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ORIGINAL ARTICLE

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

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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.

Keywords Rarity · Small populations · Extinction vortex · Alpine 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).

For plants, recent studies on mainly non-alpine 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, 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). In

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this context, alpine plant populations are often naturally small, fragmented and isolated. This raises the question of whether small populations of alpine species also show negative fitness characteristics. As alpine species generally exhibit lower genetic diversity and higher genetic differentiation than lowland species (Reisch and Rosbakh 2021), we expect a positive relationship between population size and fitness also in alpine species. Alternatively, alpine species might have adapted to occur only in small and isolated populations by high levels of local adaptation. In this case, we will not observe a relationship between population size and fitness.

In a meta-analysis of the relationship between population size and fitness, rare species tended to show stronger relationships than 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 (declining species). In contrast, many rare alpine species are naturally rare, meaning they have existed for a long time in only few, isolated populations within a small geographic range size due to factors other than human activity. For instance, delayed recolonization of suitable habitats from glacial refugia due to low dispersal capacities and narrow niche breaths during the Holocene may have influenced the distribution of many alpine plant species (Dullinger et al. 2012). To the best of our knowledge, no study has specifically examined the relationship between population size and fitness in naturally rare species. In the following study, "rare" applies to a species characterized by a natural restricted geographic range size and a low occupancy, i.e. a low number of occupied sites within this range. If the pattern of reduced fitness and lower genetic diversity often observed in many rare species (Boyd et al. 2022) also holds true for naturally rare species, they may show strong relationships between fitness and population size. If mean population fitness is already low, negative genetic and biological (e.g. pollinator attraction) characteristics of a small population size could further reduce mean population fitness. Conversely, species with historically small population sizes and low genetic diversity often have a lower genetic load than those with larger populations due to the more efficient removal of partially deleterious recessive alleles in inbred populations (purging) (van der Valk et al. 2019). If populations of naturally rare species have undergone purging, negative fitness characteristics of a small population size may be absent in naturally rare species.

Here, we studied the relationships between population size and fitness in four common and four rare congeneric alpine plant species in 2 consecutive years (2020, 2021) in the Swiss Alps. We studied population size and 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, each pair consisting of one common and one naturally rare species. As introduced earlier, naturally means that the species is rare since a long time due to other reasons than human activities. There is no universally accepted definition of rarity (Crisfield et al. 2024). However, the term is commonly used to describe species characterized by a restricted geographic range (extent in which a species occurs), habitat specificity (range of habitat types in which a species occurs) and local abundance (typical population size) (Rabinowitz 1981). We defined species rarity based on geographic range (large vs. small) and occupancy (many vs. few occupied sites). We quantified geographic range size and occupancy throughout the European Alps based on the distribution maps and occurrence numbers from GBIF (GBIF.org 2020). We quantified occupancy within Switzerland based on the Info Flora database, which collects occurrence data on vascular plants in Switzerland up to a 1×1 km scale (infoflora.ch 2020).

Androsace chamaejasme Wulfen (*Primulaceae; Seslerion* and *Caricion firmae*; Delarze et al. 2015), *Gentiana acaulis* L. (*Gentianaceae*; *Nardion*; Delarze et al. 2015), *Potentilla crantzii* (Crantz) Fritsch (*Rosaceae; Seslerion*; Delarze et al. 2015) and *Viola calcarata* L. (*Violaceae; Nardion* and *Poion alpinae*; Delarze et al. 2015) are common herbaceous plant species that are present over a wide geographic range with many occupied sites throughout the Swiss (Lauber et al. 2018; infoflora.ch 2020; Fig. 1) and European Alps (GBIF.org 2020). *Androsace puberula* Jord. & Fourr. (*Caricion curvulae*, Delarze et al. 2015), *Gentiana alpina* Vill. (*Caricion curvulae*, Delarze et al. 2015), *Potentilla nivea* L. (*Elynion*, Delarze et al. 2015) and *Viola lutea* Huds. (*Seslerion*, Delarze et al. 2015) are naturally rare herbaceous plant species which occur only within a restricted geographic range with few occupied sites through the Swiss (Lauber et al. 2018; infoflora.ch 2020; Fig. 1) and European Alps.

The rare study species except *V. lutea* tend to occur at higher elevation sites than their common congeneric partner species (Supporting information SI4). Furthermore, the rare study species except *V. lutea* typically occur in their

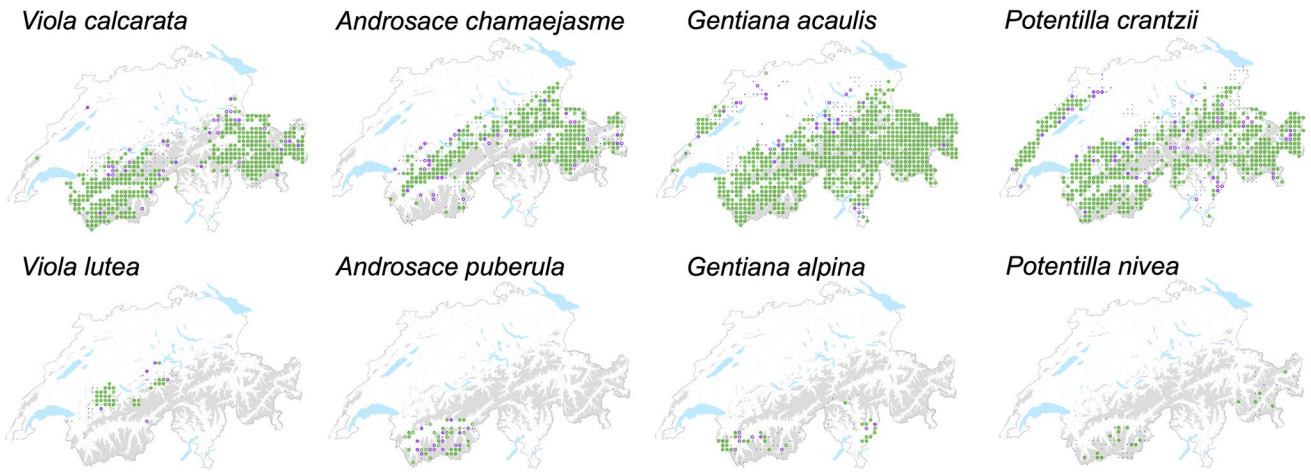

Fig. 1 Distribution maps of the four common (upper row) and the four rare (lower row) study species. Green dots indicate validated species observations, purple dots indicate species observations which have not yet been validated. © Distribution maps / Info Flora

habitat type and only rarely in other habitat types (Delarze et al. 2015). With the exception of *G. acaulis,* our common study species are not character species, which means that they likely occur also in other habitat types (Delarze et al. 2015). The pattern of three rare species being rather habitat specialists and three common species being rather habitat generalists reflects our species selection criteria: subalpine-alpine distribution, congeneric relationships, grassland habitat, geographic range, and occupancy. All study species are perennial, insect pollinated and able to reproduce also clonally. Both *Potentilla* species are facultative apomicts, which means they can produce seeds asexually.

Seed collection

For each species, we visited 10–13 different populations (N = 92) at various elevations (1390–2810 m.a.s.l.) in 2 consecutive years (2020, 2021) in the Swiss Alps (see Supporting information for sampling locations). We selected the populations based on the precise occurrence data from the Info Flora database (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. The minimum distance between two conspecific populations was 100 m.

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 (morphologically integer) 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 3 months from December to February (mean temperature and mean air humidity during these 3 months in Bern are – 0.97 °C and 78.67%; climate-data.org 2023). We selected 3 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 3 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 5 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 5 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 3 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, genus 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 did not occur in smaller populations than common species ($p = 0.22$; Fig. 2; 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. 3b, c; Table 1). Plants of small populations tended to produce seeds with lower germination probabilities ($p = 0.16$; Fig. 3e; 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. 4; Table S2 and S4 Supporting information). In the rare *P. nivea*, plants of small populations

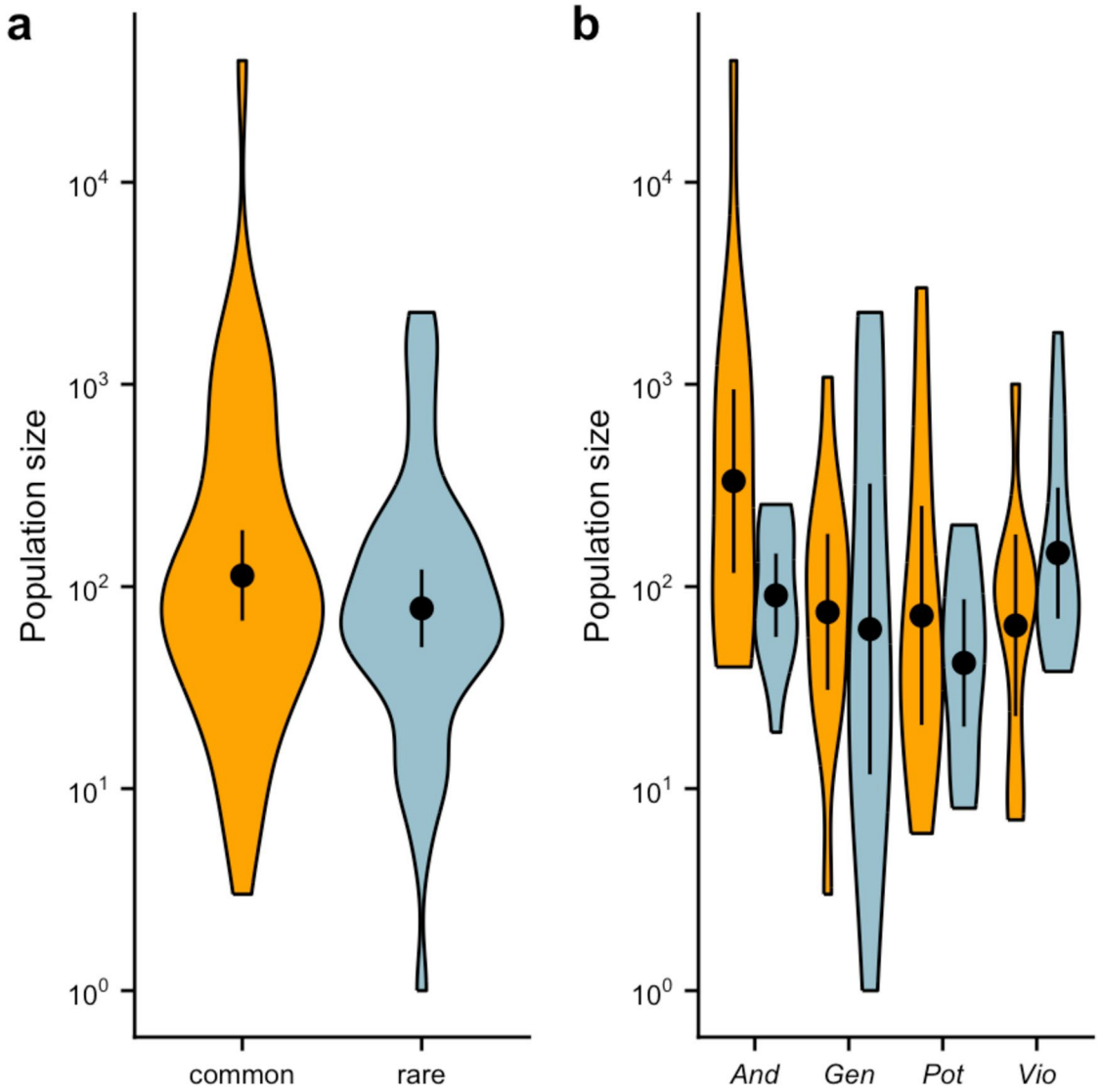

Fig. 2 Population sizes of four common and four rare alpine plant species. Shown are the densities of different population sizes for rare and common species (**a**) and for the four congeneric species pairs (And = Androsace, Gen = Gentiana, Pot = Potentilla, Vio = Viola; **b**). Differences between groups were not significant. Error bars show upper and lower limits of 95% confidence intervals. Blue bars indicate rare species and yellow bars indicate common species

produced seeds with significantly lower germination probabilities than plants of large populations ($p < 0.001$; Fig. 4; 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. 4; 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).

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. 3a; Table 1). Plants of rare species also produced significantly heavier seeds than plants of common species ($p < 0.01$; Table 1). This pattern was driven by plants of the rare *A. puberula*, which produced extremely large seeds compared to all other species. Plants of rare species germinated significantly

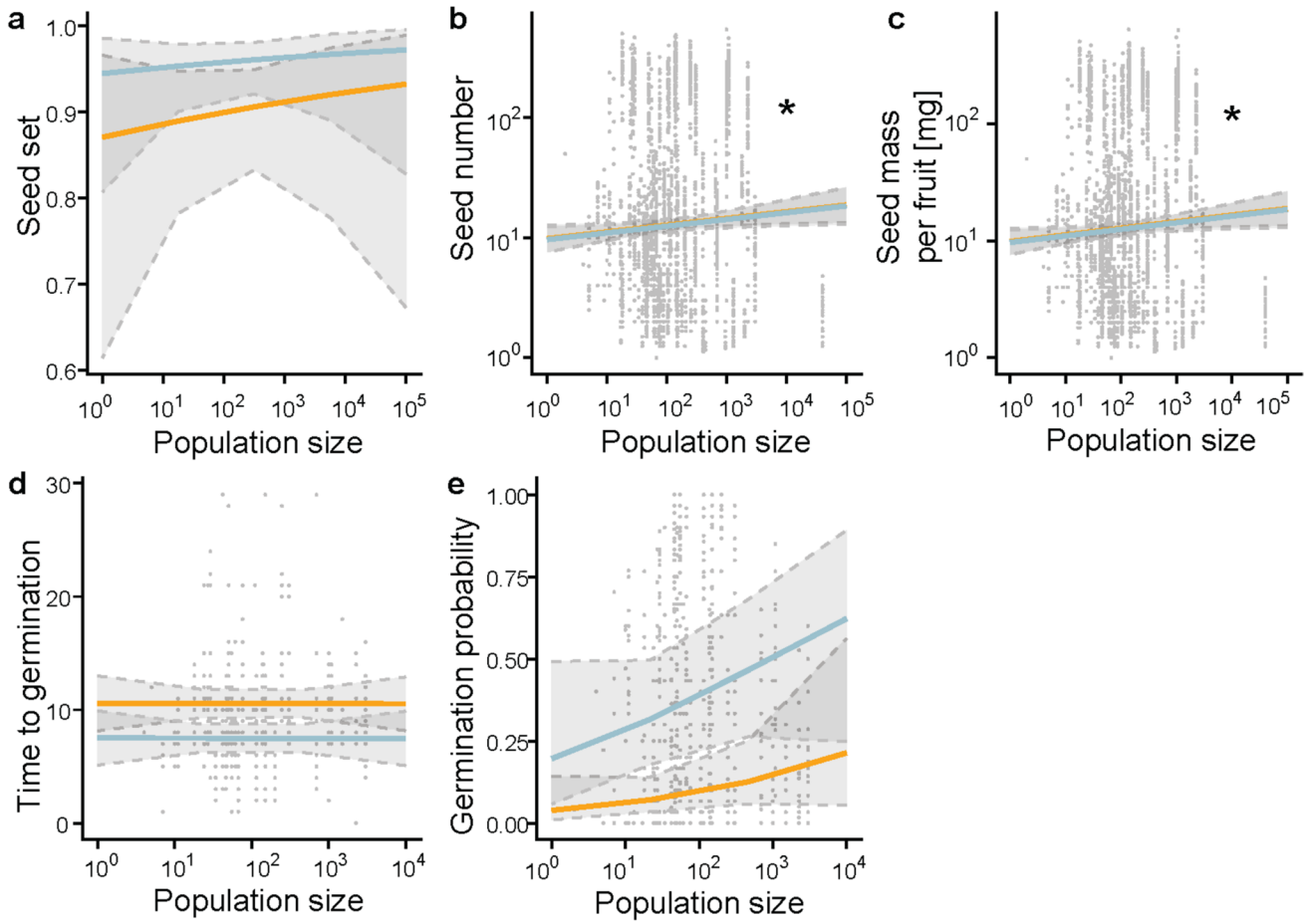

Fig. 3 Relationships between population size and fitness in four rare and four common alpine plant species. Shown are effects of population size predicted by mixed effect models on seed set (**a**), seed number (**b**) and total seed mass per fruit (**c**) across all eight species, and on time to germination (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. Significance levels are given for population size as an explanatory term in the final model: P < 0.1; °, P < 0.05; *, P < 0.01; **, P < 0.001; ***

earlier than common species ($p < 0.001$; Fig. 3d; 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. 3e; 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. 3b, c; Table 1). Across all species, none of the fitness traits were significantly affected by the interaction between rarity and population size.

Discussion

Population size affects fitness in alpine species

In general, population sizes did not differ between rare and common species. Small populations were frequent both among the rare and among the common study species. Therefore, the risk of local extinction due to environmental or demographic stochasticity, which is higher for small populations (Lande 1993), does not differ between the rare

Table 1 ANOVA tables of mixed effect models investigating the effects of population size and rarity on fitness traits across the eight study species

		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

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; ***

and the common study species. Overall, the significant positive relationships of seed number and total seed mass per fruit with population size (Fig. 3b, 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

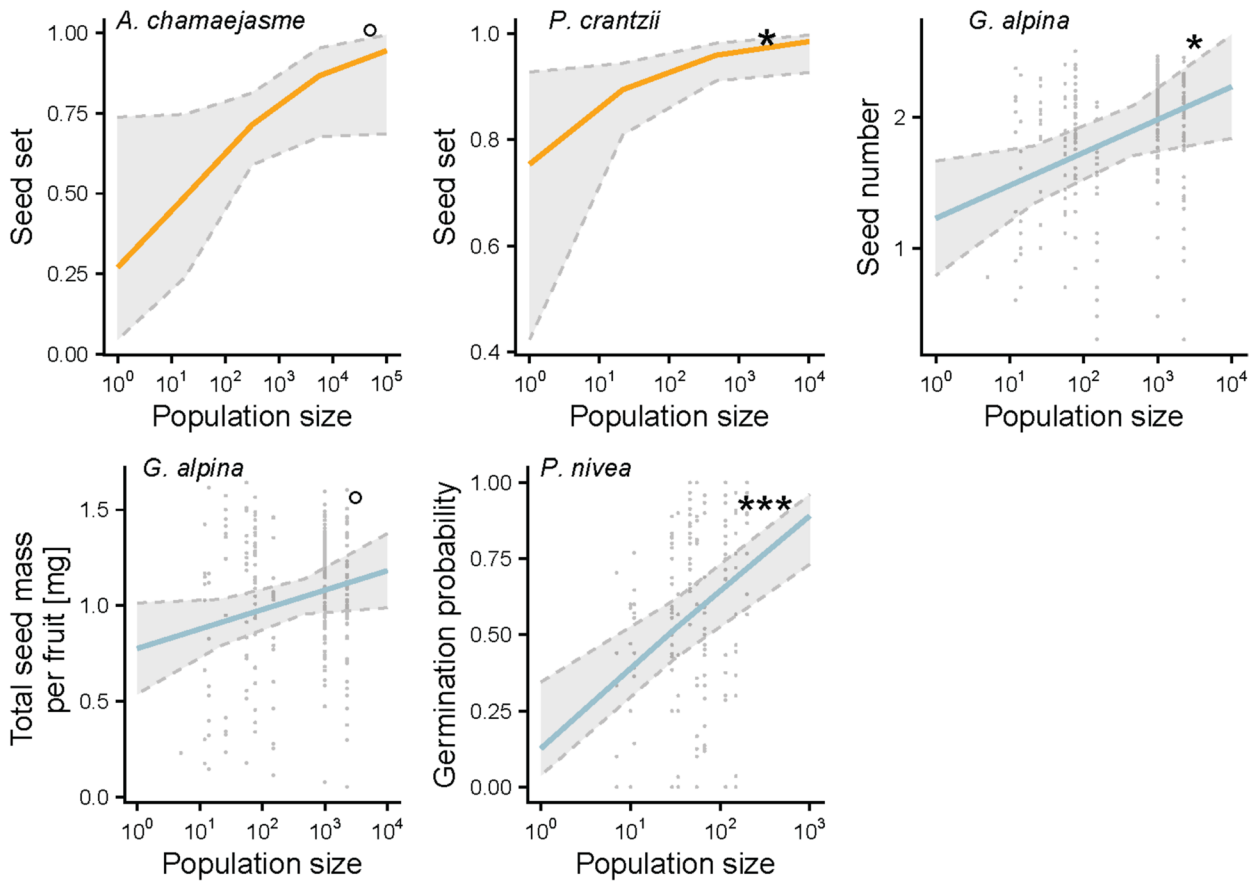

Fig. 4 Relationships between population size and fitness in *A. chamaejasme*, *P. crantzii*, *G. alpina* and *P. nivea*. Fits of mixed effect models and upper and lower limits of 95% confidence intervals are drawn for fitness traits that were marginally or significantly affected by population size when 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. Significance levels are given for population size as an explanatory term in the final model: $P < 0.1$; °, $P < 0.05$; *, $P < 0.01$; **, $P < 0.001$; ***

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. Furthermore, a low seed number may have resulted in small population sizes, leaving the causality of the relationship between population size and seed number unclear. Also, habitat quality may affect population size and plant fitness (de Vere et al. 2009). To assess the relative importance of habitat quality and population size for plant fitness, common garden studies spanning multiple generations should include the habitat parameters of the original sites into their analyses. 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, 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 our naturally rare study species are well adapted to their environment. Purging of genetic load in populations of naturally rare species might be a potential explanation of this observation. However, data on genetic diversity and crossing experiments would be needed to test this hypothesis.

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 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).

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). 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. Therefore, short- and longterm fitness traits should be studied over several years to obtain data that are more reliable and to integrate across different traits over multiple generations.

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 and were not able to break seed dormancy, 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.

Overall, our results do not confirm the broad observation of reduced fitness and reduced survival in rare species (Boyd et al. 2022). This aligns with findings of Paulů et al. (2017), who studied 18 congeneric species pairs from central European mountains and similarly found no evidence of reduced individual fitness in rare species. Hence, our naturally rare study species might be well adapted to their environment and factors other than low plant fitness likely contribute to their rarity. As introduced earlier, delayed Holocene recolonization of suitable habitats has shaped the current ranges of many alpine species (Dullinger et al. 2012). Biological factors such as limited seed dispersial capacities, establishment limitations and narrow ecological niches may explain reduced post-glacial migration (Dullinger et al. 2012). In the case of our rare study species, distribution patterns are unlikely to result from low seed dispersal capacity but may instead be driven by long-term establishment constraints and/or ecological factors.

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

We hypothesised that relationships between population size and fitness are different between rare and common species. However, relationships between fitness and population size were present both in rare and common species. Therefore, in our study species, small populations may be at risk of entering an extinction vortex independently from species rarity.

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 small populations of these species

might enter an extinction vortex. 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.

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.* This does not mean that small populations of these species may not enter an extinction vortex. It is likely that the relationship is simply weaker in these species and therefore not significant because of 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 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. Our results indicate that other species characteristics than rarity might influence whether populations can enter an extinction vortex, such as different reproductive strategies. 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 small populations of alpine plant species may face the risk of entering an extinction vortex. To gain a better understanding of the underlying mechanisms, additional studies that consider genetic diversity are necessary. Relationships between population size and fitness were present both 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.

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Author contributions H. I., D. P and M. F. conceived the ideas and designed the methodology, H. I. collected the data and analyzed the data, H. I. wrote the manuscript with substantial input from D. P. and M. F. on the final draft. All authors gave final approval for publication.

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Data availability Data available on request.

Declarations

Conflict of interest We declare no conflict of interest.

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