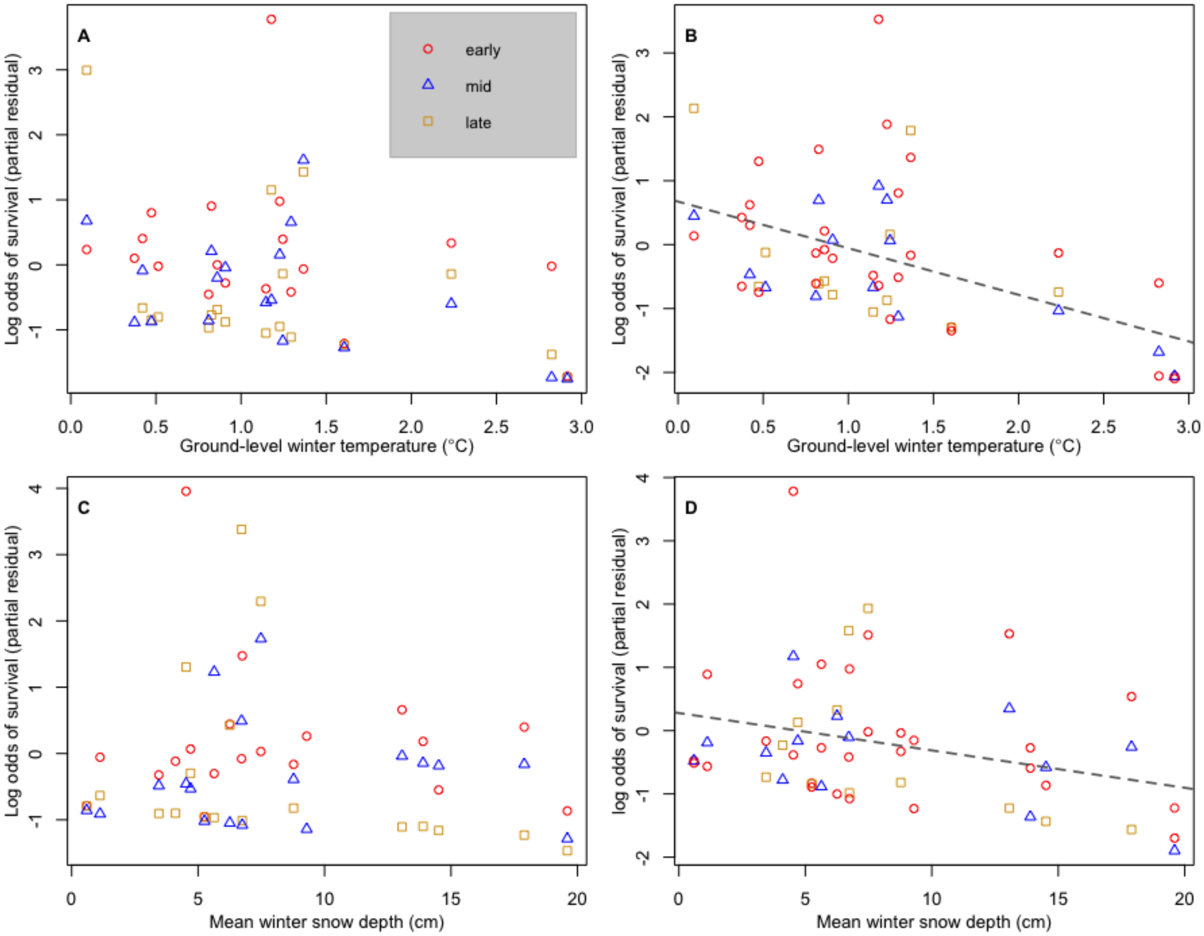

Figure 13: *In the full model, predicted ground-level winter temperature and winter snow depth both displayed unexpected significant negative relationships with survival to adulthood (B, D). Neither of these predictors was significant when the other was removed, however (A, C). It thus seems that these negatively correlated predictors may offset one another's negative effects in the field. Partial residual plots approximate the relationship between the log odds of survival to adulthood and a given predictor after accounting for all other predictors in the model.*

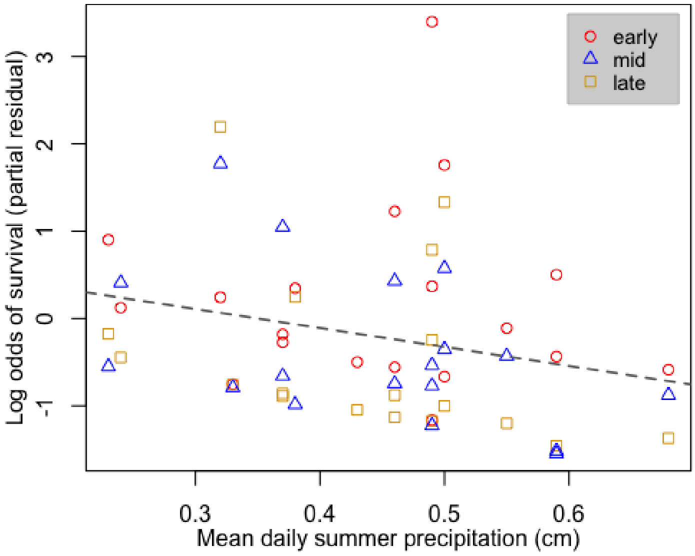

Figure 14: *Survival to adulthood showed a significant negative relationship with mean summer precipitation in the full model. The partial residual plot approximates its relationship with the log odds of survival after accounting for all other predictors.*

Models of Mean Seeds/Plant

Seed production was significantly lower in the mid site than in the early site when density was unaccounted for (t=2.38, p=0.023; Table 12; Figure 15). Density did not show any significant relationship with mean seeds/plant, however. As was the case with survival to adulthood, neither density nor site were significant predictors when they were both considered in the full model. The loss of significant differences between sites when density was considered indicates that the site differences may have been driven in part by density, but density's lack of significance in any model suggest that any density dependence is weak and indistinguishable from other variation in site qualities.

	Density-Only	Site-Only	Full Model
Intercept	**4.081****	**4.519****	**4.475****
ln(Mean density per quadrat)	0.275		0.0718
Mid site (vs. Early)		**-0.855***	-0.747
Late site (vs. Early)		-0.572	-0.541
Ground-level winter temperature	0.452	0.449	0.448

Spring temperature	0.0416	-0.0125	0.000485
Summer temperature	0.323	0.265	0.277
Spring precipitation	-0.00916	-0.0169	-0.00955
Summer precipitation	0.125	0.138	0.134
Spring/summer irradiance	0.137	0.153	0.149
Model R^2	0.258	0.317	0.319

Table 12: *Mean seeds per plant was not associated with either conspecific density or environmental factors. Seed production was lower on average in the mid site than the early site, but this difference was only significant when their different population densities were not accounted for. Here we report coefficients and R^2 values for all models of ln(mean seeds/plant). All predictors are standardized by mean and standard deviation, so coefficients represent the average change in ln(mean seeds/plant) associated with a one-standard-deviation increase in predictor value. Coefficients that are significantly different from zero (Welch's t-test for predictor slopes, F-test for* R^2*) are bolded and labeled with asterisks (*:* $p<0.05$*, **:* $p<0.01$*).*

No environmental factors had significant relationships with ln(mean seeds/plant) in any model (Table 12). Consequently, none of the models tested explained a significant amount of variation in the response overall. There is thus little evidence that reproductive output of Hopkins Forest's garlic mustard populations is sensitive to either variation in environmental conditions or conspecific density.

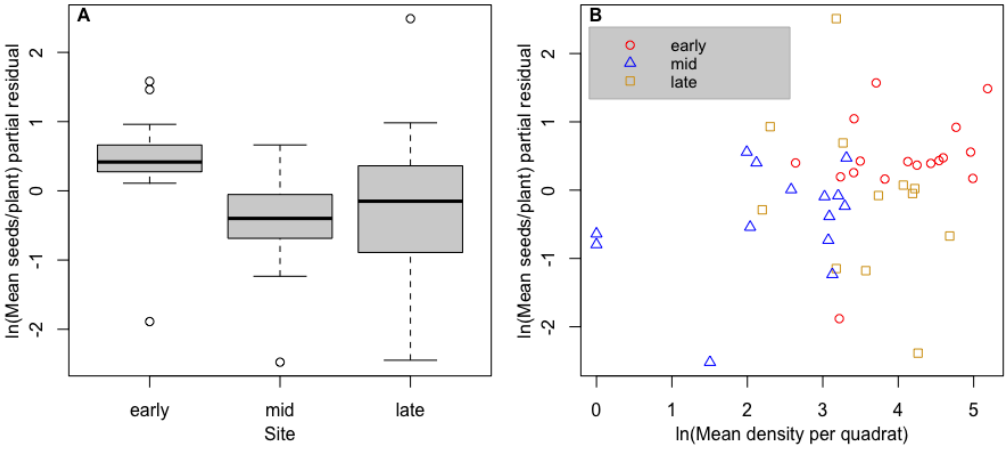

Figure 15: *On average, ln(mean seeds/plant) differed significantly between the early and mid sites when garlic mustard density was not accounted for (A). This difference lost significance in the full model, however. Differences in average density between sites may have contributed to the inter-site variation in ln(mean seeds/plant), but ln(mean seeds/plant)'s relationship with density was non-significant even when site was not accounted for (B). Partial residual plots approximate the shape of these predictors' relationships with ln(mean seeds/plant) after accounting for the environmental predictors in the model.*

Discussion

Summary of Results

All three study populations showed unexpected gradual declines in population density from 1998-2015, though densities also fluctuated widely and showed temporary increases in the late 2000s. Populations at all sites stabilized at consistently low densities by 2016, and none had showed notable signs of recovery by the final year of data (2019). The three populations all showed evidence of biphasic cycling prior to 2016, with alternation between years of high rosette density and years of high adult density. Biphasic cycles were synchronous across the three sites in certain years, most notably 2004-2009, so that the same life stage dominated across all three sites in a given year.

Sites showed notable differences in vegetative community, deer disturbance, and litter depth, density, and species origin. The mid site had the thickest and densest leaf litter and showed the least evidence of deer presence. The late site had slightly but significantly lower snow depth than the others across two sampling days. Garlic mustard populations also differed notably across sites, with the highest population densities in the early site and the lowest in the mid. There was strong evidence that, on average, population growth rate was highest in the early site. We also found evidence that survival from rosette to adult life stages was higher and seed production reduced in the mid site relative to the early site, but these differences were likely at least partly driven by the two sites' differences in mean population density

Intrinsic population growth rate (r) showed strong negative density dependence, with greater population densities associated with lower growth rates. Survival from rosette to adulthood and seed production were not density-dependent, however. Population growth rate was significantly negatively correlated with mean spring temperature but significantly positively correlated with mean summer temperature, winter temperature, and winter snow depth. It also had significant positive relationships with both summer and fall precipitation. Survival from rosette to adulthood showed unexpected negative correlations with winter temperature, snow depth, and summer precipitation. Seed set did not show sensitivity to any environmental factors.

Population Dynamics over Time

The garlic mustard populations at all three of our field sites underwent a striking decline over the course of the study, with reduced fluctuations in population densities after 2010 culminating in stable low densities and constant age structures from 2016-2019. Declines in density of older garlic mustard populations have previously been observed at both regional and local scales (Lankau *et al.* 2009; Blossey *et al.* 2021). Similar declines have been observed for other invasive species, but the mechanisms driving them are often poorly understood (Simberloff and Gibbons 2004). Lankau *et al.* (2009) observed lower allelochemical concentrations and reduced negative effects on native species in older garlic mustard populations, suggesting that long-term population declines are linked to loss of allelopathic and competitive ability. Our data offer opportunities to further test this hypothesis, as we have observed abundance of co-occurring *Arisaema triphyllum* and other native species over the twenty-two years of study. Another valuable avenue of research would be to compare allelopathy of our study populations to that of the many younger and more aggressive populations in the area.

The evidence for gradual population declines of garlic mustard does not negate the species' deleterious effects, but it does suggest that populations may be less destructive in the long-term than previously believed. More work is needed to determine to what extent native plant and soil communities recover following garlic mustard population decline. Research to date indicates that mycorrhizal communities still show partial effects of invasion after six years of experimental garlic mustard removal (Lankau *et al.* 2014) but that soil community diversity largely recovers in garlic mustard stands more than 50 years old (Lankau 2011). Long-term decline of garlic mustard suggests that control efforts are best directed towards preventing new invasions rather than controlling well-established ones, as established forest populations can be expected to become less vigorous in the future.

Our populations showed evidence of biphasic population cycles prior to their stabilization at low densities, alternating between years with high rosette density and years with high adult density. Such cycles have been predicted or observed in other study populations (Pardini *et al.* 2009; Van Riper, Becker, and Skinner 2010; Davis *et al.* 2014). The biphasic cycles involved large fluctuations in densities of each life stage, which further matches the behavior of Van Riper *et al.* (2010)'s populations. They were most evident in periods with denser peak populations, supporting Pardini *et al.* (2009)'s hypothesis that the biphasic cycles are driven by competition between the two life stages. When populations decreased in 2016-2019 biphasic cycling disappeared completely.

Biphasic cycles at our sites occurred synchronously during a high-density period (2004-2009), with all three sites having the same dominant life stage in each of these years. This might suggest that seeds are dispersed between sites during years with large populations, promoting shared dynamics, or else that similar environmental factors drove increases in a particular life stage across the three sites. Further study of the synchronous period would offer more insight into these potential connections between the three populations.

Sensitivity to Conspecific Density, Environmental Variation, and Site Differences

Our models of intrinsic growth rate offered strong evidence that population growth was negatively density-dependent. Negative density dependence has previously been observed in garlic mustard (Pardini *et al.* 2009; Phillips-Mao *et al.* 2014; Stinson *et al.* 2019), and is believed to be an important driver of both the biphasic cycles (Pardini *et al.* 2009) and population declines (Lankau *et al.* 2009) that we and other authors have seen. We found no evidence that survival from rosette to adulthood or mean seeds per plant were associated with density, however. While there is previous evidence that survival to adulthood may be negatively density-dependent (Nuzzo 1993b; Stinson et al. 2019), these correlations were also relatively weak.

Given the lack of evidence for relationships between density and survival to adulthood or reproductive output, our populations' negative density dependence seems driven by effects on germination and seedling survival. Thus, it appears that while young life stages are vulnerable to intraspecific competition this pressure is released among more mature and less dense rosette and adult stages. It is unclear to what extent our evidence that density dependence is limited to early life stages can be generalized to other garlic mustard populations, but our results nonetheless offer an important indication that density effects may not apply equally across the plant's life cycle.

As was the case with density dependence, our results suggest that seed and seedling life stages are particularly vulnerable to environmental variation. Intrinsic growth rate showed high sensitivity to environmental conditions, with five statistically significant environmental predictors in the full model. These five predictors had nonsignificant or opposite relationships with survival to adulthood and mean seeds/plant, however, indicating that the relationships identified in our models of growth rate were likely driven by responses of younger life stages.

Our study does not closely track seed viability, germination, or seedling survival, but our results suggest these early-life processes are particularly vulnerable to external factors and might thus be fertile areas of future study.

Unlike the overall population growth rate, the mean number of seeds produced per plant was remarkably insensitive to both density and environmental predictors. While other factors not considered in our models could be of importance in determining seed production, the lack of statistical significance across our eight independent variables suggests that reproductive fitness of those individuals that survive to adulthood is largely random and not driven by external factors like environment or conspecific density. This insensitivity further supports Pardini *et al.* (2009)'s suggestion that control efforts should be focused on adult plants. While younger individuals may be vulnerable to environmental hazards or intraspecific competition, those that reach reproductive age appear to face few external barriers to successful reproduction besides human control. Removal of adult plants is thus a key step in reducing future success of populations, provided they are removed before they contribute to the population's next generation by producing seed.

Models of survival to adulthood showed significant but surprising results, with probability of survival from rosette to adult life stages negatively associated with winter temperature, snow depth, and summer precipitation. This might indicate that overly favorable conditions lead rosettes to become more vulnerable. Plants might, for example, reduce investment in anti-freezing or allelopathic measures in response to less environmental stress; increases in toxic secondary metabolites due to environmental stress have been observed for other plant species, supporting this possibility (Lovett, Holt, and Christen 1994; Karageorgou, Levizou, and Manetas 2002). More research will be necessary to understand the factors that might drive these results, however.

Our models identified significant differences between sites for intrinsic growth rate, survival to adulthood, and mean seeds per plant, though site differences in these vital rates could only be confidently distinguished from density dependence for intrinsic growth rate. Our sites also displayed large differences in population density. The relatively large population and high growth rate in our early-successional site confirm previous findings that forest edge microhabitats support larger populations than interior forest (Meekins and McCarthy 2001; Stinson *et al.* 2019). Other key differences between sites which might be of importance in determining habitat invasibility include white-tailed deer disturbance (Eschtruth and Battles 2009; Knight *et al.* 2009) and litter depth and quality (Meekins and McCarthy 2001). Relationships between garlic mustard success and leaf litter remain relatively unstudied; given the notable differences in litter depth, density, and species origin between our field sites this might offer a promising direction for future research.

Relationships with Specific Environmental Factors

Taken together, our findings that intrinsic growth rate was positively associated with winter temperatures but negatively associated with spring temperatures imply support for the hypothesis that garlic mustard germination requires intermediate temperatures in the late winter and early spring. Our field results expand the mostly lab-derived evidence in support of this hypothesis (Lhotská 1975; Baskin and Baskin 1992; Blossey, Nuzzo, and Dávalos 2017). Winter snow depth also had a positive relationship with growth rate, indicating that increased depth of the snow layer was associated with greater garlic mustard success even after controlling for the insulating effect of simple snow presence. Associations between garlic mustard and snow depth have not been explored, so our observation of a significant relationship between the two suggests that further study through snow removal experiments or microhabitat comparisons of snow depth would be appropriate. The connection between temperature and garlic mustard populations suggests that the species' invasive range might be expected to shift northward with continued climate warming in order to maintain optimal temperatures and snow cover.

Increased summer and fall precipitation were both associated with significant increases in growth rate, suggesting that these seasons are particularly water-limiting for garlic mustard. Previous work has found that wetter sites tend to be associated with higher density, germination and survival of garlic mustard (Byers and Quinn 1998; Meekins and McCarthy 2001; Haines *et al.* 2018), though an experimental manipulation of rainfall did not cause significant effects on garlic mustard individuals (Hochstedler and Gorchov 2007). Increased precipitation may also promote seed dispersal directly by water (Meekins and McCarthy 2001) or on wet mammal fur (Loebach and Anderson 2018). Our results use the novel method of interannual comparison to expand on the preexisting spatial data in support of garlic mustard's positive association with moisture.

Solar irradiance was the only predictor found to have no significant relationships with population growth, survival to adulthood, or mean seeds/plant. Previous studies have shown conflicting effects of irradiance, with reports of increased garlic mustard biomass with greater light availability (Anderson, Dhillion, and Kelley 1996; Dhillion and Anderson 1999) but also of decreased seedling recruitment (Phillips-Mao *et al.* 2014). It is thus possible that counteractive effects of irradiance at different life stages limited our ability to find results. Our irradiance measurements relied on the assumption that the sugar maple-dominated canopy above the sugarbush weather station was reflective of shading in the garlic mustard sites. The lack of observed relationships between irradiance and our garlic mustard populations may thus result from differences in the shade provided by the sites' dominant tree species, or from site-scale variation in irradiance due to gaps in the forest canopies. Comparisons of solar irradiance between sites or quadrats, rather than through time, would avoid the assumption of similar canopy behavior and offer a better direction for investigating effects of light availability on our populations.

Conclusion

Garlic mustard continues to pose threats to native ecosystems, but data from our populations as well as others show that older populations typically become less invasive. While these results are encouraging, more work is necessary to determine the rate of ecosystem recovery following local garlic mustard decline. Our work confirms previous evidence for biphasic population cycles and negative density dependence, but finds that density dependence is only likely to be significant for early life stages (seeds and seedlings). Early life stages were also found to be particularly vulnerable to environmental variation. These results confirm that control efforts should be focused on adult plants, which are less vulnerable to abiotic factors and less likely to benefit from reduced density following control. Adult plants should be removed before seed development to prevent them from contributing to soil seed banks and future generations.

Our models of garlic mustard growth rate support previous findings that populations benefit from moderate winter/spring temperatures and increased moisture; they also identify effects of snow depth as an interesting avenue for future research. We failed to find any evidence for relationships between solar irradiance and our garlic mustard populations, but spatial comparisons of irradiance in our field sites might offer a more accurate picture of how the populations vary with light availability. Overall, our 22-year study of garlic mustard demography confirms the natural decline and negative density dependence of forest populations. It also suggests that population growth depends on complex interactions between environmental factors such as precipitation, temperature, and winter snow depth. These results point to key areas of future study that would further expand current knowledge of garlic mustard's invasion biology and its potential response to future global change.

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Appendix

Appendix A: ANOVA models comparing litter and snow between study sites

The tables below report output of analysis of variance (ANOVA) models used to test statistical significance of differences in litter and snow depths between the three study sites. Terms with F-test p-values <0.05 were considered significant and are bolded in the tables. ‘*’ denotes p-value<0.05, ‘**’ denotes p-value<0.01. Litter depth differed significantly between study sites only, while snow depth differed significantly between study sites, individual quadrats, and sampling days. The model of snow depth also had a significant interaction between study site and sampling day due to different rates of snowmelt between the sites.

Litter Depth	Sum of squared errors	Mean squared error	F-statistic	F-test p-value
Study site	**242.3**	**121.2**	**13.82**	**3.84×10^{-6}****
Quadrat	33.2	33.21	3.789	0.0539
Sampling day	0.3	0.28	0.031	0.859
Site × Quadrat	25.1	12.53	1.430	0.243
Residuals	1077.9	8.76		

Snow Depth	Sum of squared errors	Mean squared error	F-statistic	F-test p-value
Study site	**349.7**	**174.8**	**14.97**	**7.08×10^{-7}****
Quadrat	**763.1**	**31.8**	**3.171**	**3.81×10^{-6}****
Sampling day	**1961.3**	**1961.3**	**167.9**	**Near-zero****
Site × Day	**88.2**	**44.1**	**4.396**	**0.0135***
Quadrat × Day	347.1	14.5	1.442	0.0900
Residuals	2166.0	10.0		

Appendix B: p-values for models of growth rate, survival, and seed production

P-values for the models of intrinsic growth rate, survival from rosette to adult life stages, and ln(mean seeds per plant) were omitted from Tables 10-12 for the sake of simplicity but are reported below. P-values for independent variables were generated from Welch's t-tests of model coefficients. P-values for the overall model were generated from F-tests in the case of growth rate and seeds/plant and from a likelihood ratio test in the case of survival to adulthood. P-values <0.05 were considered significant and are bolded in the tables. '*' denotes p-value<0.05, '**' denotes p-value<0.01.

Intrinsic growth rate (r)	Density-Only	Site-Only	No Snow Depth	No Winter Temperature	Full Model
Intercept	0.646	0.659	**0.0205***	**5.11×10^{-3}****	**8.06×10^{-4}****
ln(Mean density per quadrat)	**8.43×10^{-4}****		**5.65×10^{-6}****	**1.00×10^{-6}****	**1.60×10^{-7}****
Mid site (vs. Early)		0.828	**1.91×10^{-3}****	**3.32×10^{-4}****	**3.94×10^{-5}****
Late site (vs. Early)		0.818	**0.0485***	**0.0163***	**3.59×10^{-3}****
Spring temperature	0.346	0.953	0.384	0.191	**0.0219***
Summer temperature	0.220	0.545	0.486	0.174	**0.0274***
Ground-level winter temperature	0.640	0.510	0.808		**0.0332***
Snow depth	0.445	0.397		0.0557	**4.54×10^{-3}****
Spring precipitation	0.406	0.371	0.455	0.597	0.488
Summer precipitation	0.272	0.893	0.308	0.145	**0.0110***
Fall precipitation	0.0697	0.277	0.0532	**0.0207***	**3.52×10^{-3}****
Spring/summer irradiance	0.547	0.483	0.586	0.685	0.681
Fall/winter irradiance	0.937	0.912	0.924	0.832	0.685
Overall model	**0.0420***	0.829	**2.52×10^{-3}****	**5.92×10^{-4}****	**1.95×10^{-4}****

Survival from rosette to adult	Density-Only	Site-Only	No Snow Depth	No Winter Temperature	Full Model
Intercept	**Near-zero****	**Near-zero****	**1.08×10^{-9}****	**2.53×10^{-9}****	**1.06×10^{-10}****
ln(Mean density per quadrat)	0.128		0.417	0.837	0.827
Mid site (vs. Early)		**0.0191***	0.353	0.149	0.0930
Late site (vs. Early)		0.490	0.624	0.640	0.476
Ground-level winter temperature	**0.0156***	**0.0128***	0.116		**0.0144***
Snow depth	0.0856	**0.0201***		0.268	**0.0308***
Summer precipitation	**0.0483***	**0.0282***	0.122	0.250	**0.0302***
Fall precipitation	0.328	0.292	0.548	0.603	0.298
Fall/winter irradiance	**0.0371***	0.0794	**0.0319***	0.161	0.0913
Overall model	**0.0112***	**6.02×10^{-3}****	0.0768	0.173	**0.0137***

ln(Mean seeds per plant)	Density-Only	Site-Only	Full Model
Intercept	**Near-zero****	**Near-zero****	**Near-zero****
ln(Mean density per quadrat)	0.0972		0.738
Mid site (vs. Early)		**0.0233***	0.133
Late site (vs. Early)		0.136	0.175
Ground-level winter temperature	0.0551	0.0545	0.058
Spring temperature	0.0416	0.941	0.998
Summer temperature	0.106	0.170	0.165
Spring precipitation	0.968	0.940	0.967
Summer precipitation	0.478	0.420	0.441
Spring/summer irradiance	0.438	0.376	0.396
Model R^2	0.132	0.0809	0.133