Translocation of an arctic seashore plant reveals signs of maladaptation to altered climatic conditions

Hällfors M.H.[*a,b], Lehvävirta S. [a,c], Aandahl T.R.[d], Lehtimäki I.-M.[a], Nilsson L.O. [d,e], Ruotsalainen A.L.[f], Schulman L.E.[a], Hyvärinen M.-T.[a]

[a] Botany Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland.

[b] Research Centre for Environmental Change, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland.

[c] Department of Landscape Architecture, Planning and Management, Swedish University of Agricultural Sciences, Alnarp, Sweden

[d] Division of Environment and Natural Resources, Norwegian Institute of Bioeconomy Research (NIBIO), P.O. Box 115, NO-1431 Ås, Norway.

[e] Halmstad University, PO Box 823, SE-30118 Halmstad, Sweden.

[f] Department of Ecology and Genetics, P.O. Box 3000, FI-90014 University of Oulu, Finland.

[*] corresponding author. Contact information: Maria Hällfors, Research Centre for Environmental Change, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland, e-mail: maria.hallfors@helsinki.fi; phone: +358 40 721 34 74

Abstract

Ongoing anthropogenic climate change alters the local climatic conditions to which species may be adapted. Information on species' climatic requirements and on variation in intraspecific adaptation to climate is necessary for predicting the effects of climate change on biodiversity. We used a climatic gradient to test whether populations of two allopatric varieties of an arctic seashore herb (*Primula nutans* ssp. *finmarchica*) show adaptation to their local climatic conditions and how a future warmer climate may affect them. Our experimental set-up combined i) a reciprocal translocation within the distribution range of the species with ii) an experiment testing performance of the sampled populations in warmer climatic conditions south of their range. We monitored survival, size, and flowering over four growing seasons as measures of performance. We found that plants of both varieties performed better in experimental gardens towards the north. Interestingly, highest up in the north, representatives of the southern variety outperformed the northern one. Supported by weather data, this suggests that the range of both varieties is at least partly outside their climatic optima. Further warming would make the current environments of both varieties even less suitable. Our results thus show maladaptation of populations of both varieties to their current home environments and that their overall performance is lower in warmer conditions. We conclude that *Primula nutans* ssp. *finmarchica* is already suffering from reduced viability related to changes in climate, and that further warming may be detrimental to this subspecies, especially the northern variety. These results reveal that it is not sufficient to run reciprocal experiments: adaptation needs also to be tested outside the current range of the focal taxon in order to include historic conditions to which they have possibly adapted over time.

Keywords

botanic garden, conservation, global change, local adaptation, Siberian primrose, threatened species, transplant experiment

Introduction

Ongoing climate change threatens biodiversity and is predicted, and even shown, to lead to declines in populations and to extinctions of species (Ceballos et al., 2015; Dawson et al., 2011; Díaz et al., 2019; Settele et al., 2014; Urban, 2015). How the threat of climate change on biodiversity is manifested in the response of species and populations is crucial for understanding their abilities to cope with the change. Plants offer several key functions in ecosystems, such as carbon assimilation and biomass production, and thereby provide resources for other species. The ability of populations to respond, *in situ*, to shifting environmental conditions can be a result of plasticity towards a broad range of conditions, or it can be mediated through evolutionary adaptation (Chevin et al., 2010; Gao et al., 2018; Gienapp et al., 2008; Merilä & Hendry, 2014).

Phenotypic plasticity can allow organisms to respond rapidly to changes in the environment, and hence, it has often been viewed as the main strategy to respond to environmental changes (Merilä, 2012). In contrast, evolutionary processes are often slow, especially for species with long generation times, such as perennial plants. Some species are showing signs of acclimatization or adaptation to new conditions, whereas others are either declining or dispersing to new areas with a favourable environment (Lenoir & Svenning, 2015; Parmesan & Yohe, 2003; Pöyry et al., 2009). To predict the effects of climate change on biodiversity and to plan effective

conservation strategies, we need both evaluations of how the current distribution areas of species are changing, and approximations of the genetic and phenotypic potential of species to endure these changes.

Species are often used as the basic taxonomic unit in plant conservation and predictions on the effects of environmental change usually relate to the species level (Frankham et al., 2012). Populations of a particular species may, however, be locally adapted, and therefore have divergent affinities to abiotic conditions (Banta et al., 2012) and show intraspecific differences in climatic tolerance (Atkins & Travis, 2010; Hill et al., 2011). However, in their review on local adaptation in plant species, Leimu and Fisher (2008) found that local adaptation of populations to environmental conditions is not as widespread as often assumed. Local adaptation may be favoured mostly in cases where populations occur in differing environments and gene flow between them is restricted (Kawecki & Ebert, 2004). According to Kawecki and Ebert (2004) “the resident genotypes would have on average a higher fitness in their local habitat than genotypes originating from other habitats”. Understanding and taking into account intraspecific variation in the adaptation to climatic conditions is necessary to reach balanced estimates of climate change impact at the level of populations (Hällfors et al., 2016; Valladares et al., 2014). The speed of climate change may outpace the ability of populations to respond adaptively, thereby causing maladaptation instead of adaptation or acclimatization. Thus, the need to estimate the effect that climate change has had on natural populations to date, has become increasingly evident (Anderson & Wadgymar, 2020; Franks et al., 2007; Kooyers et al., 2019; Thomann et al., 2015; Wilczek et al., 2014; Zenni et al., 2014).

Manipulative experiments have the potential to provide information on how strong a role climate plays in defining favourable conditions of a species or population (Hargreaves et al., 2014; Kawecki & Ebert, 2004; Kreyling et al., 2014; Pelini et al., 2012). Results from experiments where the climatic conditions for the focal taxa are altered can be incorporated into species distribution models to improve predictions (Greiser et al., 2020). By reciprocally transplanting individuals of two or more populations to conditions representing a foreign environment and a home environment, we can effectively measure intraspecific variation that allow maintaining fitness under varying temperature conditions (Blanquart et al., 2013; Kawecki & Ebert, 2004). Experiments can also test species' responses to future conditions, for example, through treatments mimicking increased temperatures, and inform us about the extent to which plasticity contributes towards population resilience under climate change. Furthermore, such experiments can reveal locally adaptive fixed traits, which would signify that the survival of the species in the future would require either rapid microevolution *in situ* or assisted migration (*sensu* Hällfors et al., 2014) to new favourable areas.

Here, we describe a study on Siberian primrose (*Primula nutans* ssp. *finmarchica* (Jacq.) Á. Löve & D.), in which we sampled populations of two of its varieties (the northern var. *finmarchica* and the southern var. *jokelae* L. Mäkinen & Y. Mäkinen); while acknowledging that our sampling did not cover the varieties' full distribution, for clarity we refer to the populations of the different varieties by 'variety'. We performed i) a reciprocal transplant experiment and ii) an experiment of out-of-range transplantation. The former tests the importance of intraspecific local adaptation versus insensitivity towards temperature (Fig 1 (b) versus (c)), (Fig 1 (c) versus (d)). The experiment was conducted across four growing seasons using a botanic garden network

in Finland, Norway, and Estonia (Fig. 1). Our five experimental gardens represent the i) home environments of both varieties, forming the reciprocal component in the experiment (Oulu and Svanvik; Fig 1), as well as ii) treatments simulating potential future climates in gardens occurring outside of the range of the species (Tartu, Helsinki, Rauma; Fig 1). We test the effect of the genotype G (variety) and the environment E (garden or annual temperature) and their interaction (GxE) on the performance of plant individuals:

performance ~ G + E + G*E

Specifically, we hypothesised that i) the varieties are adapted to local climatic conditions and thus would show higher performance in their home environments (Fig 1 (b)). Additionally, ii) both varieties would show lower performance in the out-of-range environments but the southern variety would have higher performance than the northern one in locations with higher temperatures outside the species' natural range (Fig 1 (b)). No intraspecific local adaptation would be revealed by equally high viability of both varieties in both environments (Fig 1 (c)) while no affinity towards conditions within the species range should result in an equally high performance of the species within and outside of its range (Fig 1 (d)). However, because climate change has already proceeded (IPCC, 2019), the process of adaptation may be lagging behind and populations may in fact be maladapted to current climatic condition (Anderson & Wadgymar, 2020; Kooyers et al., 2019; Wilczek et al., 2014). This scenario of climate change induced maladaptation (Fig 1 (e)) needs to be taken into account in contemporary translocations studies. Our study set-up thus allows us to disentangle climatic affinity and on the occurred and predicted effects of global warming on the Siberian primrose.

Materials and Methods

Study species and seed sampling

Siberian primrose (*Primula nutans*) is a small-statured perennial herb with a discontinuous, circumpolar distribution. The Fennoscandian subspecies *P. nutans* ssp. *finmarchica* (Jacq.) Á. Löve & D. Löve is a red-listed species (VU in Norway and Finland) with a disjunct distribution (Fig 1). It comprises two morpho-ecological varieties (Mäkinen & Mäkinen, 1964): var. *finmarchica* (the northern variety) grows on the shores of the Arctic Sea, while var. *jokelae* (the southern variety) occurs by the Bothnian Bay and the White Sea (Fig. 1 (a)). It is a habitat specialist that mainly grows in seashore and riverside meadows (Kreivi, Aspi, & Leskinen, 2011; Mäkinen & Mäkinen, 1964). It propagates sexually by seeds and vegetatively by stolons growing from the wintering buds and the rosettes (Mäkinen & Mäkinen, 1964). The species is insect-pollinated and produces copious seeds that spread by gravitation, via water flows, and possibly also with birds (Ulvinen 1997).

Due to the geographic distance (c. 400-550 km) between its two varieties var. *jokelae* and var. *finmarchica* (referred to in this study as the southern and the northern variety, respectively) and the lack of obvious adaptations for efficient gene flow between the areas, the varieties are presumably genetically isolated, which is also reflected in their genetic differences (Kreivi et al., 2011). Moreover, a recent study showed that the main areas where the varieties occur are climatically different (Hällfors et al., 2016; also see Fig 2 (a)), and an earlier experiment indicated a clear difference in the requirement of colder night conditions for flower induction in the northern variety compared to southern variety (Mäkinen & Mäkinen, 1964).

We sampled seeds from wild populations of both varieties of *Primula nutans* ssp. *finmarchica* in August to September 2012 (Fig. 1 (a), Table S1). Seeds of the southern variety were collected in five sites in Haukipudas and Ii in Finland, and seeds of the northern variety from six sites in Sør-Varanger in Norway. Voucher specimens from each sampling site are deposited at the herbarium of the Finnish Museum of Natural History (H *sensu* Thiers 2016). From each site we collected seeds from 10 - 53 individuals (as available, following seed collecting guidelines; ENSCONET, 2009; Table S1) to obtain a representative sample. The number of seeds obtained from the collected capsules of each sampled individual varied from 0 to *c.* 200. We stored the seed lot from each maternal individual separately and left them to dry and ripen at room temperature for a minimum of two weeks after which we placed them in a freezer (-18 to -20°C) for cold stratification to break dormancy. The seeds were kept in these conditions for about six months, until used to produce plant material for the translocation experiment (in spring 2013).

Experimental design and plant material

We set up a common garden experiment in 2013 in five botanic gardens located in Estonia and Finland, and on research station grounds in Norway (Fig 1 (a); Table S2). We chose to use botanic gardens as testing grounds instead of natural sites to avoid genetic contamination of natural populations by introducing alien genotypes, as well as for logistical reasons and legal restrictions of introducing species outside their natural range. For a detailed description on the experimental set-up, see Supplementary Material Text S1.

To describe the performance of individuals, we measured their survival, size, and flowering

(whether they flowered, how many flowers they produced, and when) from year 2014 to 2016. The fitness of genotypes can be described as the relative success with which they transmit their genes to the next generation (Silvertown & Charlesworth, 2001). Because of the limited temporal extent of our study and because we do not measure the individual's fitness through its ability to produce viable progeny, we focus on key plant performance measures likely to correlate with fitness. Survival is a definite measure of fitness as a dead individual cannot transmit genes, but survival can also be stochastic. Also, the physical size of an individual and reproductive output, such as abundance of flowering, tend to correlate with plant fitness (Silvertown & Charlesworth, 2001). Each spring (2014, 2015, and 2016) we recorded flowering presence and abundance. In the autumn of the same years, we recorded survival and photographed each surviving plant from above. We assessed plant size from photographs, through digitally cutting out and measuring the area (cm^2) of the visible vegetative parts. We used the size at the time of planting as a measurement of original size, but 24 individuals lack data on that due to missing photographs or insufficient resolution. These individuals were therefore not included in the analyses, wherefore our total N is reduced from 614 to 590.

Weather and climatic data

For describing the climatic conditions at the seed sampling sites and experimental gardens, we obtained data on historic climatic conditions (1970-2000; 10 minutes resolution) and future projections (CMIP5 for 2050, 10 minutes resolution, HADGEM2-ES model) through the Worldclim database (Fick & Hijmans, 2017). These climatic data were downloaded in R using the *getData* function in the *raster* package. Additionally, we describe weather conditions during the experimental years (Figs 2b and S5-6) and model plant performance as a function of mean

annual temperature in the experimental gardens during 2013-2016 (see below). The weather data were obtained from the Gridded Agro-Meteorological Data in Europe (Joint Research Centre, 2014), which contains meteorological parameters from European weather stations interpolated on a 25x25km grid. We used the function *biovar* in the package *dismo* to calculate bioclimatic variables of the weather data in R.

We present historic and predicted mean annual temperature and mean temperature of the warmest quarter for the seed sampling sites and experimental gardens and as a mean across experimental years for each garden in Figure 2. The same variables are also shown explicitly for each year in each garden in Figure 3. Several additional bioclimatic variables, including annual precipitation sum, are shown in figures in Fig S5 and S6.

In addition to modeling plant performance as a function of experimental garden and other variables, we conducted an alternative model using weather data instead of experimental garden. As the weather parameter we chose annual mean temperature at the experimental gardens across experimental years. Weather parameters tend to be highly correlated among each other, and we do not know which specific aspects of temperature these plants respond to. Thus, mean annual temperature functions as a large scale descriptor of differences between experimental gardens.

The current climatic conditions in Tartu, Helsinki, and Rauma roughly correspond to the anticipated future climatic conditions in Oulu and thus the occurrence area of the southern variety (Fig 2). The historic conditions in Oulu roughly correspond to the future conditions in Svanvik and thus the occurrence area of the northern variety (Fig 2).

The weather conditions during the experimental years differed between the experimental gardens in accordance with what we expected when designing the experiment (Fig. 2, Fig. S5). However, the observed temperatures were warmer than the historic means. In essence, this means that the experienced temperature conditions in Svanvik resembled the historic average temperatures in Oulu, while the experienced temperatures in Oulu resembled, or were even warmer than, the historic average temperatures in the out-of-range gardens in Rauma, Helsinki, and Tartu (Fig 2). The variation in bioclimatic variables between gardens and years are shown in Fig 3 and Fig S6.

Statistical analyses

To test the performance of the two varieties in the different gardens we analysed their combined performance using aster models (Geyer, Wagenius, & Shaw, 2007; Shaw et al., 2008). They allow the joint analysis of several components of life history that together quantify differences in performance, such as survival, flowering and flowering abundance. The complete model (Fig. S3) included plant survival and flowering in each year (0 or 1; bernoulli error distribution) plus flowering abundance (zero-truncated poisson distribution of error) that are conditional on survival in the previous year. Whether a plant flowered or not is also conditional on that it had survived in the year of flowering. The abundance of flowers per individual is further conditional on that the individual flowered that year.

These combined responses were modeled using the *aster* call in the aster package (Geyer et al., 2007; Geyer, 2017) in two main models: one testing the effect of *Garden*, and one testing the effect of *Temperature* (mean annual temperature over 2013-2016). Specifically, the responses

were modeled as a function of *original size* at planting (continuous, square-root and centered; see Fig S4 for distribution of original size per variety and experimental garden), *Variety* (categorical: Southern and Northern) and either *Garden* (categorical, 5 levels) or *Temperature* (continuous) and the interaction between *Variety* and either *Garden* or *Temperature*. To rule out an effect of *planting time* (early or late summer) we also ran a model including this variable, it did not improve model fit (results not shown). The estimated mean value parameters represent overall flowering output, that is, the expected flower count during the whole experiment for plant of average original size (Geyer, 2019). We estimate these for each variety at each experimental garden and hereafter refer to these predicted values as the overall performance.

As we assumed that random variation between the three *Plots* in each garden and between the five to six *Seed sampling sites* of each variety, we also fitted random-effect aster models for both main fixed effects (i.e. for the *Garden* and *Temperature* model) using the *reaster* function in the *aster* package (Geyer, 2017). Predicting plant performance based on random effects models is not straightforward nor directly possible within the aster models package (Geyer et al., 2019; Charles J. Geyer, Ridley, Latta, Etterson, & Shaw, 2013; although see Charles J. Geyer, Ridley, Latta, Etterson, & Shaw, 2010). Nevertheless, as the estimates for the fixed effects were very similar for both the aster models including only fixed effects and the models also including random effects (see Table S4 for the Garden-models and Table S5 for the Temperature-models) we obtain predicted values of plant performance based on the fixed effects- models using the *predict* function in the *aster* package (Tables S6 and S7). However, for assessing statistical significance of fixed effects we conducted likelihood ratio tests (anova) of the full random effects model versus models excluding individual variables (Table 1).

Summarizing results using local adaptation metrics

For the reciprocal part of the trial, we calculated the local adaptation metrics from the mean estimated combined predicted values obtained through the fixed effects Garden-model (Table S6). There are three main approaches to make quantitative comparisons of local adaptation from performance measures (Blanquart et al., 2013). The sympatric-allopatric contrast (henceforth called *ΔSA*) focuses on the *difference* between the average performance of the genotypes in their home environment and non-home environment. Thus, it describes how well the genotypes overall fit their home-environments. The home vs. away approach (henceforth called *HA*) in turn describes the *home environment quality* for each tested genotype, and is measured by the difference between the fitness of a genotype in its home environment and all other tested environments (away). Finally, the local vs. foreign approach (henceforth called *LF*) describes the *genotype quality* for each tested home environment, and is measured by the difference between the fitness of a genotype in its home environment and the mean fitness of all other genotypes when exposed to the same environment. These three conceptual approaches relate to different aspects of local adaptation, all of which lie in the interest of our study: the overall habitat quality, the overall quality of the variety, and how the two varieties fit the different environmental conditions.

In our study, we estimated plant performance over four years, by predicting mean performance for an average sized plant of each variety in each experimental garden (based on the GLM model). We use these estimated measures of performance to calculate local adaptation metrics. Specifically, *ΔSA* for the *subspecies as whole* is the difference between the mean performance

(p) of both varieties (northern, N, southern S) in their home (H) environments and that in the test (away, A) environment:

$$\Delta SA = \frac{p_{NH} + p_{SH}}{2} - \frac{p_{NA} + p_{SA}}{2}$$

The Home vs. Away metric (*HA*) for each *variety* is the difference between the performance of each variety in its home environment and that in its away environment.

$$HA_S = p_{SH} - p_{SA}$$

$$HA_N = p_{NH} - p_{NA}$$

The Local vs. Foreign metric (*LF*) for each *garden* is the difference between the performance of the local variety and that of the foreign variety.

$$LF_S = p_{SH} - p_{NA}$$

$$LF_N = p_{NH} - p_{SA}$$

The performance -estimates range between 0.04 and 5.7 and were therefore scaled to range between 0 and 1. The *HA*, *LF* and *SA* metrics will, therefore, range between -1 and 1, with values around zero indicating negligible differences in performance. The closer the value is to 1, the stronger is the evidence for positive response of the local genotype in the environment, or suitability of the environment for the genotype, and values close to -1 show the opposite.

All data management and analyses were conducted in R (version 3.5.3; R Core Team 2019).

Results

Plant survival

Altogether, 110 out of 590 (18.6%) plant individuals survived in the experiment by 2016. Low survival is common in transplantation experiments (Dalrymple, Banks, Stewart, & Pullin 2012) but there were large differences in survival between the varieties and the gardens in our experiment. The survival percentage across gardens was from 8.8% (27/307) for the northern variety and 29.3% (83/283) for the southern variety. The survival percentage varied between the gardens from 5.8% in Tartu (9/155) to 51% in Svanvik (52/102; Fig. 4, Table S3). Individuals of the southern variety survived at a higher percentage every year and in each garden (Fig 3; Table S3).

Overall survival was higher for the southern variety (Fig. 4; Table S3) even though the difference in survival between the varieties varied according to the garden. The northern variety survived best in Svanvik (representing its home environment), followed by the next garden further south, Oulu. Its survival was low in the out-of-range gardens (Rauma, Helsinki, and Tartu). The southern variety showed roughly the same trend, surviving worst in Tartu and best in the northernmost garden, Svanvik (Fig 4).

Flowering and plant size

Raw data on flower presence, flowering abundance and size (cm^2) are presented in Figure S7 both as averaged across all planted individuals and across all individuals that were alive in the specific year. Overall, of all the planted individuals, flowering was most frequent and abundant,

and plants were of the biggest sizes in Svanvik. The Southern variety also grew well and flowered abundantly in Helsinki. When considering only the surviving individuals, however, both varieties flowered frequently and abundantly in Tartu and Rauma and the surviving individuals of the southern variety grew big in all southern gardens. However, in many cases the number of surviving individuals was very low, for example, only one individual of the northern variety was alive in Tartu in 2016 (Table S3), but it flowered.

Overall performance

Both the Garden and Temperature models revealed similar and significant differences between the varieties in their overall performance (Table 1; Fig 5). Specifically, the Garden model indicated increased performance of both varieties in gardens further towards the north but revealed substantial differences between the varieties (Fig 5a; Table S6). Likewise, the Temperature model revealed a significant negative effect of mean annual temperature on the performance on both varieties, however with stronger negative effect on the northern variety (Fig 5b; Table S7). Indeed, we found a significant interaction effects between variety vs. experimental garden (Fig 5a; Table 1) and annual temperature (Fig 5b; Table 1). In addition, the original size at planting had a highly significant effect on plant performance in both models (Table 1).

Of the random effects *Plot* explained a significant proportion of the residual variance (change in deviance when Plot was omitted from the model 40 versus 60 for the Garden and Temperature models, respectively) while *Seed sampling site* explained a marginal and non-significant proportion of the residual variation (Table 1; Tables S4 and S5).

The overall performance estimated using aster models provides an estimate of overall contribution of flowers per variety in each garden while conditional on survival and presence of flowers. These predicted values (Fig 5., Table S6 and S7), or overall performance, of the southern variety were highest in Svanvik, followed by Helsinki (however with overlapping standard deviations of estimates; Fig. 5 and Table 1). The southern variety performed equally well in Oulu, Rauma, and Tartu. The overall performance of the northern variety followed our hypothesis (Fig 1a) by showing the highest performance in its home-environment Svanvik, followed by Oulu, and performed less well in all three out-of-range gardens (Tartu, Helsinki, and Rauma).

Local adaptation metrics

We calculated local adaptation metrics (Table S8) based on the estimates of overall performance for the fixed effect Garden model (Table S6) of the two varieties in the reciprocal part of the experiment. For the southern variety, the *HA*-value of -0.71 indicates that it experiences reduced habitat quality in its home environment, as it thrives better away (in Svanvik) than at home (in Oulu). The *LF* of 0.26, however, indicates that the southern variety possesses superior quality in Oulu since it still does better at home than the tested foreign northern variety does in Oulu. For the northern variety, the *HA* of 0.22 indicates that it experiences superior habitat quality in its home environment (Svanvik) compared to in the tested away-environments (Oulu). Nevertheless, the *LF* of -0.75 indicates that this variety is of reduced quality in its home environment, as the foreign (southern) variety performs better there. Mean ΔSA for the subspecies as a whole was -0.25 indicating an overall negative fit of the environments for the subspecies.

Discussion

Our results reveal clear patterns of adaptation to macroclimatic conditions at the subspecies level. In general, both varieties show their best performance within the species' range. The southern variety showed higher overall performance in all experimental gardens. The overall survival, size, and flowering frequency and abundance tended to be higher for the southern variety. This is in line with an earlier greenhouse experiment where the northern variety flowered only in cold night conditions (12 h 21°C, 12 h 5°C versus 24h 21°C) whereas the southern variety flowered only in continuously warm conditions but showed increased vegetative growth in the cold night conditions (Mäkinen & Mäkinen, 1964).

We did not find characteristic indications of local adaptation at the variety level when looking at the performance of the sampled populations per experimental garden. Individuals of both varieties survived best, and flowered more frequently and abundantly, in the northernmost garden Svanvik. This is reflected by the local adaptation metrics, where the *LF* metric indicated that the southern variety was superior in the home environment of the northern. Further, the overall performance proxy, the sympatric-allopatric contrast, suggests that the varieties may already be maladaptated to their current conditions. In addition, when considering the weather conditions during the experimental years compared to the historic climatic conditions (Fig 2 (b), Fig S5), a conclusion of local adaptation becomes more parsimonious. This is evidenced by, for example, the fact that the mean annual temperature in Svanvik during the experiment resembled that of Oulu's historic mean, and the mean annual temperature in Oulu resembled that of the three southern gardens' historical means. Thus, the conditions that we aimed to mimic through our experimental design had in practise shifted locations one step towards the north, making the

interpretation of the results in relation to our hypotheses perplexing.

Maladaptation is presumably increasing due to climate change, as the rapid change outpaces the ability of species to adapt or migrate, and conditions reach beyond the extent of temperature tolerance (Crespi, 2000; Kooyers et al., 2019). Our finding that the varieties did not show the highest performance in their home area is in line with studies showing signs of maladaptation to current climatic conditions in plant species (see Anderson & Wadgymar, 2020; Gellie et al., 2016; Kooyers et al., 2019; Wang, et al., 2019; Wilczek et al., 2014). Although maladaptation may be increasing because of climate change, it can also be caused by underlying population genetic structures, such as genetic drift or founder effects (Crespi, 2000; Leimu & Fischer, 2008) related to the biogeographic history of the populations. The two varieties of Siberian primrose probably became spatially separated during the end of the last glacial period (Mäkinen & Mäkinen, 1964), which first allowed colonization of emerging areas and later fragmented the population through diminishing suitable habitat as land masses reformed from underneath the receding ice shelves (see Kreivi et al., 2011). Indeed, genetic and allelic diversity is known to be remarkably low in populations of Siberian primrose (Kreivi et al., 2011). However, the consistent pattern of increased performance of both varieties from south to north, suggests that maladaptation caused by recent change in climate is a major driving force for the results of this study.

Potential confounding effects

While our results suggest a strong impact of climate on the Siberian primrose, they cannot be interpreted as fully conclusive. Large-scale translocation experiments are complex, and it is

important to evaluate potential methodological pitfalls. Transplantation experiments along the north-south axis necessarily contain confounding effects, such as day length (Saikkonen et al., 2012), which cannot be removed in a transplantation study. Despite the rigorous measures to standardise treatments in all gardens (See Text S1), we had only one experimental garden at each latitude (albeit with three plots in each experimental garden). Therefore, random variation in care, pressure from weeds, and weather events may have confounded the climatic signals. For example, some plots may have experienced short periods of drought despite our regime of additional watering. The roughly three-year observation period of our study may also not fully represent the prevailing climates in the trial gardens, since inter-annual variation in weather may mask mean climatic differences. Long-term studies would even out annual variations, and allow the measurement of characteristics that become available later in a plant's life cycle and population development (seed production and germination, adaptation across generations, etc.).

In our study, plants that were larger at the time of planting showed higher overall performance. Previous studies of reintroductions have shown that the best results (the highest numbers of surviving plants) are gained by using mature plants or seeds (Dalrymple et al., 2012). However, in an experimental study, we believe that using mature plants can be confounded since they may be affected by the climatic conditions of the experimental garden where they are propagated for the experiment, thus possibly biasing the results through stronger priming effects (see below for a discussion of the potential effect of Helsinki on the Southern variety). Also, early stages in the life cycle may be the ones most susceptible to climate change as they define the environments to which post-germination life-stages of the individuals are exposed (Donohue et al., 2010), wherefore they should not be omitted from a test setting. On the other hand, while running

experiments from seeds would have allowed us to evaluate performance through germination, this might have risked the experiment in case of failure to germinate. In fact, even in the relatively stable greenhouse conditions, the germination percentage of these varieties ranged between 27-69% (depending on the sampling site; Lehtimäki 2016).

The seeds of each variety were sampled within one region each within a c. 10 km radius (Fig 1, Table S1). Thus, from the data at hand we cannot infer patterns across the complete ranges of the varieties. Nevertheless, previous studies have shown that the genetic variation within each variety is relatively low (Kreivi et al., 2011) and that the varieties occur in distinct climatic environments (Hällfors et al. 2016). Thus, it is plausible to assume that individuals across the range of each variety would respond similarly to environmental conditions. We did, however, not control for, or try to remove, maternal carry-over effects, for instance through growing a first generation in identical and controlled conditions and then utilizing the progeny of these for the trials. However, the random effect of seed sampling site did not significantly increase the explanatory power of residual variation.

Another useful performance measure would have been seed production of the tested individuals from the experimental locations and germination of these seeds. However, because of limited resources and the possibility of hybridization between the two varieties, we restricted our observations to the most readily observable performance measures of the planted populations. Although germinability of seeds is a more conclusive indicator of reproductive capacity and population fitness, flowering is also an important indicator of the existence of a necessary life cycle stage towards offspring. In addition, for this species, flowering has been shown to be an

important fitness-reflecting factor, as failure in flowering is connected to increased extinction risk of the species (Björnström et al., 2011).

Why the southern variety thrived relatively well in Helsinki remains unclear. The raw proportion of surviving individuals in Helsinki (31%) was not substantially higher than that in Oulu and Rauma (24.5 and 23%, respectively). However, the overall performance estimate, which describes population-level flowering output, was substantially higher in Helsinki (4.1) than in the variety's home environment in Oulu (1.69) and in Rauma (1.01). We suspect that this could have been caused by the above-mentioned difference in general maintenance or weather conditions that we were unable to capture through long-term means. Because the individuals were propagated together in common conditions in Helsinki, the difference between these conditions and those of the experimental garden, where the individuals ended up, could additionally explain the high performance in Helsinki. If the individuals planted in Helsinki were primed to the Helsinki conditions, this might explain the higher performance of them compared to the other southern gardens and to Oulu. However, as this higher performance was not seen for the northern variety (although the varieties may be differentially affected by priming) we suspect that the main cause was stochastic effects.

<u>The effect of climate change on the Siberian primrose</u>

In this study, we have elucidated the role that plasticity towards varying temperature conditions can play within the boundaries of local adaptation for the Siberian primrose and its two varieties. We conclude that, especially for the northern variety, the existing plasticity towards warmer conditions is negligible. As the climate continues to change, migration northwards could enable

the varieties of this species to cope with increasing temperatures. However, because of its poor dispersal ability and limited temperature tolerance, the available options for this species are restricted to the production of characteristics suitable for the new climatic conditions *in situ*, through evolutionary adaptation. Nevertheless, it remains unclear how big a role evolutionary adaptation will play under climatic change in relation to temperature tolerance (Arnold et al., 2019; Charmantier & Gienapp, 2014; Gienapp et al., 2008; Nicotra et al., 2010). It is also not clear whether selection can act to increase or decrease plasticity to allow larger variation among phenotypes, which could then respond adaptively to a range of temperature conditions (Arnold et al., 2019).

Our raw data indicate that those individuals that did survive in the southernmost gardens tended to be big and to flower frequently and abundantly (Fig. S7). Thus, the elimination of individuals that are maladapted to the conditions in each experimental garden leaves a survivor population for which the impact of climate is not as decisive. The adaptive performance of the remnant plants in the out-of-range gardens highlights how individual features may be a key determinant for continued survival when a population goes through a bottleneck (Carson, 1990). Whether such a small founding population of a genetically impoverished species could form a viable population under rapidly changing conditions in natural conditions is, however, unlikely. However, experiments on the evolutionary potential in this species are needed to draw more solid conclusions.

Siberian primrose, a poor disperser with small and fragmented populations that harbour low genetic variability and a limited thermal tolerance, is an example of a species likely to suffer

from lack of adaptive capacity under rapid climatic change. Proactive conservation methods, such as assisted migration, may be needed in order to maintain this species. Overall, our results give cause for concern about the viability of the Siberian primrose, especially for the northern variety, for which the detrimental effects of climate change may become evident within the coming decades.

Lessons for translocation trials under altered climate conditions

The results of this study also highlight a critical point in testing for local adaptation and plasticity under the rapidly changing climate. If populations are not able to track ongoing changes, only experiments both within and outside the current range of the species (or variety) can provide accurate information regarding local adaptation and plasticity, as maladaptation must be considered as a scenario (e.g., Anderson & Wadgymar, 2020; Gellie et al., 2016; Kooyers et al., 2019; Wilczek et al., 2014). Climate change thus gives cause for re-examining traditional reciprocal and out-of-range common garden experiments (Anderson & Wadgymar, 2020), and to plan experiments with climatic and weather data at hand. Comparing responses to current versus "historical" conditions offers a powerful approach (Anderson & Wadgymar, 2020; Franks et al., 2007; Merilä & Hendry, 2014; Thomann et al., 2015). Together with continued monitoring of population abundances (Cotto et al., 2017) such studies can provide early warning signals for species that may be close to tipping points and to going extinct.

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Author's contributions

MHH, SL, and MH conceived the idea and designed methodology, LS contributed to the selection of experimental gardens; MHH and LS collected seeds; MHH, SL, IL, and MH produced plant material and coordinated the experiments; all authors took part in setting up the experiments and collecting the data; MHH analyzed the data and led the writing of the manuscript. All authors contributed critically to the manuscript drafts and gave final approval for publication.

Data accessibility

The data are available through GitHub at https://github.com/MariaHallfors/Primula-nutans-translocation

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Figure legends and tables

FIGURE 1. Geographical distribution of seed sampling sites and experimental gardens (a), and hypotheses of plant performance in experimental gardens (b-e). Panel (a) shows the geographical distribution of seed sampling sites and experimental gardens with occurrences of *Primula nutans* ssp. *finmarchica* marked by dark grey points: Var. *finmarchica* occurs by the Arctic Sea in N-Norway and var. *jokelae* by the Bothnian bay in Finland and Sweden and the White Sea in Russia. Red = seed sampling sites of the southern variety (var. *jokelae*) in Finland; Blue= seed sampling sites of the northern variety (var. *finmarchica*) in Norway. Source for occurrences of Siberian primrose: Global Biodiversity Information Facility (GBIF 2013); Kastikka (Finnish plant distribution database; Lampinen, Lahti, & Heikkinen 2012); Hertta (database of Finnish Environment Institute, unpublished data); occurrences in Russia based on information from herbarium specimens (from collections in the herbarium of the Finnish Museum of Natural History [H *sensu* Thiers 2016] and the herbarium of the University of Turku [TUR *sensu* Thiers 2016] and the distribution map by Hultén and Fries [1986]). Panels (b-e) show hypothesized overall performance of the tested varieties in all experimental gardens following opposing underlying scenarios of (b) local adaptation at the varietal and subspecies level, (c) local adaptation at the subspecies level, (d) tolerance (through plasticity) towards all tested conditions (including those not currently present within the occurrence area of the subspecies), and (e) maladaptation caused by climate change (see text for hypotheses). Dashed area demarks within-range gardens, i.e. the reciprocal part of the experiment. Red= southern variety; blue = northern variety.

FIGURE 2. Climatic and weather conditions of seed sampling sites and experimental gardens. (a) Mean annual temperature and (b) mean temperature of warmest quarter (°C; mean temperature for the three months during which temperatures were highest in each year). Black points show historic mean temperatures (1970-2000; 10 minutes resolution; (Fick & Hijmans, 2017) and gray points show the future

projections of mean temperatures (CMIP5 for 2050, 10 minutes resolution, HADGEM2-ES model; (Fick & Hijmans, 2017) for each experimental gardens and seed sampling sites (Northern= seed sampling sites of the northern variety; Southern= seed sampling sites of the southern variety). For experimental gardens, open circles show mean temperature during the experimental years 2013-2016. The experimental gardens and seed sampling sites within the species range is outlined by a dashed gray box, whereas the blue box indicates the sites within the range of the northern variety and the red box the sites within the range of the southern variety. Corresponding figures for precipitation sum and other climatic variables in Fig S5. The future temperatures in Oulu approach the historic ones in Tartu, Helsinki and Rauma, and the future temperatures in Svanvik approach the historic ones in Oulu. During the experiment, mean temperatures were higher than the historic means. The conditions in Svanvik corresponded with historical means in Oulu. Those in Oulu approached the historic means in the southern gardens.

FIGURE 3. Temperature conditions in the experimental gardens over the course of the experiment (2013-2016). (a) Mean annual temperature and (b) mean temperature of the warmest quarter (mean temperature for the three months during which temperatures were highest in each year) per garden and year.

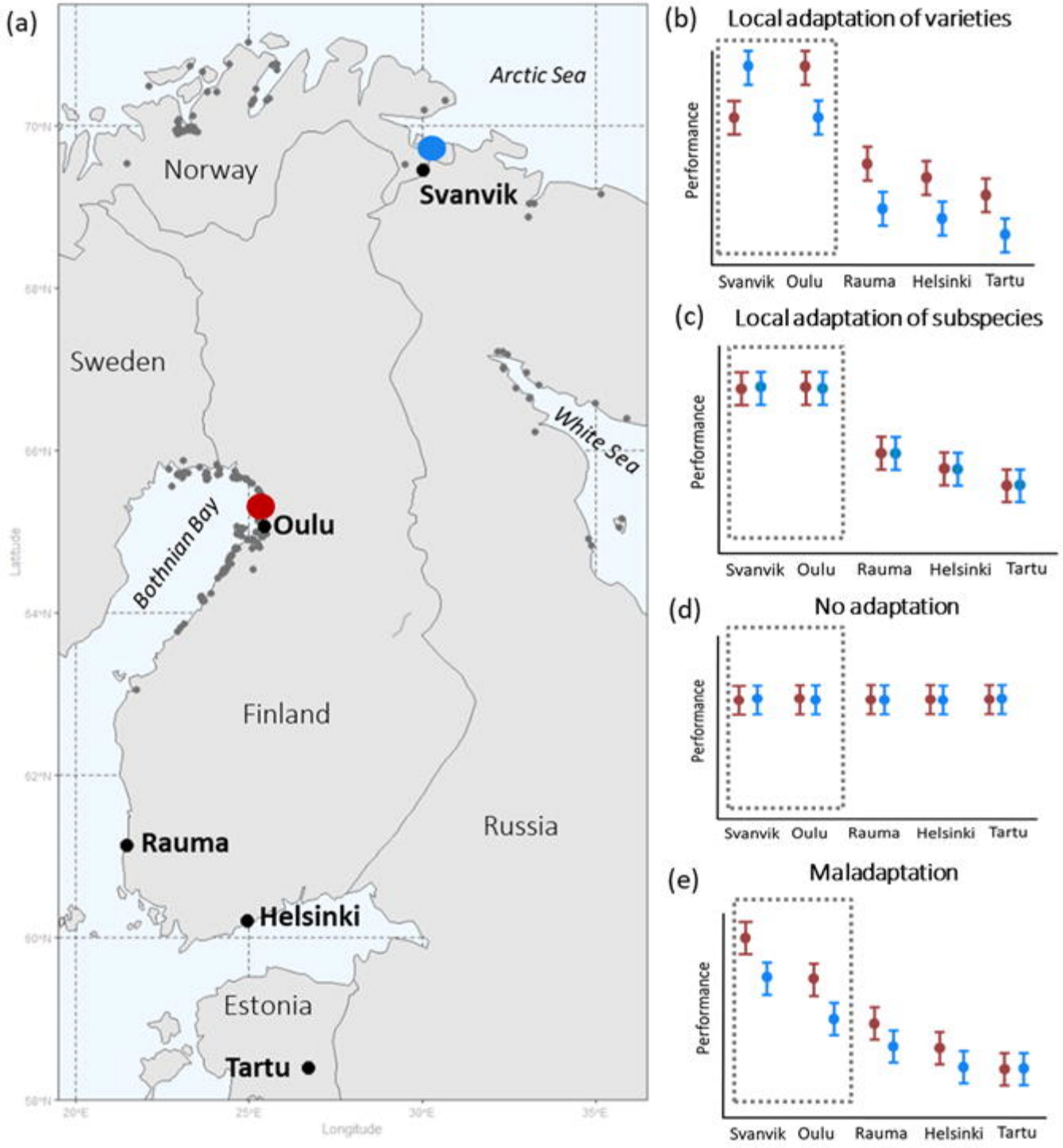
FIGURE. 4. Mean survival per variety across gardens and years. The total number of individuals planted in 2013 appear at the top of the plot (both original plants and additional plants due to high die-off in the first summer). Red points = southern variety; blue points = northern variety. The size of the point indicates year: big point= 2014; medium point= 2015; small point = 2016. Exact numbers of individuals per year and garden and percentage decrease over year are presented in Table S3.

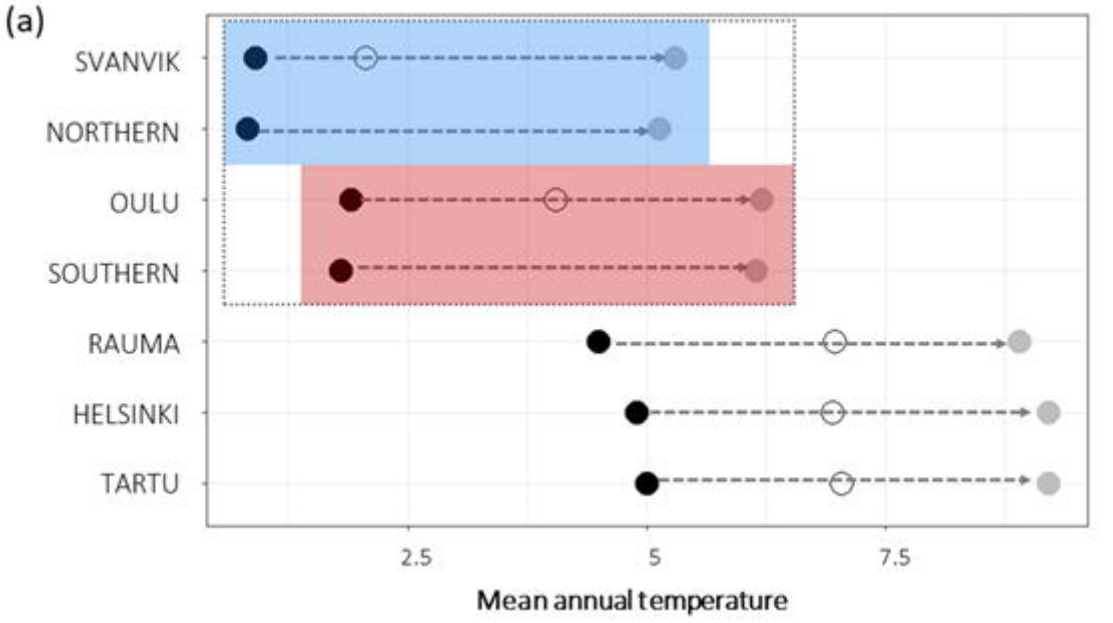
FIGURE 5. Predicted overall performance of the two varieties across (a) experimental gardens, and (b) mean annual temperature over the experimental period 2013-2016. Predictions are made for plants of

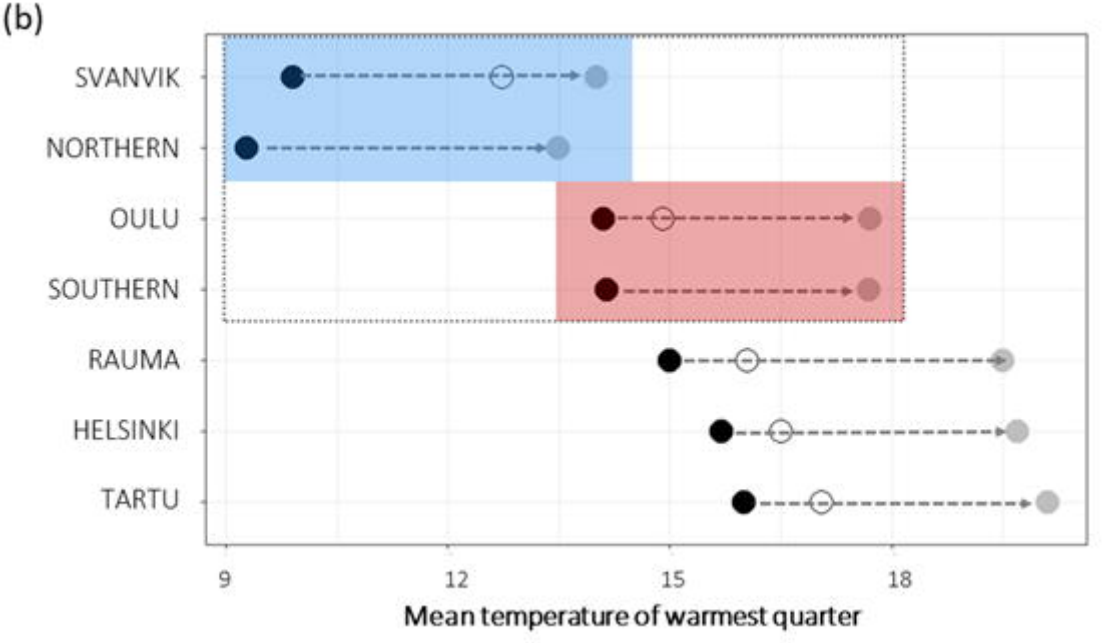
average original size and based on the fixed effects aster model (i.e., not including *Plot* and *Seed sampling site* as random effects). Red= southern variety; blue= northern variety.

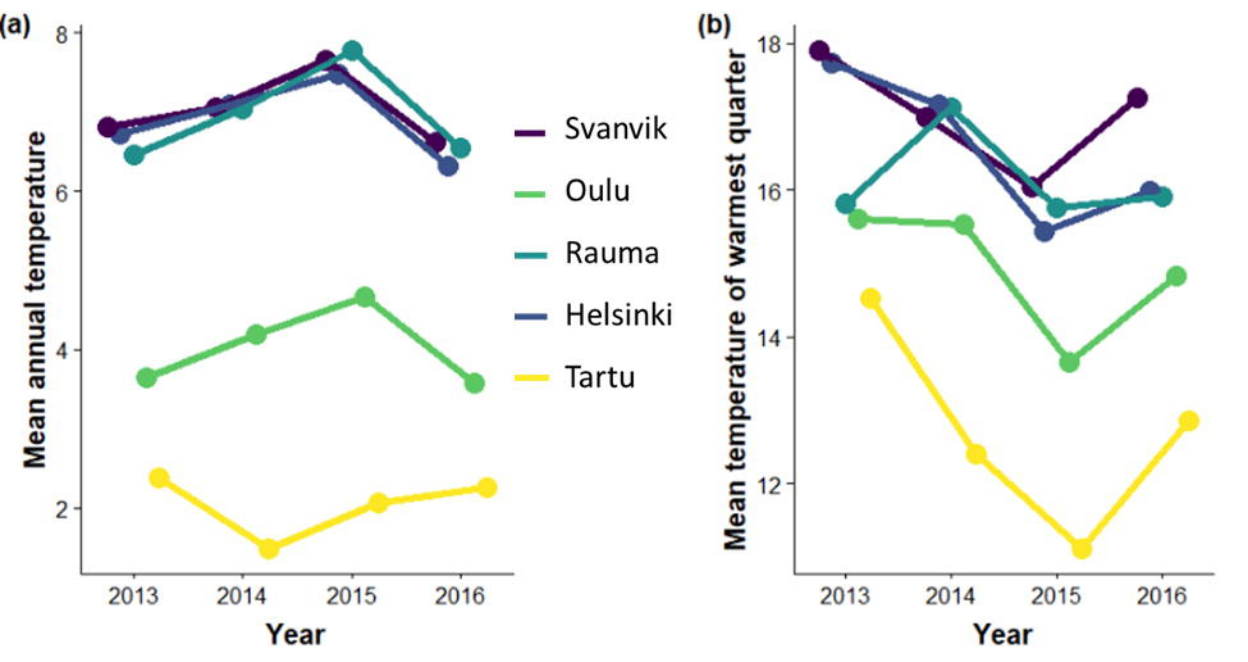
TABLE 1. Change in deviance when a single variable was omitted from the full random effects models. Summary from comparing aster models testing the fixed effects of experimental garden (left-hand side of table) or annual temperature (right hand side of table), variety and original size on plant performances, as well as *Plot* and *Seed sampling site* as random effects. Statistical significance of predictor variables was assessed using likelihood ratio tests, that is, a model where one variable was omitted was compared to the full model using anova.

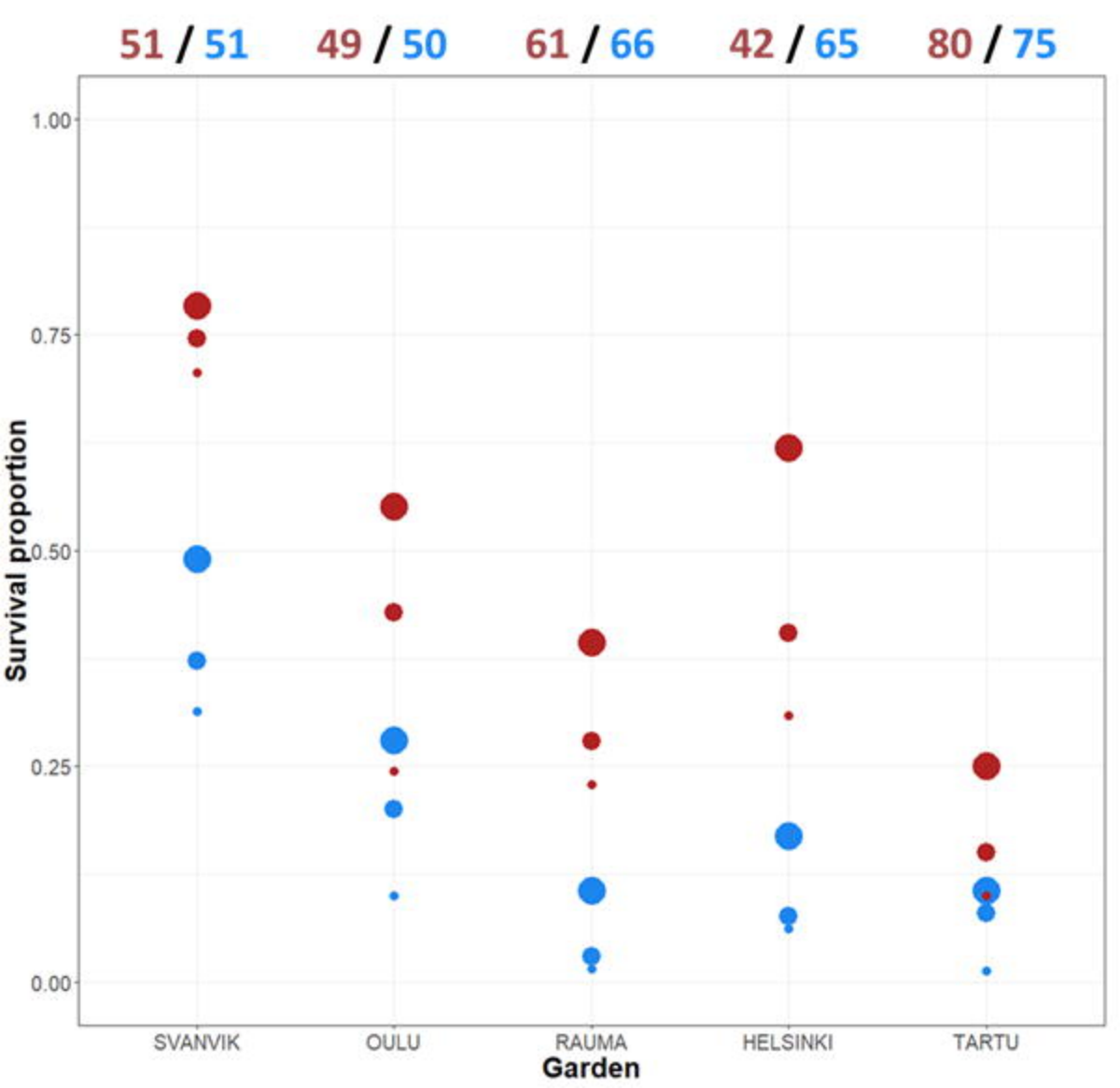
Garden-model				Annual temperature -model		
p-value	df	Change in deviance	Variable	Change in deviance	df	p-value
<0.001	1	62.4	Original size	60.2	1	<0.001
<0.05	4	11	Variety:Garden/Ann.Temp.	8.8	1	<0.01
<0.01	5	20	Variety (+ Variety:Garden/Ann. Temp.)	17.2	2	<0.001
<0.05	8	19.6	Garden/Ann. Temp. (+ Variety:Garden/Ann. Temp.)	14.2	2	<0.001
<0.001	0	46	Plot	60	0	<0.001
0.09	0	1.8	Seed sampling site	2.2	0	0.07

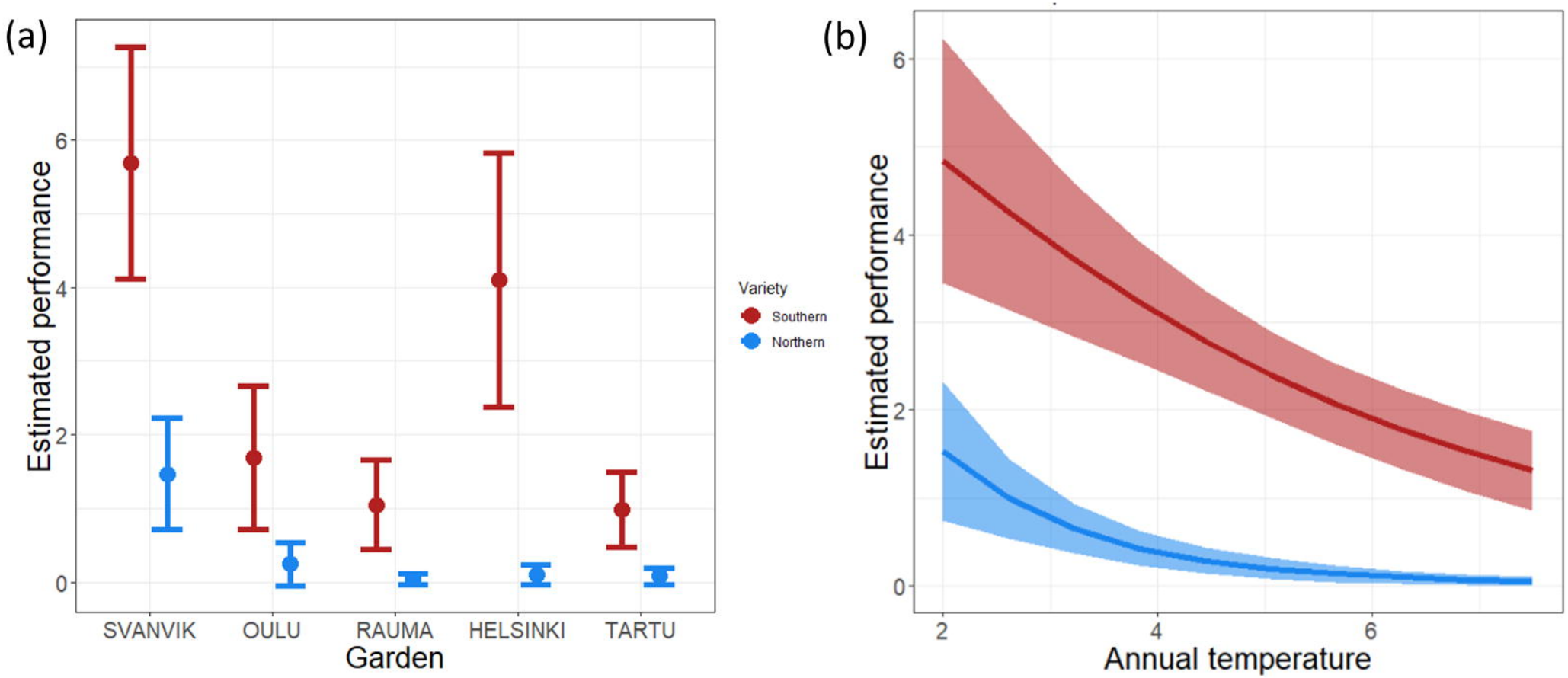

(a)
Arctic Sea
Norway
Svanvik
Sweden
White Sea
Bothnian Bay
Oulu
Finland
Russia
Rauma
Helsinki
Estonia
Tartu
70°N
68°N
66°N
64°N
62°N
60°N
58°N
20°E
25°E
30°E
35°E
Latitude
Longitude
(b)
Local adaptation of varieties
Performance
Svanvik
Oulu
Rauma
Helsinki
Tartu
(c)
Local adaptation of subspecies
Performance
Svanvik
Oulu
Rauma
Helsinki
Tartu
(d)
No adaptation
Performance
Svanvik
Oulu
Rauma
Helsinki
Tartu
(e)
Maladaptation
Performance
Svanvik
Oulu
Rauma
Helsinki
Tartu


(a)
SVANVIK
NORTHERN
OULU
SOUTHERN
RAUMA
HELSINKI
TARTU
2.5
5
7.5
Mean annual temperature


(b)
SVANVIK
NORTHERN
OULU
SOUTHERN
RAUMA
HELSINKI
TARTU
9
12
15
18
Mean temperature of warmest quarter


(a)
Mean annual temperature
8
6
4
2
2013
2014
2015
2016
Year
Svanvik
Oulu
Rauma
Helsinki
Tartu
(b)
Mean temperature of warmest quarter
18
16
14
12
2013
2014
2015
2016
Year


51 / 51
49 / 50
61 / 66
42 / 65
80 / 75
1.00
0.75
0.50
0.25
0.00
Survival proportion
SVANVIK
OULU
RAUMA
HELSINKI
TARTU
Garden


(a)
Estimated performance
0
2
4
6
SVANVIK
OULU
RAUMA
HELSINKI
TARTU
Garden
Variety
Southern
Northern
(b)
Estimated performance
0
2
4
6
2
4
6
Annual temperature