RESEARCH ARTICLE

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# Population climatic history predicts phenotypic responses in novel environments for *Arabidopsis thaliana* in North America

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**PREMISE**: Determining how species perform in novel climatic environments is essential for understanding (1) responses to climate change and (2) evolutionary consequences of biological invasions. For the vast majority of species, the number of population characteristics that will predict performance and patterns of natural selection in novel locations in the wild remains limited.

**METHODS**: We evaluated phenological, vegetative, architectural, and fitness-related traits in experimental gardens in contrasting climates (Ontario, Canada, and South Carolina, USA) in the North American non-native distribution of *Arabidopsis thaliana*. We assessed the effects of climatic distance, geographic distance, and genetic features of history on performance and patterns of natural selection in the novel garden settings.

**RESULTS**: We found that plants had greater survivorship, flowered earlier, were larger, and produced more fruit in the south, and that genotype-by-environment interactions were significant between gardens. However, our analyses revealed similar patterns of natural selection between gardens in distinct climate zones. After accounting for genetic ancestry, we also detected that population climatic distance best predicted performance within gardens.

**CONCLUSIONS**: These data suggest that colonization success in novel, non-native environments is determined by a combination of climate and genetic history. When performance at novel sites was assessed with seed sources from geographically and genetically disparate, established non-native populations, proximity to the garden alone was insufficient to predict performance. Our study highlights the need to evaluate seed sources from diverse origins to describe comprehensively phenotypic responses to novel environments, particularly for taxa in which many source populations may contribute to colonization.

**KEY WORDS** *Arabidopsis*; Brassicaceae; common garden; evolutionary ecology; introduced range; invasion ecology; natural selection; non-native distribution; novel environments; plasticity; range expansion.

In light of global climate change and biological invasions, there is a pressing need to predict organismal phenotypes and fitness in distinct climatic environments (e.g., Cahill et al., 2014; Leighton et al., 2012; Zenni et al., 2014; Louthan et al., 2015; Etterson et al., 2016). Experiments that document and dissect the mechanisms determining variation in organismal performance are needed to better predict and understand species' distributions and climate responses (Hargreaves et al., 2014; Estrada et al., 2016; Lee-Yaw et al., 2016). While adaptive plasticity has been intensively investigated for decades as a critical mechanism in relation to invasive species dynamics (Ghalambor et al., 2007; Nicotra et al., 2010; Davidson et al., 2011), data on genetically based variation in survival and reproduction in novel environments are lacking. In addition, studies addressing how selection acts on ecologically important traits in novel or non-native climate regimes are required to evaluate the role of evolutionary responses to new aspects of habitat experienced in response to climate change; such studies will ultimately inform processes acting during range shifts or expansions (Diamond, 2018). In the present study, we used common garden experiments to determine the role of climate and genetic ancestry in determining the performance of the ruderal *Arabidopsis thaliana* at two contrasting locations that represent novel climate regimes at the northern and southern extremes of its non-native range in eastern North America.

For non-native species, the establishment and persistence of annual plant populations will be determined by numerous, potentially interacting ecological and evolutionary forces (Keller and Taylor, 2008; Colautti and Lau, 2015). For example, the source of colonizing populations (whether geographically close or distant; Bossdorf et al., 2005; Lavergne and Molofsky, 2007; Dlugosch and Parker, 2008; Wilson et al., 2009), the genetic relatedness among propagules, how well the selective environment of the source matches the new colonizing location (Sexton et al., 2009), the availability of habitat patches, the potential of migrating genotypes to survive and reproduce in the colonizing environment due either to opportunistic plasticity or to environmental matching, and short-term evolutionary responses can all contribute to population establishment and persistence (Dudash et al., 2005; Colautti and Lau, 2015). It is difficult to predict how natural selection—the primary mechanism of evolutionary change that could lead to adaptation—will act in novel climatic environments in the non-native range (Rutter and Fenster, 2007; Sexton et al., 2009). On one hand, it may be that currently unoccupied habitats are similar to the source environment, and thus little or weak directional selection is seen to shift species traits (Fig. 1A). On the other hand, it may be that unoccupied habitats are qualitatively different from those experienced by source populations, and as a consequence we would predict directional selection acting on ecologically important traits (because directional selection is the form of selection most likely to change mean phenotypes; Fig. 1B, C). As commonly reported with invasive species, colonizers can originate in a single direction from nearby populations and few genetic origins (e.g., Sexton et al., 2009), or they may be from a suite of geographically and genetically widespread populations (e.g., Dlugosch and Parker, 2008; Samis et al., 2012). Disentangling these possibilities requires measuring selection on experimental lines sourced from different locations and genetic backgrounds grown together in novel habitats.

Transplant experiments comparing the suitability of populations for establishment success in novel habitats have produced mixed results, suggesting that a range of evolutionary and ecological mechanisms are at play in novel habitats (e.g., Angert and Schemske, 2005; Samis and Eckert, 2009; Malyshev et al., 2016; Stevens and Emery, 2015; reviewed by Hardie and Hutchings, 2010; Hargreaves et al., 2014). As a consequence, studies that compare the potential of genetically differentiated populations from multiple locations to grow in the same novel environments are required to enable a more complete understanding of colonization success (Peterson et al., 2016). One could posit that migrants coming from populations geographically closer to the new habitat will outperform other potential longer-distance migrants (e.g., from the center of the non-native distribution), given proximity, general similarities in climate over broad geographic areas, and likely shared patterns of natural selection (Sexton et al., 2009). Alternatively, dispersers from distant populations—perhaps with similar components of climates despite longer geographic distance—could outperform local migrants (Fig. 1A–C). Established populations of non-native species are of particular interest, as geographically distant populations may share genetic history from the native range, which can be estimated and accounted for with population genetic methods (Samis et al., 2012).

We evaluated whether climatic similarity or population genetic history of source populations were involved in predicting the performance of a geographically diverse set of non-native genotypes of the ruderal and genetic model *A. thaliana* when grown outside northern and southern habitat limits in relation to features of geography and climate experienced within the species' currently known distribution in North America. Although numerous experiments with *A. thaliana* have been performed within the non-native range (e.g., Rutter and Fenster, 2007; Richards et al., 2012; Hamilton et al., 2015; Table 1; Appendix S1), most have only planted source populations from the native range into a single garden site, hence limiting their generality to only some components of success in novel environments. However, these studies have also supported hypotheses that attributes of latitude, temperature, and precipitation represent significant predictors of flowering, size at flowering, architecture, or reproductive success in a common garden setting (e.g., Rutter and Fenster, 2007; Richards et al., 2012; Hamilton et al., 2015; Table 1; Appendix S1). However, the exclusion of non-native populations from experimental plantings in the non-native range not only avoids inclusion of germplasm that has already become established in a novel geographic location, but also

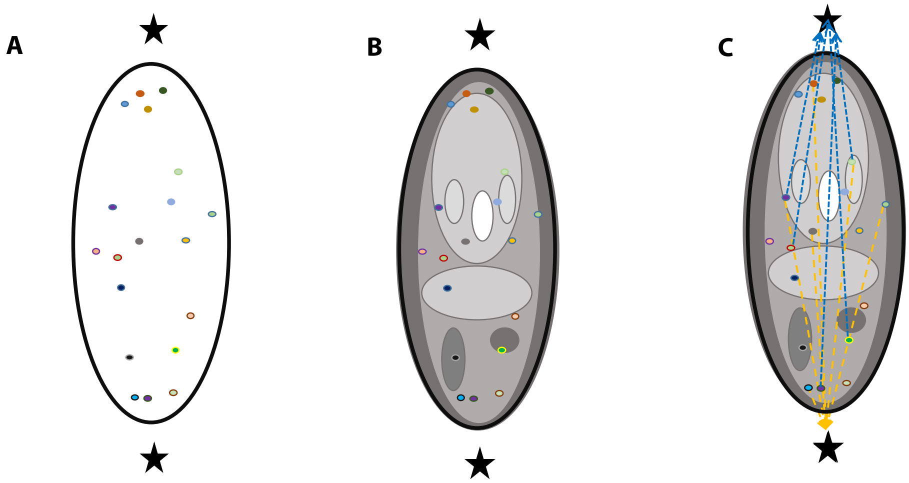

**FIGURE 1.** Hypothetical non-native distribution for a ruderal species, in which populations have long been established in the introduced area. Importantly, the populations are from a mixture of native origins and numerous independent introductions. (A) Black oval is the documented non-native distribution, color dots are individual established populations, and black stars are novel ecological sites. (B) Overlay of climate features in contour-style plot for the entire non-native range, with shared colors (white and shades of gray) indicating shared climate or other ecological features that covary with climate. (C) Dotted arrows are the routes of colonization to novel sites (indicated by stars). In these scenarios, novel environments are colonized by several populations of mixed origins, from throughout the non-native distribution, with no single point of introduction and spread. Field experiments are needed to determine the potential of putative source populations to persist in novel garden sites.

**TABLE 1.** Summary of 52 field common garden studies of *Arabidopsis thaliana* (1997–2018) planted into native and non-native geographic locations, with number of common gardens per study and whether the seeds for plants used in the gardens originated from native or non-native populations (see Appendix S1 for additional details and citations).

| | | | Number of studies with | | | | |
|---|---|---|---|---|---|---|---|
| **Study location** | **Continent** | **Total # of studies** | **1 garden** | **≥2 gardens** | **Native seed source only** | **Non-native seed source only** | **Native and non-native seed sources** |
| Native | Asia | 2 | 2 | 0 | 2 | 0 | 0 |
| | Europe | 31 | 18 | 13 | 30 | 0 | 1 |
| Non-native | North America | 19 | 14 | 5 | 14 | 3 | 2 |

precludes the ability to ask questions related to the source population's proximity to novel climate in unoccupied habitat. The few experiments conducted with local non-native populations planted into non-native environments have uncovered both abiotically (shade; Callahan and Pigliucci, 2002) and biotically (herbivory; Mauricio and Rausher, 1997; Mauricio et al., 1997; Mauricio, 1998) mediated selection, yet limited differentiation among local populations in critical timing, architecture, rosette, or reproductive traits (Callahan and Pigliucci, 2002). Differentiation among populations was more apparent when diverse sources from throughout the non-native range were grown in a single common garden (Griffith et al., 2004; Samis et al., 2012). While demonstrating limited evidence of local adaptation, Griffith et al. (2004) provided evidence that a distant population had higher reproductive output than a population close to the garden site. However, differential selection on germination timing across distinct sites highlights the critical importance of germination in establishment phase of non-native population biology (Donohue et al., 2005a, 2005b, 2005c). Building on these important studies with non-native wild *Arabidopsis* populations, we consider performance at two distinct sites in the non-native range that differ in multiple aspects of climate. We examine the contributions of shared ancestry (despite diverse geographic origins; Samis et al., 2012) and shared climate history on variation in fundamental life-history traits in novel locations.

Specifically, we asked the following series of questions. First, does climatic or geographic distance between non-native, source populations from throughout eastern North America and our experimental garden sites predict patterns of trait variation and performance after accounting for shared population genetic ancestry? Based on theoretical predictions for colonization and spread of invasive species, we hypothesized that source populations closest to the novel garden habitats (geographically or in climate attributes) would perform better than those from farther away because of a shared history in similar climates. Alternatively, populations established in northern areas may outperform those from southern areas (but see Griffith et al., 2004), due to the climate history in colder winter environments uncovering phenotypic variation (e.g., detecting hidden reaction norms; Schlichting, 2008). Second, what are the patterns of natural selection in experimental and contrasting garden sites of the non-native distribution for critical phenological, architectural, and vegetative traits all previously shown to respond to climate (Appendix S1)? And are patterns of selection similar between the two garden locations? We hypothesized that distinct climates at the two sites would lead to different selection pressures between gardens. Specifically, given differences in season length, temperature, and precipitation throughout the season in Ontario, Canada (ON), and South Carolina, USA (SC), we predicted distinct patterns of natural selection on flowering onset, size at reproduction, and aboveground architecture. Third, what is the relative contribution of genetic ancestry vs. differences in climate for plant traits and performance at two distinct novel environments? We hypothesized that genetics and diverse patterns of introduction history among geographically close populations would contribute to variation in performance within and across novel garden locations, despite the importance of population climatic history for performance.

## MATERIALS AND METHODS

### Study species

We transplanted *A. thaliana* seedlings from the species' non-native range in eastern North America into gardens at the University of Toronto (Toronto, Ontario; hereafter "ON garden"; 43.661, 79.401) and the College of Charleston (Charleston, South Carolina; hereafter "SC garden"; 32.783, 79.939) and near the northern and southern extents of the North American range. The distribution was determined by examination of publicly available digitized herbarium locations (e.g., SERNEC at http://sernecportal.org) and stock center collection localities (https://arabidopsis.org). Data from the USDA Plants database were also examined (citation materials referencing Florida indicate that no specimens are known from the state, in contrast to what the current USDA species distribution map suggests; http://florida.plantatlas.usf.edu/Excluded.aspx?xml:id=1153). Our garden sites were selected to represent novel climatic environments occurring near non-native distributional limits in eastern North America. At the onset of the garden experiment (2008), the southernmost population was reported from SC at 33.14N, although more recently digital records of inland populations at 32N have been added. Likewise, no self-sustaining populations were present in the greater Toronto area at the experiment date, although some have become established in the intervening decade; we note that *A. thaliana* is present in more northern latitudes in Michigan farther to the west. The garden sites represent a novel geographic region for all studied populations, as the garden sites were unoccupied by *A. thaliana* populations. Although climatic distinction between garden locations is multivariate, our two sites differ in temperature and precipitation in early spring, when plants experience cues for flowering. From March through April, based on 30 yr average conditions, ON average temperature is 0–6°C (low −4°C to high 11°C) with diurnal temperature range (dtr) of ~8.5°C, and precipitation range is 60–67 mm rain, whereas in SC average temperature is 14–18°C (low 8°C to high 25°C) with dtr ~13.2°C, and precipitation range is 76–102 mm. The experiment included 35 North American source populations (and a total of 198 maternal lines). We used a combination of lines from the Arabidopsis Biological Resource Center (https://abrc.osu.edu) and sampled wild populations spanning the east-coast non-native distribution (see open access map doi/10.1002/ece3.262; Samis et al., 2012). We grew all seeds for one generation in growth chambers at the University of Toronto. Because this species is largely selfing, we allowed plants to self to bulk seed, and then germinated experimental plants locally in SC and ON prior to transplanting, as described in Samis et al. (2012) and summarized here.

### Replicate calibrated common gardens

We cold treated *A. thaliana* seeds for 7 d at 5°C in the dark before germination in the glasshouse, and transplanted seedlings into outdoor gardens at the University of Toronto (ON garden) and the College of Charleston (SC garden). Seedlings were hand transplanted at 10 cm spacing into five spatially replicated, outdoor raised garden beds (blocks) at each location ($n = 990$ plants/garden) when ~1 wk old, with one replicate per maternal line per block. The ON garden was planted on the urban campus at the University of Toronto (N43.661, W79.401) in October 2008 and represents the northern geographic extent of the non-native range (Platt et al., 2010). We planted the SC garden between the two wings of the urban glasshouse (N32.783, W79.939) in December 2008. This garden represents the southern climatic and geographic edge of the east-coast non-native range (Appendix S2), yet herbarium records indicate that populations have been established in inland areas of SC for ≥150 yr (C. J. Murren and M. T. Rutter, unpublished data). We aimed to focus on climatic differences between sites, and thus filled raised beds with ProMix potting mix to standardize edaphic features. We matched the timing of transplanting at each garden to mimic when germination in the wild occurs in populations in the southern and northern regions of the species' non-native range.

### Plant phenotypes

In both gardens, we measured phenotypes representing phenology, morphology, and architecture (guided by references in Appendix S1). We recorded flowering phenology (including days to bolting and to flowering; but given their tight correlation, only days to bolting is reported) every 1–2 d and noted whether each transplant survived to reproduction. At bolting, we recorded vegetative characters, including the width of the rosette (to nearest 0.1 cm) and total rosette leaf count, which have been shown to be distinct across populations and environments (e.g., Callahan and Pigliucci, 2002). After senescence, we harvested the aboveground portion of mature plants and allowed them to dry in paper bags. We then recorded architectural characters: total number of secondary branches, and height of the inflorescence (primary stem, to nearest 0.1 cm). Finally, we counted all successful fruit (based on the presence of full or dehisced siliques) as our measure of reproductive fitness. Collectively, these traits measure features of size (rosette diameter and height), developmental timing (number of rosette leaves, production of which ceases at flowering), phenology (flowering time in days), shape/apical dominance/architecture (branch number), and reproductive performance (fruit number). We completed data analyses on traits associated with flowering or measured at maturity (i.e., on plants that survived to reproduce).

### Data analyses

***Evaluating within-garden performance based on geographic and climate distance from non-native-seed source's geographic location***—To assess whether climate history in the non-native range of non-native populations predicted phenology, growth, and fitness within gardens in novel geographic locations, we first developed measures of climate distance. To capture the multivariate nature of habitat variation across the broad geographic scale from which our non-native-seed source populations were drawn, we used principal components to describe climatic variation at each source population and our common gardens. Principal components were generated using R (version 3.3.2) and pca function in the FactoMineR package (Sebastien et al., 2008). The correlation matrix used all climate variables available in the dataset in order to capture a comprehensive measure for the North American populations in the North American field site where seeds were collected as the historical selective regime, and which we describe as climate history. In this metric, we used temperature mean, minimum, and maximum; precipitation; diurnal temperature range; ground frost; water vapor; cloud cover; and wet-day data extracted from the Climate Research Unit, University of East Anglia, high-resolution 1961–1990 dataset, version 2.1 (Mitchell and Jones, 2005), for the latitudinal and longitudinal coordinates of each location (35 non-native population source sites, plus two gardens). Collectively, these climate variables summarize aspects of both the mean of the climate and its variability (e.g., diurnal temperature range, wet-day frequency). As in Samis et al. (2012), we used climate data for October–April, the period when plants experience conditions leading up to the initiation of flowering. Given that a focus of our study was whether the difference in climate history of non-native population source sites compared to the transplant site predicted performance, we calculated a Euclidean distance metric based on the difference between pairs of principal components (PCs; employing PC1–PC5, which explained 98% of the variation) at seed source location in North America (hereafter "seed source") and those of each garden, following Noël et al. (2011) and Ferguson et al. (2016) and using the dist() function in R (R Core Team, 2016). We refer to this metric as climate distance (CD).

We then used linear regression models to assess the association of distance from seed source (Euclidean CD and geographic distance [GD] separately) with mean phenotype per line in R (R Core Team, 2016). We ran separate models for each garden:

$$Y = \mathrm{CD} + \mathrm{ancestry} \qquad \text{(Eq. 1)}$$

$$Y = \mathrm{GD} + \mathrm{ancestry} \qquad \text{(Eq. 2)}$$

where $Y$ is the phenotype and "ancestry" is log-contrast transformed ancestry coefficients from a STRUCTURE model reported by Samis et al. (2012). Samis et al. (2012) reported STRUCTURE models for non-native populations including single-nucleotide polymorphism (SNP) haplotypes across 136 loci and generated coefficients for $K = 2$ ancestral populations with little geographic pattern to the clusters identified by STRUCTURE. K = 2 was the best-supported $K$ as determined by the Evanno method (Evanno et al., 2005). SNP data available for 175/198 lines were used in the experiments described here. We included ancestry coefficients because variation among maternal lines may also be due to population genetic structure associated with demographic history. Using $\mathrm{AIC}_c$, we compared distance models (climate distance CD vs. geographic distance GD) to assess whether climatic distance or simple geographic distance (which would be correlated with spatially varying factors alone) were better predictors of within-garden performance. We chose not to fit a single model with both climate distance and geographic distance as predictors because of the high correlation between the two ($r$ ~ 0.9) and multi-collinearity in the model with both CD and GD (VIF > 5.3 for the ON garden and VIF > 8.6 for the SC garden).

***Selection analyses***—We measured selection in two ways. First, because plants in the ON garden spent many weeks under snow or ice, many of them did not survive long enough to express traits measured at reproduction. Consequently, to evaluate whether there was selection on survival, we used logistic regression with climate distance as a predictor variable and survival status (the number that survived to reproduction out of the total planted, per line) as a fitness estimate. To account for uneven available lines within populations, we performed a complementary analysis by randomly sampling one line per population and then estimating the logistic regression; we then repeated the random sampling and logistic regression 10,000 times. From the analyses of random samples, we used the median logistic regression coefficient as our point estimate and determined 95% confidence intervals from the 2.5th and 97.5th percentiles.

Second, for plants that survived to reproduce within each garden, we estimated selection differentials and gradients from genotypic selection analyses for relative fitness on standardized plant traits within gardens (Lande and Arnold, 1983; Griffith et al., 2004). We standardized all quantitative traits to mean = 0 and SD = 1 by garden, including measures of flowering phenology (days to bolting), size, and architecture (rosette diameter and rosette leaves at bolting, and plant height and total branches at maturity). We calculated relative reproductive fitness based on mean fruit production for all plants that survived to reproduce within each garden. We ran linear genotypic selection analyses based on line means within gardens (Rausher, 1992; analyses based on population means were qualitatively similar and did not change our interpretation and therefore are not presented), and phenotypic selection analyses using all data.

***Cross-garden performance***—We evaluated cross-garden performance using two complementary approaches. First, we assessed whether the climate history of the non-native source predicted divergence in performance across gardens using regressions of trait differential performance (a measure of plasticity) between gardens onto the climate of the seed source location. Our logic was that climate through the growing season at the site of origin could have imposed selection for different phenotypes (flowering, size, architecture), which themselves could show varying plasticity when planted into two novel environments. We calculated plasticity in performance as the trait difference between gardens by line (value in SC garden – value in ON garden). We used PC1 and PC2 to estimate climate of the seed source location (PC1 explained 75% of the variation and PC2 explained 13%, both of which have eigenvalues >1); we did not use climate distance because that metric applies to each garden separately, and our hypotheses were about trait and performance differences between the two gardens. All models also accounted for population structure using our genetic measure of ancestry (described above).

In addition, we ran G × E analyses as mixed models including garden as the fixed effect, and including source population, genotype (i.e., line) within population, their interactions with garden, and experimental block within gardens as random effects. We present model results only for traits showing significant relationships with climate from the cross-garden analyses described above. Model results for other traits did not reveal any biologically meaningful associations and are not discussed further. Selection and plasticity analyses were conducted in SAS version 9.4 (mixed procedure).

## RESULTS

Transplant survival was high in both gardens, with the large majority of plants surviving to reproduce. However, survival to flowering was higher in the southern (SC) garden, with 86% of transplants surviving (850/990) compared to 64% (637 transplants) in the northern (ON) garden. A small number of plants in each garden were lost after reproduction and before harvest and thus are excluded from traits recorded at maturity.

Overall, plants in the SC garden bolted and flowered earlier (day of the year and days after transplanting), grew larger, and produced more fruit than plants in the ON garden, and these differences were significant between gardens for all traits (Table 2; Fig. 2). Despite the variation in trait means between gardens, the dispersions in trait values (CV) were similar (Table 2). Lifetime fruit production varied within and between gardens (CV at ON = 65%, at SC = 56%), with plants in the SC garden tending to produce more fruit (silique count range: 0–4058, median = 451) than plants in the ON garden (range: 15–3619, median = 309).

## PERFORMANCE, ANCESTRY, AND DISTANCE FROM SEED SOURCE

Principal component analysis of the climatic aspects of source habitats clearly distinguished between source population sites and gardens (Appendix S2). PC1 varied primarily with climatic variables associated with temperature throughout the year and with water vapor (Appendix S3), whereas PC2 was most strongly associated with winter precipitation, spring diurnal temperature range, and other attributes of winter climate, in general.

The distribution of climate distances indicates that all source locations, which tend to be in relatively northern latitudes, are ecologically closer (in Euclidean space) to the ON garden (for all sources, mean climate distance to ON garden ± SD = 8.1 ± 5.0) than to the SC garden (17.3 ± 5.8). Climate distance was significantly and positively correlated with geographic distance from seed source

**TABLE 2.** Summary of quantitative traits (line means ± SE for 194–196 lines from 34 populations) measured on *Arabidopsis thaliana* plants originating in the introduced range and grown in outdoor, replicated experimental gardens in Toronto, Ontario (ON), and Charleston, South Carolina (SC). All quantitative traits were measured on reproductive plants only. CV = coefficient of variation.

| | ON garden | | SC Garden | |
|---|---|---|---|---|
| **Trait** | **Mean ± SE** | **CV** | **Mean ± SE** | **CV** |
| Days to bolt [a] | 197.3 ± 0.16 | 1.1 | 80.8 ± 0.40 | 6.9 |
| Rosette diameter at flowering (cm) | 3.0 ± 0.04 | 20.9 | 7.5 ± 0.09 | 16.6 |
| Rosette leaves at flowering | 29.2 ± 0.38 | 18.0 | 37.9 ± 0.53 | 19.8 |
| Final height (cm) | 28.6 ± 0.34 | 16.7 | 38.0 ± 0.46 | 16.7 |
| Total branches | 22.1 ± 0.92 | 58.0 | 34.5 ± 1.37 | 55.3 |
| Fruit count | 316.7 ± 14.7 | 64.9 | 552.2 ± 21.8 | 55.6 |

[a] Plants in the SC garden were planted ~90 d later than plants in the ON garden and within a few days of the end of the calendar year to match regional population germination; differences between gardens persist even if calculated as bolting day of the year.

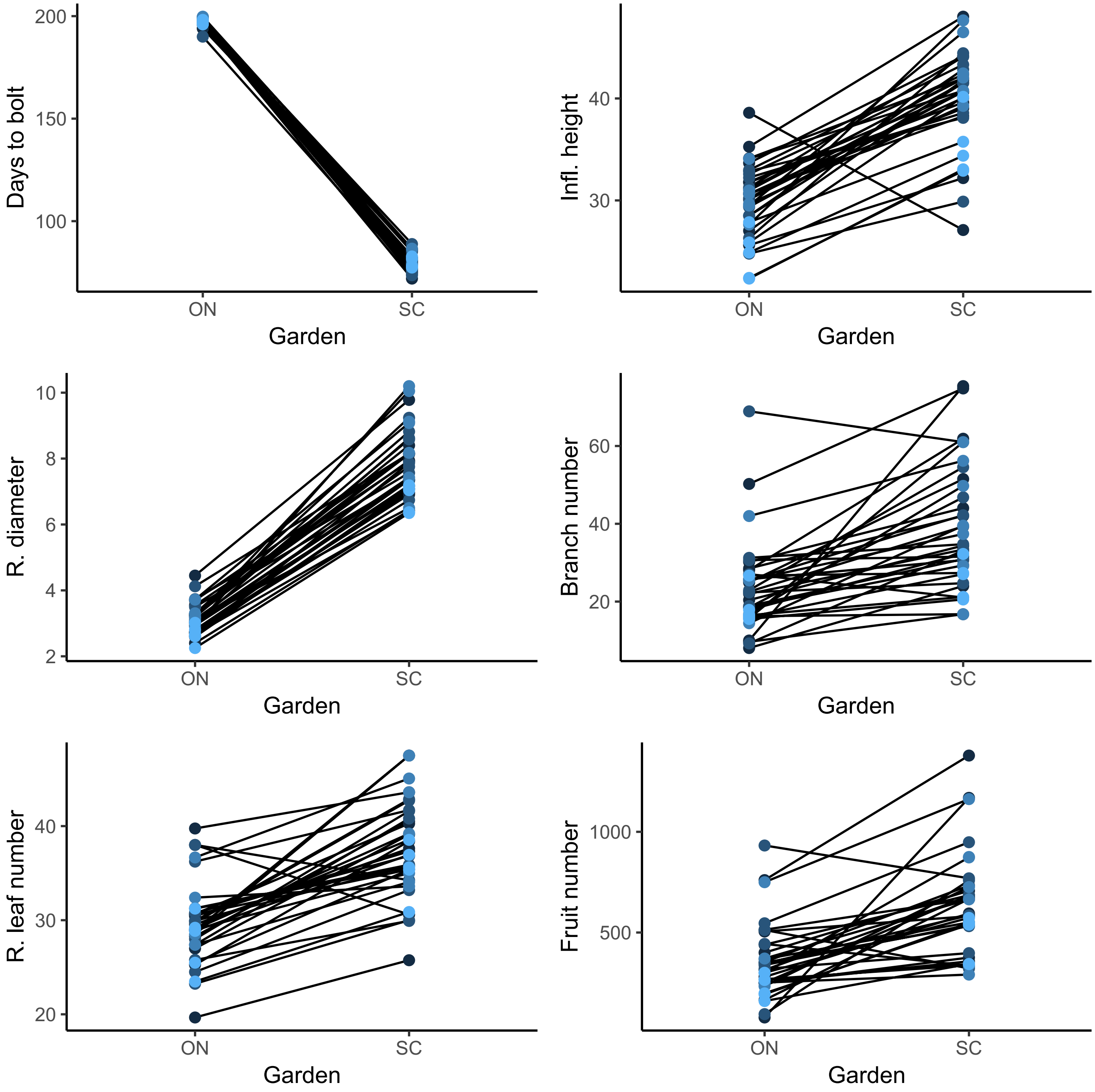

**FIGURE 2.** Reaction norms of inbred lines of North American *Arabidopsis thaliana*—when planted in northern (ON = Ontario, Canada) and southern (SC = South Carolina, USA) outdoor experimental gardens—for days to bolting, rosette diameter at bolting, rosette leaf number, inflorescence height, branch number, and total fruit production. Each line represents a mean of a unique population ($N = 35$ source populations), with point colors representing relative position along PC1 (from light = above 0, to dark = below 0; see Appendices S2 and S3).

(in kilometers) to each garden (to ON garden: $r = 0.896$, $P < 0.0001$; to SC garden: $r = 0.899$, $P < 0.0001$; $n = 35$ source populations).

The relationship between performance in the common garden and climate distance from seed source varied between gardens as measured in linear regression models accounting for genetic ancestry (which is significant for all traits in both gardens; Table 3). In both gardens, climate distance was negatively associated with plant height (ON, $P = 0.018$; SC, $P < 0.0001$; Table 3); that is, plants were tallest when climatically closer to home. In the SC garden, plants farther from home bolted later ($P < 0.0001$) and had more rosette leaves at bolting ($P = 0.007$), but had fewer fruit ($P = 0.004$) than plants climatically closer to home. In all cases, significant trait associations

**TABLE 3.** Multiple regression testing for an association of phenology and architecture traits with climate distance (estimate ± SE) of source populations of *Arabidopsis thaliana* from the gardens in Toronto, Ontario (ON), and Charleston, South Carolina (SC). All models used inbred line means ($N$ = 172–175 per trait). Climate distance (CD) represents the difference between source home and garden sites in Euclidean space, and "ancestry" equals log contrast of ancestry coefficients calculated from SNP data in STRUCTURE (see text for further details). Significant results are in bold.[a]

| | | Non-native source populations | |
|---|---|---|---|
| **Trait** | **Effect** | **ON garden** | **SC garden** |
| Days to bolt | CD | −0.014 ± 0.028 | **0.29 ± 0.053** $^{***}$ |
| | Ancestry | **0.22 ± 0.094** $^{*}$ | **−1.09 ± 0.22** $^{***}$ |
| Rosette diameter | CD | −0.010 ± 0.008 | −0.003 ± 0.013 |
| | Ancestry | **0.12 ± 0.027** $^{***}$ | **0.32 ± 0.051** $^{***}$ |
| Rosette leaves | CD | 0.003 ± 0.070 | **0.23 ± 0.077** $^{**}$ |
| | Ancestry | **0.74 ± 0.23** $^{**}$ | **−0.79 ± 0.32** $^{*}$ |
| Height | CD | **−0.14 ± 0.059** $^{*}$ | **−0.16 ± 0.060** $^{**}$ |
| | Ancestry | **0.83 ± 0.19** $^{***}$ | **1.82 ± 0.24** $^{***}$ |
| $\text{Log}_{10}$ total branches | CD | −0.0025 ± 0.004 | 0.0017 ± 0.002 |
| | Ancestry | **0.029 ± 0.012** $^{*}$ | **0.040 ± 0.0097** $^{***}$ |
| $\text{Log}_{10}$ Fruit count | CD | −0.0059 ± 0.003 | **−0.0064 ± 0.002** $^{**}$ |
| | Ancestry | **0.030 ± 0.012** $^{*}$ | **0.044 ± 0.0090** $^{***}$ |

[a] Significance of parameter estimates indicated as *$P$ < 0.05, **$P$ < 0.01, ***$P$ < 0.0001.

with climate distance occurred even after accounting for population genetic structure detected with ancestry coefficients (Table 3).

Significant associations detected between plant traits and climate distance were also detected with geographic distance for some traits (days to bolting and rosette leaves in the ON garden; Table 3; Appendix S3) but not others (fruit production in the SC garden, $P$ = 0.071; plant height in both gardens, both $P$ > 0.18; Appendix S4A). In several cases the GD and CD models explained similar amounts of variation in the data; but in four cases (days to bolt, height, and fruit in the SC garden, and height in the ON garden), the CD distance model was a better fit to the data (Appendix S4). The GD model was never detected to be a better fit to the data than the CD model. Model comparisons revealed that climate distance models were a better fit than geographic distance models alone in several instances (Appendix S4B).

### Traits associated with fitness

A logistic regression suggested a significant negative association between climate distance and survival to reproduction in the ON garden; in other words, survival to reproduction was lower among lines from climates more dissimilar to the ON garden (logistic regression coefficient = −0.0309, $\chi^2$ = 10.69, $P$ = 0.0011). When we randomly sampled only a single line per population, the median estimate of this relationship was largely unaffected, although percentile confidence intervals overlapped zero (logistic regression coefficient = −0.0367, 95% confidence interval: −0.0883 to 0.0109). These data suggest a trend for lower survival of lines from climatically more distant source populations when moved north, with the statistical significance being driven by unequal sampling of lines within populations.

Genotypic selection analyses support the expectation that quantitative traits measured upon and after completion of flowering are associated with fitness (Table 4; see also phenotypic selection analyses in Appendix S5). Selection for earlier reproduction (days to bolting: negative selection gradient and differential) was detected for populations in both gardens. Evidence that flowering at a larger size leads to increased fitness was mixed and varied between measures of rosette size across gardens. Rosette diameter exhibited clear evidence of positive linear selection in both gardens, whereas selection on rosette leaf number was detected only for plants in the ON garden (significantly positive differential) and not in the SC garden. There was also evidence of moderately positive selection on height and strong positive selection on branch production in both gardens (Table 4).

In contrast to expectations, plants growing at the southern extent of the species' distribution appear to experience similar selection pressures to those growing at the northern extent, particularly through total branch production, plant size, and phenology. However, developmental aspects of rosette size (leaf count) associated with reproduction may play a more important role in the north than in the south.

### Cross-garden performance

We also asked whether variation in climatic history, which includes seasonal variation at seed sources (Appendices S2 and S3), predicted the level of plasticity (cross-garden performance) detected among lines. Plasticity in days to bolting (Figs. 2 and 3) and the number of rosette leaves counted at bolting declined with increasing scores on PC1, while plasticity in plant height increased along PC1 (Appendix S6) when also controlling for the effects of PC2 and ancestry. Given that PC1 is tightly correlated with climate distance to each garden ($r^2$ > 0.87) and increases with decreasing latitude ($r^2$ = 0.88; see also Appendices S2 and S3), these data suggest that plants originating at seed source sites that are ecologically (and geographically) close to the SC garden (or far from the ON garden) displayed lower plasticity in phenology and developmental size at bolting, and higher plasticity in height than plants originating at the other end of the ecological cline (Fig. 2). Plasticity in phenology also increased with increasing scores on PC2 and may suggest that plasticity in this trait is also associated with overwinter precipitation conditions, which were differently experienced in the ON garden than in the southern SC garden.

Our examination of genotype and environment interactions (G × E) for plant traits in which we detected significant effects of climate on plasticity (days to bolting, rosette leaves, and plant height) revealed significant interactions between source population and garden for all three traits (all $P$ < 0.007), as well as between inbred line genotype and garden for days to bolting ($P$ < 0.0001; Appendix S7).

## DISCUSSION

We detected substantial genetic variation among populations within each garden, significant plasticity in quantitative traits between gardens, and evidence that plasticity for some traits was associated with climate distance from seed source in the non-native range. On average, plants at the garden at the SC garden bolted earlier, grew larger, and produced more fruit than plants at the ON garden. However, natural selection on traits was strikingly similar between gardens. Climate history appears to be an important predictor of performance in many cases even after accounting for patterns of genetic ancestry, although for some traits, ancestry alone is the important predictor of performance. Below, we discuss these results in the context of what is known about the species from primarily native

**TABLE 4.** Genotypic selection differentials (S) and gradients (β) for *Arabidopsis thaliana* based on standardized traits per garden in Toronto, Ontario (ON), and Charleston, South Carolina (SC), and relative fitness to each garden's mean fruit production. Analyses were conducted by garden. Parameter estimates (± SE) significantly different from zero are in bold ($P < 0.05$). $N$ is the number of lines used at each garden.

| | Non-native source populations | | | |
|---|---|---|---|---|
| | ON garden $N = 194$ | | SC garden $N = 195$ | |
| Traits | S | β | S | β |
| Days to bolt | **−0.17 ± 0.05** | **−0.04 ± 0.014** | **−0.23 ± 0.04** | **−0.18 ± 0.03** |
| Rosette diameter | **0.42 ± 0.04** | **0.07 ± 0.02** | **0.55 ± 0.05** | **0.18 ± 0.06** |
| Rosette leaves | **0.21 ± 0.02** | −0.01 ± 0.02 | 0.11 ± 0.06 | 0.01 ± 0.04 |
| Height | **0.33 ± 0.04** | **0.05 ± 0.02** | **0.30 ± 0.05** | −0.02 ± 0.04 |
| Total branches | **0.85 ± 0.02** | **0.76 ± 0.02** | **0.76 ± 0.04** | **0.61 ± 0.04** |

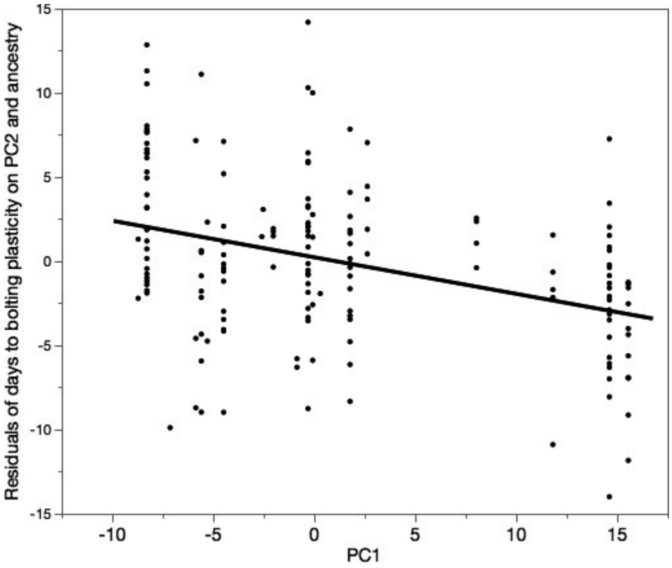

**FIGURE 3.** Partial regression of cross-garden plasticity (accounting for PC2 and ancestry) and PC1 of climate history in North America for each source population (estimate = −0.21 ± 0.04, $N = 171$, $r = +0.13$). Values on the $y$-axis represent residuals of a regression of days to bolting plasticity (SC [South Carolina, USA] garden trait value − ON [Ontario, Canada] trait value) on both climate PC2 and the log contrast of our estimate of ancestry from genetic markers (see text for details). Note that in the text, we discuss the full model including all three effects (see also Appendix S5).

range field experiments and accessions, as well as from a general understanding of invasion biology and adaptation as ranges expand into novel environments and for non-native sites more broadly.

### Does climate or geographic distance predict performance in gardens in novel northern and southern regions?

While not necessarily representative of other taxa, the striking number of common garden experiments conducted with *A. thaliana* allows for a unique context across diverse germplasm and across native and non-native sites (summarized in Table 1). The majority of experiments have used material originating from populations in the native range (94%, or 48 of 51 distinct experiments), and 67% (32/48) of experiments using native-range germplasm are conducted in the native range. Moreover, of the 19 distinct experiments conducted in the non-native range, the majority of these did not include genotypes from North America (74%; 14/19). Over 20 yr of common garden experiments (1997–2018; Table 1; Appendix S1), only six experiments (with data reported in 13 publications) have included lines originating from the non-native range (Mauricio and Rausher, 1997; Mauricio et al., 1997; Mauricio, 1998; Callahan and Pigliucci, 2002; Griffith et al., 2004; Donohue et al., 2005a, b, c; Huang et al., 2010; Samis et al., 2012; Stock et al., 2015; Gould and Stinchcombe, 2016; Rubio et al., 2018; details in Appendix S1). Despite the vast amount of work done on *Arabidopsis* as a model organism, and the large amount of work conducted on invasive species (reviewed by Colautti et al., 2009), it is noteworthy that there are so few studies of how local genotypes performed in the non-native range. Although only a small number of common garden experiments with more than one site have sampled distinct ecological conditions experienced in the wild (e.g., Wilczek et al., 2009; Fournier-Level et al., 2011; Ågren and Schemske, 2012; Rutter et al., 2018), our work builds on their findings. Our results add a new dimension to the examination of genetic variation in the wild for a ruderal plant species by assessing performance of genetically and geographically diverse populations in distinct gardens and accounting for home-site climate as a potential factor for success at novel sites in eastern North America (Table 1).

Our experiment sampled populations from across a geographically and ecologically broad portion of the species' non-native range, with germplasm material from across the range surviving to reproduce at both gardens. The genetic material represents diverse origins with limited relationship to geographic location (Samis et al., 2012). However, compared to seed source locations, conditions at the SC garden were farther from the source-site climate history experienced by the majority of populations used in this experiment than conditions at the ON garden. Nevertheless, a larger proportion of plants in the SC garden survived to reproduce, and they did so at a higher rate (more fruit, larger size) than plants at the northern ON garden, indicating success in the southern novel environment. Because we transplanted seedlings into the common gardens, our study has not assessed early life-history trait variation (for seed performance variation in non-native gardens, see Donohue et al., 2005a, 2005b, 2005c), or the impact of ecological conditions on early life stages, which may be important distinctions between the two novel sites. Given that many studies assessing variation in germination success have been conducted in the native range (e.g., Montesinos et al., 2009; Manzano-Piedras et al., 2014; Postma and Ågren, 2016), and that the few from the introduced range provide varied support for geographically structured genetic variation in field germination success in novel habitats (Griffith et al., 2004; Donohue et al., 2005a; Huang et al., 2010), it remains an area open for additional inquiry of how shared ancestry, shared climate history, and environment may interact to affect seed success in novel sites (see also Roles et al., 2016). For example, contrasting performance in the colder overwinter temperatures experienced at the inland southern range extreme with that experienced at the near-coastal SC garden (C. J. Murren, unpublished data) may help disentangle the effects of winter temperature from other variables that vary by location.

We also detected variation between traits in their association with climate distance. In the SC garden, fitness (i.e., fruit production) declined with increasing distance from seed source, whereas rosette leaf number tended to increase. Taken together, these data suggest that an increased mismatch between source and site leads to a relative reduction in fitness and increased allocation to growth prior to reproduction in order to reproduce at all. Although the pattern that fitness declines generally holds for most species tested at geographic limits (Hargreaves et al., 2014), given that most studies do not also report vegetative characteristics recorded pre-maturity, support for this pattern is difficult to assess. This general pattern may be especially noteworthy in predicting invasion and colonizing success in novel sites when the specific combination of genetic and ecological attributes leads to robust reproduction. That we were unable to detect significant associations between climate distance and performance for plants in the ON garden could be due to limited potential to detect an effect of distance given that fewer sources originated climatically or geographically far from the ON garden site. In support of that hypothesis, we found that lines originating from the southern portion of our sampling range (South Carolina, Georgia, and North Carolina, USA) had lower average fruit production and were shorter in stature than lines from farther north when planted at the ON garden. These data are consistent with the interpretation of regional-scale climatic adaptation or filtering at the initial establishment phase in non-native populations of *A. thaliana* in North America, due to the performance differences across gardens. These data support efforts to broadly survey patterns of performance across large geographic and ecological ranges (Wilczek et al., 2009), studies that account for variation between source and transplant sites (e.g., Rutter and Fenster, 2007) and that consider the diversity of environmental factors imposing selection on local populations (De Frenne et al., 2013; Hamilton et al., 2015).

Given the multivariate difference in climate between southern Ontario and near-coastal South Carolina, it is worth considering whether variation detected between gardens can be attributed to the different planting schedules used for each garden (ON garden planted ~90 d before the SC garden). We based experimental planting schedules on naturalized population germination in the field, which ensured that plants in each garden experienced environmental conditions typical for local winter annual plants. However, seasonal and timing differences between gardens meant that plants at the ON garden experienced snow cover and freezing temperatures while overwintering as rosettes (likely explaining lower survival) and were still under snow when plants in the SC garden transitioned to flowering (snow is not typical for the garden site or local populations at any point in the winter; C. J. Murren, personal observation). However, plants in both garden locations transitioned to flowering with the onset of local spring conditions. The suggestion from this experiment that day length and/or the transition to warmer weather is a more critical cue for the optimal time to reproduce than number of growing days or other developmental reproductive signals has also been supported by results from other common garden experiments in the native range (Ågren and Schemske, 2012; Blackman, 2017). It seems that the factors associated with the onset-of-spring cue for the time to reproduce are shared, yet the critical value and absolute timing are site specific (De Frenne et al., 2013).

Important predictors of successful invasion of new sites include phenotypic plasticity in ecologically relevant traits and genetic variation for the traits required to survive and reproduce (e.g., Nicotra et al., 2010). For species with broad geographic ranges, there is ample evidence of range expansion, plasticity, and ecotypic variation, as well as constraints to response to novel environments (e.g., Pujol and Pannell, 2008; Colautti et al., 2013; LaRue et al., 2018), including for *A. thaliana* (Callahan and Pigliucci, 2002; Weinig et al., 2002; Lempe et al., 2005; Wilczek et al., 2014). These data support the assertion that colonization success in novel environments is determined by a combination of site ecology, source population climate, and genetic history (Ghalambor et al., 2007; Colautti and Lau, 2015). While a growing number of large common garden studies have been conducted in the *Arabidopsis* native range (e.g., Fournier-Level et al., 2011; Ågren and Schemske, 2012; Wilczek et al., 2014; Appendix S1), specific contrasts of native and non-native gardens quantifying additional environmental parameters (Estrada et al., 2016) will inform future research decisions in the non-native range of this and other ruderal species.

### Selection at two climate sites: same or different?

Data from our experiments provide two important insights on the association of fitness and quantitative traits. First, predictions that the experience of different climates (e.g., shorter vs. longer growing season, distinct overwintering conditions) in gardens at two distributional extremes of the non-native range would lead to different fitness–trait associations were not supported. This pattern is distinct from other invasive species with directional invasion fronts (e.g., Colautti and Barrett, 2013). Our results suggest that shared features of climate, likely driving shared features of the microhabitat and surrounding vegetation, are more important drivers of selection than geographic location per se. For example, selection on early bolting and large size at maturity across gardens in our study is consistent with selection detected across shading regimes (Callahan and Pigliucci, 2002) and herbivory scenarios (Murren et al., 2005), as well as across a genetically variable sample from within the non-native range planted in Kentucky (Griffith et al., 2004). It also seems likely that more consistent use of an expanded set of traits might lead to new insights in a system for which there is a growing, yet diverse, literature (e.g., Appendix S1). To that point, we detected evidence of a strong association between total branch number, an architectural trait that is infrequently reported in *A. thaliana* studies, and fitness (also reported by Callahan and Pigliucci, 2002; Rutter and Fenster, 2007), but only weak evidence that rosette leaf count, a commonly measured trait describing the full vegetative size prior to the onset of flowering, is associated with fitness. Field studies that address selection across a range of ecological and genetic conditions across distinct novel sites are thus still needed (e.g., Donohue et al., 2005a, 2005b, 2005c; Huang et al., 2010).

Previous studies in *Arabidopsis* (Caicedo et al., 2004; Stinchcombe et al., 2004) provide strong evidence for latitudinal variation in bolting time, a critical phenological trait known to be environmentally sensitive (see also Callahan and Pigliucci, 2002; Wilczek et al., 2009). Here, we detected selection on early flowering in two climatically distinct gardens despite differences in date of flowering onset. Experiments including germplasm that has successfully passed through the sieve of successful dispersal, establishment, and expansion in North America provide additional insights into the significance of local climate history in determining patterns of selection and further invasive processes in geographic space or through time in response to climate change (Colautti and Lau, 2015).

## CONCLUSIONS

Studies assessing a broad geographic scale of phenotypic variation in the wild remain limited (Table 1; Appendix S1), particularly for populations in the non-native range. The evaluation of wide germplasm resources in multiple environments is necessary for comprehensive descriptions of phenotypic responses to novel variation from evolutionary ecology and conservation perspectives (Richards et al., 2006; Ghalambor et al., 2007). Understanding phenotypes in novel environments or those conditions that are spatially or ecologically distinct from a species' current range, and that may represent potential habitat for readily dispersing species, including ruderals, will be important for uncovering cryptic genetic variation (Paaby and Rockman, 2014) and hidden reaction norms (Schlichting, 2008). While such insights can aid in restoration and reintroduction projects for native species of threatened conservation status or in agricultural germplasm development, assessment of incremental climate changes in the native range may have important differences from the response of non-native species spreading into new non-native habitats as occurs during many biological invasions.

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## AUTHOR CONTRIBUTIONS

J.R.S. and C.J.M. conceived the idea. All authors designed the methodology. K.E.S. and C.J.M. collected and analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m4bm589 (Samis et al., 2019).

## SUPPORTING INFORMATION

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

**APPENDIX S1.** *Arabidopsis thaliana* common garden (CG) or reciprocal transplant (RT) published studies with plants grown outdoors under ambient conditions in the native range (A = Asia, E = Europe) or in the non-native range (NA = North America).

**APPENDIX S2.** Principal component analysis for non-native (open circles) range *Arabidopsis thaliana* populations used in experimental gardens in Toronto, Ontario (ON = closed triangle) and Charleston, South Carolina (SC = closed square).

**APPENDIX S3.** Factor loadings for each climate variable (October–April) used in principal component analysis (only the first three components are shown) for 35 North American populations of *Arabidopsis thaliana* and two experimental gardens (details in the text).

**APPENDIX S4A.** Multiple regression testing for an association of phenology and architecture traits with geographic distance (GD, estimate ± SE) of source populations from each garden.

**APPENDIX S4B.** Comparison of GD and CD models for traits in Table 3 and Appendix S3. $\Delta_i$ AIC (= $\text{AIC}_i - \text{AIC}_{\text{min}}$) for the model with the higher AIC (between the geographic distance [GD] and climate distance [CD] models).

**APPENDIX S5.** Phenotypic selection analyses of standardized traits on relative fitness, separately for each garden, including only non-native populations.

**APPENDIX S6.** Evaluation of plasticity across gardens using regression models (parameter estimates ± SE) for the difference in *Arabidopsis thaliana* traits recorded in experimental gardens in Toronto, Ontario (ON), and Charleston, South Carolina (SC).

**APPENDIX S7**. Evaluation of plasticity across garden performance and genetic variation for plasticity at both the line and population level for North American populations of *Arabidopsis thaliana*.

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