

## SPECIAL FEATURE: LONG-TERM DYNAMICS AND IMPACTS OF PLANT INVASIONS

# Climate and rapid local adaptation as drivers of germination and seed bank dynamics of *Alliaria petiolata* (garlic mustard) in North America

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## Summary

**1.** Local differences in climate conditions may facilitate rapid evolutionary changes in introduced plants to optimize timing of germination or ability to survive in seed banks, which may constitute beneficial demographic adaptations during range expansions. Understanding differences in germination requirements and emergence patterns across a species' range is critical for demographic modelling and potential invasive species control efforts.

**2.** We assessed germination responses of *Alliaria petiolata* using seeds collected from 10 populations spanning much of the North American distribution of the species. We compared germination responses under different stratification regimes in a growth chamber over 2.5 years, and evaluated seedling emergence in a common garden in Ithaca, New York over 13 years. We further evaluated how climate overlap between Ithaca and original collection sites influenced emergence patterns.

**3.** In the laboratory, germination of all populations was similar and highest at 4 °C stratification. Seeds exposed to sub-zero temperatures delayed germination and population responses were variable. In the common garden, seedlings from most populations emerged over 13 years, and emergence patterns were strongly influenced by population. Annual emergence was positively correlated with spring temperature and inversely correlated with number of spring days with minimum temperature below freezing. Climate overlap between the common garden and original collection location enhanced germination, but common garden climate conditions over the course of the 13-year experiment and population identity had greater explanatory power.

**4. Synthesis.** Laboratory germination tests did not reflect seedling emergence under field conditions. After 150 years of residence time in North America, *Alliaria petiolata* populations have developed striking differences in their responses to local climates and stratification requirements suggesting that a complex interplay of pre-adaptation, rapid evolutionary changes, and phenotypic plasticity result in locally adapted populations.

**Key-words:** climate modelling, germination, invasion, local adaptation, seed bank

## Introduction

The evolution of terrestrial plants has created diverse life-forms that can thrive under extreme climates and growing conditions. The vast majority of species produce seeds, some only once in their lifetime, allowing dispersal and giving rise to new generations. A nearly ubiquitous feature across all taxa is seed dormancy, which can range from a few weeks or months to decades

or centuries (Finch-Savage & Leubner-Metzger 2006). Many seeds, depending on specific habitat requirements of seedlings or adult plants, require very specific cues to break dormancy ranging from biotic (gut passage with scarification of the seed coat, or presence of mutualists in orchids), to smoke (for fire-adapted species), salt water exposure, rainfall, cold–warm cycles, to specific photoperiod requirements (Finch-Savage & Leubner-Metzger 2006; Willis *et al.* 2014; Fuzessy *et al.* 2016).

Specific environmental sensitivity of dormant seeds can have major implications for dispersal, colonization, plant demography, speciation and extinctions (Willis *et al.* 2014). All environments can undergo unpredictable fluctuations in

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climate and biota (e.g. predators, dispersal vectors, competitors, pollinators and mutualists), thus growing conditions may vary from day to day, seasonally, annually and over decadal or evolutionary time frames. Seed dormancy is thought to have evolved as a bet hedging strategy where organisms faced with unpredictable futures trade-off average fitness to reduce variance in fitness (Gremer & Venable 2014). The classic examples are desert annuals, where plants have a single season to complete development and seed set. If conditions are (or turn) unfavourable during a season, spreading germination over multiple seasons can avoid complete reproductive failure and local extinction (Gremer & Venable 2014). Plants, as well as some fungi (Graham, Smith & Simons 2014) and insects (Rajon *et al.* 2014), use dormancy as a type of forecasting to deal with future conditions based on their evolutionary histories. Dormancy, and differences among species and populations, appears to evolve, as predicted by theory, in proportion to bad years encountered in any particular locale (Evans *et al.* 2007; Simons 2009; Graham, Smith & Simons 2014; Rajon *et al.* 2014).

Seed dormancy can function as dispersal through time, and is influenced by factors such as previous land-use history, herbivory, maternal environment, position of seeds on the mother plant, latitude and altitude (Andersson & Milberg 1998; Donohue & Schmitt 1998; Baeten *et al.* 2010; Colautti & Barrett 2010; Delye *et al.* 2013; Vidigal *et al.* 2016). Germination sets in place a process that ultimately determines seedling recruitment, and has relevance for plant fitness and persistence (Cochrane *et al.* 2015), regardless of whether plants complete their life cycle in a few weeks, months or centuries. The existence of inter-population variation in germination and growth responses, including latitudinal clines, is a well-known phenomenon enabling selection to optimize germination, flowering and seed production to the most favourable periods of the growing season (Colautti & Barrett 2013; Wilczek *et al.* 2014; Cochrane *et al.* 2015; Vidigal *et al.* 2016).

Establishment requires seedling to be physiologically matched to local biotic and abiotic conditions, and/or with the ability to maintain fitness through phenotypic plasticity (Hulme & Barrett 2013). Local climates and growing conditions that vary through the range of a plant species allow selection to favour genotypes with local adaptations that manifest themselves along environmental gradients, for example salinity (Beaton & Dudley 2013), precipitation (Leiblein-Wild & Tackenberg 2014) or growing season length (Colautti & Barrett 2010; Novy, Flory & Hartman 2012). However, while there is abundant evidence for among-population variation in seedling emergence, growth and establishment, recent evidence (Cochrane *et al.* 2015) questions the validity of environmental gradients as drivers of this inter-population variation. Furthermore, past and contemporary climate change have caused adaptation lags in species where genotypes from historically warmer climates show higher performance than local genotypes (Wilczek *et al.* 2014). Differences in performance among genotypes suggest that local adaptive optima have shifted with recent climate changes over a species' native range.

Long-distance dispersal events, including introduction of non-native species, can remove seeds or propagules from their evolved local optima. That introduced species are able to establish and thrive has variously been linked to many different factors, including ability to do well in human-altered landscapes (Buckley, Bolker & Rees 2007), lack of natural enemies (Keane & Crawley 2002) and evolution of increased competitive abilities (Blossey & Nötzold 1995). Yet it has also been suggested that evolution, simply by chance, may have created superior pre-adapted genotypes elsewhere that are better adapted locally than their native competitors (Sax 2000). Pre-adaptation, phenotypic plasticity and rapid adaptation to novel growing locations for introduced plant species has received enormous attention by scientists in an attempt to explain their success (Sakai *et al.* 2001; Richards *et al.* 2006; Colautti & Barrett 2013; Dlugosch *et al.* 2015). These investigations documented widespread local adaptation in introduced species that surprisingly matches local adaptations of native species (Flores-Moreno & Moles 2013; Oduor, Leimu & van Kleunen 2016) and materializes within a few generations (Williams, Kendall & Levine 2016). These rapid adaptations do not involve morphological features but more often physiological or chemical changes in response to climate, competitors, mutualists or natural enemies (Faillace & Morin 2016; Kilkenny & Galloway 2016; Colautti *et al.* 2017).

We evaluated contributions of seed and germination traits to the demographic success of the European biennial herb garlic mustard (*Alliaria petiolata*) in North America. The species originates from temperate and oceanic western Europe (Meekins, Ballard & McCarthy 2001; Durka *et al.* 2005), and thrives in continental winter conditions of Canada (46°N) as well as >2000 km south in the heat of Georgia (34°N; Nuzzo 1993). However, reports of low seed bank duration and alternating populations of rosettes and flowering plants in southern (Baskin & Baskin 1992) but not northern locales (Cavers 1995) suggest novel germination responses and population dynamics in the introduced range. Seed and seed bank dynamics are important factors determining *A. petiolata* demography (Davis *et al.* 2006; Evans *et al.* 2012) and we used seeds collected from across the current range of the species in eastern North America in both a common garden and growth chamber experiments to assess whether local differences in climate resulted in locally adapted *A. petiolata* populations. While the typical approach to assess local adaptation involves reciprocal transplant gardens (Maron *et al.* 2004; Williams, Auge & Maron 2008; Moloney *et al.* 2009; Hulme & Barrett 2013; Wilczek *et al.* 2014), we avoided the logistically and financially difficult task of managing multiple gardens over many years by incorporating climate modelling using conditions at the seed collection sites (Nadeau & Fuller 2015). We evaluated the following hypotheses: (i) Germination of seeds collected from populations across eastern North America peak in experimental treatments that represent climate conditions at collection locations indicating local adaptation and (ii) Seed banks are short-lived ( $\leq 5$  years) regardless of collection location in eastern North America.

## Materials and methods

### EXPERIMENTAL ORGANISM

*Alliaria petiolata* (Brassicaceae) is an obligate self-fertile Eurasian biennial herb first recorded in North America in 1868 on Long Island, New York (Nuzzo 1993). The species now occurs from southern Canada south to Georgia, and from New York and Quebec west to Oregon and British Columbia, and even Alaska (Nuzzo 1993; Rollins 1993; Blossey *et al.* 2001). Genetic evidence suggests that *A. petiolata* was likely introduced from multiple European (British Isles, north and central Europe) source populations with similar oceanic climates (Meekins, Ballard & McCarthy 2001; Durka *et al.* 2005). The species shows high among-population genetic variation (Meekins, Ballard & McCarthy 2001) and undergoes rapid evolutionary change in North America (Lankau *et al.* 2009). Phenology of *A. petiolata* varies with local climates; but typically seeds germinate in spring (often under leaf litter or even snow; B. Blossey, pers. obs.), and seedlings form small rosettes in late spring/early summer. Rosettes overwinter and in the following spring additional leaf production is followed by bolting and flowering. Seeds ripen, drop and plants senesce in summer (Byers & Quinn 1998).

### GERMINATION UNDER LABORATORY CONDITIONS

At the time we initiated our experiment (1997), available information suggested that *A. petiolata* seeds are dormant at maturity (Baskin & Baskin 1992) and dormancy is broken by 100 days of 1–4 °C (Lhotska 1975; Baskin & Baskin 1992; Anderson, Dhillon & Kelley 1996), with exhaustion of the seed bank after 3 years (Kinzel 1926; Cavers, Heagy & Kokron 1979; Roberts & Boddrell 1983; Baskin & Baskin 1992).

We obtained seeds as bulk collections from  $\geq 30$  plants/site from over 30 sites across the range of *A. petiolata* in eastern North America. We stored seeds dry in paper bags at room temperature and selected 10 populations representing the range of distribution and climatic regimes for our laboratory germination trials (Fig. 1; Table S1, Supporting Information). We developed seven stratification regimes representing temperature conditions of the collection sites, ranging from mild southern winters without soil freezing (regimes 1 and 2) to increasingly colder and longer winters with longer duration of sub-zero (°C) temperatures (regimes 3–7, Table 1). We chose constant over fluctuating temperature regimes because *A. petiolata* germination occurs in early spring in buffered locations under leaf litter or snow (B. Blossey, pers. obs.), which limits temperature changes.

We filled Petri dishes (6 cm diameter) with 1.4 g autoclaved potting soil (Farfard Canadian growing mix No. 1-P, Agawam, MA, USA) and 7 ml water for moist stratification. For each population, we evenly distributed 50 randomly selected seeds across the soil surface in each of five Petri dishes, for a total of 350 experimental units (5 replicates  $\times$  7 stratification regimes  $\times$  10 populations). We sealed each Petri dish with parafilm to limit moisture loss.

We established treatments with exposure to sub-zero temperatures first to allow a simultaneous first exposure of all treatments to 4 °C on 5 May 1998. We exposed Petri dishes to sub-zero temperatures in a commercial freezer (–15 °C; Frigidaire, Martinez, GA, USA), to 4 °C in a commercial refrigerator (Frigidaire), and to summer temperatures (30 °C) in a reach-in incubator (Environmental Growth Chambers, Chagrin Falls, OH, USA). We checked Petri dishes for germination every week until day 60 (4 July 1998) and then every other day until day 115 (25 August 1998) followed by weekly to monthly checks through 6 November 2000 when the experiment terminated. We added



**Fig. 1.** *Alliaria petiolata* seed collection locations in eastern North America. Triangle indicates location of the common garden in Ithaca, New York; gray circles indicate collection locations from which seed was only used in laboratory experiments. Distance between 10° of latitude and longitude is approximately 1100 km. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**Table 1.** Initial stratification conditions for *Alliaria petiolata* seeds representing increasingly northern climates (refer to text for details regarding treatments)

Treatment	Temperature regime
Southern winters	
1	Continuous 4–7 °C
2	70 days at 4 °C, 40 days at 30 °C, then continuous 4 °C
Northern winters	
3	70 days at 4 °C, 40 days at 30 °C, 30 days –15 °C, then continuous 4 °C
4	30 days at 4 °C, 30 days –15 °C then continuous 4 °C
5	Seeds kept frozen (–10 to –15 °C) for 15 days, then continuous 4 °C
6	Seeds kept frozen (–10 to –15 °C) for 30 days, then continuous 4 °C
7	Seeds kept frozen (–10 to –15 °C) for 60 days, then continuous 4 °C

water as needed to maintain appropriate moisture condition for germination throughout this period. We defined germination as emergence of the radicle and we removed seeds once they germinated. We maintained all treatments at 4 °C until there was little or no germination for 90 days. From 17 June 1999 onwards, we exposed all Petri dishes of all treatments to 30 °C (representing summer conditions) for 60 days before returning them to 4 °C. We maintained all Petri dishes at 4 °C until 19 April 2000, before returning them to 30 °C for 62 days to simulate a second summer. We then returned Petri dishes to 4 °C and after 917 days terminated all treatments on 6 November 2000.

### EMERGENCE IN COMMON GARDEN

To test *A. petiolata* seedling emergence under field conditions, we selected a 5 m  $\times$  10 m area under dappled shade in Ithaca, New York (Fig. 1). The distance to the closest known *A. petiolata* plant was >50 m. We removed leaf litter by raking, then applied glyphosate (Roundup, Monsanto Agricultural Products Company, St. Louis, MO, USA) on 18 and 24 September 1997 to remove existing vegetation. We rototilled soil to a depth of 20–30 cm and further levelled and raked the site on 23 October 1997 to prepare the seedbed.

As experimental units we constructed 40 cages (30 cm × 30 cm × 30 cm) using 1.3 cm diameter CPVC pipe. To secure each cage to the ground, we hammered each of the four corner pipes 10 cm into the ground. We arranged cages in three rows (25 cm spacing within rows, 50 cm spacing between rows) and on 5 November 1997 we enclosed each cage with a gauze bag (white NOSEUM netting; Balson Hercules Group, Providence, RI, USA). We tied each bag at the top and buried the lower 10 cm of gauze to prevent addition or removal of seeds by above-ground seed vectors or predators (rodents, insects and birds). Over time we repaired or replaced gauze bags as needed. We did not manipulate or prevent access by below-ground seed predators such as soil pathogens or earthworms, which are ubiquitous at the site (particularly *Lumbricus* spp.).

We selected 7 of the 10 populations tested under laboratory conditions for germination under field conditions (Fig. 1) based on seed availability. We randomly assigned cages to one of seven populations or a control treatment that did not receive seeds ( $N = 5$  replicates per treatment). On 6 November 1997, we sowed 500 seeds evenly on the bare soil in each cage, then tamped seed lightly to ensure seed–soil contact, covered the soil in all cages with 5 cm of sugar maple (*Acer saccharum*) leaf litter. To maintain a thin leaf litter layer, we added 5 cm of maple leaves on 9 October 2000.

We recorded emergence of *A. petiolata* seedlings in all 40 cages for 13 years (1998 through 2010) by checking each cage at weekly to tri-weekly intervals and recording seedling emergence (defined as seedlings having one or two cotyledons present above the leaf litter). We removed all emergents. As seasonal emergence patterns became clear, we were able to reduce the frequency of checks without compromising data accuracy. In the first season (1998), we started emergence checks at snowmelt and continued through 1 September 1998. We initiated emergence checks each year immediately after snow melt, but in 1999, we terminated emergence checks in mid-July and for the remainder of the experiment (2000–2010), we terminated emergence checks by mid-June.

## STATISTICAL ANALYSES

We evaluated effects of population source, temperature regime under laboratory conditions and their interaction on proportion of seeds germinating with a generalized linear model (GLM) with binomial errors. We applied a second GLM (binomial errors) to evaluate effect of venue (common garden and controlled condition-temperature regime 1), population source and their interaction on total proportion of seeds emerging. We evaluated fit of GLM models via percent deviance explained by each model.

We evaluated effect of population source on total *A. petiolata* emergence after 13 years in the common garden with a GLM with binomial errors. We recorded two *A. petiolata* seedlings emerging in control plots over the 13 years—these observations were removed for all analyses. To model *A. petiolata* emergence over time, we employed generalized additive mixed models (GAMMs) with binomial errors, including population as a random effect. Generalized additive models are a nonparametric approach that can account for nonlinear relationships through the use of splines (Hastie & Tibshirani 1990). Based on initial data exploration, we modelled temporal effects as a nonlinear response and climate variables as linear responses (see below for description of climate variables). We fitted three sets of GAMM models: in the first set, models had a separate time smoother for each site; in the second set, models had common smoothers for groups of sites with similar emergence patterns; and in the third set, models had a single smoother across all sites. We did not test for

interactions among climate variables and time. Residual inspection did not indicate violation of normal distribution or constant variance assumptions. We selected the best model based on Akaike information criterion (Burnham & Anderson 2002) and fitted all models in R statistical software (R Core Team 2014) using gamm function in the mgcv package (Wood 2011). Proportion emerging each year was based on the number of seed present at the beginning of a given year (= total seeds sown minus those that emerged in previous years).

To evaluate effects of climate at the common garden in Ithaca on *A. petiolata* emergence (GAMM models detailed above), we obtained mean monthly temperature, total monthly precipitation, and number of days with minimum and maximum temperature below the freezing point at the closest weather station (Table S1) from the National Climatic Center (NCDC 2014). Year data points reflected monthly averages October–December of the previous year and January–May of the current year.

We evaluated the climate overlap between the common garden and original collection sites with Matusita's measure of distributional overlap index (Lu, Smith & Good 1989) as applied in Nadeau & Fuller (2015). The unitless index varies between 0 and 1 and quantifies the overlapping area between probability distributions describing climate at the common garden and climate at the original collection sites. The index ( $\rho$ ) is defined as

$$\rho = (Q * R) \quad \text{eqn 1}$$

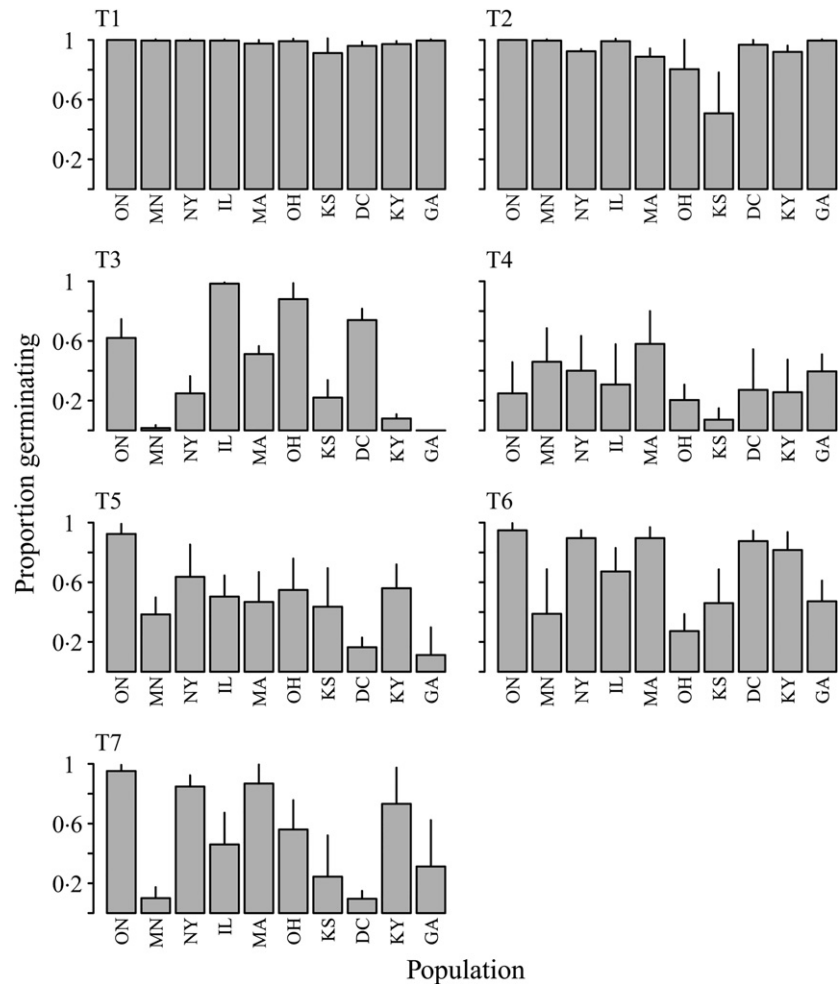
where  $Q$  is a measure of the change in means for weather variables included in the analysis and  $R$  is a measure of the correlation among weather variables (Nadeau & Fuller 2015). We used current climate (1980–2010) at each collection site and the common garden and represented climate as a joint probability of mean monthly temperature, mean total precipitation per month and number of days with minimum temperature below freezing. We excluded days with maximum temperature below freezing because this variable had no effect on *A. petiolata* emergence in the common garden (see Results section). We obtained climate data from the closest weather station to our collection sites with complete records for the study period (Table S1; NCDC 2014). We applied a bootstrap procedure to calculate 1000 estimates of overlap,  $R$ , and  $Q$  and to test if estimated values differ from estimates at the common garden. Finally, we evaluated effect of climate overlap on total *A. petiolata* emergence via a GLM with binomial errors.

## Results

### LABORATORY

We recorded germination from all populations and in all treatments up to 647 days after experimental setup. Under ideal conditions (regime 1, 4 °C constant), germination began after as little as 60–70 days, reached 25% within 70–80 days, and in just a few days germination rates increased from 25 to 75% for most populations (Table S2). Germination was significantly affected by treatment, population and their interaction ( $P < 0.001$ , 90% of deviance explained). Regimes 1 and 2 (temperatures always above 0 °C) averaged 94% germination, significantly higher than the average 48% germination in regimes 3–7 (exposed to –15 °C for varying lengths of time) with regime 1 the ideal laboratory condition to maximize germination (Fig. 2). Exposing stratified seeds to elevated temperatures (regime 2, Table 1) suppressed germination within a few days but synchronized germination when seeds were once





**Fig. 2.** Proportion of *Alliaria petiolata* seeds germinating under seven different temperature regimes (see Table 1). Data are means  $\pm$  1 SE of five replicates for each of 10 source populations in eastern North America (see Fig. 1;  $N = 50$  seeds/source population). For two letter source location details see Table S1.

again exposed to 4 °C (Fig. S1). Total germination varied among populations and ranged from 81% average across all treatments for ON to 41% for KS. Germination of each population was significantly dependent on temperature regime (Fig. 2). For example, IL, OH and DC reached 98, 88 and 74% germination in regime 3, whereas MN, GA and KY germination averaged less than 10% under the same conditions. Furthermore, while seeds from OH outperformed KY in regime 3 (88 and 8% germination respectively), the opposite occurred under regime 6 (27 and 82% respectively).

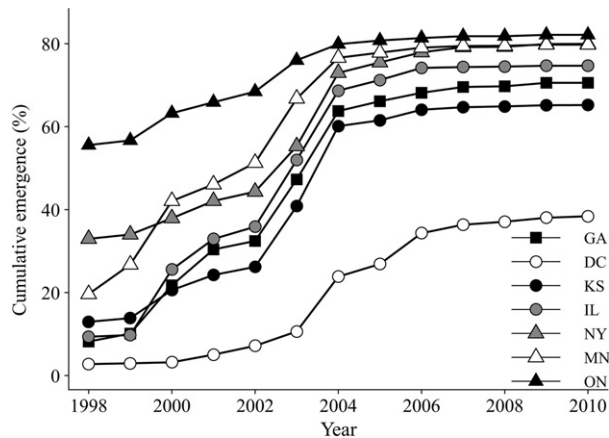
Total germination of all populations evaluated in laboratory and common garden studies (Figs 2 and 3) was significantly higher in regime 1 than in the common garden ( $P < 0.001$ ) averaging 98 and 70% germination across all populations respectively. However, higher germination in regime 1 depended on population identity (significant venue  $\times$  population interaction;  $P < 0.001$ ) with the greatest increase (field to regime 1) for DC (150% increase), followed by GA (41%), KS (39%), IL (33%), MN (25%), NY (24%) and ON (22%).

#### COMMON GARDEN

Seedlings emerged for 13 consecutive years for three of seven populations (Fig. 3), and 12 consecutive years for the remaining four populations (seedlings from MN emerged

every year except year 11). Average *A. petiolata* emergence after 13 years was 70% across the seven populations but emergence rate varied among populations ( $P < 0.001$ , 60% of deviance explained) and was significantly lower for DC (38%) than for all other populations (Fig. 3). As under ideal germination conditions in the laboratory, seedling emergence was synchronized over a very short early spring period (Fig. S2). We recorded the highest and similar total emergence for the four most northern populations: ON (82%), MN (80%), NY (80%) and IL (75%). Total emergence from GA (71%) was significantly lower than ON, but did not differ from MN, NY or IL. Emergence from KS (65%) was significantly lower than emergence from the four northern populations but did not differ significantly from GA. Seedling emergence per year varied throughout the study period and populations responded differently (Figs 3 and 4). The emergence peak recorded in 2004 was coincident with a year with few spring days with minimum temperature  $\leq 0$  °C (Fig. 5).

While seedling emergence varied among populations and years, all populations followed a similar pattern in response to temperature and precipitation in the common garden. Results from the best model indicated that emergence over time was dependent on population source and was negatively correlated with mean monthly temperature ( $-0.19 \pm 0.03$ ;



**Fig. 3.** Cumulative emergence (%) of *Alliaria petiolata* over a 13-year period in a common garden in Ithaca, New York. Seeds were collected in summer 1997 from seven source populations in eastern North America (see Fig. 1) and planted in fall 1997. Data are means of five replicates/source population ( $N = 500$  seeds/replicate; standard errors omitted for clarity; for two letter source location see Table S1).

$P < 0.001$ ) and with the number of spring days with minimum temperature below freezing (estimate =  $-0.09 \pm 0.006$ ;  $P < 0.001$ ; see Fig. S3 for climate conditions at collection locations). All other climate variables were not significant and dropped from the final model.

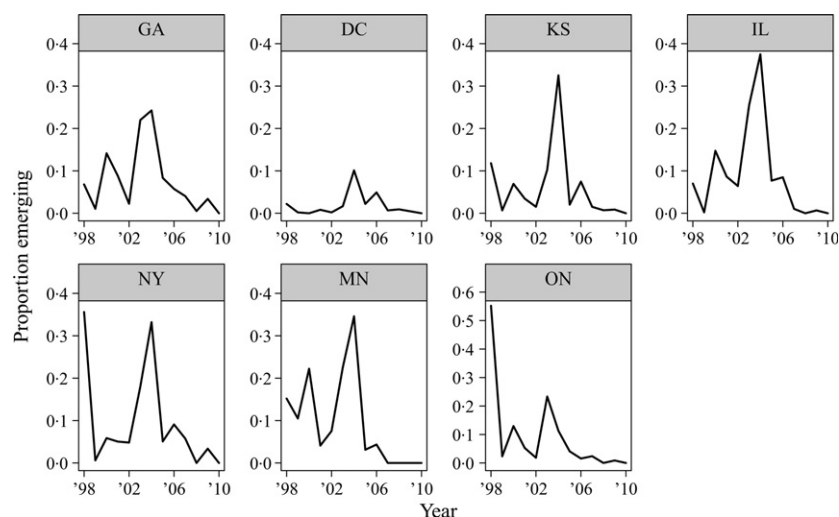
After accounting for climate, model results indicated that *A. petiolata* seedling emergence declined over time for all populations except DC, but the pattern of decrease depended on population (Fig. 6). DC and MN presented unique emergence patterns, and NY and ON, and IL, KS and GA formed two distinct groups (Fig. 6).

Climate overlap index between the common garden and original collection locations ranged from 0.03 to 0.67 (Fig. 7), with higher overlap between the New York common

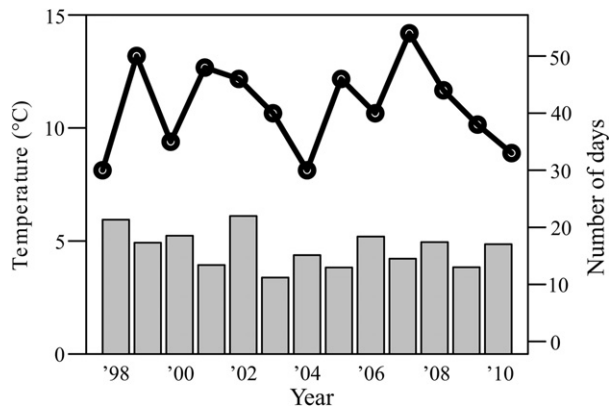
garden and northern locations (IL, MN and ON) and lower overlap between New York and southern locations (DC, GA and KS). The average contributions of changes in the means of weather variables included in the analysis to the overlap index ( $Q$ , Equation 1) ranged from 0.02 to 0.77 and were significantly different ( $\alpha < 0.05$ ) for all populations. Changes in the variance-covariance matrix (i.e. correlation among variables,  $R$ , Equation 1) ranged from 0.70 to 0.90 and were significantly different for DC ( $P = 0.01$ ) and GA ( $P = 0.02$ ) only. The climate overlap index had a significant positive effect on total germination after 13 years (estimate  $\pm$  SE:  $0.39 \pm 0.03$ ,  $z = 12.39$ ,  $P < 0.001$ ), explaining 27% of deviance. A parallel model including population instead of climate overlap index (see above) explained 60% of deviance, indicating that climate overlap, although highly significant, did not fully explain population variation.

## Discussion

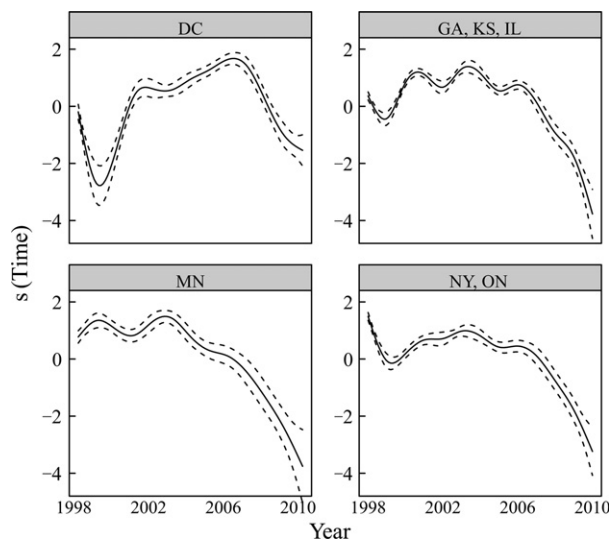
Seed dormancy and germination requirements are critical determinants of colonization and establishment success (Willis *et al.* 2014), and expected to be under strong and geographically variable selection pressure (Donohue 2009). Indeed we found support for our first hypothesis that germination of seeds is highest when experimental treatments reflect climate conditions at collection locations. As hypothesized, greater climate overlap between conditions at collection locations and the common garden resulted in higher seedling emergence suggesting local adaptation. The diversified responses among populations were best explained by conditions at the common garden location in Ithaca. Climate conditions at original collection locations (temperature, precipitation) had less explanatory power. Phenotypic plasticity (Richards *et al.* 2006) likely contributes to the ability of *A. petiolata* to thrive across its range in North America, but our modelling efforts



**Fig. 4.** Annual proportion of *Alliaria petiolata* seeds from seven source populations in eastern North America (see Fig. 1) emerging over a 13-year period in a common garden in Ithaca, New York. Proportion is based on the number of available seed at time  $t$  (= total seeds sown minus those that emerged in previous years). Data are means of five replicates/source population ( $N = 500$  seeds/replicate at planting); standard errors omitted for clarity; note different y-axis scale for ON. For two letter source location details, see Table S1.



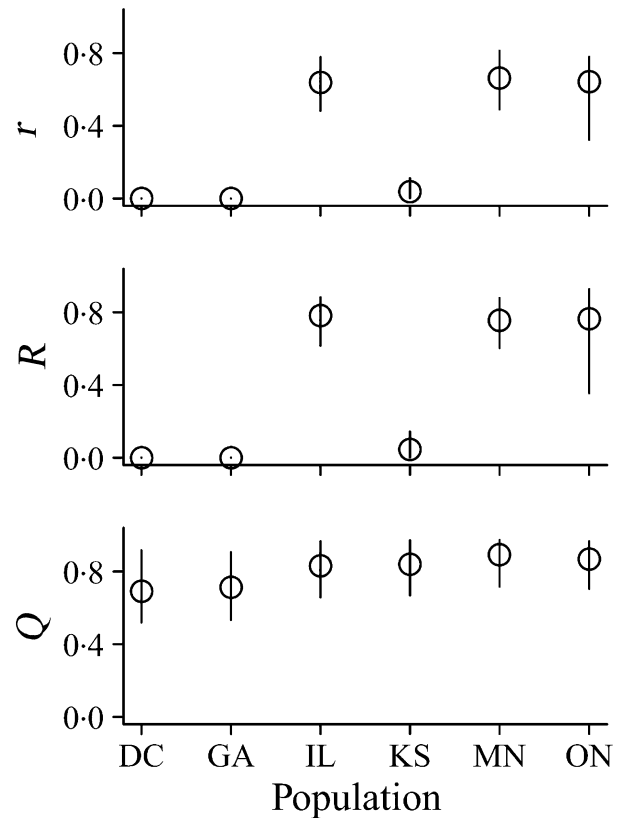
**Fig. 5.** Average mean monthly temperature °C (gray bars) in September to May and number of spring days with minimum temperatures  $\leq 0$  °C per year (black line) at common garden location in Ithaca, New York for the duration of the emergence experiment (1998–2010). Year indicates monthly averages in October to December of previous year and January to May of current year.



**Fig. 6.** Emergence of *Alliaria petiolata* as a function of time from 1998 to 2010 when exposed to conditions in a common garden in Ithaca, New York. Seeds were collected from seven different source populations in eastern North America (Fig. 1). Generalized additive model smooth curves (solid line) with 95% credible intervals (dashed lines) grouping sites with similar emergence pattern. Model output is based on data obtained from five replicates/source population ( $N = 500$  seeds/replicate; for two letter source location details see Table S1).

documented the important contribution of climate conditions at original collection locations to seedling emergence patterns. Variable intra-population dormancy responses for *A. petiolata* are likely a function of small-scale differences in maternal environments (Finch-Savage & Leubner-Metzger 2006; Donohue *et al.* 2010, 2012; Alba, Moravcova & Pysek 2016) with mother plants and developing seeds responding to and integrating seasonal climatic conditions, herbivory, presence of mutualists or pathogens (Andersson & Milberg 1998; Baeten *et al.* 2010; Renne *et al.* 2014).

Our data suggest that local adaptation to optimize germination responses in *A. petiolata* evolved over 10–30



**Fig. 7.** Climate overlap index between common garden in Ithaca, New York and other seed source populations ( $r$ , top panel), the contribution of differences in the mean ( $R$ , middle panel), and the contribution of differences in the variance-covariance matrix ( $Q$ , bottom panel; see Fig. 1 for source locations). We defined climate as mean monthly temperature, mean total precipitation per month (previous fall and current winter and spring) and total number of spring days with minimum temperature below freezing (for two letter source location details see Table S1).

generations. Similar rapid evolutionary change over the course of a few generations in native and introduced species is an adaptive response to variable local environments, including climate or natural enemy pressure (Sakai *et al.* 2001; Carroll 2011; Agrawal *et al.* 2013; Sultan *et al.* 2013; Oduor, Leimu & van Kleunen 2016; Williams, Kendall & Levine 2016). There is evidence for other rapid evolutionary changes involving *A. petiolata*, including root glucosinolate concentrations, which appear to be a function of residence time (Lankau *et al.* 2009; Evans *et al.* 2016). Furthermore, there is evidence that some native species have adapted to *A. petiolata* presence and chemistry including microbial communities (Lankau 2011), many native plants (Lankau 2012, 2013; Lankau & Nodurft 2013) and the butterfly *Pieris oleracea* (Morton *et al.* 2015). Collectively rapid evolutionary change in the introduced range allowing *A. petiolata* to thrive in novel environments may be followed by equally rapid eco-evolutionary feedback in native species; i.e. ecological and evolutionary novelty wears off reducing initial negative impacts (Hierro & Callaway 2003; Callaway *et al.* 2008; Mangla, Inderjit & Callaway 2008; Wolfe *et al.* 2008).

In the laboratory, different populations from across a >2000 km latitudinal climate gradient showed no clines in germination but rather idiosyncratic responses to our treatments. Germination was enhanced by temperatures just above freezing as reported previously (Lhotska 1975) and did not require higher temperatures (Raghu & Post 2008) nor scarification (Sosnoskie & Cardina 2009; Yasin & Andreassen 2015). Onset of higher temperatures (>20 °C) effectively suppressed germination even of stratified seeds. In the common garden, emergence was lower (60–80%) than predicted by laboratory experiments (nearly 100%) with overall similar patterns but with irregular peaks and valleys that may occur for a decade following seed set, but no biennial cycles (Pardini *et al.* 2009; Shyu *et al.* 2013). Major differences in germination occurred in early years and our climate modelling revealed that populations could be placed into four groups with distinct germination patterns but they did not align along latitudinal clines (Colautti & Barrett 2010; Wilczek *et al.* 2014; Alba, Moravcova & Pysek 2016). However, alignment of seedling emergence or growth along environmental gradients or geography is not a ubiquitous phenomenon preventing reliable generalizations about underlying environmental or genetic causes (Cochrane *et al.* 2015).

Soil seed banks buffer *A. petiolata* against bad years and we found that seeds can remain viable for extended periods, and much longer than the 3–5 years previously reported (Kinzel 1926; Lhotska 1975; Cavers, Heagy & Kokron 1979; Roberts & Boddrell 1983; Baskin & Baskin 1992; Byers & Quinn 1998; Susko & Lovett-Doust 2000). Data on seed dormancy and seed bank dynamics are rarely available and not often collected using long-term field data (Menges 2000). Only our extended data collection period discovered irregular periodic germination responses driven by local climate at our common garden. This pattern introduces interesting challenges in demographic models that typically do not capture such fluctuations (Menges 2000). Years with low seedling emergence may not indicate an exhausted seed bank but rather viable seeds awaiting appropriate cues to break dormancy. The long seed viability explains, in part, success of *A. petiolata* in North America even in the face of continuous management efforts (Murphy *et al.* 2007).

We cannot ascertain whether ‘missing’ seeds in the common garden remained viable in the seed bank, were removed by predation, disease or other factors, or germinated but failed to emerge. We cannot exclude the possibility that with additional time, and/or soil disturbance, remaining viable seeds could germinate. Earthworms, which affect seed banks and plant communities through burial and selective consumption (Milcu, Schumacher & Scheu 2006; Quackenbush *et al.* 2012; Nuzzo, Dávalos & Blossey 2015; Cassin & Kotanen 2016), could have buried or consumed *A. petiolata* seeds. Similarly, fungal pathogens are major seed mortality factors (Blaney & Kotanen 2001; Wagner & Mitschunas 2008; Gallery, Moore & Dalling 2010; Wassie *et al.* 2010) and important contributors in plant invasions (Beckstead & Parker 2003) and negative soil feedbacks (Flory & Clay 2013; van der Putten *et al.* 2013).

Our combination of laboratory and a long-term common garden experiment showed important differences in *A. petiolata* germination responses among venues. We could quickly break dormancy for all populations when we stratified seeds at constant 4 °C in the laboratory, but we detected extended dormancy and delayed fluctuations in germination in a common garden. These differences in response to common garden and laboratory conditions question validity of commonly used approaches to study germination (typically under laboratory conditions) to make inferences about evolutionary responses (Simons & Johnston 2006; Simons 2014). These venue-influenced differences are a major handicap to fully understand the life history of individual species, ecological or evolutionary adaptations or importance of resulting data for demographic models or invasive species management. Seeds, plants or other organisms do not experience constant environments and their evolutionary responses are shaped by field conditions (Hulme & Barrett 2013) that integrate climate, competitors, mutualists and natural enemies.

Our finding of a long-lived seed bank has major implications for land managers trying to prevent spread or attempting local eradication of *A. petiolata*. Seed bank dynamics have a major effect on *A. petiolata* demography (Davis *et al.* 2006; Pardini *et al.* 2009; Evans & Davis 2011; Pardini, Drake & Knight 2011; Evans *et al.* 2012) and managers need to plan for a decadal time frame to exhaust seed banks or eliminate populations, which has never been successful (Drayton & Primack 1999; Hochstedler *et al.* 2007; Slaughter *et al.* 2007; Shartell, Nagel & Storer 2012). A re-assessment of management needs and approaches appears overdue.

While investigations of local adaptation typically involve multiple common gardens with reciprocal transplants (Moloney *et al.* 2009; Hulme & Barrett 2013; Wilczek *et al.* 2014), common gardens only sample a limited proportion of the environments organisms are exposed to, hence the recommendations to add experimental manipulations (Hulme & Barrett 2013). Such approaches face significant logistical and financial challenges. Furthermore, local differences in resources, land-use history, presence of mutualists, antagonists or competitors are all likely to have influences on seed survival, dormancy, germination (Susko & Lovett-Doust 2000; Donohue 2009; Donohue *et al.* 2010, 2012; Postma & Agren 2015) or plant growth, further complicating data interpretation. We believe our novel approach to assess importance of climate at original collection locations through a modelling effort using Matusita’s measure of distributional overlap index (Lu, Smith & Good 1989; Nadeau & Fuller 2015) offers an interesting alternative approach. We first identified important climatic variables that affected germination and then assessed their contribution in determining germination of seeds from different populations in our common garden. Our approach has the distinct advantage that many more local climates can be ‘sampled’ and some of the problems associated with common gardens in different settings such as differences in biotic assemblages can be avoided. We acknowledge shortcomings of using 30-year averages, and our modelling does not include influences of local biota at original collection



locations. But to the best of our knowledge, this is the first time that our climate modelling approach has been applied to help explain success of an invasive species or effects of common garden climate on observed results.

After only 150 years of residence in eastern North America, *A. petiolata* populations show diversified responses to differences in germination conditions that suggest rapid evolutionary change driven, at least in part, by local climate conditions. Our combined results suggest, as documented for other species (Hillstrom & Don 2011; Hahn *et al.* 2013; Monty *et al.* 2013; Hufft & Zelikova 2016), a complex interplay of pre-adaptation, rapid evolutionary changes and phenotypic plasticity (Richards *et al.* 2006) that together achieve thriving locally adapted *A. petiolata* populations.

## Authors' contributions

B.B. and V.N. conceived the idea, implemented experimental designs and collected data; and A.D. conducted data analyses. All authors contributed to writing the M.S.

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## Data accessibility

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.5k1f6> (Blossey, Nuzzo & Dávalos 2017).

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Fig. S1.** Proportion of *Alliaria petiolata* seeds collected at 10 locations in North America (Fig. 1) germinating over 2 years under germination conditions of Regime 2 (see Table 1).

**Fig. S2.** Number of *Alliaria petiolata* seeds emerging per Julian day in a common garden in Ithaca, New York.

**Fig. S3.** Average mean monthly temperature °C (grey bars) September to May and number of spring days with minimum temperatures ≤ 0 °C per year (black line) at seven different source populations in eastern North America (Fig. 1), for the duration of the emergence experiment (1998–2010).

**Table S1.** Collection site two letter ID, City and State/Province name (ordered from the most northern to the most southern location), approximate Lat-Long coordinates and closest weather station from which we obtained climate details.

**Table S2.** Number of days to reach 25, 50, or 75% germination and the number of days to increase from 25 to 75% of germination when exposed to constant 4 °C (temperature regime 1, Table 1) for *A. petiolata* seeds collected from 10 populations (see Fig. 1) from across the range of the species in eastern North America.