Climate Effects on Native Plants in Swiss Botanical Gardens

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von
Christine Föhr
von Eriswil (BE)

Leiter der Arbeit:
Prof. Dr. Markus Fischer
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Chapter 1

General introduction

The impact of climate change on plant performance

Recent anthropogenic climate change has led to a mean global temperature increase of 0.74°C in the last century (IPCC 2007). Similar trends have been observed in Switzerland, with a mean temperature increase of 1.2°C/100 years, a decrease in number of frost days, an elevational rise of the zero degree level, and increase of precipitation in winter (Klimareport Meteoschweiz 2014). Abiotic factors such as temperature and precipitation directly influence vital physiological processes such as photosynthesis, respiration and growth in plants (Hughes 2000, Gurevitch et al. 2006). As every plant is physiologically adapted to the environment in which it is growing, changing climatic conditions may affect plant survival and reproduction. As a consequence, increasing mortality rates and decreasing reproductive rates within the populations may compromise the persistence of plant populations in the long-term. The change in abundance or the complete disappearance of a particular species in a habitat will have an impact on the community composition as other species will take over the available space (Hughes 2000, Lenoir et al. 2010, Gornish & Tylianakis 2013) and species interactions may become disrupted or altered (Parmesan 2006). Changes in the presence or abundance of species and altered species interactions may have an impact on the ecosystem as species traits directly influence ecosystem properties (Chapin et al. 2000, Hooper et al. 2005). Thus, by influencing the performance of plants, changing climatic conditions may ultimately lead to major changes at the community and ecosystem levels. Understanding the effects of climate change on plant performance is therefore essential to anticipate potential negative effects on species, communities and ecosystems and will help to set conservation priorities.

Modeling studies predict that under ongoing climate change some species will no longer be able to grow at their present locations because of temperature or drought stress or changed interactions (e.g. competitive exclusion) with other species (Thomas et al. 2004, Ibáñez et al. 2006). As a result, many species are shifting their distribution range in latitude or elevation as they move together with the climate to which they are adapted (Grabherr et al. 1994, Sturm et al. 2001, Walther et al 2002, Parmesan & Yohe 2003, Stöckli et al. 2011, Pauli et al. 2012). However, species might be hindered in their movement by natural obstacles such as mountain ranges or large waters and by habitat fragmentation (Higgins et al. 2003, Meier et al. 2012). Furthermore, sessile organisms such as plant species might not be able to move fast enough due to dispersal limitation (Midgley et al. 2006, Engler et al. 2009). Thus, the movement ability of many plant species is unlikely to keep up with the expected fast climate change (Corlett & Westcott 2013, Cunze et al. 2013). For dispersal limited species, persistence under novel climatic conditions by adjusting their phenotype to the changing conditions (phenotypic plasticity) or by rapid genetic evolution (adaptation) is essential (Thuiller et al. 2008, Chevin et al. 2010).

Transplantation and warming experiments have shown varying responses of plant performance to higher temperatures. For example, plant growth mainly increased under warmer conditions but sometimes also decreased (Arft et al. 1999, de Valpine & Harte 2001, Peñuelas et al. 2004, Trtikova et al. 2010, De Frenne et al. 2011). Studies that investigated the effect of increasing temperature on plant survival and reproduction reported a higher mortality (Angert & Schemske 2005) and higher as well as lower reproductive success (Arft et al. 1999, De Frenne et al. 2011).

However, most of the studies focused on one or few species which limits their strength and the generality of their conclusions. In addition, although positive responses in growth and reproduction have been detected, the long-term costs for these changes are largely unknown (Corlett & Westcott 2013). Moreover, if the magnitude of climate change exceeds the species' tolerance or their ability for rapid evolutionary response, negative consequences for plant performance and population persistence are likely to occur, and species extinction risk will increase (Jump & Peñuelas 2005).

Climatic conditions, particularly temperature, can strongly influence the timing of important plant life-history events, such as flowering time (Forrest & Miller-Rushing 2010). It has been shown that many plant species respond to global warming by flowering earlier in the season (Fitter & Fitter 2002, Menzel et al. 2006, Gordo & Sanz 2010, Ibáñez et al. 2010). Flowering earlier in the year can negatively affect the reproductive success of the plants (Burgess et al. 2007, Scheepens & Stöcklin 2013) due to an increased risk of flower bud damages by late frost events (Inouye 2008) and possible temporal mismatches in plant-pollinator interactions (Memmott et al. 2007, Hegland 2009, Kudo & Ida 2013, Petanidou et al. 2014). Such temporal mismatches in plant-pollinator interactions may occur as species vary in their temporal sensitivity and therefore respond differently to environmental cues (Parmesan & Yohe 2003, Forrest 2015). Mismatches in plant-pollinator interactions may contribute to an overall degradation of the interaction network within the community, if novel plant-pollinator interactions cannot be formed (Memmott et al. 2007, Kaiser-Bunbury et al. 2010, Burkle et al. 2013, Revilla et al. 2015). This may have substantial negative consequences on the persistence of both the plant and the pollinator populations.

Rare and threatened plant species may be particularly susceptible to climate change (Maschinski et al. 2006; Marrero-Gómez 2007; Lawson 2010). They often occur in small and isolated populations of low genetic diversity which may be caused by genetic drift and inbreeding (Karron 1997). Low genetic diversity might negatively affect viability (Oostermeijer et al. 2003, Leimu et al. 2006) and through the loss of potentially adaptive alleles also the adaptive potential of the plant populations (Husband & Campbell 2004, Willi et al. 2006, Leimu and Fischer 2008, Jump et al. 2009). Additionally, species with restricted ranges often have a low dispersal ability (Gaston 1994). Weak dispersal would limit the plants' ability to colonize new ecologically suitable habitats and shift their range with the climate they are adapted to. Rare plant species might also have more specialized plant-pollinator-interactions to increase the probability that removed pollen is deposited on the stigma of a conspecific plant (Orians 1997, Sargent & Otto 2006). However, specialized plant-pollinator interactions may render them particularly vulnerable in case of phenological mismatches and impede successful reproduction. Thus, due to the combination of multiple factors, especially rare and threatened plant species may face an increased extinction risk in future if effective conservation measures are not taken in time (Gurevitch et al. 2006).

Consequences of ex-situ conservation for adaptation

Species extinction risk is predicted to increase substantially in the next decades as a result of climate change (Thomas et al. 2004, Thuiller et al. 2005a). To prevent the potential loss of thousands of plant species, plant conservation needs to be an urgent priority (Wyse Jackson & Kennedy 2009). Plant conservation in the natural environment (in situ) alone is often not sufficient anymore for preserving threatened species, especially when the local populations are eradicated due to habitat destruction (Maunder et al. 2004, Havens et al. 2004). Thus, the conservation of plants outside their natural environment (ex situ) has become an important tool to complement in-situ conservation by providing plants for habitat restoration and reintroduction programs (Maunder et al. 2004, Havens et al. 2004). Accordingly, one of the targets of the Global Strategy for Plant Conservation, which was set up under the Convention on Biological Diversity (CBD) in 2002, and updated in 2010, is to preserve at least 75% of threatened plant species in ex-situ collections, and to provide at least 20% of them for reintroduction and habitat restoration programs.

However, the ex-situ collections raise specific difficulties, as target plants are removed from their natural habitat and introduced to novel and artificial environments (Havens et al. 2004, Husband & Campbell, 2004). In the short term, changes in abiotic or biotic conditions might have a negative impact on plant performance and impede survival and reproduction of the plants. In the long term, plant populations might adapt to the novel conditions (Havens et al. 2004, Schaal & Leverich 2004) and alter important life-history traits (Ensslin et al. 2011, Schröder & Prasse 2013a, Schröder & Prasse 2013b). Unintentional selection during cultivation such as e. g. propagation of especially well-developed plant individuals might further enhance such adaptive responses (Husband & Campbell 2004, Rolston 2004, Ensslin et al. 2011). As a result, species may lose their ability to adapt to their natural habitat and may become unsuitable for restoration and reintroduction (Schröder & Prasse 2013b).

Furthermore, ex-situ populations most often originate from very few individuals (Husband & Campbell 2004). Therefore, the genetic variation of ex-situ populations is usually low (Husband & Campbell 2004, Rucińska & Puchalski 2011, Lauterbach et al. 2012, Brütting et al. 2012). Thus, the risk of a further loss of genetic diversity due to genetic drift and inbreeding and a resulting reduction of the viability (Oostermeijer et al. 2003) and the adaptive potential of the plant populations in ex-situ collections is very high (Husband & Campbell 2004, Willi et al. 2006, Leimu and Fischer 2008, Jump et al. 2009). As a consequence, ex-situ plant populations often are of limited value for conservation programs (Maunder et al. 2001).

Botanical gardens as study sites

History of botanical gardens

"*Botanical gardens are institutions holding documented collections of living plants for the purposes of scientific research, conservation, display and education.*" (BGCI 2015)

Botanical gardens have been centers for scientific studies since their earliest foundation in the 1540s in northern Italy (Rutherford 2015). The first botanical gardens, then called physic gardens, were founded by the universities of Pisa, Padua and Florence with the aim to grow medicinal plants for the education of students and medical research. Soon, more botanical gardens were founded, and in the 17th century botanical gardens were established in most of the European countries. By that time, the botanical gardens had started to acquire also plants other than medicinal ones. Especially rarities and novelties from distant lands were much sought. With the progressing colonization of the world and the increase in maritime trade, more and more exotic plants were brought back to Europe, and the plant collections in the botanical gardens increased and diversified. Thanks to improvement of glasshouse design and technology, exotic plants could be cultivated and propagated in temperate regions. In the late 19th century the botanical gardens had broadened their scientific scope. In addition to the study of medicinal plants, crop research especially of exotic introductions like cotton, coffee and rubber became a major objective of many botanical gardens. By the early 20th century, crop experimentation declined and botanical gardens finally developed their crucial role in plant conservation and public education.

Currently, over 3000 botanical gardens and arboreta in about 150 countries world-wide harbor more than 100’000 taxa, which is almost one third of the world’s described vascular plant species (BGCI 2015).

Research in botanical gardens

Botanical gardens with their large taxonomically and ecologically diverse plant collections provide ideal research facilities for studies on plant anatomy, physiology, taxonomy, genetics, phylogeny, evolution, biogeography and ecology (Dosmann 2006, Donaldson 2009, Primack & Miller-Rushing 2009). Because of their vast and diverse collections, they facilitate the realization of multi-species studies that are required to search for general patterns and mechanisms in nature (van Kleunen et al. 2014). Furthermore, in botanical gardens many species are grown together under similar climatic conditions that often differ from the conditions in natural habitats (Primack & Miller-Rushing 2009). This feature makes them ideal study sites to address many questions related to climate change (Donaldson 2009, Primack & Miller-Rushing 2009, Ali & Trivedi 2011, Blackmore et al. 2011).

In botanical gardens, species performance under changing climatic conditions can be observed over time. For example, species benefiting from the warmer conditions and growing more vigorously than in the past can be identified as well as species that suffer from the effects of climate change (Primack & Miller-Rushing 2009). Furthermore, species responses to novel climatic conditions can also be studied by assessing the performance of species that are growing in botanical gardens outside their natural vegetation zone (Jalili et al. 2010, Hällfors et al. 2011).

Various projects involving botanical gardens have been started to observe and record plant phenology and its changes over time, such as e. g. the International Phenological Gardens project (IPG) (Menzel 2000, Chmielewski & Rötzer 2001). In this project the phenology of 23 tree and shrub species has been recorded at ca. 50 botanical gardens across Europe since 1959 (Chmielewski & Rötzer 2001). These observations revealed that spring events advanced on average by 6.3 days due to climate change within the period of 1959 to 1996 (Menzel 2000). Other studies have been realized using the botanical gardens' herbarium specimen or photographs to compare past and present timings of phenological events (Primack et al. 2004, Miller-Rushing et al. 2006).

Many botanical gardens today are also actively involved in plant conservation (Havens et al. 2006). Their facilities and the gardeners' expertise for growing plants enables the gardens to hold ex-situ collections of rare and endangered plant species (Donaldson 2009, Blackmore et al. 2011) These plants are used for reintroduction projects (e. g. Aguraiuja 2011, Noel et al. 2011) and to study the demographic, reproductive, ecological and genetic processes (e. g. Forrester & Runkle 2000, Hollingsworth et al. 2005, Oldfield 2009, Ensslin et al. 2011, Rucínska & Puchalski 2011, Baker et al. 2014) that are ultimately important for the species' successful conservation management (Donaldson 2009, Ali & Trivedi 2011).

This thesis

The aim of this thesis is to provide further insight into climate effects on plant performance, and into the question whether rare plant species are more sensitive to changing climatic conditions than common plant species. To achieve rather general inferences and conclusions, I studied multiple common and rare native plant species originating from different altitudinal zones cultivated in botanical gardens across Switzerland.

In chapter two of this thesis, I study the effect of changing climatic conditions on plant performance. So far, studies addressing this issue usually concentrated on a small number of mainly short-lived species. I studied the performance of a large taxonomically and ecologically diverse set of 165 native perennial plant species in five lowland and five alpine botanical gardens in Switzerland. I specifically asked whether plant survival, growth and reproduction is different for species naturally growing at similar, higher or lower elevations than in the particular botanical garden they are growing in. Moreover, I studied whether species with a narrower geographic or climatic range respond stronger than species with a wider geographic or climatic range.

In chapter three, I assess how changing climatic conditions affect plant phenology and whether plant species are able to establish plant-pollinator interactions in a novel environment. Therefore, I assessed in the lowland Botanical Garden of Bern (Switzerland) the flowering onset of 185 native plant species originating from different altitudinal zones and counted with a team of helpers flower visitors on these plant species. Furthermore, I tested whether the changing climatic conditions affect the phenology of rare and common plant species differently, and whether rare and common species vary in their ability to establish novel plant-pollinator interactions.

In chapter four, I compare the adaptive responses to cultivation and to novel climatic conditions of rare and common alpine plant species grown in different botanical gardens. In two experimental sites at subalpine level and in the lowland I measured germination rate, seedling survival and seedling growth of three related rare and common alpine species pairs grown from seeds from lowland garden populations, alpine garden populations and natural populations.

In chapter five, I summarize the results and conclude how changing climatic conditions affect plant performance of rare and common plant species.

Chapter 2

Warmer climate than in their natural range reduces the performance of 165 native plant species across 10 botanical gardens in Switzerland

Christine Föhr & Markus Fischer

Abstract

Assessing plant species responses to changing climate is crucial to anticipate potential impacts of climate change on biodiversity and to set conservation priorities. However, experimental studies usually concentrate on a small number of mainly short-lived species to address this issue. We used the outdoor plant collections of five lowland and five alpine botanical gardens in Switzerland to study the effect of climate on the performance of a large and taxonomically and ecologically diverse set of 165 native perennial herbaceous plant and sub-shrub species. We asked whether plant survival, growth and reproduction were different for species naturally growing at similar, higher or lower elevations than the botanical garden they were growing in and whether species with a narrower geographic or climatic range were more affected than species with a wider geographic or climatic range. Species survival and especially reproduction of plant species were reduced at lower elevations, and thus warmer conditions, than their natural occurrence, whereas they were not affected at higher elevations. This indicates that the 165 perennial plant species are generally not adapted to the warmer climate at lower elevations. This implies that the persistence of long-lived plant species might be impaired under future climate change.

Introduction

Recent anthropogenic climate change has induced shifts in species distributions in latitude and elevation, as species try to track the climate to which they are adapted (Grabherr et al. 1994; Sturm et al. 2001; Walther et al 2002; Parmesan & Yohe 2003; Stöckli et al. 2011; Pauli et al. 2012). However, the movement of many plant species is unlikely to keep up with the rate of expected future climate change (Corlett & Westcott 2013). For them persistence under novel warmer climatic conditions is essential to avoid extinction (Thuiller et al. 2008). Thus, assessing the performance of plants under novel climatic conditions is required to anticipate potential negative impacts of climate change on biodiversity and to set conservation priorities.

The ability of species to persist under novel climatic conditions depends on their life history (Thuiller et al. 2008). In the short-term, species with long-lived plants are likely to persist longer in the face of climate change than species with short-lived ones. However, for long-term persistence successful reproduction is crucial. Assessing whether longer-lived and shorter-lived species differ in their responses to novel climatic conditions requires the comparison of a large number of species with different life spans (van Kleunen et al. 2013). However, previous experimental studies investigating the response of plant species to novel climatic conditions mostly involved few (Lambrecht et al. 2006; Hovenden et al. 2008; De Frenne et al. 2009) and short-lived species with a short generation time (Jump & Peñuelas 2005).

Moreover, geographic and climatic distribution range may affect species responses to novel climates. Rare plant species may be specifically susceptible to climate change (Maschinski et al. 2005; Marrero-Gómez 2007; Lawson 2010) and plant species that naturally grow under a broader range of different climatic conditions are expected to be more tolerant to novel climatic conditions than climatically restricted species are (Thuiller et al. 2005). However, studies directly comparing the response of plants of rare and common species, or of species with different climatic ranges, to climate change are remarkably scarce.

Botanical gardens are ideal study sites for assessing the performance of a large number of perennial plants with different geographic and climatic range sizes under novel climatic conditions (Primack & Miller-Rushing 2009). Botanical gardens can be seen as large common garden experiments themselves, as their large and diverse plant collections are grown under common conditions. Additionally, many species in botanical gardens are growing outside their natural range. Most often this concerns alpine species that are grown in botanical gardens in the lowland, where the plants experience warmer and generally drier conditions than in their natural habitat. Switzerland, with its pronounced elevational gradient, has a long tradition of lowland and alpine botanical gardens (Gremaud 2007), which together provide an excellent opportunity for studying plant performance at different elevations and therefore different climatic conditions.

We assessed the performance of 165 native perennial plant species growing in 10 botanical gardens in Switzerland, five in the lowlands and five in the in the mountain region of the Alps to address the following questions: (1) How do climatic conditions affect the performance of perennial plant species in botanical gardens, specifically if they do not match the conditions the plant species are naturally exposed to? (2) Are common plant species more tolerant to novel climate than rare plant species are? (3) Are plant species that grow under a broader range of different climatic conditions more tolerant to novel climatic conditions than climatically more restricted species are?

Methods

Study sites

We assessed plant performance in 10 botanical gardens in Switzerland (Fig. 1, Table 1). Five of the gardens are situated in the alpine region at elevations above 1200 m a. s. l., the other five gardens are situated in the lowlands below 700 m a. s. l.

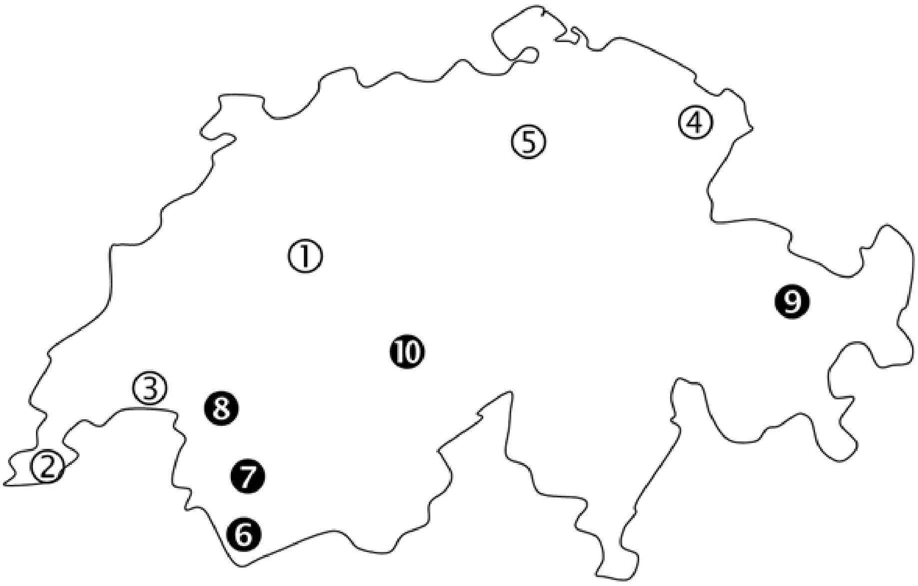

Figure 1 *Locations of the 10 botanical gardens in Switzerland. Numbers with white background represent lowland gardens, numbers with black background represent alpine gardens.*

Table 1 *The 10 botanical gardens. Their elevations are derived from Gremaud (2007).The vegetation zone indicates the assigned value based on the temperature indicator value T (Landolt 2010), which classifies the average air temperature during the growth period of a plant (1 coldest, 5 warmest).*

No.	Botanical garden	Locality	Coordinates	Mean elevation [m a.s.l.]	Vegetation zone
1	Botanical Garden of Bern	Bern	46.95°N, 7.44°E	518	4
2	Botanical Garden of Geneva	Geneva	46.23°N, 6.15°E	380	4
3	Botanical Garden of Lausanne	Lausanne	46.51°N, 6.62°E	420	4
4	Botanical Garden of St. Gallen	St. Gallen	47.44°N, 9.41°E	700	4
5	Botanical Garden of Zurich	Zurich	47.36°N, 8.57°E	436	4
6	Alpine Garden "Flore-Alpe"	Champex	46.03°N, 7.11°E	1520	2.5
7	Alpine Garden "La Thomasia"	Pont-de-Nant	46.25°N, 7.11°E	1260	2.5
8	Alpine Garden "La Rambertia"	Rochers-de-Naye	46.43°N, 6.98°E	2000	1.5
9	Alpine Garden Schatzalp	Schatzalp	46.80°N, 9.81°E	1910	2
10	Alpine Garden Schynige Platte	Schynige Platte	46.65°N, 7.91°E	1975	2

Assessment of plant performance

We selected all herbaceous plants and sub-shrubs that were growing in at least five of the botanical gardens. Thus, we assessed the performance of 165 native perennial plant species belonging to 40 different families (species list in Appendix, Table S1). We validated the taxonomic status of the species according to the Angiosperm Phylogeny Website (Stevens 2001). All species were growing outdoors under the ambient climatic conditions of the botanical gardens. In all gardens interspecific competition was mitigated by regular weeding and plants were irrigated when necessary, as part of the normal gardening procedures.

As measures of plant performance we assessed survival, growth and reproductive success, as these traits directly affect fitness (Violle et al. 2007). To assess survival and reproduction we asked the responsible gardeners in each garden to fill out a questionnaire in August 2010 in which they had to assign each species to one of the three following categories:

1. The species was repeatedly planted in the past but never survived
   or the species needs regular replanting
   or a lot of extra care in order to survive.
2. The species survives without extra care, but does not reproduce.
3. The species survives without extra care and reproduces.

The assignment of the species to these categories was based on the experience of the gardeners with the species over several years including 2010. Reproduction was assessed as successful when seedlings of the species were regularly found in the garden populations.

To assess whether a species grows well in a particular botanical garden site compared with its growth under natural climatic conditions, we measured the height of the largest individual of each species in July and August 2010 in each botanical garden. We then compared the measured value to the maximum height known from the literature (Lauber & Wagner 2007) and we calculated the log response ratio of measured height/maximum height for each individual, from now on called height ratio. The higher the ratio, the better the species grew in a particular garden.

As the plant species were grown under different light conditions and on different substrate, we recorded the positions of the plant species in the gardens concerning light/shade and humus content of the substrate with a visual estimation and categorization into three light conditions (shade/semi-shade/light) and three soil conditions (low humus content/moderate humus content/high humus content).

Climatic, distributional and ecological variables

The 10 botanical gardens were situated at two elevational levels, high (> 1200 m a. s. l., Table 1) and low (< 700 m a. s. l.). To quantify the difference between the climate of the botanical gardens and the climate of the species natural range we assigned each botanical garden to a vegetation zone according to the Landolt Temperature indicator value T (Landolt 2010, Table 1). The Landolt T indicator value characterizes the average air temperature during the growth period of a plant. It largely corresponds with the average elevational range of the plant species in the Alpine region (Landolt 2010). We calculated the difference between the garden values and the species values to obtain a measure of climatic mismatch for each species in each garden. The calculated values ranged from -3.5 to 3. Due to computational reasons we grouped the calculated values into three factor levels: higher elevation for values ranging from -3.5 to -1, similar elevation for values from -0.5 to 0.5, lower elevation for values from 1 to 3. Higher and lower elevation, respectively, referred to the elevation of the botanic gardens where the species grew compared with their natural average elevational range.

As a proxy of the rarity or commonness of each of the 165 species we also obtained data on species geographic range size as percentage of survey plots (60-100 km^2) in Switzerland where the species naturally occur (Lauber & Wagner 2007) and the range of variation of the T indicator value (small or large variation) as a proxy for climatic range size of all species (Landolt 2010).

Statistical analysis

We tested the relationship between climatic mismatch, species geographic range size and species climatic range size and plant performance for the two binary response variables survival (yes/no) and reproduction (yes/no) and for the continuous response variable height ratio (Table 2). The binary response variables survival and reproduction were based on the performance categories to which the gardeners assigned each species in the questionnaire. We limited the analysis of reproduction to those plants which had survived.

We analysed the data using generalized linear mixed effect models (GLMM) with a binomial distribution for the binary response variables survival and reproduction and with a Gaussian distribution for the continuous response variable height ratio. We performed the GLMM with the function *lmer* of the *lme4* package (Bates & Maechler 2009) implemented in the statistical software R 2.14.1 (R Development Core Team 2011). We corrected for taxonomy by including family and species, nested within family, as random factors. As additional random factor we included the botanical gardens.

For model selection we first fitted all the fixed terms (low elevation versus high elevation gardens, climatic mismatch, species geographic range size, climatic range size, shade and substrate) and their two-way interactions. We did not include interactions with the covariates shade and substrate. Then we reduced the models of fixed terms by stepwise deletion of non-significant terms starting with the interactions. After each deletion of a non-significant term we compared the resulting model with the previous one using likelihood-ratio tests (Zuur et al. 2009). In the final model we kept variables that resulted in a statistically significant change in deviance when deleted from the model as well as the variables and interactions of major interest, i.e. climatic mismatch, climatic mismatch x species geographic range size, climatic mismatch x species climatic range size. We carried out Tukey post-hoc tests and obtained estimates and standard errors for each factor level with the *multcomp* package in R (Hothorn et al. 2008). Finally, we tested the significance of random effects by comparing the models with and without each random effect with log likelihood-ratio tests (Bolker et al. 2008).

Table 2 *Set of explanatory variables used in the analyses.*

Variable	Units or categories	Source
Fixed terms		
Elevational level	Lowland garden (< 700 m a. s. l.), alpine garden (> 1200 m a. s. l.)	Gremaud (2007)
Climatic mismatch	Difference between vegetation zone of garden and temperature indicator value T of each species	Landolt (2010)
Species geographic range size	% of survey plots in Switzerland where the species is present	Lauber & Wagner (2007)
Species climatic range size	Variation of T indicator value (small/large)	Landolt (2010)
Covariables		
Shade	Shade, semi-shade, light	Föhr, personal observation
Substrate	Humus content (low, moderate, high)	Föhr, personal observation
Random terms		
Species	165 plant species	Lauber & Wagner (2007)
Family	40 plant families	Stevens (2001)
Garden	10 botanic gardens	

Results

More than half of the plant populations growing in the botanical gardens survived without extra care and regularly produced seedlings (58.6%). 37.5% of the plant populations survived without extra care but did not reproduce. Only 4.0 % of the plant populations needed regular replanting or a lot of extra care to survive.

The influence of climatic mismatches between botanical gardens and species natural range on plant performance

Climatic mismatches between the botanical gardens and the natural elevational ranges of our study species had significant effects on plant survival and reproduction, but not on growth (Table 3, Fig. 2). Plant survival was reduced when the plants grew at lower elevations than their natural range. However, the effect was small. Only 6.7% of the plants growing at lower elevations did not survive. Overall, survival rates were very high (>90%; Fig. 2a). Plant reproduction was strongly impaired for plants growing at elevations lower than the ones at which they were naturally occurring, but not for plants growing at higher elevations (Fig.2b).

Plants grew less high in the alpine gardens than in the lowland gardens (Table 3). However, climatic mismatches between gardens and natural ranges of the species did not significantly influence plant growth (Table 3, Fig. 2c). Thus, our study plant species appear to be able to adjust their growth to the prevailing climatic conditions.

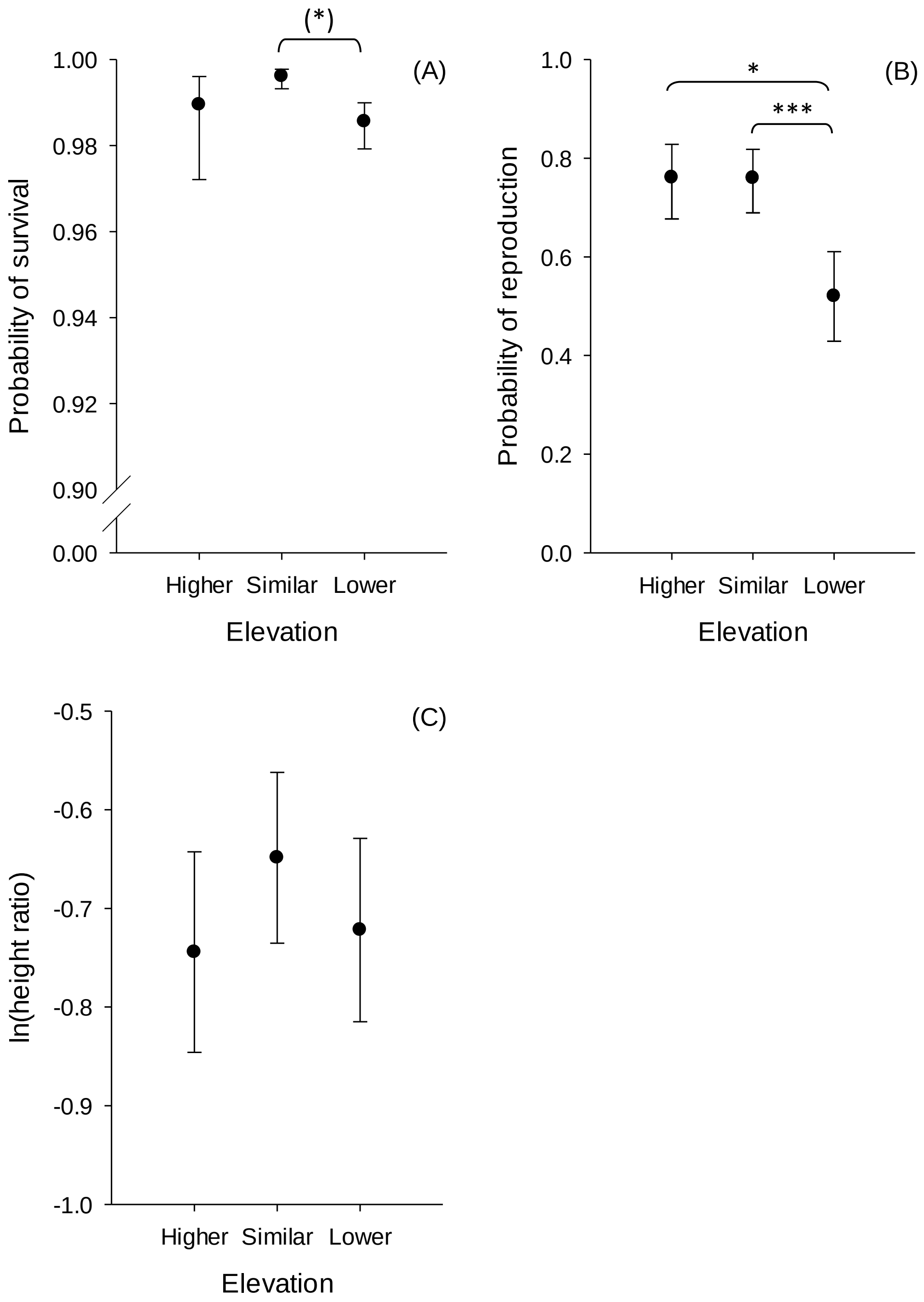

Figure 2 *Influence of climatic mismatch on plant survival (A), plant reproduction (B) and plant growth (ln(height ratio); C). Higher, similar and lower elevation refers to the elevation of the garden sites compared to the species natural average elevational ranges. For the graphs of survival and reproduction we transformed the model estimates (Table 4) to probabilities. Error bars indicate SE. Asterisks in the figure indicate significance levels according to Tukey post-hoc tests: ***: P < 0.001, *: P < 0.05, (*): P < 0.1.*

***Table 3** Summary table of GLMM analyses of plant performance. The parameter estimates and χ^2 likelihood-ratios of the single fixed factors are all derived from models without the interactions included. The variances of the random factors are derived from the final models. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$.*

	Survival (N=1011)		**Growth (N=995)**		**Reproduction (N=976)**	
	Estimates ± SE	χ2	Estimates ± SE	χ2	Estimates ± SE	χ2
Fixed effects						
Elevational level		0.255		14.138 ***		
Lowland garden	4.405 ± 0.385		-0.577 ± 0.076			
Alpine garden	5.158 ± 0.431		-0.810 ± 0.076			
Climatic mismatch		7.557 *		5.368		18.96 ***
Lower elevation	4.223 ± 0.369		-0.722 ± 0.093		0.082 ± 0.368	
Similar elevation	5.543 ± 0.558		-0.649 ± 0.087		1.150 ± 0.353	
Higher elevation	4.542 ± 0.991		-0.744 ± 0.102		1.156 ± 0.417	
Species climatic range size		1.042		0.007		1.915
Small range	4.377 ± 0.351		-0.698 ± 0.088		0.593 ± 0.391	
Large range	4.966 ± 0.622		-0.691 ± 0.102		1.063 ± 0.422	
Species geographic range size	1.074 ± 0.984	0.179	-0.062 ± 0.060	0.014	0.917 ± 0.255	20.55 ***
Shade		7.464 *				
Shade	3.525 ± 0.469					
Semi-shade	5.000 ± 0.514					
Light	4.597 ± 0.375					
Substrate				11.89 **		
Low humus content			-0.800 ± 0.080			
Moderate humus content			-0.648 ± 0.085			
High humus content			-0.609 ± 0.081			

***Table 3** continued*

	Survival (N=1011)		Growth (N=995)		Reproduction (N=976)	
	Estimates ± SE	χ2	Estimates ± SE	χ2	Estimates ± SE	χ2
Climatic mismatch x Elevation level		6.011 *				
Lower elevation x Lowland garden	4.380 ± 0.429					
Lower elevation x Alpine garden	5.704 ± 0.713					
Similar elevation x Lowland garden	0.196 ± 0.001					
Similar elevation x Alpine garden	5.833 ± 0.608					
Higher elevation x Lowland garden	0.195 ± 0.003					
Higher elevation x Alpine garden	4.419 ± 0.784					
Climatic mismatch x Geographic range size		3.792		2.091		4.097
Lower elevation x Geographic range size	2.969 ± 1.009		-0.666 ± 0.108		-0.435 ± 0.457	
Similar elevation x Geographic range size	4.406 ± 1.152		-0.580 ± 0.104		0.820 ± 0.449	
Higher elevation x Geographic range size	5.516 ± 1.754		-0.794 ± 0.116		2.086 ± 0.518	
Climatic mismatch x Climatic range size		0.301		2.566		0.989
Lower elevation x Small range	4.178 ± 0.416		-0.692 ± 0.097		-0.027 ± 0.382	
Lower elevation x Large range	4.517 ± 0.754		-0.763 ± 0.124		0.485 ± 0.465	
Similar elevation x Small range	5.552 ± 0.665		-0.676 ± 0.093		1.059 ± 0.370	
Similar elevation x Large range	5.801 ± 1.035		-0.601 ± 0.111		1.311 ± 0.427	
Higher elevation x Small range	3.684 ± 0.794		-0.778 ± 0.114		0.930 ± 0.456	
Higher elevation x Large range	5.209 ± 1.542		-0.740 ± 0.122		1.213 ± 0.477	
Random effects	Variance		Variance		Variance	
Garden	0.36		0.001		1.016	***
Family	< 0.001		0.080	**	< 0.001	
Family/Species	2.836	**	0.194	***	0.899	***

The influence of species geographic and climatic range size on plant performance under novel climatic conditions

Overall, plant species with a smaller geographic range more often failed to reproduce than plant species with a larger geographic range did (Table 3, Fig. 3). This effect was independent of the climatic mismatches between botanical gardens and natural ranges of the species (Table 3). This indicates that plant species with a narrow geographic range were not more sensitive to novel climatic conditions in the botanical gardens than species were with a large geographic range. Similarly, plant species with a large climatic range did not perform better than species with a narrow climatic range when they were grown outside their natural climatic conditions (Table 3).

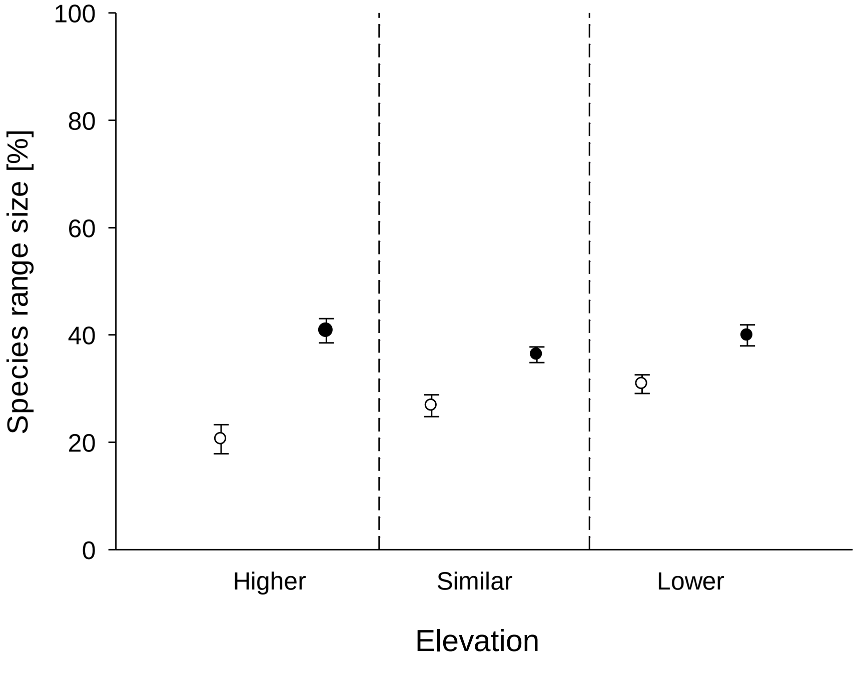

Figure 3 *Influence of species geographic range on reproduction of plant species at different climatic mismatches. Higher, similar and lower elevation refers to the elevation of the garden sites compared to the species natural average elevational ranges. The values on the y-axis represent the percentage of survey plots in Switzerland where the species is present. Means and SE are shown. ○: no reproduction, ●: reproduction.*

Discussion

Plant performance under novel climatic conditions

In a comprehensive survey we assessed the plant performance of 165 perennial plant species in 10 botanical gardens at elevations from 380 - 2025 m a. s. l. . The assessed plants were mostly grown for several years in a climate different to the one they naturally occurred in. In addition to temperature changes the assessed plants also experienced changed precipitation regimes in the botanical gardens. The plants were only watered in cases of drought which are normally rare in Switzerland. Therefore, the plants growing at lower elevations mostly experienced warmer and drier conditions, as altitude is negatively correlated with temperature and in general positively correlated with precipitation in Switzerland (Körner 1999). A warmer and drier climate largely corresponds to the predictions of climate change for Switzerland (Zubler et al. 2014). Thus, our study offers insights about how the predicted climate change might influence plant performance in the future.

We found that plant survival and reproduction were reduced when the plants grew at lower elevations than they naturally do. This suggests that the 165 long-lived plant species generally were impaired by the warmer climatic conditions. This extends findings of Angert and Schemske (2005), who reported greatly reduced survival of *Mimulus lewisii* due to heat stress when planted below its elevational range. So far, it was generally assumed that at lower elevations plant species are not limited by climate, but rather by biotic interactions, such as competition (Brown et al. 1996; Normand et al. 2009). In contrast, our findings from botanical gardens, where biotic interactions such as competition and herbivory are greatly reduced, suggest that abiotic conditions matter largely for species performance at lower elevations.

The strongly reduced reproductive success of the plants growing at lower elevations can have several reasons. Plant species from higher elevations often have physiological adaptations to low temperatures (Körner 1999). Under warmer climatic conditions at lower elevations, these adaptations could be responsible for the reduced performance of the plant species. Especially decreasing reproductive success at or beyond species range limits is often explained by a lower availability of resources and a higher demand on resources for maintenance at the expense of reproduction (Gaston 2009). This, however, is not a likely explanation for the plant populations growing under the controlled growing conditions of the botanical gardens. The vast majority of the assessed plants were successfully flowering (personal observation, Föhr), therefore reproduction was most likely impeded during pollination, fruit or seed production. It is possible that changes in phenology due to extended growing season length at lower elevations influenced the reproductive performance of the plant species (Inouye 2008; Haggerty and Galloway 2011). There is ample evidence for extended growing seasons causing plants to flower earlier in the year (Walther et al. 2002; Parmesan and Yohe 2003; Menzel et al. 2006; Haggerty & Galloway 2011). E.g. earlier flowering is the rule in the botanical garden of Bern, where many of the assessed alpine plant species flower one or even two months earlier than in their natural habitat (Föhr, personal observation). Earlier flowering has been found to prolong fruit maturation, reduce seed production and delay seed germination (Burgess et al. 2007). Moreover, it can increase the risk of frost damage of flower buds, inflorescences and developing fruits (Inouye 2008). Furthermore, phenological changes can disrupt plant-pollinator interactions and consequently impede successful pollination (Hegland et al. 2009). It will be interesting to test whether reduced plant reproductive success under warmer climatic conditions is indeed mediated by changed phenology.

In our study plant survival and reproductive performance was not significantly affected when plants were grown at higher elevations than their natural ranges. Similarly, Samis and Eckert (2009) found high plant fitness of the dune plant *Camissoniopsis cheiranthifolia* north of its natural range. However, most studies that investigated plant performance at and above an elevational species limit (Angert & Schemske 2005; Trtikova et al. 2010) or at latitudes north of the natural species range (Griffith & Watson 2006; Van der Veken et al. 2012) reported lower plant survival and reproductive success, suggesting that plant species are limited by harsh climatic conditions at higher elevations (Brown et al. 1996; Normand et al. 2009). As many of our study plant species were species with montane to alpine distributions and the highest botanical garden in our study was situated at 2000 m a. s. l., our choice of alpine gardens possibly did not cover a sufficiently large elevational gradient to detect the expected decrease in plant performance at higher elevations. As we know of no alpine garden above 2000 m a. s. l. in Switzerland (Gremaud 2007), a similar study with botanical gardens situated along a large latitudinal gradient could possibly yield further insight into the influence of a cooler climate on plant performance.

Plant growth was not significantly affected by the climatic mismatch between the botanical gardens and the species natural ranges, but by elevation in general. Regardless of their natural elevational range, plant species grew less in the alpine botanical gardens, which is in line with generally slower plant growth at higher elevations (Körner 1999). This suggests a plastic growth response of our 165 plant species to elevation, generalizing reports by Haider et al. (2012) and Trtikova et al. (2010) on the performance of thirteen non-native herbaceous plant species along an elevational gradient in Tenerife (Haider et al. 2012) and of the invasive species *Erigeron annuus* in the Swiss Alps (Trtikova et al. 2010). Thus, most plants appear able to grow taller at warmer temperatures.

Plant survival was overall very high, regardless of climatic mismatches between the natural species ranges and the botanical gardens. This high survival may be due to the benign growing conditions in botanical gardens (Primack & Miller-Rushing 2009; Hällfors et al. 2011; Herben et al. 2012), where plants are watered in the rare cases of drought, pest outbreaks are controlled and weeding mitigates competition by other species. Survival is likely to be lower in nature, especially due to biotic interactions, such as competition (Hällfors et al. 2011). Therefore, even though perennial plants can persist for a certain time under novel climatic conditions in botanical gardens, it is not certain that they can persist in nature. Furthermore, without successful reproduction they may eventually face extinction in the long-term (Gaston 2009).

The influence of species geographic and climatic range size on plant performance under novel climatic conditions

In our study, species with a large geographic range were more likely to reproduce than species with a small geographic range. This finding is in line with earlier studies reporting a lower reproductive success of rare species than of common species (Kunin & Gaston 1997; Eriksson & Jakobsson 1998; Murray et al. 2002; Lavergne et al. 2004; Lavergne et al. 2005; Rymer et al. 2005; Boieiro et al. 2010). Additionally, rare species often have lower genetic variation due to small and isolated populations and may therefore be particularly sensitive to climatic changes (Jump & Peñuelas 2005; Primack

2006; Willi et al. 2006; Leimu & Fischer 2008). In our study, however, rarer species did not suffer more from a novel climate than more common species. While 26 of our 165 study plant species are listed in the Swiss Red List of Vascular Plants and Ferns (Moser et al. 2002), only seven are endangered or critically endangered. Possibly the low number of critically rare species in our study did not allow us to detect a relationship between rarity and sensitivity to climatic change. Furthermore, as rare plant species in botanical gardens often originate from seeds with garden origin (Maunder et al. 2001), the assessed plants might have already undergone a selection process under novel climatic conditions in another botanical garden and therefore they might have been pre-adapted to conditions different to those in their natural ranges (Havens et al. 2004). Unfortunately, the origin of the plant individuals assessed in our study had not been recorded by the botanical gardens. Therefore we could not assess the likelihood of such pre-adaptation, which might possibly have masked differences in plant performance between rare and common plant species in response to climatic mismatches.

In our study, species performance in the botanical gardens did not depend on the climatic range size of the plant species, whether species were grown inside or outside their natural climatic conditions. This contradicts the prediction that plant species with a large climatic range, and thus experiencing a wide range of different climatic conditions in their natural habitat, should have high climatic tolerance (Thuiller et al. 2005). We classified the climatic mismatch between botanical garden and the species natural range based on the actual elevational ranges of the species as reported in the Flora Indicativa (Landolt 2010). This approach captures the realized, but not the fundamental climatic range of our study species. It would thus be interesting to see whether species with a wider fundamental climatic range would be more tolerant to transplantation than the ones with a narrower one. Moreover, as responses of individual plants or populations to different climate can vary (Banta et al. 2012) and the individual niche breadths may therefore be more narrow than the ones of whole species, investigating the influence of climatic mismatches on plant performance at the intraspecific level might allow us to reveal plant species especially sensitive to climate change and to forecast future trends in species distribution changes.

Conclusion

Our multi-species assessment showed that the performance of 165 perennial plant species was impaired under warmer climatic conditions. Plant survival was slightly reduced, but remained high, while reproduction was strongly impaired. This suggests that plant species are likely to persist under climate change in the short term, but not in the long term, for which successful reproduction is essential. Under novel climatic conditions neither more common species nor species with a broader climatic range were able to perform better than rarer species or species with narrower climatic range, which suggests high generality of our finding of reduced performance under warmer than normal conditions.

Acknowledgements

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Supporting material

Table S1 *List of plant species assessed in the botanical gardens. Sub-shrubs are marked with an asterisk. The vegetation zone indicates the assigned value based on the temperature indicator value T (Landolt 2010), which classifies the average air temperature during the growth period of a plant and corresponds with the average elevational range of the plant species in the Alpine region. 1 = alpine and nival zone, 2 = subalpine zone, 3 = montane zone, 4 = colline zone, 5 = very warm colline zone.*

Plant species	**Family**	**Vegetation zone**
Achillea clavenae	Asteraceae	1.5
Adonis vernalis	Ranunculaceae	5
Agrimonia eupatoria	Rosaceae	4
Alchemilla alpina	Rosaceae	1.5
Alchemilla conjuncta	Rosaceae	2
Allium carinatum	Amaryllidaceae	3.5
Allium lusitanicum	Amaryllidaceae	3
Allium schoenoprasum	Amaryllidaceae	2.5
Allium victorialis	Amaryllidaceae	2
Androsace lactea	Primulaceae	2.5
Anemone narcissiflora	Ranunculaceae	2
Anemone nemorosa	Ranunculaceae	3.5
Anemone sylvestris	Ranunculaceae	4.5
Antennaria dioica	Asteraceae	2
Anthericum liliago	Asparagaceae	4
Anthericum ramosum	Asparagaceae	3.5
*Anthyllis montana**	Fabaceae	3.5
Aquilegia vulgaris	Ranunculaceae	3
Armeria alpina	Plumbaginaceae	1
Arnica montana	Asteraceae	2
*Artemisia absinthium**	Asteraceae	4
*Artemisia campestris**	Asteraceae	3.5
Artemisia glacialis	Asteraceae	1
Artemisia umbelliformis	Asteraceae	1
Arum maculatum	Araceae	4
Asphodelus albus	Xanthorroeaceae	3
Astrantia major	Apiaceae	2.5
Athamanta cretensis	Apiaceae	2
Biscutella laevigata	Brassicaceae	2
Buphthalmum salicifolium	Asteraceae	3
Bupleurum longifolium	Apiaceae	3
Bupleurum ranunculoides	Apiaceae	2
Campanula barbata	Campanulaceae	2
Campanula cervicaria	Campanulaceae	4
Campanula cochlearifolia	Campanulaceae	2
Campanula persicifolia	Campanulaceae	4
Campanula thyrsoides	Campanulaceae	2
Carex baldensis	Cyperaceae	2.5
Carex firma	Cyperaceae	1.5

Plant species	**Family**	**Vegetation zone**
Carlina acaulis	Asteraceae	3
Cephalaria alpina	Caprifoliaceae	2.5
Chelidonium majus	Papaveraceae	3.5
Chenopodium bonus-henricus	Amaranthaceae	2.5
Cicerbita plumieri	Asteraceae	2.5
Clematis recta	Ranunculaceae	4.5
Colchicum autumnale	Colchicaceae	3
Convallaria majalis	Asparagaceae	3.5
Coronilla coronata	Fabaceae	4
*Coronilla vaginalis**	Fabaceae	2.5
Cortusa matthioli	Primulaceae	2
Crepis pyrenaica	Asteraceae	2.5
Dactylorhiza maculata	Orchidaceae	3
Delphinium elatum	Ranunculaceae	2
Dianthus carthusianorum	Caryophyllaceae	4.5
Dianthus gratianopolitanus	Caryophyllaceae	3.5
Dianthus superbus	Caryophyllaceae	3.5
Dianthus sylvestris	Caryophyllaceae	3
Digitalis grandiflora	Plantaginaceae	2.5
Doronicum pardalianches	Asteraceae	4.5
Draba aizoides	Brassicaceae	1.5
Dracocephalum ruyschiana	Lamiaceae	2
Elyna myosuroides	Cyperaceae	1.5
Epilobium angustifolium	Onagraceae	3
Epilobium fleischeri	Onagraceae	2
Erigeron uniflorus	Asteraceae	1
Erinus alpinus	Plantaginaceae	2.5
Eryngium alpinum	Apiaceae	2
Erysimum rhaeticum	Brassicaceae	3
Euphorbia cyparissias	Euphorbiaceae	3
Festuca violacea	Poaceae	1.5
Galium verum	Rubiaceae	3.5
Gentiana acaulis	Gentianaceae	1.5
Gentiana asclepiadea	Gentianaceae	3
Gentiana cruciata	Gentianaceae	3
Gentiana lutea	Gentianaceae	2.5
Gentiana pannonica	Gentianaceae	2
Geranium nodosum	Geraniaceae	4
Geranium sanguineum	Geraniaceae	3.5
Geranium sylvaticum	Geraniaceae	2.5
*Globularia cordifolia**	Plantaginaceae	2.5
Globularia nudicaulis	Plantaginaceae	2
Gypsophila repens	Caryophyllaceae	2
*Helianthemum nummularium**	Cistaceae	3
Hepatica nobilis	Ranunculaceae	4
Hieracium aurantiacum	Asteraceae	2.5
Hieracium lactucella	Asteraceae	3
Hieracium peletierianum	Asteraceae	3.5
Hieracium villosum	Asteraceae	2
Horminum pyrenaicum	Lamiaceae	2
Hugueninia tanacetifolia	Brassicaceae	2
*Hypericum coris**	Hypericaceae	3
*Iberis saxatilis**	Brassicaceae	3.5

Plant species	Family	Vegetation zone
Iris graminea	Iridaceae	4.5
Laserpitium siler	Apiaceae	3.5
Leontopodium alpinum	Asteraceae	1.5
Leucanthemum adustum	Asteraceae	2.5
Lilium martagon	Liliaceae	3
Linaria alpina	Plantaginaceae	1.5
Lotus corniculatus	Fabaceae	3
Lotus maritimus	Fabaceae	4
Luzula lutea	Juncaceae	1.5
Luzula nivea	Juncaceae	2.5
Matthiola valesiaca	Brassicaceae	3.5
Menyanthes trifoliata	Menyanthaceae	3
Meum athamanticum	Apiaceae	2.5
Origanum vulgare	Lamiaceae	3.5
Oxyria digyna	Polygonaceae	1
Paradisea liliastrum	Asparagaceae	2
Peucedanum ostruthium	Apiaceae	2
Polemonium caeruleum	Polemoniaceae	2.5
Polygonatum odoratum	Asparagaceae	3
Polygonum bistorta	Polygonaceae	2.5
Potentilla aurea	Rosaceae	1.5
Potentilla erecta	Rosaceae	3
Potentilla palustris	Rosaceae	3
Primula auricula	Primulaceae	1.5
Primula elatior	Primulaceae	3
Pseudolysimachium spicatum	Plantaginaceae	3.5
Ranunculus gramineus	Ranunculaceae	4.5
Ranunculus parnassiifolius	Ranunculaceae	1.5
Rhodiola rosea	Crassulaceae	1.5
Sanguisorba minor	Rosaceae	3.5
Sanguisorba officinalis	Rosaceae	3.5
Saponaria lutea	Caryophyllaceae	1.5
Saponaria ocymoides	Caryophyllaceae	3
Saxifraga aizoides	Saxifragaceae	2
Saxifraga cotyledon	Saxifragaceae	2.5
Saxifraga cuneifolia	Saxifragaceae	2.5
Saxifraga oppositifolia	Saxifragaceae	1
Saxifraga paniculata	Saxifragaceae	2
Saxifraga rotundifolia	Saxifragaceae	2.5
Scabiosa lucida	Caprifoliaceae	1.5
Scutellaria alpina	Lamiaceae	2
Sedum album	Crassulaceae	3
Sedum anacampseros	Crassulaceae	1.5
Sedum rupestre	Crassulaceae	4.5
Sempervivum montanum	Crassulaceae	1.5
Sempervivum tectorum	Crassulaceae	4
Sempervivum wulfenii	Crassulaceae	1.5
*Senecio abrotanifolius**	Asteraceae	2
Senecio alpinus	Asteraceae	2.5
Sibbaldia procumbens	Rosaceae	1
*Sideritis hyssopifolia**	Lamiaceae	2.5
Silene coronaria	Caryophyllaceae	4.5
Silene dioica	Caryophyllaceae	3

Plant species	**Family**	**Vegetation zone**
Silene flos-jovis	Caryophyllaceae	2.5
Silene saxifraga	Caryophyllaceae	2.5
Silene vallesia	Caryophyllaceae	3
Solidago virgaurea	Asteraceae	3.5
Stachys alopecuros	Lamiaceae	2.5
Stachys officinalis	Lamiaceae	3.5
Succisa pratensis	Caprifoliaceae	3
Tanacetum vulgare	Asteraceae	4.5
*Teucrium chamaedrys**	Lamiaceae	4.5
Thalictrum aquilegifolium	Ranunculaceae	2.5
Thalictrum minus	Ranunculaceae	3.5
Thlaspi montanum	Brassicaceae	3.5
*Thymus serpyllum**	Lamiaceae	3.5
Tofieldia calyculata	Tofieldiaceae	2.5
Trollius europaeus	Ranunculaceae	2.5
Valeriana montana	Caprifoliaceae	2
Valeriana supina	Caprifoliaceae	1
*Veronica fruticans**	Plantaginaceae	1.5
*Veronica fruticulosa**	Plantaginaceae	2
Vincetoxicum hirundinaria	Apocynaceae	3.5

Chapter 3

Phenological shifts and flower visitation of 185 lowland and alpine species growing in a lowland botanical garden

Christine Föhr, Mialy Razanajatovo, Mark van Kleunen, Markus Fischer

Abstract

Many plant species respond to global warming by phenological shifts, usually with an earlier flowering onset. However, the variability in flowering responses to changed climatic conditions is large. Furthermore, it is likely that rare plant species, due to low genetic variation, may be less able to shift their phenology than common ones. If plant species respond to global warming by shifting their flowering phenology, plant-pollinator interactions may become disrupted. However, it is vital for reproduction, and thus for long-term population survival, that plant species can attract sufficient pollinators. This might be especially difficult for rare species that may depend on few or single pollinator species. To assess how climatic conditions affect the phenology of common and rare plant species, and whether the plant species successfully attract pollinators, we assessed flowering onset and counted flower visitors of 185 native plant species originating from different altitudinal zones in the lowland Botanical Garden of Bern, Switzerland. At monthly census dates from March to August 2011, we recorded the insect-pollinated plant species that had started to flower, and we observed flower visitors. Plants from high altitudes flowered earlier in the lowland garden and showed more pronounced phenological shifts than plants from lower altitudes, independent of whether they were rare or common. The number and duration of flower visits and the number of flower visitor groups were independent of the altitudinal zone of plant origin and of species rarity or commonness. Thus, our study suggests that rare and common alpine plants will generally respond to climate change by an earlier onset of flowering, and may be able to establish novel interactions with pollinators.

Introduction

Current climate affects ecosystems and species worldwide (IPCC 2007). Many plant species respond to global warming by distributional and phenological shifts (Parmesan & Yohe 2003, Parmesan 2006, Sedlacek et al. 2015), the latter most visibly by an earlier flowering onset (Fitter & Fitter 2002, Menzel et al. 2006, Gordo & Sanz 2010, Ibáñez et al. 2010). The timing of flowering is important for plants because flowering at the wrong time can negatively affect seed production and thus plant fitness (Burgess et al. 2007, Scheepens & Stöcklin 2013) due to possible temporal mismatches in plant-pollinator interactions (Memmott et al. 2007, Hegland 2009, Kudo & Ida 2013, Petanidou et al. 2014). Therefore, adjusting flowering phenology to changing climatic conditions can be essential for the persistence of plant populations (Anderson et al. 2012).

Although the flowering period of many plant species shifts towards earlier flowering at higher temperatures, several studies reported large variability in species responses (Fitter & Fitter 2002, Primack et al. 2009, Diez et al. 2012, Cornelius et al. 2013, CaraDonna 2014). While some species change their phenology radically, other species are not changing at all. Other studies have identified life history traits (e. g. lifespan), abiotic drivers (e. g. frost, drought) and biotic drivers (e.g. pollinators, competition) as factors influencing phenological responses of plant species to changing climate (Pau et al. 2011, Wolkovich et al. 2014, Forrest & Miller-Rushing 2010). Mechanisms that allow species to shift their flowering phenology are phenotypic plasticity and evolutionary change (Parmesan 2006, Forrest & Miller-Rushing 2010, Anderson et al. 2012, Matesanz & Valladares 2014, Wolkovich et al. 2014). Reduced genetic variation can both limit the evolutionary potential to respond to global change (Willi et al. 2006, Leimu & Fischer 2008, Jump et al. 2009) and the expression of plasticity in plant populations (Kéry et al. 2000, Fischer et al. 2000, Pluess & Stöcklin 2004). Therefore, rare plant species, which often occur in small and isolated populations with reduced genetic variation (Karron 1997, Willi et al. 2006, Leimu et al. 2006), might be less able to shift their phenology under changing climatic conditions than common species are. If rare species fail to adjust phenologically to warmer climate, either by plastic response or by evolutionary change, their persistence might be severely threatened in the long term. However, we are not aware of any study that has explicitly tested whether the ability of rare species to shift their flowering phenology is lower than that of common species.

Most flowering plant species rely on insect pollination (Ollerton et al. 2011). If plant species and their pollinators do not manage to track their ideal climatic conditions either by shifting their distribution or their phenology in exactly the same way, vital mutualistic species interactions might become disrupted, and plant reproduction might be impeded (Memmott et al. 2007, Hegland 2009, Kudo & Ida 2013, Petanidou et al. 2014). While such phenological mismatches have been found (Memmott et al. 2007, Burkle et al. 2013, Kudo & Ida 2013), it is also possible that novel plant-pollinator interactions develop (Petanidou et al. 2008, Burkle et al. 2013). Studies investigating the ability of species to integrate into novel plant-pollinator networks are still rare and most often concern non-native plant species (Memmott & Waser 2002, Vilà et al. 2009, Razanajatovo et al. 2015). Furthermore, studies investigating whether rare species can establish novel plant-pollinator interactions are lacking. Plant species should evolve pollinator specialization when they are rare, to increase the probability that removed pollen is deposited on the stigma of a conspecific plant (Orians 1997, Sargent & Otto 2006). Therefore rare species might be even less able to form new plant-pollinator interactions than common species. This may render rare plant species particularly vulnerable to pollinator limitation if they are affected by phenological mismatches.

Botanical gardens are ideal study sites for investigating the influence of changing climatic conditions on plant species phenological responses and their interactions with pollinators (Primack & Miller-Rushing 2009). They harbor large and diverse plant collections, including many rare species, under similar climatic conditions. Additionally, many species in botanical gardens are growing outside their natural climatic range, e.g. alpine species growing in botanical gardens in the lowland, where the plants experience warmer conditions than in their natural habitats.

We assessed how changes in climatic conditions affect the flowering phenology of common and rare plant species from different altitudinal zones in Switzerland, and whether these species are able to attract sufficient pollinators at lower altitude. To this end, we analysed measures of flowering onset, which we had recorded for 185 native plant species in the Botanical Garden of Bern in 2011, with flower visitation of the same individuals in the same year. While we had used the counts of flower visitor earlier to compare the 185 native with 261 exotic species (Razanajatovo et al. 2015), we combine them here with the unpublished flowering onset data to compare native species originating from different altitudinal zones and rare and common native species. We addressed the following questions: (1) Do alpine and montane plants start to flower earlier compared to colline (lowland) plants under warmer climatic conditions below their natural altitudinal distribution? (2) Are shifts in flowering phenology more pronounced for common than for rare plant species? (3) Can species growing outside their natural altitudinal range successfully attract flower visitors and thereby integrate into novel pollination networks? And if yes, does this ability differ between rare and common plant species?

Methods

Study site and data collection

In summer 2011, we assessed the onset of flowering and observed flower visitors on 185 native plant species originating from different altitudinal zones in the Botanical Garden of Bern, Switzerland (46.95° N, 7.44° E; Table S1). The Botanical Garden is situated at an altitude of 501-537 m, which is part of the colline altitudinal zone. It has an average annual rainfall of 1028 mm/year and a mean annual temperature of 8.1°C. Outdoors, it harbors about 4,500 alien and native plant species in a total area of 2.5 ha.

On six monthly dates during the growing season, 24 March, 19 April, 24 May, 27 June, 29 July and 29 August 2011, we recorded all insect-pollinated plant species that had started flowering. For each species, we measured characteristics likely to determine how conspicuous and attractive they are for flower visitors. As an estimate for species abundance and density in the garden, we estimated the total area which each of these plant species covered in the botanical garden (i.e. abundance) and the number of flower units per m^2 (i.e. flower unit density). A flower unit was defined as a unit of one or more flowers from which an insect has to fly in order to reach the next unit (Dicks et al. 2002), e.g. one capitulum with multiple flowers of an Asteraceae species was considered to be one flower unit. Furthermore, we recorded the exposure of the plants to direct sunlight at the moment of observation (yes/no).

A few days after each of these dates, we recorded flower visitors on the newly flowering plant species. During each census we observed 20 to 45 plant species. Because flower visitor activity depends strongly on the weather and the time of day, we carried out each census on a sunny day and within the time frame of approximately two hours in the early afternoon (c. 1 a.m. to 3 p.m.). For each flowering species, we observed 10 flower units, if available, simultaneously for 15 minutes. If there were fewer than 10 flower units available, we noted the number of observed flower units. We counted all flower visitors that made contact with reproductive organs of the observed flower units, and thus were likely to be pollinators. We assigned the flower visitors to broad taxonomic groups (ants, bee flies, bees, beetles, bumblebees, butterflies, flies, hover flies, moths and wasps), and recorded the number of observed visits and the duration of visits using a watch. We recorded the duration of visits because long visitation periods may increase the likelihood of successful pollination (Ollerton et al. 2007).

Climatic, flowering and distributional variables

We compared our data on the onset of flowering in the garden with literature data on the flowering period in nature (Landolt 2010) to calculate a potential phenological shift in units of months. We considered the whole flowering period in nature to take the natural variation in flowering onset into account.

As an indicator value for the climate of the natural occurrence of each species, we used the Landolt T indicator value (Landolt 2010), which characterizes the average air temperature during the growth period of each species of the Swiss flora. It largely corresponds with the altitudinal vegetation zone where a species occurs (Landolt 2003). The T indicator values of the observed plant species in the Botanical Garden of Bern ranged from 1 (alpine and nival zone) to 5 (very warm colline zone). In addition, we obtained the range of the T indicator value (small or large variation) for each species as a proxy for climatic tolerance (also from Landolt 2010).

As a proxy for the rarity or commonness of the plant species, we grouped the plant species into two groups according to their status in the Red List of

Ferns and Vascular Plants for Switzerland (Moser et al. 2002): threatened (red list status vulnerable, endangered or critically endangered) and not threatened (red list status least concern and near threatened). We considered the threatened species as rare because according to the IUCN criteria of the Red Lists they fulfill one or more of the following criteria: severe population decline, restricted distribution, small population sizes, increased risk of extinction (IUCN 2001). Accordingly we classified 44 of the 185 species (24%) as rare.

Data analysis

Flowering phenology

To assess how the natural altitudinal range, temperature tolerance and rarity of a species influences the month of flowering onset in the Botanical Garden of Bern, we first fitted a linear mixed model (using the lme function of the nlme package (Pinheiro et al. 2015) in the R software, version 3.1.2 (R Core Team 2014)). We included the T indicator value (1-5), the range of the T indicator value (small or large variation) and red list status (threatened or not threatened) as a fixed terms. We also included the interaction of T indicator value with red list status to assess whether the flowering phenology of rare and common plant species is differently affected by novelty of the climatic conditions. To account for taxonomy, we included family as a random factor.

To analyze whether the natural altitudinal range, temperature tolerance and rarity of species influence the shift in flowering phenology of the plants in the Botanical Garden, we fitted an ordered logistic regression with a 3-level response of the calculated difference between the month of recorded flowering onset in the garden and the flowering period as indicated in the literature. The three levels of the response were: flowering two or more months earlier, flowering one month earlier, no change. The explanatory variables were the same as in the analysis of flowering onset. For this analysis, we used the polr function of the MASS package (Venables & Ripley 2002) in the R software, version 3.1.2 (R Core Team 2014).

Flower visitation

Of the total sample size of 185 plant species, 141 species were visited by insects. The number of flower visitors depended strongly on the month of observation with few observed flower visitors in March and April and a peak of flower visitors in June and July. To avoid a temporal bias, we calculated the percentage of flower visitors of the total number of observed flower visitors per census for each plant species (= flower visit percentage).

To assess whether plant species growing outside their natural climatic range are able to successfully attract flower visitors, we fitted linear mixed effect models using the lmer and glmer functions of the lme4 package (Bates et al. 2014) in the R software, version 3.1.2 (R Core Team 2014). The explanatory variables were the same as in the analyses of flowering onset and phenological shift. Our response variables were the number of insect visits, the duration of visits and the number of flower visitor groups during the 15-minute observation period. For the analyses of the duration of flower visits and the number of flower visitor groups, we only included the plant species with recorded flower visits, i.e. we excluded zeros. We log-transformed the number and duration of insect visits to ensure a Gaussian data distribution. For the number of flower visitor groups, we used a binomial distribution.

To account for some species having fewer than ten observed flower units, we fitted the number of observed flower units as a fixed term before red list status and T indicator value. We also included log(total area covered by the species), log(number of flower units per m^2) and exposure to direct sun as fixed terms, as these factors might influence the attractiveness to flower visitors. To reduce collinearity and to facilitate comparisons among estimates, we centered and scaled the covariates to a mean of zero and a standard deviation of one (Schielzeth 2010). We accounted for the six census dates by including date as a random term in all models. Additionally, we included plant family as a random factor to account for taxonomy. We tested the significances of the fixed terms using log-likelihood ratio tests (Zuur et al. 2009).

To test whether the different flower visitor groups prefer plant species from a specific altitudinal vegetation zone, we performed Pearson's chi-squared tests. For the calculation, we grouped plant species with T values from 1 to 2.5 (alpine to lower subalpine distribution), 3 to 3.5 (montane and lower montane distribution), and 4 to 5 (colline to very warm colline distribution) together to obtain three categories with sufficient numbers of species. Similarly, we tested whether the different flower visitor groups prefer common over rare plant species with Pearson's chi-squared tests with two categories (rare/common). As the flower visitor groups can either visit many plant species from the different categories (flower visit diversity) or visit individual plant species many times (flower visit intensity), we tested both scenarios. As moths and butterflies were observed only two and five times respectively, we excluded these flower visitor groups form the analyses. As some frequencies were low, we ran Monte Carlo simulations with 999 replications to calculate the p-values.

Results

Flowering phenology

Month of flowering onset did not differ significantly between rare and common species (Table 1), but was positively correlated with the T indicator value. This indicates that plants naturally growing at higher altitudes flower earlier in the year when grown at lower altitude than plants from lower altitudes do (Table 1, Figure 1A).

Table 1 *Results of a linear mixed effects model testing how altitudinal plant origin (assessed as T indicator value and its range of variation) and red list status influence flowering onset of 185 plant species in a botanical garden. Shown are degrees of freedom in the numerator (df1) and denominator (df2), F-values and levels of significance (*: P < 0.05, **: P < 0.01, ***: P < 0.001).*

Response Variable	**Month of flowering onset**			
Fixed factor	**df1**	**df2**	***F***	
Red list status	1	142	3.78	
Species climatic range (variation of T)	1	142	0.35	
T indicator value	1	142	16.86	***
Red list status x T indicator value	1	142	0.05	
Random factor		Std Dev	Std Dev Resid	
Family		0.910	1.264	

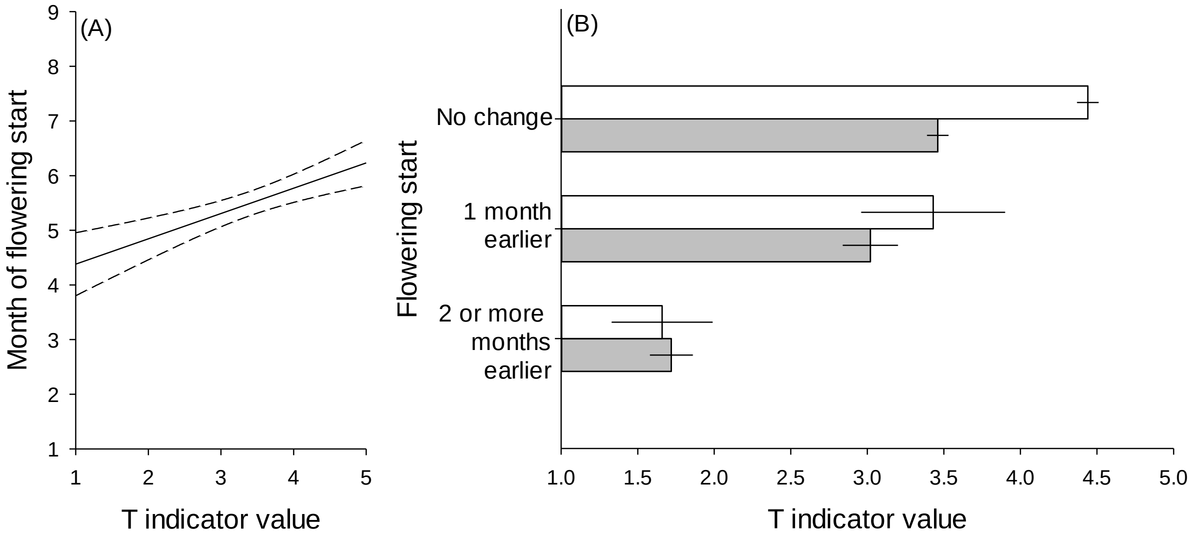


Figure 1 *Effect of T indicator value on flowering phenology (A) and phenological shifts (B) of plants in a botanical garden. Shown are the regression line with 95%-confidence intervals in graph A and means and standard errors of rare species (empty bars) and common species (filled bars) in graph B.*

The phenological shift in flowering start of a species was also strongly related to the T indicator value (Table 2). Plants that flowered two or more months earlier in the lowland garden than in their natural habitat were the ones with low T indicator values which would indicate alpine species (Figure 1B). Plant species that flowered one month earlier than in their natural habitat had an overall mean (±SE) T indicator value of 3.1±0.2, which largely corresponds to a montane distribution. The plants that underwent no phenological shift had the highest mean T indicator value (3.7±0.1). This value is close to the T indicator value of a colline distribution (4) which corresponds to the altitude of the Botanical Garden of Bern.

Table 2 *Results of an ordinal logistic regression testing how altitudinal plant origin (assessed as T indicator value and its range of variation) and red list status influence phenological shifts of 185 plant species in a botanical garden. Shown are estimates, SE, t-values and levels of significance (*: P < 0.05, **: P < 0.01, ***: P < 0.001).*

Response Variable	**Phenology shift**			
Fixed factor	**Estimate**	**SE**	***t***	
Red list status	-0.851	1.604	-0.531	
Species climatic range (variation of T)	0.870	0.442	1.968	*
T indicator value	1.540	0.263	5.857	***
Red list status x T indicator value	0.059	0.456	0.130	

Species climatic range (variation of T) also had a significant effect on whether the species had undergone a phenological shift in flowering start (Table 2). Of the 19 plant species that underwent a large phenological shift of two or more months, 18 plant species had a small climatic range (= 94.7%). Of the plant species that underwent a small (n=30) or no (n=136) shift the species with a small climatic range represented 66.7% and 61.8%, respectively. As the mean T indicator value of both the plant species with a large climatic range and the plant species with a small climatic range was the same (3.4), this result suggests that plant species with a small climatic range more readily shift their flowering onset if climatic conditions change.

Flower visitation

We observed a total of 1751 flower visits during the six census dates. Independent of the red list status of the plant species, the number of flower visits (mean = 9.5), the duration of the individual visits (mean = 18.5 s) and the number of flower-visitor groups (mean = 1.5) were not affected by the altitudinal zone of plant origin (T indicator value; Table 3, Figure 2). Thus, plants growing outside their natural altitudinal distribution seem to be generally able to successfully attract flower visitors.

Figure 2 *Effect of T indicator value on the flower visit percentage, i.e. the mean percentage of flower visits received at six monthly census dates in 2011. Shown are means and standard errors for rare species (empty bars) and common species (filled bars).*

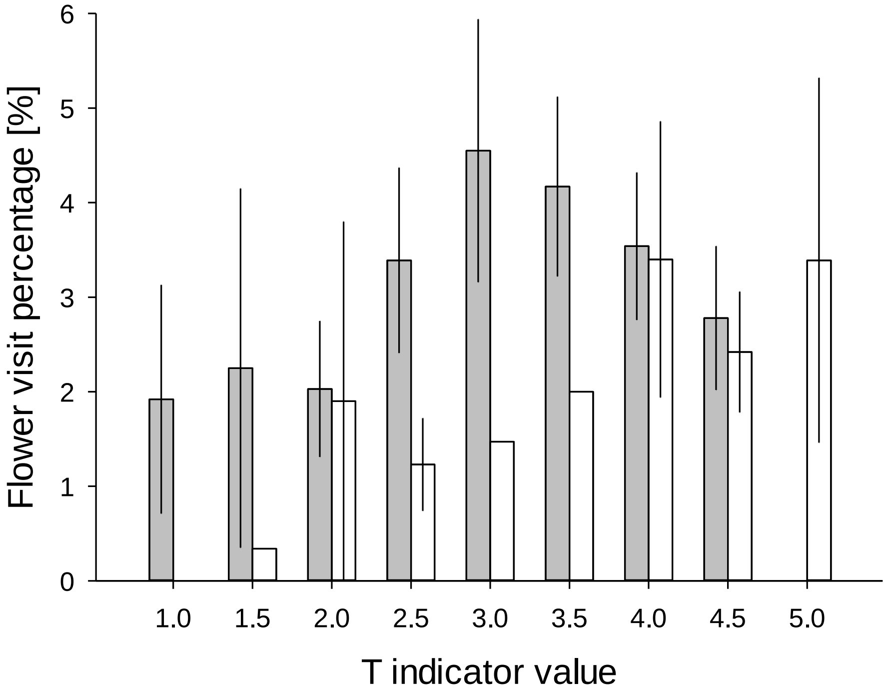
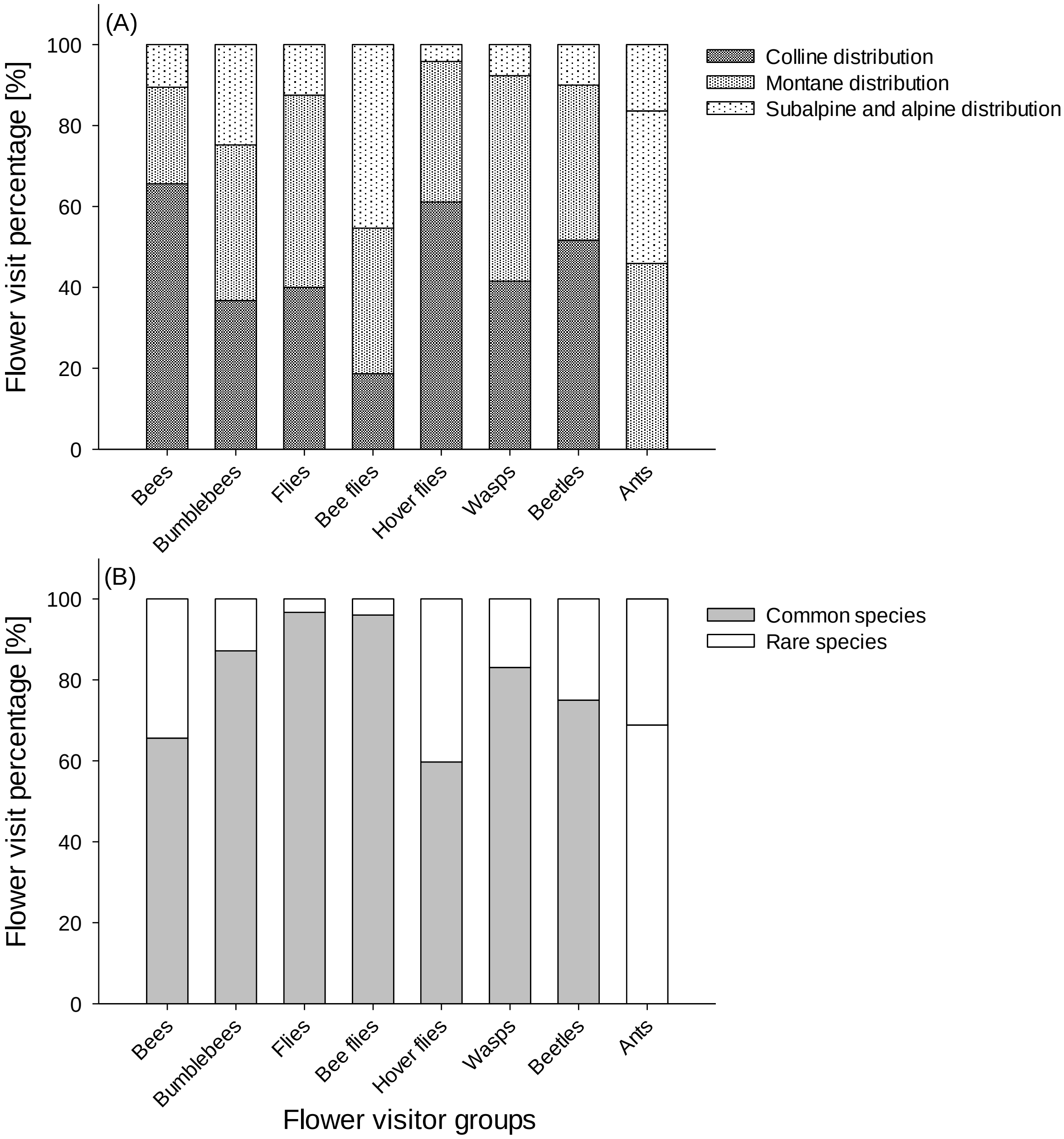


Table 3 *Results of a linear mixed effects model testing how altitudinal plant origin (assessed as T indicator value and its range of variation) and red list status influence the flower visit percentage (= percentage of total amount of flower visitors counted during census), the duration of individual flower visits and the number of flower visitor groups in a botanical garden. Shown are degrees of freedom, χ^2-values and levels of significance (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).*

Response Variable	**Flower visit percentage**			**Duration of visits**			**Number of flower-visitor groups**		
Fixed factor	**df**	**χ2**		**df**	**χ2**		**df**	**χ2**	
Number of observed flower units	1	4.951	*	1	2.666		1	1.466	
Area covered by the species	1	0.583		1	0.233		1	0.214	
Number of flower units per m^2	1	0.002		1	0.605		1	0.516	
Exposure to sun	1	61.560	***	1	20.998	***	1	22.835	***
Red list status	1	0.990		1	0.003		1	0.656	
Species climatic range (variation of T)	1	3.563		1	0.007		1	0.714	
T indicator value	1	0.445		1	0.847		1	0.945	
Red list status x T indicator value	1	0.001		1	0.015		1	0.176	
Random factor									
Family	1	2.801		1	6.217	*	1	<0.0001	
Date of observation	1	<0.0001		1	1.342		1	<0.0001	

Bees were the most abundant flower visitors in the botanical garden. They accounted for 54.1% of all flower visits and visited 61.0% of all observed plant species (Figure S1). We neither found differences in flower-visitor diversity between plant species from different altitudinal zones ($\chi^2 = 12.0$, $p = 0.610$) nor between rare and common plant species ($\chi^2 = 6.0$, $p = 0.529$). Thus, flower visitor groups did not differ in their preference for plant species of a certain category. However, we found differences in flower visit intensity for the plant species from different altitudinal vegetation zones ($\chi^2 = 201.9$, $p = 0.001$) and between rare and common plant species ($\chi^2 = 128.2$, $p = 0.001$). This means that the flower visitor groups did prefer individual plant species from particular species categories (Figure 3).

Figure 3 *Mean percentage of flower visits of plant species of colline, montane and subalpine/alpine distribution (A) and of rare and common plant species (B) per flower visitor group.*



Discussion

Flowering phenology

In line with results of earlier studies investigating phenological responses of mountain plants to warmer temperatures (Hülber et al. 2010, Scheepens & Stöcklin 2013, Sedlacek et al. 2015), we found pronounced shifts of two or more months in flowering phenology of alpine plants growing below their natural altitudinal distribution in the lowland Botanical Garden of Bern. One alpine plant species, *Draba fladnizensis,* started flowering in March and therefore four months earlier than in its natural habitat (Table S1). For alpine plants, adjusting phenology to ambient climatic conditions is essential to successfully complete their life cycle as the growing season at high altitudes is usually short and highly variable (Hülber et al. 2010, Pau et al. 2011, Wolkovich et al. 2013). Therefore, it is to be expected that many alpine plants start flowering as early as possible in the season, and also readily shift their flowering start if the climatic conditions change. Earlier flowering can either lead to a prolonged flowering period or to a shift of the entire flowering period (Dunne et al. 2003, Gímenez-Benavides et al. 2011, CaraDonna et al. 2014). A prolonged flowering period can lead to a higher flower number, resulting in more fruits and therefore ultimately improve plant fitness (Gímenez-Benavides et al. 2011). A shift of the entire flowering period can, on the other hand, affect pollination success directly by disruption of plant-pollinator interactions or allowing the maintenance of such interactions (Memmott et al. 2007, Hegland 2009, Kudo & Ida 2013, Petanidou et al. 2014) or indirectly by altered co-flowering patterns in the community influencing competition or facilitation of pollination (Ghazoul 2006, Mitchell et al. 2009). Regardless of whether the plants will benefit from earlier flowering or suffer fitness losses, phenological changes will likely lead to changes in species interactions and species compositions in ecological communities (Hülber et al. 2010, CaraDonna et al. 2014).

Among our 185 plant species, rare and common ones did not significantly differ in their flowering onset and phenological shift. This suggests that rare species are not less plastic or adaptive than common species are in this respect. Rare species often occur in small and isolated populations, and plants in small populations have been shown to have a lower potential of responding appropriately to climatic changes (Fischer et al. 2000, Paschke et al. 2003). However, plant populations in botanical gardens are all generally fairly small, independent of rarity status (Ensslin et al. 2011, Lauterbach et al. 2012). Thus, if bottleneck effects reduced the potential to respond to climatic change, they might have acted similarly for both rare and common species. Furthermore, the high temporal and spatial environmentally heterogeneity in alpine habitats might select for high plasticity in plants (Baythavong & Stanton 2010, Lázaro-Nogal et al. 2015) or promote genotypes with different response patterns to coexist eventually allowing evolutionary change (Gram & Sork 2001). Thus, heterogeneity of the habitat of origin and within-population genetic variability might be more important factors influencing plastic and adaptive responses of plants to climatic change than rarity or population size (Berg et al. 2005).

By using monthly censuses of flowering onset in the botanical garden to assess phenological shifts, we could not detected shorter shifts of only one or two weeks, and therefore we may have underestimated the phenological response of some plant species (Miller-Rushing et al. 2008). However, our assessment is likely to represent the mean advancement of phenology of a population instead of that of a small subset of less representative early-flowering individuals. Such first flowering dates can strongly depend on population size, because it is more likely to observe an early flowering plant in large populations (Miller-Rushing et al. 2008). For successful reproduction and persistence in the long term, the mean advancement of phenology might be more important than changes in flowering time at the extreme of the distribution of flowering dates (Hegland et al. 2009). Nevertheless, a direct comparison with flowering time of the plants in their natural habitat would have allowed us to measure phenological shifts at a finer temporal resolution. However, such a comparison would not have been feasible in nature for the large number of assessed species. Due to this large number of species, we also consider our results on phenological shifts as very robust, despite the coarse temporal steps of one month.

The results of our study suggest that alpine plants will generally respond to climate change by flowering earlier. Whether such phenological shift will lead to fitness costs (Burgess et al. 2007, Scheepens & Stöcklin 2013) or rather to enhanced plant performance (Cleland et al. 2012, Springate & Kover 2014), increased risk of frost damage (Inouye 2008), temporal mismatches in plant-pollinator interactions (Memmott et al. 2007, Hegland 2009, Kudo & Ida 2013, Petanidou et al. 2014) or changes in plant communities (CaraDonna et al. 2014) remains to be further investigated.

Flower visitation

In our study, the number of flower visitors, flower-visit duration and the number of flower visitor groups did not depend on the natural altitudinal zone of origin of the assessed plants. Thus, the plant species of alpine and montane origin were able to attract a similar amount of flower visitors as the plant species from colline origin in the Botanical Garden of Bern. This finding is in line with several studies that found a remarkable plasticity of plant-pollinator interactions over time, resulting in novel interactions and switching of interaction partners (“rewiring”; Alarcón et al. 2008, Petanidou et al. 2008, Dupont et al. 2009, Burkle et al. 2013). Thus, plant-pollinator interactions seem to be more flexible than previously thought, and disrupted plant-pollinator interactions due to shifts in phenology or distribution might be replaced by new interactions (Memmott et al. 2007, Alarcón et al. 2008, Petanidou et al. 2008). However, as the botanical-garden pollinator community may not be representative for all lowland pollinator communities, this should be tested at more locations.

The flexibility of plant-pollinator interactions can have different underlying reasons. Petanidou et al. (2008) found that many plant and pollinator species, which interact with only one species in one year, can be generalists in other years. Thus, as studies investigating pollination networks are mostly based on short sampling periods, specialization in plant-pollinator interactions might be highly overestimated (Waser et al. 1996, Petanidou et al. 2008). Additionally, pollinators might adjust their foraging behavior continually to the availability of resources (Fontaine et al. 2008, Kaiser-Bunbury et al. 2010, Burkle & Alarcón 2011), as predicted by the optimal foraging theory (Emlen 1966, MacArthur & Pianka 1966). Thus, when a preferred floral resource is rare or absent, pollinators switch to a more abundant plant species. In the Botanical Garden of Bern, this flexibility in foraging behavior might be especially important for the present pollinators as plant species diversity is very high but, with the exception of a small number of abundant species, the majority of the plant populations are equally small (C. Föhr, personal observation). Additionally, the plant species from higher altitudes that start flowering early in the season in the lowland garden appear to provide a welcome food source for pollinators when other floral resources are still scarce. Thus, the large variety of continuously available food sources in the Botanical Garden of Bern might have enhanced the flexibility of the foraging behavior of the present pollinators.

In our study, we did not detect any difference between rare and common plant species in their ability to attract pollinators. Furthermore, we also found no difference in the number of observed flower visitor groups between the rare and the common plant species. Considering that rare plant species mostly appeared to be specialists in plant-pollinator networks studied so far (Vázquez & Aizen 2003, Sargent & Otto 2006), this is an interesting result. However, as we did not determine the flower visiting insects to the species level, we may not have been able to detect truly specialized interactions between plants and pollinators. Still, our study does not support the idea that rare plant species are more at risk of disrupted plant-pollinator interactions than common species are.

By assessing flower visitation more than once per plant species and for a longer time, we might have been able to detect variation in the number of flower visits during the day and during the whole flowering period of the plants. However, by limiting the observation time, we were able to integrate a large number of different plant species, which increases generalizability of the results and is essential for reasons of statistical power (van Kleunen et al. 2014). As a next step, it might be interesting to test whether flower visits actually lead to pollination and fertilization of the plants, and thus whether the plants can fully integrate into a novel pollination network by successfully reproducing.

In general, the consequences of disrupted plant-pollinator interactions by phenological or distributional shifts may be mitigated by the flexibility of pollination networks (Memmott et al. 2007, Alarcón et al. 2008, Petanidou et al. 2008). However, the possibility for new plant-pollinator interactions to emerge relies on a sufficiently high species diversity (Kaiser-Bunbury et al. 2010). A sufficiently large species-pool offers more options for new interaction combinations than a community with only few species. Thus, even though pollination networks seem to be partly resilient to the loss of existing plant-pollinator interactions, there is no guarantee that the disruption of interactions cannot lead to the extinction of species and the impairment of pollination services eventually, especially in the case of ongoing biodiversity loss (Memmott et al. 2007).

Conclusion

Our results showed that alpine plant species generally flowered earlier when growing in a botanical garden below their natural altitudinal distribution regardless of whether they were common or rare. This suggests that alpine plant species generally tend to adjust their phenology to changing climate. Furthermore, the alpine plant species we assessed in our study seemed to be able to attract flower visitors in the lowland. Thus, plant-pollinator interactions seem to be flexible, and novel interactions may mitigate the consequences of disrupted plant-pollinator interactions caused by phenological or distributional shifts.

Acknowledgements

We thank all volunteers who helped with the data collection; the Botanical Garden of Bern for allowing the flower visitor observations; Corina del Fabbro and Daniel Prati for statistical advice; Andreas Ensslin and Steffen Boch for helpful comments on the manuscript.

Supporting material

Figure S1 *Number of flower visits (A) and visited plant species (B) per flower visitor group.*

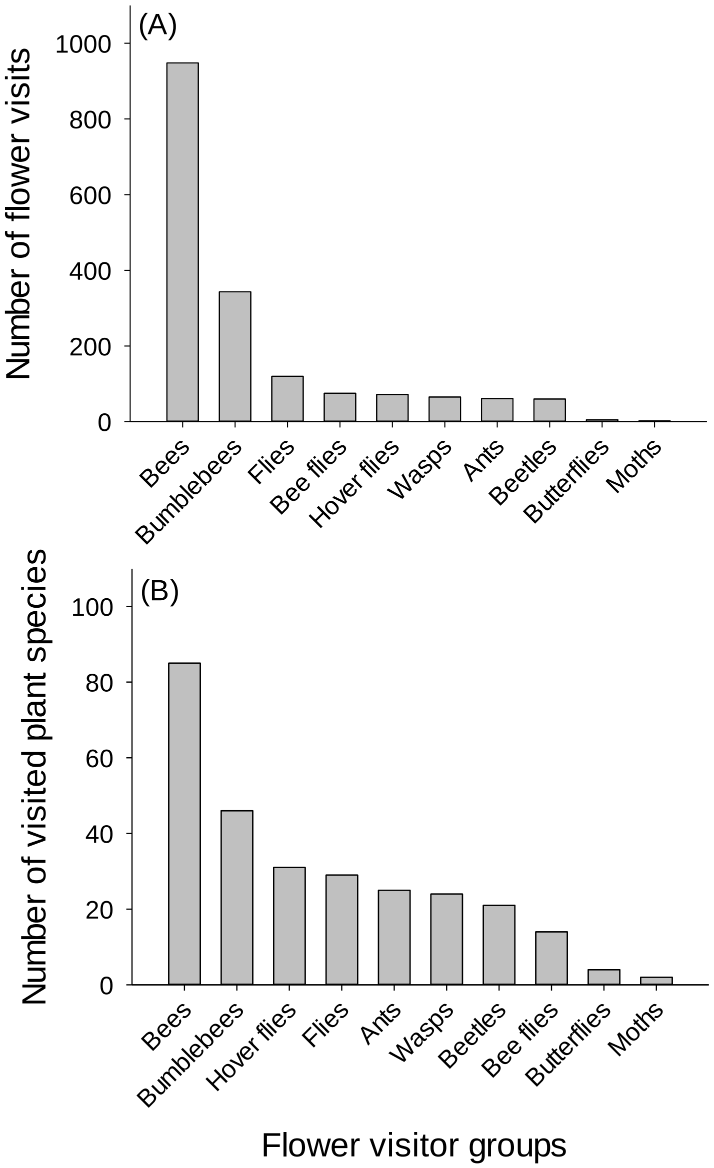


Table S1 *List of plant species assessed in the Botanical Garden of Bern. The T indicator value (Landolt 2010) classifies the average air temperature during the growth period of a plant and corresponds with the average altitudinal zone of occurrence of the plant species in the Alpine region. 1 = alpine and nival zone, 2 = subalpine zone, 3 = montane zone, 4 = colline zone, 5 = very warm colline zone.*

Plant species	**Family**	**T indicator value**	**T variation**	**Red list status**	**Flowering period in nature [months]**	**Flowering onset in botanical garden [month]**	**Number of flower visitors**	**Mean flower visitation duration [s]**	**Number of flower visitor groups**
Achillea millefolium	Asteraceae	3	large	LC	6 - 9	7	16	32	2
Achillea nobilis	Asteraceae	4.5	small	LC	6 - 8	6	34	3	2
Aconitum vulparia	Ranunculaceae	3	large	LC	6 – 8	5	5	2	1
Ajuga reptans	Lamiaceae	3.5	large	LC	4 - 7	4	17	2	3
Allium schoenoprasum	Amaryllidaceae	2.5	large	LC	5 - 8	5	10	12	2
Alyssum alpestre	Brassicaceae	2	small	EN	7 - 8	4	0	0	0
Androsace vitaliana	Primulaceae	1.5	small	NT	6 - 7	3	0	0	0
Anemone nemorosa	Ranunculaceae	3.5	large	LC	3 - 5	3	3	3	2
Anemone sylvestris	Ranunculaceae	4.5	small	CR	4 - 5	4	1	3	1
Anthemis arvensis	Asteraceae	4	large	VU	5 - 10	6	20	5	2
Anthericum ramosum	Liliaceae	3.5	large	LC	6 - 8	7	11	15	3
Aposeris foetida	Asteraceae	2.5	small	LC	6 - 7	4	0	0	0
Arabis alpina	Brassicaceae	2	large	LC	3 - 10	4	0	0	0
Arabis subcoriacea	Brassicaceae	2	small	LC	6 - 7	4	0	0	0
Aristolochia clematitis	Aristolochiaceae	4.5	small	VU	5 - 8	5	0	0	0
Artemisia umbelliformis	Asteraceae	1	small	LC	7 - 8	5	1	6	1
Aster amellus	Asteraceae	3.5	small	LC	8 - 9	7	3	2	1
Aster linosyris	Asteraceae	4.5	small	NT	8 - 9	8	24	12	3
Baldellia ranunculoides	Alismataceae	4.5	small	CR	6 - 7	8	0	0	0
Buphthalmum salicifolium	Asteraceae	3	small	LC	6 - 9	5	20	8	4

Table S1 *continued*

Plant species	Family	T indicator value	T variation	Red list status	Flowering period in nature [months]	Flowering onset in botanical garden [month]	Number of flower visitors	Mean flower visitation duration [s]	Number of flower visitor groups
Bupleurum falcatum	Apiaceae	4	small	LC	7 – 9	6	10	136	3
Caltha palustris	Ranunculaceae	3	large	LC	3 - 5	3	1	1	1
Cardamine pentaphyllos	Brassicaceae	3	small	LC	4 - 5	3	31	1	5
Carduus defloratus	Asteraceae	2.5	large	LC	6 - 8	5	2	22	1
Centaurea calcitrapa	Asteraceae	4.5	small	DD	7 - 10	8	1	2	1
Centaurea nigriscens	Asteraceae	3	small	LC	6 - 9	8	45	11	3
Centranthus angustifolius	Caprifoliaceae	4.5	large	NT	6 - 8	5	0	0	0
Cerastium arvense ssp. strictum	Caryophyllaceae	2	large	LC	4 - 7	4	2	4	1
Chelidonium majus	Papaveraceae	3.5	large	LC	4 - 9	4	2	10	1
Cichorium intybus	Asteraceae	4	small	LC	7 - 9	8	2	13	2
Cirsium acaule	Asteraceae	2.5	large	LC	7 - 9	7	19	14	1
Cirsium eriophorum	Asteraceae	2.5	large	LC	7 - 9	7	41	38	5
Conium maculatum	Apiaceae	4.5	small	VU	6 - 9	7	0	0	0
Consolida regalis	Ranunculaceae	4	small	VU	6 - 9	8	1	2	1
Cornus mas	Cornaceae	4.5	small	LC	3	3	0	0	0
Coronilla minima	Fabaceae	5	small	VU	6 - 7	6	10	3	2
Corydalis cava	Papaveraceae	3.5	small	LC	3 - 4	3	6	4	3
Corydalis lutea	Papaveraceae	4	large	LC	3 - 9	4	2	13	1
Corydalis solida	Papaveraceae	3.5	small	LC	3 - 5	3	14	16	2
Cyclamen purpurascens	Primulaceae	4	large	LC	6 - 10	7	0	0	0
Daphne laureola	Thymelaeaceae	3.5	small	LC	3 - 4	3	0	0	0
Daphne mezereum	Thymelaeaceae	3	large	LC	2 - 6	3	3	1	2
Dianthus seguieri	Caryophyllaceae	3.5	small	LC	6 - 9	7	5	19	2
Dianthus sylvestris	Caryophyllaceae	3	large	LC	6 - 7	6	8	2	1
Dictamnus albus	Rutaceae	4.5	small	VU	5 - 6	5	3	2	1

Table S1 *continued*

Plant species	Family	T indicator value	T variation	Red list status	Flowering period in nature [months]	Flowering onset in botanical garden [month]	Number of flower visitors	Mean flower visitation duration [s]	Number of flower visitor groups
Digitalis grandiflora	Plantaginaceae	2.5	small	LC	6 - 8	5	21	6	2
Digitalis lutea	Plantaginaceae	3.5	large	LC	6 - 8	5	5	2	2
Draba aizoides	Brassicaceae	1.5	small	LC	3 - 7	3	1	30	1
Draba fladnizensis	Brassicaceae	1	small	LC	7 - 8	3	0	0	0
Draba incana	Brassicaceae	1.5	small	CR	6	5	1	1	1
Dryas octopetala	Rosaceae	1.5	large	LC	5 - 8	4	0	0	0
Echium vulgare	Boraginaceae	4	large	LC	5 - 10	6	45	4	3
Epilobium angustifolium	Onagraceae	3	small	LC	6 - 8	6	6	4	2
Epilobium fleischeri	Onagraceae	2	small	LC	7 - 9	7	16	7	3
Epilobium hirsutum	Onagraceae	3.5	small	LC	6 - 9	8	10	3	1
Erica carnea	Ericaceae	2	small	LC	2 - 6	3	9	1	5
Erica vagans	Ericaceae	5	small	CR	6 - 9	7	1	35	1
Erigeron atticus	Asteraceae	2	small	NT	7 - 9	5	8	15	1
Erinus alpinus	Plantaginaceae	2.5	small	LC	5 - 7	5	0	0	0
Eryngium campestre	Apiaceae	5	small	EN	7 - 9	7	4	287	3
Erythronium dens-canis	Liliaceae	5	small	VU	3 - 4	3	4	30	2
Eupatorium cannabinum	Asteraceae	3.5	small	LC	7 - 9	7	10	10	2
Falcaria vulgaris	Apiaceae	4.5	small	EN	7 - 10	7	15	73	1
Galanthus nivalis	Amaryllidaceae	4	small	NT	2 - 3	3	0	0	0
Galium glaucum	Rubiaceae	4	small	VU	5 - 7	5	2	4	2
Genista tinctoria	Fabaceae	4.5	small	LC	6 - 8	7	1	4	1
Gentiana alpina	Gentianaceae	1	small	VU	6 - 7	4	0	0	0
Gentiana asclepiadea	Gentianaceae	3	small	LC	8 - 10	7	3	2	1
Geranium nodosum	Geraniaceae	4	large	NT	5 - 8	6	38	4	3
Geranium pyrenaicum	Geraniaceae	4	small	LC	5 - 9	4	2	3	1
Geranium sanguineum	Geraniaceae	3.5	large	LC	5 - 7	8	13	4	2

***Table S1** continued*

Plant species	Family	T indicator value	T variation	Red list status	Flowering period in nature [months]	Flowering onset in botanical garden [month]	Number of flower visitors	Mean flower visitation duration [s]	Number of flower visitor groups
Globularia cordifolia	Plantaginaceae	2.5	large	LC	5 - 7	4	5	4	1
Globularia nudicaulis	Plantaginaceae	2	small	LC	6 - 8	4	0	0	0
Gypsophila repens	Caryophyllaceae	2	large	LC	5 - 8	5	0	0	0
Helianthemum apenninum	Cistaceae	4.5	small	VU	5 - 7	7	1	75	1
Helianthemum canum	Cistaceae	4.5	small	VU	5 - 6	7	6	11	2
Helianthemum nummularium ssp. grandiflorum	Cistaceae	1.5	small	LC	6 - 9	7	4	1	1
Helianthemum nummularium ssp. obscurum	Cistaceae	4	small	LC	5 - 8	6	1	42	1
Helleborus foetidus	Ranunculaceae	3.5	small	LC	2 - 4	3	3	10	1
Helleborus niger	Ranunculaceae	3.5	small	NT	12 - 5	3	3	83	2
Helleborus viridis	Ranunculaceae	3.5	large	NT	2 - 4	3	4	6	2
Hepatica nobilis	Ranunculaceae	4	small	LC	3 - 5	3	0	0	0
Hieracium hoppeanum	Asteraceae	2.5	small	LC	6 - 8	4	0	0	0
Hieracium pilosella	Asteraceae	3	large	LC	5 - 10	7	0	0	0
Hieracium staticifolium	Asteraceae	2.5	small	LC	7 - 8	5	2	4	1
Hieracium tomentosum	Asteraceae	3	small	NT	6 - 7	6	17	8	2
Hieracium umbellatum	Asteraceae	4	small	LC	8 - 10	8	43	10	3
Horminum pyrenaicum	Lamiaceae	2	small	NT	6 - 8	5	4	21	1
Hugueninia tanacetifolia	Brassicaceae	2	small	VU	7	5	11	63	4
Hypericum perforatum	Hypericaceae	4	large	LC	7 - 8	7	9	35	2
Inula helvetica	Asteraceae	4.5	small	VU	5 - 6	8	0	0	0
Iris pseudacorus	Iridaceae	4	small	LC	5 - 6	5	29	34	4
Iris sibirica	Iridaceae	4	small	VU	5 - 9	5	24	16	3

Table S1 *continued*

Plant species	**Family**	**T indicator value**	**T variation**	**Red list status**	**Flowering period in nature [months]**	**Flowering onset in botanical garden [month]**	**Number of flower visitors**	**Mean flower visitation duration [s]**	**Number of flower visitor groups**
Knautia arvensis	Caprifoliaceae	3.5	large	LC	6 - 9	7	25	10	2
Knautia dipsacifolia	Caprifoliaceae	3	large	LC	5 - 8	7	7	14	2
Lamium album	Lamiaceae	4	large	LC	6 - 7	4	2	5	1
Lathyrus niger	Fabaceae	4.5	small	LC	6 - 7	5	14	13	3
Legousia speculum veneris	Campanulaceae	4.5	small	VU	6 - 9	6	4	1	1
Leonurus cardiaca	Lamiaceae	4.5	small	EN	4 - 5	6	58	5	4
Leucojum aestivum	Amaryllidaceae	4.5	small	VU	6 - 7	3	2	5	2
Linum alpinum	Linaceae	2	small	NT	5 - 8	4	0	0	0
Lithospermum officinale	Boraginaceae	4	small	NT	6 - 8	5	17	2	1
Lomelosia graminifolia	Caprifoliaceae	4.5	small	VU	5 - 6	7	24	16	3
Lonicera nigra	Caprifoliaceae	2.5	small	LC	7 - 9	4	6	3	1
Lycopus europaeus	Lamiaceae	3.5	small	LC	5 - 7	7	0	0	0
Lysimachia nemorum	Primulaceae	3	large	LC	6 - 9	5	8	3	1
Lythrum salicaria	Lythraceae	4	small	LC	7 - 9	7	18	5	3
Malva alcea	Malvaceae	4	small	LC	2 - 4	6	15	4	3
Malva sylvestris	Malvaceae	4	small	LC	5 - 9	7	69	5	5
Matricaria recutita	Asteraceae	4	large	LC	5 - 9	8	12	23	4
Minuartia capillacea	Caryophyllaceae	3	small	VU	6 - 8	6	8	2	1
Narcissus pseudonarcissus	Amaryllidaceae	3	large	NT	3 - 4	3	9	423	2
Nasturtium officinale	Brassicaceae	4	large	LC	5 - 9	5	0	0	0
Nepeta cataria	Lamiaceae	4.5	large	EN	7 - 9	8	16	5	3
Nepeta nuda	Lamiaceae	4.5	large	EN	7 - 8	6	41	2	1
Nigella arvensis	Ranunculaceae	4.5	small	EN	6 - 9	7	28	19	2
Onobrychis arenaria	Fabaceae	4	large	NT	5 - 8	6	11	2	2
Onosma helvetica	Boraginaceae	4.5	small	EN	5 - 7	6	1	1	1
Origanum vulgare	Lamiaceae	3.5	small	LC	7 - 9	7	10	6	4

***Table S1** continued*

Plant species	Family	T indicator value	T variation	Red list status	Flowering period in nature [months]	Flowering onset in botanical garden [month]	Number of flower visitors	Mean flower visitation duration [s]	Number of flower visitor groups
Orlaya grandiflora	Apiaceae	5	small	VU	5 - 8	6	79	18	3
Ornithogalum nutans	Liliaceae	5	small	VU	3 - 5	4	0	0	0
Petrorhagia saxifraga	Caryophyllaceae	4.5	small	LC	6 - 9	6	16	3	2
Pimpinella major	Apiaceae	3.5	large	LC	6 - 9	7	22	17	4
Potentilla arenaria	Rosaceae	4	small	EN	4 - 5	4	1	10	1
Potentilla erecta	Rosaceae	3	small	LC	6 - 9	6	7	6	3
Potentilla frigida	Rosaceae	1	small	LC	7 - 8	4	4	10	2
Potentilla micrantha	Rosaceae	4.5	small	LC	3 - 5	3	1	30	1
Potentilla palustris	Rosaceae	3	small	LC	5 - 7	5	30	20	3
Potentilla thuringiaca	Rosaceae	4	large	VU	5 - 7	4	6	36	2
Primula acaulis	Primulaceae	4.5	large	LC	3 - 4	3	2	3	1
Primula auricula	Primulaceae	1.5	small	LC	4 - 6	4	0	0	0
Primula elatior	Primulaceae	3	large	LC	3 - 7	3	0	0	0
Prunus mahaleb	Rosaceae	4.5	small	LC	4 - 5	4	4	15	3
Pulmonaria helvetica	Boraginaceae	3.5	small	VU	3 - 5	3	2	9	2
Pulmonaria montana	Boraginaceae	4	small	NT	3 - 5	4	2	4	2
Ranunculus arvensis	Ranunculaceae	4.5	small	VU	5 - 7	6	0	0	0
Rhododendron ferrugineum	Ericaceae	2	large	LC	5 - 7	8	2	103	1
Salvia glutinosa	Lamiaceae	3	small	LC	7 - 9	8	2	2	1
Salvia officinalis	Lamiaceae	5	small	VU	5 - 7	7	12	5	4
Salvia verticillata	Lamiaceae	4	large	NT	6 - 9	6	31	7	1
Sambucus ebulus	Caprifoliaceae	4	large	LC	7 - 8	7	1	680	1
Samolus valerandi	Primulaceae	4.5	small	CR	6 - 9	7	0	0	0
Sanicula europaea	Apiaceae	3.5	large	LC	5 - 7	5	13	4	3
Saponaria ocymoides	Caryophyllaceae	3	small	LC	5 - 9	5	0	0	0
Saponaria officinalis	Caryophyllaceae	4.5	small	LC	7 - 9	7	0	0	0

***Table S1** continued*

Plant species	Family	T indicator value	T variation	Red list status	Flowering period in nature [months]	Flowering onset in botanical garden [month]	Number of flower visitors	Mean flower visitation duration [s]	Number of flower visitor groups
Saxifraga granulata	Saxifragaceae	4	small	EN	4 - 6	4	0	0	0
Saxifraga rotundifolia	Saxifragaceae	2.5	small	LC	6 - 9	5	0	0	0
Scabiosa lucida	Caprifoliaceae	1.5	small	LC	7 - 9	5	34	15	1
Scabiosa triandra	Caprifoliaceae	4.5	small	LC	6 - 9	8	8	23	2
Scilla bifolia	Liliaceae	4.5	large	LC	3 - 4	3	0	0	0
Scrophularia nodosa	Scrophulariaceae	3	large	LC	6 - 8	5	21	3	2
Scutellaria alpina	Lamiaceae	2	small	NT	6 - 8	7	1	20	1
Securigera varia	Fabaceae	4	small	LC	6 - 8	7	7	4	1
Sedum album	Crassulaceae	3	large	LC	6 - 9	7	19	88	3
Senecio alpinus	Asteraceae	2.5	small	LC	7 - 9	6	17	27	3
Senecio aquaticus	Asteraceae	4	small	NT	6 - 10	8	2	165	1
Sideritis hyssopifolia	Lamiaceae	2.5	small	VU	7 - 9	6	4	6	2
Silene dioica	Caryophyllaceae	3	large	LC	4 - 9	7	2	6	1
Silene suecica	Caryophyllaceae	1	small	NT	7 - 8	4	2	4	2
Solanum nigrum	Solanaceae	3.5	small	LC	6 - 10	7	0	0	0
Solidago virgaurea	Asteraceae	3.5	small	LC	7 - 9	7	35	7	4
Sorbus chamaespilus	Rosaceae	2	small	LC	6 - 7	4	5	7	1
Stachys alopecuros	Lamiaceae	2.5	small	VU	6 - 8	5	5	3	2
Stachys germanica	Lamiaceae	4.5	large	VU	6 - 8	6	26	3	1
Stachys palustris	Lamiaceae	3.5	small	NT	6 - 9	8	18	5	1
Stachys recta	Lamiaceae	3.5	large	LC	6 - 9	6	15	3	3
Staphylea pinnata	Staphyleaceae	4.5	small	VU	5 - 6	4	0	0	0
Symphytum officinale	Boraginaceae	3.5	small	LC	5 - 8	7	5	4	1
Tanacetum vulgare	Asteraceae	4.5	large	LC	6 - 9	8	7	34	2
Teucrium chamaedrys	Lamiaceae	4.5	large	LC	6 - 8	7	11	6	4
Teucrium scorodonia	Lamiaceae	3.5	large	LC	6 - 9	6	24	4	1

Table S1 *continued*

Plant species	**Family**	**T indicator value**	**T variation**	**Red list status**	**Flowering period in nature [months]**	**Flowering onset in botanical garden [month]**	**Number of flower visitors**	**Mean flower visitation duration [s]**	**Number of flower visitor groups**
Thymus polytrichus	Lamiaceae	2	large	LC	6 - 9	7	23	11	2
Trifolium rubens	Fabaceae	4	large	NT	6 - 7	6	26	5	3
Tussilago farfara	Asteraceae	3	large	LC	3 - 5	3	2	20	1
Valeriana montana	Caprifoliaceae	2	small	LC	5 - 7	4	0	0	0
Valeriana supina	Caprifoliaceae	1	small	NT	7 - 8	4	0	0	0
Verbascum densiflorum	Scrophulariaceae	4	small	LC	6 - 9	8	0	0	0
Verbascum nigrum	Scrophulariaceae	4	large	LC	5 - 9	7	4	8	2
Verbascum phlomoides	Scrophulariaceae	4.5	small	CR	6 - 9	7	29	12	4
Veronica fruticulosa	Plantaginaceae	2	small	LC	6 - 7	5	0	0	0
Vinca minor	Apocynaceae	3.5	small	LC	3 - 5	4	1	5	1
Vincetoxicum hirundaria	Apocynaceae	3.5	large	LC	6 - 8	6	1	3	1
Viola arvensis	Violaceae	3.5	large	LC	3 - 10	6	0	0	0
Viola reichenbachiana	Violaceae	3	large	LC	4 - 5	4	1	2	1
Viola tricolor	Violaceae	4	small	LC	5 - 8	7	0	0	0

Chapter 4

Adaptive responses to cultivation and to novel environmental conditions in rare and common alpine plant species grown in botanical gardens

Christine Föhr & Markus Fischer

Abstract

Ex-situ collections play an important role in the conservation of plant species. However, new environmental conditions and unintentional selection may result in adaptive responses of important life-history traits in cultivated wild species under ex-situ cultivation. As a consequence, this may impede successful reintroduction of the threatened plants into the wild.

The ability of a plant to adapt to novel environmental conditions might be influenced by the commonness of the plant species. We therefore compared plant performance of three related rare and common alpine species pairs grown from seeds from lowland garden populations, alpine garden populations and natural populations in experimental gardens at subalpine level and in the lowland. We hypothesized that the offspring of plants grown in ex-situ collections would differ in important traits from the offspring of wild plants, and that offspring of alpine plants grown in lowland gardens would show reduced performance compared to offspring of plants of alpine ex-situ collections under alpine environmental conditions. We found differences in germination rates, seedling survival and seedling growth between plants originating from ex-situ collections and plants of wild origin. The germination rate of the plants with garden origin was higher than the germination rate of the plants of wild origin. Additionally, the common species with garden origin survived better at lowland study site compared to plants with wild origin, and the plants with garden origin had a higher seedling biomass at the subalpine study site compared to the plants with wild origin. We also found evidence of maladaptive responses. Seedlings of rare plant species originating from lowland gardens had a lower survival rate compared to seedlings of plants with alpine garden origin when grown at the subalpine level.

The changes in plant performance we detected in the offspring of plants grown in ex-situ collections and under novel environmental conditions suggest that adaptive responses of plants in ex-situ collections are likely. Thus, the planning and realization ex-situ cultivation programs should be conducted with great care. We strongly recommend that ex-situ cultivation of alpine plants should be realized under their natural environmental conditions and that unintentional selection by gardening practices should be avoided.

Introduction

Many plant species are currently threatened by habitat loss, habitat degradation and climate change (Thomas et al. 2004, Thuiller et al 2005, Hahs et al. 2009). To prevent the potential loss of tens of thousands of plant species, plant conservation in their natural environment (in situ) therefore needs to be an urgent priority (Wyse Jackson & Kennedy 2009). However, as in-situ conservation alone is often not sufficient anymore for preserving threatened species, the conservation of plants outside their natural environment (ex situ) has become an important tool to complement in-situ conservation (Maunder et al. 2004, Havens et al. 2004). Accordingly, the Global Strategy for Plant Conservation, which was set up under the Convention on Biological Diversity (CBD) in 2002, and updated in 2010, aims at preserving at least 75% of threatened plant species in ex-situ collections, and to provide at least 20% of them for restoration and reintroduction programs.

However, the ex-situ collections raise specific difficulties (Havens et al. 2004, Husband & Campbell, 2004). Unlike in-situ conservation, the target plants are removed from their natural habitat and introduced to novel and artificial environments whose conditions differ from the ones at the original populations (Havens et al. 2004, Husband & Campbell, 2004). These different conditions may be caused by changes in nutrients, water, light, temperature, competition with other species, or other biotic interactions. In the short term, survival and reproduction of the species might be reduced due to the physiological impact of the novel environment. In the long term, species might adapt to the novel abiotic and biotic conditions (Havens et al. 2004, Schaal & Leverich 2004) and alter important life-history traits such as germination (Ensslin et al. 2011, Schröder & Prasse 2013a) or growth (Schröder & Prasse 2013b). Unintentional selection during cultivation might further enhance such adaptive responses (Husband & Campbell 2004, Rolston 2004, Ensslin et al. 2011). As species become adapted to the conditions at the ex-situ site, they may lose their adaptations to their natural habitat and they may therefore become unsuitable for restoration and reintroduction (Schröder & Prasse 2013b).

Ex-situ populations most often originate from very few individuals (Husband & Campbell 2004). The ex-situ collections therefore undergo a process similar to a founder event with genotypes that are not fully representing the genetic variation of the source population. The consequences may be genetic drift and inbreeding leading to a loss of genetic diversity which might negatively affect viability (Oostermeijer et al. 2003) and the adaptive potential of the commonly small plant populations in ex-situ collections (Husband & Campbell 2004, Willi et al. 2006, Leimu and Fischer 2008, Jump et al. 2009). Rare and threatened species are particularly threatened by drift and inbreeding already in nature as they often occur in very small and isolated populations (Karron 1997), and those processes might be further enhanced in the usually small ex-situ populations (Husband & Campbell 2004, Schaal & Leverich 2004). Therefore, common plant species that originate from more genetically diverse populations might suffer less from the loss of genetic diversity in ex-situ collections than rare species and might also have a larger potential to adapt to the novel environmental conditions of the ex-situ cultivation site.

Reduced genetic diversity in ex-situ populations has already been reported for several case studies (Rucińska & Puchalski 2011, Lauterbach et al. 2012, Brütting et al 2012). However, whether this also results in a change in life-history traits of plants in ex-situ cultivation and a decrease of performance, which could be maladaptive in case of reintroduction, has rarely been investigated (Husband & Campbell 2004, Ensslin et al. 2011). Furthermore, whether rare and common plants are differently affected by adaptive trait changes and maladaptation has not been tested so far.

Alpine plants are often cultivated in botanical gardens in the lowland and there they experience environmental conditions outside of their natural range. As most alpine plants possess particular adaptations to the environmental conditions at high altitudes, adaptive responses to lowland cultivation could result in maladaptation to their natural habitat. Thus alpine plants in botanical gardens provide the opportunity to test to what extent cultivated species adapt to the novel and artificial environmental conditions in the gardens and whether the cultivation outside their natural conditions results in maladaptation when the plants are grown in the original alpine environment.

We compared important life-history traits of three pairs of common and rare alpine plant species originating from lowland gardens, alpine gardens and wild populations and planted to two experimental gardens at lowland and subalpine elevations. We addressed the following questions: (1) Does offspring of plants cultivated in ex-situ collections differ in performance from offspring of plants of wild origin? (2) Do offspring of plants cultivated in lowland botanical gardens show reduced performance compared with offspring of plants cultivated in alpine botanical gardens when grown in the original alpine environment, indicating maladaptation? (3) Are such maladaptive responses more pronounced in common species than in rare species?

Materials and Methods

Study species

We chose three congeneric or confamilial pairs of rare and common alpine plant species for the study: *Eryngium alpinum* L. (rare) and *Astrantia major* L. (common) (Apiaceae), *Saponaria lutea* L. (rare) and *Saponaria ocymoides* L. (common) (Caryophyllaceae), *Carex baldensis* L. (rare) and *Carex sempervirens* Vill. (common) (Cyperaceae). The chosen species are cultivated in several botanical gardens in Europe and therefore seeds were available from different sources.

Astrantia major and *Eryngium alpinum* are perennial hemicryptophytes that grow in meadows and in tall forb communities at upper montane to subalpine elevations (Landolt 2010). *Carex sempervirens* and *C. baldensis* are perennial hemicryptophytes that grow in meadows at upper montane to lower alpine elevations. *Saponaria lutea* is a perennial hemicryptophyte that grows in meadows and pastures at upper subalpine and lower alpine elevations, and *S. ocymoides* is a perennial chamaephyte that occurs on rocky slopes at montane elevations. In the Red list of ferns and vascular plants for Switzerland (Moser et al. 2002) *E. alpinum* and *C. baldensis* are listed as vulnerable, *S. lutea* is listed as endangered.

Sampling of the populations

15 European lowland botanical gardens and 7 European alpine botanical gardens provided seed material for the study (Table 1). The seed material was collected in 2010 and 2011. For most of the species we obtained seeds from two to five different gardens per garden type (lowland or alpine), seeds of *C. sempervirens* were obtained from two lowland gardens, but only available from one alpine garden. The botanical gardens could not provide information on the number of sampled plants and population size, and only 13 of 45 gardens could provide information on the duration of cultivation in the garden and on the site of plant origin.

Additionally, we collected seeds of each species from two to five wild populations from populations in Switzerland, France, Italy and Austria. In the wild populations, we collected seeds from 10 to 50 individuals. The sampled populations consisted all of at least 100 individuals. Seed origins and the number and altitude of populations of origin are shown in Table 1.

Table 1 *Seed origins and population numbers of the study species.*

Species	Lowland botanical gardens	Alpine gardens	Wild
Eryngium alpinum	Bern CH (501-537 m a. s. l.) Geneva CH (382 m a. s. l.) Neuchâtel CH (543 m a. s. l.) Oberhof D (832-868 m a. s. l.) University of Regensburg D (400 m a.s. l.) Tübingen D (409-490 m a. s. l.) University of Vienna A (172 m a. s. l.)	"Flore-alpe", Champex CH (1500 m a. s. l.) "La Thomasia", Pont-de-Nant CH (1260 m a. s. l.) "La Rambertia", Rochers-de-Naye CH (2000 m a. s. l.) Schynige Platte, Schynige Platte CH (1950-2000 m a. s. l.)	Belles Raies, Haut-Intyamon CH (1700 m a. s. l.) Les Verraux, Col du Jaman CH (1650 m a. s. l.) Pradas, Verzegnis I (1300 m a. s. l.) Rochers-de-Naye CH (1832 m a. s. l.)
Astrantia major	Adorf D (494 m a. s. l.) Bern CH (501-537 m a. s. l.) Krefeld D (34-39 m a. s. l.) Oberhof D (832-868 m a. s. l.) University of Vienna A (172 m a. s. l.)	"Rezia", Bormio I (1350-1400 m a. s. l.) "Flora-alpe", Champex CH (1500 m a. s. l.) "La Thomasia", Pont-de-Nant CH (1260 m a. s. l.) "La Rambertia", Rochers-de-Naye CH (2000 m a. s. l.)	Grimmialp, Diemtigtal CH (1268 m a. s. l.) Lauterbrunnen CH (915 m a. s. l.) Schynige Platte CH (1980 m a. s. l.) Sefinental CH (1259 m a. s. l.)
Saponaria lutea	Bern CH (501-537 m a. s. l.) Montet, Villers-lès-Nancy F (267-287 m a. s. l.) Munich-Nymphenburg D (515 m a. s. l.) Oberhof D (832-868 m a. s. l.)	"Rezia", Bormio I (1350-1400 m a. s. l.) "Flore-alpe", Champex CH (1500 m a. s. l.) "Saussurea", Pavillon du Mont Fréty I (2173 m a. s. l.) Schynige Platte, Schynige Platte CH (1950-2000 m a. s. l.)	Col du Petit Mont Cenis F (2182 m a. s. l.) Randinascia, Robiei CH (2243 m a. s. l.)
Saponaria ocymoides	Bern CH (501-537 m a. s. l.) Geneva CH (382 m a. s. l.) Siena I (280-350 m a. s. l.) Tübingen D (409-490 m a. s. l.) University of Vienna A (172 m a. s. l.)	"Flore-alpe", Champex CH (1500 m a. s. l.) Villacher Alpe, Villacher Alpe A (1500 m a. s. l.)	Biel CH (502 m a. s. l.) Binn CH (1323 m a. s. l.) Guttet CH (1488 m a. s. l.) Lötschberg southern slope CH (900 m a. s. l.) Rüttenen CH (605 m a. s. l.)
Carex baldensis	Bern CH (501-537 m a. s. l.) Frankfurt on the Main D (112 m a. s. l.) Geneva CH (382 m a. s. l.) Munich-Nymphenburg D (515 m a. s. l.) Salzburg A (440 m a. s. l.)	"Flore-alpe", Champex CH (1500 m a. s. l.) "La Thomasia", Pont-de-Nant CH (1260 m a. s. l.)	Grigna, Lecco I (1200 m a. s. l.) Grigna, Lecco I (1480 m a. s. l.) Ofenpass CH (2316 m a. s. l.)
Carex sempervirens	Frankfurt on the Main D (112 m a. s. l.) Graz A (380 m a. s. l.)	"Flore-alpe", Champex CH (1500 m a. s. l.)	Männlichen CH (2080 m a. s. l.) Obergurgl, Oetztal A (2266 m a. s. l.) Schynige Platte CH (1980 m a. s. l.) Sefinental CH (1259 m a. s. l.) Testa del Caricatore, La Thuile I (1900 m a. s. l.)

Study sites

We set up our common garden experiments in two botanical gardens in Switzerland, the Botanical garden of Bern and the alpine botanical garden on the Schynige Platte. The Botanical garden of Bern is situated in the city of Bern (46.95° N, 7.44° E) at an altitude of 501-537 m a. s. l. on a southwest exposed slope. Mean annual precipitation in Bern is 1028 mm and mean annual temperature is 8.1°C. The alpine garden is situated on the Schynige Platte in the Bernese Oberland (46.65° N, 7.91° E) at an altitude of 1950-2000 m a. s. l. . Mean annual precipitation on the Schynige Platte is about 2000 mm, mean annual temperature about 1°C. The experimental site on the Schynige Platte was facing southeast.

Germination and seedling establishment

Prior to sowing we counted and weighed all seeds. In September and November 2011 we sowed 6 batches of 10 seeds per species and garden or per wild population of origin in 9 cm-diameter clay pots in the alpine garden and in the Botanical garden of Bern. We covered the pots with garden fleece to avoid seed predation by animals. We then left the pots outside during winter in both gardens for a natural cold stratification. In spring 2012, to assess the germination rate, we counted the seedlings regularly from mid-March until mid-April in Bern and on the Schynige Platte after snowmelt during the month of June.

After germination we planted the seedlings individually into pots with potting soil (Ricoter 140, Aarberg, Switzerland) in both gardens. To avoid desiccation of the seedlings we used 9 cm-diameter clay pots in the alpine garden and lowered the pots into the ground soil. In Bern, we planted the seedlings in 1 l plastic pots in the botanical garden and placed them in concrete flower beds. Neither of the two pot sizes were limiting the seedlings root space, and both procedures corresponded to the common gardening practice in the two gardens With 6 replicates per species and seed origin and (1-) 2 – 4 different seed origins per population type (lowland garden, alpine garden, wild) we obtained 310 pots in the alpine garden and 331 pots in the Botanical garden of Bern. The difference in pot number was caused by some lack of *S. ocymoides* seedlings. We re-randomized the pots regularly and watered and weeded the pots when necessary.

In late August and early September we harvested the plantlets, dried them at 80°C for at least 48 h and weighed the dry biomass.

Statistical analysis

To study the effect of ex-situ cultivation on seed mass, germination and seedling performance of common and rare plant species we compared the plants of alpine garden origin and of wild origin. To study the effect of adaptation to novel climatic conditions on seed mass, germination and seedling performance of common and rare plant species we compared the plants of lowland garden origin and alpine garden origin.

We used linear mixed effect models with population type (alpine garden and wild population or lowland garden and alpine garden respectively), experimental site (Botanical garden of Bern and Alpine garden of the Schynige Platte) and rarity status (rare/common) as fixed effects. Species pair, species nested in species pair and seed origin nested in species were treated as random effects. We included seed mass as covariate in the analysis of germination rate and seedling size at the start of the experiment as covariate in the analysis of biomass. To avoid zero-inflation in our models, we analysed seedling performance in two different models with seedling survival and biomass of the surviving seedlings as response variables. When necessary, we log-transformed response variables to meet model assumptions. To test for differences among combinations of population type, experimental site and rarity status, we calculated pre-defined contrasts.

We repeated the analyses for each plant species separately with population type (alpine garden and wild population or lowland garden and alpine garden, respectively) and experimental site (Botanical garden of Bern and Alpine garden of the Schynige Platte) as fixed effects and seed origin (population) as random effect. Again we included seed mass as covariate in the analysis of germination rate and seedling size at the start of the experiment as covariate in the analysis of biomass. In the separate analyses of each species models with seedling survival as response failed to converge in both *Saponaria* species. Therefore, we included the seedlings that did not survive with zero biomass in the analysis of biomass for all species. We log-transformed the values to meet model assumptions.

We performed the analyses with the packages *nlme* (Pinheiro et al. 2014), *lme4* (Bates et al. 2014) and *multcomp* (Hothorn et al. 2008) implemented in the statistical software R 3.1.2 (R Development Core Team 2014).

Results

Effect of ex-situ cultivation on alpine plant performance

The germination rate of seeds originating from alpine gardens was significantly higher than the germination rate of seeds collected in the wild (Figure 1A; Table 2). Seedlings derived from ex-situ plants also had a higher survival than those derived from wild populations, and this difference was dependent on the rarity status of the species and on the experimental site

(Figure 1B). While offspring of common plant species cultivated in botanical gardens survived better than offspring of common plants from wild populations in the lowland experimental site, offspring of rare plants from ex-situ collections survived slightly better than rare plants from wild populations in the subalpine experimental site.

In the subalpine experimental site the seedlings of garden origin grew to significantly larger biomass than the seedlings of wild origin, while the biomass of seedlings of garden origin was not different of that of seedlings of wild origin in the lowland experimental site (Figure 1C).

In summary, these results indicate that offspring originating from cultivated populations generally performed better than offspring originating form wild populations.

Figure 1 *Effect of ex-situ cultivation (population type alpine garden/wild) on germination (A), effect of of ex-situ cultivation (population type alpine garden/wild), experimental site (Bern/Schynige Platte), status (rare/common) and their interactions on seedling survival (B) and effect of of ex-situ cultivation (population type alpine garden/wild), study site (Bern/Schynige Platte) and their interaction on seedling biomass. ■: Common species, □: Rare species. Shown are means and standard errors. The stars above the lines indicate significant differences according to pre-defined contrasts ((*): P < 0.1, *: P < 0.05, **: P < 0.01, ***: P < 0.001).*

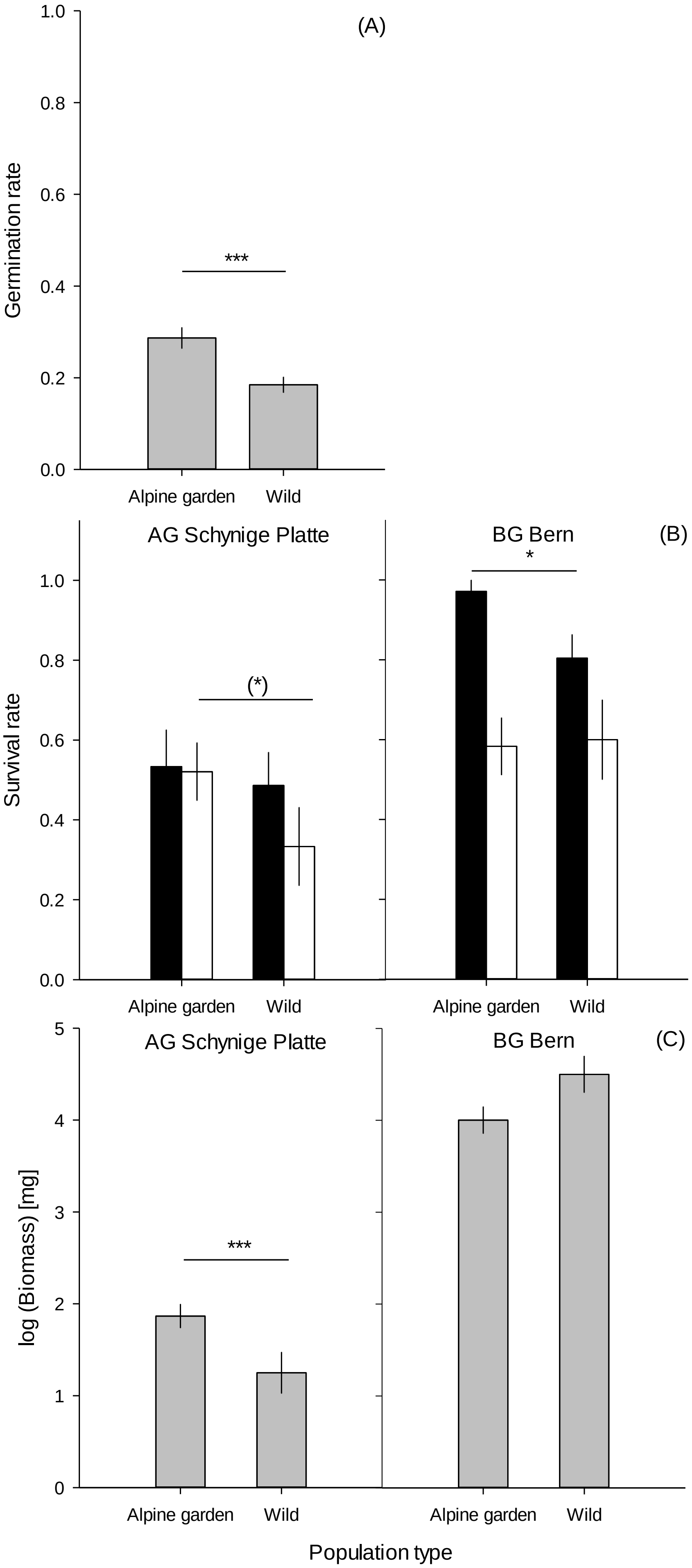

(A)
Germination rate
1.0
0.8
0.6
0.4
0.2
0.0
***
Alpine garden
Wild
AG Schynige Platte
BG Bern
(B)
Survival rate
1.0
0.8
0.6
0.4
0.2
0.0
(*)
*
Alpine garden
Wild
Alpine garden
Wild
AG Schynige Platte
BG Bern
(C)
log (Biomass) [mg]
5
4
3
2
1
0
***
Alpine garden
Wild
Alpine garden
Wild
Population type

Table 2 *Effect of ex-situ cultivation (population type alpine garden/wild), experimental site (Bern/Schynige Platte) and status (rare/common) and their interactions on seed mass, germination, seedling survival and seedling biomass. Shown are degrees of freedom in the numerator (df1) and denominator (df2), F-values and levels of significance for the analyses of seed mass and seedling biomass, and the degrees of freedom, χ^2-values and levels of significance for the analyses of germination and seedling survival. Levels of significance are: (*): P < 0.1, *: P < 0.05, **: P < 0.01, ***: P < 0.001.*

	Seed mass				**Germination**			**Survival**			**Biomass**			
Fixed effects	**df1**	**df2**	**F**	**p**	**df**	**χ^2**	**p**	**df**	**χ^2**	**p**	**df1**	**df2**	**F**	**p**
Experimental site	-	-	-		1	42.761	***	1	25.500	***	1	149	269.460	***
Rarity status	1	2	1.583		1	31.010	***	1	0.990		1	1	0.220	
Population type	1	31	0.641		1	35.391	***	1	4.750	*	1	21	2.130	
Experimental site x Rarity status	-	-	-		1	31.345	***	1	2.710	(*)	1	149	14.060	***
Population type x Experimental site	-	-	-		1	0.000		1	0.010		1	149	7.850	**
Population type x Rarity status	1	31	0.001		1	0.777		1	0.260		1	21	0.440	
Population type x Experimental site x Rarity status	-	-	-		1	1.946		1	5.980	*	1	149	3.730	(*)
Seed mass	-	-	-		1	4.080	*	-	-		-	-	-	
Plant height at start of experiment	-	-	-		-	-		-	-		1	149	120.100	***
Random effects	Std Dev	Std Dev Resid			Variance	Std Dev		Variance	Std Dev		Std Dev	Std Dev Resid		
Species pair	0.014				1.319	1.148		0.697	0.835		0.000			
Species (Species pair)	< 0.0001				0.000	0.000		0.711	0.843		0.763			
Seed origin (Species / Species pair)	0.009	0.010			1.325	1.151		< 0.0001	< 0.0001		0.116	0.804		

Effect of adaptation to lowland garden conditions on plant performance in an alpine environment

Ex-situ cultivation in lowland gardens did not affect seed mass of the test species (Table 3). In the subalpine experimental site the seeds of the rare species from alpine garden plants germinated marginally significantly better than seeds from lowland garden plants (Figure 2A). Moreover, in the subalpine experimental site significantly more offspring of rare plant species grown in alpine gardens survived than offspring of rare plant species grown in lowland gardens did (Figure 2B). We detected no such difference in survival for offspring of common species at the same site. At the lowland experimental site the offspring of plants grown in lowland gardens did not survive better than the offspring of plants grown in alpine gardens. Seedling biomass of the seedlings with alpine garden origin and lowland garden origin was not significantly different in the subalpine experimental site (Figure 2C). Thus, the growth of offspring of alpine plants does not seem to be affected by ex-situ cultivation under environmental conditions in lowland gardens.

In summary, our results indicate that alpine plants may adapt to lowland garden conditions and in consequence offspring of rare plant species show decreased germination and survival when they are reintroduced into their natural range.

Figure 2 *Effect of adaptation (population type alpine garden/lowland garden), experimental site (Bern/Schynige Platte), status (rare/common) and their interactions on (A) germination and (B) seedling survival and (C) effect of of adaptation (population type alpine garden/lowland garden), study site (Bern/Schynige Platte) and their interactions on seedling biomass. ■: Common species, □: Rare species. Shown are means and standard errors. The stars above the lines indicate significant differences according to pre-defined contrasts ((*): P < 0.1, *: P < 0.05, **: P < 0.01, ***: P < 0.001).*

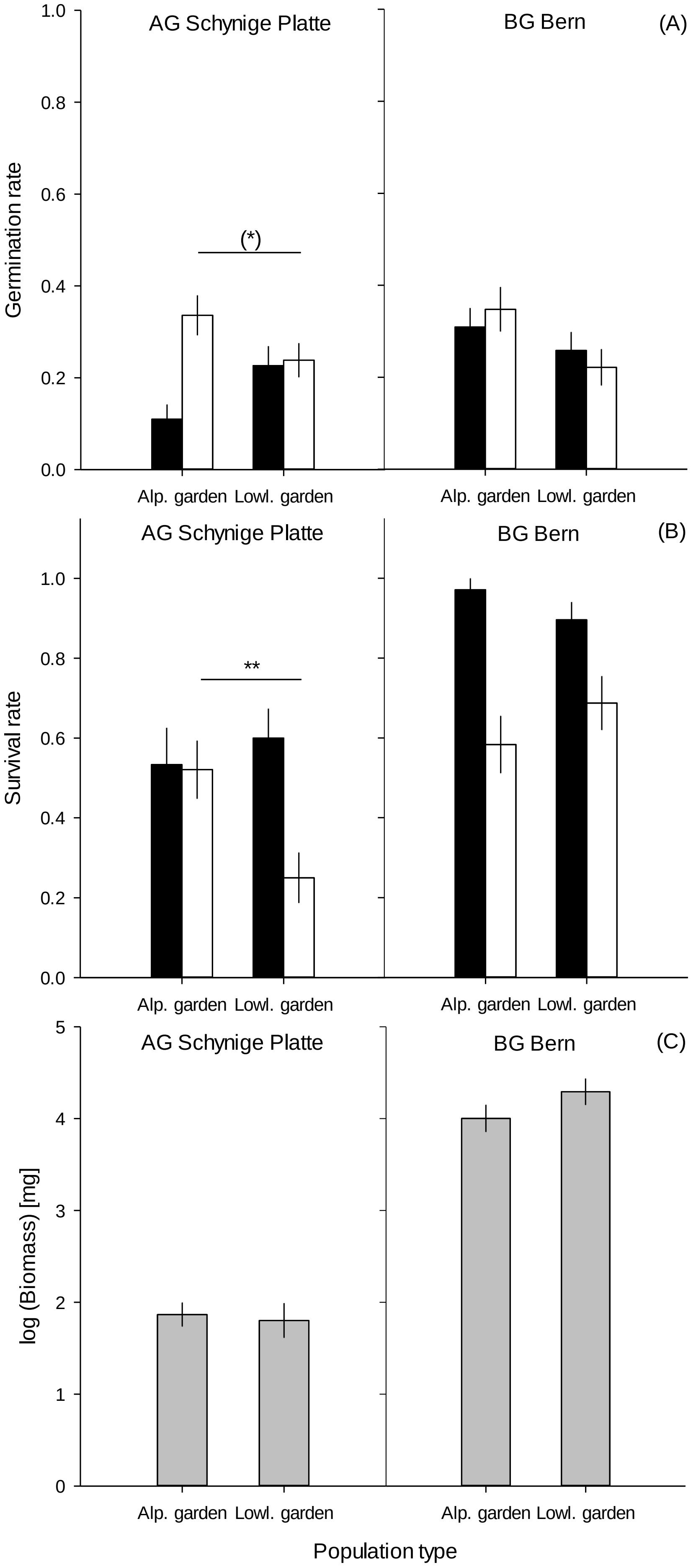

(A)
AG Schynige Platte
BG Bern
Germination rate
1.0
0.8
0.6
0.4
0.2
0.0
(*)
Alp. garden
Lowl. garden
Alp. garden
Lowl. garden
(B)
AG Schynige Platte
BG Bern
Survival rate
1.0
0.8
0.6
0.4
0.2
0.0
**
Alp. garden
Lowl. garden
Alp. garden
Lowl. garden
(C)
AG Schynige Platte
BG Bern
log (Biomass) [mg]
5
4
3
2
1
0
Alp. garden
Lowl. garden
Alp. garden
Lowl. garden
Population type

***Table 3** Effect of adaptation (population type alpine garden/lowland garden), experimental site (Bern/Schynige Platte) and status (rare/common) and their interactions on seed mass, germination, seedling survival and seedling biomass. Shown are degrees of freedom in the numerator (df1) and denominator (df2), F-values and levels of significance for the analyses of seed mass and seedling biomass, and the degrees of freedom, χ^2-values and levels of significance for the analyses of germination and seedling survival. Levels of significance are: (*): $P < 0.1$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.*

	Seed mass				**Germination**			**Survival**			**Biomass**			
Fixed effects	**df1**	**df2**	**F**	**p**	**df**	**χ^2**	**p**	**df**	**χ^2**	**p**	**df1**	**df2**	**F**	**p**
Experimental site	-	-	-		1	2.880	(*)	1	44.700	***	1	183	412.300	***
Rarity status	1	2	0.123		1	0.060		1	1.620		1	1	0.500	
Population type	1	32	3.322		1	3.919	*	1	0.990		1	24	1.100	
Experimental site x Rarity status	-	-	-		1	21.395	***	1	1.840		1	183	7.500	**
Population type x Experimental site	-	-	-		1	0.843		1	2.630		1	183	8.100	**
Population type x Rarity status	1	32	0.229		1	0.600		1	0.770		1	24	0.200	
Population type x Experimental site x Rarity status	-	-	-		1	6.816	**	1	8.550	**	1	183	0.200	
Seed mass	-	-	-		1	0.278		-	-		-	-	-	
Plant height at start of experiment	-	-	-		-	-		-	-		1	183	84.700	***
Random effects	Std Dev	Std Dev Resid			Variance	Std Dev		Variance	Std Dev		Std Dev	Std Dev Resid		
Species pair	0.013				2.108	1.452		0.164	0.405		0.000			
Species (Species pair)	0.003				0.000	0.000		0.800	0.895		0.855			
Seed origin (Species / Species pair)	0.009	0.010			1.612	1.270		0.290	0.538		0.050	0.744		

Discussion

Our study on the performance of offspring of ex-situ cultivated and wild plants of rare and common alpine plant species showed that ex-situ cultivation enhanced plant performance during the early life stages of the test species. This influence differed between rare and common species and between the lowland and alpine experimental sites. The rare species showed signs of a maladaptive response, which mostly affected seedling survival.

Effect of ex-situ cultivation on alpine plant performance

Ex-situ cultivation had a generally positive influence on germination and early seedling growth and survival in our study, and this influence depended on the rarity status of the species and on the environmental conditions of the experimental site.

The germination rate of seeds with garden origin was higher than the one of seeds with wild origin. Increased germination rates as a consequence of cultivation have also been found in plants of the rare species *Cynoglossum officinale* L. (Ensslin et al. 2011) and the common species *Plantago lanceolata L.* and *Lotus corniculatus L.* (Schröder & Prasse 2013a). Increased germination rates could indicate reduced dormancy and a faster germination caused by unintentional selection by gardeners, who often prefer planting out only the early germinants (Havens et. al 2004, Ensslin et al. 2011, Schröder & Prasse 2013a). However, such changes in germination characteristics might be maladaptive in natural environments. Seed dormancy is a strategy that may ensure survival during a season of unfavorable environmental conditions for seedling establishment (Vleeshouwers et al. 1995, Baskin & Baskin 1998). This is particularly important for alpine plant species for which too early germination in spring or in autumn could cause high seedling mortality. Reduced dormancy after several generations of ex-situ cultivation might therefore render the seeds of cultivated plants unsuitable for reintroduction.

Contrary to our expectation, ex-situ cultivation had no negative effects on seedling survival under the novel environmental conditions at the lowland experimental site. The survival rate of the common species was even higher for the plants with garden origin, although the high survival rate was mostly influenced by one species – *Astrantia major* - only. As ex-situ plantings often suffer from inbreeding (Husband & Campbell 2004, Schaal & Leverich 2004) which can reduce the adaptive potential of the plants (Husband & Campbell 2004, Willi et al. 2006, Jump et al. 2009), we would have expected an increased mortality rate of plants with garden origin and especially of the rare species at the lowland experimental site. It might, however, be possible that the survival rate of the plants with garden origin was influenced by pre-adaptation to cultivation which masked the effect of genetic diversity.

Ex-situ cultivation also influenced growth of plant offspring positively, though only in the subalpine experimental site, i.e. under conditions corresponding to the ones of natural environments of these species. At the lowland experimental site, seedling biomass was higher than at the subalpine experimental site regardless of population type, which suggests a mainly plastic growth response in the warmer climate. Increased growth of arctic-alpine plant species under warmer temperature has also been reported in meta-analyses of warming experiments (Arft et al. 1999, Elmendorf et al. 2012). The increased seedling growth of plants with garden origin at the subalpine experimental site, on the other hand, might also indicate further unintentional selection of larger or faster growing plants in the botanical gardens. Similar to the changes in germination characteristics, changes in plant growth might be maladaptive for plant offspring when reintroduced to natural conditions. In stress-dominated environments such as mountain ecosystems, fast growth mostly leads to reduced stress tolerance in plants (Körner 1999). Cultivated plants that are adapted to the benign garden conditions might therefore fail to survive or suffer a severe fitness loss after reintroduction in their natural habitat, as was shown by Schröder & Prasse (2013b) in a case study with offspring of cultivated *Lotus corniculatus L.* and *Plantago lanceolata L.*

Effect of adaptation to lowland garden conditions on plant performance in an alpine environment

In our study, we found evidence for maladaptive responses for the rare, but not for the common, species. At the subalpine experimental site the offspring of plants grown in alpine gardens survived considerably better than the offspring of plants grown in lowland gardens (Table 3, Figure 2C). In the lowland experimental site, the survival rate of the rare species was slightly but not significantly higher for plants with lowland garden origin. These results suggest that the alpine plants grown in lowland botanical gardens can adapt to the novel environmental conditions there and as a consequence their offspring may suffer from increased seedling mortality when grown at their natural elevation range.

We expected that common plant species with their potentially genetically more diverse populations might adapt more readily to novel environmental conditions. Alternatively, the common plants might have reacted plastically to the novel environmental conditions they encountered in the lowland botanical gardens. The cultivation of the rare species in the lowland gardens on the other hand might have resulted in an elimination of genotypes that could not cope with the novel environmental conditions. This could have resulted in maladaptation of the plants to the environmental conditions at the subalpine experimental site.

Adaptation to novel environments might require a long time especially for perennial plant species with a longer lifespan and a longer generation time than short-lived species (Jump & Peñuelas 2005). Generally, the studied perennial plant species were growing in the gardens for several years up to decades. However, as the exact time span of cultivation was only available for 13 of the total of 45 garden populations in the lowland gardens, we cannot study whether time span had an effect on adaptive responses and whether this differed between rare and common species. While we therefore cannot rule out the possibility that the rare species might have been cultivated a longer time in the lowland botanical gardens than the common species, we consider this as quite unlikely.

Perspectives for future research in botanical gardens

We investigated the influence of ex-situ cultivation and maladaptation on early plant life stages which are considered most sensitive to genetic processes such as inbreeding depression (Kolb & Durka 2012, de Vere et al. 2009). However, additional maladaptive responses might show also at later life stages, e. g. in the reproductive phase of the plants, or after reintroduction into the natural habitat of the species (Husband & Schemske 1996, Havens et al. 2004). Therefore, a similar study over the timespan of several years might render further interesting insights about the influence of ex-situ cultivation on plant performance.

Furthermore, the performance of rare and common plants originating from botanical gardens and the wild and growing under different environmental conditions also depend on the genetic variation of the source and ex-situ populations (Husband & Campbell 2004). Thus, studies also considering genetic variation and levels of inbreeding would be a next step to gain further insights into the roles of inbreeding or maladaptive processes in ex-situ cultivation.

Finally, including the sizes and ages of the ex-situ populations would help to find out how fast microevolutionary processes actually act ex-situ and to determine the minimum viable population size for ex-situ cultivations. So far, detailed information on plant populations in botanical gardens, such as origin or cultivation period, is only rarely available (Maunder et al. 2001, Ensslin et al. 2011). With the growing awareness of the importance of detailed record keeping in botanical gardens, these and other interesting questions about adaptation processes might be tackled by botanical gardens in the future and the insights would help to improve ex-situ cultivation for reintroduction.

Conclusion

We studied the influence of ex-situ cultivation in botanical gardens on offspring performance of common and rare alpine plant species. Compared with offspring of wild plants, we found changes in germination rates, seedling survival and seedling growth in offspring of cultivated plants. Ex-situ cultivation affected both rare and common species. When growing them in an alpine environment, we also found evidence for maladaptive responses of offspring of the assessed rare species after cultivation in lowland gardens. Based on our findings we caution against unintentional selection in ex-situ cultivations and strongly recommend that alpine plants should be cultivated ex situ only within their natural climatic range.

Acknowledgements

We thank all the botanical gardens that provided seed material for the experiment; the staff of the Botanical garden of Bern and the Alpine garden of the Schynige Platte for the help with the set-up and the realization of the experiment; Corina del Fabbro, Juliane Preukschas and Madalin Parepa for their assistance during the harvest of the biomass; Corina del Fabbro for statistical advice; Andreas Ensslin and Anne Kempel for helpful comments on the manuscript.

Supporting material

Figure S1 *Effect of ex-situ cultivation (population type alpine garden/wild) and experimental site (Bern/Schynige Platte) on germination of the six test species. ●: Astrantia major, ○: Eryngium alpinum, ▲: Saponaria ocymoides, △: Saponaria lutea, ■: Carex sempervirens, □: Carex baldensis. Filled symbols represent common species, empty symbols represent rare species. Shown are means and standard errors. Significant effects of experimental site (ES), population type (PT) and their interactions (ES x PT) on germination rate are indicated ((*): P < 0.1, *: P < 0.05, **: P < 0.01, ***: P < 0.001).*

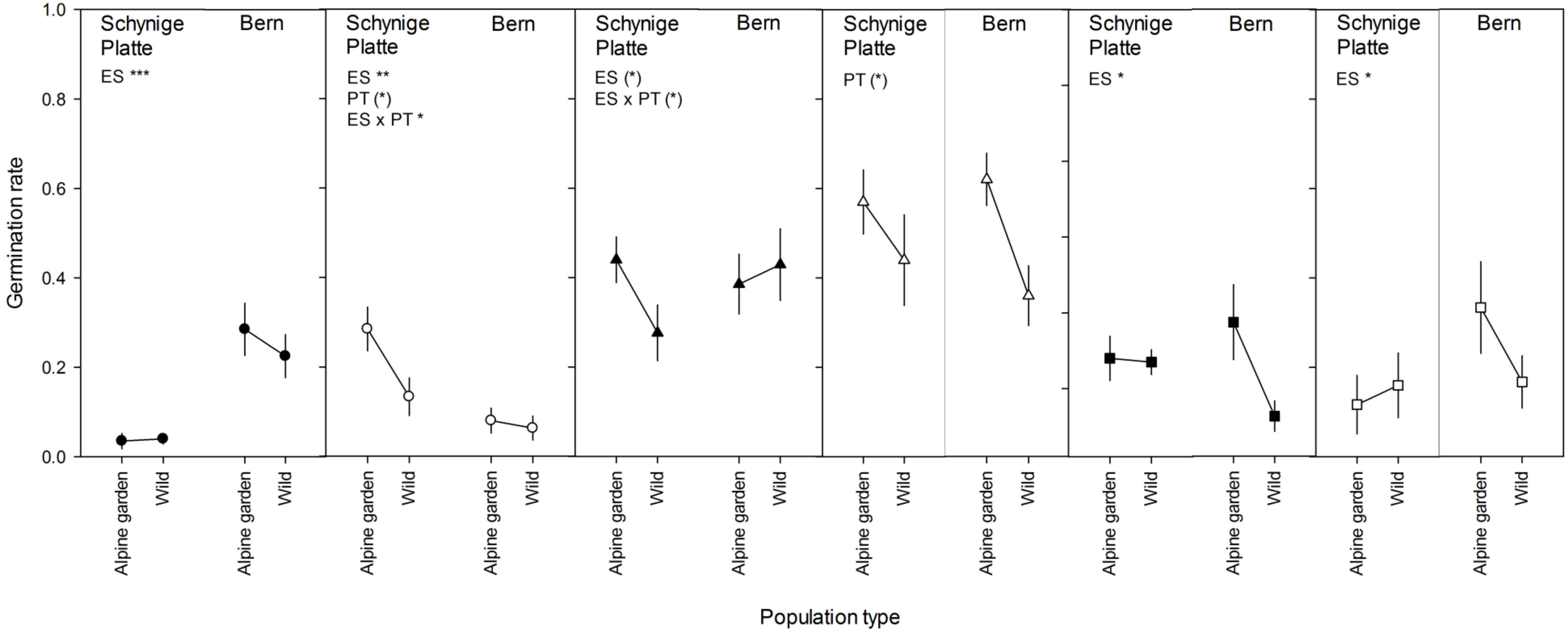


Figure S2 *Effect of ex-situ cultivation (population type alpine garden/wild) and experimental site (Bern/Schynige Platte) on seedling biomass of the six test species (dead seedlings included).* ●*: Astrantia major,* ○*: Eryngium alpinum,* ▲*: Saponaria ocymoides,* △*: Saponaria lutea,* ■*: Carex sempervirens,* □*: Carex baldensis. Filled symbols represent common species, empty symbols represent rare species. Shown are means and standard errors. Significant effects of experimental site (ES), population type (PT) and their interactions (ES x PT) on biomass are indicated ((*): P < 0.1, *: P < 0.05, **: P < 0.01, ***: P < 0.001).*

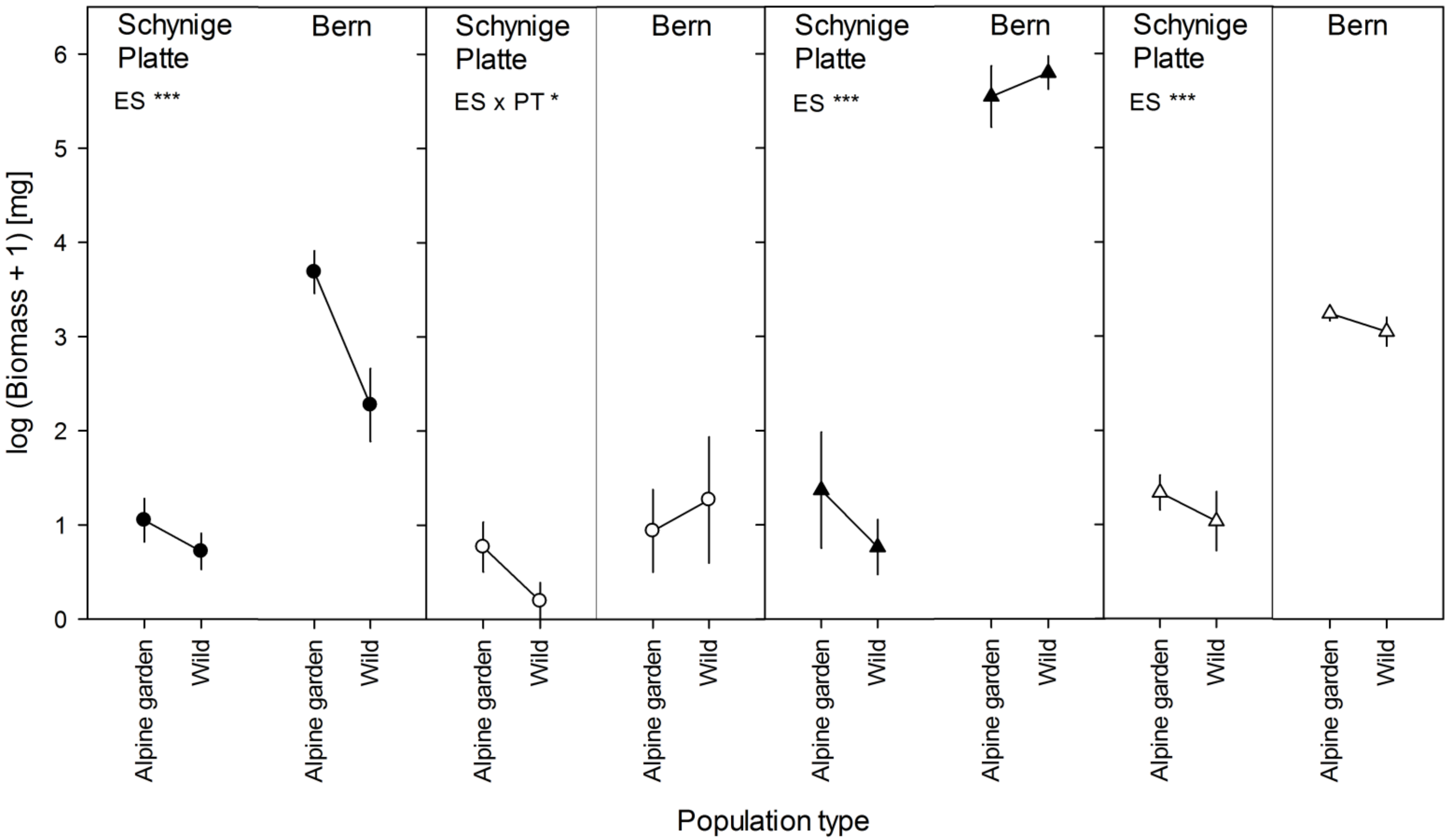


Figure S3 *Effect of adaptation (population type alpine garden/lowland garden) and experimental site (Bern/Schynige Platte) on germination of the six test species. ●: Astrantia major, ○: Eryngium alpinum, ▲: Saponaria ocymoides, △: Saponaria lutea, ■: Carex sempervirens, □: Carex baldensis. Filled symbols represent common species, empty symbols represent rare species. Shown are means and standard errors. Significant effects of experimental site (ES), population type (PT) and their interactions (ES x PT) on germination rate are indicated ((*): P < 0.1, *: P < 0.05, **: P < 0.01, ***: P < 0.001).*

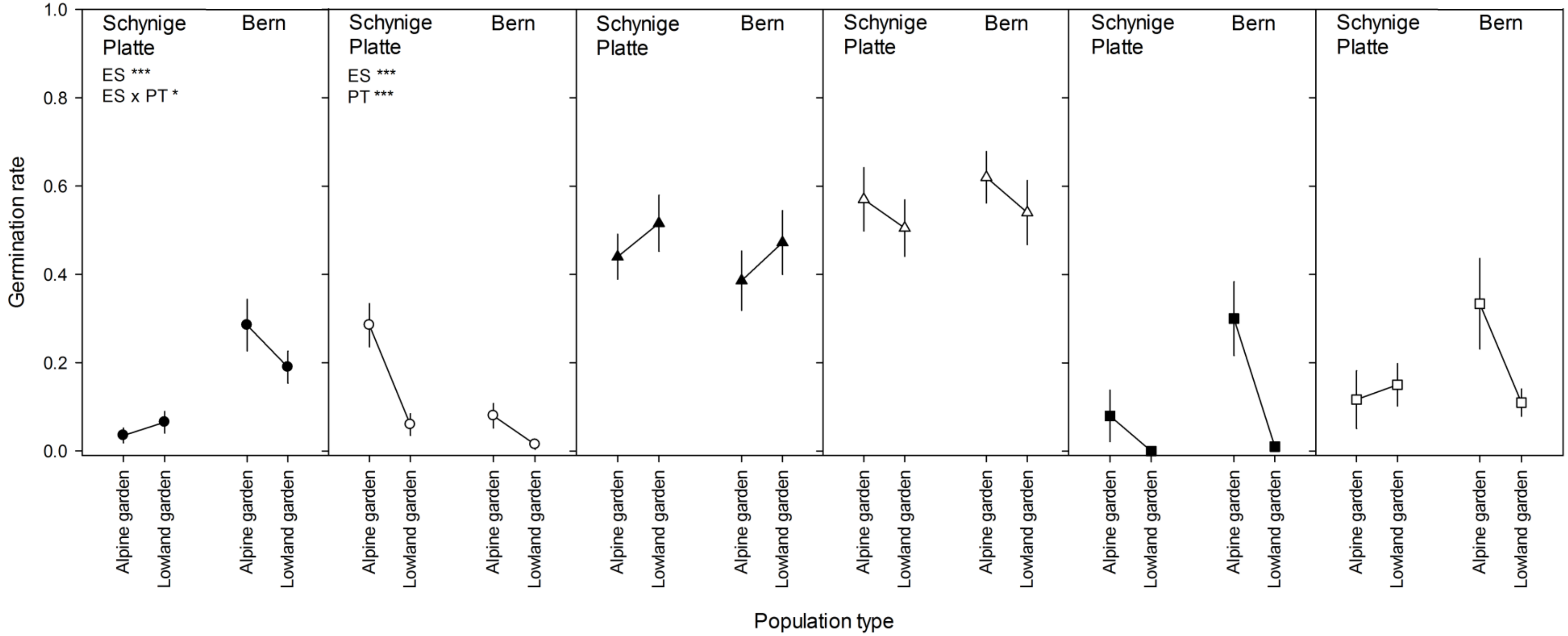
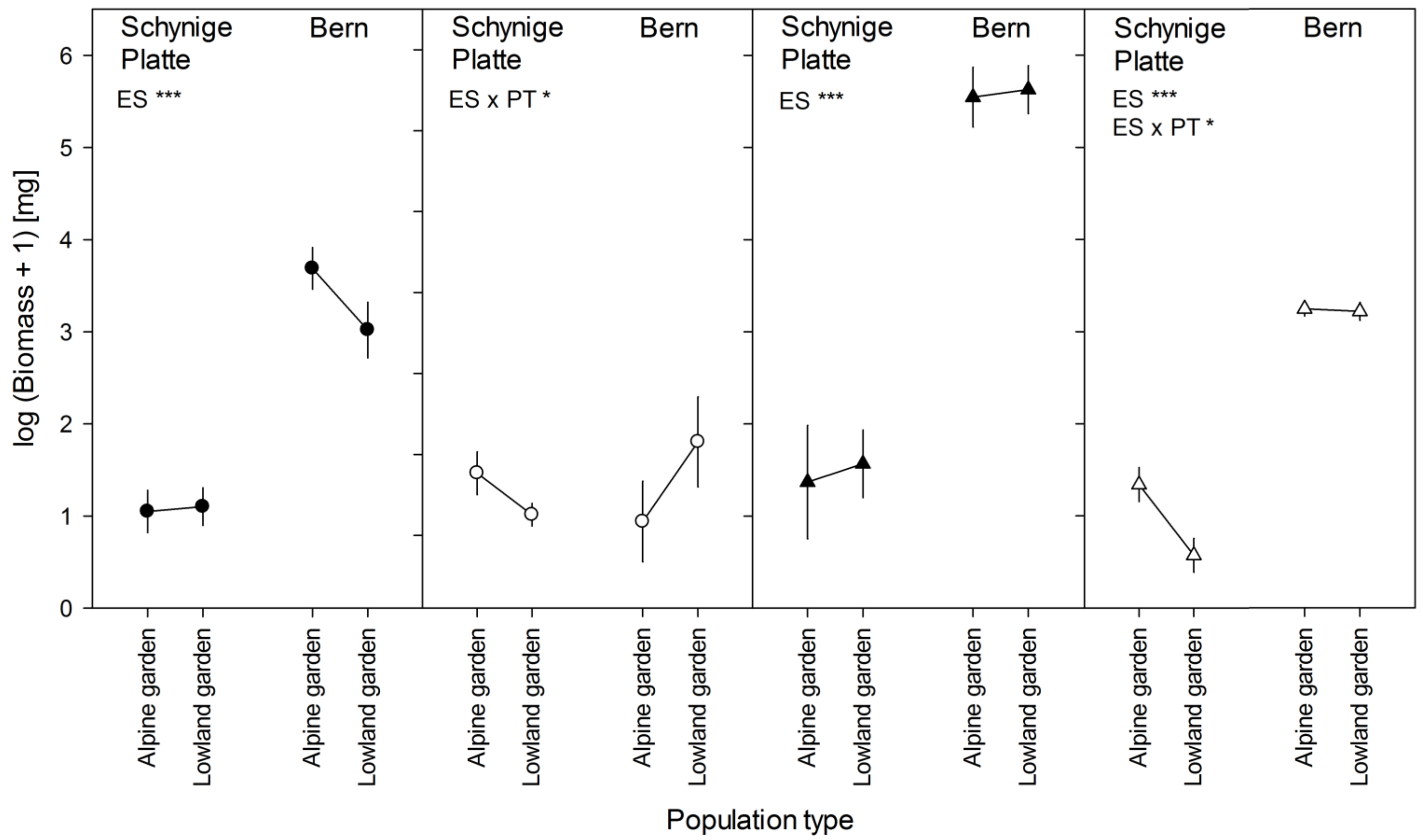


Figure S4 *Effect of adaptation (population type alpine garden/lowland garden) and experimental site (Bern/Schynige Platte) on seedling biomass of the six test species (dead seedlings included). ●: Astrantia major, ○: Eryngium alpinum, ▲: Saponaria ocymoides, △: Saponaria lutea, ■: Carex sempervirens, □: Carex baldensis. Filled symbols represent common species, empty symbols represent rare species. Shown are means and standard errors. Significant effects of experimental site (ES), population type (PT) and their interactions (ES x PT) on biomass are indicated ((*): P < 0.1, *: P < 0.05, **: P < 0.01, ***: P < 0.001).*



Chapter 5

Summary and conclusions

The impact of climate change on plant performance

Understanding the extent and the ways in which changing climatic conditions affect plant performance is currently among the major challenges in plant ecology. As climate directly influences vital physiological processes in plants, changing climatic conditions may likely influence the performance and persistence of plant populations and plant species, the composition of plant communities, and ultimately ecosystem properties.

One of the observed responses to recent climate change is that many species are shifting their distribution range in latitude or elevation to move with the climatic conditions to which they are adapted (Grabherr et al. 1994, Sturm et al. 2001, Walther et al 2002, Parmesan & Yohe 2003, Stöckli et al. 2011, Pauli et al. 2012). However, species that are not able to keep up with the rate of expected future climate change will have to persist under novel climatic conditions by phenotypic plasticity or by adaptation to the novel climatic conditions in order to avoid extinction (Thuiller et al. 2008).

Among the species affected by climate change rare and threatened plant species may be particularly susceptible to changing conditions (Maschinski et al. 2006; Marrero-Gómez 2007; Lawson 2010). Their generally low genetic diversity might negatively affect their viability (Oostermeijer et al. 2003, Leimu et al. 2006) and the adaptive potential of the plant populations (Husband & Campbell 2004, Willi et al. 2006, Leimu and Fischer 2008, Jump et al. 2009). As a consequence, their long-term persistence may be impeded and their extinction risk may increase substantially.

So far, studies investigating the direct effect of climate change, e.g. of a temperature increase on plant performance, have shown varying results. Furthermore, they most often focused on one or few mainly short-lived species, which renders general conclusions and comparisons between rare and common species difficult.

In my thesis, I therefore aimed to assess the effect of changing climatic conditions on the performance of rare and common plant species. To allow for drawing general conclusions I addressed my research questions using multi-species studies which I carried out in botanical gardens.

In chapter two, I studied the effect of changing climatic conditions on the performance of a large and taxonomically and ecologically diverse set of 165 native perennial plant species growing in the outdoor plant collections of five lowland and five alpine botanical gardens in Switzerland. I assessed whether plant survival, growth and reproduction were different for species naturally growing at similar, higher or lower elevations than the botanical garden they were growing in and whether species with a narrower geographic or climatic range were more affected than species with a wider geographic or climatic range. Species survival and especially reproduction of plant species were generally reduced at lower elevations, and thus warmer conditions, than their natural occurrence. Neither more common species nor species with a broader climatic range were able to perform better than rarer species or species with narrower climatic range under the novel conditions. These finding suggests that the persistence of long-lived plant species might be impaired under future climate change, regardless whether they are rare or common.

Climatic conditions not only have a direct effect on plant performance but also strongly influence the timing of important life-history events such as flowering (Forrest & Miller-Rushing 2010). Thus, many plant species respond to global warming by flowering earlier in the season (Fitter & Fitter 2002, Menzel et al. 2006, Gordo & Sanz 2010, Ibáñez et al. 2010). The timing of flowering is crucial as it can affect the reproductive success of the plants. Again, rare plant species may be less able to shift their phenology under changed climatic conditions than common ones due to a reduced adaptive potential. Furthermore, as species may respond differently to environmental cues temporal mismatches in plant-pollinator interactions may occur (Memmott et al. 2007, Hegland 2009, Kudo & Ida 2013, Petanidou et al. 2014). The disruption of important plant-pollinator interactions can have substantial negative consequences for the persistence of both the plant and the pollinator species (Memmott et al. 2007, Kaiser-Bunbury et al. 2010, Burkle et al. 2013, Revilla et al. 2015). Rare plant species might be particularly vulnerable to such consequences of phenological mismatches due to more specialized plant-pollinator-interactions (Orians 1997, Sargent & Otto 2006).

In chapter three, we assessed flowering onset and counted flower visitors of 185 rare and common native plant species originating from different vegetation zones in the lowland Botanical Garden of Bern, Switzerland. At monthly census dates from spring to late summer we recorded the insect-pollinated plant species that had started to flower and observed their flower visitors. Plants naturally growing at higher altitudes flowered earlier in the lowland garden and showed pronounced phenological shifts, independent of whether they were rare or common. The number and duration of flower visits and the number of flower visitor groups were independent of plant origin and of species rarity or commonness. Thus, the plant species naturally growing at high altitudes could attract a similar amount of flower visitors as the plant species naturally growing in the lowland. These results suggest that alpine plants will generally respond to climate change by an earlier onset of flowering, that plant-pollinator interactions are flexible, and that novel interactions may mitigate the consequences of disrupted plant-pollinator interactions caused by phenological or distributional shifts, both for rare and common species.

Consequences of ex-situ conservation for adaptation

Ex-situ collections play an important role in the conservation of plant species. However, novel climatic conditions and unintentional selection may result in adaptive responses of important life-history traits in wild species under ex-situ cultivation. These adaptive responses may affect plant performance and may impede successful reintroduction of the threatened plants into the wild.

In chapter four, I studied the influence of ex-situ cultivation and novel environmental conditions on plant performance by setting up a common garden experiment at two altitudinal levels. I compared germination and seedling performance of three related rare and common alpine species pairs grown from seeds from lowland garden populations, alpine garden populations and natural populations in experimental gardens in the subalpine level and in the lowland. I found differences in germination rates, seedling survival and seedling growth between plants originating from ex-situ collections and plants of wild origin. Moreover, rare and common species responded differently to cultivation under novel environmental conditions. Also, both rare and common species were affected by ex-situ cultivation. When growing the plants in a subalpine environment, I found evidence for maladaptive responses of offspring of the assessed rare species after cultivation in lowland gardens. Thus, the performance of offspring of ex-situ cultivated plants under novel climatic conditions suggests that adaptive responses of plants to the conditions in ex-situ collections are likely and that these adaptive responses can turn maladaptive when offspring are planted back to high-altitude environments.

Botanical gardens as study sites

Botanical gardens with their large taxonomically and ecologically diverse plant collections provide ideal research facilities for studies on plant performance. They facilitate the realization of multi-species studies that are required to search for general patterns and mechanisms in ecology (van Kleunen et al. 2014). Furthermore, in botanical gardens many species are grown together under similar climatic conditions that often differ from the conditions at their natural habitats of origin (Primack & Miller-Rushing 2009). This feature makes them ideal study sites to address many questions related to climate change research (Donaldson 2009, Ali & Trivedi 2011, Blackmore et al. 2011, Primack & Miller-Rushing 2009).

Additionally, today many botanical gardens are actively involved in plant conservation and hold ex-situ collections of rare and endangered plant species (Havens et al. 2006, Donaldson 2009, Blackmore et al. 2011). Therefore, botanical gardens are also ideal sites to study demographic, reproductive, ecological and genetic processes of rare and threatened plant species (e. g. Forrester & Runkle 2000, Hollingsworth et al. 2005, Oldfield 2009, Ensslin et al. 2011, Rucínska & Puchalski 2011, Baker et al. 2014) that are ultimately important for successful conservation management (Donaldson 2009, Ali & Trivedi 2011).

Final conclusions

In conclusion, climate appears to have a strong effect on plant performance and important life-history events such as flowering. Both rare and common plant species seem to be similarly affected. Interspecific interactions, such as plant-pollinator interactions, however, seem to be flexible and might therefore compensate disrupted interactions caused by phenological or distributional shifts. Nevertheless, changes in the performance of rare species due to novel climatic conditions may strongly increase their extinction risk in the future. Moreover, changes in the performance of common species may alter the structure and dynamics of the community and largely affect ecosystems.

Novel climatic conditions affect the performance of plants in ex-situ cultivation. Furthermore, they can lead to maladaptive responses of the plants if they are reintroduced into conditions similar to their natural habitats. My thesis therefore highlights the risk of unintentional selection in ex-situ cultivations and its possible consequences. Thus, I strongly recommend that alpine plants should be cultivated ex-situ only within their natural climatic range.

I addressed the question how changing climatic conditions affect plant performance in general and in ex-situ cultivation in particular by using the large and diverse plant species collections of botanical gardens. The botanical gardens offered an excellent opportunity to study plant performance under novel climatic conditions. Furthermore, they proved to be ideal study sites to perform multi-species studies that are essential for detecting general patterns of plant species responses to novel climatic conditions. I strongly recommend that botanical gardens should more often be integrated into ecological research activities, as they have resources that are beneficial for addressing many different questions in ecology, global change and conservation science.

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Erklärung

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Titel der Arbeit: Climate Effects on Native Plants in Swiss Botanical Gardens

Leiter der Arbeit: Prof. Dr. Markus Fischer

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe o des Gesetztes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

Bern, 7. August 2015 Christine Föhr

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