Global Ecology and Conservation 52 (2024) e02973

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Demographic responses to competition with surrounding vegetation in subalpine plant species

Hyungsoon Jeong [a], Yong-Chan Cho [b], Eunsuk Kim [a,*]

[a] *School of Earth Sciences and Environmental Engineering, Gwangju Institute of Science and Technology, Gwangju 61005, South Korea*
[b] *Forest Biodiversity Research Division, Korea National Arboretum, Pocheon 11186, South Korea*

ARTICLE INFO

Keywords:
Elasticity
Integral projection model
Interspecific competition
Life-table response experiment contribution
Population growth rate
Vegetation gradient

ABSTRACT

Alterations in biotic interactions alongside climatic factors are proposed to affect the extinction risks of alpine and subalpine plant species. We examined the population demography of *Primula farinosa* along gradients of vegetation coverage to assess how the population viability of high mountain plants would alter in response to changing competitive intensities. Size-based integral projection models were constructed for plots with varying vegetation coverages. Complementary to the demographic survey, the performance of *P. farinosa* was evaluated in controlled environments when grown with its naturally co-occurring plant, *Sanguisorba hakusanensis*. In field sites, population growth rates (λ) of *P. farinosa* declined as surrounding vegetation coverage increased. The means, elasticities, and life-table response experiment (LTRE) contributions of the vital rates also changed, but the alteration patterns depended on the vital rates. Juvenile survival (JS), adult survival (AS), and flowering probability (FP) were lower in plots with denser vegetation while the decrease of AS was not statistically significant. Notably, the elasticity of AS exhibited a positive, whereas the elasticities of JS and FP exhibited negative regression coefficients for vegetative coverage. AS and FP showed more pronounced LTRE contributions in declining λ than JS. Significant reductions in JS and FP were also observed when plants were grown with *S. hakusanensis* in growth-chamber environments. Both field and chamber studies demonstrated a competitive interaction between *P. farinosa* and neighboring vegetation, affecting diverse demographic parameters. Altered elasticities would mitigate or exacerbate the impact of decreased mean vital rates on λs in denser vegetation, emphasizing the importance of evaluating both elasticity and the mean of vital rates to predict population persistence under changing biotic interactions.

1. Introduction

Although biotic interactions, including competition, are often considered incidental to a species' range, recent studies propose their significant role in shaping species distribution (Morris et al., 2020; Wisz et al., 2013). In particular, competition, in addition to climatic factors, can be a determinant of altered species distribution under global climate change conditions (Brooker, 2006; HilleRisLambers et al., 2013; Lenoir et al., 2020; Sanczuk et al., 2022; Zellweger et al., 2020). Understanding how demographic parameters respond to competitive interaction is essential to evaluate its effects on the viability of existing plant populations or potential range shift into novel habitats (Morris et al., 2020; Sanczuk et al., 2022).

---

* Corresponding author.
E-mail address: eunsukkim@gist.ac.kr (E. Kim).

https://doi.org/10.1016/j.gecco.2024.e02973
Received 5 January 2024; Received in revised form 28 April 2024; Accepted 1 May 2024

For instance, plant performance in alpine and subalpine areas has been considered vulnerable to changing climatic factors (Pepin et al., 2015; Theurillat and Guisan, 2001). Notably, altered climatic conditions can change competitive interactions with neighboring plants, which can threaten population persistence in current habitats (Brooker, 2006; Dullinger et al., 2012; Nomoto and Alexander, 2021). Plant species in high-altitude environments exhibit varied responses to altered climatic conditions, possibly influencing their interactions with neighboring plant species. Grasses, sedges, and rushes grow more rapidly at increased temperatures, enhancing their competitive abilities over other coexisting plant species (Bret-Harte et al., 2004; Brooker and van der Wal, 2003). Furthermore, plant species at lower altitudes can encroach into higher-altitude habitats in response to climate change, becoming novel competitors to existing alpine plant species. This surge in vegetation can detrimentally affect the performance of alpine plants, resulting in decreased population growth rates (Alexander et al., 2015; Broadbent et al., 2022; Nomoto and Alexander, 2021; Shepard et al., 2021).

A useful methodology to assess the impact of temporally changing conditions on population persistence is to characterize population demography across spatial environmental gradients (Andrello et al., 2020; Sheth and Angert, 2018). Given that competitive intensity is likely to change in the future, a demographic study along a gradient of neighboring vegetation abundance can provide information on how population demography would respond to altered competitive intensity in the future. It could evaluate whether population growth rates (λ) and mean values of vital rates change across vegetation gradients, providing information on changes in population size (Caswell, 2000). The elasticities of vital rates can be used to quantify their relative significance to λ (Benton and Grant, 1999; Franco and Silvertown, 2004). The life-table response experiment (LTRE) contribution can assess the impacts of altered vital rates on λ (Maldonado-Chaparro et al., 2018; Villellas et al., 2015).

In this study, we conducted a demographic study of four *Primula farinosa* natural populations in Korea (Fig. S1). *P. farinosa* is a rosette-forming herbaceous plant native to northern Europe and Asia (Hambler and Dixon, 2003). In Korea, *P. farinosa* inhabits grasslands and crevices of mountaintops at altitudes higher than 1000 m a.s.l. Plants occurred along a gradient of neighboring vegetation abundance at the study sites, spanning from open bare ground to densely vegetated surroundings. In European *Primula* species, their growth and floral display can be diminished by surrounding vegetation's growth and litter accumulation (Ågren et al., 2006; Ehrlén et al., 2005). Managing tall vegetation through grazing or mowing has been proposed as an effective strategy for conserving *Primula* natural populations (Endels et al., 2007; Lindborg and Ehrlén, 2002; Wehn, 2009). We constructed integral projection models (IPMs) along vegetation gradients across study sites and assessed three key descriptors of vital rates, including mean value, elasticity, and LTRE contribution to λ.

Although demographic study along a vegetation gradient can offer insights into plant responses to surrounding vegetation at the population level, it is important to note that the results may be compounded with various micro-environmental factors in the field. We performed a growth chamber experiment to remove micro-environmental factors and tried to confirm that *P. farinosa* interacted competitively with the surrounding vegetation. Among co-occurring plant species, *Sanguisorba hakusanensis* was selected as the testing species because it was frequently observed in *P. farinosa* habitats and shared belowground space, even in narrow rock crevices (H. Jeong, per. obs.). Since elevated temperatures can alter the strength of competitive interaction (Bret-Harte et al., 2004; Brooker and van der Wal, 2003), we assessed the plant performance under two temperature regimes.

This study aimed to address the following questions: (1) Does the population growth rate of *P. farinosa* decline as the coverage of the surrounding vegetation increases? (2) Which vital rates are affected by vegetation coverage and contribute to the observed change in population growth rates? (3) Does the presence of *S. hakusanensis* affect the performance of *P. farinosa*?

2. Materials and methods

2.1. Demographic census

We conducted demographic surveys from 2018 to 2021 to examine the dynamics of four *Primula farinosa* populations using an integral projection model (IPM). Ten 1 × 1 m^2 plots were established at each of four sites: Cheonhwangsan (CH), Gayasan (GY), Hallasan (HL), and Jirisan (JR) in 2018 (Fig. S1). Each plot contained 16−66 plants and 1250 plants in total were tagged in 2018. Seedlings newly established since 2019 were also tagged. Plant life history and morphological traits of tagged plants were measured at the beginning (April and May) and end (August and September) of the growing season. Census-to-census survival, rosette diameter, and the number of flowers and fruits were recorded. The dataset encompassed 3692 life history records as of 2021 (N_{2018}=1250, N_{2019}=1159, N_{2020}=1151, N_{2021}=132). The number of seeds per fruit was counted using three to five plant individuals grown near the plots.

In study sites, neighboring plants that reached sufficient height to cover *P. farinosa* included *Sanguisorba hakusanensis* (Rosaceae), *Carex lanceolate* (Cyperaceae), *Carex sabynensis* (Cyperaceae), and *Sasa quelpaertensis* (Poaceae). *S. hakusanensis* is a perennial species commonly found in the middle of the mountainous regions (< 600 m a.s.l.) of the Korean Peninsula and is frequently encountered in the habitat of *P. farinosa*. The two perennial species of *Carex* are distributed across Northeast Asia and occasionally accumulated litter at the study sites. *S. quelpaertensis*, a perennial species, was observed only at the Halla site on Jeju Island. This species thrives at an elevation range of 600−1900 m a.s.l.

Each plot was subdivided into 10 × 10 cm^2 subplots to determine whether aboveground tissues of plant species other than *P. farinosa* were present. The coverage of the surrounding vegetation was quantified for each plot as the number of subplots with non-*P. farinosa* plants divided by the total number of subplots (100). Average vegetation coverages of sites had a negative correlation with altitudes of sites, while the calculated Spearman correlation coefficient was not statistically significant (Spearman's orrelation coefficient = − 0.80, P = 0.333). Surrounding vegetation occurred in clusters rather than uniformly in the study sites. The measured coverage values of a cluster tended to be over 5% and increase by 5–10% within a plot. Additionally, the measured coverage values exhibited seasonal and annual variations of up to 5% in subplots due to the growth and senescence of aboveground tissues (H. Jeong, personal observation). Taking these factors into consideration, the measured coverage of the surrounding vegetation was rounded to the nearest ten percentage points and subsequently assigned to each plot to incorporate the coverage into the life table response experiment (LTRE) analysis. The measurements of vegetation coverage ranged from 10% to 80% across study sites.

2.2. Structure and analyses of the demographic model

All modeling and statistical analyses were performed using R 4.1.2 (R Core Team 2013). First, the IPM was constructed for overall study sites and for each site across four years to evaluate population growth rates and elasticities. In addition, the IPM for each plot was constructed to examine demographic responses to gradients of vegetation coverage. In IPMs, the size distribution in year $t+1$ is determined by the main kernel function $\boldsymbol{K}$ of the size distribution in year t, which is further decomposed into a survival/growth sub-kernel function $\boldsymbol{P}$ and a fecundity sub-kernel function $\boldsymbol{F}$ (Merow et al., 2014). The model is

$$n_{t+1}(z') = \int_L^U \boldsymbol{K}(z,z')n_t(z)dz = \int_L^U [\boldsymbol{P}(z,z') + \boldsymbol{F}(z,z')] \quad n_t(z)dz \tag{1}$$

where n is the size distribution, z is the plant size (mm) at time t, z' is the plant size at time $t+1$, and U and L are the upper and lower limits of plant size (1.1 × the maximum size observed and 0.9 × minimum size observed) respectively. The $\boldsymbol{P}$ sub-kernel ($\boldsymbol{P}(z,z')$) and $\boldsymbol{F}$ sub- kernel ($\boldsymbol{F}(z,z')$) are decomposed into vital rates as follows (Merow et al., 2014):

$$\boldsymbol{P}(z,z') = s(z) \times g(z,z')$$

$$\boldsymbol{F}(z,z') = p_{flowering}(z) \times \quad n_{head}(z) \times \quad n_{seeds} \times p_{establishment} \times C(z') \tag{2}$$

where s is the annual survival probability, g is the annual growth rate, $p_{flowering}$ is the probability of flowering, n_{head} is the number of flowers, n_{seeds} is the number of seeds per flower, $p_{establishment}$ is the probability that a germinated seedling survives till the next census, and $C(z')$ is the seedling size (mm) distribution.

Vital rates were modeled in relation to plant size. Generalized linear models (GLMs) with binomial error distributions were used for $s(z)$ and $p_{flowering}(z)$, GLMs with Poisson distributions were used for $n_{head}(z)$, and linear models with Gaussian distributions were used for $g(z,z')$. The model was constructed for each plot using census data collected over four years. The models included the year and individual effect as a fixed factors to control for yearly variation and individual heterogeneity because models with the year and individual as random factors often did not coverge. We tested models with linear or quadratic terms of plant size and selected the model with the lowest Akaike Information Criterion (AIC) value as the best-fitting model. The n_{seeds} were constant in the IPM models as mean values across all censuses. *P. farinosa* in Sweden exhibits a short-term persistent seed bank, probably due to its tiny seed size (0.047 mg, SD = 0.012, n = 215) (Lindborg and Ehrlén, 2002). In addition, the removal of the seed bank stage from the demographic model has a negligible effect of on the population growth rate (Lindborg and Ehrlén, 2002). Considering these previous results, the seed bank was not included in the model, and the $p_{establishment}$ was set to a constant as the average ratio between seedling recruitment and seed production across all censuses.

We used the *IPMpack* package to construct the IPMs (Metcalf et al., 2013). The IPMs with a resolution of 100 × 100 cells were filled with the demographic rates (τ) by applying the midpoint rule on discretized vital rates (Ellner and Rees, 2006). The deterministic population growth rate (λ) was estimated from the IPM of each plot (Easterling et al., 2000). The 95% confidence intervals of λ were determined at four sites using 1000 bootstrapped samples. To assess the demographic significance of vital rates in λ, the sensitivity and elasticity for the $\boldsymbol{K}$ kernel were calculated (De Kroon et al., 2000; Hegland et al., 2010) using the *popbio* package (Stubben and Milligan, 2007). The sensitivity ($S_K(z,z')$) and elasticity ($E_K(z,z')$) of $\boldsymbol{K}$ kernel is

$$S_K(z,z') = \frac{\partial\lambda}{\partial K}(z,z'), E_K(z,z') = \frac{K(z,z')}{\lambda} \bullet S_K(z,z') \tag{3}$$

We used the life table responses experiment (LTRE) to assess the effect of vegetation coverage on λ. For the LTRE contribution, we used the midway method (Caswell, 2000). The IPM kernel obtained from each plot with distinct coverage (A^C) was compared with the overall IPM kernel obtained from the model that included all individuals (A^M). The coverage effect (α) was approximated as the difference between λs of A^M and A^C as follow:

$$\lambda^C \cong \lambda^M + \alpha \tag{4}$$

where λ^C is the population growth rate of each plot, and λ^M is the population growth rate of the overall IPM. The LTRE coverage effect for each vital rate was calculated by summing the differences in all kernel elements between A^C and A^M, which were subsequently multiplied by the average sensitivity of A^C and A^M (Hegland et al., 2010) as follows:

$$\widetilde{\alpha} = \lambda^C - \lambda^M \approx \sum_p (\tau^p_{C,v} - \tau^p_{M,v}) S_{K^v}\big|_{\frac{1}{2}(A^C + A^M)} \tag{5}$$

where $\tau^{p}_{C,v}$ is the p^{th} kernel element (demographic rate) of each IPM kernel (A^{C}) consisting of the vital rate (v) function, $\tau^{p}_{M,v}$ is the p^{th} kernel element (demographic rate) of the overall IPM kernel (A^{M}) consisting of the vital rate (v) function and $S_{K^{v}}$ is the average sensitivity.

To evaluate the effects of surrounding vegetation coverage on λ and vital rates, linear regression analyses were performed using the *lme4* package (Bates, 2010). The regression model included the site as a random factor to control for the site effect. Vital rates, including survival, growth, and fecundity, were analyzed. The stasis in the same plant size given survival and retrogression to the smaller plant size given survival were excluded from the analysis. Vital rates were expressed as mean, elasticity, and LTRE contribution. These descriptors were calculated separately for plants in juvenile (before reproduction) and adult stage (after reproduction). A plant was classified as an adult if its rosette diameter was larger than the average of the minimum rosette sizes of flowering individuals across years (23 mm in the CH site, 21 mm in the GY site, 26 mm in the JR site, and 22 mm in the HL site) (Jeong et al., 2022; Lindborg and Ehrlén, 2002). Plants with rosette diameters smaller than this threshold were juveniles. Regression coefficients of the coverage of surrounding vegetation against each parameter of vital rates were estimated.

To assess the demographic significance of vital rates in the variation of λ across different levels of vegetation coverage, we conducted two correlation analyses. First, we calculated Spearman's correlation coefficients between the LTRE effects of vital rates and the deviation of λ of each plot to the λ of overall IPM. A strong correlation indicates that changes in these vital rates consistently contribute to the variation in λ across vegetation coverage (Jongejans et al., 2010). Second, Spearman's correlation coefficients were calculated for all pairs of vital rates' LTRE effects. According to Villellas et al. (2015), a negative correlation indicates opposing responses of vital rates to environmental gradients, which can demographically compensate for a negative impact of one vital rate on λ. The permutation tests in the *wPerm* package were used to evaluate the statistical significance of the correlation coefficients (Weiss, 2015). To assess whether the number of negative correlations was higher than expected by chance, a null distribution of the significant negative correlations was created using 10,000 random permutations of the LTRE effects (Villellas et al., 2015).

2.3. Experimental design and statistical analyses of the growth-chamber experiment

The seeds of *P. farinosa* and *S. hakusanensis* were collected from four sites (CH, JR, GY, and HL). Seeds of each species from the same site were mixed and soaked in a 100 mM gibberellic acid (Sigma, Darmstadt, Germany) solution to facilitate germination. After soaking for 24 h, the treated seeds were sprinkled into flats filled with a blend of commercial soil (ShinSung Mineral Co., Kyeonggi-do, Korea) and decomposed granite (1:1.5 v/v). The flats were placed in a walk-in chamber for one month, maintaining a temperature of 18 °C and a photoperiod of 12/12-h light/dark with 200 μmol s^{-1} m^{-2} PAR intensity. As seeds from the CH and GY sites rarely germinated, we used seedlings from seeds from the JR and HL sites.

After four weeks of maintenance, seedlings with true leaves were transplanted into individual plastic pots (80 mm diameter) filled with the same soil medium used for seed germination. To simulate interspecific competition, a seedling of *P. farinosa* and a seedling of *S. hakusanensis* from the same site were randomly chosen and planted approximately 2 cm apart in a single pot. As negative controls, two randomly selected *P. farinosa* seedlings from the same site were planted in pots without *S. hakusanensis*. One hundred twenty pots were used for interspecific competition, and the same for the control.

We designated 18 °C as the control temperature, representing the average temperature during the growing season from May to September at the Jirisan site (H. Jeong, unpublished data). The elevated temperature was set at 20 °C considering the prediction of 1.9 – 4.7 ℃ increase above current temperature in South Korea by the late 21st century (Suh et al., 2016). The transplanted plots were maintained in a walk-in chamber at 18 °C for one week. Subsequently, these pots were randomly assigned into one of two walk-in chambers, each operating at 18 °C or 20 °C. Both chambers were illuminated with 200 μmol s^{-1} m^{-2} PAR intensity and a 12/12-h light/dark photoperiod. All pots were placed following a completely randomized design (CRD) in each chamber and irrigated twice weekly. To mitigate the potential chamber effect, we relocated all pots to alternate chambers every two weeks. After three months of temperature treatment, all plants were transferred to a chamber at 4–6 °C and underwent a vernalization period for two months. The plants were then moved back to the walk-in chambers at 18 °C or 20 °C and grown for two months.

We recorded the survival and rosette diameter of *P. farinosa* before vernalization and at the end of the experiment. The number of flowering heads was counted after vernalization. Because the leaves of *S. hakusanensis* withered during vernalization, the length of the longest leaf and the number of stems of *S. hakusanensis* were measured before vernalization.

One *P. farinosa* individual in each pot was designated as a focal plant. Linear mixed models were used to assess the effects of interspecific competition and temperature treatments on the traits of focal *P. farinosa* individuals. The models included competition, temperature, and their two-way interaction as fixed factors. The source population was also included as a fixed factor to control for differences between source populations. The survival rate and probability of flowering in *P. farinosa* were evaluated using a generalized linear mixed model with a binomial error distribution. The morphological traits of *S. hakusanensis* and *P. farinosa* were examined using the same model as above with a Gaussian error distribution. Post-hoc analyses were performed using the Bonferroni adjustment. In four control pots with two *P. farinosa* individuals, one *P. farinosa* died during the experiment; therefore, it was excluded from the analyses.

3. Results

3.1. Population growth rates and elasticities at testing sites

The population growth rate (λ) of *P. farinosa* from the overall IPM kernel was 0.980 (± 0.005, 95% CI), indicating a decline in population size. Plant individuals with rosette diameters ranging from 35 to 55 mm constituted around 22% of testing populations. They exhibited relatively high survival rates and reproductive capacities for seedling establishment (Fig. S2). In addition, those plants showed high sensitivity and elasticity values, showing their critical role in maintaining population size (Fig. S2). The elasticities of small individuals (< 10 mm) and the establishment of seedlings were also considerable, while values were relatively low (Fig. S2).

When λs at four sites were estimated separately, the CH ($\lambda = 1.027 \pm 0.006$, 95% CI) and HL ($\lambda = 1.063 \pm 0.006$, 95% CI) populations had λ values higher than 1 (Fig. S3). In contrast, λs at the GY ($\lambda = 0.968 \pm 0.007$, 95% CI) and JR ($\lambda = 0.957 \pm 0.008$, 95% CI) sites were lower than 1, suggesting that the sizes of those populations were expected to decline. Similar to the elasticities of the overall IPM, the adult stage showed relatively high elasticities at all sites (Fig. S4). At the GY and JR sites, where the decline of population size was anticipated, seedling establishment and juvenile growth showed lower elasticities than those at the CH and HL sites (Fig. S4).

3.2. Relationship between the coverage of surrounding vegetation and demographic parameters

The study plots of *P. farinosa* exhibited a significant regression coefficient of λ against the vegetation coverage gradients (Fig. 1). Most plots at the HL site showed low vegetation coverage, while plots with high coverage were located at the JR site. When the site effect was controlled for, the λ was predicted to decline with an increase in vegetation coverage (regression coefficient (SE) = – 0.187 (0.061), $t = -3.053$, $R^2_{adjust} = 0.204$, $P < 0.01$) (Fig. 1, Table S1).

The survival rate of the entire life stage exhibited a negative regression coefficient against the coverage of surrounding vegetation with marginal statistical significance (regression coefficient (SE) = – 0.123 (0.065), $t = -1.906$, $P = 0.064$) (Fig. 2, Table S1). Such effect manifested at the juvenile stage (regression coefficient (SE) = – 0.267 (0.132), $t = -2.031$, $P < 0.05$). Survival rate at the adult stage also had a negative relationship with the vegetation coverage, although the observed regression coefficient was not statistically significant (regression coefficient (SE) = – 0.064 (0.054), $t = -1.202$, $P = 0.237$). No relationship was detected between the vegetation coverage and the progressive growth at the juvenile (regression coefficient (SE) = – 0.005 (0.027), $t = -0.204$, $P = 0.839$) and adult (regression coefficient (SE) = – 0.019 (0.047), $t = -0.397$, $P = 0.694$) life stages (Fig. 2, Table S1). Although the regression coefficient of fecundity was not statistically significant (regression coefficient (SE) = – 0.001 (0.001), $t = -0.974$, $P = 0.336$), flowering probability, a component of fecundity kernel, decreased as the coverage of surrounding vegetation increased (regression coefficient (SE) = – 0.417 (0.156), $t = -2.681$, $P < 0.05$) (Fig. 2, Table S1).

The elasticities for several vital rates changed with the coverage levels. The elasticity of survival across all life stages increased as vegetation coverage increased (regression coefficient (SE) = 0.116 (0.033), $t = 3.469$, $P < 0.01$) (Fig. 3, Table S2). Similarly, the elasticity of adult survival tended to increase (regression coefficient (SE) = 0.224 (0.064), $t = 3.516$, $P < 0.01$) while the response of juvenile survival showed an opposite trend (regression coefficient (SE) = – 0.108 (0.031), $t = -3.423$, $P < 0.001$). A declining elasticity was also found for fecundity (regression coefficient (SE) = – 0.114 (0.033), $t = -3.425$, $P < 0.01$) (Fig. 3, Table S2). The elasticities of flowering probability ($p_{flowering}$) and number of seeds (n_{seeds}) showed the same trend as the elasticity of fecundity because the ***F*** kernel was directly influenced by the fecundity components (Griffith, 2017). There was a rise in the growth elasticity at the adult stage against the coverage gradient (regression coefficient (SE) = 0.062 (0.029), $t = 2.100$, $P < 0.05$); however, such trend was not detected at the juvenile stage (regression coefficient (SE) = – 0.043 (0.051), $t = -0.847$, $P = 0.403$) (Fig. 3, Table S2).

Significant regression coefficients for the LTRE contributions of survival were found in relation to the coverage of surrounding

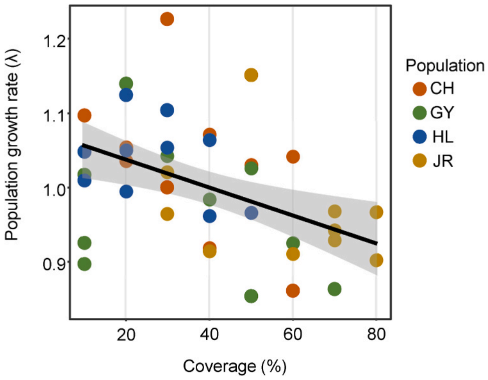

Fig. 1. Population growth rate (λ) and vegetation coverage across four testing sites. Points correspond to the population growth rate of each plot as projected from the integral projection models (IPMs). The black line is the fitted line from a linear regression, and the gray shading is the 95% confidence interval. Regression statistics are given in Table S1.

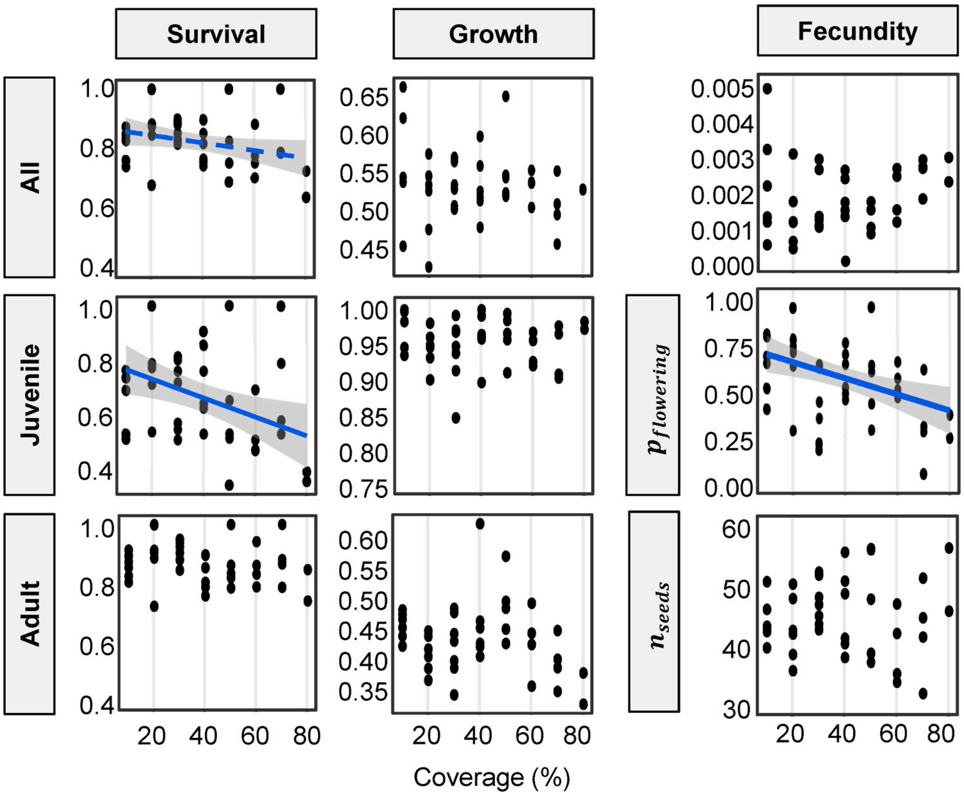

Fig. 2. Mean vital rates across vegetation coverages. $p_{flowering}$ depicts the probability of flowering and n_{seeds} depicts the number of seeds per flower. The blue lines are fitted linear regression lines against vegetation coverage. The significant regression line ($P < 0.05$) is solid, and the marginally significant regression line ($0.05 < P < 0.1$) is dashed. Gray shading shows the 95% confidence interval. Regression statistics are given in Table S1.

vegetation at both juvenile (regression coefficient (SE) = – 0.015 (0.007), t = – 2.160, $P < 0.05$) and adult (regression coefficient (SE) = – 0.121 (0.056), t = – 2.50, $P < 0.05$) stages (Fig. 4, Table S3). As the coverage of surrounding vegetation increased, LTRE contribution of survival shifted from positive to negative values (Fig. 4), indicating that reduced λ in high vegetation plots (Fig. 1) was attributable to the reduction in survival rate. The LTRE contribution of fecundity did not show a relationship with the vegetation, but the probability of flowering ($p_{flowering}$) had a significant negative regression coefficient (regression coefficient (SE) = – 0.101 (0.044), t = – 2.295, $P < 0.05$). No statistically significant coefficients were detected for the LTRE contributions of growth and number of seeds (n_{seeds}) against the vegetation coverage.

The LTRE contribution of survival and fecundity to the population growth rate positively correlated with the λ deviation from λ of the overall IPM model across varying vegetation coverages (Fig. 5). This indicates that decreasing LTRE effects of survival and fecundity consistently amplified the decline of λ in plots with high neighboring vegetation. No statistically significant negative correlation between the LTRE effects of vital rates was detected, and consequently, the number of negative correlations did not exceed what would be expected by chance (Fig. S5). Thus, the reduction of juvenile survival and flowering probability in abundant surrounding vegetation was not demographically offset by increases in other vital rates.

3.3. Effects of interspecific competition and temperature on the survival, growth, and reproduction of P. farinosa

Interspecific competition with *S. hakusanensis* affected various traits of *P. farinosa* (Table S4). Before vernalization, competition reduced both rosette diameter (F = 8.641, $P < 0.01$) and survival rate (χ^2= 9.012, $P < 0.01$) (Table S4). After vernalization, *P. farinosa* grown with *S. hakusanensis* exhibited a lower survival rate by 17% (Fig. 6a; χ^2= 9.384, $P < 0.01$) compared to those grown with another *P. farinosa*. The interspecific competition also diminished flowering probability (Fig. 6b; χ^2= 19.339, $P < 0.001$), such that only 5% of individuals reproduced in the interspecific competition treatment, while around 25% of plants produced flowers in the control treatment. The effect of interspecific competition on rosette diameter was not detected after vernalization, likely because reproducing plants under intraspecific competition would allocate resources to reproduction rather than growth.

Before vernalization, the seedlings of *P. farinosa* exhibited longer rosette diameters under warming temperature than control temperature (Table S4). In contrast, no difference in rosette diameter was detected between the temperature treatments after vernalization (Fig. 6c, Table S4). The survival rate decreased due to warming temperature before vernalization (χ^2= 3.284, $P = 0.066$), and at the end of the experiment (χ^2= 16.328, $P < 0.001$) (Fig. 6a). Temperature treatment did not affect the probability of flowering

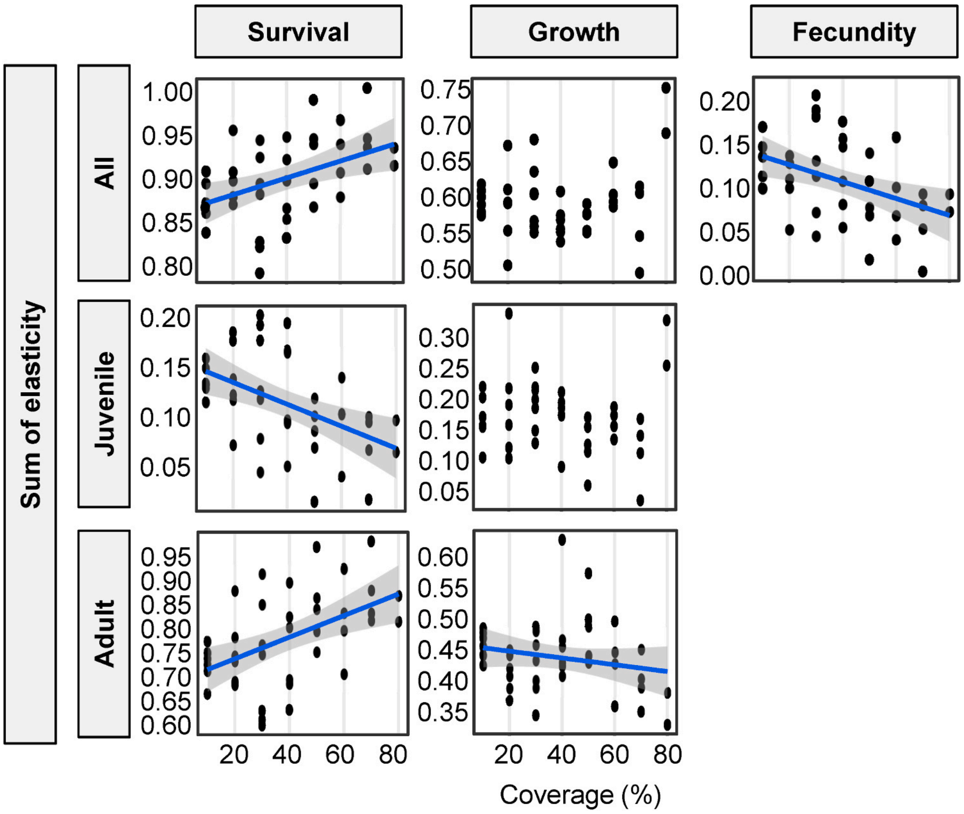

Fig. 3. The sum of elasticities of vital rates across vegetation coverages. The blue lines are fitted linear regression lines against vegetation coverage. Separate analyses were conducted for each life stage. The elasticities of flowering probability ($p_{flowering}$) and the number of seeds (n_{seeds}) showed the same trend as the elasticity of fecundity (Griffith, 2017), so they are not shown in the figure. The significant regression line ($P < 0.05$) is solid, and the marginally significant regression line ($0.05 < P < 0.1$) is dashed. Gray shading shows the 95% confidence interval. Regression statistics are given in Table S2.

(Fig. 5b, Table S4) or the number of flowering heads (Fig. 6d, Table S4).

The seedlings of *S. hakusanensis* exhibited more stems ($F = 8.539$, $P < 0.01$) and larger leaves ($F = 4.783$, $P < 0.05$) under warming temperature than under control temperature (Fig. S6). However, no interaction between competition and temperature treatments was detected (Table S4), indicating that temperature increments did not alter the effects of competition on survival, growth, and reproduction.

4. Discussion

This study demonstrated that the coverage of surrounding vegetation had a negative relationship with the population growth rate (λ) and some vital rates of *P. farinosa* in natural habitats (Fig. 1, Fig. 2). When *P. farinosa* grew with *S. hakusanensis* in controlled environments, their survival rate and the probability of flowering were lower than those without *S. hakusanensis*, suggesting that declining λ observed in the field can be attributed to the competitive interactions between *P. farinosa* and co-occurring plants.

4.1. Population growth rate and vital rates of P. farinosa across the coverage of surrounding vegetation

The study plots with higher vegetation coverage tended to have lower λ values. Among the nine demographic plots with 60% or more vegetation coverage, eight exhibited λ values less than one (Fig. 1), indicating that their population sizes are declining. Additionally, two vital rates, survival and probability of flowering, decreased with increasing vegetation coverage (Fig. 2). Previous studies showed that reducing neighboring vegetation could enhance plant performance and population viability, while they explored demographic outcomes following artificial interventions such as mowing management or grazing history (Endels et al., 2007; Hegland et al., 2010; Lennartsson and Oostermeijer, 2001; Wehn and Johansen, 2015; Wilsey and Polley, 2003). Our results underscore that varying degrees of neighboring vegetation in natural habitats can influence vial rates and λ.

Evaluating multiple demographic descriptors (mean, elasticity, and LTRE contribution) can offer a more comprehensive understanding of population demography under altered environmental conditions (Andrello et al., 2020; Sheth and Angert, 2018; Villellas et al., 2015). First, the mean survival rate for the entire life stage decreased in plots with higher vegetative coverage (Fig. 2). Notably,

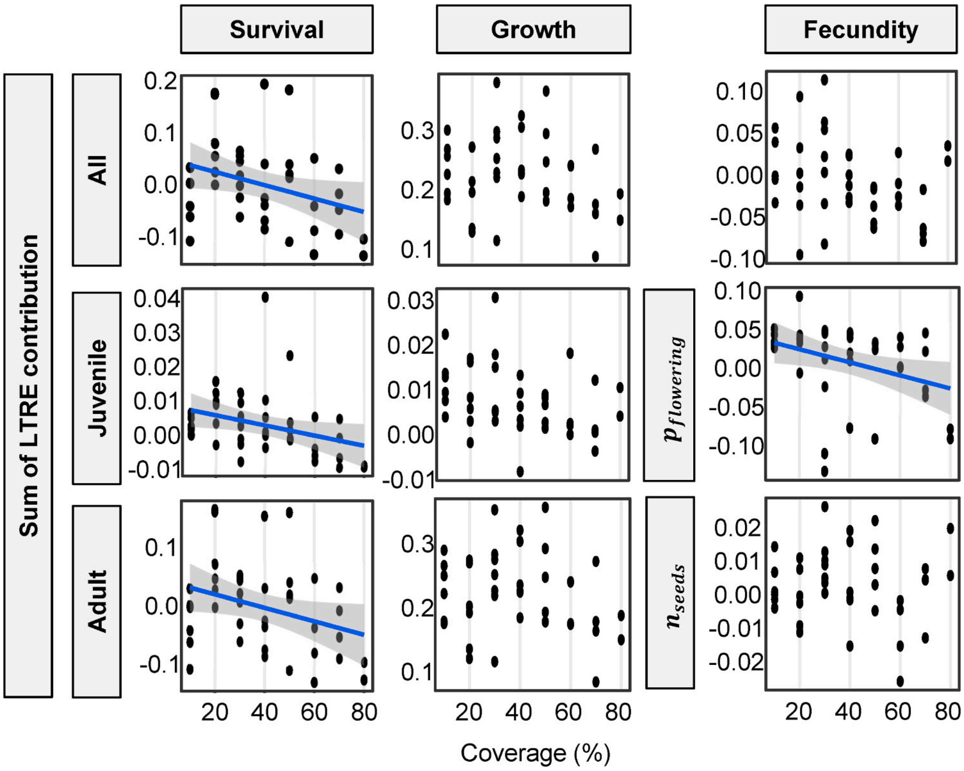

Fig. 4. The sum of life table response experiment (LTRE) contributions of vital rates across vegetation coverages. The blue lines are fitted linear regression lines against vegetation coverage. Separate analyses were conducted for each life stage. The significant regression line ($P < 0.05$) is solid and gray shading shows the 95% confidence interval. Regression statistics are given in Table S3.

the elasticity of survival increased (Fig. 3), indicating the heightened demographic impact of survival on λ. This increased elasticity of survival appears to amplify the negative effect of a declining survival rate on λ, leading to a more negative LTRE contribution of survival to λ. In a similar way, increasing elasticity of adult survival likely induced pronounced negative LTRE contribution to λ even though the decrement of adult survival was not statistically significant in response to surrounding vegetation.

Furthermore, our study showed that juvenile survival exhibited a lower mean value in denser vegetation plots, accompanied by diminished elasticity (Fig. 2, Fig. 3). These results are consistent with a demographic study of *A. alpina* conducted along an altitudinal gradient. In that study, both mean growth and its elasticity decreased with altitude, effectively mitigating the adverse effects of reducing growth on λ (Andrello et al., 2020). Similarly, in the case of a vegetation gradient, the attenuation of λ due to low juvenile survival in high vegetation plots is potentially offset by its low elasticity, resulting in the minute LTRE contribution of juvenile survival to the overall decline in λ (Fig. 4). Thus, decreases in λ in plots with higher vegetative coverage can be attributed to alterations in both vital rates and their corresponding elasticities.

Flowering reproduction has been deemed limited in demographic significance in alpine plants, such as *P. farinosa*, due to the high juvenile mortality in high-altitude environments. Instead, adult survival has been identified as a critical factor contributing to population persistence, partly because many alpine plant species engage in clonal reproduction under barren conditions (Silvertown et al., 1993; Stöcklin and Bäumler, 1996; Weppler et al., 2006). In the case of *P. farinosa*, plants produce heterostylous flowers that limit selfing and rarely reproduce clonally (Arnold and Richards, 1998; Lindborg and Ehrlén, 2002). Increased vegetative coverage was associated with reduced flowering probability and its negative LTRE contribution to λ, suggests that reduced flowering probability plays a role in deteriorating λ (Fig. 2 and Fig. 3). In alpine plants conducting flowering reproduction, vital rates in relation to flowering reproduction need to be considered as a potential factor influencing population viability under changing environments.

4.2. *Negative effect of interspecific competition on survival and flowering probability of P. farinosa*

The field-based demographic study demonstrated a decline in both the survival and flowering probability of *P. farinosa* as the surrounding vegetation coverage increased, suggesting the potential adverse effects of neighboring plants on the performance of *P. farinosa*. Nevertheless, there are alternative explanations for these observations. For example, the micro-environmental conditions under which *P. farinosa* coexists with other plant species may not be optimal for its growth, leading to compromised survival rates and flowering probabilities. To further explore this, a growth chamber experiment was conducted, in which *P. farinosa* was grown with *S. hakusanensis* in a single pot. The results showed that the coexistence of *P. farinosa* with *S. hakusanensis* led to lower survival rates and

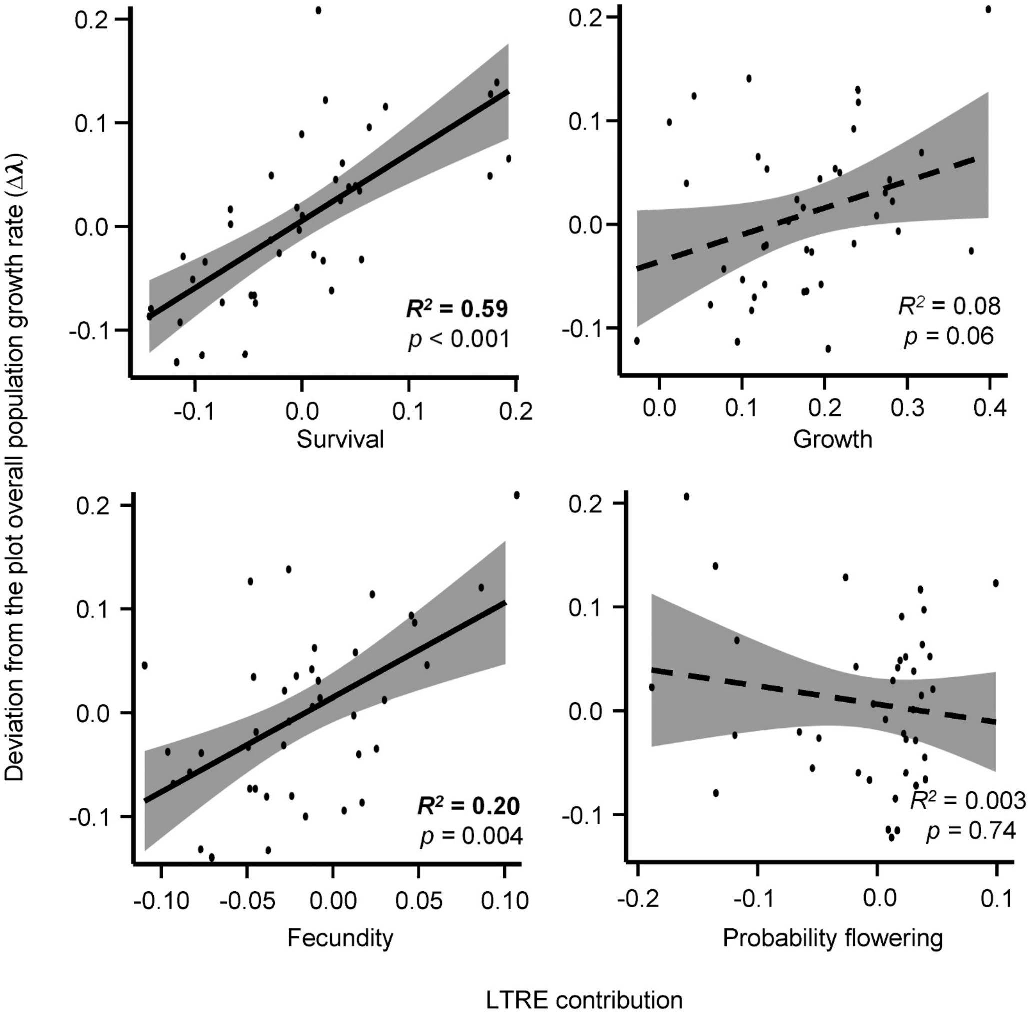

Fig. 5. Correlations between variation in population growth rate (λ) and variation in the LTRE contribution of vital rates. Separate analyses were conducted for each life stage. Spearman's correlation coefficients were calculated, and correlations with statistical significance ($P < 0.05$) by permutation test are represented by solid trend lines.

reduced flowering probability compared to those with other *P. farinosa* plants (Fig. 6). We acknowledge that the growth-chamber experiment applied competition treatments using a single species and evaluated the consequences of competition at a relatively early stage of the plant life cycle. With such limitation, however, the results are consistent with field observations, suggesting that neighboring vegetation, including *S. hakusanensis,* likely has a competitive interaction imposing constraints on the survival and flowering probability of *P. farinosa* in field environments.

In high-altitude environments with cold temperatures and strong winds, coexistence with other plant species often facilitates plant performance by providing wind protection, soil moisture conservation, or elevated air temperatures, which can potentially enhance community productivity (Bertness and Hacker, 1994; Carlsson and Callaghan, 1991). However, both field observations and growth chamber experiment consistently indicated that the current neighboring vegetation at the study sites had adverse effects on the vital rates and population growth rate of *P. farinosa*. Interspecific competition has been reported in other alpine plant species. Belowground competition for nutrients can reduce the growth, survival, and fertility of plants by consuming the available resources (Brooker, 2006; Casper and Jackson, 1997). In rosette-forming plants like *Primula* species, height and litter accumulation of surrounding vegetation can affect survival, floral display, and growth by limiting light availability or altering soil nutrients (Ågren et al., 2006; Ehrlén et al., 2005; Endels et al., 2007; Wehn and Johansen, 2015). Since both below- and aboveground competition likely affect the performance of *P. farinosa*, more refined manipulative studies are needed to identify the competitive mechanism affecting the vital rates of *P. farinosa* in field environments.

Environmental conditions, such as temperature, often influence the outcomes of interspecific competition (Brooker and van der Wal, 2003; Shepard et al., 2021). Leaf growth of *S. hakusanensis* increased under the elevated temperature treatment (Fig. S6); therefore, we initially anticipated that the stimulated growth of *S. hakusanensis* might have a more pronounced negative effect on the performance of *P. farinosa*. Notably, our analysis did not detect any statistically significant interaction between competition and

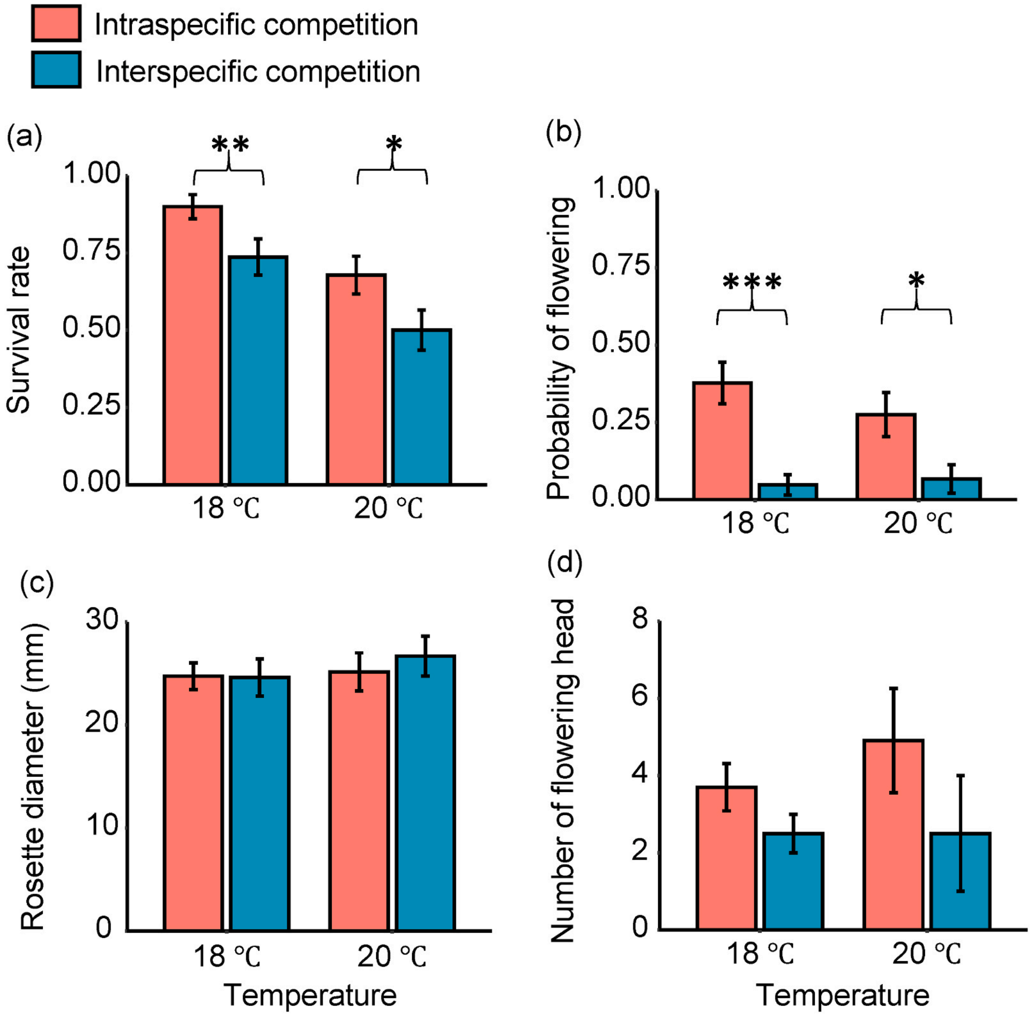

Fig. 6. Effect of competition and temperature treatments on vital rates of *P. farinosa*. Vital rates were measured at the end of the experimental period. The asterisks are the results of the Bonferroni *post-hoc* analyses. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

temperature (Table S4), suggesting that the adverse effects of competition were consistent regardless of the temperature treatment. Considering that our growth-chamber study was conducted for only eight months under two temperature regimes, it remains possible that the competition effect could vary with temperature in a long-term study with varying temperatures.

In conclusion, our results support the hypothesis that competitive interaction is a determining factor influencing the population persistence of alpine plant species (Brooker, 2006; Dullinger et al., 2012; Nomoto and Alexander, 2021). In addition to the negative effect of increasing temperature on survival (Jeong et al., 2021), higher neighboring vegetation can decrease survival and the probability of flowering, which consequently deteriorates λ of *P. farinosa* populations. If climate change increases the competitive ability of the current surrounding vegetation (Brooker and van der Wal, 2003) or if novel, strongly competitive plant species expand from lower altitudes (Nomoto and Alexander, 2021), it likely pose a new threat to *P. farinosa* in its current habitats. Since the elasticities of vital rates also change with vegetation coverage, altered mean values and elasticities of vital rates should be considered when assessing the effects of competitive interactions on population persistence.

CRediT authorship contribution statement

Yong-Chan Cho: Writing – review & editing, Validation, Resources, Methodology, Conceptualization. **Hyungsoon Jeong:** Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eunsuk Kim:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The authors thank D.Y. Lee and H.G. An for their help in conducting annual censuses and demographic analyses. This study was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (NRF-2021R1I1A2047635) and Korea National Arboretum (Project No. KNA1–2–26, 16–4).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02973.

References

Ågren, J., Fortunel, C., Ehrlén, J., 2006. Selection on floral display in insect-pollinated *Primula farinosa*: effects of vegetation height and litter accumulation. Oecologia 150, 225–232.

Alexander, J.M., Diez, J.M., Levine, J.M., 2015. Novel competitors shape species' responses to climate change. Nature 525, 515–518.

Andrello, M., de Villemereuil, P., Carboni, M., Busson, D., Fortin, M.J., Gaggiotti, O.E., Till-Bottraud, I., 2020. Accounting for stochasticity in demographic compensation along the elevational range of an alpine plant. Ecol. Lett. 23, 870–880.

Arnold, E., Richards, A., 1998. On the occurrence of unilateral incompatibility in *Primula* section Aleuritia Duby and the origin of *Primula* scotica Hook. Bot. J. Linn. Soc. 128, 359–368.

Bates, D.M., 2010. lme4: Mixed-effects modeling with R. Springer, New York.

Benton, T.G., Grant, A., 1999. Elasticity analysis as an important tool in evolutionary and population ecology. Trends Ecol. Evol. 14, 467–471.

Bertness, M.D., Hacker, S.D., 1994. Physical stress and positive associations among marsh plants. Am. Nat. 144, 363–372.

Bret-Harte, M.S., García, E.A., Sacré, V.M., Whorley, J.R., Wagner, J.L., Lippert, S.C., Charpin III, F.S., 2004. Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. J. Ecol. 92, 635–647.

Broadbent, A.A., Bahn, M., Pritchard, W.J., Newbold, L.K., Goodall, T., Guinta, A., Snell, H.S., Cordero, I., Michas, A., Grant, H.K., 2022. Shrub expansion modulates belowground impacts of changing snow conditions in alpine grasslands. Ecol. Lett. 25, 52–64.

Brooker, R.W., 2006. Plant–plant interactions and environmental change. N. Phytol. 171, 271–284.

Brooker, R., van der Wal, R., 2003. Can soil temperature direct the composition of high arctic plant communities? J. Veg. Sci. 14, 535–542.

Carlsson, B.A., Callaghan, T.V., 1991. Positive plant interactions in tundra vegetation and the importance of shelter. J. Ecol. 973–983.

Casper, B.B., Jackson, R.B., 1997. Plant competition underground. Annu. Rev. Ecol. Syst. 28, 545–570.

Caswell, H., 2000. Matrix population models. Sinauer, Sunderland, MA.

De Kroon, H., Van Groenendael, J., Ehrlén, J., 2000. Elasticities: a review of methods and model limitations. Ecology 81, 607-618.Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature climate change 2, 619-622.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nat. clim. change 2, 619–622.

Easterling, M.R., Ellner, S.P., Dixon, P.M., 2000. Size-specific sensitivity: applying a new structured population model. Ecology 81, 694–708.

Ehrlén, J., Syrjänen, K., Leimu, R., Begona Garcia, M., Lehtilä, K., 2005. Land use and population growth of *Primula veris*: an experimental demographic approach. J. Appl. Ecol. 42, 317–326.

Ellner, S.P., Rees, M., 2006. Integral projection models for species with complex demography. Am. Nat. 167, 410–428.

Endels, P., Jacquemyn, H., Brys, R., Hermy, M., 2007. Reinstatement of traditional mowing regimes counteracts population senescence in the rare perennial *Primula vulgaris*. Appl. Veg. Sci. 10, 351–360.

Franco, M., Silvertown, J., 2004. A comparative demography of plants based upon elasticities of vital rates. Ecology 85, 531–538.

Griffith, A.B., 2017. Perturbation approaches for integral projection models. Oikos 126, 1675–1686.

Hambler, D.J., Dixon, J.M., 2003. *Primula farinosa* L. J. Ecol. 91, 694–705.

Hegland, S.J., Jongejans, E., Rydgren, K., 2010. Investigating the interaction between ungulate grazing and resource effects on *Vaccinium myrtillus* populations with integral projection models. Oecologia 163, 695–706.

HilleRisLambers, J., Harsch, M.A., Ettinger, A.K., Ford, K.R., Theobald, E.J., 2013. How will biotic interactions influence climate change–induced range shifts? Ann. N. Y. Acad. Sci. 1297, 112–125.

Jeong, H., Cho, Y.-C., Kim, E., 2021. Differential plastic responses to temperature and nitrogen deposition in the subalpine plant species, *Primula farinosa* subsp. *modesta*. AoB Plants 13, plab061.

Jeong, H., Cho, Y.-C., Kim, E., 2022. Site-specific temporal variation of population dynamics in subalpine endemic plant species. Sci. Rep. 12, 19207.

Jongejans, E., Jorritsma-Wienk, L.D., Becker, U., Dostal, P., Mildén, M., De Kroon, H., 2010. Region versus site variation in the population dynamics of three short-lived perennials. J. Ecol. 98, 279–289.

Lennartsson, T., Oostermeijer, J.G.B., 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. J. Ecol. 451–463.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., Grenouillet, G., 2020. Species better track climate warming in the oceans than on land. Nat. Ecol. Evol. 4, 1044–1059.

Lindborg, R., Ehrlén, J., 2002. Evaluating the extinction risk of a perennial herb: demographic data versus historical records. Conserv. Biol. 16, 683–690.

Maldonado-Chaparro, A.A., Blumstein, D.T., Armitage, K.B., Childs, D.Z., 2018. Transient LTRE analysis reveals the demographic and trait-mediated processes that buffer population growth. Ecol. Lett. 21, 1693–1703.

Merow, C., Dahlgren, J.P., Metcalf, C.J.E., Childs, D.Z., Evans, M.E., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R., McMahon, S.M., 2014. Advancing population ecology with integral projection models: a practical guide. Methods Ecol. Evol. 5, 99–110.

Metcalf, C.J.E., McMahon, S.M., Salguero-Gómez, R., Jongejans, E., 2013. IPM pack: an R package for integral projection models. Methods Ecol. Evol. 4, 195–200.

Morris, W.F., Ehrlén, J., Dahlgren, J.P., Loomis, A.K., Louthan, A.M., 2020. Biotic and anthropogenic forces rival climatic/abiotic factors in determining global plant population growth and fitness. Proc. Natl. Acad. Sci. 117, 1107–1112.

Nomoto, H.A., Alexander, J.M., 2021. Drivers of local extinction risk in alpine plants under warming climate. Ecol. Lett. 24, 1157–1166.

Pepin, N., Bradley, R.S., Diaz, H., Baraër, M., Caceres, E., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M., Liu, X., 2015. Elevation-dependent warming in mountain regions of the world. Nat. Clim. Change 5, 424–430.

Sanczuk, P., De Lombaerde, E., Haesen, S., Van Meerbeek, K., Luoto, M., Van der Veken, B., Van Beek, E., Hermy, M., Verheyen, K., Vangansbeke, P., 2022. Competition mediates understorey species range shifts under climate change. J. Ecol. 110, 1813–1825.

Shepard, I.D., Wissinger, S.A., Greig, H.S., 2021. Elevation alters outcome of competition between resident and range-shifting species. Glob. Change Biol. 27, 270–281.

Sheth, S.N., Angert, A.L., 2018. Demographic compensation does not rescue populations at a trailing range edge. Proc. Natl. Acad. Sci. 115, 2413–2418.

Silvertown, J., Franco, M., Pisanty, I., Mendoza, A., 1993. Comparative plant demography–relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J. Ecol. 465–476.

Stöcklin, J., Bäumler, E., 1996. Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. J. Veg. Sci. 7, 45–56.

Stubben, C., Milligan, B., 2007. Estimating and analyzing demographic models using the popbio package in R. J. Stat. Softw. 22, 1–23.

Suh, M.-S., Oh, S.-G., Lee, Y.-S., Ahn, J.-B., Cha, D.-H., Lee, D.-K., Hong, S.-Y., Min, S.-K., Park, S.-C., Kang, H.-S., 2016. Projections of high resolution climate change for South Korea using multiple-regional climate models based on four RCP scenarios. Part I: surface air temperature. Asia-Pac. J. Atmos. Sci. 52, 51–169.

Theurillat, J.-P., Guisan, A., 2001. Potential impact of climate change on vegetation in the European Alps: a review. Clim. Change 50, 77–109.

Villellas, J., Doak, D.F., García, M.B., Morris, W.F., 2015. Demographic compensation among populations: what is it, how does it arise and what are its implications? Ecol. Lett. 18, 1139–1152.

Wehn, S., 2009. A map-based method for exploring responses to different levels of grazing pressure at the landscape scale. Agric., Ecosyst. Environ. 129, 177–181.

Wehn, S., Johansen, L., 2015. The distribution of the endemic plant *Primula scandinavica*, at local and national scales, in changing mountainous environments. Biodiversity 16, 278–288.

Weiss, N., 2015. Package 'wPerm'.

Weppler, T., Stoll, P., Stöcklin, J., 2006. The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant *Geum reptans*. J. Ecol. 94, 869–879.

Wilsey, B.J., Polley, H.W., 2003. Effects of seed additions and grazing history on diversity and productivity of subhumid grasslands. Ecology 84, 920–931.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A., Guisan, A., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol. Rev. 88, 15–30.

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., 2020. Forest microclimate dynamics drive plant responses to warming. Science 368, 772–775.