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Lagging adaptation to warming climate in *Arabidopsis thaliana*

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Contributed by Johanna Schmitt, April 8, 2014 (sent for review June 14, 2013; reviewed by Steven J. Franks and Julie R. Etterson)

If climate change outpaces the rate of adaptive evolution within a site, populations previously well adapted to local conditions may decline or disappear, and banked seeds from those populations will be unsuitable for restoring them. However, if such adaptational lag has occurred, immigrants from historically warmer climates will outperform natives and may provide genetic potential for evolutionary rescue. We tested for lagging adaptation to warming climate using banked seeds of the annual weed *Arabidopsis thaliana* in common garden experiments in four sites across the species' native European range: Valencia, Spain; Norwich, United Kingdom; Halle, Germany; and Oulu, Finland. Genotypes originating from geographic regions near the planting site had high relative fitness in each site, direct evidence for broad-scale geographic adaptation in this model species. However, genotypes originating in sites historically warmer than the planting site had higher average relative fitness than local genotypes in every site, especially at the northern range limit in Finland. This result suggests that local adaptive optima have shifted rapidly with recent warming across the species' native range. Climatic optima also differed among seasonal germination cohorts within the Norwich site, suggesting that populations occurring where summer germination is common may have greater evolutionary potential to persist under future warming. If adaptational lag has occurred over just a few decades in banked seeds of an annual species, it may be an important consideration for managing longer-lived species, as well as for attempts to conserve threatened populations through *ex situ* preservation.

climate adaptation | adaptation lag | local adaptation | provenance test

Rapid climate change has already caused species range shifts and local extinctions (1) and is predicted to have greater future impacts (2). As the suitable climate space for a species shifts poleward (3), populations previously well adapted to the historical climate in a particular region may experience strong selection to adapt to rapidly warming local temperatures (4–10). Rapid evolutionary response to climate change has already been observed (11, 12), but it remains unclear whether evolutionary response can keep pace with rapidly changing local adaptive optima (6, 8, 13–15). If local adaptation is slower than the rate of climate change, the average fitness of local populations may decline over time (7, 14, 16, 17), possibly resulting in local extinctions and range collapse at the warmer margin. Where such lag exists, we expect that local seeds banked for conservation may no longer be well adapted to their sites of origin (18). However, such adaptational lag may be mitigated by migration or gene flow from populations in historically warmer sites if those populations are better adapted to current conditions in a site than local populations (8, 13, 19, 20). Although adaptational lag has been predicted (4–6, 8, 14, 15, 19, 21, 22), the distinctive signature of mismatch between local population performance and current climate optima has not yet been explicitly demonstrated in nature.

Despite evidence for local adaptation in many organisms (23), there have been few explicit tests for the role of specific climate factors in shaping local fitness optima (4, 9, 13). Such tests require growing many genotypes from populations spanning a range of climates in common gardens across a species' range to decouple climate of origin from geographic variation in other selective factors (4, 6, 14). If adaptation to local climate has occurred, then genotypes from climates similar to each planting site are expected to have high fitness in that site relative to genotypes from dissimilar climates (6). However, if local adaptive optima have shifted with rapid warming trends over the last 50 y, we expect that banked genotypes from historically warmer climates will have higher fitness within a site than banked genotypes of local origin (6, 21, 22).

We tested for lagging adaptation to climate using *Arabidopsis thaliana*, a naturally inbreeding annual species that inhabits a broad climate space across its native Eurasian range (24). *A. thaliana* exhibits strong circumstantial evidence of climate adaptation, including geographic clines in ecologically important life-history traits (25–28) and in candidate genes associated with these traits (29, 30), as well as genome-wide associations of single nucleotide polymorphisms with climatic factors (31–34). To test explicitly for local adaptation to climate we measured the lifetime fitness of more than 230 accessions from banked seeds originating from a broad range of climates in replicated field experiments in four sites across the species' native climate range

Significance

If adaptive evolution cannot keep up with rapid climate change, populations and even species may decline or go extinct. Such adaptational lag is predicted, but evidence is scarce. We tested for lagging adaptation to warming climate in banked seeds of the annual weed *Arabidopsis thaliana* in common garden experiments in four sites across the species' native European climate range. Genotypes originating in climates historically warmer than the planting site had higher relative fitness than native genotypes in every site. This result suggests that local adaptive optima have shifted rapidly with recent climate warming across the species' native range, and that the potential for adaptational lag deserves consideration in conservation and management decisions for many species.

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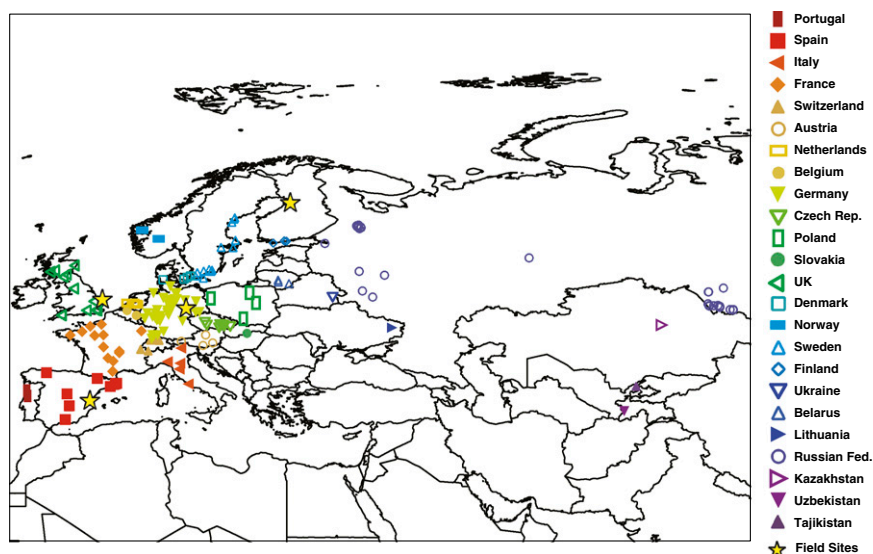


Fig. 1. Map of common garden sites and sites of origin of the 241 native *A. thaliana* accessions represented in our experiments.

(Fig. 1). We observed that genotypes originating in historically warmer climates outperformed local genotypes, particularly at the northern range limit.

Results

Absolute fitness varied dramatically across our field sites in Spain, England, Germany, and Finland, and among spring, summer, and autumn cohorts in our English site. Average fecundity was highest in our Halle, Germany site and lowest in Oulu, Finland (Dataset S1 and Table S1). Differences in absolute fitness among sites may reflect differences in edaphic factors, environmental stresses, or biotic factors as well as climate and growing season length. To test for evidence of regional adaptation, we therefore examined genotype relative fitness within each planting. Relative fitness is the basis for selection among genotypes within any particular growth environment (35) and is a good predictor of the outcome of selection across heterogeneous environments (36). Accessions from different regions differed significantly in relative fitness within each planting site (Fig. 2). Iberian accessions performed well in Spain, UK accessions in England, and German accessions in Germany, suggesting broad-scale regional adaptation (Fig. 2). However, although Nordic accessions achieved their highest relative fitness in our most northern, Finnish planting location, their relative fitness in Oulu was still lower than that of German accessions (Fig. 2 and Fig. S1). Relative fitness of accessions declined significantly and monotonically with increasing physical distance of the site of origin from each common garden site except in Finland, where accessions with the highest average fitness came from locations on average ~1,000 km distant from the garden site (Fig. S2).

Fitness was significantly heritable within each of the experimental plantings, providing evidence of genetic variation among accessions (Table S2). However, the genetic basis of fitness varied among planting locations. Genetic correlations in fitness between plantings in Spain, England, and Germany were weakly positive or nonsignificant. Accession mean fitness in Finland was not significantly correlated with fitness in any other site, except for a negative correlation with fitness in Spain (Table S2), suggesting a genetic tradeoff in performance between the northern and southern range limits. Correlations in accession mean fitness across years were moderate but significant ($P < 0.05$) for winter annual cohorts in Spain ($r = 0.43$) and Germany ($r = 0.48$), where a subset of accessions was planted in both 2006 and 2007.

To test whether regional differences in relative fitness were associated with climate, we regressed relative fitness within each experimental planting on absolute climatic distance of an accession's site of origin from the planting site. In Valencia, Norwich, and Halle, relative fitness declined significantly with climatic distance of an accession's site of origin from the planting site (Fig. S3 and Tables S3 and S4), suggesting a role for climate in regional adaptation. In Finland, however, a significant quadratic term indicated that genotypes from climates most similar to the historical climate for the planting site did not have the highest relative fitness (Fig. S3).

Absolute climate distance cannot distinguish asymmetries in fitness between accessions derived from areas colder and warmer than the growth climate, although such asymmetries are predicted under adaptational lag to warming temperature. To test for such lag, we regressed relative fitness in each planting against mean annual and seasonal temperatures in the site of origin. Relative fitness was significantly associated with mean annual and seasonal temperatures in the site of origin in all four planting sites, and in all three seasonal plantings within England (Fig. 3, Figs. S4 and S5, Table 1, and Table S3). However, the optimal native temperature varied across sites and seasons and was in every case warmer than the estimated historical climate of the common garden site. In the autumn plantings in Finland and Germany (2006), as well as the spring planting in England, there was a significant quadratic relationship between fitness and mean annual, April, and October temperature in the site of origin, with accessions originating in sites with intermediate temperatures having higher relative fitness than accessions from warmer or cooler sites. In Spain, at the southern range limit, as well as in the Norwich autumn and summer plantings, relative fitness increased linearly with mean temperature in the site of origin, such that the "optimum" native temperature was at or beyond the warmest values in our sampled population range (Table 1, Table S4, Fig. 3, and Figs. S4 and S5). In Spain in 2007, accessions from warmer climates of origin had higher fitness, as observed for the larger sample in 2006 (Tables S3 and S4). In Germany, we saw similar estimated effect sizes of temperature for the 2 y (Table S4), although our reduced sample size in 2007 provided little power to detect the quadratic effects on fitness observed at this site with the larger 2006 accession sample.

Across the four sites, the optimal native temperature for the autumn cohort was lowest in Finland, followed by Germany, then

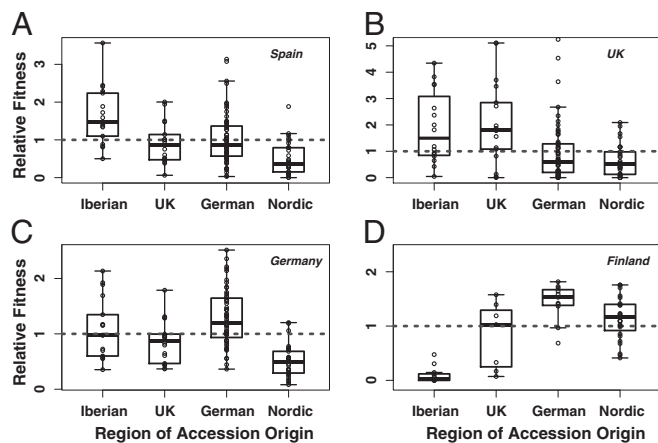


Fig. 2. Local adaptation by region in accessions of *A. thaliana*. In autumn cohorts at three of our four field sites—(A) Norwich, United Kingdom; (B) Halle, Germany; and (C) Valencia, Spain—accessions from the same region as the garden site had the highest fitness. In D, Oulu, Finland, accessions from Germany had higher fitness than more local Nordic accessions. Box-and-whisker plots of relative fitness for ecotypes from each region within each autumn planting are displayed. For each experimental planting, Kruskal–Wallis tests demonstrated that accessions from these four regions differed in relative fitness ($\alpha = 0.05$).

England and Spain, as expected if there is a history of local adaptation to climate across the species range. However, in each case the optimal native temperature was higher than the historic temperature in the planting site, but similar to the actual April and October temperatures recorded on site during the experiment (Table 1, Fig. 3, and Fig. S5) (37). We observed a similar mismatch between the latitude of common garden sites and the optimum native latitude of origin estimated from the accessions in all of the plantings. The optimal latitude of origin decreased from Finland to Germany to England and Spain, but was always south of the actual latitude in each planting site in both 2006 and 2007 (Table 1 and Table S3). Thus, genotypes from southern populations in historically warmer climates had higher average fitness than genotypes from the local latitude in every planting site.

We also observed differences in optimal mean native temperatures and latitudes among seasonal cohorts in England, demonstrating that for annual plants adaptation to climate can depend on the growth season. In the Norwich summer and autumn plantings, where seedlings experienced warm temperatures for several months, selection monotonically favored accessions originating in warmer climates. In contrast, in the cooler spring planting, accessions originating in sites with a mean April temperature of 11.4 °C had higher relative fitness than accessions from warmer or cooler climates. This optimal native temperature was warmer than the historical mean for the site, but very similar to the actual April temperature recorded during the experiment (Table 1). Thus, selection can favor adaptation to different thermal environments in different seasonal cohorts within a site.

The accessions in this study were banked in the stock center over a period of nearly 70 y. If these collections were collected uniformly in space and time across that period, we might expect that accessions collected earlier would show greater adaptational lag than more recently collected populations from the same region. Unfortunately it was not possible to test this prediction using our entire sample, because different geographic regions were largely sampled in different decades, with early collections concentrated in western and central Europe and more recent collections concentrated in other parts of the species range (Dataset S1). We found no association between date of collection and fitness in

a core set of 56 accessions from Germany, the region that spanned that largest range of collection dates (1939–1993).

Discussion

Our results provide evidence for broad-scale adaptation to regional climate across *A. thaliana*'s native European range as well as for adaptational lag. In all of our experimental plantings, southern “immigrants” from historically warmer climates had higher relative fitness on average than local genotypes, particularly at the northern range margin in Finland. These results suggest that climatic optima for *A. thaliana* populations have shifted rapidly since the collection of the accessions used in our experiment. The observation of adaptational lag over a few decades in banked seeds of a short-lived annual plant suggests that such lag should be considered in planning for conservation and management of many species.

On a broad regional scale, local genotypes on average had higher relative fitness than genotypes from other regions in every planting site except Finland, at the northern range limit (Fig. 2). Nevertheless, the relative fitness of Nordic genotypes was higher in Finland than in any other site, suggesting that they were best adapted to northern conditions (Fig. S1). For example, in the summer planting in Norwich, many Nordic accessions grew

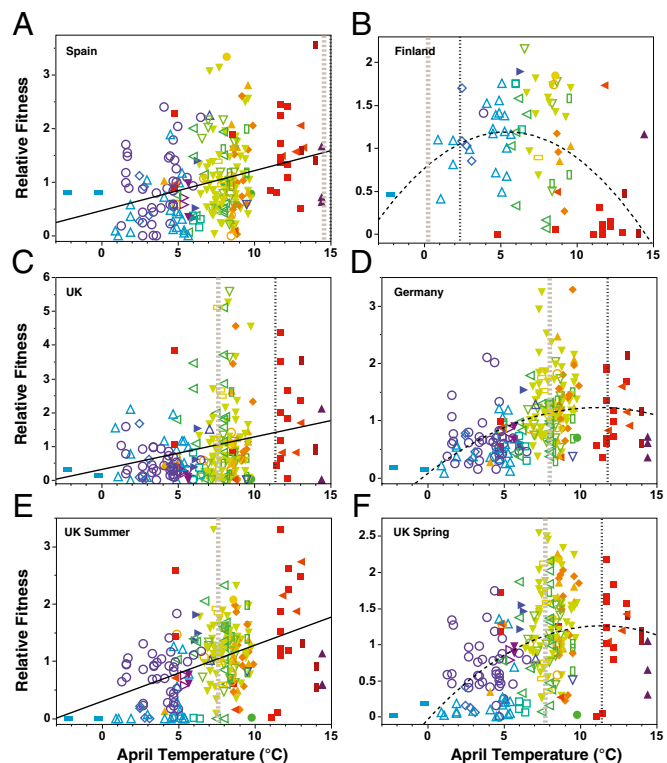


Fig. 3. Lagging adaptation to April temperature in a large sample of accessions from throughout the native range of *A. thaliana*. In autumn cohorts in (A) Valencia, Spain; (B) Oulu, Finland; (C) Norwich, United Kingdom; and (D) Halle, Germany, historic April temperatures were cooler than experienced April temperatures, which were closer to the predicted optimum. Selection also favored accessions from historically warmer climates in (E) summer and (F) spring cohorts planted into the Norwich, UK, common garden site. Lines of linear (solid) or quadratic (dashed) best fit, significant at $P \leq 0.006$ are shown (Table S4). Warmer-colored symbols denote accessions from more southerly locations, with each color and shape combination characterizing a single country of origin (legend details in Fig. 1). Vertical gray lines show the recent historic April temperature, whereas vertical black lines show the April temperature during the experimental planting at each site.

Table 1. Patterns of selection on climate of accession origin demonstrate geographic variation in selection and lagging adaptation to temperature

Location and season	United Kingdom			Germany	Spain	Finland
	Summer	Spring	Autumn	Autumn	Autumn	Autumn
Temperature, °C						
Historic mean annual	10.0	10.0	10.0	9.0	16.9	1.9
Optimal mean annual	>16	13.9	>16	12.5	>16	7.0
Historic April	7.7	7.7	7.7	8.1	14.5	0.4
Growth April	11.4	11.4	11.4	11.8	15.0	2.3
Optimal April	>15	11.4	>15	11.2	>15	5.4
Historic October	11.0	11.0	11.0	9.6	18	2.8
Growth October	13.7	13.7	13.7	13	—	5.8
Optimal October	>17	14.8	>17	13.7	>17	7.7
Latitude, ° N	52.6	52.6	52.6	51.5	39.6	65.1
Optimal latitude, ° N	43.7	46	<37	46.8	<37	54.2

Historic temperature data are based on 30-y climate normals, and temperatures from the year of growth are based on hourly air temperature averages made at on-site weather stations. Optimal values of temperature and latitude of accession origin were determined from selection analyses of field-measured fitness (Tables S3 and S4).

vegetatively but failed to flower, possibly because they did not receive sufficient chilling to satisfy their vernalization requirements (38). Conversely, accessions from the Iberian peninsula had low survival in Finland, possibly due to low cold tolerance (29). Thus, different selective mechanisms may contribute to adaptation in different geographic regions (31, 32, 39–41). These results are consistent with evidence for adaptation on a broad geographic scale in a wide range of species (23, 42–45). However, the wide geographic diversity of accessions available for *A. thaliana* also permitted us to test explicitly for a signature of adaptation to climate (4, 13, 14) and explore the genetic basis of local adaptation.

The weak genetic correlations we observed between different planting sites suggest regional differences in the genetic basis of fitness in *A. thaliana*. In particular, fitness in Finland was weakly correlated with fitness in the other sites and displayed a negative genetic correlation with fitness in Spain. Local adaptation in our most northern site may thus have a distinct genetic basis and contribute to a tradeoff between adaptation to local environments at the northern and southern climatic range limits of *A. thaliana*. This quantitative genetic evidence for local adaptation is corroborated by results from a genome-wide scan showing that SNP alleles associated with fitness differed among these same sites, and that alleles conferring greater fitness within a site were locally abundant and climatically differentiated relative to genomic controls (31).

This study provides, to our knowledge, the first direct field test of regional climate adaptation in *A. thaliana*, although several previous studies have measured the fitness of natural accessions in the field in this species (26, 28, 39, 41, 46–51). Reciprocal transplant experiments between northern and southern sites show evidence of local adaptation but were not designed to distinguish the role of climate (41). We tested for adaptation to climate by deploying a large geographically diverse sample in multiple sites across the native climate range and measuring real-time fitness in each site. A broad-scale signal of climate adaptation was detectable despite considerable genetic variation in fitness within regions. Such variation is not surprising given the diverse smaller scale processes contributing to local environmental heterogeneity for this species. Other studies in *Arabidopsis* have found genetic evidence suggestive of local adaptation on a fine geographic scale (e.g., refs. 26, 39, 52, and 53). Potential drivers at these smaller scales include local pathogen pressure (54–57), disturbance (53), and edaphic factors (39, 58). Nevertheless clear patterns of broad-scale regional adaptation as well as lagging adaptation to climate were consistently apparent

overlaid on this variation. This direct observation of climatic adaptation under field conditions validates several recent studies that inferred climatic adaptation from genomic data (31–34, 59) or observations of population differentiation or clinal life history variation in common gardens (26, 27, 41, 51, 60–62).

The most striking result of this study is the observation that southern genotypes from historically warmer climates consistently outperformed local genotypes in all four field sites across the species' European climate range. Thus, local banked genotypes collected several decades ago no longer match the fitness optima measured in the years of our field experiments, in which temperatures consistently exceeded historical averages. Although we found no effect of year of collection on fitness in any planting for a core set of German ecotypes collected between 1939 and 1993, that sample did not provide a strong test of temporal change in adaptational lag as the sampled decades displayed little directional change in annual temperature anomalies compared with more recent rapid warming trends (63, 64).

Fitness optima are likely to vary within sites from year to year, and interannual climate variability may allow warm-adapted genotypes or species to colonize historically cooler climates in warm years (such as during our experiment) but prevent persistence in subsequent cool years (65, 66). It is therefore possible that the adaptational lag we observed may reflect episodic past strong selection against warm-adapted genotypes by extreme cold events, particularly in Finland. However, a directional warming trend has already occurred in Europe and is predicted to continue in the future (67), suggesting that warm years like those of our experiments will be increasingly common in the future. If so, continued directional shifts of local fitness optima are likely, and gene flow or migration from historically warmer regions could increase mean population fitness (14, 16, 19, 22). Short-term climatic variation may help to maintain standing genetic variation in climatic tolerance within populations and allow introgression of warm-adapted traits from southern migrants during warm years or seasons. However, genetic potential for adaptation to track warming temperatures at the southern range limit may be limited (4, 14, 16).

Climatic optima also shifted among seasonal cohorts within the Norwich site. Such seasonal variation in selection may help to maintain genetic variation in climatic tolerance in populations with multiple generations per year. Thus, populations occurring where summer germination is common may have greater potential for adaptation to future warming. Germination timing in itself is likely to contribute to climate adaptation, as suggested by observations of clinal variation (26, 30, 68). However, because our experimental design required us to synchronize germination,

we could not assess the contribution of this life stage to the adaptational lag we observed.

Whether evolution can drive adaptation in the face of future climate change will depend upon the heritability, genetic covariance structure, and plasticity of adaptive traits within populations, as well as migration rates (4–7, 10, 21). Our results suggest that high standing genetic variation and/or substantial gene flow from more southern *A. thaliana* populations will be necessary for adaptive evolution to keep pace with predicted rates of future warming. The lagging adaptation to warming temperatures that we observed for *A. thaliana* occurred over just a few decades, suggesting that similar lags may be likely for other plant species conserved in *ex situ* seed banks. Studies designed to measure rates of adaptation (e.g., ref. 69), and to compare measured evolutionary rates with rates of climate change (15, 70), will be vital to a fuller understanding of the importance of adaptational lag (4–7, 10, 19, 21). Nonetheless, the rapidly shifting climate optima observed for this annual species suggest that adaptational lag is likely to occur within individual lifetimes for some longer-lived species. The possibility that climatic optima of local populations may not keep pace with rapid climate change deserves consideration in future forestry and conservation management decisions.

Methods

Common Garden Experiments. During the years 2006–2008, we measured real-time fitness in the field with a geographically diverse panel of *A. thaliana* accessions in four common garden sites spanning the species' native European climate range: Oulu, Finland; Norwich, United Kingdom; Halle, Germany; and Valencia, Spain (Fig. 1). We grew a panel of *A. thaliana* accessions (ecotypes) derived from the US and European stock centers as well as recently collected and bulked seed from Central Asian populations contributed by K. J. Schmid (University of Hohenheim, Stuttgart, Germany) (71, 72) (Dataset S1 and Fig. 1). Accessions used in this experiment were collected from wild populations between the late 1930s and 2002, with most ecotypes having been sampled from 1939 to 1991 [<http://arabidopsis.org> (73) and Dataset S1]. Using these banked seeds from stock center-derived inbred lines (accessions or "ecotypes"), originally collected from natural populations, it is possible to measure lifetime fitness of replicated individuals in multiple locations. Seeds for the field experiment were taken from a common bulking generation in which all accessions were grown at 20 °C with 14-h days.

We planted between 15 and 20 replicates of each accession in a randomized block design in four common garden sites spanning the climate range of the species' native distribution (Oulu, Finland; Norwich, United Kingdom; Halle, Germany; and Valencia, Spain) as described in ref. 37 and Table S1. We grew an autumn-germinating winter annual cohort at all sites. The mild oceanic climate of Norwich also supports spring- and summer-germinating cohorts of *A. thaliana* that behave as rapid-cycling annuals, and we therefore established spring and summer cohorts to measure seasonal variation in selection at this site (Table S1). As described by Wilczek et al. (37), seeds for these experiments were stratified for 4 d at 4 °C in 0.1% agar before sowing in the greenhouse under close-to-ambient light and temperature conditions. Seedlings were transplanted within 14 d of sowing into the field. Within each fully randomized block, plants were arrayed in an 80 cm × 450 cm grid at 10-cm spacing [360 accessions per block including the native accessions interspersed with additional genotypes for other studies], except in Oulu where the array was 80 cm × 150 cm (for 120 accessions per block).

Fitness estimates were based on a subsample of 5 to 15 complete blocks at each planting, with an average of 7.3 replicates per accession per planting (Table S1). Individuals were harvested from the field at senescence and the branching architecture, number of siliques, and representative silique length were recorded. Individuals from the subsampled blocks that survived transplanting but failed to reproduce were assigned a fitness of 0. Occasionally, individuals lacking a field-recorded date of death could not be found among the harvested plants; these points were treated as missing data. In the subsampled blocks, we collected fitness data from at least 94% of the plants that survived transplanting (with the proportion of missing data ranging from 0.9% in Oulu to 5.6% in Halle, with an average across all plantings of 2.8% missing data). In total, our sample of fitness estimates from genetically distinct native accessions (*Location and Climate Information for A. thaliana*

Accessions) consisted of more than 7,200 measurements from individuals that were tracked in the field (Table S1).

We estimated fitness as the product of total silique number and (representative) silique length, with the latter serving as a proxy for number of seeds per fruit (74, 75). Silique number and seed proxy were highly correlated in all plantings ($0.978 < \text{Spearman's } \rho < 0.992$; $0.970 < \text{Pearson's } r < 0.987$), and analyses of performance using number of siliques as the measure of fitness gave nearly identical results.

Within each planting, we calculated the family mean fitness for each accession. The relative fitness of each accession was then estimated as the family mean fitness divided by the average family mean fitness in that planting (35, 76).

Location and Climate Information for *A. thaliana* Accessions. We determined site of origin for each accession using the collection information available from The Arabidopsis Information Resource (<http://arabidopsis.org>) and the Nottingham Arabidopsis Stock Centre (<http://arabidopsis.org.uk>) in concert with town location information from Google Earth (www.google.com/earth/), as well as published information for accessions included in our sample (71, 72). Physical distance between each accession location and each common garden site was taken as the great-circle distance between the two, calculated using the haversine formula. For each accession site of origin as well as for each common garden location, we obtained climate normals (averages from 1961 to 1990) of monthly temperatures, frost days, precipitation amounts, and wet days—mapped over the world on a 10-min grid—from the Climate Research Unit [CRU CL 2.0 (77)]. Bioclimatic variables including mean annual temperature (BIO1) based on averages from 1960 to 1990 were obtained at the 10-min scale from WorldClim (78). Data from these two sources were used to estimate the recent historical climate at each accession site of origin and common garden site. We also calculated the actual growth temperatures of these sites during our experiments using data from onsite weather stations (37). We used the average of the daily maximum and minimum temperatures to calculate mean growth temperature for October and April (77). As our on-site weather stations were only active during our planting seasons, we could not make a comparable estimate of mean annual temperature for the year of planting. The autumn cohort in Valencia was not planted until November (following natural germination patterns of nearby populations; see also ref. 79), and we therefore do not have a plant-relevant estimate of on-site October temperature here (Fig. S5). Similarly, we do not display the April temperature for the Norwich summer cohort (Fig. 2) because this planting was not established in the field until mid-May.

Analyses of performance relative to estimated climate of origin were restricted to accessions whose provenance fell within the potential native range of -11° to 86° E and 35° to 71° N (80). Six locations were clear outliers on the basis of bioclimatic variables (e.g., Mahalanobis distance of >10 when all 19 bioclimatic variables were considered for our accession sample). We excluded accessions from these six locations (Kil, Lc, Na, Pa, Pi, and Tu), at least four of which occurred within or at the edge of mountain ranges, suggesting that 10-min resolution climate estimates may not accurately describe *Arabidopsis* population microclimates here. Where accessions in our sample were found to be identical across a panel of genome-wide SNPs (81), only one representative accession was included. Accessions identical to the common laboratory strains Ler and Col were considered to be the result of contamination (see also ref. 82) and discarded; otherwise we retained the accession represented in the greatest number of field plantings. In most cases identical accessions were derived from the same location, but all identical accessions were excluded when these were attributed to different sites of origin. Our final sample of genetically distinct native accessions for which we had field-collected fitness data consisted of 78 to 241 accessions per planting, with a median of 231.5 (Dataset S1 and Table S1). We planted all 241 accessions at Valencia and Halle and a subset of 230 to 232 at Norwich. The autumn planting in Oulu contained a core collection of 78 accessions chosen to represent the broad range of phenotypic and geographic variation present within the larger set. We collected fitness data for at least 95% of the Oulu-represented accessions in each other planting as well (Dataset S1).

To test for broad-scale local adaptation, we classified accessions into four regions: German (from Germany), United Kingdom (from the United Kingdom), Iberian (from Spain or Portugal), and Nordic (from Denmark, Norway, Sweden, or Finland). We then compared performance of accessions in native versus nonnative regions (Fig. 2 and Fig. S1). Transforming fitness data can lead to erroneous conclusions about the outcome of selection across heterogeneous environments (36), and we therefore analyzed the more easily interpretable measure of relative fitness within environments. As our data did not meet the assumption of ANOVA, however, for each experimental planting, we performed nonparametric Kruskal–Wallis tests

that demonstrated that accessions from each of these four regions differed in relative fitness (at $\alpha = 0.05$).

To determine the basis and extent of local adaptation, we calculated both physical distance and an index of climate distance of each accession site of origin from each planting site. To generate estimates of the native climate niche, we obtained occurrence records of *A. thaliana* from within the native range from the Global Biodiversity Information Facility Web portal (www.gbif.org). We supplemented these records with data from recent collections in underrepresented areas (71, 83) to generate a better estimate of the complete species' distribution in climate space. We reduced overlapping records to one occurrence per 10-min grid cell. Our final sample of *A. thaliana* occurrence consisted of 4,980 unique grid cell records in the native range for which we were able to obtain climate data (data available upon request). Using data from the CRU CL 2.0 (77), we calculated separately the first four principal component (PC) axes (using correlation matrices) for the *A. thaliana* climate envelope space as characterized by monthly temperature (mean and number of frost days) and precipitation (mean amount and number of rainy days) variables. These first four PC axes accounted for 97.0% and 95.4% of the variation in monthly temperature and precipitation, respectively (Table S5). After calculating the position of each common garden location in climate space along these PC axes, we calculated climate distance between each accession and each common garden location as the Euclidian distance along the eight PC axes. Just as for physical distance, each accession was therefore closer in climate distance to some growth sites (common gardens) than to others.

Climate and physical distance to a given field site were significantly positively correlated in all cases. For the sample of accessions grown within a given site, physical distance explained 44–84% of the variation in climate distance (Fig. S6). The most physically proximate accessions were often among the most similar to the growth site in climate space, but the most distant accessions were never furthest in climate space.

Performance Relative to Climate and Location. To determine whether individual climate variables were associated with local adaptation, we determined the relationship between fitness and selected bioclimatic, temperature, and precipitation estimates that had been identified a priori as potential candidate indicators of adaptation to climate. For each climate variable considered, we calculated linear and quadratic fit of the climatic variable versus accession relative fitness in that planting (Tables S3 and S4). We explicitly tested for adaptation to temperature in October and April because temperatures in these months have been implicated as determining factors for the climatic range limits for *A. thaliana* (24) and because one or both of these months fall within the growing season for the majority of natural annual cohorts in European locations. An earlier study of *A. thaliana* found a strong relationship between estimates of diurnal temperature range (dtr) [CRU variable dtr (77)] at the site of origin and accession performance in the field in Maryland (47); however, we found that these temperature range variables explained less of the variance in fitness than corresponding monthly average temperatures.

Our final analysis of local adaptation examined three location variables (latitude, longitude, and physical distance to planting site) and five climatic variable estimates [mean annual temperature (BIO1), mean annual precipitation (BIO12), October mean temperature, April mean temperature, and climate distance to planting site (Tables S3 and S4)]. Many individual climate variables (monthly values of average temperature, frost days, precipitation and rainy days; see above) were included in our metric of climate distance (Table S5). For each climate and location variable considered, we estimated linear and quadratic fit of the environmental variable versus accession relative fitness in that planting. Tables S3 and S4 show estimates of the (unstandardized) selection differentials (S , the slope parameter from a simple linear regression) and gradients (γ , double the quadratic regression parameter) (84) for each climate and location variable. Where quadratic components were negative and significant at $\alpha = 0.05$, the value of the climate or location variable giving the highest fitness (i.e., the predicted optimum) was calculated; where quadratic components were positive and significant at $\alpha = 0.05$, the boundary value of the climate or location variable giving the highest fitness was calculated. Where quadratic components were not significant at $\alpha = 0.05$ but linear components were, we assumed that the optimum lay at or beyond the upper or lower boundaries of our sample (Table 1 and Tables S3 and S4). A Bonferroni correction for the number of climatic and location comparisons conducted per trait ($n = 8$) yielded an adjusted $\alpha = 0.006$. However, we chose to display marginal polynomial fits in any case with this noted as a gray ($0.006 < P < 0.05$) rather than a black ($P < 0.006$) line in Figs. S2, S4, and S5. In each case, where the polynomial fit was marginal the linear fit was significant at $\alpha = 0.006$ (Tables S3 and S4).

The differential response of fitness observed in Oulu to climate and location variables was not due to the reduced accession sample, as restricting performance analyses to the 78 Oulu-represented accessions (Dataset S1) did not reveal any qualitatively different patterns in fitness associations with environment and location.

In Halle and Valencia, we planted a subset of 27 to 28 accessions in fall 2007 to test for year-to-year variation in relative fitness. Plants in Halle and Valencia were sown October 3 and November 14, respectively, within one week of the 2006 calendar planting date. Seedlings were placed in randomized blocks into the same field site using the same procedure and with the same arrangement as the previous year's cohorts (described above).

Dates of collection for accessions collected up to 1987 were derived from ref. 73 where available. Rough dates of collection were sometimes assigned based on collector identity (when collectors contributed other accessions over a short and known time scale). Other dates were assigned based on first publication of data from accession and/or separately published information about the acquisition/collection of seeds from natural populations (e.g., refs. 72 and 85). We tested whether observed patterns of local adaptation or adaptational lag were influenced by date of collection by subsetting ecotypes according to collection date (pre-1950, 1951–1976, and post-1976). We then tested whether the relationship between fitness and selected bioclimatic, temperature, and precipitation estimates (Tables S3 and S4) differed among these subsets by comparing linear and quadratic regressions carried out separately for each time-restricted subset. Unfortunately, year of collection was strongly confounded with geographic region of origin, which both reduced our power to detect adaptational lag and also introduced a potential bias. Using German accessions, for which we have good representation from many collection dates, we also regressed fitness on year of collection and to test whether adaptational lag was greater in accessions collected earlier.

Genetic Components of Fitness. Broad sense heritabilities (V_G/V_P) were estimated from restricted maximum likelihood (REML) variance components by taking the variance attributed to (inbred homozygous) accession divided by the total phenotypic variance (accession plus block and error). The heritability of relative fitness was significant at $\alpha = 0.05$ in all plantings (Table S2). Cross-environment genetic correlations in fitness were calculated using two methods. First, we used family (accession) means in each planting and calculated the pair-wise correlation between plantings (method 1) (86). This method of estimating cross-environment correlation tends to yield estimates that are smaller in magnitude and is therefore conservative in testing the hypothesis that genetic correlation is different from 0 (86). We also calculated cross-environment correlation between each pair-wise set of plantings using REML variance components from a single analysis including block in the total environmental variance (method 5) (86). This method is conservative if one wishes to determine whether or not correlation is different from 1, although concerns have been raised about the accuracy of this method (87). The pattern of correlation among plantings was very similar by both measures although, as expected, estimates of cross-environment correlation derived from family means were smaller in magnitude (closer to 0) than those from REML (Table S2). The reduced cross-environment correlation between the Oulu autumn and other plantings was not due to the reduction in shared accessions between Oulu and other sites. Recalculations of cross-environment correlations among other plantings calculated from a sample restricted to Oulu-represented accessions showed approximately equal or even slightly elevated estimates of cross-environment correlation. Statistical analyses were conducted in JMP (www.jmp.com) and R (www.R-project.org).

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