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Author(s): Florence Nicolè, Johan P. Dahlgren, Agnès Vivat, Irène Till-Bottraud and Johan Ehrlén

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# Interdependent effects of habitat quality and climate on population growth of an endangered plant

Florence Nicolè<sup>1</sup>, Johan P. Dahlgren<sup>2\*</sup>, Agnès Vivat<sup>3</sup>, Irène Till-Bottraud<sup>4</sup> and Johan Ehrlén<sup>2</sup>

<sup>1</sup>Laboratoire BVpam, Université de Lyon, Université de Saint-Etienne, F-42000 Saint-Etienne, France; <sup>2</sup>Department of Botany, Stockholm University, SE-10691 Stockholm, Sweden; <sup>3</sup>Pôle Natura 2000, Campana 05600 Mont Dauphin, France; and <sup>4</sup>Laboratoire d'Ecologie Alpine, Université Joseph Fourier, 38041 Grenoble, France

## Summary

1. To predict the viability of populations, it is essential to clarify how performance depends both on large-scale environmental changes, such as climate warming, and on the local habitat. However, in spite of their potential importance, effects of interactions between large-scale environmental changes and the local environment on population viability have rarely been examined.

2. We investigated how population dynamics of the endangered alpine plant *Dracocephalum austriacum* depend on local habitat quality and climatic variation, as well as how effects of climate depend on local habitat. We used lasso regression shrinkage and integral projection models to identify effects on vital rates and population growth rates in seven populations over seven annual transitions.

3. Populations on steeper slopes had lower survival and stochastic population growth rate than populations on more gentle slopes. In years with low spring temperatures and high summer temperatures, survival and population growth rate were lower. In addition, the negative effects of high summer temperatures did depend on local habitat quality, being more negative in populations on steeper slopes.

4. Combining the net positive effects of high spring temperature and the net negative effects of high summer temperature on plant vital rates with predicted climate change over the next 30 years suggested that effects on *D. austriacum* would be relatively small.

5. *Synthesis.* Our results show that different aspects of a warmer climate may have opposing effects on populations, and that climatic effects may depend on local habitat quality. Such interactive effects should be accounted for when determining effects of large-scale environmental changes on population and community dynamics.

**Key-words:** climate change, *Dracocephalum austriacum*, global warming, integral projection model, local environment, plant population and community dynamics, slope, spatio-temporal variation, temperature

## Introduction

Linking environmental variation over time and space to individual performance and population dynamics is a central objective in ecology. Spatial variation in environmental factors may occur over many different scales and has been shown to influence population dynamics in many systems (e.g. Alvarez-Buylla 1994; Horvitz, Tuljapurkar & Pascarella 2005). Temporal variation in environmental factors may be important to population dynamics both in terms of long-term trends and short-term fluctuations. Sessile organisms, like plants, are

likely to be particularly vulnerable to temporal environmental variation because they are slow in tracking favourable conditions. Long-term environmental changes with potentially large impact on plant population viability include succession, global warming, altered land use and other human-induced habitat alterations. Short-term fluctuations in environmental factors shown to have substantial effects on plant population dynamics include flooding (Smith, Caswell & Mettler-Cherry 2005; Schleuning, Huaman & Matthies 2008) and other catastrophic events (Åberg 1992; Menges & Kimmich 1996; Pascarella & Horvitz 1998). Also, temporal variation in biotic interactions has been shown to have important effects on plant population dynamics (Horvitz, Tuljapurkar & Pascarella 2005; Maron & Crone 2006; Kolb, Ehrlén & Eriksson 2007). One important,

\*Correspondence author. E-mail: johan.dahlgren@botan.su.se

but little explored, aspect of temporal variation in the factors influencing population dynamics is that the amount of variation and the effects of this variation will often depend on local environmental conditions (Maschinski *et al.* 2006; Schleuning, Huaman & Matthies 2008; Davison *et al.* 2010).

Linking vital rates and population viability to key environmental factors is also important because long-term management of species will inevitably be associated with the management of environmental factors (Fieberg & Ellner 2001; Gotelli & Ellison 2006; Sutherland 2006). In a spatial context, demographic models that include environmental factors can be used to determine how habitat quality influences population viability (Dahlgren & Ehrlén 2009). Temporal variation is often included in population models in terms of stochastic variation among years. Linking among-year variation in population performance to environmental variation is likely to improve predictions of demographic models in many cases. For example, it enables exploration of the effects of climate change on population viability in a more direct way (cf. Maschinski *et al.* 2006; Jenouvrier *et al.* 2009; Jongejans *et al.* 2010; Jonzen *et al.* 2010). Lastly, effects of environmental changes such as global warming are likely to depend on local environmental conditions. Examinations of how interactions between temporal variation in climatic variables and local environmental conditions affect population dynamics are therefore of major importance to enhance predictions of future local population viability.

In this study, we investigated environmental effects on population growth rate of the endangered plant *Dracocephalum austriacum*, which in our study region remains as a few isolated and genetically differentiated relict populations in exposed alpine habitats (Bonin *et al.* 2007). We linked variation in population dynamics in seven populations over seven annual transitions to a set of local environmental factors as well as to variation in temperature and precipitation among years. We used the lasso regression shrinkage method to identify the environmental factors influencing vital rates. To examine how vital rate variation translates into differences in population growth rate, we used an extension of matrix models, Integral Projection Models (IPM; Easterling, Ellner & Dixon 2000; Ellner & Rees 2006). We asked three questions: (i) Can among-population variation in vital rates and population growth rate be linked to differences in habitat quality? (ii) Can differences in local population growth rates among years be linked to climatic variation? And (iii) do effects of climate depend on local habitat quality?

## Materials and methods

### STUDY SYSTEM

The Austrian Dragonhead (*D. austriacum* L., Lamiaceae) is a long-lived perennial plant occurring from the Pyrenees to the Caucasus, with scattered populations in Western Europe (Bensettiti *et al.* 2002). The plant is 20–50 cm high, with hairy stems and large blue-violet insect-pollinated flowers (3.5–5 cm in length). *Dracocephalum austriacum* does not spread clonally and seeds lack adaptations for dispersal. It usually occurs in habitat patches where competition

with other plants is low and competition with shrubs and trees may have a negative effect on performance (Olivier *et al.* 1995). *Dracocephalum austriacum* is listed as Vulnerable by the World Conservation Union (IUCN) and is protected under National, European and international legislation (Red List of French Endangered Flora, Habitats Directive, Bern Convention). Threats include pillaging, trampling and damage by grazing cattle (Bensettiti *et al.* 2002). Previous studies with this species have shown large population differences in adaptive genetic variation (Bonin *et al.* 2007) and positive correlations between population heterozygosity and stochastic population growth rate (Nicolè 2005). The present field study was carried out in 7 of the 15 known French populations of *D. austriacum*. The study populations occur in the subalpine zone (1250–2000 m a.s.l.) of the Alps, on exposed, xeric, stony grasslands or heaths, preferentially on calcareous, thin soils (Lauber & Wagner 1998). Populations vary widely in size, density, habitat characteristics and soil composition (see Appendix S1 in Supporting Information). The northernmost population, Bessans, experiences a mountain climate while the southernmost population, Reynier, experiences a Mediterranean climate.

### DATA COLLECTION

In each population, 2–4 permanent plots, initially comprising 60–79 established individuals per population, were censused annually. Population censuses were done at peak flowering (mid-June–mid-July) from 1999 to 2006 (except Bessans, see Appendix S1). Each individual was identified by a number and its location within the plot was recorded. Every year, all new seedlings were included in the study. For each individual, we recorded the state (dead, flowering or non-flowering), the height of the highest stem and the number of stems. Size was defined as the logarithm of the product of plant height and number of stems. Individual growth was defined as the difference in size between years.

We examined the effects of 12 local environmental factors on among-population variation in population dynamics, and the effects of temperature and precipitation on among-year variation. As we did not have a large enough sample size to simultaneously test the effects of all environmental variables, we restricted the final statistical analysis to five variables: soil nitrogen, ground slope, the angle of orientation of the slope (aspect), population density and latitude. In addition, we included genetic factors (heterozygosity) in the analyses because of previously documented effects (see Study system). Longitude, altitude, soil carbon content, carbon : nitrogen ratio, soil depth, vegetation composition and total population size were omitted because they were correlated with other variables or were considered less likely to affect population dynamics based on previous knowledge about the system. Total nitrogen concentration was measured in soil from five pooled samples (3–4 g each), homogeneously distributed in each permanent plot, that was dried and finely ground (500 µm). N quantities were measured with an Elementary Analyser Flash EA 1112 (ThermoElectron, Waltham, MA, USA; see Viard-Cretat *et al.* 2009 for a detailed protocol). Ground slope inclination at each individual was described by a semi-quantitative index ranging from 0 (flat, 0°) to 3 (very steep, over 45°), where levels 1 and 2 were judged in the field to be equally spaced between levels 0 and 3. The aspect of the slope was measured at the population level with a compass. Aspects ranged from NE (45°) to S (180°). Population density was calculated as the average of the yearly mean number of stems per square metre in permanent plots. Heterozygosity was estimated by genotyping 20 individuals per population with dominant AFLP molecular markers [amplified fragment length polymorphism,

see Bonin *et al.* (2007) for details concerning sampling and protocols], and assuming Hardy–Weinberg equilibrium. The Bayesian default method of the software AFLP-SURV was used to calculate the mean within-population expected heterozygosity (Vekemans 2002).

We correlated temporal variation in population dynamics to differences in temperature and precipitation. *Dracocephalum austriacum* grows in exposed locations in the subalpine area and based on our knowledge of the species, we expected that during the spring, water availability is usually sufficient and temperature limits growth, while during the summer, temperatures are higher and water is short in supply. We thus predicted that individual performance should be positively influenced by high temperatures in spring and unaffected, or possibly positively affected, by low precipitation in spring due to the negative correlation with light availability. In summer, performance should be negatively influenced by high temperatures and low precipitation, because both these factors may lower soil water content. We also expected that effects of environmental conditions in the spring should affect vital rates in the same year, whereas effects of environmental conditions in the summer should mainly affect vital rates the following year (censuses were performed in the middle of the growing season). Accordingly, we calculated four climate variables assumed to be important for population growth from year  $t$  to year  $t + 1$ : mean temperature and rainfall in the summer year  $t$  (mean over May, June, July and August, encompassing the entire growing season including fruit development), and mean temperature and rainfall in late spring in year  $t + 1$  (mean over May and June, between emergence and flowering). Weather conditions in May and June were included in both spring and summer measures because we expected conditions being favourable early in the season, i.e. high temperatures, to also increase the probability that plants suffer from drought later during the season. We used monthly temperature and rainfall data 1999–2006 from the meteorological stations closest to the respective populations: Embrun (6°30'12" E, 44°34'00" N) for Largentiere, Escoyères, Champcella and Reynier; Valjouffrey (6°01'06" E, 44°52'48" N) for Valsenestre and St. Christophe; and Challes-Eaux (5°58'30" E, 45°33'30" N) for Bessans (Météo-France data). Distances to the nearest meteorological station were 86 km for Bessans, 17 km for Champcella, 28 km for Escoyères, 23 km for Largentiere, 36 km for Reynier, 18 km for St. Christophe and 6 km for Valsenestre.

#### INTEGRAL PROJECTION MODEL

Integral projection models are similar to matrix population projection models, which simulate population growth over discrete time steps. They differ in that populations do not have to be divided into classes but state variables (size in this case) can be continuous (Easterling, Ellner & Dixon 2000). A general IPM can be expressed as:

$$n(y, t + 1) = \int_L^U [F(x, y) + P(x, y)]n(x, t)dx,$$

where  $x$  is state year  $t$ ,  $y$  is state year  $t + 1$ ,  $n$  is the population density function and  $L$  and  $U$  describe the range of possible states. Probability density functions of reproduction,  $F(x, y)$ , and state transition,  $P(x, y)$ , constitute the continuous projection kernel.

For *D. austriacum*, a function of individual growth, predicting future sizes based on the current size, was obtained by fitting a linear regression of size year  $t + 1$  on size year  $t$ . The distribution of future sizes was modelled as normally distributed with the residual standard error of the regression fit used as an approximation of the true stan-

dard deviation. Probability functions of survival of established individuals and of flowering were obtained by logistic regressions on size. The growth function was multiplied by the function of survival of established individuals to give the state transition function,  $P(x, y)$ . The function describing reproduction,  $F(x, y)$ , was the product of the size-dependent probability function of flowering, the mean number of seedlings in year  $t + 1$  per number of flowering individuals in year  $t$ , and a probability function of the seedling size distributions. The seedling size distribution in each population and each year was described by a normal distribution with the observed mean and standard deviation. Parameters of models for all *Dracocephalum* populations are summarized in Appendix S2. The R code used for the computer implementation of the model was based on the one provided in Ellner & Rees (2006).

We used the IPMs to calculate deterministic population growth rates for each year and population (as the dominant eigenvalue of the matrix representing the projection kernel,  $\lambda$ ). Stochastic growth rates ( $\lambda_{\text{stoch}}$ ) were calculated for each population as the geometric mean proportional change in population size over 10 000 model iterations, where one yearly projection kernel was randomly drawn for each iteration. To simulate effects of environmental factors and climate change in different local environments, we formulated an IPM of an average, hypothetical population where vital rates were estimated using mixed-effects regression models including plant size and environmental factors with an effect on growth rate as fixed effects. Stochasticity was included in this IPM as the yearly variation of intercept and slopes quantified by random effects in the regression models (cf. Rees & Ellner 2009). To take correlations of intercepts and slopes within and among vital rates into account in the IPM, random components of vital rate models were drawn for each transition utilizing Cholesky decomposition of the covariance matrix of all parameters, in the R package 'mvtnorm'.

#### STATISTICAL ANALYSES

To investigate which combination of environmental factors best described differences in vital rates and population growth rates among populations and years, we first determined which factors affected population growth rate by using the lasso method for parameter shrinkage and selection in regression models (Tibshirani 1996). On the individual level, we then fitted linear and generalized linear mixed-effects models of vital rates, including the variables found to be related to population growth rate.

Regression shrinkage methods using penalized estimation can be used to avoid overestimation when fitting models with few degrees of freedom (Witten & Tibshirani 2009). The lasso algorithm maximizes model fit under 'L<sub>1</sub> penalization', which can be seen as a cap on the sum of the absolute value of all coefficients in the model. In the lasso, some regression coefficients are frequently shrunk to zero, which means the method can be used for variable selection. The lasso is likely a more reliable tool for variable selection and estimation than best subset selection methods in cases with many parameters and small sample sizes, as is generally the case in analyses of among-population differences (Dahlgren 2010). We used the package 'penalized' in R 2.8.1 (R Development Core Team 2008) to fit lasso models of among-population variation in stochastic growth rates, with soil nitrogen, ground slope, aspect, population density, latitude and heterozygosity as candidate predictor variables. Optimal shrinkage was calculated by cross-validation. We also used the lasso to fit models of yearly variation in population growth rates. In these models, the candidate predictor variables were the four climate variables, the variables associated with differences in growth rate between populations

and all two-way interactions. Interactions between climate variables and environmental variables were included to test if climatic effects on population growth rate depend on local habitat characteristics.

Mixed-effects models of survival, growth and flowering were fitted using the 'lme' and 'glmmPQL' functions in the 'nlme' and 'MASS' R packages respectively. Populations and population-years were used as grouping variables to account for the structure of the environmental data. Intercepts and regression slopes for size and ground slope varied randomly. The random parameters were used to include yearly environmental variability in the IPMs. Due to convergence failures when fitting the statistical models, ground slope was only included as a fixed effect when determining yearly variation, and population was omitted as a grouping variable when testing the significance of factors. At the population level, we tested for environmental effects on yearly variation in seedling size and establishment. The regression models were simplified by omitting parameters with  $P > 0.5$  in Wald tests, to avoid overfitting. Interaction terms were tested first and if kept, all lower-level terms were also retained in the models. The resulting regression models, used for the IPM projections, included only parameters with  $P \leq 0.15$  and lower-level parameters. Further model simplification was not attempted because it has been found to reduce the reliability of predictions (Harrell 2001).

#### PREDICTING EFFECTS OF CLIMATE CHANGE

To simulate possible effects of a temperature increase on *D. austriacum*, we used a scenario of global warming suggested by the Intergovernmental Panel on Climate Change (IPCC). The scenario used, 'A1B', is based on assumptions of economic, demographic and technological development that would presumably lead to a relatively large temperature increase (a mean increase by 3.4 °C until 2080; Pachauri & Reinsinger 2007). Mean monthly temperatures simulated for the study region were obtained from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model data set (model CNRM CM3, grid point with mean latitude = 6.98° and longitude = 45°; Meehl *et al.* 2007). The predicted mean temperature increased linearly for both springs and summers (as defined in the Data collection section) and we fitted regression lines to the simulated data to determine the yearly mean spring and summer temperatures. The resulting temperatures were multiplied with the ratios of mean observed temperature in the study area to the predicted mean temperature, for the study years (0.61 for spring and 0.68 for summer). We also simulated scenarios with lower temperature increases (A2 and B1), but the results were similar and are not presented.

We assumed vital rates to be affected by temperature in accordance with the statistical analyses and projected future population sizes over 30 years from 2006. Simulations were iterated 20 000 times for hypothetical populations on the lowest, mean and highest slope inclinations. Variance in temperature was assumed to be the same as observed over the study period. However, recent climatic models for the study area predict that the variation in summer temperature and drought incidence will increase (Seneviratne *et al.* 2006). We therefore also examined effects of different levels of variation in summer temperature in additional simulations.

#### Results

Yearly long-term deterministic population growth rate ( $\lambda$ ) ranged from 0.52 to 1.29 (Fig. 1). In all populations,  $\lambda$  was below unity during at least one transition. Among-year variation in  $\lambda$

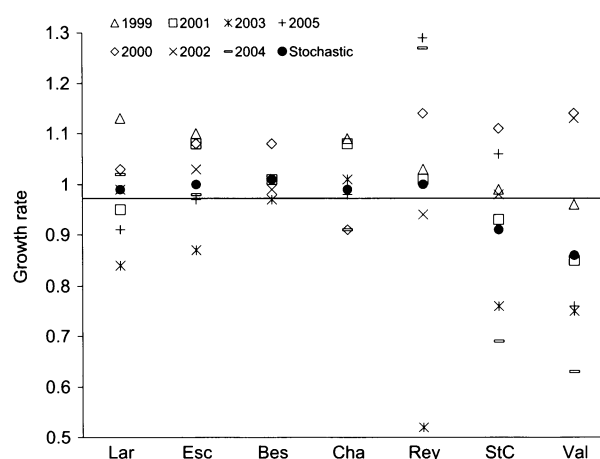
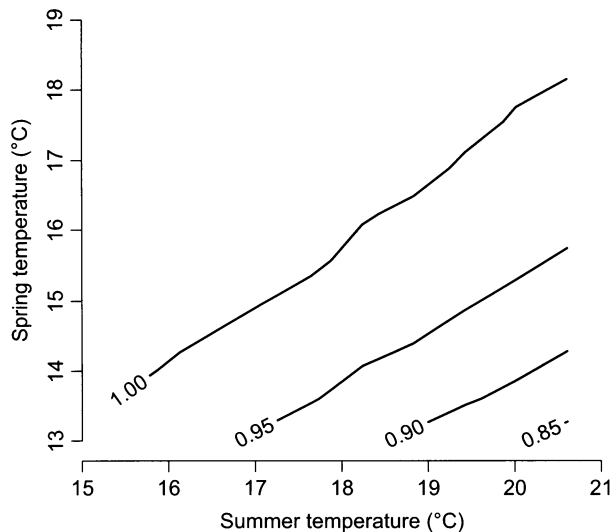


Fig. 1. Stochastic and yearly deterministic growth rate for each population of *Dracocephalum austriacum* over the census period (1999–2006). Populations are ordered with ground slope increasing from left to right. Lar = Largentiere, Esc = Escoyères, Bes = Bessans, Cha = Champcella, Rey = Reynier, StC = St. Christophe, Val = Valsenestre.

was higher than the variation among populations. Mean population growth rate was lowest (0.82) in 2003–2004, when there was a severe summer drought. The Reynier population, the only population that experiences a Mediterranean climate, showed the widest range of variation in  $\lambda$ , including both the lowest and highest values observed during the study. In this population, stochastic growth rate was 0.04 lower than the mean of yearly rates. For the six other populations, with lower temporal variation in population growth rates, stochastic rates were only slightly lower than means of yearly rates (arithmetic mean difference = 0.01). Stochastic growth rate was well below unity in the St. Christophe and Valsenestre populations, but close to unity in the remaining populations.

Environmental factors partly explained both spatial and temporal variation in population growth rate. Lasso regression models of relationships between spatial variation in environmental factors and stochastic population growth rates identified only a negative effect of ground slope ( $\lambda_{\text{stoch}} = 1.13 - 0.085 \times \text{slope}$ ). Eighty-two percent of the individuals in our study occurred on steep or very steep slopes (slope index 2 or 3). Mean observed slope indices for populations ranged from 1.65 to 2.59. Yearly population growth rate from year  $t$  to year  $t + 1$  was positively affected by spring temperature in year  $t + 1$  and negatively affected by summer temperature in year  $t$  (Fig. 2). We found no effect of precipitation. Importantly, however, higher summer temperatures had a more negative effect on population growth rate on steeper slopes, as shown by the negative effect of the interaction between summer temperature and slope ( $\lambda = 1.21 + 0.016\{\text{spring temp.}\} - 0.014\{\text{summer temp.}\} - 0.007\{\text{summer temp.} \times \text{slope}\}$ ; the main effect of slope was shrunk to exactly zero).

Regression models of vital rates showed that the negative effect of slope acted on population growth rate mainly via survival, but also via the probability of flowering of large individuals (see Table 1 for all environmental parameters included in



**Fig. 2.** Contour plot of the combined effects of observed spring and summer temperatures (°C) on stochastic population growth rate of *Dracocephalum austriacum*, predicted for a population on an average slope in an integral projection model with temperatures affecting vital rates as in Table 1.

the IPM, and Appendix S3 for graphical representations). The positive effect of spring temperature acted mostly via growth; growth of large individuals increased with increasing spring temperature. There was also a marginally significant positive effect of spring temperature on survival, but no effect on flowering. The negative effects of summer temperature occurred mainly via survival, while there was a positive effect of summer temperature on flowering probability. The negative interactive effect of slope and summer temperature acted on population growth rate via survival of larger individuals (Fig. 3). No associations were found between climatic or local environmental factors and seedling establishment or seedling size.

With no change in the temperature regime, *D. austriacum* populations on mean slopes were predicted to decrease by 25% over 30 years. The predicted increases in temperature over 30 years based on the IPCC data were 1.0 °C for springs and 1.1 °C for summers. Simulating the effects of changes in spring and summer temperatures suggested that population sizes of *D. austriacum* on average should decrease slightly less than with unchanged temperatures (resulting in a decrease by 23% over 30 years). This was because the positive effects of increasing spring temperatures balanced the negative effects of increasing summer temperatures on population growth rate. Effects of increasing temperatures differed only very little between simulations of populations of different slope, but populations on steep slopes were predicted to not be affected by increasing temperatures in the long run, while populations on gentle slopes were predicted to be positively affected (the trajectories for steep slopes in Fig. 4 converge the last years of simulation, whereas the lines for gentle slopes continually diverge). Increasing variation in summer temperature had a relatively small effect on the average population trajectory (increasing the SD by 25% for the whole simulated time period

**Table 1.** Mixed-effects regression models of effects of climate and local environment on vital rates, used for parameterization of an integral projection model for *Dracocephalum austriacum* (see text). Survival and flowering were modelled with logistic regression and growth was modelled with linear regression. All parameters were ln-transformed and centred prior to analysis. Parameters with  $P > 0.50$  based on Wald  $t$ -tests were removed unless higher-level interactions were present. Parameters with  $P < 0.05$  are in bold print

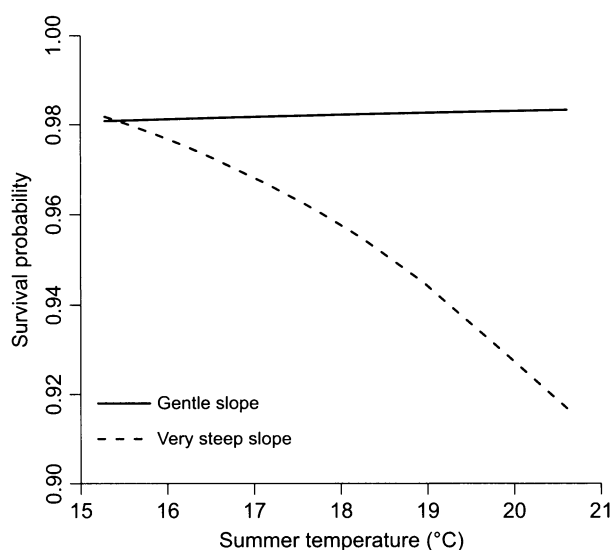
	Estimate	$t$	$P$	Random effect
<b>Survival</b>				
Intercept	2.57	12.17	< 0.001	SD = 0.43
Size	<b>0.93</b>	<b>12.95</b>	<b>&lt; 0.001</b>	SD = 0.18
Slope	-0.26	-1.63	0.10	
Spring temperature	5.11	1.89	0.066	
Summer temperature	<b>-2.91</b>	<b>-0.95</b>	<b>0.035</b>	
Size × Slope	-0.14	-1.55	0.12	
Size × Summer temperature	0.32	0.35	0.72	
Slope × Summer temperature	-3.08	-1.45	0.15	
Size × Slope × Summer temperature	<b>-2.32</b>	<b>-1.96</b>	<b>0.0498</b>	
<b>Growth</b>				
Intercept	0.13	4.79	< 0.001	SD = 0.000
Size	<b>0.78</b>	<b>26.76</b>	<b>&lt; 0.001</b>	SD = 0.059
Spring temperature	-0.37	-0.96	0.34	
Summer temperature	-0.62	-1.45	0.15	
Size × Summer temperature	-0.53	-1.49	0.14	
Size × Spring temperature	<b>0.64</b>	<b>2.02</b>	<b>0.044</b>	
<b>Flowering</b>				
Intercept	-0.35	-1.07	0.28	SD = 1.64
Size	<b>1.33</b>	<b>13.32</b>	<b>&lt; 0.001</b>	SD = 0.33
Slope	<b>0.36</b>	<b>1.97</b>	<b>0.048</b>	
Summer temp	<b>8.59</b>	<b>2.35</b>	<b>0.023</b>	
Size × Slope	<b>-0.35</b>	<b>-3.01</b>	<b>0.003</b>	

corresponded to an increase of approximately 0.1% in mean temperature, for a population on a mean slope).

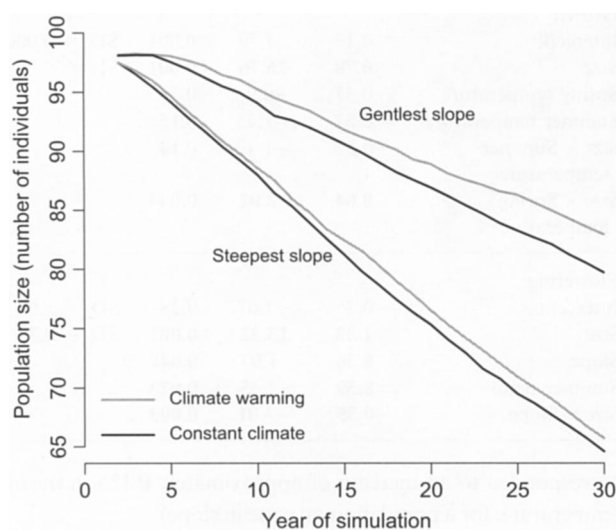
## Discussion

Our results with the endangered alpine plant species *D. austriacum* show that both local environmental factors and climatic variation among years influence population dynamics, and that the effects of climate depend on local habitat quality. The fact that, under environmental conditions similar to those observed during the study, average populations were predicted to decrease underscores the vulnerability of the few isolated relict populations of this species that remain in the Alps (Bensettiti *et al.* 2002; Bonin *et al.* 2007).

Of the studied environmental variables, only ground slope influenced among-population variation in stochastic population growth rates; inclination in ground slope was negatively related with  $\lambda_{\text{stoch}}$  and the two declining populations occurred on the steepest slopes. Effects of slope inclination on population growth acted mainly via survival in *D. austriacum*.



**Fig. 3.** Predicted effect of observed summer temperature (°C) on probability of survival of large individuals (75th percentile of observed sizes) on gentle slopes (slope index 1), and very steep slopes (slope index 3), based on the regression model in Table 1.



**Fig. 4.** Simulated trajectories of *Dracopis austriacum* populations on the gentlest and the steepest observed population-level ground slope inclinations, experiencing observed spring and summer temperatures and during increasing temperature due to climate warming. The projections are based on relationships between vital rates and environmental factors (see Table 1), as well as IPCC predictions of future temperatures (see Materials and methods). Lines are median population sizes from 20 000 model iterations.

Topography has been found to influence adult mortality also in other species in the European Alps (Dullinger, Dirnböck & Grabherr 2004). In this study, we did not experimentally investigate the mechanism behind the relationship between population growth rate and slope. However, it is likely to be at least partly associated with differences in soil thickness and water-retaining capacity. Uprooting rate is also likely to increase with increasing slope because of decreasing soil thickness as well as shifting rocks and earth. Uprooting was observed after shifting

earth in Valsenestre and St. Christophe (F. Nicolè, personal observation). An alternative mechanism is that, effects on plant performance are mediated by soil nutrient concentrations. In our study, nitrogen to carbon ratio was significantly correlated with slope (Spearman  $\rho = -0.79$ ,  $P = 0.048$ ). However, the fact that total nitrogen concentration had no effect on population growth rate suggests that effects via uprooting and drought are more important.

We examined the effects of genetic variation on differences in growth rate between populations, because a previous study with this species documented a positive relationship between heterozygosity and population viability (Nicolè 2005). The lack of a significant relationship in the present study that included also environmental factors suggests that the correlation between heterozygosity and population viability may have been caused by environmental covariation. At this point, it is thus unclear whether genetic diversity affects population dynamics in this species.

Among-year variation in population growth rate was synchronized between populations and correlated with spring and summer temperature but not with precipitation. The results suggested that warm summer temperatures had negative effects on population growth rate, acting mainly through survival. In particular, the exceptionally warm summer in 2003 resulted in very low population growth rates. Several previous studies with perennial plants have documented negative effects of summer drought on population growth rates (e.g. Riba, Pico & Mayol 2002; Davison *et al.* 2010; Toräng, Ehrlén & Ågren 2010). A study with *Centaurea corymbosa*, a perennial herb occurring in the same geographical region and in similar habitats, did, however, not reveal any negative effects of summer droughts (Freville *et al.* 2004). In our study, we found that flowering probability increased the year after a warm summer, counteracting the negative effects of survival on population growth rate. In general, such opposed effects on different vital rates may lead to smaller effects of climatic and environmental factors on population growth rate than anticipated (Doak & Morris 2010). Furthermore, lasso regression models suggested that warm spring temperatures had positive effects on population growth rate. This effect of spring temperature was acting mainly by increasing growth. A likely explanation for this effect is that plants have sufficient supply of water early in the season and that increased temperatures therefore have mainly positive effects on plant metabolism. Other authors have suggested that milder springs will enhance population growth rate by extending average annual growing seasons in the subalpine and alpine belts (Jolly *et al.* 2005), as well as in other regions (Myneni *et al.* 1997; Parmesan 2006).

The location of our studied populations at the edge of the distribution range of the species could be expected to make them particularly sensitive to climatic variation. However, as a result of counteracting negative effects of higher summer temperatures and positive effects of higher spring temperatures, the estimated average effect of future climate warming predicted by IPCC scenarios on the population growth rate of *D. austriacum* was relatively small. These results illustrate that



global warming may have both positive and negative effects on species performance and that the net consequence for population viability depends on how sensitive population growth rate is to the different effects.

An important finding in our study was that effects of climate on population growth rate were partly dependent on local habitat quality. Populations on steeper slopes suffered from more negative effects of high summer temperatures on plant survival than populations on gentle slopes. Negative plant responses to high summer temperatures may be explained by increased evapotranspiration and associated declines in soil moisture (Penuelas *et al.* 2004). This negative effect of high summer temperatures is probably more severe at steeper slopes because these have thinner soils resulting in a lower water-retaining capacity. The effect of the interaction between summer temperature and slope observed in our study suggests that the effects of future climate warming may differ among sites. In our simulations, however, net effects of climate warming on *D. austriacum* population trajectories were very small and it would take much larger temperature increases to make the interaction effect important over short to moderate time spans. Furthermore, plant populations at steep slopes may possibly be able to adapt to increased temperatures in the long term. Several other studies with plants have shown that effects of climatic variation may depend on local environmental conditions (e.g. Schleuning, Huaman & Matthies 2008; Davison *et al.* 2010). Taken together, these results illustrate that interactions with the local abiotic environment should constitute an important part of predictions of population viability under climate change.

Using IPMs to link environmental and climatic factors to population growth rates via vital rates, together with the lasso regression shrinkage method to identify the best environmental predictors, constitutes a powerful method to understand population dynamics and predict the effects of environmental changes on population growth. This is particularly true for systems where the number of factors potentially influencing population dynamics is large relative to the number of populations or years monitored. Our results with the endangered alpine plant species *D. austriacum* illustrate that the factors influencing spatial and temporal variation in population dynamics may be interdependent. Future studies should therefore preferably investigate causes of spatial variation in effects of large-scale environmental changes such as global warming, to better understand the effects on population and community dynamics.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Characteristics of the seven studied populations of *D. austriacum*.

**Appendix S2.** Parameters of the integral projection model for each *D. austriacum* population.

**Appendix S3.** Plots of the fitted relationships in Table 1.

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