Population ecology of four common and four rare alpine plant species

Inaugural dissertation of the Faculty of Science

University of Bern

Presented by

Hannah Inniger

from Adelboden (BE)

Supervisors of the doctoral thesis:

Prof. Dr. Markus Fischer

Institute of Plant Sciences, University of Bern

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Prof. Dr. Marco Herwegh

Public defence at the Institute of Plant Sciences, University of Bern

26th March 2024

Promotion committee

Prof. Dr. Markus Fischer

Institute of Plant Sciences, University of Bern

Dr. Daniel Prati

Institute of Plant Sciences, University of Bern

Prof. Dr. Jürg Stöcklin

Department of Environmental Sciences, University of Basel

Chair

Prof. Dr. Matthias Erb

Institute of Plant Sciences, University of Bern

“Plants stand still and wait to be counted…”

(Harper 1977)

Contents

Typical windy ridge at Col de Tsofeirat, Valais.

Chapter 1

General introduction

Alpine environments are characterised by harsh climatic conditions, extreme environmental heterogeneity and high disturbance frequency (Scherrer and Körner 2010). Simultaneously, these environments include hotspots of plant diversity and belong to the most species-rich regions in the world (Körner 2021). The vascular plant flora of the European Alps comprises approximately 4530 species, which is 40 % of the native flora of Europe (Ozenda and Borel 2003). This makes the Alps a fascinating research area for many plant ecologists (Körner 2021).

Alpine plants

Populations of alpine plant species have undergone adaptations to grow in spatially isolated habitats with frequent environmental disturbance (Stöcklin et al. 2009). Due to the pronounced topographical heterogeneity and patchiness of habitats, populations of alpine species are often considered as naturally fragmented (Pluess and Stöcklin 2004; Ægisdóttir et al. 2009; von Büren and Hiltbrunner 2022). Plant reproduction in alpine environments is a challenge, as the growing season is extremely short and exposed to extreme weather conditions, which makes the successful germination and establishment of seedlings uncertain (Bliss 1971; Kobiv 2018). Thus, alpine species are generally highly specialized (Körner 2021). Nevertheless, many species are common and are found in numerous populations throughout the alpine environment (Aeschimann et al. 2004; Lauber et al. 2018). There are also rare alpine species that are present in only a few populations within small geographic ranges (Aeschimann et al. 2004; Lauber et al. 2018). This leads to interesting questions regarding which factors are important for the performance of individual plants and populations in alpine species and how rare species differ from more widespread species.

Population ecology of plants

Investigating the factors that determine plant performance at the level of individuals and populations is a major concern of population ecology (Silvertown and Charleswordth 2009; Gibson 2015). Population ecologists aim to understand what determines the abundance of species and how individuals of a population interact with the surrounding environment (Charles and Godfray 2009). Thereby, a population is a group of individuals belonging to the same species living within the same area (Silvertown and Charleswordth 2009; Gibson 2015). Since plants are sessile organisms, the habitat plays a decisive role in determining the performance of individuals and of populations (Menges 1991). In addition to the habitat, species characteristics and characteristics of the population influence plant performance. Effects of habitat-, population- and species characteristics on plant performance have been researched across numerous plant species (e.g. Lienert 2004; Leimu et al. 2006; Nicole et al. 2011; Jacquemyn et al 2012; Kempel et al. 2020; Kiesewetter and Afkhami 2021; Boyd et al. 2022; Bürli 2022). However, relationships between the different determinants of plant performance are complex and only few studies assess habitat-, species- and population variables together (e.g. Leimu 2010). This is especially true for alpine species, despite their interesting ecology.

Importance of habitat quality for plant performance

The habitat includes many abiotic and biotic factors that vary across space and time (Gibson 2015). While the abiotic environment includes all non-living factors within a habitat, such as microclimatic conditions (temperature, moisture level), soil chemistry (pH, nutrient availability) and disturbance, the biotic environment comprises all living factors within a habitat, ranging from individuals of the same species to individuals of species of other trophic levels (Gibson 2015).

The fundamental niche of a species is the range of abiotic and biotic environmental variables under which the species can survive and reproduce (Hutchington 1957; Chase and Leibold 2009; Fig. 1). In contrast, the realised niche characterises the actual micro-habitat a population of a species occupies. It reflects the actual relationship between the plant and its habitat (Gibson 2015). As a result of biotic interactions or random processes, the realised niche is, in fact, smaller than the fundamental niche (Körner 2021). The actual habitat occupied, or realised niche, can be of varying quality for a species, depending on how close it is to the fundamental optimum of the species (Fig. 1). Therefore, it is plausible that the performance of individuals and of populations of a species could be explained by the distance of the occupied habitat to the fundamental optimum of the species, in other words, by habitat quality.

For example, acidic or eutrophic habitats can restrict population sizes of species that rather prefer non-acidic and nutrient-poor habitats (Boerrigter 1995; Vergeer et al. 2003). Furthermore, previous studies have demonstrated negative effects of reduced habitat quality on plant performance, measured from the number of flowers, recruits, seeds and seed germination (Fischer and Matthies 1998; Vergeer et al. 2003; de Vere et al. 2009; Adriaens et al. 2009; Leimu 2010). Habitat quality was assessed by the absolute mean of environmental variables, such as abiotic soil conditions, topography, disturbance levels, light levels and levels of competition (Vergeer et al. 2003; de Vere et al. 2009; Adriaens et al. 2009; Nicole et al. 2011).

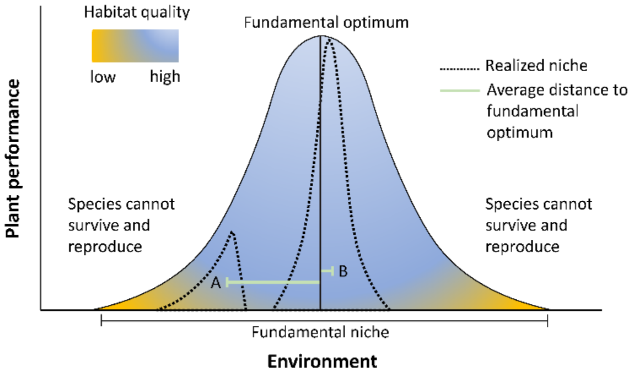

Fig. 1 Schematic representation of the species ecological niche. The realized niches of two populations are indicated with A and B, with A representing a population growing in a habitat further away from the fundamental niche optimum than population B.

Given the diversity of plant species and their different ecological niches, it is obvious that various environmental factors affect the performance of individuals and populations differently for individual species. Thus, more relative and abstract measures of habitat quality could be useful to compare the relationship between plant performance and habitat quality across numerous species. Examples of such variables include local abiotic conditions relative to the target species optimum, habitat heterogeneity and local plant diversity. However, these aspects of habitat quality remain largely unstudied.

Importance of population size for plant performance

Population size is usually regarded as fundamentally important factor for eco-evolutionary processes within species (Gilpin and Soulé 1986; Ellstrand and Elam 1993; Leimu et al. 2006; Hoffmann et al. 2017). Many plant populations are small due to different reasons and as such, encounter various problems. First, small populations have an increased risk of local extinction caused by random catastrophes, demographic and environmental stochasticity (Lande 1993; Menges 1998; Matthies et al. 2004). Additionally, important interactions with mutualists are often less frequent in small populations. For instance, pollinator visits can be reduced in small populations because they are less attractive to pollinators, which can result in a reduced reproductive output (Jennersten 1988; Agren 1996).

Genetic consequences of a small population size include the loss of genetic variation through drift and higher inbreeding levels (Barrett and Kohn 1991; Ellstrand and Elam 1993; Young et al. 1996). Individual fitness has been observed to be reduced in small populations of many species due to inbreeding and loss of heterozygosity (Oostermeijer et al. 1994; Fischer and Matthies 1998; Leimu et al. 2006). Long term, the negative feedback between small population size, genetic variation and individual fitness can reduce the populations’ ability to adapt to changing environmental conditions and eventually to local extinction (Ellstrand and Elam 1993; Young et al. 1996). This process is known as the extinction vortex (Gilpin and Soulé 1986; Höglund 2009; Fig. 2).

Historically, research investigating the relationships between plant performance, population size, and habitat quality has focused on individual fitness as quantified by average values of seed- and size-related traits, as well as on mean offspring performance. Evidence on a few species suggest that variation in plant traits is as well affected by population size and habitat quality (Boerrigter 1995; Karbstein et al. 2023). Furthermore, local adaptation is more frequently observed in large than in small plant populations (Leimu and Fischer 2008). Individual fitness, within-population trait diversity and the presence of local adaptation are features of a population that determine whether the population can survive in the current and future environment. To date, studies that combine these aspects of plant performance are lacking.

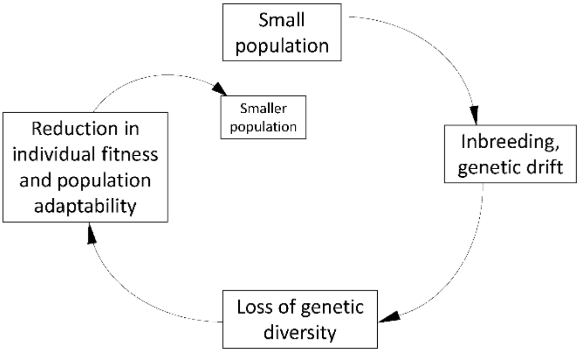

Fig. 2 Schematic representation of the extinction vortex. Adapted from Höglund (2009).

Importance of rarity for plant performance

Plants have evolved different life history strategies to survive in their environment (Adler et al. 2014). Some species grow slowly and reproduce irregularly, but live for a long time. Other species are short-lived, but grow quickly and produce many seeds in a short time (Adler et al. 2014). While some species have broad niches and occur in many different habitats, others are more specialised and have narrow ecological niches that are less abundant (Brown 1984). Such species characteristics can influence plant performance and how plant performance is influenced by the environment. One of the most important life history characteristics is the rarity or commonness of a species.

A common problem of rare species is that they have narrow ecological niches, which makes them habitat specialists (Brown et al. 1984; Gaston and Kunin 1997). Other typical problems of rare species are low genetic diversity, poor recruitment (Gaston and Kunin 1997; Boyd et al. 2022), low dispersal and high self-incompatibility (Gaston and Kunin 1997). Moreover, rare species can suffer more from inbreeding depression and low fertilisation efficiency (Boyd et al. 2022). In addition, relationships between plant performance and population size tend to be stronger for rare than for common species (Leimu et al. 2006).

There are different dimensions of rarity, such as habitat specificity, geographical range size and local abundance (Rabinowitz 1981; Boyd et al. 2022). However, because only a few studies have considered multiple dimensions of rarity, an understanding of the rarest of species is extremely limited (Boyd et al. 2022). Many rare species that have been studied, were widespread in the past and have recently become rare due to human activities. In contrast, many rare alpine species are naturally rare. Species that are naturally rare have evolved over long periods of time in small, isolated populations (Lienert 2004) and typically have low local abundance, small geographic range and high habitat specificity (Harrison et al. 2008). The question arises as to whether there are systematic differences between naturally rare and common species with respect to the relationships between plant performance, population size and habitat quality. Finally, there is a lack of studies that compare rare species with either related (e.g. congeners) or unrelated common species, which are needed to investigate the characteristics of rare plant species (Lienert 2004; Boyd et al. 2022).

This thesis

There are numerous unresolved questions regarding a comprehensive understanding of plant populations. This chapter introduces several of these research gaps, highlighting the limited research on the combined effects of habitat quality, species rarity and population size on plant performance.

Despite the interesting ecology of alpine species and the fact that rare and common species can be studied in the same or in similar habitats, alpine species have been scarcely studied in this respect. Additionally, the investigation of habitat quality mostly considers mean environmental values and neglects important aspects of an environment, such as heterogeneity and plant diversity. Furthermore, plant performance is mainly studied by the populations' average of seed-related traits such as seed number, seed mass and seed germination. Equally vital aspects of a population may be the presence of local adaptation, as well as the extent of within-population trait variation as a crucial prerequisite for further evolution. This thesis aims to contribute to fill these gaps of knowledge.

The objective of this thesis is to study the population ecology of eight alpine plant species (Fig. 1) and to investigate the potential determinants of plant performance. The thesis is based on 92 natural populations of four congeneric species pairs from the plant genera *Androsace* (*Primulaceae*), *Gentiana* (*Gentianaceae*), *Potentilla* (*Rosaceae*) and *Viola* (*Violaceae*). Each of the species pairs includes a common and a naturally rare species native to (sub-) alpine grasslands of Switzerland. I visited each of the populations at least twice, once in summer 2020 and once in summer 2021 to collect seeds and data on morphological traits and population size. I did vegetation records in each population to quantify abiotic conditions via vegetation-based indicator values (Landolt et al. 2010), habitat heterogeneity and plant diversity as aspects of habitat quality based on vegetation data.

I studied plant performance at the level of individuals and of populations in the field and in the greenhouse. I investigated variables of plant performance that are ecologically and evolutionary important, namely individual fitness, within-population trait diversity, population size and local adaptation. As potential determinants of plant performance, I studied species rarity, abiotic conditions, habitat heterogeneity and plant diversity. I studied population size not only as response variable to those determinants but also as an explanatory variable of individual fitness, within-population trait diversity and adaptation. Chapters 2-5 report on results in the format of scientific papers.

In **Chapter 2**, I studied whether there are correlations of seed-related traits and germination with population size among the 92 populations of my study species. This topic has been relatively intensely investigated for non-alpine species; however, alpine species have not been sufficiently studied in this regard. I further asked whether common and naturally rare species differ in the relationship between seed-related traits, germination and population size.

Chapter 3 shows effects of habitat quality on plant performance and population size among 89 populations of the eight study species. As in Chapter 2, plant performance was quantified by seed-related traits and seed germination in a common garden. The novelty of this chapter is the investigation of the combined effects of habitat quality and population size on plant performance. Additionally, I focused on habitat quality variables that have not been considered in this context so far: abiotic mismatch, habitat heterogeneity and plant diversity. In this chapter, the possible correlation between plant fitness and population size is investigated considering habitat quality, and whether systematic differences between naturally rare and common species can be observed.

In **Chapter 4**, I assessed whether within-population trait diversity can be explained by population size, species rarity and by abiotic, biotic and structural heterogeneity. To date, this has scarcely been studied. I quantified variation in individual traits as coefficient of variation (CV) and multidimensional trait diversity as trait richness, trait evenness and trait dispersion in 87 populations of the eight study species.

Chapter 5 reports results of a common garden experiment, where I investigated whether populations of four study species are adapted to local soil and soil biota. It is based on 36 small and large populations of *P. crantzii* and *P. nivea, G. acaulis* and *G. alpina*. I tested whether adaptation to local soil and soil biota is present in plants of the two genera *Potentilla* and *Gentiana*. Further, I asked whether this adaptation is different between small and large populations and between common and naturally rare species. Finally, **Chapter 6** summarises and discusses the most important findings of the study, identifies implications for future research and draws general conclusions.

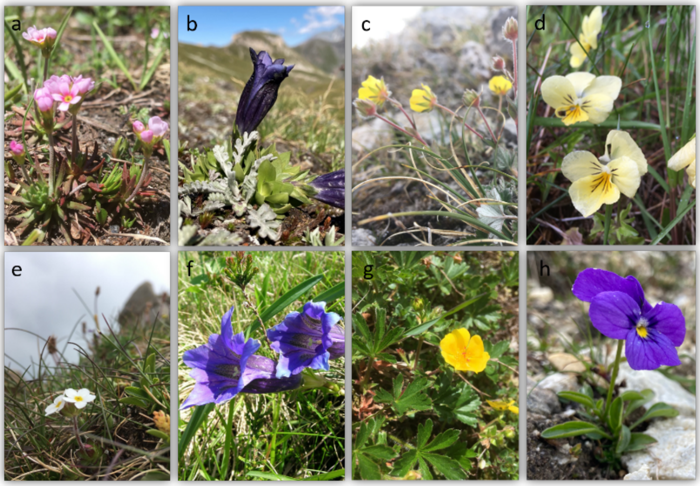

Fig. 3 This thesis concentrates on four congeneric herbaceous species pairs from four different plant families. Each of the species pairs includes a naturally rare and a common species with a (sub-) alpine distribution. The rare species studied in this thesis are (a) *Androsace puberula* Jord & Fourr. (*Primulaceae*), (b) *Gentiana alpina* Vill. (*Gentianaceae*), (c) *Potentilla nivea* L. (*Rosaceae*) and (d) *Viola lutea* Huds. (*Violaceae*). The common species studied in this thesis are (e) *Androsace chamaejasme* Wulfen, (f) *Gentiana acaulis* L., (g) *Potentilla crantzii* (Crantz) Fritsch and (h) *Viola calcarata* L. All species are native to the Swiss Alps and occur in different types of alpine grasslands (*Seslerion*, *Nardion*, *Poion alpinae*, *Elynion*, *Caricion curvulae*, *Caricion firmae*, classification typoCH, Delarze et al. 2008).

Potentilla nivea (*Rosaceae*) on Col de Tsofeirat, Valais.

Chapter 2

Relationships between fitness and population size in four common and four rare alpine plant species

Hannah Inniger, Daniel Prati, Markus Fischer

Abstract Due to habitat fragmentation and climate change, many plant populations become smaller and more isolated and thus more prone to local extinction. Whereas it is well established for lowland species that plants of small populations have lower individual fitness, alpine species have not been sufficiently studied in this respect. It is also not clear whether relationships between population size and fitness vary between naturally rare and common species. We assessed how population size and rarity affect seed set, seed mass, seed number, total seed mass per fruit, germination, time to germination, offspring survival and offspring size in four congeneric alpine plant species pairs (*Androsace chamaejasme* Wulfen, *A. puberula* Jord. & Fourr., *Primulaceae*; *Gentiana acaulis* L., *G. alpina* Vill., *Gentianaceae*; *Potentilla crantzii* (Crantz) Fritsch, *P. nivea* L., *Rosaceae*; *Viola calcarata* L., *V. lutea* Huds., *Violaceae*). Across all eight species, plants from smaller populations produced fewer seeds and had lower total seed mass per fruit than plants from larger populations. This demonstrates that population size also affects fitness in alpine species. Rare species did not have lower individual fitness than common species. Therefore, naturally rare species might be well adapted to their environment. Relationships between population size and fitness were equally pronounced in rare and common species. We conclude

that plant fitness is reduced in small populations in alpine species, also in common species.

Introduction

Due to habitat fragmentation and isolation, populations of plant species are often small and isolated (Lienert 2004; Matthies et al. 2004). Small populations can enter what is known as an extinction vortex due to environmental stochasticity (e.g. climatic variation over years, landslides, floods) and the continuous negative interaction of population size, genetic diversity and fitness (Gilpin and Soulé 1986; Fischer and Matthies 1998; Gaggiotti and Hanski 2004; Leimu et al. 2006). The genetic consequences of a small population size may include random genetic drift, inceased inbreeding and reduced gene flow between spatially isolated populations (Ellstrand and Elam 1993; Young et al. 1996). The reduced genetic diversity and accumulation of deleterious mutations will decrease the fitness of plant individuals within the population. In the long term, this can diminish the population’s ability to adapt to changing environmental conditions (Ellstrand and Elam 1993; Young et al. 1996). Recent studies on mainly non-alpine plant species demonstrate positive relationships between population size, genetic diversity and fitness, indicating the presence of an extinction vortex in small populations (Fischer and Matthies 1998; Leimu et al. 2006).

Relationships between population size and fitness have not yet been studied in herbaceous alpine plant species. Alpine environments differ in several aspects from lowland environments. High mountain regions are very species-rich and characterised by harsh conditions and a pronounced level of environmental heterogeneity and stochasticity (Scherrer and Körner 2010; Scherrer and Körner 2011; von Büren and Hiltbrunner 2022). Due to the complex topography, suitable habitats are restricted to small areas, which often allows plants to exist only in small and isolated populations (Reisch and Rosbakh 2021). In addition, limited pollen and seed dispersal and the phenological mismatch between populations of different micro habitats lead to a restricted gene flow between populations (Reisch and Rosbakh 2021). Hence, alpine species generally exhibit lower genetic diversity and higher genetic differentiation than lowland species (Reisch and Rosbakh 2021). Therefore, we expect a positive relationship between population size and fitness also in alpine species.

In a meta-analysis of the relationship between population size and fitness, no significant difference was observed between rare and common species (Leimu et al. 2006). However, most of the species that were considered as rare have become rare only recently due to human activities. In contrast, rare alpine species are naturally rare. To the best of our knowledge, no study has specifically examined the relationship between population size and fitness in naturally rare species. As rare species are generally less fit and have lower genetic diversity (Boyd et al. 2022), negative fitness consequences of a small population size might be more prominent in rare than in common species. On the other hand, populations of rare species may have undergone purging of genetic load (van der Valk et al. 2019). In this case, relationships between population size and fitness may not differ between naturally rare and common species.

Here, we studied the relationships between population size and fitness in four common and four rare congeneric alpine plant species in two consecutive years (2020, 2021) in the Swiss Alps. We studied seed-related traits (seed set, seed mass, seed number and total seed mass per fruit) in 92 populations in the field and seed germination, time to germination, offspring survival and offspring size in a greenhouse. We addressed the following questions: (I) Is there an effect of population size on the investigated fitness components? (II)

Are plants of naturally rare species less fit than plants of common species? (III) Is the effect of population size on individual fitness different among naturally rare and common species?

Methods

Study species

We selected four congeneric pairs of grassland species with a subalpine-alpine distribution from four different plant families based on expert knowledge. Each pair consisted of one common and one rare species that were phylogenetically relatively closely related and thus comparable. We defined species rarity based on geographic range (large vs. small), habitat specificity (generalist vs. specialist) and local abundance (dense vs. sparse) (Rabinowitz 1981). *Androsace puberula* Jord. & Fourr., *Gentiana alpina* Vill., *Potentilla nivea* L. and *Viola lutea* Huds. are naturally rare herbaceous plant species which occur only within a restricted geographic range with sparse local abundance through the Swiss and European Alps (Lauber et al. 2018; GBIF.org 2023). *Androsace chamaejasme* Wulfen (*Primulaceae*), *Gentiana acaulis* L. (Gentianaceae), *Potentilla crantzii* (Crantz) Fritsch (*Rosaceae*) and *Viola calcarata* L. (*Violaceae*) are common herbaceous plant species that are present over a wide geographic range with pronounced local abundance throughout the Swiss and European Alps (Lauber et al. 2018; GBIF.org 2023). Except for *V. lutea,* the rare species are strongly restricted to their habitat (Lauber et al. 2018). With the exception of *G. acaulis,* the common species are not strongly restricted to their habitat (Lauber et al. 2018). All species are perennial and insect pollinated. Both *Potentilla* species are facultative apomicts.

Seed collection

For each species, we visited 10-13 different populations (N = 92) at various elevations (1390-2810 m.a.s.l.) in two consecutive years (2020, 2021) in the Swiss Alps (see Fig. S2-5 Supporting information for sampling locations). We selected the populations based on the Info Flora database, which collects occurrence data on vascular plants in Switzerland up to a 1 x 1 kilometre scale (infoflora.ch 2020). There was no information available on the populations except the coordinates of their location. We selected the populations of the rare species as far as possible across their whole distributional range throughout Switzerland. We selected the populations of the common species within a range size comparable to their congeneric rare partner species. If a rare species had a disjunct distribution in Switzerland, such as *P. nivea* and *G. alpina*, we also sampled their common congeneric partner species within these disjunct regions.

We defined the boundaries of the population where we found the outermost individuals. For each population, we estimated population size by counting the number of fertile (flowering and fruiting) individuals. Whenever there were more than 250 fertile individuals in a population, we estimated the area of these 250 individuals and extrapolated over the area of the whole population to get an estimate of the total number of fertile individuals. For each species, we collected fruits of a total of 2-40 individuals per population, depending on the total number of fertile individuals (see Supporting information). We air-dried the fruits in paper bags directly after collection.

Quantification of fitness components

We defined seed set as a binomial variable indicating whether a fruit contained viable seeds or not. We counted and weighed the viable seeds of an individual together to the nearest milligram. We sowed a maximum of 60 seeds per individual (N = 1536) in separate pots filled with seedling soil (Substrate 167, RICOTER Erdaufbereitung AG, Aarberg). We stratified the sown seeds outside for three months from December to February (mean temperature and mean air humidity during these three months in Bern are -0.97 °C and 78.67 %; climate-data.org 2023). We selected three months of stratification, because this corresponds approximately to the minimum time span of snow cover duration in the alpine zone (Klein et al. 2016). Also, many studies used this amount of time for a successful stratification of alpine seeds (Cavieres and Sierra-Almeida 2018). Outside stratification allowed for natural freezing events, simulating overwintering of alpine seeds. We covered the pots with a thin fleece to simulate darkness by snow cover and to protect the seeds from light, birds and heavy rain. We watered the seeds weekly with a water sprayer.

After three months, we placed the pots inside the greenhouse to initiate germination (min 12 °C, 13 h light, 40 % air humidity), to approximately match spring conditions in the (sub-) alpine zone. Temperature rose up to a maximum of 20 °C depending on weather. We recorded germination every second day over five weeks by counting the total number of germinated seeds per mother plant. We defined the number of days until the first seed germinated as the germination initiation time of an individual plant. After five weeks of growth, we measured offspring size from soil to the longest leaf (stretched) of one random seedling per mother plant. Because the percentage of germinated seeds was less than 10 % among the *Androsace* and the *Viola* species, we measured offspring size only for the *Potentilla* and *Gentiana* species. We repeated germination in the following winter (2021) for the *Androsace* and *Viola* species after three months of stratification in a dark cool chamber (4 °C and weekly watering). However, the percentage of germinated seeds was as low as the previous year (< 0.5-12 %).

Statistical analysis

We performed all statistical analyses in R (R core team 2022). To test whether the fitness components depend on population size and rarity, we ran separate linear mixed models fitted by restricted maximum likelihood for seed mass, seed number, total seed mass per fruit, time to germination and offspring size using the function “lmer” from the R package "lme4" (Bates et al. 2015). We ran separate generalised linear mixed models with a binomial distribution fitted by restricted maximum likelihood for seed set, germination and offspring survival using the function “glmer” from the "lme4" package. We z-transformed numeric explanatory variables to correct for different scales and log-transformed population size (number of fertile individuals), seed mass, seed number and total seed mass per fruit to meet the assumption of a normal distribution.

We included the following variables in the following order as fixed explanatory terms in each of the full models: rarity and the rarity-genus interaction, rarity and the rarity - population size interaction, collection date, elevation and collection year. We did not include species in the models, as this would have been redundant to the genus - rarity interaction. We included population as a random term in each model. In the seed mass model, we included the number of seeds as weights to account for the varying seed number from which we calculated the average seed mass of an individual plant. In the germination and time to germination models, we included seed mass as an additional fixed factor. In the germination and time to germination models, we included tray (where we grouped the pots in the greenhouse) as an additional random factor. Due to convergence problems, we did not include elevation in the full model of germination. In the seed set model, we had to remove the interaction terms to avoid convergence problems.

To study the strength and the direction of the relationship between population size and fitness for each species, we also analysed species separately. For this purpose, we ran the same models described previously but without the genus and rarity terms.

We tested whether rare species generally occurred in smaller populations than common species. For this purpose, we ran a linear model with population size as response variable and rarity, genus, the rarity - genus interaction, collection date and elevation as explanatory variables.

We simplified models with the function “dredge” from the "MuMIn" package (Bartoń 2022) based on the Akaike information criterion (AIC), without removing the variables of interest (population size, rarity). We calculated marginal and conditional R^2 of the final models with the function “r.squaredGLMM” from the “MuMIn” package. We evaluated the final models based on normality of the residuals. We considered p-values from the ANOVA table (type II Wald χ^2-square tests for generalised mixed effect models, type III F-tests based on Satterthwaite's method for linear mixed effect models) smaller than 0.05 as significant and smaller than 0.1 as marginally significant.

Results

Effects of population size on fitness

In general, rare species tended to occur in smaller populations than common species ($p = 0.22$; Fig. 1; Table S1 Supporting information). Across all species, plants of small populations produced fewer seeds ($p < 0.05$) and had lower total seed mass per fruit ($p < 0.05$; Fig. 2b and c; Table 1). Plants of small populations tended to produce seeds with lower germination probabilities ($p = 0.16$; Fig. 2e; Table 1). This was not significant because in

G. alpina, plants of small populations tended to produce seeds that germinated better (Fig. S1 Supporting information). Seed set, seed mass, time to germination, offspring survival and offspring size did overall not depend on population size (Table 1). Seed mass, total seed mass per fruit and seed number were significantly lower in 2021 than in 2020 (Table 1), probably because the summer in 2021 was much shorter and colder than in 2020. Seed mass decreased with higher elevation ($p < 0.001$; Table 1). Germination of *P. nivea* was lower for plants from sites with higher elevation ($p < 0.01$; Table S3 Supporting information).

When we analysed the relationship between fitness and population size separately for each species, we found that plants of small populations of the common *P. crantzii* and *A. chamaejasme* had a reduced seed set ($p < 0.1$ and $p < 0.05$; Fig. 3; Table S2 and S4 Supporting information). In the rare *P. nivea*, plants of small populations produced seeds with significantly lower germination probabilities than plants of large populations ($p < 0.001$; Fig. 3; Table S3 Supporting information). In the rare *G. alpina*, plants of small populations produced fewer seeds and had lower total seed mass per fruit ($p < 0.05$ and $p < 0.1$; Fig. 3; Table S2 Supporting information). In *G. acaulis*, *A. puberula*, *V. calcarata* and *V. lutea*, fitness was not affected by population size when analysed within species (Table S3, S4 and S5 Supporting information).

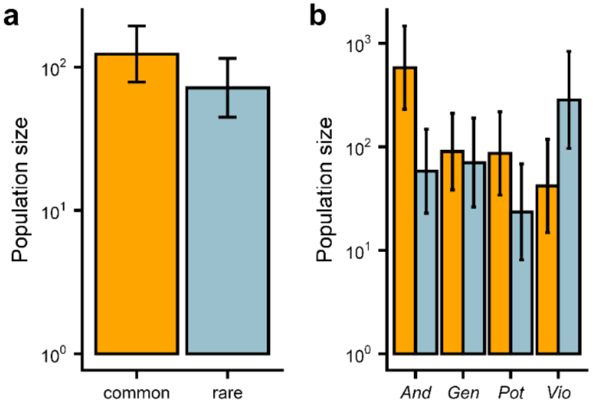

Fig. 1 Population size of four common and four rare alpine plant species. Shown are effects of rarity (a) and of the rarity - genus interaction (b) on population size in the eight study species predicted by a linear regression model (*And* = *Androsace*, *Gen* = *Gentiana*, *Pot* = *Potentilla*, *Vio* = *Viola*). Error bars show upper and lower limits of 95 % confidence intervals. Blue bars indicate rare species and yellow bars indicate common species.

Effects of rarity on fitness

Across all species, plants of rare species had significantly higher seed set than plants of common species ($p < 0.05$; Fig. 2a; Table 1). Plants of rare species also produced significantly heavier seeds than plants of common species ($p < 0.01$; Table 1). This was due to plants of the rare *A. puberula*, which produced extremely large seeds compared to all other species. Plants of rare species germinated significantly earlier than common species ($p < 0.001$; Fig. 2d; but with high residual variance; marginal $R^2 = 0.01$; Table 1). Furthermore, plants of rare species produced seeds with higher germination probability than plants of common species ($p < 0.001$; Fig. 2e; Table 1). Offspring size was significantly smaller among plants of rare species than among plants of common species ($p < 0.01$; Table 1). Seed number, total seed mass per fruit and offspring survival did not differ among plants of rare species and plants of common species (Fig. 2b and c; Table 1). Across all species, none of the fitness traits was significantly affected by the interaction between rarity and population size.

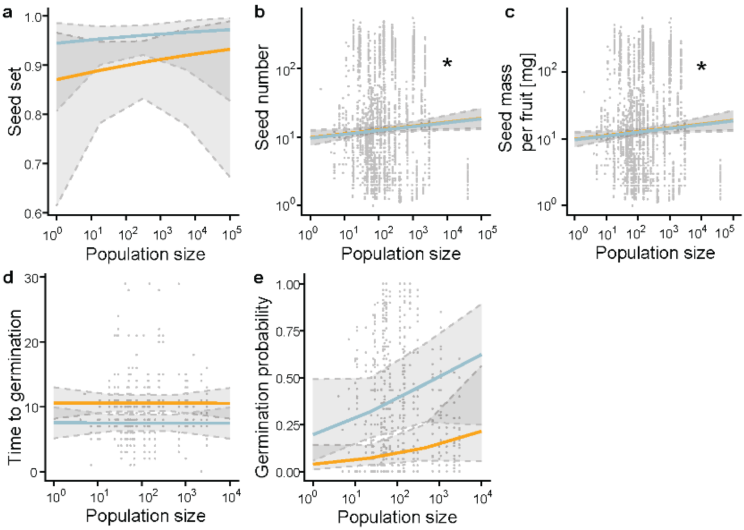

Fig. 2 Relationships between population size and fitness in four rare and four common alpine plant species. Shown are effects of population size predicted by mixed effect models on seed set (a), seed number (b) and total seed mass per fruit (c) across all eight species, and on time to germination (number of days until the first seed germinated, d) and on germination (e) across species of the genera *Gentiana* and *Potentilla*. Blue lines illustrate rare species and yellow lines represent common species. Grey shadows show upper and lower limits of 95 % confidence intervals. Grey dots indicate observed values and stars indicate significant relationships.

Table 1 ANOVA tables of mixed effect models investigating the effects of population size and rarity on fitness traits across the eight study species. Numeric variables were scaled and population size, seed mass, seed number and total seed mass per fruit were transformed with the decadic logarithm. Seed set and germination were fitted as binomial response variable (seed set: whether a fruit contained viable seeds or not, germination: number of germinated seeds, number of seeds that did not germinate, "cbind" function from base R). Final models contained only fixed effects for which there are statistical values in the table (χ^2: Chi squared, SS: sum of squares, F: F-statistics, df: degrees of freedom; type II Wald χ^2 tests for generalised mixed effect models, type III F-tests based on Satterthwaite's method for linear mixed effect models). Number of groups indicate the number of levels for each of the random effects. For the variables included in the final models, significance levels are given: P < 0.1; °, P < 0.05; *, P < 0.01; **, P < 0.001; ***.

		Seed set		Seed mass		Seed number		Total seed mass	
	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F
Fixed effects									
Rarity	1	4.45	0.04*	18.36	7.81**	0.01	0.13	0.01	0.12
Genus	3	43.77	1.7e^{-9}***	482.97	68.51***	141.48	488.03***	141.61	487.96***
Population size	1	0.21	0.65	3.28	1.39	0.5	5.21*	0.51	5.25*
Elevation	1			42.08	17.91***				
Collection date	1			727.8	309.71***				
Collection year	1			1450.66	617.33***	7.21	74.6***	7.17	74.1***
Genus : rarity	3			382.65	54.28***	7.54	26.0***	7.57	26.08***
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		3.27	1.81	0.01	0.1	0.02	0.14	0.02	0.14
Residual				2.35	1.53	0.1	0.31	0.1	0.31
Number observations			3323		2730		2728		2730
Number groups			92		90		90		90
R^2m/R^2c			0.21/0.61		0.04/0.05		0.81/0.84		0.81/0.84
		Germination		**Time to germination**		**Offspring survival**		**Offspring size**	
	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F
Fixed effects									
Seed mass	1	34.25	4.9e^{-9}***						
Genus	1	0.13	0.72	160.68	8.52**	70.32	<2e^{-16}***	0.29	53.73***
Population size	1	2.0	0.16	0.01	0.3e^{-3}	0.16	0.69	0.2e^{-2}	0.33
Rarity	1	13.2	0.3e^{-3}***	329.98	15.7***	0.36	0.55	0.06	10.64**
Genus : rarity	1	11.58	0.7e^{-3}***	0.05	8.75**			0.05	8.75**
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		2.36	1.54	0.2	0.45	0.94	0.97	0.3e^{-2}	0.06
Tray		0.07	0.26	0.8e^{-2}	0.09				
Residual				18.86	4.34			0.5e^{-2}	0.07
Number observations			701		590		590		2555
Number groups			45, 10		39, 10		39		37
R^2m/R^2c			0.26/0.97		0.01/0.03		0.66/0.93		0.51/0.7

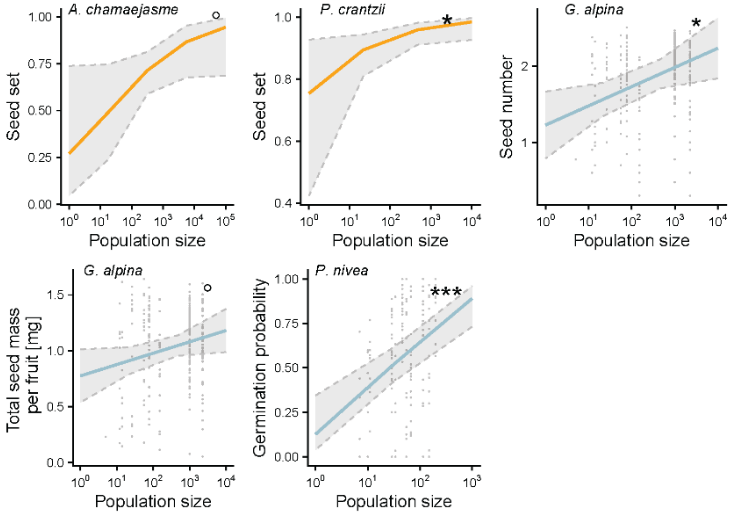

Fig. 3 Relationships between population size and fitness in *A. chamaejasme*, *P. crantzii*, *G. alpina* and *P. nivea*. Fits of mixed effect models and upper and lower limits of 95 % confidence intervals are drawn for fitness traits that were marginally or significantly affected by population size when we analyzed the eight study species separately. Total seed mass per fruit [mg] for *G. alpina* was log-transformed. Blue lines illustrate rare species and yellow lines represent common species. Grey dots indicate observed values.

Discussion

Population size affects fitness in alpine species

In general, populations of rare species tended to be smaller than populations of common species. This might increase their risk of local extinction due to environmental or demographic stochasticity (Lande 1993).

Overall, the significant positive relationships of seed number and total seed mass per fruit with population size (Fig. 2b and c) and the trend of higher germination rates in larger populations support our hypothesis of a positive relationship between population size and fitness in alpine species. Seed number is a strong indicator of plant fitness (Boyd et al. 2022) and limited seed availability is an important reproductive constraint for populations of alpine plant species (Lindgren et al. 2007; Frei et al. 2012). Germination and seedling establishment are difficult within the short reproductive season and exposed to adverse alpine conditions such as frosts or droughts (Kobiv 2018). It appears likely that populations with limited seed production and low germination rates are at higher risk of local extinction.

Different mechanisms could explain why plants of small populations produce fewer seeds. A reduced seed number can result from reduced pollination visitation, since small populations are less attractive for insects (Jennersten 1988; Agren 1996). This effect might be even stronger in alpine habitats, where insect activity is generally lower due to environmental constraints (Totland and Sottocornola 2001). Despite the absence of genetic variation and genetic differentiation data, small populations of our study species might suffer from reduced gene flow within and between populations, increased gene drift and inbreeding. This could translate into reduced individual fitness. It remains unknown whether biotic or genetic reasons (or both) explain the reduced seed number in small populations of our study species. Our results align with previous studies on lowland species, highlighting seed number as the fitness parameter most dependent on population size (Fischer and Matthies 1998; Morgan 1999). Nevertheless, experimental studies are required to understand the mechanisms underlying the relationship between population size and seed production.

We observed only positive but no negative relationships between plant fitness and population size, indicating that there might be no trade-off between seed quantity and quality in populations of our study species. While larger seeds are generally more robust under environmental stressors as for instance frost, drought or competition, smaller seeds can be produced in larger numbers with the same amount of resources (Bufford and Hulme

2021). According to Lázaro and Larrinaga (2018), trade-offs between seed quantity and quality are particularly strong in alpine species. Our results suggest that the extent to which such a trade-off is present in populations of alpine species might vary across species. However, we observed significantly lower seed mass in populations at higher elevations. This might be due to the short vegetation time, which can constrain seed mass by the short time available for seed provisioning (Baker 1972). As lower seed mass led to lower germination rates in our study species, reproduction might be limited at high elevations. This could put even more pressure on small populations that already suffer from reduced fitness.

We conclude that there is a positive relationship between population size and fitness in our study species. Therefore, small populations of these species might have an increased risk of local extinction. Moreover, large populations that experience a bottleneck due to droughts or increased competition could also fall into an extinction vortex.

Rare species do not have reduced individual fitness

Our data do not support the hypothesis that plants from rare species are less fit than plants from common species. Plants of *G. alpina* and *P. nivea* produced offspring with smaller size compared to the common *G. acaulis* and *P. crantzii*. This pattern can be explained on one hand by rarity, but on the other hand also by an adaptation of the plants of these species to high alpine habitats (Halbritter et al. 2018). Seed set and germination were even higher in rare than in common species, indicating that naturally rare species are well adapted to their environment. Therefore, our results support our alternative hypothesis that genetic load has been purged in populations of naturally rare species.

Beside the differences in seed set and germination, time to germination was significantly shorter among rare than among common species, but the variance explained by this model was very low ($R^2 m < 0.1$). Alpine species implement different germination strategies depending on the species habitat (Tudela-Isanta et al. 2018); hence, time to germination is may not provide an accurate estimate of plant fitness. Since *G. alpina* and *P. nivea* both occur at high alpine sites, the earlier onset of germination in these species could reflect adaptation to a very short vegetation time in high alpine habitats rather than an effect of rarity, *per se*. In addition, earlier germination is not necessarily advantageous, as drought or frost can threaten the seedlings. A more meaningful estimate of plant fitness might be the *variation* in time to germination. Germination is the most critical stage in a plant's life cycle and plasticity in germination could play an important role in the response of alpine species to climate change (Paulů et al. 2017).

To conclude, our results do not confirm the very general observation of a reduced fitness and reduced survival in rare species (Boyd et al. 2022). Rather, they agree with Paulů et al. (2017), who studied 18 congeneric species pairs from central European mountains and did not find reduced individual fitness in rare species. Hence, naturally rare species might be well adapted to their environment and other reasons than low plant fitness must be responsible for their rarity.

In general, the assessment of purely short-term fitness traits is a limitation of not only this study but also many others. First, alpine plants reproduce with a high variability among years, due to aspects such as variation in snowmelt time (Kudo and Hirao 2006). Therefore, alpine species should be sampled over several years to obtain data that are more reliable. Second, an important long-term fitness parameter is the population's ability to adapt to changing environmental conditions. In the context of climate change, it might be important to investigate the extent of adaptive trait plasticity (e.g. onset and duration of flowering and germination under different environmental conditions) as an indicator for adaptive capacity in alpine species.

Another limitation of our study is that the analysis of germination, time to germination, offspring survival and offspring size included only half of our study species, because the *Androsace* and *Viola* species germinated poorly (<0.5-10 %). Either the commonly known conditions needed to break seed dormancy for alpine species (cold stratification and moist-chilling, warm-cued germination and changing temperature and light conditions; Shimono and Kudo 2005; Fernández-Pascual et al. 2021) are unsuitable for these four species, or this result shows that half of our study species are mostly incapable of germination. Germination already failed in some other alpine species, regardless of the conditions (Shimono and Kudo 2005). However, this does not weaken our conclusion of a positive relationship between fitness and population size in alpine species. We still observed a positive relationship between germination and population size in the reduced dataset. In addition, we observed positive relationships between seed-related traits and population size across all eight species. For larger and elaborate germination experiments of alpine species, we strongly recommend small pilot studies in advance to define suitable germination conditions.

Relationships between population size and individual fitness are equally strong for rare and common alpine species

We hypothesised that rare species show stronger relationships between population size and fitness than common species. However, relationships between fitness and population size were equally strong in rare and common species. This again supports our alternative hypothesis that genetic load has been purged in populations of our rare study species.

On the species level, we found significant positive relationships between fitness and population size in the rare *G. alpina* and *P. nivea* and in the common *A. chamaejasme* and *P.crantzii*, indicating that an extinction vortex is ongoing in small populations of these species. Both *Potentilla* species form apomictic seeds (Hörandl et al. 2011; Nylehn et al. 2003), probably to speed up reproduction as an adaptation to short vegetation periods at high elevations (Schinkel et al. 2016). Genetic variability can be strongly reduced in small populations with a large proportion of apomicts (Adolfsson and Bengtsson 2007), which might explain the low plant fitness in small populations of our *Potentilla* species. Hence, negative effects of a small population size on individual fitness might depend on the reproductive strategy.

The fact that we did not observe significant relationships between population size and fitness on the species level in *A. puberula*, *G. acaulis*, *V. lutea* and *V. calcarata* does not mean that an extinction vortex is absent in small populations of these species. Otherwise, we would not have observed significant overall effects. It is likely that the relationship is simply weaker in these species and therefore not significant with limited statistical power.

Studies on non-alpine species found no significant difference between rare and common species; neither in the strength of the relationship between population size and fitness nor in population size *per se* (Leimu et al. 2006). Our results suggest that although naturally rare species tended to occur in smaller populations, the relationship between fitness and population size might be equally strong in naturally rare and in common alpine species. Consequently, populations of both rare and common alpine plant species may face the potential of entering an extinction vortex. The presence of an extinction vortex in alpine species could limit their ability to adapt and migrate, making them more susceptible to rapid environmental change. Hence, these species could be severely threatened by climate change, which is predicted to place high climatic and biotic pressure on alpine populations (Theurillat and Guisan 2001).

Conclusion

Our study demonstrates that individual fitness is affected by population size in alpine plant species. Across all species, individuals of small populations produced fewer seeds, a crucial trait for the survival of plant populations in harsh alpine conditions. In four out of eight species, individuals of small populations also had a reduced seed set or reduced germination ability. Until now, research has largely ignored herbaceous alpine species in the context of the relationship between population size and fitness. Our study suggests that an extinction vortex might be ongoing in small populations of alpine plant species. To gain a better understanding of the underlying mechanisms, additional studies that consider genetic diversity are necessary. Relationships between population size and fitness were equally pronounced in rare and common species, suggesting that even common alpine species might be at risk of falling into an extinction vortex. This could increase their vulnerability to environmental changes.

Acknowledgements

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Supporting information

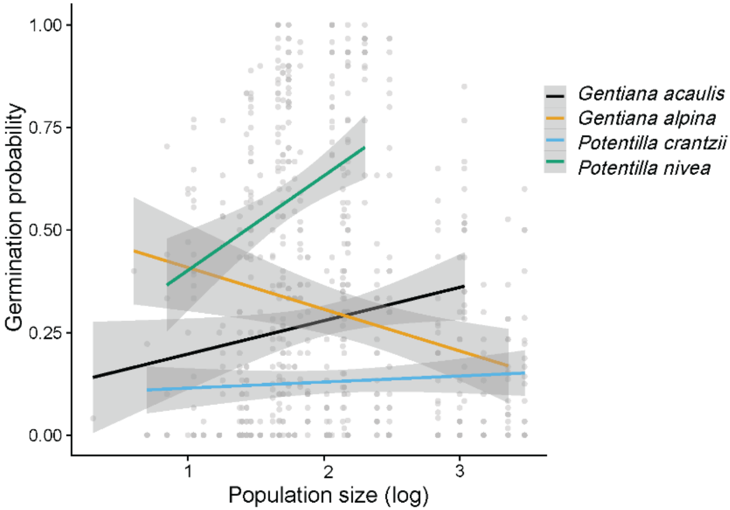


Fig. S1 Relationship between plant germination and population size in two rare (*G. alpina*, *P. nivea*) and two common (*G. acaulis* and *P. crantzii*) alpine plant species. Lines show relationships of germination probability and population size predicted by linear regression. Grey shadows indicate lower and upper limits of 95 % confidence intervals. Grey dots show observed values. When analysed by species, the relationship was significant for *P. nivea* ($p < 0.01$; Table S3).

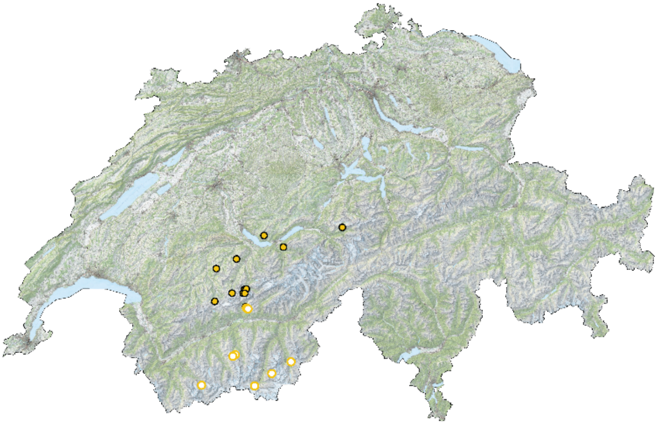


Fig. S2 Map of Switzerland (1:25000, © swisstopo) with locations of sampled populations of the common *Androsace chamaejasme* (yellow dots with black outline, N = 12) and the rare *Androsace puberula* (white dots with yellow outline, N = 11). Dots are sometimes overlapping, however, the minimum distance between two populations was 250 m. Maps were edited by Hinderling J. in QGIS.

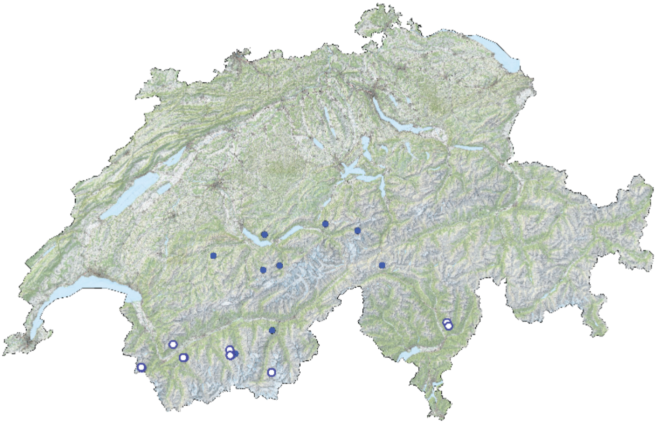


Fig. S3 Map of Switzerland (1:25000, © swisstopo) with locations of sampled populations of the common *Gentiana acaulis* (blue dots with black outline, N = 12) and the rare *Gentiana alpina* (white dots with blue outline, N = 11). Dots are sometimes overlapping, however, the minimum distance between two populations was 250 m. Maps were edited by Hinderling J. in QGIS.

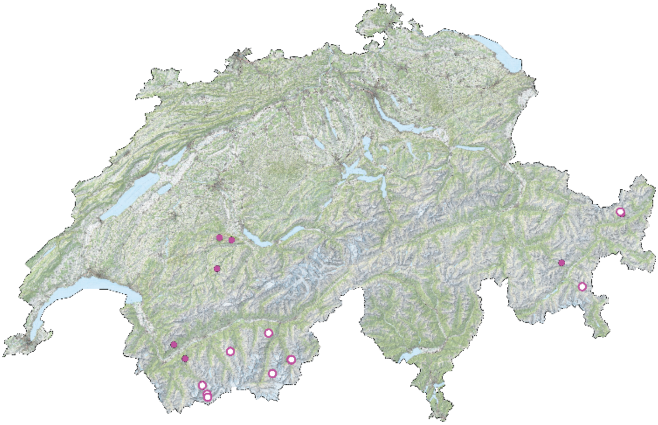


Fig. S4 Map of Switzerland (1:25000, © swisstopo) with locations of sampled populations of the common *Potentilla crantzii* (pink dots with black outline, N = 11) and the rare *Potentilla nivea* (white dots with pink outline, N = 11). Dots are sometimes overlapping, however, the minimum distance between two populations was 250 m. Maps were edited by Hinderling J. in QGIS.

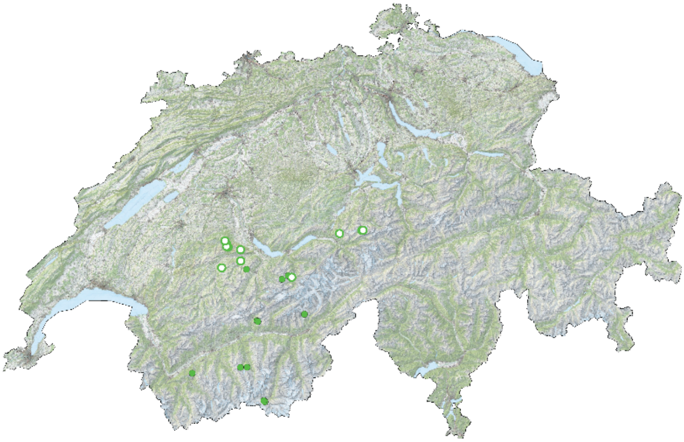
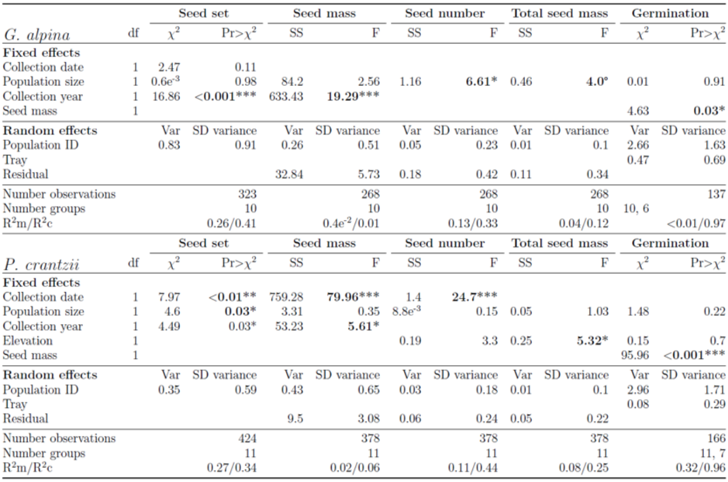


Fig. S5 Map of Switzerland (1:25000, © swisstopo) with locations of sampled populations of the common *Viola calcarata* (green dots with black outline, N = 10) and the rare *Viola lutea* (white dots with green outline, N = 11). Dots are sometimes overlapping, however, the minimum distance between two populations was 250 m. Maps were edited by Hinderling J. in QGIS.

Table S1 ANOVA table of linear model investigating the effect of rarity on population size. The full model contained rarity, genus, the rarity - genus interaction, collection date and elevation as explanatory variables. Numeric variables were z-transformed and population size was transformed with the decadic logarithm. The final model contained only response variables for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***.

		Population size	
	df	SS	F
Parameters			
Elevation	1	1.82	**4.21***
Genus	3	3.19	**2.46°**
Rarity	1	0.29	0.68
Genus : rarity	3	5.19	**4.01***
Residuals	83	35.8	
Number observations		92	
R^2		0.2	

Table S2 ANOVA tables of mixed effect models investigating the effects of population size on fitness traits among populations of the rare *Gentiana alpina* and the common *Potentilla crantzii*. We tested each fitness trait separately within species. Numeric variables were z-transformed and population size, seed number and total seed mass per fruit were transformed with the decadic logarithm. Seed set and germination were fitted as binomial response variable (seed set: whether a fruit contained viable seeds or not, germination: number of germinated seeds, number of seeds that did not germinate, "cbind" function from base R). Final models contained only fixed effects for which there are statistical values in the table (χ^2: Chi squared, SS: sum of squares, F: F-statistics, df: degrees of freedom; type II Wald χ^2-square tests for generalised mixed effect models, type III F-tests based on Satterthwaite's method for linear mixed effect models). Number of groups indicate the number of levels for each of the random effects. For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***.



		Seed set		Seed mass		Seed number		Total seed mass		Germination	
G. alpina	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F	χ^2	Pr>χ^2
Fixed effects											
Collection date	1	2.47	0.11								
Population size	1	$0.6e^{-3}$	0.98	84.2	2.56	1.16	**6.61***	0.46	**4.0°**	0.01	0.91
Collection year	1	16.86	**<0.001*** **	633.43	**19.29*** **						
Seed mass	1									4.63	**0.03***
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		0.83	0.91	0.26	0.51	0.05	0.23	0.01	0.1	2.66	1.63
Tray										0.47	0.69
Residual				32.84	5.73	0.18	0.42	0.11	0.34		
Number observations			323		268		268		268		137
Number groups			10		10		10		10	10, 6	
R^2m/R^2c			0.26/0.41		$0.4e^{-2}/0.01$		0.13/0.33		0.04/0.12		<0.01/0.97
		Seed set		Seed mass		Seed number		Total seed mass		Germination	
P. crantzii	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F	χ^2	Pr>χ^2
Fixed effects											
Collection date	1	7.97	**<0.01****	759.28	**79.96*** **	1.4	**24.7*** **				
Population size	1	4.6	**0.03***	3.31	0.35	$8.8e^{-3}$	0.15	0.05	1.03	1.48	0.22
Collection year	1	4.49	0.03*	53.23	**5.61***						
Elevation	1					0.19	3.3	0.25	**5.32***	0.15	0.7
Seed mass	1									95.96	**<0.001*** **
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		0.35	0.59	0.43	0.65	0.03	0.18	0.01	0.1	2.96	1.71
Tray										0.08	0.29
Residual				9.5	3.08	0.06	0.24	0.05	0.22		
Number observations			424		378		378		378		166
Number groups			11		11		11		11		11, 7
R^2m/R^2c			0.27/0.34		0.02/0.06		0.11/0.44		0.08/0.25		0.32/0.96

Table S3 Parameter estimates for mixed effect models investigating the effects of population size on fitness traits among populations of the common *Gentiana acaulis* and the rare *Potentilla nivea*. We tested each fitness trait separately within species. Numeric variables were z-transformed and population size was transformed with the decadic logarithm. We did not test seed set (whether fruits contained viable seeds or not) because only few plants had empty fruits (three among populations of *G. acaulis* and five among populations of *P. nivea*). Final models contained only fixed effects for which there are statistical values in the table (χ^2: Chi squared, SS: sum of squares, F: F-statistics, df: degrees of freedom; type II Wald χ^2-square tests for generalised mixed effect models, type III F-tests based on Satterthwaite's method for linear mixed effect models). Number of groups indicate the number of levels for each of the random effects. For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***.

		Seed mass		Seed number		Total seed mass		Germination	
G. acaulis	df	SS	F	SS	F	SS	F	χ^2	$Pr>\chi^2$
Fixed effects									
Elevation	1	424.8	**5.63***	0.32	0.37	4.56	**8.6***		
Collection date	1	22919.5	**303.78*****			92.73	**175.14*****		
Population size	1	4.7	0.06	0.06	0.06	0.16	0.29	1.57	0.21
Collection year	1	26587.9	**352.4*****	0.06	0.07	66.13	**124.9*****		
Seed mass	1							5.13	**0.02***
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		0.14	0.38	0.21	0.46	0.12	0.35	2.86	1.69
Tray								0.34	0.58
Residual		75.45	8.69	0.85	0.92	0.53	0.73		
Number observations			524		524		524		209
Number groups			13		13		13		13, 9
R^2m/R^2c			<0.01/<0.01		0.01/0.21		0.36/0.48		0.06/0.98
		Seed mass		Seed number		Total seed mass		Germination	
P. nivea	df	SS	F	SS	F	SS	F	χ^2	$Pr>\chi^2$
Fixed effects									
Collection date	1	32.77	**5.82***	157.79	**6.39***				
Population size	1	0.37	0.07	0.24	$0.97e^{-2}$	0.09	0.11	12.21	**<0.001*****
Collection year	1	12.89	2.29	327.9	**13.28*****	8.93	**11.12*****		
Elevation	1			39.19	1.59	3.31	**4.12°**	8.47	**<0.01****
Seed mass	1							12.88	**<0.001*****
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		0.26	0.51	0.29	0.54	0.2	0.44	0.28	0.53
Tray								0.07	0.26
Residual		5.63	2.37	0.71	0.84	0.8	0.9		
Number observations			347		347		347		189
Number groups			11		11		11		11
R^2m/R^2c			<0.01/0.05		0.07/0.34		0.1/0.27		0.49/0.83

Table S4 Parameter estimates for mixed effect models investigating the effects of population size on fitness traits among populations of the common *Androsace chamaejasme* and the rare *A. puberula*. We tested each fitness trait separately within species. Numeric variables were z-transformed and population size, seed number and total seed mass per fruit were transformed with the decadic logarithm. For *A. puberula*, we transformed seed mass with the decadic logarithm. Seed set (whether a fruit contained viable seeds or not) was fitted as binomial response variable. Final models contained only fixed effects for which there are statistical values in the table (χ^2: Chi squared, SS: sum of squares, F: F-statistics, df: degrees of freedom; type II Wald χ^2-square tests for generalised mixed effect models, type III F-tests based on Satterthwaite's method for linear mixed effect models). Number of groups indicate the number of levels for each of the random effects. For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***.

		Seed set		Seed mass		Seed number		Total seed mass	
A. chamaejasme	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F
Fixed effects									
Collection date	1	6.3	**0.01***	32.09	**17.46*****	0.19	**11.34*****	0.15	**26.72*****
Population size	1	3.64	**0.06°**	0.00	0.1e^{-3}	0.14e^{-2}	0.08	0.61e^{-3}	0.11
Collection year	1	17.58	<**0.001*****			0.53	**31.86*****	0.1	**17.4*****
Elevation	1			4.63	2.52				
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		0.84	0.92	0.17	0.41 0.62e^{-2}	0.08	0.24e^{-2}	0.05	
Residual				1.84	1.36	0.02	0.13	0.55e^{-2}	0.07
Number observations			535		370		370		370
Number groups			13		13		13		13
R^2m/R^2c			0.14/0.31		0.04/0.12		0.1/0.34		0.1/0.37

		Seed set		Seed mass		Seed number		Total seed mass	
A. puberula	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F
Fixed effects									
Collection date	1	0.9e^{-2}	<**0.001*****	0.19	17.25	0.91	**59.45*****	2.76	**149.55*****
Population size	1	0.9e^{-2}	0.92	0.3e^{-2}	0.27	0.01	0.71	0.12e^{-2}	0.06
Collection year	1	7.38	<**0.01****			1.24	**81.48*****	0.96	**51.79*****
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		8.16	2.86	0.23e^{-2}	0.05	0.49e^{-2}	0.07	0.01	0.12
Residual				0.01	0.11	0.02	0.12	0.02	0.14
Number observations			605		525		525		525
Number groups			12		12		12		12
R^2m/R^2c			0.4/0.83		0.05/0.22		0.32/0.48		0.36/0.64

Table S5 Parameter estimates for mixed effect models investigating the effects of population size on fitness traits among populations of the common *Viola calcarata* the rare *V. lutea*. We tested each fitness trait separately within species. Numeric variables were z-transformed and population size, seed mass, seed number and total seed mass per fruit were transformed with the decadic logarithm. Seed set (whether a fruit contained viable seeds or not) was fitted as binomial response variable. Final models contained only fixed effects for which there are statistical values in the table (χ^2: Chi squared, SS: sum of squares, F: F-statistics, df: degrees of freedom; type II Wald χ^2-square tests for generalised mixed effect models, type III F-tests based on Satterthwaite's method for linear mixed effect models). Number of groups indicate the number of levels for each of the random effects. For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***.

		Seed set		Seed mass		Seed number		Total seed mass	
V. calcarata	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F
Fixed effects									
Elevation	1	3.66	**0.06°**						
Collection date	1	13.15	**<0.001*****	0.02	**5.99***				
Population size	1	1.94	0.16	$0.88e^{-3}$	0.28	<0.01	0.06	0.12	0.79
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		3.31	1.82	<0.01	0.04	0.0	0.0	$1.7e^{-16}$	<0.001
Residual				<0.01	0.06	0.03	0.39	0.2	0.4
Number observations			214		83		83		83
Number groups			11		9		9		9
R^2m/R^2c			0.14/0.57		0.12/0.39		<0.01/0<0.01		<0.01/<0.01

		Seed set		Seed mass		Seed number		Total seed mass	
V. lutea	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F
Fixed effects									
Population size	1	0.45	0.5	$0.5e^{-5}$	$0.13e^{-2}$	0.07	1.21	0.02	0.19
Collection year	1	41.8	**41.8*****			0.58	9.55	0.31	**3.32°**
Elevation	1			0.09	**22.95*****	0.15	2.4	1.42	**15.44**
Collection date	1					0.14	2.37	<0.01	0.11
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Population ID		2.15	1.46	<0.01	0.04	0.01	0.11	0.02	0.15
Residual				<0.01	0.06	0.06	0.25	0.09	0.3
Number observations			330		214		214		214
Number groups			11		11		11		11
R^2m/R^2c			0.29/0.57		0.23/0.44		0.2/0.33		0.21/0.36


Example of an isolated alpine grassland on a windy ridge in the Swiss Alps.

Chapter 3

Relationships between fitness, population size and habitat quality in four common and four rare alpine plant species

Hannah Inniger, Judith Hinderling, Markus Fischer, Daniel Prati

Abstract To understand the performance of populations of plant species, it is important to study the factors that determine plant fitness. Plant fitness can depend on abiotic and biotic factors of the surrounding habitat. Additionally, plant fitness often correlates with population size, which can lead to a so-called extinction vortex in small populations. However, most studies on fitness focus either on habitat quality or on population size. Alpine and naturally rare species have received limited attention in this context. We assessed relationships between plant fitness, population size and habitat quality in an observational field study in four common and four rare alpine plant species in alpine grasslands in Switzerland. We investigated seed number and seed mass in 89 natural populations and seed germination in a common garden in a greenhouse. We carried out vegetation surveys in each population and quantified abiotic conditions, heterogeneity and plant diversity based on vegetation data. We found that plant fitness and population size were affected by abiotic conditions, heterogeneity and plant diversity. Variation in fitness and population size of common species was explained by habitat quality as much as in rare species, suggesting that they are equally vulnerable to environmental change. We found little evidence for a positive relationship between fitness and population size, however, experimental approaches are necessary to test whether an extinction vortex is present in small populations of alpine species. Our study indicates that both habitat

quality and population size might determine plant fitness in alpine and naturally rare species.

Abbreviations:
SD Standard deviation

Introduction

Alpine habitats exhibit harsh climatic conditions and extreme environmental heterogeneity (Scherrer and Körner 2010; Scherrer and Körner 2011). Consequently, populations of alpine plant species are often small and isolated (von Büren and Hiltbrunner 2022). Furthermore, many alpine species face increased abiotic and biotic pressure due to climate change (Theurillat and Guisan 2001) and significant habitat loss is projected by the end of this century (Theurillat and Guisan 2001; Dirnböck et al. 2011). The expected consequences of more competitive species migrating upward include potential reductions in the populations of rare and specialized alpine species, possibly leading to local extinctions at lower elevation distribution boundaries (Watts et al. 2022). To make predictions about the future performance of alpine plant species, particularly rare ones, it is essential to investigate potential relationships between plant fitness, population size and the present environment.

Previous research on various lowland species has demonstrated that differences in plant fitness can be accounted for by factors of habitat quality such as disturbance, soil properties, topography, vegetation structure and shading (Fischer and Matthies 1998; Vergeer et al. 2003; Adriaens et al. 2009; de Vere et al. 2009). In addition to habitat quality, population size is a crucial determinant of plant fitness in numerous lowland species (Fischer and Matthies 1998; Vergeer et al. 2003; Reed 2005; Leimu et al. 2006). Plant fitness is typically lower in small populations due to increased inbreeding and random genetic drift (Ellstrand and Elam 1993; Lienert 2004). The negative feedback loop involving small population size, lower genetic diversity and plant fitness can reduce the populations' ability to adapt to changing environmental conditions (e.g. Fischer et al. 2000) and may eventually lead to local extinction (Matthies et al. 2004). This phenomenon, known as the extinction vortex, has held significant importance in population ecology for many years (e.g. Gilpin and Soulé 1986).

For alpine species, the importance of specific habitat quality parameters for population size and plant fitness remains an unresolved question. Also, we do not know whether an extinction vortex might be ongoing in small populations of alpine plant species. To answer these questions, it is important to assess habitat quality, population size and plant fitness together. One of the most important factors that could affect population size and fitness of alpine species are local abiotic conditions relative to the target species optimum (hereafter: abiotic mismatch). On the level of the species, niche availability is among the main factors determining species distributions and range size (Sheth et al. 2020). On the level of the population, we therefore expect that populations are smaller and have lower plant fitness at sites with higher abiotic mismatch, or, in other words, at sites where the local abiotic conditions do not match the target species optimum. Because rare species are expected to have a narrower niche breadth than common species (Brown 1984), we predict a stronger relationship between population size, fitness and abiotic mismatch in rare than in common species.

Given the observed habitat homogenization due to climate change in alpine grasslands (Liberati et al. 2019), it becomes crucial to understand the influence of habitat heterogeneity on plant fitness and population size. Environmental heterogeneity can maintain genetic diversity in life history traits within plant populations, serving as a fundamental requirement for adaptation and continued evolution (Prati and Schmid 2000). This, in turn, might favor plant fitness and population size. Therefore, we expect larger populations with higher plant fitness at locations with high heterogeneity. This could be more pronounced for rare species, as they may already have lower phenotypic and genetic variation in comparison to common species. Alternatively, regardless of population size and species rarity, plants may also be well-adapted to a homogeneous environment through natural selection in the past. In this case, we might observe no positive or even a negative relationship between population size, fitness and habitat heterogeneity.

To the best of our knowledge, species richness and diversity are habitat parameters that have never been studied in relation to population size and plant fitness of target species. Species-rich sites are less likely to contain very dominant species (Huston 1979; Segre et al. 2014). Therefore, the likelihood of competitive exclusion is possibly reduced, which could benefit species with lower competitive abilities in highly diverse environments. Additionally, it is well-established that facilitation is common in alpine environments (Rose and Malanson 2012), and the occurrence and diversity of positive interactions may increase in habitats with high species diversity and richness. This could lead to higher plant fitness and eventually larger populations of individual plant species. As rare species can benefit more from facilitation than common species (Soliveres et al. 2015), rare species might show a stronger relationship between population size, fitness and plant diversity. Alternatively, high plant diversity could constrain population growth rates (Huston 1979) and there might be no correlation or even a negative correlation between population size, fitness and the diversity and richness of surrounding plant species.

The objective of the present study was to investigate whether plant fitness is related to habitat quality and population size in four common and four rare herbaceous alpine species. We investigated relationships between population size, fitness and habitat quality across 89 populations at different elevations in the Swiss Alps. We studied seed number and seed mass in the field, and seed germination in a common garden in the greenhouse. We collected vegetation data from every population, enabling the quantification of three features of habitat quality: abiotic conditions based on species indicator values (Landolt et al. 2010), habitat heterogeneity and plant diversity. We used regression analysis to answer the following research questions: (I) Can we explain variation in population size with habitat quality? (II) Can we explain variation in plant fitness with habitat quality? (III) Can we explain variation in plant fitness with population size when accounting for habitat quality? Additionally, we investigate whether there are differences between common and rare species concerning each of these questions.

Methods

Study species

We studied four pairs of congeneric herbaceous grassland species with a subalpine-alpine distribution. They comprised four different plant families and were selected based on expert knowledge. Each of the pair included one common and one rare species that were relatively closely related regarding phylogeny and hence comparable. We classified a species as rare if it had a small geographic range, low local abundance and high habitat specificity in comparison to its more common partner species (Rabinowitz 1981).

The (naturally) rare species in our study are *Androsace puberula* Jord. & Fourr. (*Primulaceae*, *Caricion curvulae*, classification typoCH, Delarze et al. 2008), *Gentiana alpina* Vill. (*Gentianaceae*, *Caricion curvulae*), *Potentilla nivea* L. (*Rosaceae*, *Elynion*) and *Viola lutea* Huds. (*Violaceae*, *Seslerion*). These species occur within a restricted geographic range with sparse local abundance through the Swiss and European Alps (Lauber et al. 2018; GBIF.org 2023). Apart from *V. lutea*, the species are strongly restricted to their habitat (Lauber et al. 2018).

The common species in our study are *Androsace chamaejasme* Wulfen (*Seslerion, Caricion firmae*), *Gentiana acaulis* L. (*Nardion*), *Potentilla crantzii* (Crantz) Fritsch (*Seslerion*) and *Viola calcarata* L. (*Nardion, Poion alpinae*). These species occur over a wide geographic range with pronounced local abundance throughout the Swiss and European Alps (Lauber et al. 2018; GBIF.org 2023). Apart from *G. acaulis*, the common species are not strongly restricted to their habitat (Lauber et al. 2018). All study species are insect pollinated and perennial. Both *P. crantzii* and *P. nivea* are facultative apomicts.

Study locations and sampling

We visited between ten and twelve populations per species (N = 89) twice during the summers of two consecutive years (2020, 2021) in the Swiss Alps. We selected the populations at elevations between 1390 to 2810 m.a.s.l. based on the Info Flora database. This database collects occurrence data on vascular plant species in Switzerland up to a 1 x 1 kilometre scale (infoflora.ch 2020). We had no information on the populations beyond their coordinates. We chose populations of the rare species as widely distributed as possible across their entire range throughout Switzerland. We chose the populations of the common species within a range size comparable to their rare species partner. The rare *P. nivea* and *G. alpina* had a disconnected distribution in Switzerland. We sampled these species in both disconnected regions and collected their common congeneric partner species within these regions, but not in the areas between them. We estimated population size by counting the number of fertile (fruiting or flowering) individuals. We defined the borders of a population where we found the outermost individuals. If there were more than 250 fertile individuals within a population, we estimated the area of these 250 individuals. We extrapolated across the entire population area to obtain an estimate of the total number of fertile individuals.

Fitness parameters

Depending on population size, we collected fruits of 2-40 randomly selected individuals once in 2020 and 2021 (see Supporting information). We sampled fewer than ten individuals for eight populations, due to a very small population size. After collecting the fruits, we air-dried them in paper bags. We counted and weighed the viable seeds of an individual plant together to nearest milligram and calculated the average seed mass. We sowed a maximum of 60 seeds per individual (N = 1536) in separate pots on seedling soil (Substrate 167, RICOTER Erdaufbereitung AG, Aarberg). We stratified the seeds after sowing from December to February outside the greenhouse in Bern, Switzerland. Mean temperature and mean air humidity during these three months in Bern are -0.97 °C and 78.67 % (climate-data.org 2023). Three months correspond approximately to the minimum duration of snow cover in the alpine zone (Klein et al. 2016) and former researchers used this time span for a successful stratification of alpine seeds (Cavieres and Sierra-Almeida 2018). Outdoor stratification facilitated natural freezing events, simulating the seeds' natural overwintering. We covered the pots with a thin fleece to protect the seeds from birds and heavy rain and to simulate darkness by snow cover. We watered the seeds weekly with a water sprayer. We placed the pots inside the greenhouse to initiate germination after stratification. We set greenhouse conditions to a minimum of 12 °C (with 14 h light and 40 % air humidity), to approximately match spring conditions in the (sub-) alpine zone. Depending on weather, temperature rose up to a maximum of 20 °C.

For five weeks, we monitored germination every other day by counting the total number of seeds that germinated per parent plant. Because less than 10 % of the seeds germinated in the *Androsace* and the *Viola* species, we repeated germination in the following winter (2021) for these species after three months of stratification in a dark cool chamber (4 °C and weekly watering). The germination rate remained equally low in early 2022 compared to the preceding year (< 0.5-12 %).

Vegetation data

We took eight circular vegetation records (diameter = 20 cm) per population in summer 2021. Since alpine vegetation can vary over very short distances (von Büren and Hiltbrunner 2022), we chose such a small plot size to investigate plant diversity, abiotic conditions and heterogeneity on a very local scale. Four records were done around four randomly chosen individuals of the target species. The other four records were done at random locations within the population, where no individuals of the target species were present, when possible within a minimum distance of one metre to individuals of the target species. We distinguished between these two record types to obtain data representing the area of the entire population. In the following, they are referred to as microsites with and without target species. For each record, we identified all vascular plants to species and, if necessary, subspecies level. We estimated the percentage cover of each species as well as of lichens, moss, bare ground, stones and litter. We measured vegetation height in each record by placing a laminated A5 sheet on the vegetation and measuring the minimum and maximum height of the corners.

Abiotic conditions

We used Landolt indicator values (Landolt et al. 2010) as a proxy for local abiotic conditions. Landolt indicator values describe the niche position of a species on a scale from one to five (Table S13 and S14 Supplementary material). Community weighted mean indicator values based on vegetation surveys are commonly used to provide information on the abiotic environment and it has been shown that they correlate well ($R^2 > 0.4$) with environmental properties measured in the field (Diekmann 2003; Descombes et al. 2020). For each record, we calculated community weighted means in the software Vegedaz (Küchler 2022) for the following indicator values: temperature (T), soil moisture (F), soil reaction (pH; R), light levels (L), humus cover (H), nutrient levels (N), soil dispersity (D) and soil salt (S). For each population, we averaged the absolute Euclidian distance between the target species indicator value and the community weighted mean of each record for each indicator value. We used this measure as an approximation of the local abiotic conditions relative to the target species optimum. In the following sections, we will refer this to mismatch in temperature, soil moisture, soil reaction, light levels, humus cover, nutrient levels, soil dispersity and soil salt. We further calculated the total abiotic mismatch per population, averaging the sum of all mismatches from each record, which we will further refer to as abiotic mismatch.

Heterogeneity

We assessed three types of heterogeneity: biotic, abiotic and structural heterogeneity. Our estimate of biotic heterogeneity was local beta diversity, which we calculated with all the records from the population with the function “beta.multi.abund” from the R package “betapart” (Baselga et al. 2018) in R (R core team 2022). Beta.multi.abund computes a balanced (β.BC.BAL) and a gradient (β.BC.GRA) component based on the Bray-Curtis index (Baselga 2013) as a measure of dissimilarity among the given sites based on species abundances. While the balanced component measures species turnover between sites, the gradient component is a measure of how many species are lost from one site to another (Baselga 2017). We used the sum of the two components (β.BC) as a measure of local beta diversity. As a measure of abiotic heterogeneity, we calculated the variation (mean standard deviation) of the community weighted mean indicator values for each record in each population. Similarly, we calculated the variation (mean standard deviation) of vegetation height and of the cover of shrubs, graminoids (species from the *Poaceae, Cyperaceae* and *Juncaceae* families), forbs, lichens, mosses, litter, bare ground and stones in each population to get an estimate of structural heterogeneity.

Plant diversity

To quantify local plant diversity, we calculated the Shannon index and Shannon evenness for each record in the software Vegedaz (Küchler 2022). While the Shannon index is a measure of the number of species, where each species is weighted by its abundance (hereafter: alpha diversity), Shannon evenness measures the equality of abundances within the community (hereafter: evenness) (Gurevitch et al. 2002). We defined the total number of vascular plant species observed across all eight records per population as gamma diversity.

Statistical analysis

We performed all the analyses in R (R core team 2022). We standardized numeric variables to a mean of zero with a standard deviation of one. We standardized seed number and seed mass within genera to a mean of zero with a standard deviation of one. We transformed population size (the number of fertile individuals) with the decadic logarithm prior to all analyses.

We used linear regression models to test whether population size depends on habitat quality. In a separate model, we first tested whether variation in population size can be explained by anthropogenic disturbance, elevation, exposition, inclination or seasonality (sampling date). Since population size was positively related to elevation (Table S1 Supporting information), we included elevation as a co-variable in each of the habitat quality models. To not over-fit the models, we built separate models for alpha diversity and evenness, gamma diversity, abiotic conditions, abiotic, biotic and structural heterogeneity. In every model, we included the habitat quality variable(s) together with the habitat quality - rarity interaction, genus, rarity and the genus - rarity interaction. Because rarity was nested in genus, we did not include species, as this would be redundant with the genus - rarity interaction. In the abiotic and structural heterogeneity models, we did not include the habitat quality - rarity interaction to not over-fit the model. For abiotic conditions, we first tested whether population size was determined by total abiotic mismatch. We tested in a second model whether variation in population size could be explained by single mismatches (temperature, soil moisture, soil reaction (pH), light level, humus cover, soil nutrients, soil dispersity and soil salt). In the abiotic heterogeneity model, we included variation in soil moisture (F), soil salt (S), nutrient levels (N), temperature (T), light levels (L) and soil reaction (R) as habitat quality variables. We did not include variation in soil dispersity and humus cover since they correlated among each other and with variation in soil reaction (Pearson’s correlation coefficients > 0.7). In the structural heterogeneity model, we included variation in vegetation height and variation of the cover of shrubs, forbs, graminoids, litter, mosses, lichens, bare ground and stones as habitat quality variables.

To test whether fitness (seed number, seed mass and germination) depends on habitat quality, we fitted separate mixed effect models for the different fitness variables. We fitted linear mixed effect models using the function “lmer” from the R package "lme4" (Bates et al. 2015) for seed number and seed mass. We fitted generalised mixed effect models using the function “glmer” (Bates et al. 2015) with a binomial distribution for germination. Due to the exceedingly low germination rates observed in the *Androsace* and *Viola* species, we excluded these species from the germination analysis. As for population size, we first tested if the response variables were influenced by anthropogenic disturbance, elevation, exposition, inclination or by seasonality. We included the significant parameters as co-variables in the habitat quality models (seed number: seasonality and year; seed mass: seasonality, year and elevation; germination: seasonality; Table S3 Supporting information). As for population size, we fitted separate models for the different habitat quality variables. In each of the habitat quality models, we included the habitat quality variable(s), the habitat quality - rarity interaction, rarity, genus and the genus - rarity interaction as fixed effects. In the abiotic and structural heterogeneity models, we did not include the interactions between the habitat quality variables and rarity to not over-fit the models. We included population as a random effect to account for spatial non-independence in all mixed models. In the germination models, we included tray (where we grouped pots in the greenhouse) as an additional random term.

Because plant fitness might depend on population size, we fitted mixed effect models as described before with the only difference being that we included population size and the population size - rarity interaction as co-variables. The objective of this was to determine whether potential effects of population size on plant fitness persist when we consider habitat quality. This allowed for further testing as to whether potential effects of habitat quality on plant fitness change when accounting for population size.

We simplified models with the function "dredge" from the package "MuMIn" (Bartoń 2022) based on the Akaike information criterion (AIC).

We kept habitat quality variables except abiotic and structural heterogeneity in the models. We also kept population size in the models, when fitted as explanatory variable. We evaluated final models based on the R^2 and on normality of the residuals. We considered p-values from the ANOVA table smaller than 0.05 as significant, and smaller than 0.1 as marginally significant (type II F-tests bases on Satterthwaite's method for linear models, type III F-tests based on Satterthwaite's method for linear mixed effect models, type II Wald χ^2 -tests for generalised mixed effect models).

Results

Relationships between population size and habitat quality

Regarding abiotic conditions, populations were smaller at sites with greater abiotic mismatch ($p < 0.05$; Fig. 1a; Table S1 Supporting information). When we tested the mismatches in temperature, soil moisture, soil reaction (pH), light level, humus cover, soil nutrients, soil dispersity and soil salt, we found that populations were significantly smaller at locations with greater mismatch in temperature ($p < 0.001$; Table S1 Supporting information). Community weighted mean temperature values were usually higher than the target species optimum. Surprisingly, populations were larger at locations with greater mismatch in soil salt ($p < 0.01$; Table S1 Supporting information). Community weighted mean values of soil salt were always higher than the target species optimum.

Regarding heterogeneity, populations were smaller at locations with higher abiotic and structural heterogeneity (Fig. 1b and d-f; Table S2 Supporting information). Drivers of these relationships were variation in light levels and variation in vegetation height, bare ground, graminoids and lichens. Population size did not depend on biotic heterogeneity ($p = 0.67$).

Regarding diversity, populations were larger at sites with higher alpha diversity ($p < 0.01$; Fig. 1g; Table S1 Supporting information) and lower evenness ($p < 0.05$; Fig. 1h; Table S1 Supporting information). Populations tended to be larger at locations with higher gamma diversity ($p = 0.1$; Fig. 1i; Table S1 Supporting information).

The population sizes of rare and common species were equally influenced by abiotic mismatch. However, population sizes of rare and common species were differently affected by abiotic heterogeneity (rarity - SD soil reaction interaction; $p < 0.05$; Fig. 1c; Table S2 Supporting information). While population size of common species did not depend on variation in soil reaction, populations of rare species were significantly smaller at locations with high variation in soil reaction ($p < 0.05$; $R^2 = 0.28$). Regarding diversity, population sizes of common species depended more on evenness than population sizes of rare species (evenness - rarity interaction $p < 0.1$; Fig. 1h; Table S1 Supporting information). In summary, population sizes in our study species depended on abiotic conditions, heterogeneity and local plant diversity. Population sizes of rare species were more affected by abiotic heterogeneity, while population sizes of common species were more affected by evenness.

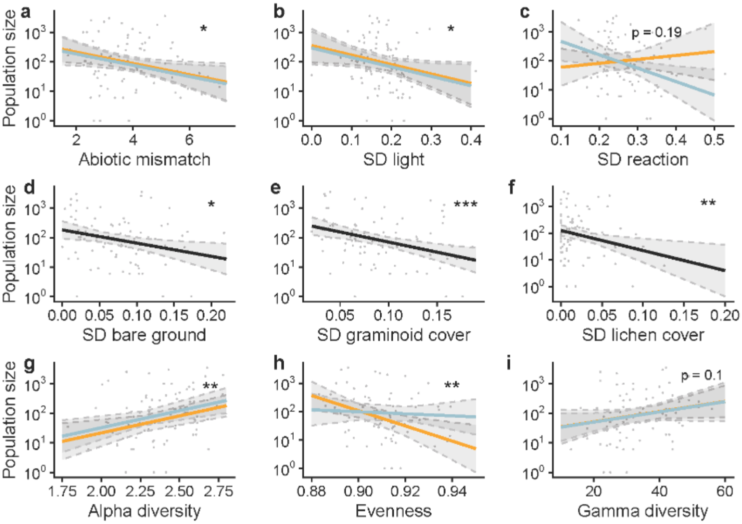


Fig. 1 Relationships between habitat quality and population size in four rare and four common alpine plant species. Lines show effects predicted by linear regression of abiotic mismatch (a), abiotic heterogeneity (b and c), structural heterogeneity (d-f), alpha diversity (g), evenness (h) and gamma diversity (i) on population size across all eight study species. Grey shadows show upper and lower limits of 95 % confidence intervals. Grey dots show observed values. Blue lines illustrate relationships for rare species and yellow lines show relationships for common species. Black lines show relationships for all eight study species when the final model did not include rarity. Significance levels are given for the main effects of habitat quality parameters: P < 0.1; °, P < 0.05; *, P < 0.01; **, P < 0.001; ***.

Relationships between fitness and habitat quality

Regarding abiotic conditions, seeds from locations with greater abiotic mismatch had lower germination probability ($p < 0.01$; Fig. 3a; Table S9 Supporting information). When analysing abiotic mismatches separately, we found that seeds from locations with greater mismatch in soil moisture and light levels had lower germination probability ($p < 0.05$; $p < 0.05$; Table S9 Supporting information). Seeds from sites with greater mismatch in soil salt had marginal higher germination probability ($p < 0.1$; Table S9 Supporting information).

Regarding heterogeneity, we found that plants from locations with higher biotic heterogeneity produced more seeds than plants from locations with lower biotic heterogeneity ($p < 0.01$; Fig. 2b; Table S4 Supporting information). Plants from locations with higher abiotic heterogeneity produced larger seeds than plants from locations with lower abiotic heterogeneity (variation in light levels; $p < 0.01$; Fig. 2e; Table S6 Supporting information). Seeds from locations with high variation in soil reaction (pH) and soil salinity had higher germination probability ($p < 0.1$; $p < 0.1$; Fig. 3c and e), whereas seeds from locations with high variation in temperature had lower germination probability ($p < 0.1$; Fig. 3d; Table S11 Supporting information). Plants from locations with high variation in forbs produced more seeds, whereas plants from locations with high variation in stones produced larger seeds ($p < 0.05$; $p < 0.001$; Fig. 2c and f; Table S4 and S7 Supporting information). Seeds from locations with higher variation in bare ground and litter had lower germination probability ($p < 0.01$; $p < 0.001$; Fig. 3f and g), whereas seeds from locations with higher variation in graminoids and stones had higher germination probability ($p < 0.001$; $p < 0.01$; Fig. 3h and i; Table S12 Supporting information). Across the entire dataset, variation in the cover of litter, stones and graminoids correlated + 0.7 (Pearson's correlation coefficient) with the mean cover of the respective variables. Variation in the cover of bare ground, lichens, mosses and shrubs correlated + 0.9 with the mean cover of the respective variables (Fig. S2 Supporting information).

Regarding diversity, plants from locations with higher evenness produced more seeds ($p < 0.05$; Fig. 2a; Table S4 Supporting information). Furthermore, plants from locations with higher gamma diversity produced smaller seeds ($p < 0.05$; Fig. 2d; Table S5 Supporting information). Germination was not dependent on alpha diversity, evenness, or gamma diversity.

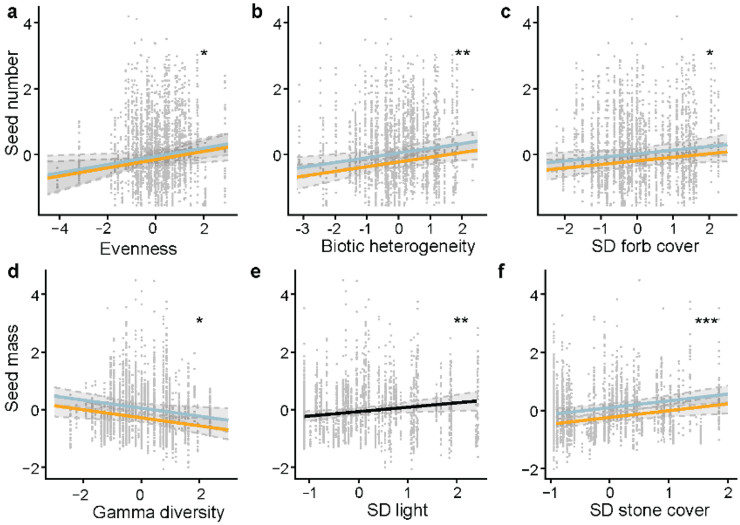


Fig. 2 Relationships between seed related fitness traits and habitat quality in populations of four common and four rare alpine plant species. Lines show effects of evenness (a), biotic heterogeneity (b) and structural heterogeneity (c) on seed number and effects of gamma diversity (d), abiotic heterogeneity (e) and structural heterogeneity (f) on seed mass predicted by linear mixed effect models. We scaled all explanatory variables to a mean of zero with a standard deviation of one. We scaled seed number and seed mass within each genus to a mean of zero with a standard deviation of one. Blue lines illustrate model fits for rare species and yellow lines show model fits for common species. Grey shadows show upper and lower limits of 95 % confidence intervals and grey dots show observed values (percentage of germinated seeds per individual plant). Significance levels are given for the main effects of habitat quality parameters: $P < 0.1$; °, $P < 0.05$; *, $P < 0.01$; **, $P < 0.001$; ***.

Plant fitness was equally affected by habitat quality in both rare and common species. Plants of rare species produced seeds with higher germination probability when they originated from locations with high biotic heterogeneity (Fig. 3b). Plants of rare species produced significantly more seeds and seeds with significantly larger seed mass (Table S4, S7 and S8 Supporting information). The effect of rarity on seed mass was due to the large seeds of *A. puberula* and disappeared when we removed the genus *Androsace* from the analysis. In summary, plant fitness depended on abiotic conditions, heterogeneity and local plant diversity across all our study species.

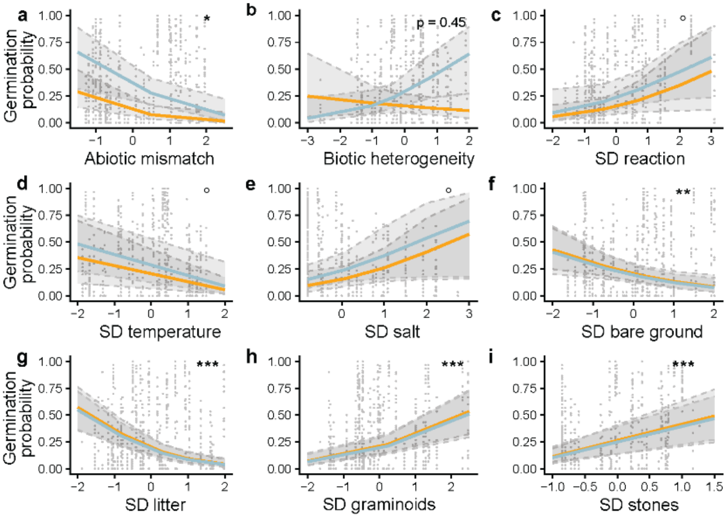


Fig. 3 Relationships between seed germination and habitat quality in populations of two common (*G. acaulis*, *P. crantzii*) and two rare (*G. alpina*, *P. nivea*) alpine plant species. Lines show effects of abiotic mismatch (a), biotic heterogeneity (b), abiotic heterogeneity (c-e) and structural heterogeneity (f-i) on germination probability predicted by generalised mixed effect models. We scaled all explanatory variables to a mean of zero with a standard deviation of one. Blue lines illustrate relationships for rare species and yellow lines show relationships for common species. Grey shadows show upper and lower limits of 95 % confidence intervals and grey dots show observed values (percentage of germinated seeds per individual plant). Significance levels are given for the main effects of habitat quality parameters: $P < 0.1$; °, $P < 0.05$; *, $P < 0.01$; **, $P < 0.001$; ***.

Effects of population size on plant fitness

We tested whether population size influenced plant fitness and whether effects of habitat quality on plant fitness changed when population size was included as a co-variable in our models. Plants from smaller populations produced fewer seeds when we considered both plant diversity and population size ($p < 0.1$; Fig. 4a; Table S4 Supporting information). Also, plants from smaller populations produced seeds with lower germination probability when we considered both structural heterogeneity and population size ($p < 0.05$; Fig. 4b; Table S12 Supporting information). Variation in seed mass was not explained by population size.

In addition, some effects of habitat quality on plant fitness changed when we accounted for population size. The difference between plants of rare and common species regarding the dependence of seed germination on biotic heterogeneity (Fig. 3b) was no longer significant (Table S10 Supporting information). The negative effects of variation in soil reaction (pH) and soil salinity on seed germination became significant when we accounted for population size ($p < 0.05$ and $p < 0.05$; Table S11 Supporting information). Furthermore, plants from locations with greater abiotic mismatch produced smaller seeds when we accounted for population size ($p < 0.1$; Table S8 Supporting information).

In summary, habitat quality influenced population size in all eight study species. Population sizes of rare species were more dependent on abiotic heterogeneity, whereas population sizes of common species were more affected by local diversity. Plant fitness was influenced by habitat quality across all species, irrespective of species rarity. When accounting for population size, two models revealed that variation in seed number and germination could be explained by population size. Three effects of habitat quality on plant fitness changed when we accounted for population size.

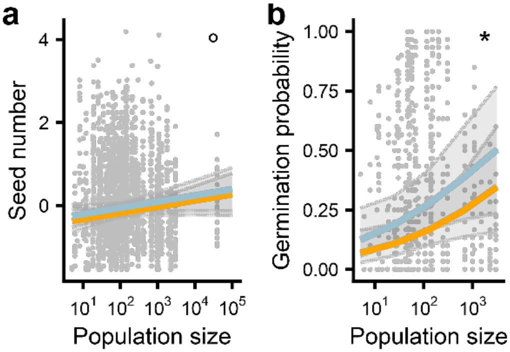


Fig. 4 Relationships between fitness and population size in eight (a) and four (b) alpine plant species. Lines show effects of population size on seed number (a) and germination probability (b) predicted by mixed effect models. We scaled seed number within each genus to a mean of zero with a standard deviation of one. Blue lines show relationships for rare species, yellow lines illustrate relationships for common species. Grey shadows show upper and lower levels of 95 % confidence intervals. Grey dots represent observed values (b: germination percentage per individual plant).

Discussion

Population size depends on abiotic conditions, heterogeneity and plant diversity

The present study shows that variance in population size of alpine plant species can be explained by abiotic conditions, habitat heterogeneity and plant diversity. While population sizes of rare and common species were equally affected by abiotic mismatch, population sizes of rare species were more sensitive to abiotic heterogeneity than population sizes of common species. In contrast, population sizes of common species were more sensitive to the surrounding plant diversity than population sizes of rare species. This suggests that populations of both rare and common species might be susceptible to local environmental changes.

Our results support the hypothesis that populations are smaller when there is high abiotic mismatch. The fact that temperature was the most important factor driving this pattern is in agreement with von Büren and Hiltbrunner (2022), who demonstrated that temperature is most critical to the distribution of species in alpine environments. Since the temperature indicator value also reflects the elevation of the species (Landolt et al. 2010), the negative relationship between population size and temperature mismatch may also reflect the upward migration of more competitive species (with higher T values). Although we cannot conclude from our data that thermophilisation of plant species has taken place in habitats of smaller populations, this is likely, as strong thermophilisation of plant species has been observed in alpine habitats over the last twenty years (Kiebacher et al. 2023). Therefore, our observations might reflect both direct and indirect effects of increased temperatures on population sizes of our study species. Previous research on alpine species has indicated that specialized species experience a reduction in population size due to climate change effects, including increased competition (Watts et al. 2022). Our study suggests that population sizes of alpine specialists *and* generalists might be susceptible to climate change effects such as increased competition.

Our results do not support the hypothesis of a positive relationship between population size and heterogeneity, since populations were even smaller at sites with higher abiotic and structural heterogeneity. In habitats with pronounced abiotic heterogeneity, microsites matching the ecological niche of the species might be less prevalent. As a result, offspring recruitment may become even more challenging, further constraining population size. The negative relationship between population size and abiotic heterogeneity was stronger for rare species, supporting the common view that rare species have more narrow niches than common species (Brown 1984; Bornand 2014; Haynes et al. 2021). The negative relationship between population size and structural heterogeneity in our study may be explained by confounding effects. As the variation in cover correlated with mean cover (Fig. S2 Supporting information), locations exhibiting high variation in graminoids may be associated with intensified competition, whereas locations with high variation in stones and lichens might indicate harsher abiotic conditions. Therefore, niche availability and competition rather than heterogeneity, *per se*, might be responsible for the negative relationship between population size and heterogeneity in our study species.

Across all of our study species, populations were larger at high alpha diversity and tended to be larger at high gamma diversity. This supports our hypothesis of a beneficial effect of local plant diversity on the population of individual species. This may be explained by the lower abundance of strong competitors and enhanced facilitation. Another benefit of an environment with high plant diversity could be a more diverse below-ground community, which can be accompanied by a stabilizing effect on plant populations (van der Heijden 2003).

We observed a negative relationship between population size and evenness mainly among our common species. According to Hillebrand et al. (2008), interspecific interactions are more important at high evenness compared to low evenness. As our common species occurred in habitats with a denser vegetation than our rare species, interspecific competition might regulate populations of our common species.

To our knowledge, this is the first study to show that population size of rare and common alpine plant species can depend on abiotic mismatch, habitat heterogeneity and plant diversity. Although further research is required to understand the underlying mechanisms of these patterns, our results demonstrate the importance of these habitat parameters for alpine plant species.

Plant fitness depends on abiotic conditions, heterogeneity and plant diversity

We detected that local abiotic conditions, habitat heterogeneity and plant diversity can significantly contribute to plant fitness in alpine species. Since the observed patterns were similar for rare and common species, all of our study species might be vulnerable to changes in habitat quality.

Our results support the hypothesis that plant fitness is lower in habitats with high abiotic mismatch. In those habitats, microsites matching the species niche are less available. Plant growth and reproductive investment, which are often correlated in alpine species (Hautier et al. 2009), are likely restricted under such conditions. Our observations align with the common view that the limitation of microsites is an important factor restricting recruitment of plant populations (Eriksson and Ehrlén 1992; Frei et al. 2012). In our study, seed germination was affected by unsuitable abiotic conditions most likely as a result of reduced reproductive effort in plants growing at microsites with low quality. This is a poor future prospect for our study species, as germination is an essential life stage (Bareke 2018). For alpine species, germination is a very delicate process and seeds often germinate poorly even under controlled conditions (Shimono and Kudo 2005; De Vere et al. 2009). Moreover, climate change is expected to shift germination into autumn, exposing germinated seeds to freezing events (Mondoni et al. 2012). Our results suggest that abiotic conditions could exert additional pressure on germination, which might increase mortality in populations of alpine plant species.

We found higher plant fitness at locations with pronounced heterogeneity. This might be explained by earlier findings of Prati and Schmid (2000), indicating that high habitat heterogeneity can maintain genetic diversity. Decades ago, an experimental demonstration established a causal relationship between environmental heterogeneity and plant fitness (Hartgerink and Bazzaz 1984). In the field, habitat heterogeneity is found to drive morphological and functional trait (Karbstein et al. 2020). This can facilitate micro-evolution, with positive consequences for survival, fitness, and resistance and resilience to climate change (Karbstein et al. 2019; Karbstein et al. 2020; Graae et al. 2018). Although we studied neither trait nor genetic diversity, it is possible that greater within-population diversity could have led to improved fitness in habitats characterized by significant heterogeneity in our study species. This was similar in rare and common species, suggesting that plant fitness of not only rare but also common alpine species could benefit from a more heterogeneous habitat.

It is important to emphasise that plants of our study species produced more seeds at higher biotic heterogeneity (beta diversity). Seed number is a strong indicator of plant fitness (Boyd et al. 2022) and limited seed availability can constrain the reproductive output of alpine plant populations (Lindgren et al. 2007; Frei et al. 2012). In addition, the number of seeds affects dispersal ability, a trait that is crucial in determining whether a species can track climate trends (Morgan and Venn 2017). Sites with a higher beta diversity might attract more pollinators, which could increase the pollination efficiency of individual plants. Alpine plants are generally pollen limited (Garcia-Camacho and Totland 2009) and there is empirical evidence that in alpine species, seed number increases at higher abundance of potential pollinators (Straka and Starzomski 2015). Our observed pattern is likely not confounded by other environmental variables (Fig. S1 Supporting information), however, in such a field study, the possibility cannot be excluded that important environmental parameters were not investigated (Fischer and Matthies 1998).

To our knowledge, this is one of the first field studies to demonstrate a link between plant fitness and abiotic, biotic and structural heterogeneity. It is important to point out that the few negative relationships between germination and structural heterogeneity do not imply that habitat homogenisation will benefit populations of our study species. Structural heterogeneity had positive effects on seed related traits, as well as on seed germination. Therefore, climate change induced habitat homogenisation and change in vegetation structure (Theurillat and Guisan 2001; Bühler and Roth 2011; Liberati et al. 2019) may have negative consequences for plant fitness in our study species.

Plant fitness depends on habitat quality and population size

We observed a positive relationship between plant fitness and population size in two of our habitat quality models. On one hand, this shows that variation in fitness can be explained by population size. On the other hand, population size may be less important for plant fitness in our study species than habitat quality, as the effect of population size mostly disappeared when both population size and habitat quality were considered. If population size and plant fitness were both positively influenced by the same habitat quality parameter, the observed positive relationship between plant fitness and population size could potentially be ascribed to an underlying habitat quality factor. However, in our study, population size and plant fitness were affected either by distinct habitat quality parameters or by the same habitat quality factor in opposing directions. This indicates that the observed reduction in seed number and germination probability in small populations may be a result of a small population size, indicating an extinction vortex in small populations of our study species. Possible explanations for this pattern might be increased genetic drift and inbreeding depression in small populations (Ellstrand and Elam 1993; Lienert 2004). Reduced seed set can also result from a low frequency of pollinator visits, since small populations are usually less attractive to pollinators (Sih and Baltus 1987; Agren 1996). However, to examine the hypothesis of an ongoing extinction vortex in small populations of our study species, it would be essential to investigate plant fitness across multiple generations in controlled conditions, thereby minimising the influence of habitat effects. Data on genetic diversity would also be required to understand the underlying mechanisms.

Conversely, some of the observed effects of habitat quality on plant fitness in this study changed when we accounted for population size. For instance, the negative effect of abiotic heterogeneity on seed germination became significant for rare species when we included population size as a co-variable. As populations of rare species were smaller at locations with pronounced abiotic heterogeneity, this pattern may be explained by the combined effects of low habitat quality and a small population size.

The present study supports previous findings that both habitat quality and population size contribute to variation in plant fitness (Fischer and Matthies 1998; Vergeer et al. 2003; Adriaens et al. 2009; Nicole et al. 2011). Our observations indicate that this might also be true also for alpine and naturally rare species.

Conclusion

Our findings show that variation in population size and plant fitness in alpine plant species can be explained by plant diversity, abiotic conditions and habitat heterogeneity. Therefore, these environmental parameters should be included when studying populations of alpine plant species. We did not find major differences between common and rare species, suggesting that populations of common and more generalist species may be equally vulnerable to changing habitat conditions as populations of rare and more specialist alpine species. Across all of our study species, we found lower plant fitness in small populations. The effect of population size on plant fitness was most of the time masked by effects of habitat quality. On the other hand, some effects of habitat quality on plant fitness were stronger when we accounted for population size. This indicates that both habitat quality and population size might be important for plant fitness in alpine species. To understand the relative importance of habitat quality and population size for plant fitness and to investigate the potential presence of an extinction vortex in small populations of alpine species, experimental methodologies are crucial.

Acknowledgements

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Supporting information

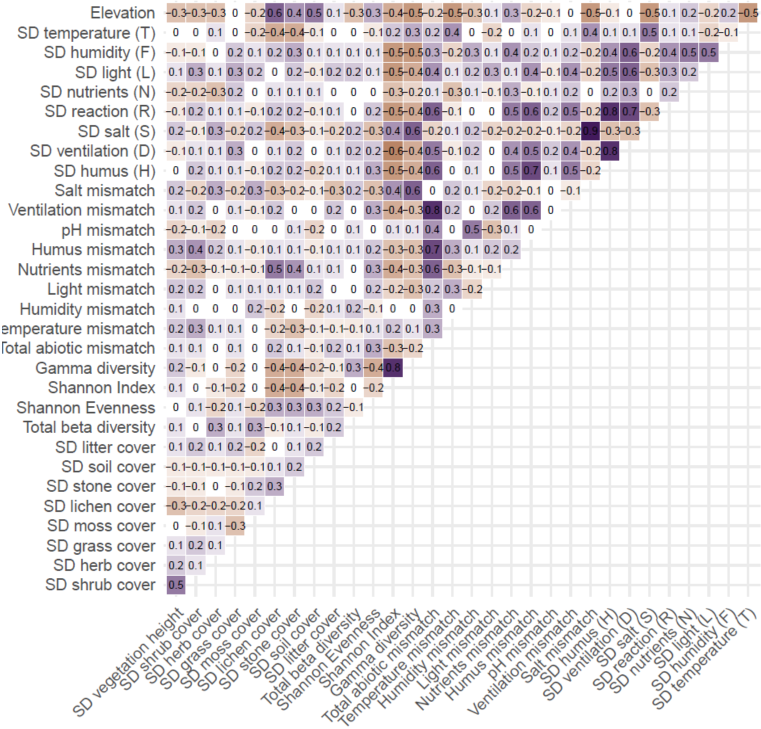
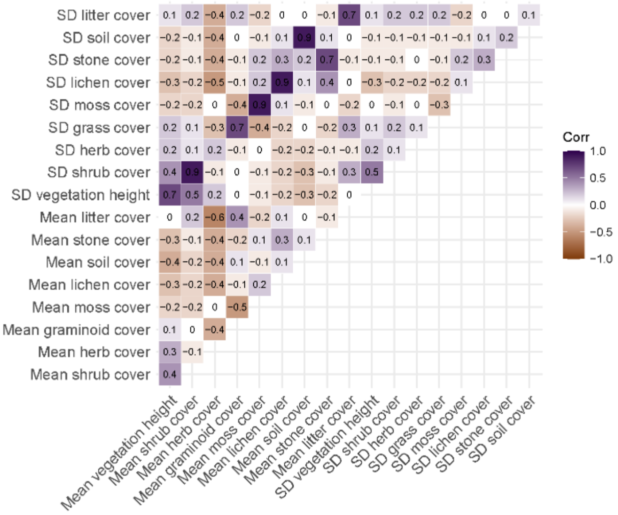


Fig. S1 Correlations among environmental variables based on 87 populations of our eight study species. Values of the Pearson rank coefficients are given (purple – positive correlation, brown – negative correlation). SD = standard deviation. See methods for a description of the variables.



	Mean vegetation height	Mean shrub cover	Mean herb cover	Mean graminoid cover	Mean moss cover	Mean lichen cover	Mean soil cover	Mean stone cover	Mean litter cover	SD vegetation height	SD shrub cover	SD herb cover	SD grass cover	SD moss cover	SD lichen cover	SD stone cover	SD soil cover
SD litter cover	0.1	0.2	−0.4	0.2	−0.2	0	0	−0.1	0.7	0.1	0.2	0.2	0.2	−0.2	0	0	0.1
SD soil cover	−0.2	−0.1	−0.4	0	−0.1	0.1	0.9	0.1	0	−0.1	−0.1	−0.1	−0.1	−0.1	0.1	0.2	
SD stone cover	−0.2	−0.1	−0.4	−0.1	0.2	0.3	0.2	0.7	−0.1	−0.1	−0.1	0	−0.1	0.2	0.3		
SD lichen cover	−0.3	−0.2	−0.5	−0.1	0.2	0.9	0.1	0.4	0	−0.3	−0.2	−0.2	−0.2	0.1			
SD moss cover	−0.2	−0.2	0	−0.4	0.9	0.1	−0.1	0	−0.2	0	−0.1	0	−0.3				
SD grass cover	0.2	0.1	−0.3	0.7	−0.4	−0.2	0	−0.2	0.3	0.1	0.2	0.1					
SD herb cover	0.2	0.1	0.2	−0.1	0	−0.2	−0.2	−0.1	−0.1	0.2	0.1						
SD shrub cover	0.4	0.9	−0.1	0	−0.1	−0.2	−0.3	−0.1	0.3	0.5							
SD vegetation height	0.7	0.5	0.2	0	−0.1	−0.2	−0.3	−0.2	0								
Mean litter cover	0	0.2	−0.6	0.4	−0.2	0.1	0	−0.1									
Mean stone cover	−0.3	−0.1	−0.4	−0.2	0.1	0.3	0.1										
Mean soil cover	−0.4	−0.2	−0.4	0.1	−0.1	0.1											
Mean lichen cover	−0.3	−0.2	−0.4	−0.1	0.2												
Mean moss cover	−0.2	−0.2	0	−0.5													
Mean graminoid cover	0.1	0	−0.4														
Mean herb cover	0.3	−0.1															
Mean shrub cover	0.4																

Fig. S2 Correlations among environmental variables based on 87 populations of our eight study species. Values of the Pearson rank coefficients are given (purple – positive correlation, brown – negative correlation). SD = standard deviation. See methods for a description of the variables.

Table S1 ANOVA tables of linear models investigating the effects of habitat quality on population size among four rare and four common alpine plant species. In model (a) we tested whether elevation, topography, disturbance and collection date affected population size without model simplification. Because population size was significantly affected by elevation, we included elevation as a co-variable in each of the habitat quality models (b-f). We tested the following habitat quality variables in separate models: total abiotic mismatch (b), single abiotic mismatches (c), alpha diversity and evenness (d), gamma diversity (e) and biotic heterogeneity (beta diversity, f). Numeric variables were z-transformed and population size was transformed with the decadic logarithm. Final models contained only fixed effects for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the statistical analysis.

		(a)		(b)		(c)	
Source of variation	df	SS	F	SS	F	SS	F
Elevation	1	2.16	**4.2***				
Inclination	2	2.2	2.15				
Exposition	10	6.84	1.33				
Disturbance	1	0.03	0.05				
Collection date	1	0.63	1.2				
Genus	3	3.66	**2.37°**	3.52	**2.31°**	5.24	**3.79***
Rarity	1	0.04	0.07	0.12	0.39	0.1	0.22
Genus : rarity	3	6.9	**4.46**	8.67	**5.67****	5.96	**4.32****
Total abiotic mismatch	1			2.59	**5.09***		
Salt mismatch	1					3.64	**7.9****
Temperature mismatch	1					5.96	**12.25*****
Residuals		34.0		40.7		35.9	
Number observations		89		89		88	
R^2 adjusted		0.37		0.25		0.32	

		(d)		(e)		(f)	
Source of variation	df	SS	F	SS	F	SS	F
Elevation	1					3.46	**5.88***
Genus	3			2.99	1.91		
Rarity	1	0.37	0.72	0.01	0.02		
Genus : rarity	3			4.26	**2.71°**		
Alpha diversity	1	4.08	**7.93****				
Evenness	1	2.82	**5.48***				
Evenness : rarity	1	1.96	**3.8°**				
Gamma diversity	1			1.44	2.75		
Beta diversity	1					0.12	0.2
Residuals		42.24		41.84		50.59	
Number observations		87		89		89	
R^2 adjusted		0.19		0.23		0.06	

Table S2 ANOVA tables of linear models investigating the effects of habitat quality on population size among four rare and four common alpine plant species. Because population size was significantly affected by elevation, we included elevation as a co-variable in each of the habitat quality models (a and b). We tested the following habitat quality variables in separate models: abiotic heterogeneity (SD indicator values; a) and structural heterogeneity (SD of vegetation height and SD of the cover of shrubs, forbs, graminoids, litter, mosses, lichen, bare ground and soil; b). Numeric variables were z-transformed and population size was transformed with the decadic logarithm. Final models contained only fixed effects for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the statistical analysis.

		(a)		(b)	
	df	SS	F	SS	F
Parameters					
Genus	3	1.62	1.11		
Rarity	1	0.16	0.32		
SD light	1	2.16	**4.41***		
SD reaction	1	0.84	1.71		
Genus : rarity	3	7.66	**5.21****		
Rarity : SD reaction	1	2.34	**4.77***		
SD bare ground	1			2.99	**5.85***
SD graminoids	1			4.37	**8.57****
SD lichen	1			3.53	**6.88***
SD vegetation height	1			1.43	**2.79°**
Residuals		38.24		42.03	
Number observations		89		87	
R^2 adjusted		0.29		0.2	

Table S3 ANOVA tables of linear models investigating the effects of habitat quality on fitness among populations of four rare and four common alpine plant species. We tested in separate models whether seed number, seed mass and germination are affected by elevation, topography, disturbance and collection date. We z-transformed seed number and seed mass within genera. Final models contained only fixed effects for which there are statistical values in the table (χ^2: Chi squared, SS: sum of squares, F: F-statistics, df: degrees of freedom; chi squared; type III F-tests based on Satterthwaite's method for linear mixed effect models; type II Wald χ^2-tests for generalised mixed effect model). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the statistical analysis.

		Seed number		**Seed mass**		**Germination**	
	df	SS	F	SS	F	χ^2	Pr>χ^2
Fixed effects							
Genus	3	3.82	1.91	0.51	0.45		
Rarity	1	2.96	**4.44***	3.41	**9.08****		
Collection date	1	15.15	**22.72*****	32.85	**87.36*****	17.83	**<0.001*****
Collection year	1	66.3	**99.44*****				
Genus : rarity	3	47.96	**23.98*****	34.14	**30.26*****		
Elevation	1			9.11	**24.23*****		
Seed mass	1					38.77	**<0.001*****
Random effects	Var	SD variance	Var	SD variance	Var	SD variance	
Population ID	0.21	0.46	0.16	0.4	2.68	1.64	
Tray					0.06	0.25	
Residual	0.67	0.82	0.38	0.61			
Number observations		3156		2647		693	
Number groups		87		86		44, 10	
R^2m/R^2c		0.21/0.39		0.31/0.52		0.31/0.97	

Table S4 ANOVA tables of linear mixed effects models investigating the effects of habitat quality on seed number among populations of four rare and four common alpine plant species. We tested in separate models whether seed number was affected by alpha diversity and evenness (a), biotic heterogeneity (beta diversity; b) and structural heterogeneity (SD of vegetation height and SD of the cover of shrubs, forbs, graminoids, litter, mosses, lichen, bare ground and soil; c). We tested whether relationships between seed number and habitat quality changed when we accounted for population size (d-f). We z-transformed seed number within genera and transformed population size with the decadic logarithm. We z-transformed all numeric variables. Final models contained only fixed effects for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; type III F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the analyses.

		(a)		(b)		(c)	
	df	SS	F	SS	F	SS	F
Fixed effects							
Genus	3	5.35	**2.7°**	2.9	1.45	2.79	**4.23***
Rarity	1	1.02	1.54	4.77	**7.16****	3.27	**4.96***
Collection date	1	13.59	**20.56*****	15.19	**22.78*****	16.39	**24.83*****
Year	1	58.25	**88.12*****	66.6	**99.91*****	54.31	**24.08*****
Genus : rarity	3	49.47	**24.45**	53.47	**26.73*****	47.68	**24.08*****
Evenness	1	3.03	**4.59***				
Alpha diversity	1	0.44	0.67			0.31	0.46
Beta diversity	1			5.08	**7.61****		
SD forbs	1					2.79	**4.23***
Random effects		Var	SD variance	Var	SD variance	Var	SD variance
Population ID		0.19	0.45	0.19	0.44	0.2	0.45
Residual		0.66	0.81	0.67	0.82	0.66	0.81
Number observations		3127		3156		3067	
Number groups		86		87		85	
R^2m/R^2c		0.22/0.39		0.22/0.39		0.22/0.4	

		(d)		(e)		(f)	
	df	SS	F	SS	F	SS	F
Fixed effects							
Genus	3	5.14	**2.57°**	2.55	1.27	4.17	2.11
Rarity	1	1.1	1.65	5.12	**7.68****	3.7	**5.6***
Collection date	1	14.37	**21.56*****	14.9	**22.34*****	16.1	**24.39*****
Year	1	66.08	**99.9*****	66.8	**100.21*****	54.51	**82.59*****
Genus : rarity	3	52.43	**26.21*****	54.76	**27.28**	49.66	**25.08*****
Evenness	1	3.59	**5.38***				
Beta diversity	1			5.09	**7.65****		
SD forbs	1					3.17	**4.8***
Population size	1	2.08	**3.12°**	1.07	1.6	1.41	2.13
Random effects		Var	SD variance	Var	SD variance	Var	SD variance
Population ID		0.2	0.44	0.19	0.43	0.2	0.45
Residual		0.67	0.82	0.67	0.82	0.66	0.81
Number observations		3156		3156		3067	
Number groups		87		87		85	
R^2m/R^2c		0.21/0.39		0.21/0.39	0.22/0.4		

Table S5 ANOVA tables of linear mixed effects models investigating the effects of gamma diversity and population size on seed mass among populations of four rare and four common alpine plant species. In model (a), we tested whether seed mass was affected by gamma diversity. In model (b), we tested whether relationships between seed mass and gamma diversity changed when we accounted for population size. We z-transformed seed mass within genera and transformed population size with the decadic logarithm. We z-transformed all numeric variables. Final models contained only fixed effects for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; type III F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the analyses.

		(a)		(b)	
	df	SS	F	SS	F
Fixed effects					
Gamma diversity	1	2.34	**6.32***	2.27	**6.15***
Genus	3	0.58	0.53	0.57	0.51
Rarity	1	1.6	**4.32***	1.57	**4.24***
Elevation	1	9.75	**26.36*****	9.46	**25.6*****
Collection date	1	44.01	**119.06*****	43.97	**118.95*****
Year	1	16.96	**45.88*****	16.95	**45.84*****
Genus : rarity	3	39.81	**35.9*****	35.25	**31.79*****
Population size	1			0.00	$3e^{-4}$
Random effects		Var	SD variance	Var	SD variance
Population ID		0.14	0.38	0.15	0.39
Residual		0.37	0.61	0.37	0.61
Number observations		2647		2647	
Number groups		86		86	
R^2m/R^2c		0.34/0.53		0.34/ 0.53	

Table S6 ANOVA tables of linear mixed effects models investigating the effects of abiotic heterogeneity and population size on seed mass among populations of four rare and four common alpine plant species. In model (a), we tested whether seed mass was affected by abiotic heterogeneity (SD of the indicator values moisture (F), soil salt (S), nutrients (N), temperature (T), light levels (L) and reaction (R)). In model (b), we tested whether relationships between seed mass and abiotic heterogeneity changed when we accounted for population size. We z-transformed seed mass within genera and transformed population size with the decadic logarithm. We z-transformed all numeric variables. Final models contained only fixed effects for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; type III F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the analyses.

		(a)		(b)	
	df	SS	F	SS	F
Fixed effects					
Genus	3	1.02	0.92	1.12	1.0
Population size	1			0.2	0.53
Rarity	1	0.75	2.01	0.68	1.81
Collection date	1	41.97	**112.55*****	42.11	**112.9*****
SD light (L)	1	3.07	**8.24****	2.83	**0.75^{-2}****
Year	1	17.47	**46.86*****	17.41	**46.67*****
Genus : rarity	3	35.48	**31.71*****	31.77	**28.4*****
Random effects		Var	SD variance	Var	SD variance
Population ID		0.14	0.38	0.15	0.38
Residual		0.37	0.61	0.37	0.61
Number observations		2647		2647	
Number groups		86		86	
R^2m/R^2c		0.31/0.5		0.31/0.51	

Table S7 ANOVA tables of linear mixed effects models investigating the effects of structural heterogeneity and population size on seed mass among populations of four rare and four common alpine plant species. In model (a), we tested whether seed mass was affected by structural heterogeneity (SD of vegetation height and SD of the cover of shrubs, forbs, graminoids, litter, mosses, lichen, bare ground and soil). In model (b), we tested whether relationships between seed mass and structural heterogeneity changed when we accounted for population size. We z-transformed seed mass within genera to zero mean and transformed population size with the decadic logarithm. We z-transformed all numeric variables. Final models contained only fixed effects for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; type III F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***. See methods for a detailed description of the analyses.

		(a)		(b)	
	df	SS	F	SS	F
Fixed effects					
SD stone cover	1	4.0	**11.94*****	4.0	**11.93*****
Genus	3	0.19	0.19	0.26	0.26
Rarity	1	1.56	**4.64***	1.62	**4.82***
Elevation	1	8.91	**26.55*****	8.96	**26.72*****
Collection date	1	33.06	**98.54*****	32.92	**98.14*****
Genus : rarity	3	31.35	**31.15*****	28.58	**28.41*****
Population size	1			0.1	0.31
Random effects		Var	SD variance	Var	SD variance
Population ID		0.14	0.37	0.14	0.37
Residual		0.34	0.58	0.33	0.58
Number observations		2549		2549	
Number groups		83		83	
R^2m/R^2c		0.3/0.5		0.3/0.51	

Table S8 ANOVA tables of linear mixed effects models investigating the effects of total abiotic mismatch and population size on seed mass among populations of four rare and four common alpine plant species. In model (a), we tested whether seed mass was affected by total abiotic mismatch. In model (b), we tested whether relationships between seed mass and total abiotic mismatch changed when we accounted for population size. We z-transformed seed mass within genera and transformed population size with the decadic logarithm. We z-transformed all numeric variables. Final models contained only fixed effects for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; type III F-tests based on Satterthwaite's method. For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***. See methods for a detailed description of the analyses.

		(a)		(b)	
	df	SS	F	SS	F
Fixed effects					
Genus	3	1.16	1.04	1.13	1.02
Total abiotic mismatch	1	0.87	2.36	1.08	**2.92°**
Population size	1			0.24	0.66
Rarity	1	3.73	**10.09****	3.61	**9.77****
Elevation	1	9.64	**26.09*****	9.55	**25.84*****
Collection date	1	17.36	**116.55*****	43.08	**116.58*****
Year	1	17.36	**46.98*****	17.26	**46.71*****
Genus : rarity	3	30.0	**27.07*****	24.43	**22.03*****
Random effects		Var	SD variance	Var	SD variance
Population ID		0.16	0.4	0.16	0.4
Residual		0.37	0.61	0.37	0.61
Number observations		2647		2647	
Number groups		86		86	
R^2m/R^2c		0.32/0.53		0.33/0.53	

Table S9 ANOVA tables of generalised mixed effects models investigating the effects of abiotic mismatch on seed germination among populations of two rare and two common alpine plant species (*G. alpina*, *P.nivea*, *G. acaulis* and *P. crantzii*). We tested in separate models whether germination was affected by total abiotic mismatch (a) and single abiotic mismatches (c-d). We tested whether relationships between germination and total abiotic mismatch changed when we accounted for population size (b). We z-transformed numeric variables and transformed population size with the decadic logarithm. Final models contained only fixed effects for which there are statistical values in the table (df: degrees of freedom; χ^2: Chi squared, type II Wald χ^2-square tests). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the analyses.

		(a)		(b)		(c)	
	df	χ^2	Pr>χ^2	χ^2	Pr>χ^2	χ^2	Pr>χ^2
Fixed effects							
Genus	3	0.06	0.81	<0.01	0.98	4.44	**0.04***
Total abiotic mismatch	1	6.73	**<0.01****	4.58	**0.03***		
Mismatch in moisture (F)	1					6.03	**0.01***
Rarity	1	1.38	0.24	0.51	0.48	0.98	0.32
Collection date	1	7.63	**<0.01****	7.6	**<0.01****	6.01	**0.01***
Genus : rarity	1	24.31	**<0.001*****	22.69	**<0.001*****	7.71	**<0.01****
Population size	1			0.01	0.91		
Random effects		Var	SD variance	Var	SD variance	Var	SD variance
Population ID		1.57	1.25 1.5	1.22	1.63	1.28	
Tray		0.07	0.26			0.07	0.26
Number observations		693		693		676	
Number groups		44, 10		44		43, 10	
R^2m/R^2c		0.56/0.97		0.58/0.97		0.56/0.97	

		(d)		(e)	
	df	χ^2	Pr>χ^2	χ^2	Pr>χ^2
Fixed effects					
Mismatch in soil salt (S)	1	2.82	**0.09°**		
Mismatch in light (L)	1			6.21	**0.01***
Genus	1	0.18	0.67	2.35	0.13
Rarity	1	2.24	0.13	13.27	**<0.001*****
Collection date	1	16.45	**<0.001*****	14.99	**<0.001*****
Genus : rarity	1	18.83	**<0.001*****	5.02	**0.03***
Random effects		Var	SD variance	Var	SD variance
Population ID		1.78	1.33	1.68	1.3
Tray		0.07	0.26	0.07	0.27
Number observations		676		676	
Number groups		43, 10		43, 10	
R^2m/R^2c		0.54/0.97		0.55/0.97	

Table S10 ANOVA tables of generalised mixed effects models investigating the effects of biotic heterogeneity (beta diversity) and population size on seed germination among populations of two rare and two common alpine plant species (*G. alpina*, *P.nivea*, *G. acaulis* and *P. crantzii*). In model (a), we tested whether germination was affected by biotic heterogeneity. In model (b), we tested whether relationships between germination and biotic heterogeneity changed when we accounted for population size. We z-transformed numeric variables and transformed population size with the decadic logarithm. Final models contained only fixed effects for which there are statistical values in the table (df: degrees of freedom; χ^2: Chi squared, $p > \chi^2$, type II Wald χ^2-tests). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the analyses.

		(a)		(b)	
	df	χ^2	Pr>χ^2	χ^2	Pr>χ^2
Fixed effects					
Beta diversity	1	0.57	0.45	0.19	0.67
Rarity	1	2.88	**0.09°**	10.1	**<0.01****
Collection date	1	18.34	**<0.001*****		
Genus	3	$0.19e^{-2}$	0.89	0.01	0.92
Beta diversity : rarity	1	4.95	**<0.05***	1.45	0.23
Population size	1			0.48	0.49
Genus : rarity	1	10.59	**<0.01****	8.02	**<0.01****
Random effects		Var	SD variance	Var	SD variance
Population ID		1.62	1.27	2.25	1.5
Tray		0.07	0.27		
Number observations		693		693	
Number groups		44, 10		44	
R^2m/R^2c		0.55/0.97		0.36/0.97	

Table S11 ANOVA tables of generalised mixed effects models investigating the effects of abiotic heterogeneity and population size on seed germination among populations of two rare and two common alpine plant species (*G. alpina*, *P.nivea*, *G. acaulis* and *P. crantzii*). In model (a), we tested whether germination was affected by abiotic heterogeneity (SD indicator values moisture (F), SD nutrients (N), SD temperature (T), SD light (L), SD reaction (R)). In model (b), we tested whether relationships between germination and abiotic heterogeneity changed when we accounted for population size. We z-transformed numeric variables to a mean of zero and transformed population size with the decadic logarithm. Final models contained only fixed effects for which there are statistical values in the table (df: degrees of freedom; χ^2: Chi squared, p > χ^2, type II Wald χ^2-tests). For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***. See methods for a detailed description of the analyses.

		(a)		(b)		
	df	χ^2	Pr>χ^2	χ^2	Pr>χ^2	
Fixed effects						
Genus	1	1.45	0.23	1.79	0.18	
Rarity	1	0.04	0.85	$0.62e^{-2}$	0.94	
Collection date	1	20.4	**<0.001*****	21.88	**<0.001*****	
SD reaction (R)	1	3.72	**0.05°**	4.89	**0.03***	
SD soil salt (S)	1	3.59	**0.06°**	4.04	**0.04***	
SD temperature (T)	1	3.68	**0.06°**	3.71	**0.05°**	
Genus : rarity	1	16.04	**<0.001*****	18.03	**<0.001*****	
Population size	1			2.16	0.14	
Random effects		Var	SD variance	Var	SD variance	
Population ID		1.55	1.25		1.36	1.17
Tray		0.07	0.26			
Number observations		693		693		
Number groups		44, 10		44		
R^2m/R^2c		0.56/0.97		0.58/0.97		

Table S12 ANOVA tables of generalised mixed effects models investigating the effects of structural heterogeneity and population size on seed germination among populations of two rare and two common alpine plant species (*G. alpina*, *P.nivea*, *G. acaulis* and *P. crantzii*). In model (a), we tested whether germination was affected by structural heterogeneity (SD of vegetation height and SD of the cover of shrubs, forbs, graminoids, litter, mosses, lichen, bare ground and soil). In model (b), we tested whether relationships between germination and structural heterogeneity changed when we accounted for population size. We z-transformed numeric variables and transformed population size with the decadic logarithm. Final models contained only fixed effects for which there are statistical values in the table (df: degrees of freedom; χ^2: Chi squared, $p > \chi^2$, type II Wald χ^2-tests). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the analyses.

		(a)		(b)	
	df	χ^2	Pr>χ^2	χ^2	Pr>χ^2
Fixed effects					
SD bare ground	1	7.42	**<0.01****	0.55	0.46
Genus	1	1.78	0.18	0.54	0.46
SD graminoids	1	15.1	**<0.001*****	18.39	**<0.001*****
SD litter	1	23.18	**<0.001*****	5.14	**0.02***
Rarity	1	0.02	0.88	1.81	0.18
Collection date	1	37.4	**<0.001*****		
SD stones	1	8.66	**<0.01****	15.82	**<0.001*****
Genus : rarity	1	35.58	**<0.001*****	19.49	**<0.001*****
Population size	1			5.27	**0.02***
Random effects		Var	SD variance	Var	SD variance
Population ID		0.74	0.86	1.25	1.12
Tray		0.07	0.27		
Number observations		671		671	
Number groups		43, 10		43	
R^2m/R^2c		0.75/0.97		0.63/0.97	

Table S13 Species indicator values according to Landolt et al. (2010). Adapted from Lauber et al. (2018) and wsl.ch (2023).

Temperature	Characterises the average temperature at which the species thrives and therefore largely reflects the altitudinal distribution of the species
1 1+ 2 2+ 3 3+ 4 4+ 5	alpine and nival (from the tree line to the snow line) lower-alpine, supra-alpine and upper-subalpine (pine-larch forests) subalpine (spruce forests without beech up to the upper limit of spruce) lower-subalpine and upper montane montane (forests with beech, silver fir, in the central Alps with scots pine) lower-montane and upper colline colline (mixed deciduous forests with oak) warm-colline very warm (only in the warmest places, main distribution southern Europe)
Soil moisture	Indicates mean soil moisture during the vegetation time
1 1+ 2 2+ 3 3+ 4 4+ 5	very dry dry moderately dry moderately dry to moderately damp moderately damp damp wet very wet flooded or under water
Soil reaction	Characteristic for the content of free H ions in the soil. The pH values are only indicative of the average occurrence, exceptions are frequent
1 2 3 4 5	Strongly acidic (pH 2.5-5.5) acidic (pH 3.5-6.5) weakly acidic to neutral (pH 4.5-7.5) neutral to weakly alkaline (pH 5.5-8.5) alkaline (pH 6.5->8.5)

Table S14 Species indicator values according to Landolt et al. (2010). Adapted from Lauber et al. (2018) and wsl.ch (2023).

Soil nutrients	Indicates the nutrient content (especially nitrogen) of the soil
1	very nutrient-poor
2	nutrient-poor
3	moderately nutrient-poor to moderately nutrient-rich
4	nutrient-rich
5	very nutrient-rich to over-fertilised
Light levels	Characteristic for the average illumination level at which the plant thrives
1	very shady
2	shady
3	semi-shady
4	bright
5	very bright
Humus cover	Indicates the humus cover of the soil
1	soils with no humus cover (bare soil indicator)
2	soils with small humus cover (indicator of mineral soils)
3	soils with intermediate humus cover
4	soils with humus, plant rooting partly in mineral soil
5	raw humus or bog, plant rooting particularly in humus
Soil dispersity	Indicates soil ventilation
1	plant on rocks, blocks or walls
2	species on rubble, gravel or soils with a high amount of skeleton
3	plant on well-drained soils rich in skeleton
4	plant on soils poor in skeleton
5	often indicator of clay or peat-soil or generally indicating lack of oxygen
Soil salt	Indicates the salt-tolerance of the plant
1	plant on salt soils, salt-tolerant species
2	species avoiding salt soils

Population of the rare *Gentiana alpina* (*Gentianaceae*) in the Valais, Switzerland.

Chapter 4

Relationships between within-population trait diversity, population size and habitat heterogeneity in four common and four rare alpine plant species

Hannah Inniger, Daniel Prati, Markus Fischer

Abstract Small populations of many plant species suffer from reduced plant fitness, which may decrease their adaptive potential. As trait diversity is a fundamental prerequisite for selection and adaptation, it is essential to investigate whether small populations have reduced trait diversity and how this depends on the surrounding habitat. While this aspect has scarcely been studied, it may be particularly important for alpine plant species in their harsh and changing environment. We studied the relationship of population size and abiotic, biotic and structural habitat heterogeneity with trait diversity in 87 populations of four common and four rare alpine plant species in the Swiss Alps. To assess habitat heterogeneity, we took eight vegetation records in each population and quantified abiotic heterogeneity via vegetation-based indicator values, biotic heterogeneity via beta-diversity among records within populations, and structural heterogeneity based on variation in shrub-, forb-, graminoid-, lichen-, moss-, stone-, litter- and bare ground cover. We measured plant height, leaf number, and the width and length of leaves and flowers for 20 plants per population and quantified variation in individual traits as coefficient of variation (CV) and multidimensional trait diversity as trait richness, trait evenness and trait dispersion. Population size explained little variance in within-population trait diversity. Abiotic heterogeneity generally increased and structural heterogeneity generally decreased within-population trait diversity across all species. For rare species, higher biotic heterogeneity reduced the CV of two traits and increased it for common species. The CV of one trait and trait richness were generally lower for rare species. As the importance of population size for trait diversity in populations of alpine species might differ across species, we suggest that it requires further investigation. We conclude that habitat heterogeneity is the most important determinant of trait diversity in our study populations and that species rarity is also a contributing factor.

Abbreviations:

CV Coefficient of variation
SD Standard deviation

Introduction

Due to habitat fragmentation and alteration, populations of many plant species become smaller and more isolated (Lienert 2004). Smaller populations typically display lower genetic diversity and reduced plant fitness in comparison to larger populations (Ellstrand and Elam 1993; Fischer and Matthies 1998; Reed 2005). Consequently, the ability to adapt to changing environmental conditions is likely to decrease (Barrett and Kohn 1991). The permanent cycle between population size, genetic diversity and fitness can lead to local extinction and is known as extinction vortex (Gilpin and Soulé 1986; Matthies et al. 2004; Leimu et al. 2006). Research on the extinction vortex has traditionally concentrated on genetic diversity and plant fitness. Hereby, fitness has mostly been assessed as the average performance of a population in terms of reproductive traits such as seed number, seed mass and seed germination (e.g. Fischer and Matthies 1998; Leimu et al. 2006). However, an equally significant ecological and evolutionary aspect of a population is within-population trait diversity, which quantifies the variability among individuals within a population across single or multiple traits. Given that trait diversity is considered as a fundamental requirement for adaptive capacity and natural selection (Schoener 2011; Bussotti et al. 2015; Karbstein et al. 2020), it is important to assess whether within-population trait diversity is also reduced in small populations. To the best of our knowledge, only the dry meadow species *Trifolium montanum* has been studied in this context so far (Karbstein et al. 2023).

Sources of trait diversity are genetic variation and the surrounding environment (Blanquart et al. 2013; Puy et al. 2021; Kemppinen and Niittynen 2022). Genetic variation can arise from genetic drift, mutation, recombination, selection and immigration (Blanquart et al. 2013) and is usually higher in large than in small populations due to lower levels of genetic drift and inbreeding (e.g. Fischer and Matthies 1998). Research in natural plant populations has demonstrated that variation in phenotype and variation in genotype are associated, especially for morphology-related traits (Karbstein et al. 2020). Therefore, large populations may have higher within-population trait diversity compared to small populations. Alternatively, within-population trait diversity might be a result of natural selection in the past as adaptation to the surrounding environment. In this case, we would not observe an effect of population size when accounting for the surrounding habitat.

Regarding the environment, recent studies indicate the significance of habitat heterogeneity in maintaining within-population trait diversity (Wellstein et al. 2013; Karbstein et al. 2020), however, not in the context of population size (but see Karbstein et al. 2023). We expect that populations occurring in more heterogeneous habitats have higher within-population trait diversity due to different adaptations to diverse microenvironments. This adaptation may occur either through the selection of well-suited genotypes, leading to genetically fixed variation, or via phenotypic plasticity (Wellstein et al. 2013; Karbstein et al. 2020). Phenotypic plasticity is the extent to which the genotype can be modified on the level of the phenotype by environmental variation (DeWitt et al. 1998). Due to potential constraints in genetic variation and phenotypic plasticity, individuals within small populations may tend to exhibit relative similarity even in the presence of pronounced heterogeneity.

An understanding of the relationships between trait diversity, population size, and habitat heterogeneity might be particularly important for alpine species. Climate change exerts notably pronounced effects on alpine ecosystems (Theurillat and Guisan 2001) and trait diversity may be a crucial prerequisite for alpine species to be able to adapt to future biotic and abiotic conditions (Rixen et al. 2022). Because populations of rare species usually exhibit lower genetic variation than populations of common species (Boyd et al. 2022), we expect that negative consequences of a small population size on within-population trait diversity might be stronger for populations of rare than for populations of common species. Similarly, habitat heterogeneity might affect within-population trait diversity less in rare than in common species due to genetic constraints. Alternatively, reasons other than reduced levels of genetic diversity and phenotypic plasticity might be responsible for rarity in alpine plant species, and we may observe no differences between rare and common species regarding the relationships between within-population trait diversity, population size and habitat heterogeneity.

Here, we investigated the relationships between trait diversity, population size and habitat heterogeneity in four common and four rare congeneric alpine grassland species. We measured morphological traits (plant height, leaf number, leaf and flower width and length) in 87 populations at different elevation sites in the Swiss Alps. We quantified within-population trait diversity with the CV of individual traits and with multidimensional diversity metrics, namely trait richness, trait evenness and trait dispersion. To assess habitat heterogeneity, we took eight vegetation records in each population and quantified abiotic heterogeneity via variation in species indicator values, biotic heterogeneity via beta-diversity among the records and structural heterogeneity based on variation in the cover of shrubs, forbs, graminoids, lichens, mosses, stones, litter and bare ground cover. We conducted an observational field study without consideration of the sources of trait diversity or the underlying mechanisms driving the observed relationships. We investigated whether variation in trait diversity in populations of our study species can be explained by (I) population size, (II) habitat heterogeneity and (III) an interaction between habitat heterogeneity and population size. Finally, we explored whether there are differences between rare and common species in respect to the relationships between within-population trait diversity, population size and habitat heterogeneity.

Methods

Study species

We selected four congeneric species pairs from four different plant families based on expert knowledge. All species are herbaceous and perennial grassland species with a (sub-) alpine distribution. Each species pair included one common and one phylogenetically closely related (naturally) rare species. We defined species rarity based on geographic range (large vs. small), habitat specificity (generalist vs. specialist) and local abundance (dense vs. sparse) according to Rabinowitz (1981).

As rare species, we studied *Androsace puberula* Jord. & Fourr. (*Primulaceae*, *Caricion curvulae*, classification typoCH, Delarze et al. 2008), *Gentiana alpina* Vill. (*Gentianaceae*, *Caricion curvulae*), *Potentilla nivea* L. (*Rosaceae*, *Elynion*) and *Viola lutea* Huds. (*Violaceae*, *Seslerion*). These species occur only within a restricted geographic range with sparse local abundance through the Swiss and European Alps (Lauber et al. 2018; GBIF.org 2023).

As common species, we studied *Androsace chamaejasme* Wulfen (*Seslerion, Caricion firmae*), *Gentiana acaulis* L. (*Nardion*), *Potentilla crantzii* (Crantz) Fritsch (*Seslerion*) and *Viola calcarata* L. (*Nardion, Poion alpinae*). These species occur over a wide geographic range with pronounced local abundance throughout the Swiss and European Alps (Lauber et al. 2018; GBIF.org 2023).

Apart from *V. lutea*, the rare species in our study are strongly restricted to their habitat (Lauber et al. 2018). Apart from *G. acaulis*, the common species in our study are not strongly restricted to their habitat (Lauber et al. 2018). *P. crantzii* and *P. nivea* are both facultative apomictic species.

Study locations

We visited ten to twelve different populations (N = 87) per species at different elevations (1390-2810 m.a.s.l.) in two consecutive years (2020, 2021) the Swiss Alps. We selected the populations from the Info Flora database, which collects occurrence data on vascular plant species in Switzerland up to a 1 x 1 kilometre scale (infoflora.ch 2020). No information about the populations was available except for the location coordinates. We first selected the populations of the rare species, so that their entirety covered as much of their whole distribution range as possible throughout Switzerland. We then selected the populations of the common species within a range size comparable to that of their congeneric rare partner species.

P. nivea and *G. alpina* have a disjunct distribution in Switzerland. We sampled populations of these species and their common congeneric partner species in both disjunct regions (see Fig. S2-5 Supporting information of Chapter 2 for sampling locations). For each population, we counted the number of fertile (flowering and fruiting) individuals as a measure of population size. Whenever a population exceeded 250 fertile individuals, we estimated the area they occupied and extrapolated this over the entire population to approximate the total number of fertile individuals. We defined the boundaries of the population where we found the outermost plants of the target species.

Within-population trait diversity

In summer 2020, we randomly selected 20 fertile individuals per population across the area of the whole population. In 16 populations, we sampled fewer than 20 individuals (N = 8-19) due to small population size (see Supporting information). For each individual, we counted the number of leaves and the number of flowers per shoot. We measured generative height (shoot and highest flower, stretched), the length and width of three leaves, and the length and width of three flowers. We assigned a phenological status to each flower measured on a scale from zero (closed bud) to eight (dispersed, Table S1 Supporting information).

As a quantification of one-dimensional trait range, we calculated the coefficient of variation (CV) for plant height, leaf number, leaf width and flower width for each population. In the following sections, this will be referred to as variation in individual traits. We did not consider variation in leaf length and flower length, as these traits were closely correlated with leaf width and flower width, respectively (Pearson's correlation coefficient = 0.6; Fig. S4 Supporting information).

The combination of individual traits in a multidimensional space represents an abstract, yet more comprehensive measure of trait diversity. Multidimensional metrics of functional diversity such as functional richness, functional evenness and functional dissimilarity quantify different dimensions of functional trait diversity and are commonly used in community ecology (Cadotte et al. 2011; De Bello et al. 2021). Analogously, these metrics can also be used to quantify the functional diversity of individuals within populations. Any trait, regardless of its functional importance, can be used to calculate a trait space. Therefore, functional diversity metrics enable the quantification of within-population trait diversity.

Trait richness is the multidimensional range of traits within a community or a population, or, in other words, the total volume of the trait space (De Bello et al. 2021; Fig. 1). Trait evenness quantifies how regularly species or individuals are distributed across the trait space (Fig. 1). Trait dispersion is a quantification of trait dissimilarity and measures how distant species or individuals are from the centre of the trait space (de Bello et al. 2021; Fig. 1). Whereas trait richness depends to some degree on the number of species or individuals, evenness and dispersion remain unaffected by the quantity of species or individuals used to compute the metric (De Bello et al. 2021).

We used the function "dbfd" from the R package "FD" (Laliberté et al. 2014) to calculate trait richness (FRic), trait evenness (FEve) and trait dispersion (FDis) for each population based on plant height, leaf number and leaf width. To test how robust the results were, we also calculated the same diversity metrics by substituting leaf width with the leaf width-length ratio.

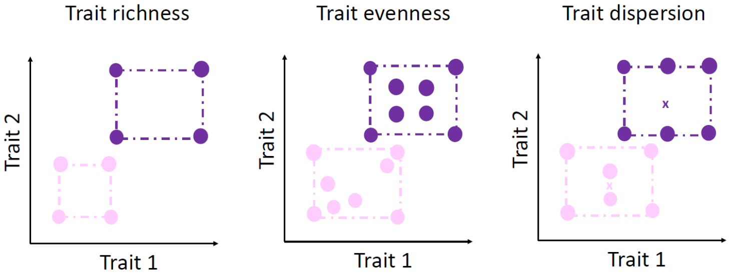


Fig. 1 Schematic representation of metrics used to quantify different dimensions of trait diversity in populations of eight alpine plant species. Trait richness, evenness and dispersion quantify the probability distribution of trait expression by individuals of a population in a multidimensional space. Dots represent individuals of two fictional populations; purple represents a population with high values each of the metrics, and pink represents a population with low values for each of the metrics. Dashed lines indicate the borders of the trait spaces, and crosses in the right graph show 'center of gravities' for each trait space. For a more detailed description of these metrics, see methods. Adapted and modified from Carmona et al. (2016) and De Bello et al. (2021).

Habitat heterogeneity

We took eight circular vegetation records (diameter = 20 cm) per population in the summer of 2021. Since alpine vegetation can vary over very short distances (von Büren and Hiltbrunner 2022), we chose such a small plot size to investigate heterogeneity on a local scale. We took four records around four randomly chosen individuals of the target species. We took another four records at random locations within the population, where no individuals of the target species were present, within a minimum distance of one metre to individuals of the target species, when possible. We distinguished between these two record types to obtain data representing the area of the entire population. For each record, we identified all vascular plants to species and, if necessary, subspecies level. We estimated the percentage cover of each species as well as of lichens, mosses, bare ground, stones and litter. We measured vegetation height in each record by placing a laminated A5 sheet on the vegetation and measuring the minimum and maximum height of the corners.

We assessed biotic, abiotic and structural heterogeneity. Our estimate of biotic heterogeneity was local beta diversity, which we calculated among all microsites of the population with the function “beta.multi.abund” from the package "betapart" (Baselga et al. 2018) in R (R core team 2022). Beta.multi.abund computes a balanced (BC.BAL) and a gradient (BC.GRA) component based on the Bray-Curtis index (Baselga 2013) as a measure of dissimilarity among the given sites based on species abundances. While the balanced component measures species turnover between sites, the gradient component is a measure of how many species are lost from one site to another (Baselga 2017). We used the sum of the two components (BC) as a measure of local beta diversity.

We used Landolt indicator values (Landolt et al. 2010) as an approximation for local abiotic conditions. Landolt indicator values describe the niche position of a species on a scale from one to five, with one referring to the lowest and five to the highest level of the respective factor (see Table S13 and S14 Supporting information of Chapter 3). Community weighted mean indicator values based on vegetation surveys are commonly used to provide information on the abiotic environment and it has been shown that they well correlate ($R^2 > 0.4$) with environmental properties measured in the field (Diekmann 2003; Descombes et al. 2020). For each record, we calculated community weighted means with the software Vegedaz (Küchler 2022) for the following indicator values: temperature (T), moisture (F), reaction (pH; R), light (L), humus (H), nutrients (N), dispersity (D) and salt (S). As a quantification of abiotic heterogeneity, we calculated the mean standard deviation (SD) of the community weighted mean indicator values for each population. As a measure of structural heterogeneity, we calculated the mean SD of the cover of shrubs, graminoids (species from the *Poaceae, Cyperaceae* and *Juncaceae* families), forbs, lichens, mosses, litter, bare ground and stones in each population.

Statistical analysis

We did all the analyses in R (R core team 2022). Abiotic and structural heterogeneity were based on population means. We excluded observations with a distance greater than four standard deviations from the mean (five populations for variation in flower width, one population in trait evenness and two populations in trait richness). We standardized all trait variables within genera to zero mean and a standard deviation of one. We standardised abiotic, biotic and structural heterogeneity to zero mean with a standard deviation of one. We transformed population size and phenotype richness with the decadic logarithm prior to whole analysis.

We used linear regression models to test whether within-population trait diversity was affected by population size and rarity. We fitted separate models with trait richness, trait evenness, trait dispersion and the variation in individual traits (CV) as response variables. Each of the models had the following structure of explanatory variables: *population size + rarity + population size x rarity + genus + genus x rarity*. We did not include species as this would have been redundant to the genus - rarity interaction. In a separate linear model, we tested whether trait diversity was affected by elevation. This model contained trait diversity as response variable and elevation, genus, rarity and the genus - rarity interaction as explanatory variables. When we tested trait richness, we included the number of individuals based on which it was calculated as weights to take into account their potential influence (Fig. S5 and S6 Supporting information). When testing the variation in flower width, we included phenology as a continuous co-variable to account for different phenological states.

To not over-fit the models, we fitted separate linear models for the different habitat heterogeneity parameters. We included the same response variables as described before and the following structure of explanatory variables: *habitat heterogeneity* + *population size* + *habitat heterogeneity x population size* + *rarity* + *habitat heterogeneity x rarity* + *genus* + *genus x rarity*. We included the habitat heterogeneity - population size interaction to account for effects of population size.

We simplified models with the function "dredge" from the package "MuMIn" (Bartoń 2022) based on the Akaike information criterion (AIC). When testing the effect of population size on within-population trait diversity, we retained population size and rarity in the model during model simplification. When testing the effect of habitat heterogeneity on within-population trait diversity, we kept population size and habitat heterogeneity in the model during model simplification. We evaluated the final models based on the R^2 and normality of the residuals. We considered p-values from the ANOVA table (type II F-tests based on Satterthwaite’s method) smaller than 0.05 as significant and smaller than 0.1 as marginally significant.

Results

Effect of population size on within-population trait diversity

Regarding variation in individual traits, variation in leaf number was generally lower in populations of rare species than in populations of common species ($p < 0.05$; Fig. 2e; Table S2 Supporting information). Across all species, we found no significant relationship between variation in individual traits and population size (Fig. 2a, e, i and m).

When we calculated multidimensional trait diversity based on plant height, leaf number and leaf width, trait richness was generally lower in populations of rare species than in populations of common species ($p < 0.01$; Fig. 3a-d; Table S4 and S5 Supporting information). Across all species, we did not observe significant relationships between multidimensional trait diversity and population size when we calculated the metrics based on plant height, leaf number and leaf width (Fig. 3a, e and i). When we calculated multidimensional trait diversity based on plant height, leaf number and the leaf width-length ratio, we observed higher trait evenness in larger populations across all species ($p < 0.05$, Fig. 4e, Table S6 Supporting information). Neither variation in a single trait nor multidimensional trait diversity was significantly affected by an interaction between population size and rarity.

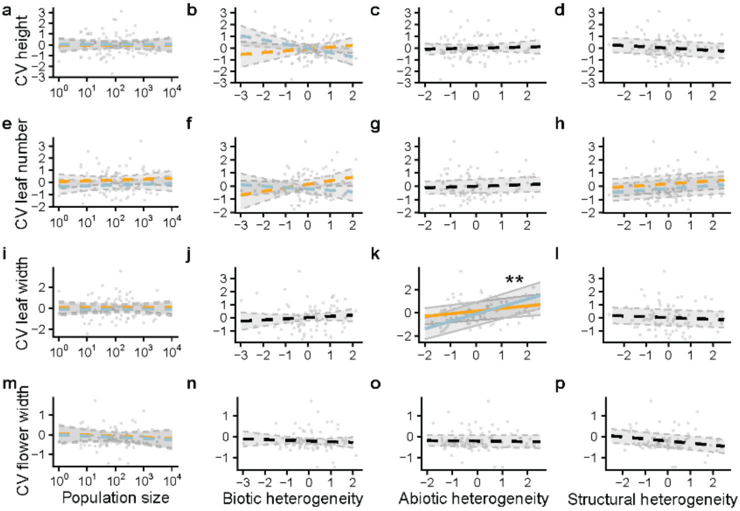


Fig. 2 Relationships between within-population variation (CV) in individual traits, population size and biotic, abiotic and structural heterogeneity among four common and four rare alpine plant species. We transformed population size with the decadic logarithm and scaled all numeric variables to zero mean with a standard deviation of one. Solid lines show significant relationships, dashed lines show non-significant relationships. Blue shows relationships for rare species and yellow shows relationships for common species. Black lines show relationships across all eight species when rarity was not included in the final model. Grey shadows show 95 % confidence intervals and grey dots show observations. Significance levels are given for the main effects: $P < 0.1$; °, $P < 0.05$; *, $P < 0.01$; **, $P < 0.001$; ***.

Effect of habitat heterogeneity on within-population trait diversity

Regarding variation in individual traits, variation in leaf width was higher at locations with high abiotic heterogeneity ($p < 0.01$; Fig. 2k; Table S3 Supporting information). Variation in leaf width was also lower at higher elevations ($p < 0.05$). The relationship between variation in plant height and biotic heterogeneity was different among populations of rare and populations of common species (significant beta diversity - rarity interaction; $p < 0.05$, Fig. 2b; Table S3 Supporting information). While variation in plant height tended to increase in populations of common species in habitats with high biotic heterogeneity, we observed the opposite among rare species. We detected the same pattern for variation in leaf number (marginal rarity - biotic heterogeneity interaction; $p < 0.1$; Fig. 2f; Table S3 Supporting information).

Regarding multidimensional trait diversity, we did not observe a relationship between trait richness, evenness and dispersion and biotic heterogeneity. Trait richness was higher in populations in habitats with high abiotic heterogeneity when we calculated the metric based on plant height, leaf number and leaf width ($p < 0.1$; Fig. 3c; Table S5 Supporting information). Trait dispersion was higher in populations in habitats with high abiotic heterogeneity, independently of how we calculated the metric ($p < 0.05$ and $p < 0.1$; Fig. 3k and 4k; Table S5 and S7 Supporting information). Trait evenness was lower in populations in habitats with high structural heterogeneity, independently of how we calculated the metric ($p < 0.05$ and $p < 0.05$; Fig. 3h and 4h; Table S5 and S7 Supporting information). Trait richness was lower in populations in habitats with high structural heterogeneity when we calculated the metric based on plant height, leaf number and the leaf width-length ratio ($p < 0.05$; Fig. 4d; Table S7 Supporting information). None of the trait diversity variables were affected by an interaction between habitat heterogeneity and population size. In addition, the positive effect of population size on trait evenness (Fig. 4e) remained significant when we accounted for habitat heterogeneity (Table S7 Supporting information).

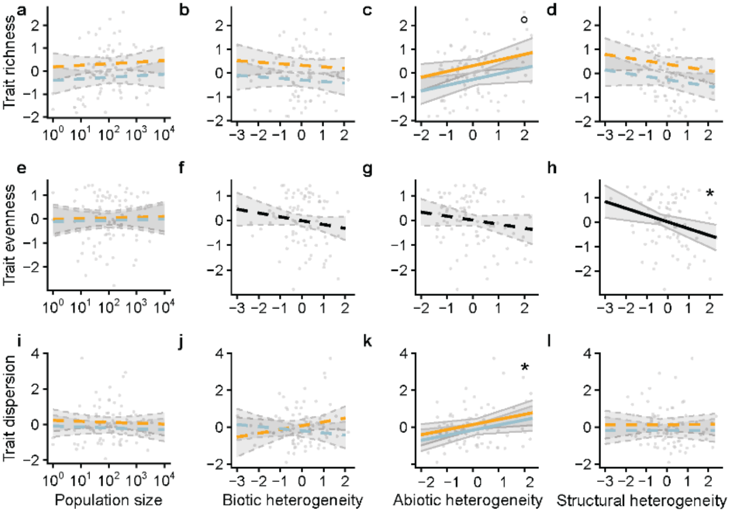


Fig. 3 Relationships between multidimensional within-population trait diversity, population size and biotic, abiotic and structural heterogeneity among four common and four rare alpine plant species. We quantified multidimensional trait diversity by calculating trait richness, evenness and dispersion based on plant height, leaf number and leaf width. We transformed population size with the decadic logarithm and scaled all numeric variables to zero mean with a standard deviation of one. Solid lines illustrate significant relationships and dashed lines indicate relationships that were not significant. Blue shows relationships for rare species and yellow shows relationships for common species. Black lines show relationships across all eight species when rarity did not significantly explain variance in our data. Grey shadows show 95 % confidence intervals for all relationships and grey dots show observations. Significance levels are given for the main effects: $P < 0.1$; °, $P < 0.05$; *, $P < 0.01$; **, $P < 0.001$; ***.

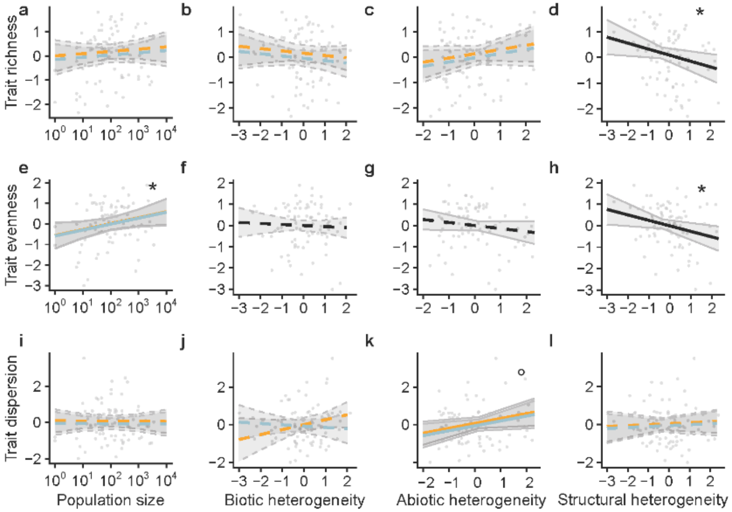


Fig. 4 Relationships between multidimensional within-population trait diversity, population size and biotic, abiotic and structural heterogeneity among four common and four rare alpine plant species. We quantified multidimensional trait diversity by calculating trait richness, evenness and dispersion based on plant height, leaf number and the leaf width-length ratio. We transformed population size with the decadic logarithm and scaled all numeric variables to zero mean with a standard deviation of one. Solid lines illustrate significant relationships and dashed lines indicate relationships that were not significant. Blue shows relationships for rare species and yellow shows relationships for common species. Black lines show relationships across all eight species when rarity did not significantly explain variance in our data. Grey shadows show 95 % confidence intervals for all relationships and grey dots show observations. Significance levels are given for the main effects: $P < 0.1$; °, $P < 0.05$; *, $P < 0.01$; **, $P < 0.001$; ***.

Discussion

Population size explained little variation in within-population trait diversity

Our findings weakly support the hypothesis of lower trait diversity in small populations of alpine plant species. Trait evenness was lower in small populations across all species (Fig. 4e). In other words, individuals from small populations were less regularly distributed within the total trait space than individuals from large populations. Variation in individual traits, trait richness and trait dispersion were not significantly influenced by population size. Thus, population size is likely not a major determinant of within-population trait diversity across the majority of our study species.

However, since we detected a significant relationship between within-population trait diversity and population size within a limited dataset, studies including more species and traits might reveal more significant relationships. As variation in physiology-related traits, such as gas exchange and photosynthesis, tends to be more related to genetic variation than variation in morphology-related traits (Geber and Griffen 2003), such traits might be more strongly related to population size. Future studies should include common garden experiments which could provide information on whether the observed trait diversity is caused by phenotypic plasticity or genetic differentiation (Westerband et al. 2021a). Furthermore, it would be crucial to evaluate the correlations between within-population trait diversity and the average fitness and growth rate of the population to assess whether the observed trait variation is adaptive, neutral or even maladaptive (Westerband et al. 2021a).

To our knowledge, there is only the study by Karbstein et al. (2023) on *Trifolium montanum* in this research area. They demonstrated that small populations of this dry grassland species had lower within-population trait diversity than large populations and concluded that small populations might have a lower adaptive capacity. In our study, slopes of the relationships between within-population trait diversity and population size tended to be different for different species (Fig. S1 and S2 Supporting information). In *P. nivea*, for example, the relationships were consistently positive, but more statistical power would have been required to analyse the effects of population size within species. This suggests that the extent to which trait diversity is reduced in small populations might vary among different species. Thus, it could be worthwhile to study trends at the species level and identify species that display significant relationships.

Our results do not support the hypothesis of a stronger relationship between trait diversity and population size in rare species. However, the CV of one trait and trait richness were generally lower for rare species. In particular, trait richness was low in populations of the rare high alpine *G. alpina*, *P. nivea* and in populations of the common high alpine *V. calcarata* (Fig. S3a and c Supporting information). This supports the previous findings of Rixen et al. (2022), who observed lower intraspecific trait variation in alpine species with higher median elevation ranges than in alpine species with lower median elevation ranges. The combined findings of Rixen et al. (2022) and our study indicate that rare species and species with a high alpine distribution could have a reduced trait diversity and therefore potentially lower adaptive potential compared to common species and species with low alpine and subalpine distribution.

Habitat heterogeneity affected within-population trait diversity in different directions

Our findings support the hypothesis that habitat heterogeneity drives trait diversity in populations of alpine plant species. In our study, the direction of this effect depended on the selected plant traits, how habitat heterogeneity was quantified and on species rarity.

Abiotic heterogeneity had the most positive effects on within-population trait diversity in our study species, both on variation in individual traits and on multidimensional trait diversity. One might argue that abiotic conditions measured via indicator values are less accurate than direct measurements in the soil. However, they provide a more robust picture of abiotic conditions over time, as they are less dependent on the time of measurement. Indeed, our observations support previous findings showing that intraspecific trait diversity is affected by abiotic heterogeneity in plant populations in colline and mountain habitats (Wellstein et al. 2013; Karbstein et al. 2020). Our study indicates that within-population trait diversity can also be driven by abiotic heterogeneity in alpine and high-alpine habitats.

Trait evenness and trait richness were lower in populations in habitats with a high structural heterogeneity. This means that individuals within these populations were not evenly spread across the trait spectrum and occupied a smaller portion of the overall trait space. In contrast, clusters of individuals shared similarities in leaf number, width, length, and plant height. This pattern diverges from our hypothesis of a general positive effect of habitat heterogeneity on within-population trait diversity. Either structural heterogeneity, *per se*, selected for relatively similar phenotypes in populations of our study species, or, structural heterogeneity was confounded with for instance decreased habitat quality or higher environmental stress level, which can decrease trait diversity in plant populations (Stanik et al. 2020). Thus, further investigations are required before drawing conclusions regarding the impact of structural heterogeneity on trait variability in populations of alpine plant species.

We hypothesised that trait diversity would be less influenced by habitat heterogeneity in small than in large populations due to constraints in genetic diversity and phenotypic plasticity. Our results do not support this hypothesis, indicating that habitat heterogeneity is affecting within-population trait diversity in our study species irrespective of population size. The positive effect of population size on trait evenness remained significant when we accounted for habitat heterogeneity and was not a hidden habitat effect. These observations indicate that habitat heterogeneity and population size affect within-population trait diversity independently from each other in our study species.

We expected that trait diversity would be less influenced or remain unaffected by habitat heterogeneity in populations of rare species due to genetic constraints. While patterns of the relationships between within-population trait diversity and abiotic and structural heterogeneity were similar for rare and common species, we observed a disparity among populations of rare and of common species regarding biotic heterogeneity. This probably explains why we did not observe an overall effect of biotic heterogeneity on within-population trait diversity. While for common species, two CVs (leaf number and plant height) tended to increase in habitats with high biotic heterogeneity, we observed the opposite for rare species. Hence, negative effects of habitat heterogeneity on within-population trait diversity were more present in rare than in common species.

In general, our findings of negative relationships between trait diversity and habitat heterogeneity contradict to the frequently observed higher trait diversity at higher heterogeneity, evident both within communities (Stark et al. 2017) and within species (Kemppinen and Niittynen 2022). However, we should not conclude that alpine and especially rare species could benefit from habitat homogenisation. Our results indicate that plant rarity could play a role in the effect of habitat heterogeneity on trait diversity in populations of alpine plant species.

To conclude, we found effects of habitat heterogeneity on within-population trait diversity in our study species, and little evidence for a positive effect of population size on within-population trait diversity. These findings align with previous studies demonstrating that the extent and direction of intraspecific trait variation vary with small-scale heterogeneity such as light levels (Carlucci et al. 2015), soil pH (Dong et al. 2020), soil nutrients (Niu et al. 2020) and climate (Westerband et al. 2021b). Our study suggests that structural, abiotic and biotic heterogeneity might also be important drivers of trait diversity in plant populations. Furthermore, our study agrees with Karbstein et al. (2023), who observed that abiotic heterogeneity was more important than population size in explaining variation in within-population trait diversity of *Trifolium montanum* in colline- and mountain habitats. We show that this might be also true in alpine plant species.

Multidimensional diversity metrics might be useful to detect significant relationships

To the best of our knowledge, no study in the field of population ecology has used multidimensional diversity metrics to quantify within population trait diversity. The present study shows that the use of such metrics might help to investigate which variables determine trait diversity in populations of plant species. We found less significance among the variation in individual traits (CV) than among the multidimensional trait diversity variables, indicating that the combination of individual traits in a multidimensional space may be important in plant populations. We therefore recommend the use of multidimensional diversity metrics when assessing relationships between trait diversity of plant populations and any factor of interest, thereby avoiding potential underestimation or oversight of existing relationships.

Conclusion

We found weak evidence for the hypothesis of population size being a driver of within-population trait diversity in alpine plant species. Our study indicates that the strength of the relationship between within-population trait diversity and population size likely varies among species, suggesting that it would be worth studying such relationships on the species level. Furthermore, habitat heterogeneity was a significant driver of within-population trait diversity in our study species. Thus, our observations emphasise the importance of considering habitat heterogeneity as influential factors when investigating trait diversity within plant populations. As within-population trait diversity was overall lower in populations of rare species, populations of these species might have a lower adaptive potential than populations of common alpine plant species. For a better understanding of the effects of population size and habitat heterogeneity on within-population trait diversity, future studies should include the investigation of a heritable base of the observed trait diversity. Our study suggests that the use of multidimensional diversity metrics could help to identify significant relationships.

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Supporting information

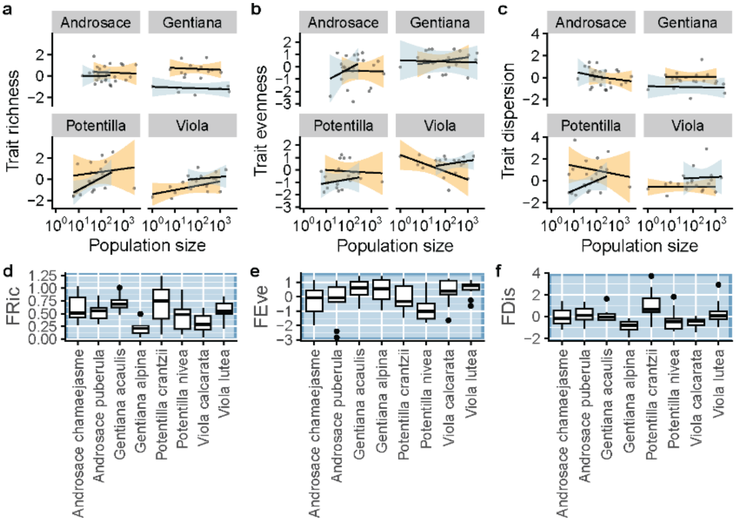

Fig. S1 Relationships between multidimensional trait diversity and population size in four rare and four common alpine plant species. We calculated trait richness (a and d), trait evenness (b and e) and trait dispersion (c and f) based on plant height, leaf number and leaf width in 87 populations of our eight study species. Trait richness and population size were transformed with the decadic logarithm and numeric variables were z-transformed. Rare species are shown in blue, common species are shown in yellow. Lines show relationships predicted by linear regression. Grey dots show observations (N = 8-13 per species), blue and yellow shadows show 95 % confidence intervals. We did not test the relationships between multidimensional trait diversity and population size within species due to limited statistical power.

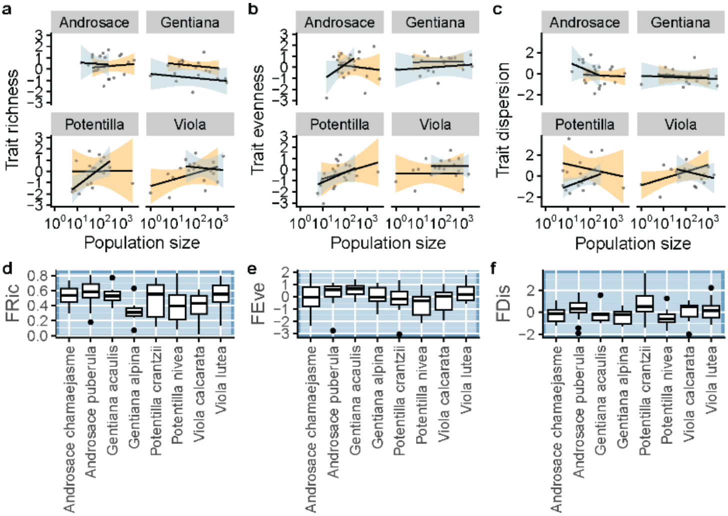

Fig. S2 Relationships between multidimensional trait diversity and population size in four rare and four common alpine plant species. We calculated trait richness (a and d), trait evenness (b and e) and trait dispersion (c and f) based on plant height, leaf number and the leaf width-length ratio in 87 populations of our eight study species. Trait richness and population size were transformed with the decadic logarithm and numeric variables were z-transformed. Rare species are shown in blue, common species are shown in yellow. Lines show relationships predicted by linear regression. Grey dots show observations (N = 8-13 per species), blue and yellow shadows show 95 % confidence intervals. We did not test the relationships between multidimensional trait diversity and population size within due to limited statistical power.

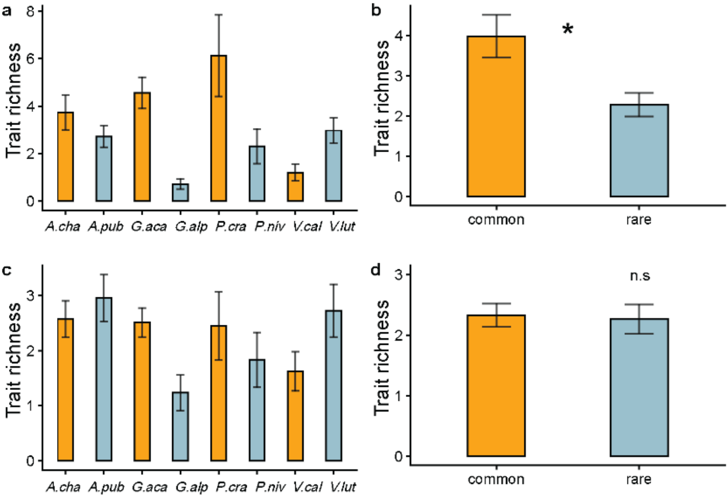

Fig. S3 Multidimensional trait richness in populations of four common and four rare alpine plant species. *A.cha = Androsace chamaejasme; A.pub = Androsace puberula; G.aca = Gentiana acaulis; G.alp = Gentiana alpine; P.cra = Potentilla crantzii; P.niv = Potentilla nivea; V.cal = Viola calcarata; V.lut = Viola lutea*. Rare species are shown in blue, common species are shown in yellow. When we calculated trait richness based on plant height, leaf number and leaf width, trait richness was significantly lower in populations of rare species (a and b). When we calculated trait richness based on plant height, leaf number and the leaf width-length ratio, the difference between rare and common species regarding within-population trait richness was no longer significant (c and d). Apart from the genus *Androsace*, however, the pattern within species pairs remained similar (a versus c).

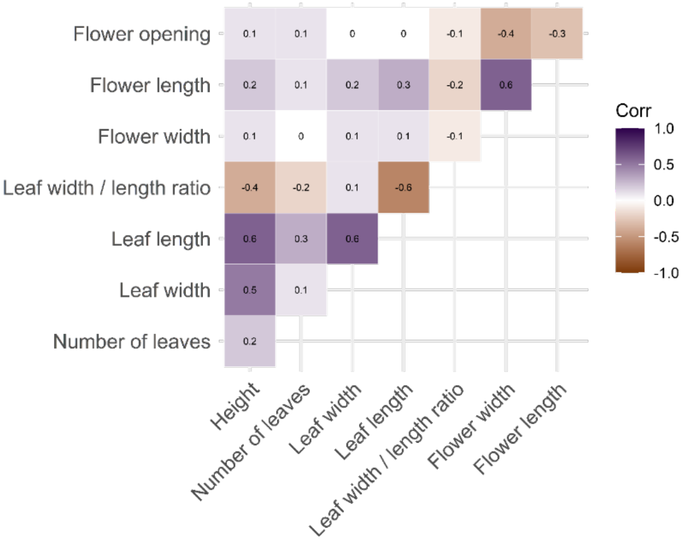

Fig. S4 Correlations among traits in 87 populations of four common and four rare alpine plant species. Values of the Pearson rank coefficients are given (purple – positive correlation, brown – negative correlation).

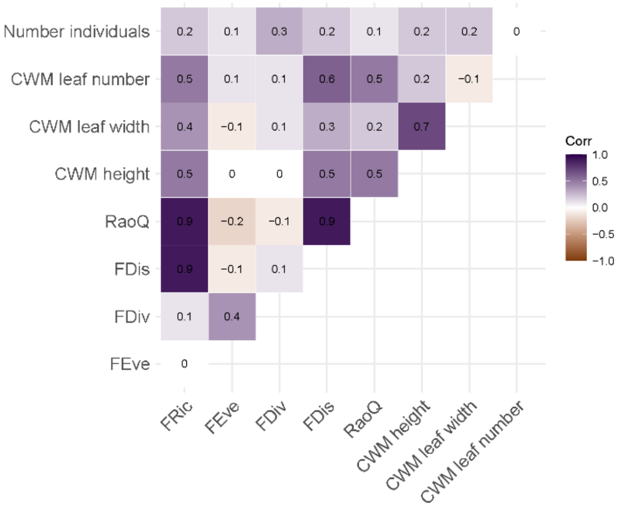

Fig. S5 Correlations among trait diversity variables across 87 populations of four common and four rare alpine plant species. CWM = community weighted mean. Number of individuals corresponds to the number of plants we used to calculate the diversity metrics RaoQ, FDis, FDiv, FRic and FEve based on height, leaf number and leaf width with the function “dbfd” from the R package “FD” (Laliberté et al. 2014). Values of the Pearson rank coefficients are given (purple – positive correlation, brown – negative correlation).

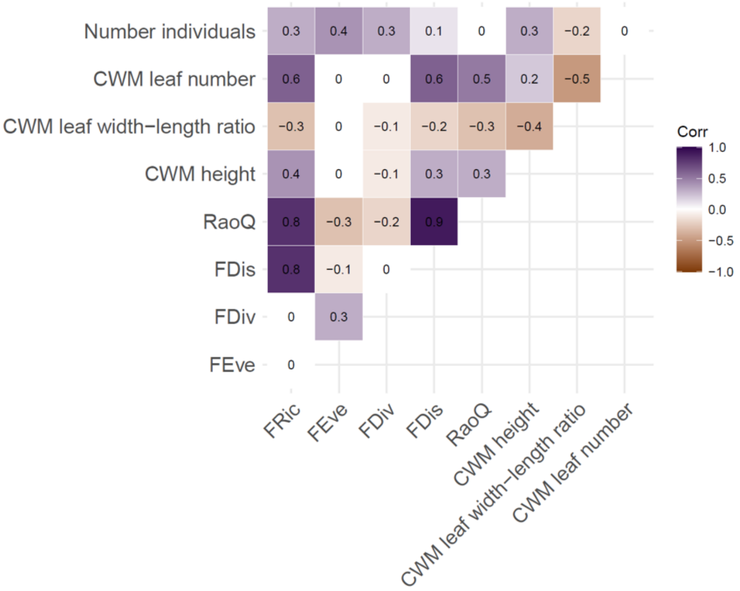

Fig. S6 Correlations among trait diversity variables across 87 populations of four common and four rare alpine plant species. CWM = community weighted mean. Number of individuals corresponds to the number of plants we used to calculate the diversity metrics RaoQ, FDis, FDiv, FRic and FEve based on height, leaf number and the leaf width-height ratio with the function “dbfd” from the R package “FD” (Laliberté et al. 2014). Values of the Pearson rank coefficients are given (purple – positive correlation, brown – negative correlation).

Table S1 Categories of flower phenology (flower opening).

0	closed bud
1	bud still closed but petals visible
2	opening flower bud
3	bud half open
4	bud almost open
5	flowering
6	fading
7	fruiting
8	dispersed

Table S2 Summary statistics of linear models investigating the effects of population size and species rarity on within-population variation in individual traits (CV) across eight alpine plant species. Trait values were z-transformed within genera. Population size and variation in leaf number were transformed with the decadic logarithm. Final models contained only parameters for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; ANOVA type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***. See methods for a detailed description of the statistical analysis.

		CV plant height		**CV leaf number**		**CV leaf width**		**CV flower width**	
Source of variation	df	SS	F	SS	F	SS	F	SS	F
Population size	1	$0.4e^{-2}$	$0.43e^{-2}$	0.22	0.23	0.0	$0.4e^{-3}$	0.07	0.29
Rarity	1	0.14	0.14	3.84	**4.08***	0.65	0.66	0.33	1.36
Phenology	1							1.06	**4.41***
Residuals SS(df)		82.86(84)		78.93(84)		82.35(84)		18.69(78)	
Number observations		87		87		87		82	
R^2multiple/adjusted		<0.01/<0.01		0.05/0.03		<0.01/<0.01		0.07/0.15	

Table S3 Summary statistics of linear models investigating the effects of habitat heterogeneity, population size and species rarity on within-population variation in individual traits (CV) across eight alpine plant species. Trait variables were z-transformed within genera. Habitat heterogeneity variables were z-transformed and population size and variation in leaf number were transformed with the decadic logarithm. We fitted separate linear models to investigate whether within-population variation in individual traits was affected by (a) biotic heterogeneity, (b) abiotic heterogeneity and (c) structural heterogeneity. Final models contained only parameters for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; ANOVA type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***. See methods for a detailed description of the statistical analysis.

(a)		**CV plant height**		**CV leaf number**		**CV leaf width**		**CV flower width**	
Source of variation	df	SS	F	SS	F	SS	F	SS	F
Biotic heterogeneity	1	1.59	1.68	0.25	0.27	0.72	0.77	0.94	0.37
Population size	1	0.07	0.07	0.44	0.46	0.09	0.1	$0.5e^{-3}$	$0.2e^{-2}$
Rarity	1	0.03	0.03	2.67	**2.85°**				
Biotic heterogeneity : rarity	1	5.27	**5.57***	2.77	**2.96°**				
Residuals SS(df)		74.78(79)		74.07(79)		76.08(81)		19.54(77)	
Number observations		84		84		84		80	
R^2multiple/adjusted		0.09/0.04		0.08/0.04		0.01/<0.01		<0.01/<0.01	

(b)		**CV plant height**		**CV leaf number**		**CV leaf width**		**CV flower width**	
Source of variation	df	SS	F	SS	F	SS	F	SS	F
Population size	1	0.04	0.04	0.4	0.42	0.4	0.51	$0.3e^{-3}$	$0.13e^{-2}$
Genus	3					1.47	0.62		
Genus : rarity	3					13.6	**5.75****		
Rarity	1			4.05	**4.28***	1.29	1.64		
Abiotic heterogeneity	1	0.18	0.18	0.26	0.28	6.33	**8.03****	0.01	0.04
Population size : abiotic heterogeneity	1			1.96	0.15	0.23	0.9		
Rarity : abiotic heterogeneity	1					1.8	2.28		
Residuals SS(df)		81.65(81)		74.87(79)		57.51(73)		19.4(76)	
Number observations		84		84		84		80	
R^2multiple/adjusted		<0.01/<0.01		0.07/0.03		0.25/0.15			

(c)		**CV plant height**		**CV leaf number**		**CV leaf width**		**CV flower width**	
Source of variation	df	SS	F	SS	F	SS	F	SS	F
Structural heterogeneity	1	0.79	0.78	0.95	0.97	0.29	0.3	0.64	2.57
Population size	1	$0.3e^{-2}$	$0.3e^{2}$	0.83	0.86	0.24	0.25	0.1	0.4
Rarity	1			2.68	2.74				
Residuals SS(df)		80.41(79)		67.09(78)		76.13(79)		18.78(75)	
Number observations		82		82		82		78	
R^2multiple/adjusted		0.01/<0.01		0.06/0.02		<0.01/<0.01		0.03/<0.01	

Table S4 Summary statistics of linear models investigating the effects of population size and species rarity on within-population trait richness, evenness and dispersion across eight alpine plant species. We calculated trait richness, evenness and dispersion based on plant height, leaf number and leaf width. Trait values were z-transformed within genera. Population size and trait richness were transformed with the decadic logarithm. Final models contained only parameters for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; ANOVA type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the statistical analysis.

		Trait richness		Trait evenness		Trait dispersion	
Source of variation	df	SS	F	SS	F	SS	F
Genus	3	42.67	1.15	15.23	**5.85****	4.94	2.06
Population size	1	3.19	0.26	0.03	0.04	0.11	0.14
Rarity	1	135.64	**10.98****	0.21	0.04	2.13	2.65
Genus : rarity	3	282.05	**7.61*****			16.66	**6.93*****
Residuals SS(df)		938.62(76)		69.39(80)		62.52(78)	
Number observations		85		86		87	
R^2multiple/adjusted		0.34/0.27		0.18/0.13		0.27/0.2	

Table S5 Summary statistics of linear models investigating the effects of habitat heterogeneity, population size and species rarity on within-population trait richness, evenness and dispersion across eight alpine plant species. We calculated trait richness, evenness and dispersion based on plant height, leaf number and leaf width. Trait values were z-transformed within genera. Habitat heterogeneity variables were z-transformed and population size and trait richness were transformed with the decadic logarithm. We fitted separate linear models to investigate whether within-population trait richness, evenness and dispersion were affected by (a) biotic heterogeneity, (b) abiotic heterogeneity and (c) structural heterogeneity. Final models contained only parameters for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; ANOVA type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the statistical analysis.

(a)		Trait richness		Trait evenness		Trait dispersion	
Source of variation	df	SS	F	SS	F	SS	F
Biotic heterogeneity	1	5.53	0.44	2.13	2.6	0.07	0.09
Genus	3	41.38	1.1	16.2	**6.58*** **	3.97	1.65
Population size	1	4.78	0.38	0.06	0.07	0.03	0.04
Rarity	1	131.32	**10.45** **			1.36	1.7
Genus : rarity	3	280.73	**7.45*** **			18.27	**7.58*** **
Biotic heterogeneity : population size	1			1.72	2.1		
Biotic heterogeneity : rarity	1					1.72	2.14
Residuals SS(df)		904.52(72)		62.34(76)		58.62(73)	
Number observations		82		83		84	
R^{2}multiple/adjusted		0.34/0.26		0.24/0.18		0.31/0.21	

(b)		Trait richness		Trait evenness		Trait dispersion	
Source of variation	df	SS	F	SS	F	SS	F
Genus	3	5.5	0.15	8.53	**3.41***	1.07	0.46
Population size	1	12.79	1.07	0.03	0.03	0.7e^{-2}	0.8e^{-2}
Rarity	1	116.34	**9.7** **			1.81	2.35
Abiotic heterogeneity	1	46.69	**3.89°**	1.03	1.26	3.43	**4.46***
Genus : rarity	3	258.89	**7.2*** **			17.95	**7.77*** **
Population size : abiotic heterogeneity	1			1.69	2.03		
Residuals SS(df)		863.35(72)		63.45(76)		56.98(74)	
Number observations		82		83		84	
R^{2}multiple/adjusted		0.37/0.29		0.23/0.17		0.33/0.24	

(c)		Trait richness		Trait evenness		Trait dispersion	
Source of variation	df	SS	F	SS	F	SS	F
Genus	3	44.81	1.22	15.45	**6.46*** **	5.37	2.13
Structural heterogeneity	1	18.01	1.47	5.54	**6.95***	0.0	0.3e^{-3}
Population size	1	1.49	0.12	0.33	0.41	0.02	0.02
Rarity	1	146.17	**11.91*** **			2.21	2.64
Genus : rarity	3	222.53	**6.04** **			15.62	**6.22*** **
Structural heterogeneity : population size	1	21.86	1.78				
Residuals SS(df)		846.95(69)		59.81(75)		60.33(72)	
Number observations		80		81		82	
R^{2}multiple/adjusted		0.37/0.28		0.25/0.2		0.28/0.2	

Table S6 Summary statistics of linear models investigating the effects of population size and species rarity on within-population trait richness, evenness and dispersion across eight alpine plant species. We calculated trait richness, evenness and dispersion based on plant height, leaf number and leaf width-length ratio. Trait values were z-transformed within genera. Population size and trait richness were transformed with the decadic logarithm. Final models contained only parameters for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; ANOVA type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: p < 0.1; °, p < 0.05; *, p < 0.01; **, p < 0.001; ***. See methods for a detailed description of the statistical analysis.

		Trait richness		**Trait evenness**		**Trait dispersion**	
Source of variation	df	SS	F	SS	F	SS	F
Population size	1	6.93	0.42	4.08	**4.18***	$0.3e^{-2}$	$0.25e^{-2}$
Rarity	1	8.71	0.53	$0.8e^{-2}$	$0.87e^{-2}$	0.43	0.42
Residuals SS(df)		1320.24(80)		80.9(83)		85.57(84)	
Number observations		83		86		87	
R^2multiple/adjusted		0.01/<0.01		0.05/0.03		<0.01/<0.01	

Table S7 Summary statistics of linear models investigating the effects of habitat heterogeneity, population size and species rarity on within-population trait richness, evenness and dispersion across eight alpine plant species. We calculated trait richness, evenness and dispersion based on plant height, leaf number and leaf width-length ratio. Trait values were z-transformed within genera. Habitat heterogeneity variables were z-transformed, population size and trait richness were transformed with the decadic logarithm. We fitted separate linear models to investigate whether within-population trait richness, evenness and dispersion were affected by (a) biotic heterogeneity, (b) abiotic heterogeneity and (c) structural heterogeneity. Final models contained only parameters for which there are statistical values in the table (SS: sum of squares, F: F-statistics, df: degrees of freedom; ANOVA type II F-tests based on Satterthwaite's method). For the variables included in the final models, significance levels are given: $p < 0.1$; °, $p < 0.05$; *, $p < 0.01$; **, $p < 0.001$; ***. See methods for a detailed description of the statistical analysis.

(a)		**Trait richness**		**Trait evenness**		**Trait dispersion**	
Source of variation	df	SS	F	SS	F	SS	F
Biotic heterogeneity	1	10.41	0.69	0.2	0.2	0.46	0.49
Genus	3	70.6	1.56			1.67	0.6
Population size	1	1.0	0.07	4.19	**4.31***	0.0	$0.2e^{-3}$
Rarity	1	12.94	0.86			0.16	0.17
Genus : rarity	3	129.75	**2.86***			9.62	**3.47***
Biotic heterogeneity : rarity	3					1.91	2.07
Residuals SS(df)		1059(70)		77.68(80)		67.4(73)	
Number observations		80		83		84	
R^2multiple/adjusted		0.17/0.07		0.05/0.03		0.19/0.08	

(b)		**Trait richness**		**Trait evenness**		**Trait dispersion**	
Source of variation	df	SS	F	SS	F	SS	F
Genus	3	72.8	1.62			1.68	0.62
Population size	1	4.85	0.32	3.8	**3.98***	0.05	0.05
Rarity	1	6.82	0.46			0.34	0.37
Abiotic heterogeneity	1	21.25	1.42	1.65	1.73	3.05	**3.39°**
Genus : rarity	3	133.74	**2.98***	12.68	**4.69****		
Residuals SS(df)		1048.79(79)		76.22(80)		66.71(74)	
Number observations		80		83		84	
R^2multiple/adjusted		0.18/0.07		0.07/0.05		0.2/0.1	

(c)		**Trait richness**		**Trait evenness**		**Trait dispersion**	
Source of variation	df	SS	F	SS	F	SS	F
Genus	3			5.11	1.93	2.79	0.99
Structural heterogeneity	1	72.41	**4.64***	4.5	**5.09***	0.16	0.17
Population size	1	0.02	$0.13e^{-2}$	1.09	1.23	0.03	0.03
Rarity	1					0.27	0.29
Genus : rarity	3					10.53	**3.75***
Residuals SS(df)		1170.49(75)		66.3(75)		67.41(72)	
Number observations		78		81		82	
R^2multiple/adjusted		0.06/0.04		0.17/0.12		0.17/0.06	

Germinating seeds and seedlings of the rare *Potentilla nivea* (*Rosaceae*) in a common garden experiment in the greenhouse.

Chapter 5

Adaptation to local soil and soil biota in small and large populations of two common and two rare alpine plant species

Hannah Inniger, Daniel Prati, Markus Fischer

Abstract

Characterising local adaptation in alpine plants is crucial to evaluate their vulnerability to environmental changes. We experimentally tested whether plants of two common and two rare alpine herbaceous species are adapted to local soil and to soil biota and whether this adaptation depends on species rarity and population size. We studied seed germination and seedling performance on local versus foreign soil, with and without soil biota among plants originating from 36 populations of *Potentilla crantzii* (Crantz) Fritsch (*Rosaceae*), *P. nivea* L., *G. acaulis* L. (*Gentianaceae*) and *G. alpina* Vill. in a reciprocal plant-soil transplant experiment in a common garden in the greenhouse. Plants of the genus *Potentilla* overall performed better on local than on foreign soil. This effect was stronger among plants of the common *P. crantzii* than among plants of the rare *P. nivea* and stronger for large than for small populations. Among plants from small populations, seedling height and the product of germination probability and seedling height even tended to be lower on local than on foreign soil, indicating maladaptation in small populations. Plant performance was negatively affected by soil biota within the genus *Potentilla*. Within the genus *Gentiana*, we found no evidence for adaptation to local soil. However, plants of the genus *Gentiana* germinated better with than without soil biota. Our findings suggest that plants of the genus *Potentilla* are adapted to local soil. Further, this adaptation is likely

influenced by population size and rarity. Finally, they indicate that soil biota may be important for a successful germination within the genus *Gentiana*.

Introduction

Local adaptation is essential in population, evolutionary, global change and conservation biology (Leimu and Fischer 2008). Plants in their habitats are influenced by interactions with other organisms (Van der Putten et al. 2001; Wardle 2006) and by environmental conditions such as climate and soil composition (Ellenberg and Leuschner 2010). Selection forces are different at different locations, which can lead to genetic differentiation among populations (Linhart and Grant 1996). Plants are locally adapted if fitness, the contribution of a plant to the next generation, is maximised in the local habitat. Local adaptation is present in many non-alpine plant species (Leimu and Fischer 2008). In alpine plants, it is likely that extreme spatial heterogeneity and natural fragmentation of habitats (Scherrer and Körner 2010; Körner 2021) produce local adaptation (Hamann et al. 2016). To date, however, few studies have investigated whether local adaptation is present in alpine species.

The standard method for testing whether plants are adapted to their local environment is the reciprocal transplant experiment, in which plants from different environments are transplanted into either different environments or corresponding test environments (Leimu and Fischer 2008; Blanquart 2013). Local adaptation is present when plants perform better in their local environment than in a foreign environment or when they perform better than conspecifics in their local environment (Blanquart 2013; Lascoux et al. 2016).

Reciprocal transplant experiments have been conducted for a number of alpine species to study local adaptation to elevational gradients (Galen et al.

1991; Stinson 2004; Byars et al. 2007; Gonzalo-Turpin and Hazard 2009; Hautier et al. 2009; Scheepens et al. 2010; Scheepens and Stöcklin 2013; Kim and Donohue 2013; Wos et al. 2022), snow cover (Stanton and Galen 1997; Stinson 2004; Sedlacek et al. 2015), competition (Pluess and Stöcklin 2005), land use (Fischer et al. 2008) and exposition (Hamann et al. 2016). At a very local scale, abiotic (soil chemistry, soil structure, soil type) and biotic (symbionts, pathogens) soil properties affect plant performance (Wardle 2006) and can act as agents of natural selection (Smith et al. 2012). However, whether alpine plants are adapted to local soil and soil biota, remains largely unstudied.

The ability to adapt to local environmental conditions may depend on characteristics of the population and of the species. The theory of quantitative genetics predicts that the potential to respond to selection, and thus the adaptive potential, decreases linearly with decreasing population size (Robertson 1960). Due to inbreeding and genetic drift, genetic diversity is often reduced in small populations (Ellstrand et al. 1993; Young et al. 1996). In contrast, large populations are predicted to produce more new mutations per generation and preserve more genetic variation against the influence of drift (Holt 1987). Hence, the strongest adaptive response is expected in larger populations (Alberto et al. 2013). Several experimental studies provide evidence for the significant impact of population size on shaping patterns of local adaptation (Leimu and Fischer 2008).

Species characteristics that could affect the adaptive response of plants include life history traits, such as mating system, longevity, or clonality. However, the meta-analysis of Leimu and Fischer (2008) found no influence of life history traits on the degree of local adaptation. Another important species characteristic that could affect local adaptation is species rarity. The prevailing assumption suggests that as the distance between populations increases, the level of local adaptation tends to increase too. This occurs due to reduced gene flow between populations, leading to higher genetic differentiation among them (Galloway and Fenster 2000). It is likely that plants of rare species occur in fewer and more isolated populations with less gene flow in between, meaning that they might be genetically more differentiated than plants of common species. Thus, local adaptation might be stronger among plants of rare species than among plants of common species. Alternatively, adaptation may be constrained by low genetic diversity and drift in populations of rare species and we might observe no local adaptation (or even maladaptation) among plants of rare species. Another possibility is that gene flow might be generally low among populations of alpine species due to the pronounced spatial heterogeneity and isolation of suitable habitats (Stöcklin et al. 2009), independent of species rarity. In this case, we would observe no difference among rare and common species in the degree of local adaptation.

Alternatively, in alpine species, gene flow could be generally limited among populations, driven by the pronounced spatial heterogeneity and the isolation of suitable habitats (Stöcklin et al. 2009), regardless of species rarity. In this case, we might not observe any difference between rare and common species regarding their adaptation to the local environment.

We experimentally tested whether small and large populations of two common and two rare alpine grassland species are adapted to local soil and soil biota in a common garden in a greenhouse. We collected seeds and soil samples in 36 natural populations of the rare *Gentiana alpina*, the common *G. acaulis*, the rare *Potentilla nivea* and the common *P. crantzii*. We studied seed germination and seedling performance on local and foreign soil with and without soil biota. Seed germination and seedling performance belong to the most critical processes of plant reproduction under the harsh environmental conditions in alpine habitats and are therefore important fitness parameters. We aimed to investigate the following research questions: (I) Are populations of our study species adapted to local soil and soil biota? (II) Do large and small populations differ in adaptation to local soil and soil biota? (III) Do populations of rare and common species differ in adaptation to local soil and soil biota?

Methods

Study species

We studied two plant species pairs, one within the genus *Gentiana* (*Gentianaceae*) and one within the genus *Potentilla* (*Rosaceae*). All study species are perennial and native to the Swiss Alps. Both congeneric species pairs include one common and one rare alpine plant species, which are phylogenetically and ecologically closely related and thus comparable. We defined species rarity based on geographic range (small versus large) and local abundance (low versus high) (Rabinowitz 1981). The rare species in this study have a scattered distribution within a relatively small geographical range across the Swiss Alps (infoflora.ch 2020). As they occur in habitats where human impact is low compared to the habitats of most other rare species, these species can be considered as naturally rare.

The rare *Gentiana alpina* Vill. occurs at high-alpine sites in acidic and nutrient-poor grasslands (*Caricion curvulae*, typoCH, Lauber et al. 2018). In Switzerland, the distribution of the species is restricted to a few populations in the central (Valais) and the southern (Ticino) Alps. According to the red list (Bornand et al. 2016), the species is potentially threatened (NT) within Switzerland. *Gentiana acaulis* L. is a character species of rather species-poor (sub-) alpine grasslands on acidic soils (*Nardion*, typoCH, Lauber et al. 2018;

Delarze et al. 2008). The species is widespread across the Swiss and European Alps.

The rare *Potentilla nivea* L. occurs in high-alpine calcareous grasslands on windy ridges (*Elynion*, typoCH, Lauber et al. 2018; Delarze et al. 2008). Within Switzerland, the species has a disjunct distribution with few populations in the central (Valais) and the eastern (Graubünden) Alps. The current red list of Switzerland categorises the species as vulnerable (VU) (Bornand et al. 2016). *Potentilla crantzii* (Crantz) Fritsch typically occurs in calcareous, species-rich grasslands at (sub-) alpine sites (*Seslerion*, typoCH, Lauber et al. 2018; Delarze et al. 2008). The species is widely distributed across the Swiss and European Alps. *P. nivea* and *P. crantzii* are facultative apomictic species.

Fig. 1 Study species: (a) *Gentiana alpina* (*Gentianaceae*), (b) *G. acaulis*, (c) *Potentilla nivea* (*Rosaceae*) and (d) *P. crantzii*.

Study locations and sampling

In summer 2021, we visited 36 populations of our study species (*G. alpina*: N = 6; *G. acaulis*: N = 10; *P. nivea*; N = 11; *P. crantzii*: N = 9). The populations were selected based on the Info Flora database, which collects occurrence data on vascular plant species in Switzerland up to a 1 x 1 kilometre scale (infoflora.ch 2020). We chose the populations of the rare species so that they covered the distribution range of the species in

Switzerland. We chose populations of their common partner species within a comparable range size.

For each population, we estimated population size by counting the number of fertile individuals. We defined the border of the population where we found the outermost individuals. Whenever we counted 250 individuals, we estimated the area that was covered by these individuals and extrapolated over the area of the total population.

We collected fruits of between four and twenty randomly selected individuals per population, depending on population size. We air-dried the fruits in paper bags directly after collecting. We took eight soil samples per population with a cylindric garden drill (depth = 10 cm, volume = 3 dl) next to randomly chosen individuals of the study species. Samples were stored separately in paper bags at 4 °C over six months until usage.

Investigation of adaptation to local soil and soil biota

To assess whether there is adaptation to local soil and to soil biota in populations of our study species, we studied seed germination and seedling in a reciprocal soil experiment in a common garden in a greenhouse. The soil treatments comprised local versus foreign soil and soil biota (‘with’ versus ‘without’). Depending on maternal seed set, between two and thirty seeds per mother plant (N = 1576) were placed in pots for each of the soil treatments: local soil with soil biota, local soil without soil biota, foreign soil with soil biota and foreign soil without soil biota.

Local soil was the mixture of the eight soil samples that were taken within the natural populations. Foreign soil was the local soil from a randomly chosen conspecific population. All soils were sieved to remove roots, stones and litter (mesh size = 1 cm). To remove soil biota, we sterilised half of the soil samples in an autoclave for one hour at 120 °C and 95 kPa. To remove biota that could have established from spores after sterilisation, we incubated the sterilised soil for 24 hours at room temperature and autoclaved it again. We inoculated seedling soil (RICOTER Erdaufbereitung AG, Aarberg) with a ratio of 9:1 with each of the treatments.

After sowing, seeds were stratified in the dark for three months at 4 °C with weekly watering. We initiated seed germination by placing the pots in a greenhouse at conditions approximately matching spring conditions in the (sub-) alpine zone (minimum temperature of 12 °C, 14 h light and 40 % air humidity). Depending on weather, the temperature rose up to a maximum of 20 °C. We counted the number of germinated seeds per pot every third day. We categorised a seed as germinating when we observed the radical tip breaking through the seed coat. We counted the number of seedlings per pot for four weeks after the first seeds started to germinate. We measured the height of the three tallest seedlings per pot for *P. crantzii* and *P. nivea* from the base of the stem to the end of the largest leaf (stretched). We did not measure seedling height for *G. acaulis* and *G. alpina*, because only few seedlings of the latter species survived.

Statistical analysis

We did all the analyses in R (R core team 2022). We defined population size as a factor with two levels: small and large. We defined small and large populations within each species based on the median. We scaled seed mass within species to zero mean with a standard deviation of one. We defined seed germination as binomial variable with the function “cbind” from base R from the number of seeds that germinated and the number of seeds that did not germinate for each mother plant (hereafter: germination probability). We defined seedling survival as the number of seedlings 25 days after the first seeds began to germinate divided by the maximum number of seedlings observed per mother plant within this time.

We tested whether populations of our study species are adapted to local soil and soil biota and whether this depends on population size and species rarity with mixed effect models. We fitted separate models using the functions “lmer” and “glmer” from the R package "lme4" (Bates et al. 2015) for the different variables of plant performance. We tested each genus separately, because *Gentiana* and *Potentilla* differ in many aspects. For *Gentiana*, we fitted a generalised mixed effect model for germination probability and linear mixed effect models for the number of seedlings, seedling survival and the product of germination probability (percentage of germinated seeds) and seedling survival. For *Potentilla*, we fitted a generalised mixed effect model for germination probability and linear mixed effect models for the number of seedlings, seedling height and the product of germination probability (percentage of germinated seeds) and seedling height. We included the following structure of fixed and random terms in each of the models: *variable of plant performance ~ local soil * soil biota * population size + local soil * soil biota * rarity + seed mass + (1|population/mother plant).* Thereby, asterisks mean that we tested each term separately as well as the two- and three-way interactions. Mother plant was included as random term (nested in population) to account for the replication of identical genotypes and identical sites. We included the number of seeds sown per mother plant as weights in all linear mixed effect models.

We tested whether seed mass was influenced by population size and rarity in a separate linear mixed effect model but seed mass did not depend on these variables. We tested for over-dispersion in generalised mixed effect models with the function “dispersion_glmer” from the R package “blmeco” (Korner-Nievergelt et al. 2015). We evaluated final models based on the R^2

and on normality of the residuals. We considered p-values from the ANOVA table smaller than 0.05 as significant and smaller than 0.1 as marginally significant (type III F-tests based on Satterthwaite's method for linear mixed effect models, type II Wald χ^2 -tests for generalised mixed effect models).

Results

Adaptation to local soil and soil biota

Within both genera, seed germination was low (mean = 17 %, SD = 0.28 %). While all seedlings of *P. crantzii* and *P. nivea* survived, seedling survival of *G. acaulis* and *G. alpina* was low (43 % in *G. acaulis* and 13 % in *G. alpina*).

Within the genus *Potentilla,* germination probability, the number of seedlings and seedling height were higher with higher average seed mass of the mother plant ($p < 0.001$, $p < 0.01$ and $p < 0.001$, Table S1 Supporting information). Within the *Potentilla* genus, germination probability and the number of seedlings were higher on local than on foreign soil ($p < 0.05$ and $p < 0.1$; Fig. 1a and b; Table S1 Supporting information). Germination probability, seedling height and the product of germination probability and seedling height were lower with than without soil biota within this genus ($p < 0.1$, $p < 0.001$ and $p < 0.001$; Table S1 Supporting information). Within the genus *Potentilla*, no significant interaction between local soil and soil biota was found for any of the studied variables of plant performance.

Within the genus *Gentiana*, seedling survival was higher with higher average seed mass of the mother plant ($p < 0.05$; Table S2 Supporting information). Within this genus, germination probability was higher with than without soil biota ($p < 0.05$; Fig. 1c; Table S2 Supporting information). Within the genus *Gentiana*, the investigated variables of plant performance were neither influenced by local soil nor by an interaction between local soil and soil biota.

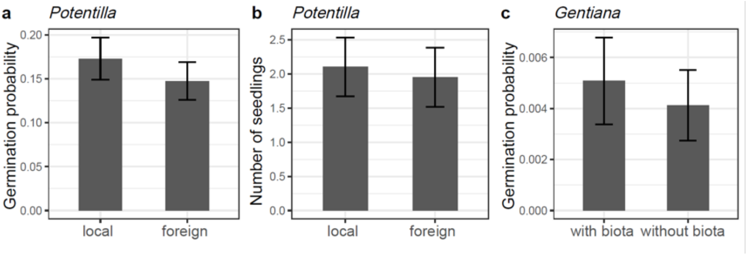

Fig 1. Significant effects of local versus foreign soil on germination probability and the number of seedlings in two species of the genus *Potentilla* (a and b) and of soil biota ('with' versus 'without') on germination probability in two species of the genus *Gentiana* (c). Shown are effects and standard errors predicted by mixed effect models. See Supporting information for ANOVA tables of mixed effect models.

Difference between small and large populations in adaptation to local soil and soil biota

Within both genera, plant performance did not significantly differ among small and large populations. Within the genus *Potentilla*, we observed that all of the studied variables of plant performance were affected by an interaction between local soil and population size (germination probability: $p < 0.05$; number of seedlings: $p < 0.1$; seedling height: $p < 0.01$; product of germination probability and seedling height: $p < 0.01$; Fig. 2a-c). Among small populations, plant performance did not differ between local and foreign soil. In contrast, plant performance tended to be higher on local than on foreign soil among large populations. Within the genus *Gentiana*, none of the investigated variables of plant performance was influenced by an interaction of population size with local soil or soil biota.

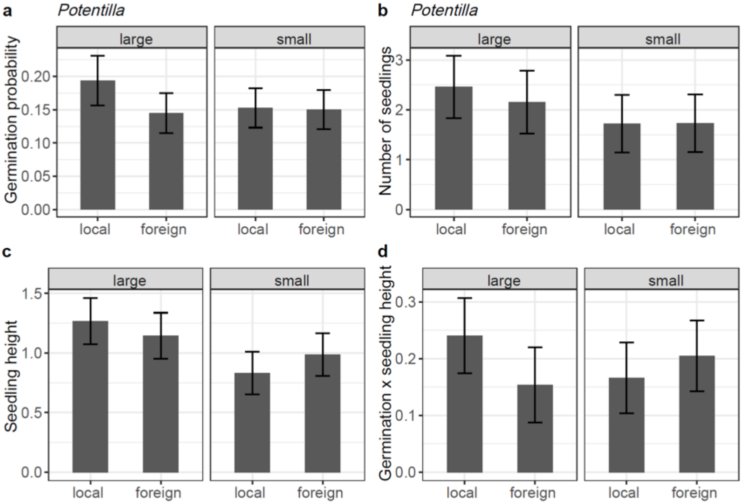

Fig 2. Significant interactions between local soil and population size on variables of plant performance in two species of the genus *Potentilla*. Shown are effects and standard errors predicted by mixed effect models. See Supporting information for ANOVA tables of mixed effect models.

Difference between rare and common species in adaptation to local soil and soil biota

Within the genus *Potentilla*, germination probability and the number of seedlings were higher among plants of the rare *P. nivea* than among plants of the common *P. crantzii*. Within the genus *Potentilla*, germination probability and the product of germination probability and seedling height were affected by an interaction between local soil and rarity ($p < 0.05$ and $p < 0.1$; Fig. 3). Thereby, the positive effect of local soil on germination probability and the product of germination probability and seedling height was stronger for the common *P. crantzii* than for the rare *P. nivea*. Among plants of the rare *P. nivea*, germination probability and the product of germination probability and seedling height tended to be lower on local than on foreign soil with soil biota, indicating maladaptation to local soil biota in this species (three-way interaction of rarity, soil biota and local soil: $p < 0.05$ and $p < 0.1$).

Within the genus *Gentiana*, germination probability, the number of seedlings and the product of germination probability and seedling survival were lower in the rare *G. alpina* than in the common *G. acaulis* ($p < 0.001$, $p < 0.05$ and $p < 0.05$). Within the genus *Gentiana*, none of the investigated variables of plant performance were significantly affected by an interaction between local soil and rarity or between soil biota and rarity.

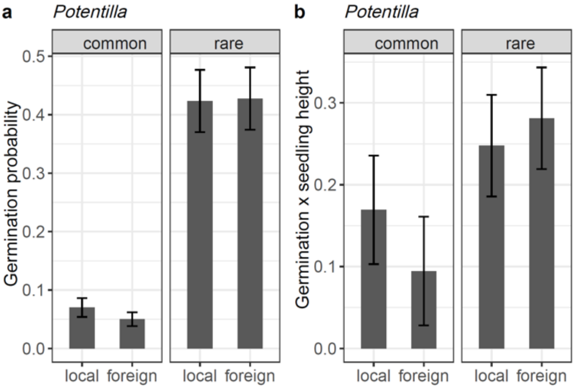

Fig 3. Significant interactions between local soil and rarity on germination probability (a) and the product of germination probability and seedling height (b) in two species of the genus *Potentilla*. Shown are effects and standard errors predicted by mixed effect models. See Supporting information for ANOVA tables of mixed effect models.

Discussion

Adaptation to local soil and soil biota differs among genera

Our results demonstrate that adaptation to local soil and soil biota differs among the genus *Potentilla* and the genus *Gentiana*. While plants of the genus *Potentilla* showed adaptation to local soil (Fig. 1a and b), plants of the genus *Gentiana* showed no adaptation to local soil. While plants of the genus *Potentilla* were consistently negatively affected by soil biota, plants of the genus *Gentiana* were positively affected by soil biota.

Our findings show that ecological differentiation is present among the study populations of the genus *Potentilla*. Since we studied adaptation to local soil in a common garden, the observed ecological differentiation likely has a genetic base. Therefore, these results indicate that there is genetic differentiation among our study populations of the genus *Potentilla*. As both *Potentilla* species are facultative apomictic species, it might be interesting to investigate how the apomictic breeding system shapes patterns of local adaptation.

As we did not identify abiotic and biotic soil properties, we do not know which soil characteristics may have driven the observed differences in plant performance. Sources of environmental variation that contribute to local adaptation are generally hard to identify, as effects (climatic variation, soil and biotic factors) are often confounded (Macel et al. 2007; Hamann et al. 2016), for instance by soil fertility. Nevertheless, given the low soil inoculum ratio (9:1) in our experiment, it can be inferred that the nutrient contents across various treatments were likely comparable. Additionally, we accounted for seed mass, thereby minimising the potential impact of maternal effects on our results. Despite not finding a significant interaction between local soil and soil biota, differences in belowground soil biota might be the drivers of the observed adaptation to local soil within the genus *Potentilla*.

Potential reasons for the lack of adaptation to local soil in plants of the genus *Gentiana* include temporal environmental variability, which may involve opposing selection pressures and thus constrain adaptation (Stearns 1992; Kawecki and Ebert 2004). Furthermore, high gene flow among populations may prevent local adaptation (Kawecki and Ebert 2004). There might only be moderate differences between habitats, selecting for similar traits and genotypes (Kawecki and Ebert 2004). Most likely, the combination of the different forces of evolution, especially of gene flow and natural selection, are responsible for the lack of local adaptation of our study populations of the genus *Gentiana*.

Negative effects of soil biota have been observed by former studies, for instance in the grass *Stipa capillaris* (Wagner et al. 2011). Generally, various groups of organisms can negatively affect plants belowground, including bacteria, protozoa and nematodes (Katan et al. 2002). Within the genus *Gentiana*, germination probability was positively affected by soil biota. Arbuscular mycorrhiza, a symbiosis where nutrient uptake is increased by fungal root colonisation, is known to be very common in gentian species (Sýkorová 2014). Because seeds do not yet have roots, however, organisms other than mycorrhizal fungi may have influenced seed germination among plants of the genus *Gentiana* in our study.

As we investigated plant performance at a very early life stage in our study species, the observed differences among the treatments could have increased with time. Considered together, our findings suggest that adaptation to local soil and to soil biota can be present in alpine plant species. Our results call for future studies on different species to draw more general conclusions on whether adaptation to local soil and soil biota is important for the evolutionary and population biology of alpine plants. Our results indicate that soil characteristics may play a role in the evolutionary biology of alpine plants.

Population size is important in adaptation to local soil within the genus Potentilla, but not within the genus Gentiana

Our findings show that within the genus *Potentilla*, adaptation to local soil is more present in large than in small populations. Within this genus, plants of small populations even tended to show maladaptation to local soil. Within the genus *Gentiana*, patterns of adaptation to local soil and soil biota were not influenced by population size. Thus, the importance of population size for shaping patterns of adaptation might differ among genera.

There are different explanations as to why small populations can fail local adaptation (Leimu and Fischer 2008). For instance, lower levels of heritable variability and beneficial mutations can decrease the evolutionary potential in small populations (Hill 1982; Weber and Diggins 1990). Furthermore, genetic drift decreases the chance of fixation of beneficial alleles in small populations, and the importance of inbreeding increases relative to the importance of mutation (Willi et al. 2006). These factors decrease the population’s capacity to response to selection (Willi et al. 2006). Finally, maladaptation can be explained by genetic drift due to a founder event, especially when founders of small populations come from contrasting habitats (Alpert 2006).

Our results are in agreement with Leimu and Fischer (2008), who found in a meta-analysis that plants from large populations are locally adapted, whereas this is not true for plants from small populations. They highlighted the clear role of population size for the evolution of local adaptation and presented the question of whether small populations lack the potential to adapt to changing environmental conditions. Our results suggest that population size can be an important determinant of local adaptation also in alpine species. Nevertheless, the strength of the relationship likely varies across genera and needs further investigation.

Species rarity plays a role in adaptation to local soil and soil biota within the genus Potentilla, but not in Gentiana

Overall, plant performance was negatively affected by rarity within the genus *Gentiana* but not within the genus *Potentilla*. While adaptation to soil biota did not differ between the rare and the common species in both genera, adaptation to local soil was stronger for plants of the common than for plants of the rare *Potentilla* species (Fig. 3). This supports our alternative hypothesis that plants of common species are more locally adapted due to higher genetic diversity and lower levels of drift. Another explanation for this pattern could be the degree of specialisation of the species. Perhaps the soils in windy ridges are all very similar, whereas the soils of (sub-) alpine grasslands of the type *Seslerion* could vary strongly according to the location. Therefore, populations of the more generalist, widespread *P. crantzii* may be subject to different selection pressures at different locations, leading to local adaptation.

According to Leimu and Fischer (2008), local adaptation in plants is much more influenced by population size than by life history characteristics such as clonality and longevity. Our study indicates that aspects of species rarity (spatial isolation, ecological specialisation), as well as population size might be important for the adaptation of alpine plants to their environment.

Conclusions

The findings of our reciprocal soil-transplant experiment demonstrate that adaptation to local soil and soil biota could play a role in evolutionary and population biology of alpine plant species, but likely differs among genera. Therefore, adaptation to local soil and soil biota should be investigated for other alpine species. Our study shows that population size and species rarity determine patterns of local adaptation within the genus *Potentilla*. Finally, our results indicate that soil biota might be important for a successful seed germination within the genus *Gentiana*.

Acknowledgements

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Supporting information

Table S1. ANOVA tables of mixed effect models testing the effects of local soil, soil biota, population size and rarity on plant performance within the *Potentilla* genus. Numeric variables were scaled. Germination was fitted as binomial response in a generalised mixed effect model (number of germinated seeds, number of non-germinated seeds, «cbind» function from base R). For the number of groups, the first number indicates the number of populations and the second number indicates the number of mother plants. χ^2: Chi squared, SS: sum of squares, F: F-statistics, df: degrees of freedom; type II Wald χ^2 tests for generalised mixed effect models, type III F-tests based on Satterthwaite's method for linear mixed effect models. For the variables included models, significance levels are given: $P < 0.1$; °, $P < 0.05$; *, $P < 0.01$; **, $P < 0.001$; ***

Potentilla		**Germination**		**Seedling number**		**Seedling height**		**Germination x height**	
	df	χ^2	Pr>	SS	F	SS	F	SS	F
Fixed effects									
Local soil	1	5.16	**0.02***	0.39	**2.77°**	0.12	0.23	0.49	0.74
Soil biota	1	2.99	**0.08°**	0.28	2	20.63	**38.97*****	28.04	**42.32*****
Population size	1	0.17	0.68	0.07	0.47	0.7	1.33	0.01	0.02
Rarity	1	57.99	**<0.001*****	1.48	**10.44****	15.14	**28.6*****	1.5	2.27
Seed mass	1	93.56	**<0.001*****	1.21	**8.57****	25.21	**47.61*****	33.06	**49.89*****
Local soil : Soil biota	1	0.39	0.53	0.02	0.17	0.03	0.06	0.15	0.22
Local soil : Population size	1	5.41	**0.02***	0.51	**3.63°**	4.2	**7.93****	5.62	**8.49****
Soil biota : Population size	1	1.57	0.21	0.06	0.4	0.14	0.25	0.48	0.72
Local soil : Rarity	1	6.88	**<0.01****	0.17	1.2	1.38	2.6	4.29	**6.47***
Soil biota : Rarity	1	0.17	0.68	$3.8e^{-3}$	0.03	11.58	**21.87*****	10.69	**16.13*****
Local soil : Soil biota : Population size	1	2.66	0.1	0.17	1.22	0.14	0.27	0.38	0.58
Local soil : Soil biota : Rarity	1	4.8	**0.03***	0.27	1.89	0.01	0.02	0.7	1.05
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Mother plant : Population		0.57	0.75	0.39	0.63	0.26	0.51	0.02	0.14
Population		0.38	0.62	0.29	0.54	0.29	0.53	0.03	0.18
Residual				0.14	0.38	0.53	0.73	0.66	0.81
Number observations			876		876		871		871
Number groups			20, 212		20, 212		20, 212		20, 212
R^2m/R^2c			0.62/0.87		0.2/0.86		0.38/0.69		0.04/0.11

Table S2. ANOVA tables of mixed effect models testing the effects of local soil, soil biota, population size and rarity on plant performance within the *Gentiana* genus. Numeric variables were scaled. Germination was fitted as binomial response in a generalised mixed effect model (number of germinated seeds, number of non-germinated seeds, «cbind» function from base R). For the number of groups, the first number indicates the number of populations and the second number indicates the number of mother plants. χ^2: Chi squared, SS: sum of squares, F: F-statistics, df: degrees of freedom; type II Wald χ^2 tests for generalised mixed effect models, type III F-tests based on Satterthwaite's method for linear mixed effect models. For the variables included models, significance levels are given: P < 0.1; °, P < 0.05; *, P < 0.01; **, P < 0.001; ***.

Gentiana		Germination		Seedling number		Seedling survival		Germination x survival	
	df	χ^2	Pr>χ^2	SS	F	SS	F	SS	F
Fixed effects									
Local soil	1	$0.5e^{-2}$	0.94	6.85	0.42	2.23	0.09	$5.6e^{-3}$	0.54
Soil biota	1	6.08	**0.01***	5.65	0.35	34.07	1.41	$2.3e^{-3}$	0.22
Population size	1	0.33	0.57	14.94	0.92	4.56	0.19	0.01	1.06
Rarity	1	13.4	**<0.001*****	93	**5.74**	48.12	1.99	0.07	**6.49***
Seed mass	1	0.56	0.56	25.17	1.55	122.09	**5.05***	0.02	2.01
Local soil : Soil biota	1	0.15	0.7	0.1	$6.3e^{-3}$	6.28	0.26	$4.2e^{-5}$	$4e^{-3}$
Local soil : Population size	1	1.43	0.23	2.1	0.13	21.28	0.88	$1.9e^{-3}$	0.19
Soil biota : Population size	1	1.76	0.19	2.8	0.17	12.12	0.5	$4.6e^{-4}$	0.04
Local soil : Rarity	1	2.06	0.15	4.57	0.28	0.33	0.01	$3.6e^{-3}$	0.35
Soil biota : Rarity	1	0.43	0.51	13.18	0.81	8.58	0.36	$7.5e^{-3}$	0.71
Local soil : Soil biota : Population size	1	0.62	0.43	8.22	0.51	13.15	0.54	$7.5e^{-3}$	0.72
Local soil : Soil biota : Rarity	1	$0.1e^{-3}$	0.99	2.1	0.13	12.11	0.5	$1.6e^{-3}$	0.16
Random effects		Var	SD variance	Var	SD variance	Var	SD variance	Var	SD variance
Mother plant : Population		1.63	1.28	0.35	0.59	0.04	0.19	$2.2e^{-4}$	0.02
Population		0.83	0.91	0.09	0.29	0.09	0.31	$4.7e^{-5}$	$6.8e^{-3}$
Residual				16.2	4.03	24.17	4.92	$4.7e^{-5}$	0.1
Number observations			684		684		170		684
Number groups			16, 144		16, 144		13, 67		16, 144
R^2m/R^2c			0.39/0.97		$0.4e^{-2}/0.03$		$0.4e^{-2}/0.01$		$0.4e^{-2}/0.03$

Small and isolated population of the rare *Potentilla nivea* at Gianda d’Albris, Graubünden

Chapter 6

Summary, general discussion and final conclusions

Summary and general discussion

Alpine habitats differ in many aspects from those of lowlands. They are characterised by harsh climatic conditions, extreme environmental heterogeneity and plant diversities that are often higher compared to the surrounding lowlands (Scherrer and Körner 2010; Scherrer and Körner 2011, Körner 2021). Populations of many alpine species have had to adapt to spatially isolated habitats and to environmental disturbances (Stöcklin et al. 2009). Due to the extremely short vegetation periods, plant reproduction is a challenge and the completion of all life stages such as flowering, fruiting, germination and successful seedling establishment is highly uncertain (Bliss 1971; Kobiv 2018). Therefore, alpine species are generally highly specialised (Körner 2021). Nevertheless, many alpine species are widespread and occur over large regions across the Alpine range (Aeschimann et al. 2004; Lauber et al. 2018). On the other hand, there are also rare alpine species that have a scattered distribution across larger geographical scales (Aeschimann et al. 2004; Lauber et al. 2018). In contrast to many non-alpine species, these species are naturally rare and factors other than human impact has caused their rarity. This leads to the questions as to how the alpine environment shapes the performance of individuals and of populations and how rare alpine species differ from alpine species that are more widespread. However, it remains largely unstudied, how population-, species- and habitat characteristics influence the performance of alpine plants.

The aim of this thesis was to evaluate the relative importance of different potential determinants of plant performance in eight alpine species. As potential determinants, I studied population size, species rarity and various aspects of habitat quality inferred from vegetation records, namely abiotic conditions (species indicator values), habitat heterogeneity and plant diversity. As variables of plant performance, I studied individual fitness, population size, within-population trait diversity and in four species also adaptation. I studied population size both as an explanatory and as a response variable, since it may be correlated to species rarity and habitat quality or to any variable of plant performance. The following sections summarise the most important findings.

Importance of habitat quality for plant performance

As plants are sessile organisms, the performance of individual plants and of populations is largely determined by the environment (Menges 1991). In this work, it has been demonstrated that different aspects of habitat quality affected different variables of plant performance across the eight study species (Table 1; in yellow). Overall, seed mass and variation in leaf width were lower at higher elevations, indicating that elevation and the harsher conditions associated with elevation restrict seed quality and select for an optimum for leaf width in the populations of the study species. On the other hand, populations were larger at higher elevations than at lower elevations, suggesting that abiotic or biotic features, or both, of lower elevation sites (e.g. stronger competition, more herbivory) are likely to limit population size in the study species.

Within habitats, abiotic conditions, habitat heterogeneity and plant diversity influenced different variables of plant performance (Chapters 3 and 4). Abiotic conditions were important both for individual fitness and for population size (Chapter 3). In habitats where abiotic conditions did not match the target species optimum (i.e. with large abiotic mismatch), populations were smaller. Plants of the genera *Potentilla* and *Gentiana* produced seeds with lower germination rates within these habitats (Chapter 3; Table 1). Therefore, the availability of the species niche influences plant performance in these alpine species. From a methodological point of view, this result demonstrates that species indicator values (Landolt et al. 2010) may be useful tools to assess habitat quality for any target species.

A novelty of this study is the finding that local plant diversity and habitat heterogeneity can affect plant performance of specific target species (Chapter 3). To the best of my knowledge, the role of plant diversity for the performance of individuals and populations of a species has not yet been investigated. Against the background of the concept of competitive exclusion (Huston 1979), the positive effects of alpha and gamma diversity on population size appear contradictory. However, we should remember that environmental conditions in alpine habitats are very harsh (Körner 2021). One of the most established ideas about positive interactions in ecology, nowadays also known as the stress-gradient hypothesis (Callaway, 2007), is that they are more frequent in stressful environments, where neighbour plants can buffer one another from physical stress (Clements et al. 1926). A greater number and diversity of positive interactions (above- and belowground) could therefore have been the reason for better performance in habitats with greater diversity. Thus, my observations support the view of many ecologists that positive interactions should be considered with more attention (e.g. Bertness and Hacker 1994).

Across all study species, habitat heterogeneity was especially influential regarding various effects on the performance of individuals and populations. The positive effect of biotic heterogeneity on individual fitness (Chapter 3;

Table 1) further supports the importance of positive interactions for populations of alpine plant species. Abiotic heterogeneity negatively affected population size while also positively influencing individual fitness and within-population trait diversity (Chapters 3 and 4; Table 1). Positive relationships between within-population trait diversity and abiotic heterogeneity have been observed in *Trifolium montanum* populations in the colline- and montane zone (Karbstein et al. 2023). This thesis shows that abiotic heterogeneity can be a driving force for trait diversity also in populations of alpine species as well as positively affecting individual fitness.

Similar to abiotic heterogeneity, structural heterogeneity negatively influenced population size but positively affected individual fitness (Chapter 3; Table 1). In contrast to abiotic heterogeneity, structural heterogeneity negatively affected to within-population trait diversity (Chapter 4; Table 1). Different aspects of habitat heterogeneity affected different variables of plant performance in different directions, showing that the effect of habitat heterogeneity on plant performance is complex and highly context dependent. Nevertheless, this thesis (Chapters 3 and 4) suggests that habitat heterogeneity may be a strong determinant of the performance of individuals and populations in alpine species.

Table 1 Summary of marginal and significant effects of species rarity (blue), population size (violet) and habitat (yellow) variables on plant performance across the chapters of this thesis. Plant performance was assessed at the level of individuals (seed- and size-related traits in the field and in the greenhouse) and at the level of populations (population size, within-population trait diversity, adaptation). Note that population size was investigated both as explanatory and as response variable. Seed germination, time to germination, seedling height and adaptation were studied for the *Gentiana* and *Potentilla* species, while all other variables of plant performance were assessed across all eight species.

Explanatory variable		**Variable of plant performance**	**Direction, chapter**	
Rarity	Rarity	Population size	-	2
		Seed set (field)	+	2
		Seed mass (field)	+	2
		Seed germination (greenhouse)	+	2
		Time to germination (greenhouse)	+	2
		Adaptation to local soil (greenhouse)	-	5
Population size	Population size	Seed number (field)	-	2, 3
		Total seed mass per fruit (field)	+	2
		Seed germination (greenhouse)	+	2, 3
		Seedling height (greenhouse)	+	2
		Within-population trait evenness (field)	+	4
		Adaptation to local soil (greenhouse)	+	5
Habitat	Elevation	Seed mass (field)	-	2
		Within-population variation in leaf width (field)	-	4
		Population size	+	2,3
	Abiotic mismatch	Population size	-	3
		Seed germination (greenhouse)	-	2
	Evenness	Population size	-	3
		Seed number (field)	+	3
	Alpha diversity	Population size	+	3
	Gamma diversity	Population size	+	3
		Seed mass (field)	-	3
	Biotic heterogeneity	Seed number (field)	+	3
	Abiotic heterogeneity	Population size	-	3
		Seed germination (greenhouse)	+/-	3
		Seed mass (field)	+	3
		Within-population variation in leaf width (field)	+	4
		Within-population trait richness & - dispersion (field)	+	4
	Structural heterogeneity	Population size	-	3
		Seed mass (field)	+	3
		Seed germination (greenhouse)	+/-	3
		Within-population trait richness & - evenness (field)	-	4

Importance of population size for plant performance

Among population ecologists, population size is considered a factor of great evolutionary significance for the survival of a population. The reduction of individual fitness due to demographic, genetic and biotic consequences of a small population size has been extensively studied in many non-alpine species and can result in an extinction vortex (Ellstrand and Elam 1993; Oostermeijer et al. 1994; Young et al. 1996; Leimu et al. 2006). Furthermore, small populations can show reduced local adaptation (Leimu and Fischer 2008) and reduced within-population trait variation (Karbstein et al. 2013). For the first time, this thesis addressed the importance of population size for the performance of alpine species.

This thesis found that plants from small populations produced fewer seeds and had lower total seed mass per fruit than plants from large populations (Chapter 2; Table 1). Within the genera *Gentiana* and *Potentilla*, seeds from large populations germinated better than seeds from small populations (Chapter 2; Table 1). However, studying the combined effects of population size and habitat quality on individual fitness revealed that positive effects of population size are masked by habitat quality (Chapter 3). Therefore, for the study species, habitat quality seems to be more important than population size for individual fitness. However, since positive correlations between individual fitness and population size were not completely absent when considering habitat quality (Chapter 3), an extinction vortex may be ongoing in small populations of the study species.

Chapter 4 of this thesis provided little evidence that population size can positively affect within-population trait diversity. This supports a former study on *Trifolium montanum* (Karbstein et al. 2023) and suggests that also in alpine species, population size may be a determinant of within-population trait diversity. As trait diversity is a fundamental prerequisite for natural selection and further evolution, it would be important to study the importance of population size for within-population trait diversity also in other alpine species. This thesis indicated that the importance of population size for within-population trait diversity might differ among different alpine plant species (Chapter 4).

Besides trait diversity, adaptation as a variable of plant performance has been relatively scarcely investigated in relation to population size. This thesis experimentally demonstrated that population size can positively affect local adaptation in plants of the genus *Potentilla* (Chapter 5). This is in line with previous findings (Leimu and Fischer 2008) and indicates that also in alpine species, small populations may fail to be locally adapted. As this probably differs between genera, alpine species need further investigation to conclude whether population size is of a similar importance for evolutionary processes as in non-alpine species. Nevertheless, the observation of reduced local adaptation in small populations (Chapter 5) further indicates that small populations can be affected by an extinction vortex.

Considered together, the positive relationships between different variables of plant performance (individual fitness, within-population trait diversity, local adaptation) and population size found in this thesis indicate that an extinction vortex might be ongoing in small populations of the study species. Finally, during the two years of my field visits, I observed the local extinction of a small population of *A. chamaejasme* and of an extremely small and sterile population of *G. alpina*. The former population covered a relatively large area but with a very scattered distribution and low population density (~70 flowering individuals within an area of 2300 m^2) and disappeared due to a landslide. The latter disappeared due to an unknown, probably stochastic process. These observations support the idea that small populations are threatened by local extinctions due to random stochastic events (Lande 1993).

Importance of rarity for plant performance

The question of the causes and consequences of the rarity of species has been a longstanding concern among biologists. Therefore, the research on species rarity in this thesis is built upon the foundation of great scientific work (Darwin 1859; Rabinowitz 1981; Kunin and Gaston 1997; Matthies et al. 2004; Boyd et al. 2022; to name only a few). In this thesis, I studied the effects of species rarity on plant performance and on the relationships between plant performance, population size and habitat quality. It is important to keep in mind that the rare species studied here are naturally rare.

Overall, rare species tended to occur in smaller populations than common species (fewer fertile individuals), suggesting that these species might be more prone to local extinction than common species due to random stochastic processes (Chapter 2). However, individual fitness was, for some variables, even higher in populations of rare than in populations of common species (Chapter 2; Table 1). This shows that these naturally rare species are well adapted to their environment. I observed no difference between rare and common species in the strength of the relationships between individual fitness and population size. This contrasts with Leimu et al. (2006), who observed a trend of individual fitness being more strongly reduced in small populations of rare than in small populations of common species. A possible explanation could be that naturally rare species have occurred in smaller populations and low abundance for a long time and have long inbreeding histories. Thus, natural selection could have purged some of the deleterious genetic load, leading to relatively high plant fitness (Ellstrand and Elam 1993; van der Valk 2019).

Overall, habitat quality affected plant performance of both rare and common species. Individual fitness and population size were equally affected by abiotic mismatch in rare and in common species (Chapter 3). This suggests that populations of naturally rare species are similarly dependent on niche availability as populations of common species (Chapter 3).

Positive effects of alpha and gamma diversity on individual fitness and population size were similar in rare and common species (Chapter 3). Nevertheless, the negative effect of evenness on population size was stronger for common than for rare species. This suggests that populations of naturally rare species may benefit overall more from high plant diversity. Furthermore, rare species tended to occur in smaller populations under high abiotic heterogeneity, whereas the opposite was observed for common species. This could be explained by narrower ecological niches in these naturally rare species, which are likely less abundant in habitats with high abiotic heterogeneity.

While I found higher individual fitness in rare species, within-population trait variation was overall lower in populations of rare than in populations of common species (Chapter 4). Despite the lack of clarity as to whether the observed trait variation is due to phenotypic plasticity or genetic variation, i.e. whether the observed variation has a heritable base, populations of these naturally rare species may have a reduced potential for adaptation to changing environmental conditions and further evolution. This is further supported by the finding that within-population trait variation tended to be positively related to habitat heterogeneity in common species, but negatively related to habitat heterogeneity in rare species (Chapter 4).

I found evidence for local adaptation in populations of the genus *Potentilla*, which was stronger among populations of the common than among populations of the rare *Potentilla* species (Chapter 5). To the best of my knowledge, local adaptation has not yet been compared systematically among rare and common species. This thesis indicates that species rarity might play a role in local adaptation and in evolutionary biology of alpine plant species.

Considered together, despite the rare species in this study having occurred in smaller populations and had lower within-population trait variation, individual fitness was high in these species compared to common congeners. Also, positive correlations between individual fitness and population size were overall not stronger in rare than in common species. The question arises as to whether this is a positive discovery for the rare species in this study or whether the common species of this study behave like rare species and should be considered as rare on a larger scale (Brown et al. 1996; Bornand 2014). As species' abundance and range size vary across space and time, rarity is a concept that depends on the scale (Gaston 1997). Within this thesis, regarding the differences between rare and common species mentioned above, I conclude that the naturally rare species of this study are overall more specialised and may have more difficulty adapting to changing environmental conditions than their common relatives.

Future directions

First, this thesis revealed that local plant diversity as well as abiotic, biotic and structural heterogeneity can strongly affect plant performance in alpine species. Thus, including these environmental variables when studying alpine plants may lead to a more complete understanding. In particular, heterogeneity seems to have complex effects on different levels of plant performance (individual, population). With respect to the expected habitat homogenisation (Bühler and Roth 2011; Liberati et al. 2019), it may be important to further explore the relationships between habitat heterogeneity and plant performance in alpine species.

Second, this thesis demonstrated that an extinction vortex might be ongoing in small populations of alpine species. Testing the hypothesis of an ongoing extinction vortex in small populations is a complex and time-consuming task, especially for alpine species which are difficult to cultivate, slow-growing and known to reproduce inconsistently across years. However, further investigations of other species are needed to better understand the vulnerability of small plant populations in alpine environments. Furthermore, knowledge of the genetic background of small populations would help to understand underlying mechanisms.

Third, despite high individual fitness, rare alpine species may have a reduced evolutionary potential. With respect to ongoing and future environmental changes in alpine habitats (Theurillat and Guisan 2001; Grabherr et al. 2010; Gottfried et al. 2012), research on more species from different alpine habitats is important to draw more general conclusions on the vulnerability of rare species. From a methodological point of view, data on genetic variation would be needed to disentangle phenotypic plasticity from heritable variation. Furthermore, this thesis shows that multidimensional diversity metrics may be useful to quantify trait variation within and among populations.

Final conclusions

This thesis demonstrated the importance of abiotic conditions, local plant diversity and habitat heterogeneity for the performance of eight alpine plant species. In particular, habitat heterogeneity affected the performance of individuals and of populations across all study species.

Additionally, this thesis showed that population size is a determinant of plant performance in the eight study species. It suggests that an extinction vortex may be ongoing in small populations of the study species.

Finally, this thesis gives new input on the population ecology of species that are naturally rare. From the results across all chapters, it is concluded that the naturally rare species in this study do not suffer from reduced individual fitness but may have a low potential for further evolution. Therefore, these species could be susceptible to environmental change


Mosaic of different alpine grasslands in October on the Col de Lona, Valais.

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Declaration of consent

On the basis of Article 18 of the PromR Phil.-nat. 19

Name/First name:	Inniger Hannah
Matriculation number:	14 116 107
Study program:	Ecology & Evolution
Title of the thesis:	Population ecology of four common and four rare alpine plant species
Supervisors:	Prof. Dr. Markus Fischer
	Dr. Daniel Prati

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 paragraph 1 litera r of the University Act of September 5th, 1996 and Article 69 of the University Statute of June 7th, 2011 is authorized to revoke the doctoral degree awarded on the basis of this thesis. For the purposes of evaluation and verification of compliance with the declaration of originality and the regulations governing plagiarism, I hereby grant the University of Bern the right to process my personal data and to perform the acts of use this requires, in particular, to reproduce the written thesis and to store it permanently in a database, and to use said database, or to make said database available, to enable comparison with theses submitted by others.

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