Weather-driven demography and population dynamics of an endemic perennial plant during a 34-year period

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Abstract

1. Increased anthropogenic influence on the environment has accentuated the need to assess how climate and other environmental factors drive vital rates and population dynamics of different types of organisms. However, to allow distinction between the effects of multiple correlated variables, and to capture the effects of rare and extreme climatic conditions, studies extending over decades are often necessary.

2. In this study, we used an individual-based dataset collected in three populations of *Pulsatilla vulgaris* subsp. *gotlandica* during 34 years, to explore the effects of variation in precipitation and temperature on vital rates and population dynamics.

3. Most of the observed conspicuous variation in flowering among years was associated with differences in precipitation and temperature in the previous summer and autumn with a higher incidence of flowering following summers with high precipitation and low temperatures. In contrast, climatic variables had no significant effects on individual growth or survival.

4. Although the weather-driven variation in flowering had only moderate absolute effects on the population growth rate, simulated persistent changes in average precipitation and temperature resulted in considerable reductions in population sizes compared with current conditions. Analyses carried out with subsets of data consisting of 5 and 10 years yielded results that strongly deviated from those based on the full dataset.

5. Synthesis. The results of this study illustrate the importance of long-term demographic monitoring to identify key climatic variables affecting vital rates and driving population dynamics in long-lived organisms.

**KEYWORDS**
climate change, demography, flowering, integral projection model, population dynamics, precipitation, *Pulsatilla*, vital rates
1 | INTRODUCTION

A fundamental question in ecology is how different abiotic and biotic environmental factors influence the distribution and abundance of species (Krebs, 1972). In recent years, the importance of this question has been accentuated due to increased anthropogenic influence on climate and other aspects of the environment. Key tasks for ecologists are therefore to assess how different environmental ‘drivers’ affect the dynamics of populations, and to predict human-induced changes in distribution and abundance. While demographic models often treat temporal variation in vital rates of individuals (e.g., growth, reproduction and survival) as stochastic, that is caused by variation in unknown factors and modelled by using observed variation, many of the current changes in the environment are directional (Ehrln & Morris, 2015). Predicting how future changes in environmental conditions will influence population dynamics of different organisms therefore requires that we identify the causal relationships between vital rates and explicit environmental drivers.

Most demographic assessments of the effects of climatic factors on population dynamics are based on studies typically performed over relatively short time periods. In a review of the effects of biotic, abiotic and anthropogenic forces on plant population growth rates, only four of 33 studies that had assessed the effects of climatic factors covered more than 10 years, and only one covered more than 20 years (Morris et al., 2020). This is problematic because it means that there will often not be sufficient information to accurately identify relationships between climatic variables and vital rates and population growth rate (Teller et al., 2016). In addition, many effects of climatic variables are difficult to investigate experimentally in a realistic way (Ehrln et al., 2016). Long-term studies are therefore often necessary to identify the factors that have a large impact on population dynamics, and to capture the effects of rare and extreme conditions. Long-term studies are also needed to detect nonlinear effects of climatic factors, such as optimal growing temperature or moisture conditions, which have been shown to be important for the population dynamics of several plant species (Dahlgren et al., 2016; Diez et al., 2014; Doak & Morris, 2010; Merow, Latimer, et al., 2014). Moreover, more than one third of plant species are classified as very rare and many of them grow in areas where the climate has been very stable for a long time (Enquist et al., 2019), meaning they might be poorly adapted to withstand the effects of climate change. Yet, there is still little information about how climate affects population dynamics of rare plants.

In this study, we used 34 years of data on climate and demography in three populations of a rare, endemic long-lived plant, *Pulsatilla vulgaris* subsp. *gotlandica*, to investigate how variation in precipitation and temperature among years influence vital rates and population growth rates, and to forecast the effects of changes in climate. The study species grows in drought-exposed habitats, and exhibits a conspicuous among-year variation in flowering. Rare endemic plants with a low dispersal ability, like the study species, often depend on microclimatic refugia and are likely to be particularly vulnerable to changes in temperature and precipitation (Enquist et al., 2019; Krause et al., 2015; Ulrey et al., 2016). At the same time, it may take considerable time before changes in climate are evident as reductions in the population sizes of long-lived plants. We addressed the following four specific questions:

1. How does among-year variation of vital rates depend on precipitation and temperature during summer and autumn? Based on the study plants that grow in areas which are exposed to severe summer droughts, we hypothesized that precipitation during the summer and autumn should be positively related to reproduction, survival and growth of individuals in the following year, and that the effects of temperature during the same period should be negative.

2. What is the effect of among-year variation in climatic conditions on population growth rate? Based on the observed slow turn over of individuals, we hypothesized that variation in climate should have relatively small effects on population growth rate compared to previously reported effects of environmental variables.

3. How will changes in climate affect future population sizes? Based on the above, we hypothesized that the effects of climate change on population sizes should be important, but only become evident after a relatively long period of time.

4. How does the duration of the study influence our ability to assess the effects of climatic factors on population growth rates? We predicted that the length of most existing plant demographic studies, that is <10 years, is likely to yield estimates that deviate from those based on longer time series.

2 | MATERIALS AND METHODS

2.1 | Study system

*Pulsatilla vulgaris* is a European hemicryptophyte. The subspecies *Pulsatilla vulgaris* subsp. *gotlandica* (Johanss.) Zämelis & Paegle is endemic to the island of Gotland in the Baltic Sea, where it occurs uncommonly in the SE part at low altitudes (maximum 30–35 m a.s.l.) in well-drained limestone areas with thin soil. The known population sizes and distribution of the taxon have increased since it was first collected in 1910 (Johansson, 1912; Peterssson, 2009). It is classified as vulnerable in the IUCN Red List of threatened species. The habitats are open to semi-open with scattered pine trees and junipers with transitions to light-open pine forests with a very low tree layer. Average annual temperature in the area is 7–8°C and total annual precipitation is 500–600 mm.

Old individuals are often tufted with several apices of the vertical rhizome. The stem is unbranched with a maximum of two stems from each apex. Flowers are terminal and solitary with a flowering period from mid-April up to the second half of May. Main pollinators are bees, especially bumblebees and the seed set
in other taxa within the genus is pollen limited (Kratochwil, 1988; Widén & Lindell, 1995). Basal leaves develop during and after anthesis. The feathery achenes develop during early summer and usually fall within 1 m distance from the plant (Lindell, 2007; Tackenberg, 2003; Tackenberg et al., 2003). Rarely, specimens with dissected sepals occur. The longest distance found between specimens sharing this deviating trait is 22 m which suggests that the dispersal ability is relatively poor (Lindell, 2007). Previous studies have not found any indication of inbreeding depression in the study populations (Lindell, 1998; T. Lindell, pers. obs. but see Wagenius et al., 2010). No permanent seed bank exists and the achenes start to lose their viability after about 1 year (Lindell, 2001; Wells & Barling, 1971). At the study sites, it takes at least a decade from germination to the first flowering event of individuals (Lindell, 2001). Most of the established plants included in the study in 1985 were still alive in 2018. A previous study with this species found that the life expectancy for 10-year-old plants was between 27 and 50 years (Edelfeldt et al., 2019). The genus is favoured by moderate grazing and initial phases of overgrowth but performance deteriorates at later stages of overgrowth (DiLeo et al., 2017; Hensen et al., 2005; Kalliovirta et al., 2006; Lindell, 2001, 2007; Walker & Pinches, 2011).

2.2 | Demographic data

Demographic data were collected each year during the period 1985–2018 in three populations, varying in size (Table 1; Table S1). Five 1 m × 1 m plots within each population were permanently marked with iron rods in July 1985. In populations 1 and 2, plots were placed along a transect running through an area with a relatively high density of individuals. The position of the first plot and the orientation of the transect were picked randomly, with the prerequisite that all plots in the transect should contain at least one flowering individual. This design resulted in a broad range of plot densities, from 1 to 12 individuals per m². In population 3, where densities were overall lower, the position of each plot was selected to include flowering individuals. In all populations, all individuals within each plot were mapped with the help of a folding rule and fixed measuring scales on a 1-m² square. In population 3, remaining individuals found outside the plots were also mapped. Survival, size and number of flowers were recorded for all individuals in each year when basal leaves were fully developed, during the second half of July or the first half of August. Size was estimated by the maximum diameter of basal leaf rosette, consisting of one or several apices. All plots were carefully searched for seedlings in each year, and new appearing seedlings were recorded and included in the study. However, in the years 1996–1998, 2007–2009 and 2016–2017, only survival and flower number of established individuals were recorded in all plots. Size of recorded individuals in these years was estimated as the mean of sizes in the preceding and the following years. No permission was required for the fieldwork.

### Table 1

Characteristics of the three study populations of *Pulsatilla vulgaris* subsp. *gotlandica*, in terms of location, composition of the tree and shrub species, approximate area covered by the study species, estimated total population size (number of established individuals), number of individuals (established individuals and seedlings) followed in the study plots, number of vascular plant species, moss species (M) and lichen species (L) observed in the study plots, soil thickness in plots and year of first report.

| Population | Position (Latitude N; Longitude E) | Woody species | Population size | Area (m²) | Number of individuals followed | Number of species of vascular plants, mosses and lichens | Soil layer | First reported |
|------------|-----------------------------------|---------------|----------------|----------|-----------------------------|-----------------|-------------|---------------|
| 1          | 57°22′56.3″N, 18°40′33.7″E | Very light-open pine forest with scattered junipers | 1,500 | <4,000 | 544 | V = 26, M = 14, L = 10 | Thin | 1939 |
| 2          | 57°23′11.7″N, 18°43′41.8″E | Semi-open with scattered pine trees and junipers | 140,000 | 140,000 | 494 | V = 27, M = 13, L = 6 | Very thin, partly bare | 1910 |
| 3          | 57°26′11.8″N, 18°47′3.4″E | Semi-open with scattered pine trees and junipers | 150 | <100 | 192 | V = 31, M = 11, L = 7 | Thin | 1966 |
2.3 | Weather data

Information about monthly precipitation and temperature at the meteorological station closest to the study populations which had records covering the entire period 1984–2017, Hemse 25 km SW population 1, was obtained from SMHI (The Swedish Meteorological and Hydrological Institute). We used information about precipitation and temperature during the period June–October to examine effects on vital rates since this is the period of active growth and establishment, and the period during which flower buds for the following year are initiated in hemicryptophytes (Raunkiaer, 1907). We used the summed precipitation (mm) and average temperature (°C) for each month during the period June–October in each year in the analyses. Records of precipitation were complete, data regarding temperatures were missing from in total 7 months scattered over the study period of 34 years. Data for these months were imputed using data from the nearby weather station Visby airport situated about 45 km N Hemse and 40 km NW population 1, and a linear regression model of the relationship of the weather variables at the two stations ($R^2 = 0.89$).

The summed precipitation June–October during the investigated period varied between 163 and 441 mm. Average monthly temperatures ranged 5–7°C between years (June 11.4–18.8°C, July 14.2–19.6°C, August 13.0–20.2°C, September 9.4–15.3°C and October 4.7–11.2°C).

Information used for the simulations of population development under predicted climate change was downloaded from SMHI (www.smhi.se, 22 April 2021). These data were based on downscalings of nine different global climate models to the regional level, and on a scenario with a RCP (Representative Concentration Pathway) value below 4.5 which corresponds to low to moderate climate change. For the study area, increases in both mean precipitation and temperature have been predicted, but with small changes in variation among years (Persson et al., 2015).

2.4 | Data analysis

Size (standardized value of diameter of the basal leaf rosette, i.e. the difference between the observed value and the mean value, divided by the standard deviation), individual flower number and survival were modelled as functions of size in either the previous year (size and survival) or the same year (flower number), density (sum of the individual sizes per plot), summed precipitation (June–October) and average monthly temperature (June–October). Precipitation and temperature variables were standardized by subtracting the mean and divided by the standard deviation. Based on statistically significant effects on flower number of interactions of size, temperature and precipitation with population in a preliminary model analysing all populations together, we continued with separate analyses of each population (Table S2). Individual ID, year and plot were included as random effects (intercepts) to account for repeated measures and the spatial data structure. Models were also run with year as a fixed continuous variable to test whether any unmeasured directional environmental change affected the populations. All vital rate models were fit using generalized linear mixed effect models (GLMM) and the glmer function in R (Bates et al., 2015; R Core Team, 2019). We also fitted generalized additive mixed models using the gamm4 package (Wood & Scheipl, 2020), but no nonlinear effects were detected and we present the GLMM results.

Survival was modelled as a logistic regression (a binomial error distribution and logit link function). Size versus size the previous year (growth) was modelled as a linear regression (Gaussian error distribution and identity link function). Wald tests assuming the degrees of freedom equal the difference between number of observations and the number of model parameters were used to calculate p-values for effects on growth. Since these tests do not account for the random effects structure, they are liberal, but were still clearly not statistically significant. Flower number was modelled using a Poisson error distribution and log link function. Despite containing many zeros, there was no problem with overdispersion when using an ordinary Poisson error distribution based on that the ratio of residual deviance over degrees of freedom was close to 1 (1.03 in a model with pooled populations). Seedling establishment rate, describing the number of new seedlings produced per flower, was estimated per population and year as the number of observed new seedlings divided by the number of flowers in the previous year. Seedling sizes were not measured in the field but approximate seedling sizes were assigned based on leaf number.

2.5 | Population model

To assess the current trend in population growth and to investigate how among-year variation in precipitation and temperature influences on population growth, we included the regression models of vital rates as components in size-structured integral projection models (IPMs) following standard methods (Easterling et al., 2000; Ellner & Rees, 2006; Merow, Dahlgren, et al., 2014). Regression models without year as a fixed effect were used in these IPMs. An IPM is a structured population projection model where at least one state variable is continuous. It is similar to a matrix population model but in an IPM the discrete matrix is replaced by the continuous kernel. In practice, the kernel is often represented by a large matrix. In the IPM, number of flowers, survival probability and size the following year were modelled as functions of size, precipitation and temperature as in the regression analyses described above. These functions were combined to form the transition kernel of the IPM, $K$, and the model is

$$n_{t+1}(x') = \int_L^U K(x', x, z) n_t(x) \, dx,$$

where $n$ is a size distribution describing the population, $t$ is time (year), $x$ is size at time $t$ and $x'$ is size at time $t + 1$, $z$ is a vector of additional covariates (temperature and precipitation), $L$ and $U$ are the lower ($-1.272$)
and upper (7.038) bounds of possible sizes, respectively, and the kernel, $K$, is

$$K(x', x, z) = s(x, z)g(x', x, z) + f(x, z)p_2p_3(x'),$$

where $s$, $g$ and $f$ describe survival, growth and number of flowers which were estimated using the regression models described above (Table S3; $g$ was modelled as a normal distribution with the mean given by the predicted value and the standard deviation by the residual standard error of the regression: 0.315, 0.266 and 0.354, for populations 1–3 respectively). In addition, $p_2$ is the probability of one flower producing one established seedling, included in the model as the average value across years (1.05, 0.86 and 1.45, for populations 1–3 respectively), and $p_3$ is the size distribution of newly established seedlings, which was modelled as a normal distribution with data pooled across years (mean $=-1.080$, $SD = 0.118$). For analyses, the kernel was converted to a 200 $\times$ 200 matrix in accordance with the midpoint rule of integration (cf. Ellner & Rees, 2006).

### 2.6 Effects of temperature and precipitation on population growth rate

The deterministic population growth rate (the dominant eigenvalue of the matrix representing the IPM kernel) was calculated per population in a model where precipitation and temperature were set to their mean observed values. The elasticity (proportional sensitivity) of population growth rate to changes in the matrix elements representing the kernel was calculated by combining the dominant right and left eigenvectors of the entire discretized kernel (Morris & Doak, 2002). Matrix elements representing transitions from established plants to seedlings were then summed to represent total fecundity elasticity. Because the summed elasticity of all matrix elements equal 1.0, one minus fecundity elasticity equals the elasticity of survival-growth transitions.

To examine the effects of temperature and precipitation on population growth rate, we calculated the deterministic population growth rates also for kernels based on temperature and precipitation varying up to 3 $SD$ away from the mean for the vital rate where we identified statistically significant effects (i.e. only flower number). To further explore the effect of climate variation, deterministic population growth rates were compared with stochastic population growth rates, incorporating yearly variation in kernels. Stochastic growth rates were calculated using standard simulation methods of randomly selecting one of the yearly transition kernels for a large number of model iterations (100,000 iterations) and calculating the geometric mean annual growth rate (Rees & Ellner, 2009). The yearly kernels were specified by incorporating the random year effects from regression models for all vital rates that did not include the two fixed climate variables. There were no consistent effects of intraspecific density on vital rates (Table S4). We found significant effects on survival in two of the three populations, but these effects were in opposite directions. The results presented below are from models without density.

### 2.7 Effects of climate change on future population sizes

To examine how predicted changes in temperature and precipitation in the study area might affect future population sizes, we simulated responses in flower number and its effects on the growth of each population over the coming 50 years. Expected changes in climatic factors were based on average predictions for our study region by the national Swedish Meteorological and Hydrological Institute, where temperature and precipitation both increase linearly (by 9% and 10%, respectively, in the coming 50 years). There was no trend in increasing variation in this data, nor did we detect such trends over our study period (Breusch–Pagan statistic $= 0.0099$, $p = 0.92$ for precipitation, and Breusch–Pagan statistic $= 0.99$, $p = 0.22$ for temperature). In our simulations, we started from populations at a stable size distribution in an environment with the temperature and precipitation observed in our final study year. For each following simulated year, a new temperature and precipitation value was sampled from normal distributions with average values that increased as predicted across years, and with a constant variance. These values were incorporated into the flower number component of the IPM kernel, and the resulting IPM was used to predict annual population growth. We iterated the 50-year simulation 10,000 times. For more realistic predictions, we examined the combined effects of changes in precipitation and temperature, but we also simulated the effects of changes in one of the climatic factors at a time in order to assess the relative impact of each factor.

### 2.8 Length of time series

To assess how the length of the time series influenced the possibility to identify the relationships between climatic variables, and vital rates and population growth rates, and investigate if similar results could have been obtained with shorter time series, we made analogous regression analyses to those described above (for flower number since it was the only vital rate where we found statistically significant effects of climatic factors) but using 10,000 randomly drawn shorter subsets, 5, 10 and 20 years, of the data. We also randomly drew sets of consecutive years but results were similar to those with years drawn randomly (data not shown). We then compared the distribution of regression coefficients of precipitation and temperature on flower number with the values estimated using all data, and the 95% confidence intervals of these estimates. Finally, we calculated the deterministic population growth rates for kernels where the effects of precipitation and temperature on flowering were substituted by the values from the simulations with subsets of 5, 10 and 20 years. This was done for environments where either
precipitation or temperature was 1 SD higher than the observed mean over the entire study period, while the other climatic factor was at its observed mean.

3 | RESULTS

There was no trend in precipitation during the study period ($R^2 = 0.03, p = 0.35$), but there was a nonlinear relationship between year and temperature, with a strong increase in temperature during the first years of the study, followed by a stabilization (second-degree polynomial model: $R^2 = 0.479, p < 0.001$; Figure S1). Temperature and precipitation were not correlated during the study period ($R^2 = 0.00, p = 0.98$). There were no consistent effects of intraspecific density on any of the vital rates (Table S4).

3.1 | Effects of climatic factors and size on vital rates

In all three populations, flower number per individual fluctuated considerably between years, and was strongly positively correlated with precipitation during June–October in the previous year (Figure 1; Table S3; Figure S2). Flower number was also negatively correlated with temperature in the previous year in all populations, although the relationship was not statistically significant in population 3 (Figure 1; Table S3; Figure S2). Individual size was positively correlated with flower number in the same year in all three populations (Table S3). Models including also a fixed effect of year suggested that trends in unmeasured factors over the study period did not influence observed correlations with weather variables (Table S5). Year as a fixed factor had a significant negative effect only in population 2. The effect of temperature was not significant in models with year as a fixed factor in this population, but models including either year or temperature had a similar fit. The effect of the temperature × precipitation interaction on the number of flowers was not significant in any population ($p > 0.4$ in all cases).

We detected no effects of climatic variables on either growth or survival in any of the populations (Table S3). In all three populations, size in 1 year was strongly positively correlated with size in the next year and with survival. Results were similar for models with and without year as a fixed factor (Table S3; Table S5).

3.2 | Effects of climatic variables on population growth rate

Higher precipitation and lower temperatures were associated with higher population growth rates (Figure 2a,b). Increases in precipitation over the investigated range were associated with
acceleratory increases in deterministic population growth rate, in particular in populations 1 and 3 (Figure 2a). Decreasing temperature had a similar but weaker effects on population growth rate (Figure 2b). Differences in effect sizes among populations were partly driven by differences in the elasticity of population growth rate to reproduction (Population 1 = 0.052, Population 2 = 0.010 and Population 3 = 0.054). Observed variation in precipitation and temperature around their mean values had only small effects on long-term growth rates, as evident from the similarity between the stochastic population growth rates and the deterministic population growth rates at average temperature and precipitation but there was still substantial variation among years (stochastic vs. deterministic population growth rate; Population 1: 0.999 vs. 1.002; Population 2: 0.987 vs. 0.988; Population 3: 0.975 vs. 0.987). The 95% confidence intervals of the stochastic growth rate calculated as the 2.5th and 97.5th percentiles of simulated yearly growth rates were 0.777–1.264, 0.770–1.161 and 0.822–1.097, for populations 1–3 respectively.

3.3 | Future population development in response to climate change

Simulations for the forthcoming 50 years suggested that predicted increases in temperature had a negative effect on population sizes, while increases in precipitation had a positive effect (Figure 3). Simultaneous increases in temperature and precipitation resulted in populations sizes that were intermediate between those predicted after changes in only one of the factors, and were closer to the predictions with no change in climate. Predicted development under scenarios of changes in climate also differed among populations. Populations 2 and 3 were predicted to decrease, both in scenarios with no change in climate and in scenarios with predicted increases in either precipitation or temperature or both. For population 1, simulations indicated a more complex pattern with a strong increase in population size in a scenario with a predicted increase in precipitation only, and smaller increases in scenarios with no change in either precipitation or temperature or with simultaneous increases in both factors. In a scenario with predicted increases in temperature only, population size decreased.

FIGURE 2 Deterministic population growth rates at precipitation levels (a) and temperatures (b) up to 3 SD away from the mean during the study period. Shaded areas represent the uncertainty in population growth rate based on the 95% confidence intervals of the climate parameters.

FIGURE 3 Simulated development of population size for three populations of Pulsatilla vulgaris subsp. gotlandica over the next 50 years under predicted scenarios of climate change. Green solid lines show population size per year when both precipitation and temperature are increasing, with green-shaded areas representing the 95% confidence intervals. Lilac dashed lines show population size per year with an increase in precipitation only. Orange dash-dotted lines show population size per year with an increase in temperature only. Blue dotted lines show population size per year with levels of precipitation and temperature from 2019 and onwards held constant.

3.4 | Effects of study duration

Models of flower number using subsets of data consisting 5 and 10 randomly selected years resulted in estimated effects of precipitation
and temperature that often strongly deviated from those yielded using the full dataset in all populations (Figure 4). Only when using 20-year subsets, effects were more similar to those estimated using the full dataset. The incorporation of the regression coefficients estimated using subsets of the data into IPM showed that also predictions of the deterministic growth rate were strongly affected by the number of years used to estimate the effects of climate variables (Figure 5).

4 | DISCUSSION

Our results suggest that weather conditions, in terms of precipitation and temperature during the period June–October, are driving the observed large variation among years in flowering in *Pulsatilla vulgaris* ssp. *gotlandica*. The short-term effect of weather-induced variation in flowering on population growth rate was relatively small, but simulations indicated that expected changes in climate can still have important long-term effects on population viability in this endemic herb. From a methodological perspective, the results indicate that investigations spanning over several decades increase the likelihood to correctly assess the effects of climatic variables on plant population dynamics over a broad range of conditions.

Concurrent with our hypothesis, variations in precipitation and temperature were identified as important drivers of the observed among-year variation in flowering. The strong effects of precipitation on the probability of individuals to flower are not fully understood. However, in our study species, flowering stems are initiated during summer and autumn the previous year, and it is likely that precipitation during this period is positively correlated with resource accumulation, which in turn influence flower initiation. Likewise, higher temperatures with increased evaporation during the same period are likely to affect flowering negatively due to increased drought stress. A long-term study of *Fumana procumbens* found similar positive effects of increasing precipitation on flowering, but also positive effects of increasing temperature (Dahlgren et al., 2016). The difference in response to temperature between this species and our study species might be related to morphology and differences in water availability at their respective sites. In the perennial herb *Astragalus scaphoides*, among-year variation in flowering is linked to variation in precipitation and the ability to accumulate carbohydrate stores (Crone et al., 2009; Tenhumberg et al., 2018).

In our study system, summer temperature and precipitation influenced population growth rates through strong effects on fecundity while we found no effects on growth or survival. This is in contrast to what has been found in most previous studies. Morris et al. (2020) reviewed 33 plant demographic studies which had examined the effects of one or several climatic variables on vital rates and population growth rates. Almost all of these studies found the effects of among-year variation in climate on growth and/or survival and no study found effects on only fecundity. It is also important to note that in long-lived plants, where the sensitivity of population growth rate to changes in growth and survival is usually markedly higher than the sensitivity to fecundity, relatively large negative effects on fecundity can be balanced by relatively small positive effects on growth or survival. For example, in the long-lived subalpine herb *Helianthella quinquenervis*, earlier snowmelt was associated with increased flower stalk abortion, but this did not contribute strongly to negative effects on population growth rates as the sensitivity of population growth rate to fecundity was low (Iler et al., 2019). Instead, the negative effects of an earlier snowmelt on population growth rate occurred mainly through effects on survival. The fact that climate only influenced fecundity in our long-lived study species implies that the negative effects of climate change on population size are likely to become apparent only after considerable time.
Our finding that weather conditions strongly affected reproduction but not growth and survival is consistent with that individuals strive to minimize the effects of environmental variation on total fitness by using stored resources primarily on vital rates with large effects on total fitness (Franco & Silvertown, 2004; Silvertown et al., 1993). Our long-lived study species has a large rhizome that gradually increases over time (Lindell, 2001), which should enable mature individuals to allocate stored resources to support growth and survival. The notion that individuals were able to minimize fitness losses in response to unfavourable climatic conditions is also supported by that the effects of observed variation in precipitation and temperature on population growth rate were only moderate, in spite of the strong effects on flower number. An ability to buffer the effects of unfavourable environmental conditions on population growth rate through differential changes in vital rates has been documented in several perennial plants (e.g. Crone, 2016; Doak & Morris, 2010; Salguero-Gomez et al., 2012), although studies with other species have shown important effects of climatic variables on both vital rates and population growth (e.g. Dalgleish et al., 2011).

Despite the fact that the effects of weather variation on population growth rates were relatively modest, our simulations suggested that predicted increases in temperature and precipitation may have important effects on future population sizes. Moreover, in our study area, both temperature and precipitation are expected to increase, and according to our simulations, these changes will partly affect the study populations in different directions. Predictions of overall changes in the future population growth rates in response to climate change are thus difficult to make for our species. It is also true that differences in local environment imply that different populations will respond in different ways to changes in climate. In our study, population growth rates differed considerably among populations which might be associated with differences in soil thickness and vegetation composition that affect the water-holding capacity. In accordance, local environmental conditions were shown to be important for differences in the effects of a warmer climate on the growth rate of Dracocephalum austriacum populations (Nicolé et al., 2011), and similar conclusions have been drawn also in other studies of perennial plants (Jongejans et al., 2010; Sletvold & Ågren, 2015; Sletvold et al., 2013; Tye et al., 2018). Taken together, our results and previous studies illustrate that population-specific responses to climatic change might be common.

While the absence of significant effects of climatic factors on vital rates with a large effect on population growth rate resulted in relatively small effects on population growth rate in our study species, the lack of intraspecific density effects on vital rates in our study suggests the predicted negative effects of climate change are not likely to be compensated for by a release from negative density dependence when populations shrink. This is in contrast to several other perennial plants, where intraspecific density has been shown to affect population responses to climatic variation (e.g. Dahlgren et al., 2016; Ehrlén & Morris, 2015; Ramula & Buckley, 2009).

We conclude that the exceptional length of this study, covering extreme and also rare climatic conditions, allowed us to better assess the effects of climate variation on population viability under current conditions, to identify the vital rate underlying population responses and to provide more solid predictions of the long-term effects of climate change, than would have been possible using shorter subsets of data. The simulations carried out with subsets of data of up to 10 years yielded results that strongly deviated from those that were based on the full dataset. The fact that demographic studies assessing the effects of climatic drivers only rarely extends over more than 10 years (Morris et al., 2020) thus implies that our current knowledge about how climatic factors influence plant population dynamics...
is insufficient and that predictions of the effects of future climate change might be unreliable. Correctly identifying relationships between climatic conditions and vital rates and population growth rates depends on both the number of years and the accuracy of yearly estimates of rates. This implies that for a given number of years, relationships will be more accurately assessed if estimates of population growth rate are based on a larger number of individuals. However, it is unlikely that large sample sizes per year will substantially reduce the number of years needed to accurately assess relationships, and many years will still be needed to capture the effects of rare and extreme conditions.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHORS’ CONTRIBUTIONS
T.L. designed and conducted the field study; T.L., J.E. and J.P.D. conceived the study questions; T.L. and J.P.D. analysed the data; T.L. wrote the first draft of the manuscript and all authors contributed to revisions.

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The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13821.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.zpc86619d (Lindell et al., 2021).

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