

Research

Ecological and evolutionary responses of an arctic plant to variation in microclimate and soil

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The arctic and alpine regions are predicted to experience some of the highest rates of climate change, and the arctic vegetation is expected to be especially sensitive to such changes. Understanding the ecological and evolutionary responses of arctic plant species to changes in climate is therefore a key objective. Geothermal areas, where natural temperature gradients occur over small spatial scales, and without many of the confounding environmental factors present in latitudinal and other gradient studies, provide a natural experimental setting in which to examine the response of arctic–alpine plants to increasing temperatures. To test the ecological and evolutionary response of the circumpolar alpine bistort *Persicaria vivipara* to temperature, we collected plant material and soil from areas with low, intermediate and high soil temperatures and grew them at three different temperatures in a three-factorial growth chamber experiment. At higher experimental soil temperatures, sprouting was earlier and plants had more leaves. Sprouting was earlier in soil originating from intermediate temperature and plants had more leaves when grown in soil originating from low temperatures. We did not find evidence of local adaptation or genetic variation in reaction norms among plants originating from areas with low, intermediate and high soil temperature. Our findings suggest that the alpine bistort has a strong plastic response to warming, but that differences in soil temperature have not resulted in genetic differentiation. The lack of an observed evolutionary response may, for example, be due to the absence of temperature-mediated selection on *P. vivipara*, the low rate of sexual recombination, or high levels of gene flow balancing differences in selection. When placed within the context of other studies, we conclude that arctic–alpine plant species often show strong plastic responses to spring warming, while evidence of evolutionary responses varies among species.

Keywords: *Bistorta vivipara*, geothermal systems, local adaptation, performance, phenotypic plasticity, soil temperature



Introduction

Climate warming is predicted to be particularly strong in the Arctic (IPCC 2014). This increase in temperature may have a major impact on the phenology, growth and reproduction of arctic plants, whose life cycles are strongly influenced by seasonal variation in temperature (Henry and Molau 1997, Callaghan et al. 2004, Gornish and Prather 2014, Semenchuk et al. 2015). To predict the long-term effects of increasing temperatures on the arctic flora, it is important to understand both immediate and evolutionary responses. For example, plant individuals may respond plastically and advance development in response to increasing spring temperatures (Anderson et al. 2012). At the same time, overall increases in temperatures might lead to changes in how strong the optimal response of development to temperature should be and the evolution of reaction norms (Valdés et al. 2018).

Plasticity allows plants to grow under variable conditions and to respond to changes in the environment (Agrawal 2001). For example, plants often germinate earlier and grow larger at higher temperatures (Stöcklin et al. 2009, Anderson et al. 2012). The optimal plastic response of plants is likely to differ depending on their local environmental conditions (Grether 2005). If there is genetic variation in plasticity, we would thus expect selection on locally adapted populations to be manifested as variation in reaction norms (Valdés et al. 2018). For example, plants that have evolved in a low-temperature environment may rapidly germinate, leaf out and flower in response to warming in spring, whereas plants from a high-temperature environment may respond more slowly to spring warming. Indeed, previous studies have found that plants from geothermally heated areas have an earlier spring phenology than plants from non-heated areas in the field, while the pattern is reversed when grown in a common environment, a phenomenon referred to as counter-gradient variation (Conover and Schultz 1995, Valdés et al. 2018).

Previous studies of how arctic plants react to increasing temperature have commonly used open-top climate chambers (Arft et al. 1999, Wolkovich et al. 2012), or examined plants growing along elevational (Frei et al. 2014) or latitudinal gradients (Toftegaard et al. 2016). These studies have demonstrated that plants growing in arctic–alpine conditions strongly respond to experimentally induced changes in temperature, and to elevational and latitudinal gradients. For example, a meta-analysis of open-top chamber experiments in the Northern Hemisphere revealed that vegetative growth and reproductive performance often increased with increasing temperatures in arctic species (Arft et al. 1999). In a reciprocal transplant experiment plants from high elevations advanced their phenology more than low and mid-altitude plants when transplanted to the warmer end of the gradient (Frei et al. 2014). However, each of these methods has its limitations. Changes in temperature along elevational and latitudinal gradients often occur together with changes in other environmental factors, and the time-scale of open-top chamber experiments is often too short to observe

evolutionary responses. Given these limitations, geothermal systems, where radiation heating causes variation in temperature over small spatial scales that persist long time periods without accompanying differences in environmental factors that vary along large-scale gradients (O’Gorman et al. 2014, Sigurdsson et al. 2016), offer an important alternative setting to explore plastic and evolutionary responses to temperature (Gudmundsdottir et al. 2011, O’Gorman et al. 2014, Sigurdsson et al. 2016, Valdés et al. 2018). For example, Iceland has many naturally occurring geothermal areas, where volcanic activity close to the surface warms water and soil through radiation heating (Gudmundsdottir et al. 2011, Zakharova and Spichak 2012). In such geothermal areas, plants of the same species frequently grow side-by-side in heated and non-heated soil.

The plastic responses and local adaptation of plants in geothermal landscapes may not only be in response to the direct effect of warming, but also due to indirect effects of warming on the local environment. For example, warming may influence soil processes like decomposition, nutrient availability and the composition of the soil community, which in turn may affect the plastic and evolutionary responses of plants (Wittenmayer and Merbach 2005, Bardgett and van der Putten 2014). Soil nutrient levels, which are frequently limited in arctic environments, are often associated with higher soil temperatures (Totland and Nylehn 1998, Sigurdsson et al. 2016). Moreover, both beneficial and antagonistic soil biota, like fungi, bacteria and archaea, might be more diverse in warmer soils (Tedesoo et al. 2014, Rasmussen et al. 2018, 2020). There is evidence that plant populations can adapt to such abiotic (Joshi et al. 2001) and biotic soil characteristics (Mursinoff and Tack 2017).

The aim of this study was to investigate plastic and evolutionary responses to variation in temperature and soil for a characteristic plant of the arctic–alpine environment. For this, we focused on *Persicaria vivipara*, which has a mixture of clonal growth and (less common) sexual reproduction. We carried out a three-way multifactorial greenhouse experiment where we grew bulbils (i.e. asexually produced axillary buds) of *P. vivipara*, collected from locations with low, intermediate and high temperatures, in soils from the same three types of locations, under low, intermediate and high soil temperatures in a climate chamber. We tested the following specific hypotheses:

- 1) Experimental heating of soil results in a higher probability of sprouting, earlier sprouting and increased size.
- 2) The bulbils planted in soils originating from heated areas have a higher probability of sprouting, sprout earlier and grow larger due to higher availability of mineralized nutrients.
- 3) Selection has resulted in a counter-gradient pattern where bulbils originating from heated sites show a weaker growth response to temperature than bulbils originating from non-heated sites.
- 4) Genetic differences among plants originating from different soil temperatures reflect local adaptation, i.e. plants

perform better under environmental conditions that correspond to conditions at their site of origin.

- 5) Both the abiotic and biotic soil environment influence the ecological and evolutionary response of plants to heating.

Material and methods

Study system

Geothermal landscapes, where magma gets close to the surface and heats soils and ground water, can act as hotspots of local adaptation (O’Gorman et al. 2014). Notably, within these landscapes the temperature can vary strongly at small spatial scales, with temperatures differing by several or tens of degrees Celsius between locations separated by only a few meters (Gudmundsdottir et al. 2011). The plant and soil microbial communities in these locations are frequently strongly affected by spatial variation in soil temperature (Friberg et al. 2009, Zakharova and Spichak 2012).

The alpine bistort *Persicaria vivipara*; synonym *B. vivipara* is a perennial herb that occurs in many parts of the Northern Hemisphere (Jonsell and Karlsson 2000). In Iceland, *P. vivipara* grows naturally in a wide range of temperature conditions (Kristinsson 2001), including geothermal areas. The herb primarily spreads clonally by bulbils and only rarely produces fertile seeds (Diggle 1997, Jonsell and Karlsson 2000). Bulbils are asexually produced bulb-like structures that replace flowers in the lower part of the inflorescence of *P. vivipara*. Bulbils have no specialized dispersal structures and often start growing within tens of centimeters from the mother plant (Bills et al. 2015). Despite the clonal spread and low dispersal distance, populations of this species are often characterized by several genetically distinct clones growing in close proximity (Bauert 1996, Diggle et al. 1998).

Origin of plants and soil

We collected plants and soil from Hengladalir, a geothermally active valley located a few tens of kilometers east of Reykjavik, Iceland. Within this area, we identified three locations with no heating (soil temperatures ca 13°C), three locations with slight heating (14–17°C) and three locations with strong heating (25–30°C). From each location, we collected soil up to a depth of ca 10 cm, which matches the root depth of *P. vivipara* (Mundra et al. 2015). Soil temperature was measured at 10 cm depth next to each mother plant and soil sample, and then averaged at the population level. At geothermally heated sites in Iceland, differences in soil temperature at 10 cm depth are little affected by air temperature (Sigurdsson et al. 2016). Thus, these temperature measurements reflect long-term differences in soil temperature between populations. All samples were taken within a 0.25 km² area, and distances between populations ranged from 50 to 630 m (Supplementary information). From the soil, we removed the litter layer and larger rocks and roots. We collected bulbils from one to three *P. vivipara* plants (henceforth

referred to as ‘mother plants’) per population, resulting in seven mother plants from each temperature category (i.e. n = 21 mother plants in total).

Experimental design

To investigate the effect of temperature and soil on plant performance, we designed a multifactorial experiment where bulbils collected at different temperatures (three levels) were grown in soils collected at different temperatures (three levels), and the soils were then experimentally heated to low, intermediate and high temperatures, to simulate the natural variation in soil temperature at the geothermal area. This resulted in 27 different treatment combinations. For each treatment combination, we had seven 82 mm diameter pots (330 ml) planted with two bulbils from the same mother plant. We distributed bulbils from each mother plant equally across treatment combinations. As maternal investment in bulbils may affect growth, we recorded bilbil mass prior to planting.

We experimentally heated the plant pots in water baths. The water baths were uniformly heated using a combination of aquarium heaters and water circulation pumps. In total there were nine water baths, three at each temperature level: 1) low temperature (13°C), 2) intermediate (18°C) and 3) high (30°C). In each water bath, we placed 21 plant pots. Water baths were placed in a climate chamber set to 13°C and a day length of 16 h.

To avoid microbial contamination, we sealed the plant pots, but filled the lower 2.5 cm with gravel and water-absorbing cloth to allow for drainage. To allow water to flow below the plant pot, we glued three metal washers under each plant pot. To avoid positional effects, the location of the plant pots was regularly randomized within the three water baths belonging to the same temperature treatment.

To disentangle the effect of soil biota from that of the abiotic soil environment (e.g. physical or chemical structure) on the probability and timing of bilbil sprouting, we set up a complementary experiment using sterile soil. For this, we applied only the low and high temperatures, resulting in eight treatment combinations and 56 plant pots. For sterilization, soil was autoclaved for 1 h at 121°C.

Plant performance measures

Plants were monitored every other day for sprouting. The day of sprouting was determined as the number of days from planting until the first sign of sprouting was observed. Vegetative plant height and number of leaves were recorded on days 84 and 126, and the length and width of the longest leaf were measured on days 97 and 159. Given the elliptical shape of the leaf lamina, and that the area of the petiole was very small, we calculated leaf size using the formula for the area of an ellipse:

$$\text{Leaf size} = \left(\frac{\text{leaf width}}{2} \times \frac{\text{leaf length}}{2} \right) \times \pi$$

Analysis

Data were analyzed using the generalized linear mixed model framework as implemented in R ver. 3.6.1 (<www.r-project.org>). We tested for significance using the *Anova* function in the *car* package (Fox and Weisberg 2019), which uses type-II Wald χ^2 tests.

To test for the impact of soil temperature and origin of plants and soil on bulbil sprouting and plant growth, we modelled sprouting (0/1), day of sprouting, plant height, number of leaves and leaf size as a function of original soil temperature, mother plant temperature, experimental soil temperature and their two- and three-way interactions. Bulbil mass was included as a covariate. To account for variation among mother plants, we included the random factor 'Mother plant'. As we planted two bulbils in each plant pot, we further included the random factor 'Plant pot' which was nested under 'Mother plant'. For probability of sprouting, we used a binomial distribution with a logit link; for day of sprouting, plant height and leaf size, we used a normal distribution with an identity link; and for the number of leaves, we used a Poisson distribution with a log link. Plant height, leaf size and day of sprouting were log transformed before analyses to meet the assumptions of heteroscedasticity and normally distributed model residuals. For the model of the number of leaves, we checked for overdispersion by using the function *check_overdispersion* in the *performance* package (Lüdecke et al. 2020).

We a priori planned to test for local adaptation in those cases where we found an interaction between mother plant temperature and original soil temperature, or between mother plant temperature and experimental soil temperature (Kawecki and Ebert 2004, Blanquart et al. 2013), using a contrast statement as implemented with the function *emmeans* in the package *emmeans* (Lenth 2019).

An effect of soil temperature at the collection site on the probability of sprouting and the date of sprouting could be due to either the abiotic or biotic soil characteristics. To disentangle the role of the soil abiotic and biotic environment, we first created a data set with data from both the field and sterile soil experiment, where we only retained those treatment combinations present in both experiments (i.e. only 'low' and 'high' temperatures). We then modelled the affected plant traits as a function of original soil temperature, mother plant temperature, experimental soil temperature and soil sterilization, including all two- and three-way interactions. As above, we included the random factors 'Mother plant' and 'Plant pot' (nested under 'Mother plant').

Results

Bulbils were more likely to sprout and sprouted earlier when grown at higher soil temperatures (Fig. 1a–b, Table 1). Plants had the smallest leaves when grown at intermediate soil temperature when measured 97 days after planting, whereas plants grown at higher soil temperatures had more

leaves when plants were measured 126 days after planting (Fig. 1c–d, Table 1). Bulbils sprouted earlier in soil originating from areas with intermediate temperature than in soil originating from low or high temperatures (Table 1, Fig. 2a). Plants had a higher number of leaves at 126 days after planting when grown in soil from a low temperature origin (Fig. 2b, Table 1). At day 159, original soil temperature and experimental soil temperature jointly affected leaf size, where plants had the largest leaves when grown in soil originating from intermediate temperature that was exposed to high experimental temperature (Supplementary information). Plant height increased with bulbil mass but was not affected by any of the experimental factors (Table 1).

Plants originating from areas with low, intermediate and high soil temperature did not differ in probability of sprouting, day of sprouting or growth traits (Table 1). We also did not detect any evidence of local adaptation in terms of an effect of the interaction between mother plant temperature and original or experimental soil temperature on sprouting probability, day of sprouting or plant growth (Table 1).

Bulbil sprouting was later in the sterile soil than in the field soil, and sprouting was earlier with experimental soil heating in both the sterile and field soil (Supplementary information).

Discussion

To investigate the immediate and evolutionary responses of the alpine bistort to variation in microclimate and soil, we grew genotypes collected along a soil temperature gradient in soils originating from the same gradient, and exposed them to different temperatures. As expected, higher experimental soil temperature advanced bulbil sprouting and led to plants with more leaves. In contrast to our prediction, sprouting was earliest in soil originating from locations with intermediate temperature, and the number of leaves was highest when plants were grown in soil from a low temperature origin. We found no evidence for either genetic variation in phenotypic plasticity or local adaptation. The microbial community in the soil advanced bulbil sprouting.

Plants sprouted earlier and had more leaves with higher experimental soil temperature. This matched our prediction, which was based on previous studies that have shown an advance of spring phenology and flowering, as well as increased plant growth, with increasing temperature (Arft et al. 1999, Valdés et al. 2018). For example, flowering phenology has been shown to advance with heating in geothermal areas (Anderson et al. 2012, Valdés et al. 2018), and plant biomass is higher in *Arctagrostis latifolia* and *Carex bigelowii* when grown at higher soil temperature (Marchand et al. 2005). Taken together, our findings suggest that the circumpolar *P. vivipara* will start growing earlier, and grow larger, with climate change.

We expected that higher mineralization rates, and associated higher availability of nutrients, in soils from high temperature would result in earlier sprouting and increased plant

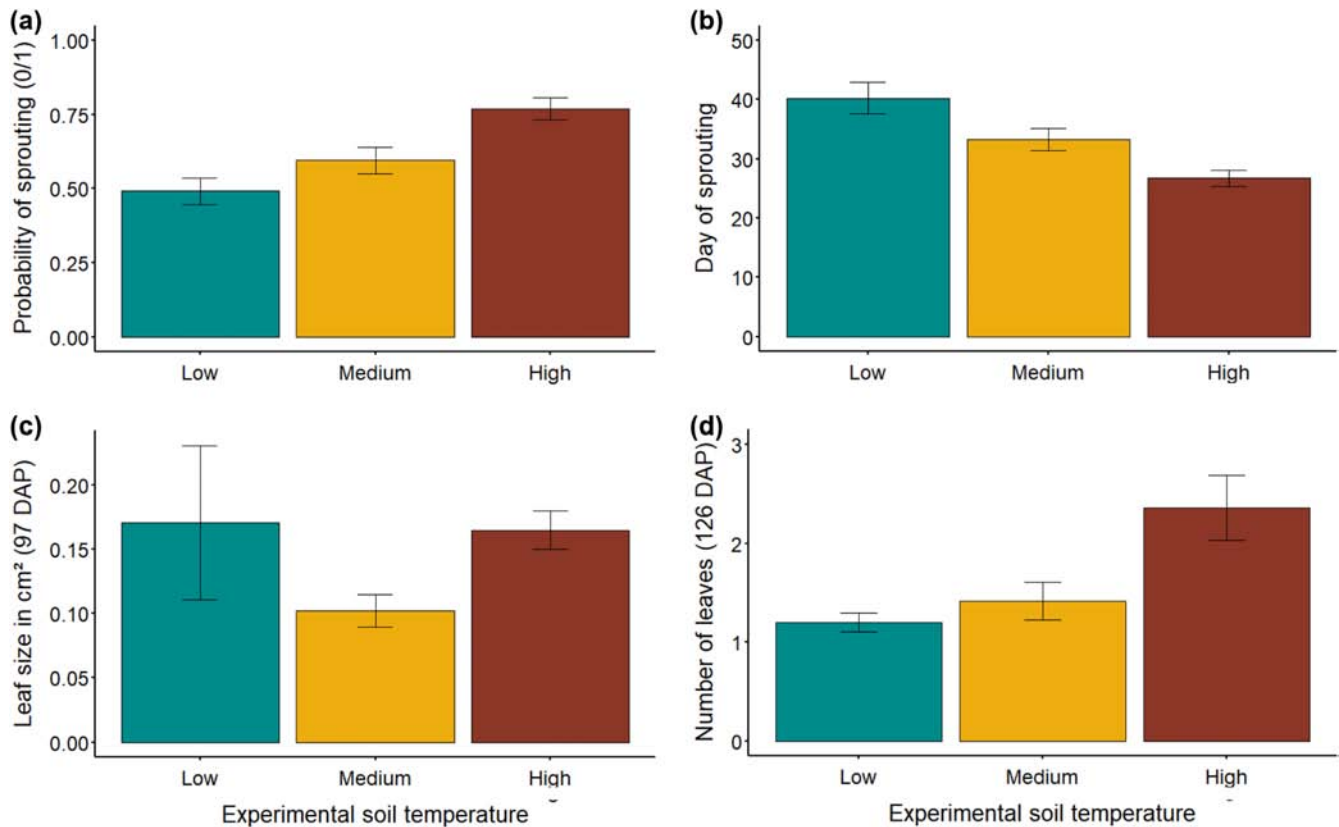


Figure 1. The impact of experimental soil temperature on bulbil sprouting and performance of *Persicaria vivipara*. Shown are the impact of experimental soil temperature on (a) probability of sprouting, (b) day of sprouting, (c) leaf size at 97 days after planting (DAP) and (d) number of leaves at 126 days after planting. Shown are means \pm SE.

performance. In contrast to this prediction, bulbils sprouted earliest in soil from the intermediate temperature origins, and plants had the highest number of leaves when grown in soil from low temperature origins. Previous studies have shown that nutrients are frequently a limiting factor in arctic ecosystems and increased temperatures enhance nutrient availability for plants and increase growth (Henry and Molau 1997, Weintraub and Schimel 2003, Semenchuk et al. 2015). Moreover, warmer soil is often associated with a more diverse soil community and higher soil biotic activity (Friberg et al. 2009, Zakharova and Spichak 2012). One possible explanation for the lack of the expected pattern is that nutrient variation across temperature gradients is limited in geothermal areas (O’Gorman et al. 2014, Sigurdsson et al. 2016), and even if mineralization is higher in soils in heated areas, this may not result in higher availability of nutrients when the soil is exposed to lower temperatures. Importantly, our findings illustrate that warming-mediated changes in the soil environment can have idiosyncratic effects on plant phenology and plant traits.

We found no evidence for genetic variation in phenotypic plasticity or local adaptation of plants to spatial variation in soil temperature. In contrast, previous studies have found adaptive patterns of phenotypic plasticity by comparing plants grown in the field and common garden (Valdés et al. 2018),

and local adaptation using reciprocal transplant experiments (Conover and Schultz 1995, Joshi et al. 2001, Anderson et al. 2012). For example, Valdés et al. (2018) found that the arctic plant *Cerastium fontanum* flowered earlier when growing in heated areas than in non-heated areas in the field, but that individuals from heated areas flowered later than individuals from non-heated areas when growing in a common garden. The lack of counter-gradient variation and local adaptation in *P. vivipara* might have three non-mutually exclusive explanations. First, absence of local adaptation might simply be the result of that selection on the investigated traits may be weak or heterogenous over time. Second, *P. vivipara* mostly propagates clonally, with low levels of sexual reproduction. While previous studies have shown considerable genetic variation in populations of *P. vivipara*, as well as in populations of other clonally reproducing plants (Bauert 1996, Diggle et al. 1998, Stöcklin et al. 2009), the reduced rate of recombination may slow down the evolutionary response to selection, and increase the probability that conditions change before populations become locally adapted. Indeed, adaptive patterns of counter-gradient variation have been demonstrated in several sexually reproducing species (Anderson et al. 2012, Valdés et al. 2018). Finally, gene flow may swamp the effect of natural selection, but as dispersal distances are low in *P. vivipara* (Bills et al. 2015), this appears a less likely

Table 1. The impact of original soil temperature (OST), mother plant temperature (MPT) and experimental soil temperature (EST), as well as bulbil mass, on the performance of *Persicaria vivipara* in field soil. Each factor had three temperature levels, i.e. low, intermediate and high temperature. Shown are p-values, with significant values in bold. The number of observations (bulbils or plants) for each response variable is given within parentheses. For test statistics and degrees of freedom see Supplementary information.

	Original soil temperature (OST)	Mother plant temperature (MPT)	Experimental soil temperature (EST)	Bulbil mass	OST × MPT	OST × EST	MPT × EST	OST × MPT × EST
Sprouting success (n=378)	0.855	0.849	<0.001	0.164	0.121	0.212	0.276	0.313
Day of sprouting (n=240)	<0.001	0.094	<0.001	0.072	0.935	0.080	0.456	0.445
Plant height on day 84 (n=217)	0.792	0.088	0.338	<0.001	0.790	0.106	0.753	0.468
Plant height on day 126 (n=77)	0.402	0.648	0.529	0.030	0.561	0.337	0.623	0.101
Leaf number on day 84 (n=217)	0.290	0.514	0.177	0.560	0.874	0.785	0.816	0.992
Leaf number on day 126 (n=77)	0.012	0.118	0.004	0.984	0.939	0.772	0.559	0.999
Leaf size on day 97 (n=162)	0.066	0.296	0.043	0.066	0.538	0.652	0.050	0.571
Leaf size on day 159 (n=48)	0.162	0.924	0.055	0.521	0.296	0.025	0.074	–

explanation. To tease apart these explanations, future studies could use quantitative genetic approaches to assess additive genetic variation for the investigated traits, as combined with a genetic or experimental assessment of gene flow.

Interestingly, bulbil sprouting was slower in the sterile soil than in the field soil, indicating that the soil microbial community stimulates sprouting. While this in part could be due to that sterilization affects nutrient levels, the observed effect agrees with previous studies, which found that soil organisms can advance phenology and influence plant growth (Wagner et al. 2014, Rasmussen et al. 2017, 2020). However, this study provided no insights into the putative adaptive nature of this pattern. Warmer soil advanced sprouting in

both field and sterile soil, indicating that temperature impacts sprouting both in the presence and absence of associated soil biota.

Our findings highlight that the circumpolar alpine bistort has a strong plastic response to temperature. We did not find evidence of an evolutionary response in the form of counter-gradient variation or other types of local adaptation. This contrasts with results from other plant species in geothermal areas, and observations made along latitudinal and elevational gradients. To better understand the exact conditions under which temperature variation is likely to lead to evolutionary responses of plant populations, we need further studies that examine a broad range of plant species and traits. We

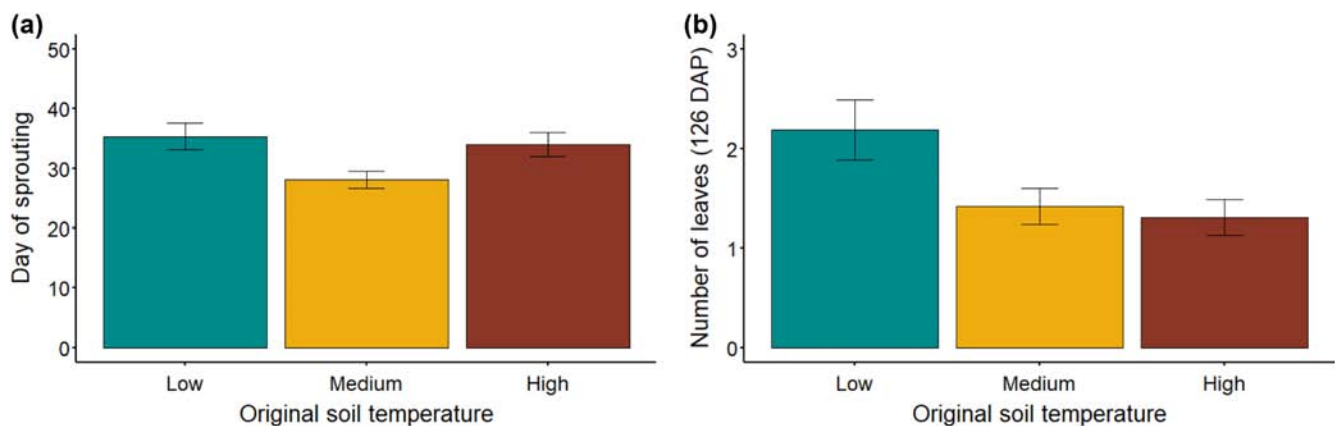


Figure 2. The impact of original soil temperature on bulbil sprouting and performance of *Persicaria vivipara*. Shown are the impact of original soil temperature on (a) day of sprouting and (b) the number of leaves at 126 days after planting (DAP). Shown are means \pm SE.

also need reciprocal transplant experiments that assess fitness differences to explore to what extent populations are locally adapted to their thermal environment, and to unravel the mechanisms underlying such adaptation. Such knowledge will allow for better predictions of the long-term evolutionary responses of arctic–alpine species to changes in climate.

Speculations

The contrast between our findings and results with other plant species suggests that the relative importance of plastic vs genetic responses to environmental variation is highly variable. This has important implications for our understanding of how arctic–alpine species will respond to a changing climate. We speculate that while plastic responses to temperature, like advances in spring phenology and increased growth, are almost universal in arctic–alpine plant species, evolutionary responses are more variable. To better understand when and where species respond evolutionarily, we must explore the roles of generation times, standing genetic diversity and gene flow. We think that the lack of an evolutionary response to temperature in *P. vivipara* may be due to the extended generation time associated with clonal reproduction, with evolutionary changes too slow to catch up with the changing environment. While clonal reproduction may turn out to explain the absence of an evolutionary response in *P. vivipara*, we stress that this prediction should still be tested in other clonally reproducing plants using rigorous experimental tests.

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.4tmpg4f7z>> (Wickander et al. 2020).

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Author contributions

Niklas Wickander: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Writing—original draft (lead); Writing—review and editing (lead). **Pil Rasmussen:** Conceptualization (equal); Formal analysis (supporting); Writing—review and editing (supporting). **Bryndís Marteinsdóttir:** Methodology (equal); Writing—review and editing (supporting). **Johan Ehrlen:** Conceptualization (equal); Writing—review and editing (supporting). **Ayco Tack:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Writing—original draft (supporting); Writing—review and editing (supporting).

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Supplementary information (available online as Appendix oik-07794 at <www.oikosjournal.org/appendix/oik-07794>).