

Climate adaptation is not enough: warming does not facilitate success of southern tundra plant populations in the high Arctic

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Abstract

Rapidly rising temperatures are expected to cause latitudinal and elevational range shifts as species track their optimal climate north and upward. However, a lack of adaptation to environmental conditions other than climate – for example photoperiod, biotic interactions, or edaphic conditions – might limit the success of immigrants in a new location despite hospitable climatic conditions. Here, we present one of the first direct experimental tests of the hypothesis that warmer temperatures at northern latitudes will confer a fitness advantage to southern immigrants relative to native populations. As rates of warming in the Arctic are more than double the global average, understanding the impacts of warming in Arctic ecosystems is especially urgent. We established experimentally warmed and non-warmed common garden plots at Alexandra Fiord, Ellesmere Island in the Canadian High Arctic with seeds of two forb species (*Oxyria digyna* and *Papaver radicum*) originating from three to five populations at different latitudes across the Arctic. We found that plants from the local populations generally had higher survival and obtained a greater maximum size than foreign individuals, regardless of warming treatment. Phenological traits varied with latitude of the source population, such that southern populations demonstrated substantially delayed leaf-out and senescence relative to northern populations. Our results suggest that environmental conditions other than temperature may influence the ability of foreign populations and species to establish at more northerly latitudes as the climate warms, potentially leading to lags in northward range shifts for some species.

Keywords: Arctic tundra, climate change, common garden experiment, experimental warming, latitudinal transplant experiment, local adaptation, plant phenology

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Introduction

Current and projected increases in global temperatures are predicted to have widespread consequences for the distribution and abundance of organisms (Parmesan, 2006). As temperatures increase, areas of suitable climate will shift poleward and upward in elevation for many species (Loarie *et al.*, 2009; Burrows *et al.*, 2014). If the degree of climate warming exceeds the ability of individuals to respond through phenotypic plasticity, local populations will become maladapted to the novel climatic conditions in their current range (Anderson *et al.*, 2012; Franks *et al.*, 2014), and evolutionary adaptation may be necessary for the *in situ* persistence of these populations (Aitken *et al.*, 2008; Shaw & Etterson, 2012; Alberto *et al.*, 2013).

For species whose distributions span a broad latitudinal range, it has been proposed that gene flow can ‘rescue’ northern populations by introducing warm-

adapted genotypes from the south (Aitken *et al.*, 2008; Sgrò *et al.*, 2011; Anderson *et al.*, 2012; Norberg *et al.*, 2012). It is similarly projected that climate warming will lead to northward range shifts of ‘pre-adapted’ southern species (Davis & Shaw, 2001; Walther *et al.*, 2002; Thuiller *et al.*, 2008; Morin & Thuiller, 2009). Both of these projections rely on the assumption that temperature is the key variable determining the establishment and success of warm-adapted immigrants at northern latitudes. However, nonclimatic factors such as soil conditions (e.g., nutrient availability or soil moisture) or biotic interactions (e.g., herbivory) might also be important determinants of distribution and abundance along latitudinal or elevational gradients (Corlett & Westcott, 2013; Brown & Vellend, 2014).

While populations of many species show evidence of local adaptation (Leimu & Fischer, 2008; Hereford, 2009), including adaptation to climate (Jump & Peñuelas, 2005; Savolainen *et al.*, 2007), the relative importance of climate vs. other environmental factors in driving local adaptation is largely unknown (Stanton-

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Geddes *et al.*, 2012; Aitken & Whitlock, 2013). If local adaptation is not driven primarily by climate but rather by nonclimatic conditions (Davis *et al.*, 1998, 2005; Alberto *et al.*, 2013), southern immigrants may not be pre-adapted to site conditions further north as the climate warms, and gene flow from southern populations could instead lead to reduced fitness in the northern populations (Edmands, 2007; Frankham *et al.*, 2011; Sexton *et al.*, 2011; Aitken & Whitlock, 2013; Schiffers *et al.*, 2013; Bourne *et al.*, 2014). The reverse is also possible: Immigrants could be at a fitness advantage if they escape the herbivores or parasites that limit their fitness in their current range (Van der Putten *et al.*, 2010; De Frenne *et al.*, 2014).

To date, direct tests of the success of poleward transplants under realistic warming scenarios in the field are extremely rare. Wilczek *et al.* (2014) transplanted several European *Arabidopsis thaliana* populations northward, and at the northernmost site found that local populations are now at a fitness disadvantage relative to southern immigrants, presumably due to recent climate warming. However, they also found strong evidence of local adaptation, with local genotypes having higher relative fitness than foreign ones at the majority of experimental sites. Several additional studies have investigated the response of multiple populations to warming using reciprocal transplants along a latitudinal or altitudinal gradient, in which climatic conditions further south or at lower elevations are considered a proxy for future conditions at the northern site (De Frenne *et al.*, 2011; Ågren & Schemske, 2012; Alexander *et al.*, 2015). However, while these studies provide important insights into the underpinnings of local adaptation, many nonclimatic conditions also vary among such sites (e.g., soil and biotic interactions), such that the role of temperature *per se* is very difficult to isolate (De Frenne *et al.*, 2013). Manipulating climate locally can permit a more direct test of how warming might alter the relative fitness of local vs. foreign genotypes. Addressing this question is especially urgent in Arctic ecosystems, where temperatures have risen by 2 °C over the past 50 years – a rate more than twice that of the global average (Weller *et al.*, 2004; IPCC, 2013).

Here, we test the hypothesis that warming at northern latitudes will confer an advantage to immigrants from southern, warm-adapted populations relative to resident individuals and that this advantage will outweigh the potential disadvantages due to adaptation to other environmental factors. We collected seeds from three to five foreign and local populations of two widely distributed and abundant Arctic plant species (focusing on *Oxyria digyna*, with additional work on *Papaver radicum*), planted them into both passively warmed and nonwarmed (control) treatments at our

high Arctic field site, and followed the survival, phenology (leaf-out and senescence), and growth of all individuals over two summers. We recorded phenology in addition to survival and growth because changes in the timing of life events have been shown to have important consequences for plant success (Willis *et al.*, 2008; Cleland *et al.*, 2012), particularly in the relatively short Arctic growing season, where mismatches between phenology and temporal environmental patterns can lead to substantially reduced fitness (Molau, 1993; Berteaux *et al.*, 2004).

If populations are locally adapted to climate (*sensu* Kawecki & Ebert, 2004), individuals from populations from warmer areas should have higher fitness (here defined as survival and plant size) in the experimentally warmed treatment than in the control treatment. These warm-adapted populations should also have higher fitness than local populations in the warmed treatment if the warming effect creates temperature conditions that resemble those at the population's home site. Conversely, if local conditions other than climate (e.g., photoperiod, soil, biotic interactions) hinder the successful establishment and growth of foreign populations even under warmer temperatures, we would expect higher fitness in the local populations in both warm and control treatments (i.e., home-site advantage).

Materials and methods

Species and site characteristics

Study species. Our study focused on two forb species: *Oxyria digyna* (L.) Hill (mountain sorrel) and *Papaver radicum* Rottb. (rooted poppy). These species were chosen because they are widely distributed and relatively abundant across the Arctic, grow readily from seed, and have been focal species of the International Tundra Experiment (ITEX; Henry & Molau, 1997) since 1992. In addition, *O. digyna* has been studied extensively along its ~40° latitudinal range (Mooney & Billings, 1961; Billings *et al.*, 1971). *Oxyria digyna* is wind pollinated (Billings, 1974), while *P. radicum* is insect pollinated (Robinson, 2014); both species are self-fertile. The maximum life span of *O. digyna* individuals has been recorded as 13–17 years in alpine and subarctic populations, respectively (Erschbamer & Retter, 2004), but the life span of high Arctic populations is unknown. The maximum life span of *P. radicum* ranges between 8 and 30 years (Lévesque *et al.*, 1997; Jónsdóttir, 2011).

Source populations. The experimental site, Alexandra Fiord (AF; 78.88°N, 75.80°W), is located on the eastern coast of Ellesmere Island in the Canadian High Arctic. The AF lowland is an 8 km² mosaic of dwarf-shrub tundra and wet sedge meadow, bounded to the east and west by high plateaus, to the south by the Twin Glacier, and to the north by the fiord. This

area is considered a 'polar oasis' due to the relatively mild conditions compared to the polar desert areas that dominate the high Arctic (Freedman *et al.*, 1994). The primary herbivores at the site are Arctic hares, lemmings, and the moth caterpillar *Gynaephora groenlandica*; large mammal herbivory at the site is generally very low and has likely been low for at least 100 years (Henry *et al.*, 1986). For an overview of the ecology of Alexandra Fiord, see Svoboda & Freedman (1994).

For our common garden experiment at the AF site, we collected seeds of *O. digyna* and *P. radicum* from local (AF) populations, as well as several 'foreign' populations. Seeds of *O. digyna* were collected from two southern sites, Latnjajaure, Sweden (68.35°N), and Barrow, Alaska, USA (71.30°N), and one northern site, Sverdrup Pass, Ellesmere Island, Canada (79.12°N). Including a more northerly site (Sverdrup Pass) allows us to determine whether patterns in phenology, size, and survival of *O. digyna* are related to a latitudinal gradient (in which case we expect a linear relationship with latitude) or home-site advantage (in which case we expect survival and plant size to decrease with increasing distance from the home site, regardless of whether the source site is north or south of AF). Because *P. radicum* was present at fewer of the seed collection sites, it is represented by only one foreign population: Resolute Bay, Cornwallis Island, Canada (74.72°N; Table 1, Fig. 1).

To test whether nearby populations growing in a warmer microclimate would have the same adaptive advantage as foreign populations from southern latitudes, we also collected seeds of *O. digyna* and *P. radicum* from the Twin Glacier site approximately 2 km to the south of AF. Plants at the Twin Glacier site are exposed to the same general weather patterns and biotic interactions as the AF populations, but grow in a microclimate that is ~0.5 °C warmer during the growing season (Labine, 1994; Bean, 2002; Edwards, 2012). Both snow melt and flowering phenology are typically advanced at the Twin Glacier foreland relative to other areas of the Alexandra Fiord lowland (Woodley & Svoboda, 1994). Plants also senesce slightly earlier at the Twin Glacier site (Woodley & Svoboda,

1994), possibly as a consequence of water limitation (Billings & Mooney, 1968; Bliss, 1971).

With the exception of Resolute Bay, mean annual air temperatures (MAT) and growing season length follow a south-to-north pattern across source populations, with the Latnjajaure population at the warmest and Sverdrup Pass at the coldest extremes (Table 1). Long-term (1960–1990) monthly 0.5° × 0.5° gridded climate data (available at http://www.ipcc-data.org/observ/clim/get_30yr_means.html) for Resolute Bay indicate that its MAT is approximately 1 °C warmer than AF, but recent data (1990–2009) from local weather stations indicate that Resolute is in fact 0.9 °C colder, on average.

Experimental design

We collected seeds from 40 individuals (mothers) of *O. digyna* and *P. radicum* spaced at least 2 m apart at the Alexandra Fiord, Twin Glacier, Sverdrup Pass, and Resolute Bay sites in 2009. The Latnjajaure and Barrow populations were collected by colleagues using the same criteria. Seeds from Barrow were collected in 2010. All seeds were collected just before seed dispersal at each site to minimize differences between populations due to seed ripeness. Seeds were air-dried and stored at 2 °C for 9–21 months. We measured average seed mass for each seed family (i.e., all seeds from the same mother) to estimate the maternal environmental effect of differential seed provisioning for each seed family and population.

In early June 2011, seeds of *O. digyna* and *P. radicum* were germinated at Alexandra Fiord in Flowerhouse® RowHouse™ (Clio, MI, USA) cold frame greenhouses to promote germination and initial establishment. Seed trays were filled with soil collected from Alexandra Fiord the previous summer and coarse-sifted to remove roots. Seedlings were planted into 44 1 m² common garden plots at Alexandra Fiord in mid-July, and each individual was marked. Seedlings were distributed according to a stratified random design, such that no two seedlings from the same seed family were planted into the

Table 1 Latitude and temperature variables for each population. Mean annual temperature (MAT) 1960–1990 is 0.5 × 0.5 gridded mean annual surface air temperature from the East Anglia Climatic Research Unit. MAT 1990–2009 is local climate station air temperature provided by collaborators at each site (~1.5 m height). Days above 0 °C is a count of the number of days with mean diurnal temperature above 0 °C at each site, averaged over the 1990–2009 period, and represents an estimate of potential growing season length. Latnjajaure, Sweden, is abbreviated to Latnja. The common garden experimental site, Alexandra Fiord, is indicated by bold lettering. The abbreviation 'n.a.' designates data that are not available

	Latnja	Barrow	Resolute Bay	Twin Glacier	Alexandra Fiord (AF)	Sverdrup Pass
Latitude	68.35°N	71.30°N	74.72°N	78.86°N	78.87°N	79.12°N
MAT, 1960–1990	−3.7 °C	−12.4 °C	−17.0 °C	n.a.	−18.8 °C	−20.8 °C
MAT, 1990–2009*	−2 °C	−11.2 °C	−15.4 °C	n.a.†	−14.5 °C	−16.1 °C
Days above 0 °C	145 ± 3	103 ± 4	74 ± 3	n.a.	91 ± 1	86 ± 2

*Because temperature data were not recorded at all local weather stations in every year, we estimated MAT 1990–2009 values for the foreign populations by calculating the average relative temperature difference between the foreign site and the AF site only in those years for which temperature data were collected at both locations and then back-calculating to MAT based on the temperature relative to AF.

†MAT was not available for the Twin Glacier site but temperature data collected during the growing season (June–August) over several years indicate that this site is approximately 0.5 °C warmer than AF (Labine, 1994; Bean, 2002; Edwards, 2012).

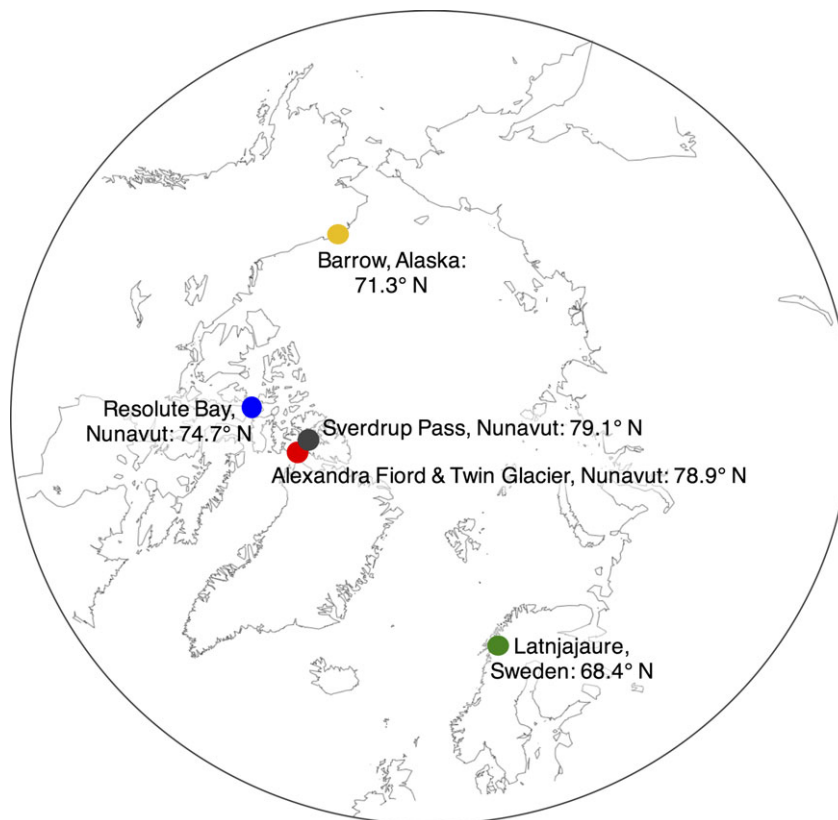


Fig. 1 Seed collection locations and latitudes. *Oxyria digyna* was collected from Latnjajaure, Barrow, Twin Glacier, Alexandra Fiord, and Sverdrup Pass; *Papaver radicum* was collected from Resolute Bay, Twin Glacier, and Alexandra Fiord.

same plot. Germination and survival of seedlings varied among source populations, and thus, the number of families and number of individuals per seed family planted into the experimental site was also unequal (see Table S1). A total of 1062 *O. digyna* and 719 *P. radicum* individuals were planted.

We randomly chose half of the common garden plots to be passively warmed using clear-sided, 1.5-m-diameter open-top chambers (OTCs; Henry & Molau, 1997; Marion *et al.*, 1997; Hollister & Webber, 2000; Bokhorst *et al.*, 2012) to simulate climate warming. High latitudes are predicted to experience substantial warming over the next century, with the bulk of warming occurring in the winter, but also increased winter precipitation that may limit the advance of the spring growing season (Kattsov & Källén, 2004; Bintanja & Selten, 2014). OTCs at AF realistically simulate these conditions; they create a year-round warming effect with greater warming in the winter than in the summer (Hollister & Webber, 2000; Bjorkman *et al.*, 2015), but snow melt dates in the OTCs do not differ significantly from the control plots, likely due to increased snow accumulation in the chambers (Bjorkman *et al.*, 2015). Thus, the effect of the OTCs on growing season length is subtle. At a nearby long-term site, OTCs increased summer temperatures by 1.7 °C (95% CI: -0.1 to 3.4) and winter temperatures by 3.3 °C (95% CI: -1.2 to 11.7) and prolonged the length of the growing season (the number of days with mean air temperatures above 0 °C) by 4% (3.6 days; 95% CI: -0.8 to 11.2), on average over 10 years of temperature records.

Temperature loggers (HOBO® Pro Series™, Onset Computer Corp., Bourne, MA, USA) were placed at a height of 10 cm in three warmed and three control plots during the peak growing season (late June–mid-July) in both 2012 and 2013. Due to microtopographic heterogeneity at the site, soil moisture varies between plots. We therefore measured soil moisture (using a handheld HydroSense® probe, Campbell Scientific Canada Corp., Edmonton, AB, Canada) in every plot in mid-July in both years. There was a slight but nonsignificant soil drying effect of the OTCs in 2013 only (Fig. S1).

Phenology and performance measurements

We recorded plant phenology and status every three days during the growing season (mid-June through early August) of 2012 and 2013. We recorded the date of first mature leaf appearance (leaf-out date) for every individual, considering a leaf mature when the emerging leaf bud unfolded completely. We additionally measured the leaf and plant dimensions of each plant twice in 2012 and three times in 2013 to estimate total leaf area for each individual. Total leaf area was estimated based on measurements of leaf width (the widest leaf at the widest point) and whole-plant diameter (maximum distance, tip-to-tip, between two opposite leaves) using linear regression. The equations were parameterized using a separate sample of 30 individuals (nonexperimental plants) that were measured by hand and then harvested and scanned

using ImageJ (U. S. National Institutes of Health, Bethesda, MD, USA) to estimate total leaf area ($R^2 > 0.95$ for both species; Fig. S2):

O. digyna: Leaf Area = $59.26 + 0.42 * \text{Leaf Width} * \text{Plant Diameter} * (\# \text{ of Leaves}/2)$

P. radiculatum: Leaf Area = $70.00 + 0.41 * \text{Leaf Width} * \text{Plant Diameter} * (\# \text{ of Leaves}/2)$

For individuals with only one leaf, the number of leaves was not divided by two as this would underestimate total leaf area for these plants. We used the maximum of the two (2012) or three (2013) total leaf area measurements in each year as an estimate of maximum leaf area of an individual (i.e., the peak size attained by a given individual during that growing season).

In 2013 only, we also recorded the presence/absence of leaf senescence in the last round of measurements in early August. Leaf senescence generally signals the end of the growing season for an individual plant (Lim *et al.*, 2007). A leaf was considered senesced if it had begun to dry up (*O. digyna*) or turn yellow (*P. radiculatum*). Survival of every individual was recorded at the end of 2013. Plants that did not have a leaf bud at any point during the 2013 growing season were considered dead.

Due to the slow growth and long time to reproductive maturity of many Arctic plant species (including the two studied here), we used overall survival and plant size as estimates of fitness, as plants did not flower during the two years of observation. Plant size has been shown to be highly correlated with reproductive fitness in many species (Samson & Werk, 1986) and is commonly used as a measure of performance in slow-growing perennial species (Rehfeldt *et al.*, 2002; Mimura & Aitken, 2010; McLane & Aitken, 2012).

Statistical analyses

We used Bayesian hierarchical modeling to determine the effect of population, treatment, and seed weight on all phenological and fitness response variables. Seed family and plot were modeled as sum-to-zero constrained random effects, with random slopes for seed family \times treatment. Models for leaf-out date and maximum leaf area additionally included a fixed effect of 'year', as these variables were measured in both 2012 and 2013. Results presented here are the mean value across both years (estimated as a derived parameter), but coefficients for the full population \times treatment \times year interaction can be found in the Tables S2 and S3. Leaf-out date and maximum leaf area were log-transformed and modeled with a univariate Normal error distribution, while survival and senescence, both binomial responses, were modeled with a Bernoulli error distribution. Estimates presented in the text are back-transformed to the original scale, or inverse-logit transformed in the case of binomial responses. Differences between populations and treatments (i.e., the population or treatment 'effect') were estimated as derived parameters. For example, the difference between leaf-out date of populations A and B was calculated by subtracting the estimate of leaf-out date for population A from that of population B at each iteration of the Markov chain, thus generating a posterior

distribution for the difference between these populations. In order to simplify interpretation of the results, in the text we consider populations or treatments to be 'significantly' different if the 95% credible interval on the difference between each paired comparison did not overlap zero. The importance of soil moisture in predicting maximum leaf area was determined in a separate model of the same structure, with soil moisture entering the model at the plot level. Soil moisture values were centered and scaled (by dividing by the standard deviation) within each year as the between-year variation in soil moisture was not of interest.

For *O. digyna*, we also characterize differences in the pattern of growth over the entire growing season. We analyzed this pattern using leaf area measurements per individual (two in 2012, three in 2013) as the response variable. Time of measurement (e.g., early summer, mid-summer, late summer) was included as a continuous fixed effect along with population, treatment, and interactions between all three. In 2013, an additional quadratic term for time of measurement was included to account for nonlinear patterns in plant growth. Random effects for seed family and plot were also included. Due to the different number of measurements in 2012 and 2013, years were analyzed separately.

Seed weight (average per seed family) was included as a family-level covariate in every statistical model for both species to account for potential differences in seed provisioning by each mother, which could affect offspring performance. For long-lived, slow-growing perennial species, time constraints often prevent growing all populations in a common garden for one or more generations to minimize these maternal effects. Thus, the potential influence of maternal seed provisioning is frequently assessed using seed mass instead (Angert *et al.*, 2008; Dlugosch & Parker, 2008; McLane & Aitken, 2012).

All analyses were conducted using JAGS (v. 3.4.0) called from R (v. 3.1.3) using the packages RJAGS (Plummer, 2014) and R2JAGS (Su & Yajima, 2015). Models were run for at least 35 000 iterations or until convergence was achieved, as determined by both visual inspection of trace plots and calculation of the Gelman-Rubin diagnostic (Gelman & Rubin, 1992; Plummer *et al.*, 2006). We used flat priors for all parameters.

Results

Survival, leaf phenology, and plant size all varied substantially among source populations in at least one species. In most cases, the local (AF) population had the greatest survival and growth, regardless of treatment, while phenology followed a latitudinal pattern, with earlier leaf-out and senescence occurring in individuals from the northernmost source populations. Differences due to the warming treatment were generally minor compared to the differences between source populations despite a strong summer warming effect in the OTCs (average daily temperature difference between OTCs and controls from day 173 to 200 was 3.7 °C in 2012 and 2.8 °C in 2013; Fig. S3). There were also large differences in plant size and leaf-out date between

years; growing season temperatures (June to early August) were 3 °C colder in 2013 than in 2012, which was the warmest summer recorded at Alexandra Fiord since continuous records began in 1989.

Oxyria digyna (mountain sorrel)

The strongest among-population differences were found for *O. digyna*, which spans the largest sampled latitudinal and temperature range of the two study species. Both phenological variables (date of leaf-out and leaf senescence) followed a clear latitudinal trend (Fig. 2a, b), with the most northerly populations leafing out only five days after snow melt and the most southerly populations more than a week later, regardless of treatment. Leaf-out date was earlier for all populations in the warmed treatment in 2012 but not in 2013

(Table S2a, Fig. S4). In the control plots, northern populations were also more likely to senesce by early August than southern populations (Fig. 2b, Table S2b). There was a general tendency for warming to lead to an increased probability of early senescence in the southern populations and a decreased probability of early senescence in the northern population, but a treatment effect was not significant for any individual population.

In contrast to the monotonic latitudinal trends for phenology, both survival and growth of *O. digyna* demonstrated a pattern of home-site advantage, with the local (Alexandra Fiord and Twin Glacier) populations demonstrating the highest survival and growth compared to populations from either lower or higher latitudes (Fig. 2c, d, Table S2c, S2d). Foreign populations decreased in both survival and leaf area with increasing distance from their own home site,

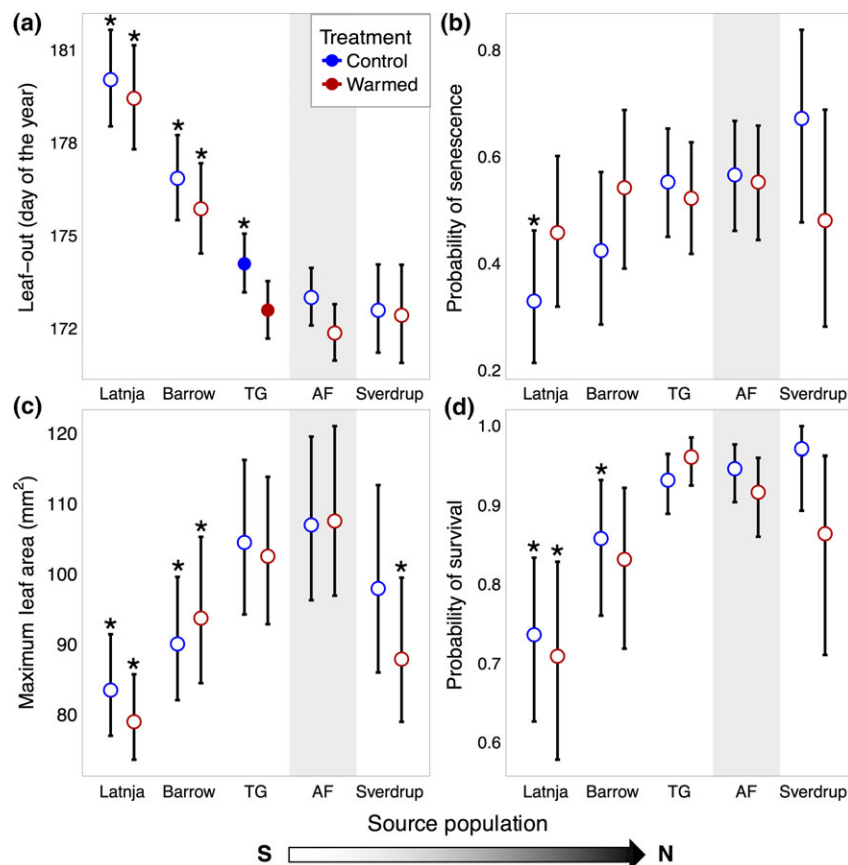


Fig. 2 Leaf-out date (a), probability of senescence by early August (2013 only; b), maximum leaf area (c), and probability of survival at the end of 2013 (d) for *Oxyria digyna*. Populations are ordered from south to north along the x-axis; the gray shaded area indicates the 'home' (AF) population. All points are estimated means from a Bayesian hierarchical model; error bars are 95% credible intervals on the means. Asterisks designate 'significant' differences between a given population and the home (AF) population in the same treatment, as determined by the 95% credible interval on the difference between each pair of estimated means. Filled circles designate a 'significant' treatment effect for a given population (here, only leaf-out date for the TG population); open circles indicate no significant treatment effect for that population. For variables measured in two years (leaf-out date and leaf area), points are the mean of both years. Latnja = Latnjajaure (Sweden), TG = Twin Glacier, AF = Alexandra Fiord.

regardless of treatment. Spatial variation in soil moisture did not contribute to population-level differences in leaf area or to the magnitude of the treatment effect (Table S2c).

Populations of *O. digyna* also differed in their patterns of growth over the summer (Fig. 3). In 2013, plants from southern latitudes (especially Latnjajaure, Sweden, the southernmost site) continued to grow throughout the summer and reached or maintained their maximum size in early August, while northern populations reached their maximum size in mid-late July and then began to decline (leaf senescence). In 2012, plants were measured only twice during the growing season, but results were consistent with the pattern observed in 2013. The overall treatment effect also differed between years; plants in the warmed treatment were generally larger than those in the control plots in 2012 (at peak size) but smaller in 2013; however, treatment differences were not significant in either year (Table S4a, S4b).

Papaver radicum (rooted poppy)

Leaf-out date of *P. radicum* differed by source population and treatment, as well as an interaction between the two (Fig. 4a, Table S3a). Leaf-out occurred ~2 days earlier in the warming treatment for the Resolute and Twin Glacier populations (95% CI = 0.17–3.41 and 0.42–3.87 days for Resolute and Twin Glacier, respectively), but not the Alexandra Fiord population (95% CI = –1.88 to 1.44 days).

As with *O. digyna*, senescence of *P. radicum* occurred earlier overall in the northern (Twin Glacier and AF) populations than in the southern (Resolute) population (Fig. 4b, Table S3b). In contrast to *O. digyna*, however, the warming treatment led to advanced senescence in the northernmost (AF) population, while having no effect on the southern (Resolute) population.

Similar to *O. digyna*, leaf area for *P. radicum* was greatest for the local (AF) or near-local (Twin Glacier) populations and smallest for the foreign population (Resolute; Fig. 4c, Table S3c). As with leaf-out date, leaf area for the Twin Glacier population differed by warming treatment, although the difference was not significant (95% CI = –0.80 to 14.67 mm² larger in the warming treatment). The other populations (Resolute and AF) did not vary by treatment. Soil moisture was not an important predictor of leaf area for any population (Table S3c).

Survival was universally high for *P. radicum* (96–99%); thus, there were no significant differences in survival among populations or between treatments (Fig. 4d; Table S3d).

Seed weight

Seed weight was not an important predictor in any model for *O. digyna* (Table S2a–d), suggesting that the potential maternal effect of seed provisioning did not likely have a large influence on the patterns shown here. In contrast, seed weight was an important predictor of leaf-out date and maximum leaf area for

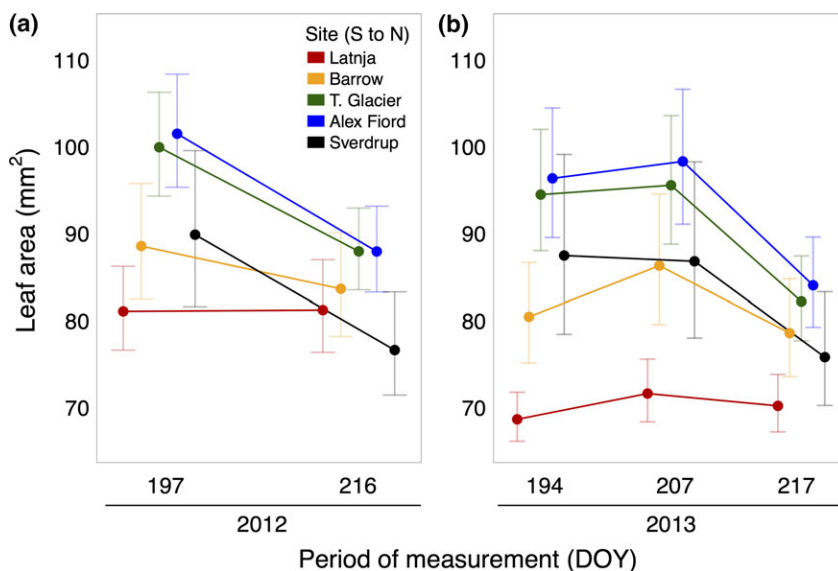


Fig. 3 Leaf area (mm²) of *Oxyria digyna* throughout the 2012 and 2013 growing seasons (DOY = day of the year). Individuals were measured twice in 2012 (mid-July and early August) and three times in 2013 (early and late July and early August). Points are modeled means (\pm 95% credible interval) per population, averaged over both treatments, for each measurement period with linear and quadratic (2013 only) terms for time. Populations are ordered from south (red) to north (black).

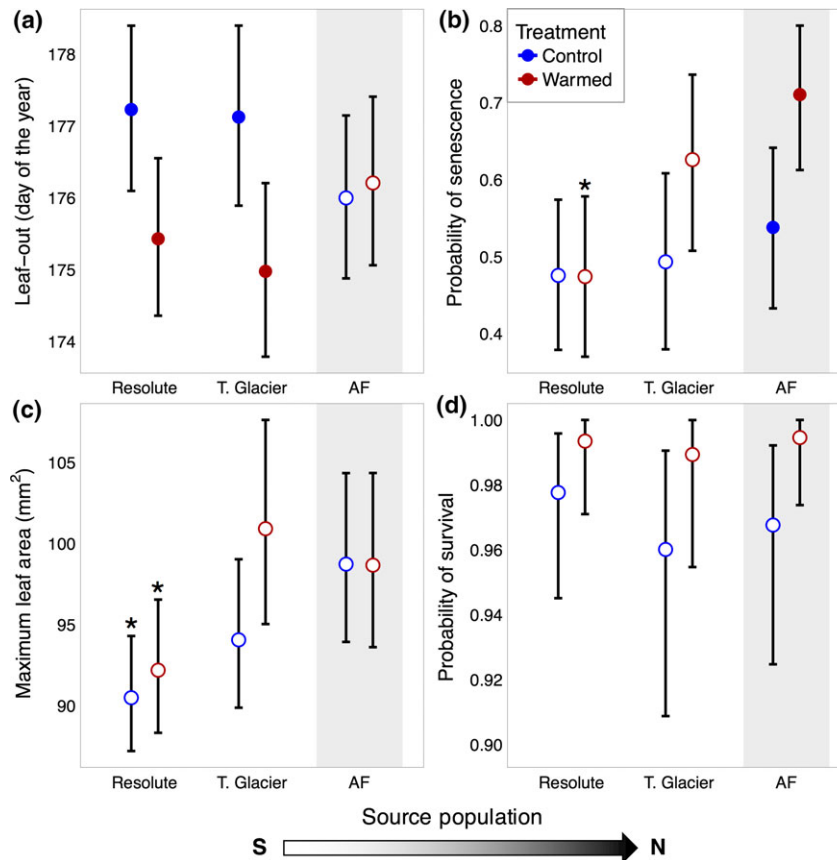


Fig. 4 Leaf-out date (a), probability of senescence by early August (2013 only; b), maximum leaf area (c), and probability of survival at the end of 2013 (d) for *Papaver radicum*. Populations are ordered from south to north along the *x*-axis; gray shaded area indicates the 'home' (AF) population. All points are estimated means from a Bayesian hierarchical model; error bars are 95% credible intervals. Asterisks designate 'significant' differences between a given population and the home (AF) population in the same treatment, as determined by the 95% credible interval on the difference between each pair of estimated means. Filled circles designate a 'significant' treatment effect for a given population (e.g., leaf-out date for Resolute and T. Glacier); open circles indicate no significant treatment effect for that population. For variables measured in two years (leaf-out date and leaf area), points are the mean of both years. T. Glacier = Twin Glacier, AF = Alexandra Fiord.

P. radicum, as the 95% credible interval on the slope of the relationship between seed weight and each response variable did not overlap zero (Table S3a, S3c). Interestingly, the relationship between seed weight and maximum leaf area was negative (95% CI = -0.18 to -0.02), suggesting that lighter seeds led to larger adult plants in the two years after planting. Because we included seed weight as a covariate in every model, the results presented here reflect population and treatment effects while taking into account the influence of family-level variation in seed weight on the response variable of interest.

Discussion

The results of our study do not support the hypothesis that warming at a given site will favor immigrants from more southerly populations. Local populations of the

two species studied here had higher survival and/or grew larger than foreign populations, regardless of the latitude of the foreign population and regardless of warming treatment. This indicates that local populations may have a general 'home-site advantage' even under warmer conditions and suggests that environmental factors other than temperature could hinder the establishment of southern immigrants in the Arctic. Although maximum size might represent a functional trait under selection (e.g., if small stature confers an adaptive advantage under harsh conditions), rather than only a fitness proxy, several studies have demonstrated that maximum plant size is under stronger genetic constraints in high Arctic than in low Arctic populations (Billings & Mooney, 1968 and references therein). This, in combination with corresponding patterns for survival in *O. digyna*, suggests that the difference in plant size between local (high Arctic)

populations and low Arctic populations is due to better performance and not genetically controlled differences in size.

Implications for species' responses to climate change

The general advantage of local over foreign populations in both study species, regardless of treatment or geographic origin of those foreign populations, points to the importance of local adaptation to factors other than temperature. Even in 2012, the warmest summer ever recorded at Alexandra Fiord, local populations performed better than all foreign populations (particularly for *O. digyna*, the best represented species). This pattern held even in the warmed plots, where the combination of experimental warming and the record atmospheric temperature and predominantly clear sky conditions led to warming treatment temperatures more than 5 °C warmer than the mean ambient temperature of the previous two decades. This result contrasts somewhat with a recent study of *Arabidopsis thaliana* populations in Europe, in which the northernmost population demonstrated lower fitness than a more southern population at the northern site, presumably due to elevated temperatures in the present relative to historical averages (Wilczek *et al.*, 2014).

While it is often predicted that gene flow from warm-adapted, southern populations will 'rescue' northern populations as temperatures increase (Anderson *et al.*, 2012; Norberg *et al.*, 2012), the results of our experiment suggest that maladaptation of southern genotypes to nonclimatic local conditions at northern latitudes may outweigh their presumed adaptation to warmer temperatures. If this result generalizes to other species and systems, it would have important implications for the implementation of assisted gene flow, in which warm-adapted, southern genotypes are deliberately introduced to northern populations in order to promote their adaptation to increasing temperatures (Kreyling *et al.*, 2011; Weeks *et al.*, 2011; Aitken & Whitlock, 2013). Assisted gene flow is already underway in some areas (O'Neill *et al.*, 2008) and has been proposed as a potential conservation strategy in several others (Broadhurst *et al.*, 2008; Vitt *et al.*, 2009). The reduced fitness of southern populations in a northern environment even under warmed conditions, as we observed, suggests that assisted gene flow from southern populations might actually negatively impact native populations, at least in the short term until recombination and selection can occur (Frankham *et al.*, 2011; Aitken & Whitlock, 2013; Bourne *et al.*, 2014). This highlights the importance of testing for adaptation to site conditions other than temperature when selecting source populations for assisted gene flow.

The importance of local adaptation to nonclimatic conditions demonstrated here also has implications for the immigration of species beyond their current northern range limits. Many studies have found that range shifts in many plant species and populations are lagging behind the rate of temperature change (Grabherr *et al.*, 1994; Harsch *et al.*, 2009; Bertrand *et al.*, 2011; Corlett & Westcott, 2013; Wilczek *et al.*, 2014; Savage & Vellend, 2015), but it is generally unknown whether this lag is due to dispersal limitation or nonclimatic constraints on the ability of southern immigrants to establish and grow (Lafleur *et al.*, 2010; Savage & Vellend, 2015). The failure of warmer temperatures to facilitate the success of 'warm-adapted' populations demonstrated in our study suggests that the latter explanation may contribute to these lags. Our results highlight the potential importance of adaptation to environmental conditions in addition to climate, and suggest that evolutionary adaptation to novel conditions will likely have to occur in concert with the northward movement of species and genotypes, as was the case for historical range shifts as well (Davis *et al.*, 2005). An important future research direction is testing the degree to which these conclusions apply to other systems and taxa.

The Twin Glacier population in our study provides an interesting comparison of the importance of adaptation to small-scale variation in climate. The Twin Glacier and AF populations are only ~2 km apart with no physical barriers between them, suggesting that some between-population gene flow likely does occur. However, genetic differentiation has been revealed by transplant experiments over much shorter physical distances at the AF site (~500 m; A.D. Bjorkman, E.R. Frei, M. Vellend & G.H.R. Henry, unpublished data). This 'local' standing genetic variation could be of key importance in promoting adaptive evolution as climate change progresses (Jump & Peñuelas, 2005 and references therein). In our study, the ~0.5 °C warmer Twin Glacier populations generally performed similarly to the AF populations in the control plots. However, the Twin Glacier populations of both species responded positively (earlier leaf-out and/or larger size) to the warming treatment, while the AF population did not. In fact, the mean plant size of the Twin Glacier *P. radicum* population in the warming treatment was slightly (although not significantly) larger than that of the AF population. The differential response to warming between the two 'local' populations in our study could indicate that an important source of warm-adapted genes is likely to come from nearby warmer microclimates within the same general region, rather than from populations far to the south (Crawford, 2008; Hof *et al.*, 2011). These regional populations are already

adapted to the local photoperiod, herbivores, and many other environmental factors and thus may have an advantage over southern immigrants.

Phenology and growth

As asynchrony between environmental events and phenological responses can have strong negative consequences for plant growth and fitness, plants that are able to respond quickly to seasonal cues will have the most time for growth and reproduction (Stinson, 2004; Andrés & Coupland, 2012). This is particularly true in high Arctic ecosystems, where a delay of one week can be nearly a sixth of the growing season. Our results revealed a clear latitudinal trend in phenology, with individuals from northern populations leafing out and senescing earlier than those from southern populations. The delayed leaf development of individuals from southern populations relative to northern populations (up to 8 days for *O. digyna*) is likely at least partly responsible for their smaller size. Experimental warming did not always cause earlier leaf-out, but when it did, it nearly always led to greater plant size as well (relative to the same population in the control treatment), suggesting that earlier leaf-out was usually advantageous.

Strong latitudinal patterns of spring phenology have been observed in other species (Johnsen *et al.*, 1996; Raven *et al.*, 1999) and suggest that a combination of factors, which may include a differential response of populations to photoperiod (Mooney & Billings, 1961), and variation in speed of response to springtime snow melt (Wipf, 2010) are important determinants of plant performance. Such among-population differences are often explained by differences in required heat accumulation for dormancy release (Campbell & Sugano, 1979; Johnsen *et al.*, 1996; Yu *et al.*, 2010; Cook *et al.*, 2012), although in our study the effect of experimental warming on leaf-out dates was inconsistent, and varied by population, species, and year.

The timing of fall senescence also affects plant success, as fall freezing events that occur before the plant has fully hardened could be extremely detrimental (Taschler & Neuner, 2004; Inouye, 2008). Southern populations of *O. digyna* showed fewer signs of leaf senescence at the end of the growing season than local populations, which may have contributed to their lower survival rate. As both fall senescence in response to photoperiod and dormancy release in response to spring warming are heritable traits (Shaver & Kummerow, 1992; Prock & Körner, 1996; Fracheboud *et al.*, 2009; Andrés & Coupland, 2012), selective pressure may lead to evolution in these traits as the climate warms.

In sum, this is one of the first studies to experimentally test the hypothesis that warming at northern latitudes will facilitate the success of southern immigrants. The results have important implications for our understanding of how species will respond to climate change. Many species distribution models are based on the prediction that species will track their optimal climate northward (Davis *et al.*, 1998; Pearson & Dawson, 2003), and it is often proposed that northward gene flow will promote adaptation to warming conditions at northern latitudes (Davis & Shaw, 2001; Anderson *et al.*, 2012; Norberg *et al.*, 2012). Conversely, the predominant trend in our study was that of local-population advantage, even under experimental warming. This highlights the importance of local adaptation to nonclimatic factors when considering how species will respond to future warming and suggests that evolution, either of local populations to novel climatic conditions or of foreign populations and species to novel nonclimatic environmental conditions, will play a critical role in these responses.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

- Figure S1** Soil moisture in both treatments and years.
- Figure S2** Comparison of estimated and actual leaf area for both species.
- Figure S3** Temperature in warmed and control treatments in 2012 and 2013 at the experimental site.
- Figure S4** Leaf-out date of *Oxyria digyna* in both years.
- Table S1** Total number of families of each population for each species.
- Table S2** Coefficients from Bayesian model output for (a) leaf-out date, (b) probability of senescence, (c) maximum leaf area, and (d) probability of survival for *O. digyna*.
- Table S3** Coefficients from Bayesian model output for (a) leaf-out date, (b) probability of senescence, (c) maximum leaf area, and (d) probability of survival for *P. radicata*.
- Table S4** Coefficients from Bayesian model output predicting among-population differences in growth patterns of *O. digyna* in (a) 2012 and (b) 2013.