

Climate warming alters effects of management on population viability of threatened species: results from a 30-year experimental study on a rare orchid

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Abstract

Climate change is expected to influence the viability of populations both directly and indirectly, via species interactions. The effects of large-scale climate change are also likely to interact with local habitat conditions. Management actions designed to preserve threatened species therefore need to adapt both to the prevailing climate and local conditions. Yet, few studies have separated the direct and indirect effects of climatic variables on the viability of local populations and discussed the implications for optimal management. We used 30 years of demographic data to estimate the simultaneous effects of management practice and among-year variation in four climatic variables on individual survival, growth and fecundity in one coastal and one inland population of the perennial orchid *Dactylorhiza lapponica* in Norway. Current management, mowing, is expected to reduce competitive interactions. Statistical models of how climate and management practice influenced vital rates were incorporated into matrix population models to quantify effects on population growth rate. Effects of climate differed between mown and control plots in both populations. In particular, population growth rate increased more strongly with summer temperature in mown plots than in control plots. Population growth rate declined with spring temperature in the inland population, and with precipitation in the coastal population, and the decline was stronger in control plots in both populations. These results illustrate that both direct and indirect effects of climate change are important for population viability and that net effects depend both on local abiotic conditions and on biotic conditions in terms of management practice and intensity of competition. The results also show that effects of management practices influencing competitive interactions can strongly depend on climatic factors. We conclude that interactions between climate and management should be considered to reliably predict future population viability and optimize conservation actions.

Keywords: climate change, *Dactylorhiza lapponica*, demography, global warming, land-use change, long-term monitoring, mowing, plant population dynamics, regional variation, rich fen

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Introduction

Climate change is currently considered a major threat to biodiversity, and numerous species extinctions and range shifts are predicted in future scenarios (Thomas *et al.*, 2004; Pereira *et al.*, 2010). The changes in abiotic conditions induced by climate change can have direct effects on organisms, e.g., in terms of altered vital rates caused by changes in temperatures and water availability (e.g., Nicolè *et al.*, 2011; Salguero-Gómez *et al.*, 2012). However, climate change may also influence performance indirectly, via interactions with other species (Fox *et al.*, 1999; Suttle *et al.*, 2007; van de Pol *et al.*,

2010). Under extreme conditions, like in deserts and arctic and alpine environments, direct effects are likely to dominate (Nicolè *et al.*, 2011; Jenouvrier *et al.*, 2012; Salguero-Gómez *et al.*, 2012), whereas in many other habitats, indirect effects via changes in competitive relationships should be more important (Brooker, 2006; Adler *et al.*, 2012). Moreover, both direct and indirect effects of climate change on organisms may vary among habitats, because effects are the result of interactions between large-scale changes in climate and local habitat conditions (Brook *et al.*, 2009; Nicolè *et al.*, 2011; Bütof *et al.*, 2012; Peery *et al.*, 2012). From a conservation perspective, this implies that land use and management currently favouring a certain species may become less favourable in a changing climate. Consequently, management actions designed specifically to preserve rare or threatened species will need to be modified, and

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modifications need to be tailored to local conditions. To examine how the negative effects of climate change on biodiversity can be mitigated by additional conservation efforts or by modified land use practices, we therefore need to simultaneously evaluate effects of climate and management at the scale of populations.

Climatic variation may affect many parts of a plant's life cycle, including germination (Levine *et al.*, 2008), flowering dynamics (Inouye *et al.*, 2002; Pfeifer *et al.*, 2006a) and survival probability (Simons *et al.*, 2010). Climatic effects might differ among vital rates and effects can even be in opposed directions (Hutchings, 2010; Nicolè *et al.*, 2011). Likewise, a specific management practice may increase some vital rates and lower others (Sletvold *et al.*, 2010). Assessment of effects over the entire life cycle is therefore necessary to determine impacts of climate change on population dynamics and viability. In many habitats, climate warming is also likely to increase plant growth and thereby intensify competition. Management experiments manipulating the intensity of competition will therefore be useful for separating direct effects of climate warming from indirect effects due to changed competitive interactions.

To reliably predict long-term viability and design optimal management under climate change, it is essential to link climatic factors and management practices to vital rates of individuals (Dahlgren & Ehrlén, 2009, 2011; Toräng *et al.*, 2010). This should preferably be done on a spatial scale capturing important local habitat characteristics, because the impact of variation in climate and land use is likely to differ among geographic regions (Bütöf *et al.*, 2012), and vary along gradients in latitude, altitude and oceanity. Similarly, it is important to cover a temporal scale that allows potential interactive effects of climate change and management to be quantified. Although management decisions are increasingly based on quantitative predictions from matrix models (Ehrlén *et al.*, 2005; Crone *et al.*, 2011), such predictions, in turn, are often based on short-term data from a single site. To assess the threats that changes in climate pose to biodiversity and to identify appropriate management actions, long-term demographic data from multiple sites is likely to be particularly valuable (Morris *et al.*, 2008; Jongejans *et al.*, 2010).

Here, we ask how climatic variation affects vital rates and population viability directly in a focal plant species, and if direct effects are counteracted by indirect effects via competing species. We also examine how the net effects of climatic variation depend on the local habitat, and predict how climate warming will impact plant population growth in the near future. Lastly, we discuss if management plans for threatened species need to be adjusted as a consequence of climate change.

To address these questions, we use two long-term datasets on the rare orchid *Dactylorhiza lapponica*. We link variation in vital rates in non-managed versus traditionally mown plots to variation in temperature, precipitation and length of the growing season over three decades in populations from one oceanic and one more continental climatic region in Norway. In this traditionally managed system of the boreal region, land use practices, such as mowing and grazing, typically decrease competition. Based on this and on knowledge of the ecology of *D. lapponica*, we hypothesized that: (i) Temperature and length of the growing season limits population growth, whereas water availability is likely to be sufficient throughout the growing season and negatively affect plant performance through waterlogging in years with high rainfall; (ii) Climatic factors with a positive influence on vital rates have stronger effects in mown plots where competition is reduced, whereas climatic factors with a negative influence on vital rates have stronger effects in unmanaged plots where competition is more intense; and (iii) The positive effects of increasing temperature are stronger in the inland population where growing seasons are shorter, and the negative effects of increasing precipitation are stronger in the coastal population where summer rainfall is higher. In addition, we examine if there are temporal trends in the climatic variables at both sites, and use climatic trends and estimated relationships between climatic variables and vital rates to predict future population growth rate.

Material and methods

Study species

Dactylorhiza lapponica (Laest. ex Hartm.) Soó is a nonclonal, tuberous orchid limited to Fennoscandia, Scotland and alpine areas in Central Europe (Delforge & Harrap, 2006). It has been included in the *D. russowii/traunsteineri* complex, but recent studies recognize it as a distinct taxon (Pedersen, 2010). In Fennoscandia, *D. lapponica* is found in open lawn communities of extremely rich (calcareous) fens and springs in the boreal vegetation zones (Moen, 1990, 1999; Moen *et al.*, 2012). Individuals emerge aboveground approximately 2 weeks after snow melt, usually in late May to early June. Vegetative individuals form a leaf rosette that is fully grown by the end of June, whereas the rosette of flowering individuals continue to grow during the flowering period, which lasts 3–4 weeks from mid-late June. Flowering individuals produce a single inflorescence with approximately 3–15 flowers without any nectar production. In August, leaves wither and above-ground structures decay, and the new replacement tuber grows roots and a new shoot which emerges next spring. Flower primordia are formed in autumn (Øien & Pedersen, 2005). The minute seeds mature in August, and are spread by a passive ballistic mechanism. Seeds are short-lived (<1 year) and the average field

germination probability is 11% (Øien *et al.*, 2008). The underground seedling stage is believed to last for a minimum of 1 year, as germination experiments suggest that the growing season in Scandinavia is too short to allow above-ground emergence as vegetative individuals during the first year after seed dispersal (Øien *et al.*, 2008). The first flowering event is estimated to occur at the earliest 5 years after germination (Øien & Moen, 2002).

Study areas

From 1981 to 2010, we collected demographic data in two nature reserves in central Norway; the coastal Tågdalen site (63°03'N, 9°05'E) and the inland Sølendet site (62°40'N, 11°50'E). Both areas are situated at the transition between the middle and northern boreal zone. The Tågdalen area has a markedly oceanic climate with on average a 5 day longer growing season compared with the Sølendet area, which is more continental (Table S1). Both areas are dominated by open fens, mixed with birch-wooded areas. Base-rich phyllites dominate the geology, and springs overflow the fens with calcareous water (pH > 7), resulting in large areas with extremely rich fen vegetation (cf. Moen *et al.*, 2012). Both areas were formerly used for haymaking, but this practice diminished in the 20th century, and ceased altogether around 1950. Traditionally, fens were scythed every second year.

The studied populations occupy sloping fens (3–8 degree of slope) with species-rich lawn communities dominated by *Carex* spp., *Molinia caerulea* and *Trichophorum cespitosum* in the field layer and *Campylium stellatum* and *Scorpidium cossonii* in the bottom layer. The mean field layer production (estimated based on the scythed biomass every second year) is 109 g m⁻² in both areas.

Mowing treatments

In both populations, mowing was reintroduced as a management practice in the mid-1970s. Permanent plots of 5 m × 2.5 m were established in localities with two or more plots per locality, with at least one mown and one control plot in each at the start of the experiment. Mown plots were scythed in August every second year, mimicking traditional use. Control plots have been left unmown since traditional use ceased. In this study we included data collected in six localities in the inland population (10 control and 12 mown plots) and in 12 localities in the coastal population (12 control and 6 mown plots).

Demographic data

Since 1981, all flowering individuals have been permanently marked and their positions inside the study plot were recorded. New individuals have thus been included in the monitoring from the year they were first observed flowering, and subsequently followed irrespective of reproductive status. We censused plots in early July each year, and noted plant flowering status and number of flowers. Vegetative plants were recorded in three separate classes; small (1–2

leaves with a total leaf area < 2 cm²), medium (2–3 leaves with a total leaf area 2–6 cm²) and large (2–4 leaves with total leaf area > 6 cm²) individuals. From 2004, the number of fruits produced was recorded in early August. Missing individuals that later reappeared were recorded as dormant. Individuals were considered dead the third consecutive year after last emergence, and mortality was assumed to occur in the first year of disappearance. It is uncertain whether dormancy (i.e., vegetative or prolonged dormancy, *sensu* Shefferson, 2011) exists in *D. lapponica*, as no tubers have been found in attempts to excavate missing individuals (Sletvold *et al.*, 2010). The absence of an individual may also reflect herbivory prior to the yearly census (A. Moen, D.-I. Øien; pers. obs.), representing the recovery period after damage (e.g., Gregg, 2011). However, the mechanism causing individuals to be missing at the time of the census does not affect the matrix model output.

Climatic data

The Norwegian Meteorological Institute provided spatially interpolated estimates of temperature and precipitation for both sites, with target elevations of 460 and 725 m above sea level (a.s.l.) for Tågdalen and Sølendet respectively. For Tågdalen, temperature and precipitation data recorded at Rindal station (5 km E, 231 m a.s.l.) were used, whereas snow cover data was estimated from recordings at Søvatnet station (22 km NE, 306 m a.s.l.). For Sølendet, we used precipitation and snow cover data recorded at Brekken station (3 km SE, 712 m a.s.l.) and temperature data recorded at Røros station (25 km SW, 628 m a.s.l.). Temperature estimations were performed with residual kriging, whereas triangulation with terrain adjustment was used to estimate precipitation (Tveito *et al.*, 2005).

We calculated monthly effective temperature sum (ETS) from a formula developed by Laaksonen (1979) for the boreal zone: $ETS = \sum_{m=a}^b T_m - 5^\circ$, where T_m is mean daily temperature, and a and b are the third day of the first and last snowfree, five day period with mean $T_m > 5^\circ\text{C}$ respectively. We defined the length of the growing season as the period between a and b . Precipitation data was aggregated to monthly sums.

Our aim in this study was to investigate how variation in temperature, precipitation and length of the growing season influenced variation in vital rates. To examine the hypothesized relationships, we calculated four climatic variables: spring temperature sum (from the start of the growing season to the end of June, covering the period from leaf emergence to flowering), summer temperature and summer rainfall sum (July and August, covering the period from flowering to withering of aboveground parts) and total length of the growing season. More specifically, we expected that high spring temperatures in year t positively affect size and fecundity in the same year, whereas high summer temperatures in year t positively affect survival and probability of growth from year t to $t + 1$ and flowering in year $t + 1$. We expected high summer precipitation in year t to negatively affect survival and probability of growth from year t to $t + 1$ and flowering in year $t + 1$. Finally, we expected that the length of the growing

season in year t is positively related to probabilities of survival and growth from t to $t + 1$ and flowering in year $t + 1$.

Statistical modelling and analyses

To examine the effects of climate and mowing on vital rates in year $t + 1$, we used generalized linear mixed models (GLMM; the `glmer` function in the `lme4` package in R 2.12.1; Bates *et al.*, 2011; R development core team 2011) including the four climatic factors (spring temperature year $t + 1$, summer temperature year t , summer precipitation year t , length of the growing season year t), mowing treatment (control vs. mown) and the interactions between climatic factors and mowing treatment. We also included life stage (small, medium, large) as a fixed factor. Year, locality, plot and individual identity (except in the model of survival) were included as grouping variables with random intercepts (i.e., random factors) to account for potential correlations among errors and for the fact that the fixed effects varied at different levels. Effects of the climatic variables (year level) and mowing treatment (plot level) on individuals could thus be analysed using the same statistical model. All vital rates were modelled separately for the two populations.

To limit model complexity, we excluded interactions among climatic variables, and between life stage and other factors. Variables and interactions in the full model were removed if this decreased model AIC (Akaike's Information Criterion). These model simplifications facilitated the interpretation of climatic and mowing effects when vital rates were included as components of the matrix models (see below). The subset models were stable, i.e., removing a variable had only minor effects on the remaining relationships (suggesting low collinearity).

Survival, state transition probability of surviving individuals (growth, stasis or shrinkage) and flowering probability were analysed with logistic regressions, whereas number of flowers (reproductive individuals) was analysed with Poisson regression. State transitions of surviving individuals were analysed in two steps using two dichotomous response variables. First, we analysed the probability of growth (grown/not grown). Second, we analysed the probability of stasis vs. shrinkage for individuals that had not grown. We used this two-step method rather than mixed effects ordinal logistic regressions because slightly different data were used (small individuals cannot shrink and large and flowering individuals cannot grow), and because the latter type of model cannot be fitted using standard GLMM packages such as `glmer`. Dormancy was included as a form of shrinkage in these analyses (reoccurrence was not seen as growth, as all dormant individuals emerged the year after). We regarded all flowering individuals as belonging to the largest size class, and thus treated observed transitions from smaller size classes to flowering individuals as growth followed by flowering. In analyses of flowering probability, only large vegetative individuals and flowering individuals were included.

We assumed that all relationships between vital rates and climatic variables were linear over the observed range. We tested this assumption by including second degree polynomial

terms for spring temperature, summer temperature and precipitation. Although some relationships were significantly curved, main trends were linear (determined visually from plots), and we chose to use linear models to limit the complexity and avoid convergence failure of the models. To improve convergence, all continuous predictor variables were standardized (to a mean of 0 and a variance of 1) prior to analyses.

For both populations, we constructed matrix population models with the classes: (i) dormant plants; (ii) small plants; (iii) medium sized plants; (iv) plants above the threshold size for flowering; and (v) seeds (Appendix S1). Transition probabilities were calculated from the regression models and combined with observed means of transitions not modelled using regressions. The latter were: the probability of reaching a certain class after dormancy; the probability of dormancy for small individuals (this was not included as shrinkage in the growth models due to low sample sizes); the probability of growing or shrinking two size classes, and; germination probability (2 years after seed production). Thus, effects of the climatic variables and the mowing treatment were included in the matrix models via the statistical models of survival, growth/stasis/shrinkage, flowering probability and flower production. For each population and mowing treatment, we calculated the asymptotic population growth rate, λ , which corresponds to the dominant right eigenvalue of each matrix. We estimated λ at the population mean value of all climatic factors. To quantify how each climatic factor affected population growth in a manner that simplified comparisons of effect sizes we calculated λ for each factor over the range of ± 2 standard deviations of observed values, while keeping all other factors constant.

The total effects of mowing treatment and climatic factors on population growth rate were decomposed into contributions from different life cycle transitions using LTRE (life table response experiment; Caswell, 2001) analyses. In LTRE analyses, the contribution of matrix elements to differences in population growth rate obtained from two (in this case) transition matrices is determined. This is done by first constructing a reference matrix (a matrix with all elements being the mean of the compared matrices) and a difference matrix (a matrix with the difference in each element). Sensitivity values for the reference matrix are then multiplied with the elements of the difference matrix. The sensitivity of a matrix element, α , is defined as $\delta\lambda/\delta\alpha$. In the present analyses, mown plots were compared with control plots, and matrices representing high vs. low levels of the climatic factors (mean ± 2 SD) in both mown and control plots were also compared.

Results

Mowing

Mowing every second year reduced mean population growth rate in both populations (Fig. 1). At mean value of all climatic factors, estimated population growth rates (λ) in control and mown plots were 1.01 and 0.99 in the coastal population, and 0.94 and 0.90 in the inland population respectively. In the coastal population, mowing

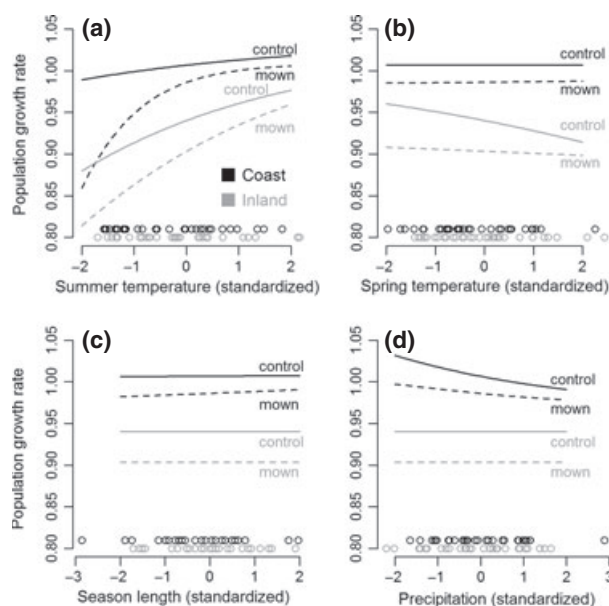


Fig. 1 Population growth rate of *Dactylorhiza lapponica* in relation to the climatic factors summer temperature (a), spring temperature (b), season length (c) and precipitation (d) in control (solid line) and mown (dashed line) plots in the coastal (black) and inland (grey) population. Circles are observed climatic values during the 30-year study period.

affected survival positively, but growth, flowering probability and flower production negatively (Table 1). LTRE-analyses showed that the decline in growth rate in mown plots was mainly caused by the reduction in fecundity (Fig. 2a). In the inland population, mowing reduced both survival and growth, but increased flowering probability (Table 1). At mean value of all climatic factors, the lower growth rate in mown plots was explained by reductions in survival and growth, and effects on small and medium sized individuals were most important (Fig. 2b).

Summer temperature

In both populations, growth rate increased with summer temperature the previous year, and the increase was stronger in mown plots compared with control plots (Fig. 1a). In the coastal population, variation across the range of observed summer temperatures had small effects on growth rate in control plots compared to in mown plots (0.99–1.02 vs. 0.85–1.00), whereas in the inland population, there was a considerable increase in population growth rate with summer temperature in both treatments (0.80–0.95 vs. 0.88–0.98). Population growth rate was more sensitive to summer temperature at low temperatures (Fig. 1a). The increase in population growth rate with summer temperature was caused by a positive effect on survival in both

populations, and also on growth and stasis in the inland population (Table 1). The stronger increase in population growth rate with increasing summer temperature in mown plots compared with control plots was due to treatment-dependent effects on survival in the coastal population, and on growth in the inland population (significant summer temperature \times treatment interactions; Table 1). In the coastal population, survival of small and medium sized plants made the largest contribution to the strong increase in population growth rate with summer temperature in mown plots, whereas all size classes contributed approximately evenly to the weaker increase in unmanaged plots (Table 1; Fig. 2c,d). In the inland population, temperature effects on growth of small and medium sized individuals made the largest contribution in both mowing treatments (Table 1; Fig. 2e,f). The particularly strong negative effect of mowing after cold summers in the coastal population was mainly explained by reduced growth in all size classes, and to some degree by lower fecundity (Fig. 2g). At high summer temperatures, the negative effects of mowing on growth and fecundity were almost balanced by the positive effect on survival, resulting in only minor effects on population growth rate (Fig. 1a).

Spring temperature

Population growth rate declined with spring temperature in control plots in the inland population (Fig. 1b). This decline was the result of reduced survival and growth (Table 1), and effects were similar in all life cycle stages (Fig. 2h). In the coastal population, growth rate did not vary with spring temperature in any treatment (Fig. 1b).

Length of the growing season

In mown plots in the coastal population, a long growing season increased the probability of growth and flowering in the following year (Table 1), resulting in a weak increase in population growth rate with increasing season length (Fig. 1c). In the inland population and in control plots in the coastal population, variation in length of the growing season had no effect on population growth rate (Fig. 1c).

Summer precipitation

Population growth rate was negatively related to summer precipitation in the coastal population, but not in the inland population (Fig. 1d). Precipitation reduced the probability of growth and increased the probability of shrinkage in the coastal population, and effects were

stronger in mown plots compared with control plots (significant precipitation \times treatment interactions; Table 1). Precipitation also reduced the number of flowers in both treatments (Table 1). In mown plots, a positive effect of precipitation on flowering probability (Table 1) counteracted the negative effects on other vital rates, leading to a weaker net effect of precipitation on population growth rate (Table 1, Fig. 1d). LTRE analyses showed that the negative effect on next year's flower production constituted the largest contribution

to the decline in growth rate with increasing precipitation in the control plots (Fig. 2i). In the mown plots, negative effects on growth and stasis contributed more to the decrease in population growth rate with precipitation.

Effects of climate change

Of the climatic factors that affected population growth rate, only summer temperature recordings showed any

Table 1 Generalized linear mixed model results of the effects of mowing (control vs. every second year), summer temperature, spring temperature, length of the growing season, summer precipitation and their interactions on vital rates in the coastal and inland populations of *Dactylorhiza lapponica*. Effects of life cycle stage (2 = medium, 3 = large) are also shown [estimates and statistical tests for these are in relation to stage 1 (the intercept)]. Models were estimated including the factors year, locality, plot and individual identity as grouping variables with random intercepts (data not shown)

Vital rate	Coastal population		Inland population	
	Parameter	Estimate \pm SE	Parameter	Estimate \pm SE
<i>Survival</i>	Intercept	3.12 \pm 0.24***	Intercept	2.19 \pm 0.22***
	Mowing	0.33 \pm 0.28	Mowing	-0.45 \pm 0.21*
	SumT	0.24 \pm 0.15	SumT	0.32 \pm 0.14*
	Stage 2	0.40 \pm 0.18*	SpringT	-0.16 \pm 0.14
	Stage 3	0.26 \pm 0.17	Stage 2	0.37 \pm 0.12**
	Mowing \times SumT	0.79 \pm 0.22***	Stage 3	0.25 \pm 0.11*
			Mowing \times SpringT	0.17 \pm 0.079*
<i>Growth</i>	Intercept	0.43 \pm 0.21*	Intercept	0.37 \pm 0.12**
	Mowing	-0.57 \pm 0.33	Mowing	-0.36 \pm 0.10***
	SumP	-0.098 \pm 0.12	SumT	0.17 \pm 0.10
	SeasonL	0.016 \pm 0.11	SpringT	-0.032 \pm 0.10
	Stage 2	-1.09 \pm 0.091***	Stage 2	-1.03 \pm 0.086***
	Mowing \times SumP	-0.46 \pm 0.13***	Mowing \times SumT	0.20 \pm 0.085*
	Mowing \times SeasonL	0.30 \pm 0.13*	Mowing \times SpringT	-0.21 \pm 0.090*
<i>Stasis</i>	Intercept	1.09 \pm 0.21***	Intercept	-0.92 \pm 0.79
	Mowing	-0.78 \pm 0.31*	Mowing	-0.037 \pm 0.13
	SpringT	-0.00071 \pm 0.12	SumT	0.18 \pm 0.093*
	SumP	-0.14 \pm 0.13	SpringT	-0.15 \pm 0.10
	Stage 3	-2.23 \pm 0.084***	SeasonL	-2.23 \pm 0.084*
	Mowing \times SpringT	0.30 \pm 0.14*	Stage 3	-1.50 \pm 0.076***
	Mowing \times SumP	-0.43 \pm 0.14**	Mowing \times SumT	-0.13 \pm 0.078
			Mowing \times SpringT	0.18 \pm 0.075*
<i>Prob. flow</i>	Intercept	3.26 \pm 1.24**	Intercept	0.41 \pm 0.21
	Mowing	-3.55 \pm 1.59*	Mowing	0.71 \pm 0.14***
	SumP	-0.031 \pm 0.12		
	SeasonL	-0.018 \pm 0.0096		
	Mowing \times SumP	0.35 \pm 0.16*		
	Mowing \times SeasonL	0.032 \pm 0.012**		
<i>No. flow</i>	Intercept	1.92 \pm 0.057***	Intercept	1.90 \pm 0.061***
	Mowing	-0.12 \pm 0.063		
	SumP	-0.12 \pm 0.034***		

Prob. flow = Probability of flowering, No. flow = Number of flowers.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$ based on Wald tests.

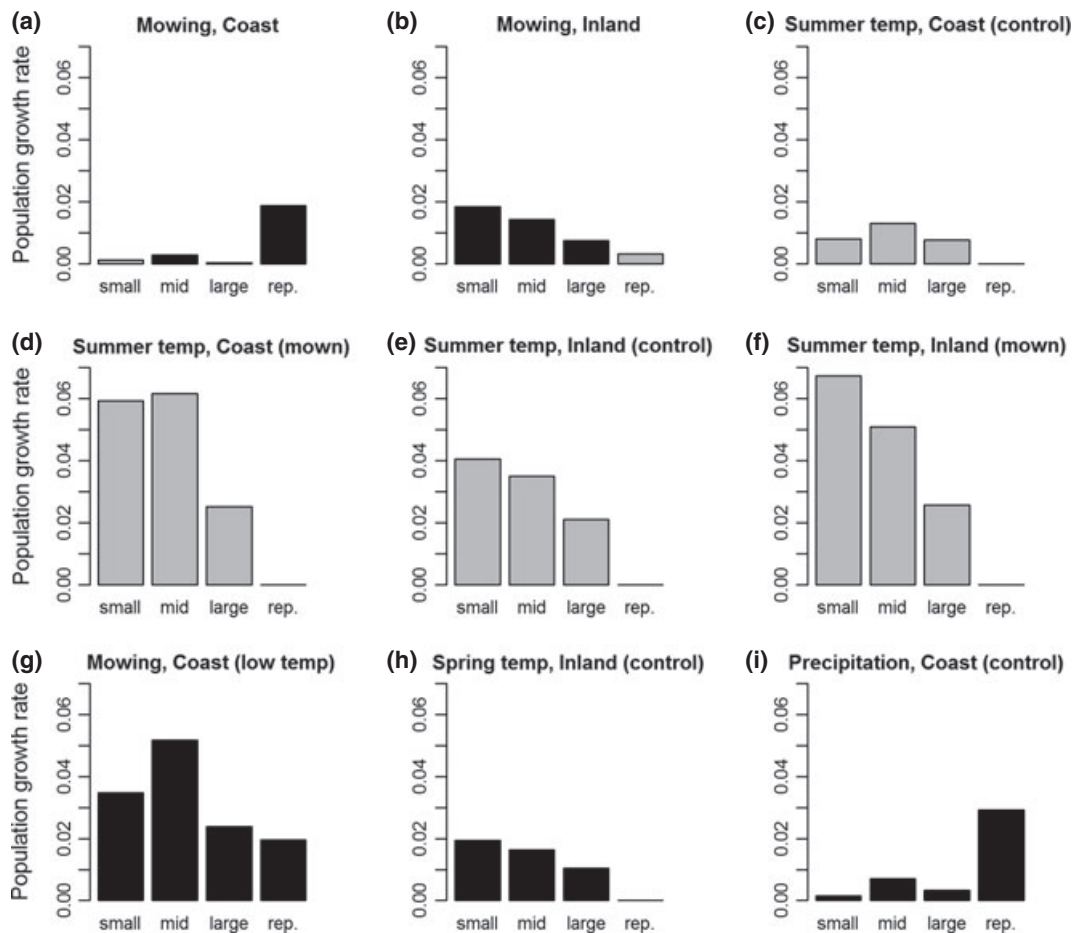


Fig. 2 The impact on population growth rate of differences in vital rates between mown vs. control plots or years with high vs. low values of climatic factors. Values for each class (survival-growth in small, medium and large individuals, and reproduction) are LTRE-contribution values summed over transition matrix columns. Black and grey bars indicate negative and positive effects of mowing or an increase in the environmental factor, respectively.

evidence of changes in central tendency (mean) during the 30 years of the study (linear regression of standardized temperature on time in the coastal and the inland population: $b = 0.059$, $P = 0.003$ and $b = 0.034$, $P = 0.11$ respectively). These trends correspond to substantial average temperature increases of 2.32 °C and 1.34 °C (1.78 and 1.03 standard deviations) in the next 30-year period in the coastal and inland population, respectively (cf. Fig. 1). In the coastal population, the predicted warming would increase average population growth rate from 1.01 to 1.02 in control plots, and from 0.99 to 1.01 in mown plots. In the inland population, average growth rate would increase from 0.94 to 0.96 in control plots, and from 0.90 to 0.94 in mown plots.

Discussion

This study on a herbaceous plant suggests that climate change may have both direct and indirect effects on

population viability, and that the effects of large-scale changes in climate depend on local habitat conditions.

It also demonstrates that the effects of management on population viability may strongly depend on climate. An important overall implication is that management practices for rare and threatened species will often need to adapt to variation in climatic factors at both global and local scale, and that such flexibility can alleviate potential negative effects of climate change.

In both studied populations of *Dactylorhiza lapponica*, climatic factors had significant effects on vital rates and population dynamics.

Summer temperature was the factor that most strongly influenced population growth rate, mainly as a result of higher survival. Over the observed range in summer temperature, growth rate increased by 3% and 11% in the coastal and inland population respectively. In the fen habitat of the studied species, water availability is likely to be sufficient throughout the growing season, and high temperatures

should have positive effects on resource acquisition and storage. In contrast, warm summers have been associated with low population growth rate of plants occurring in habitats that are prone to summer drought (Riba *et al.*, 2002; Tor ng *et al.*, 2010; Nicol  *et al.*, 2011; Bucharov  *et al.*, 2012). In the coastal *D. lapponica* population, high summer precipitation reduced population growth rate via negative effects on individual growth and flower production in the next season. An oceanic climate is associated with high water saturation due to a combination of low evaporation and high precipitation, and it is likely that fens at the coastal site become waterlogged in periods of heavy rainfall (cf. Crawford, 2000). Population growth of many types of plants have been reported to be affected by various climatic factors, including a positive association with autumn temperature in the grassland orchid *Himantoglossum hircinum* (Pfeifer *et al.*, 2006b), negative associations with drought and early season frost in the desert plant *Cryptantha flava* (Lucas *et al.*, 2008; Salguero-G mez *et al.*, 2012), and positive associations with summer temperature and precipitation, respectively, in the sagebrush steppe plants *Artemisia tripartita* and *Hesperostipa comata* (Dalglish *et al.*, 2011). Apparently, direct effects of temperature and precipitation affect population viability in many types of environments, but exactly which climatic factors and at what time of the year they are important should depend on the habitat and phenology of the focal species.

The effects of climatic factors on population viability of the studied orchid depended on management practice, suggesting that both direct and indirect effects are important. Effects of climatic factors in mown and unmanaged plots were mostly in the hypothesized direction, and management-dependent differences corresponded to expected consequences of differences in competition. The positive effects of summer temperature on vital rates and population growth rate of *D. lapponica* were stronger in mown plots, and the negative effects of precipitation were stronger in control plots. These interactions between climate and management can probably be explained by a combination of direct effects on habitat conditions and of indirect effects via competition. Mowing prevents litter accumulation, reduces the density of the field layer, and increases the amount of thermal radiation reaching the soil, which could enhance the positive effect of warm summers through higher photosynthetic or mycotrophic activity (Kotowski *et al.*, 2001;  ien & Moen, 2002; Kyt viita & Ruotsalainen, 2007). In addition, mowing is likely to reduce inter-specific competition. In particular, this should allow small plants to capitalize on favourable environmental conditions, or conversely, be less affected by adverse

conditions. Indirect effects mediated by changes in competitive interactions may also explain the negative effect of higher spring temperatures in the inland population, which was found primarily in control plots where management had not reduced competition. This pattern would be expected if a high spring temperature favours competing species more than it favours *D. lapponica*, and this seems likely as these species-rich fen margin communities include tall graminoids like *Molinia caerulea* and shrubs like *Betula nana* (Moen *et al.*, 2012), that may get a head start by high spring temperatures. Climatic effects on competition have rarely been examined in detail (Levine *et al.*, 2010), but some recent studies on animals have shown that climatic factors may impact competitive relationships via multiple pathways (Ulvan *et al.*, 2012) and via effects on other trophic levels (Gillespie *et al.*, 2012). These results suggest that indirect effects mediated by competition are likely to be common, and play an important role for the net impact of climate change on the viability of populations and structure of communities (cf. Davis *et al.*, 1998). Even though the exact role of species interactions in population and community responses to climate change remains a challenge (Gilman *et al.*, 2010; Adler *et al.*, 2012), predictions based on models including even simple estimates of indirect effects should be more reliable than approaches ignoring such effects. Experimental approaches that separate direct and indirect effects will thus be a key to improve our ability to predict how species will respond to climate change.

The fact that effects of climatic variables on population viability depended on management has important implications for the design of optimal management practices. The increasing trend in summer temperature over the last three decades in the study areas suggests that the effect of the prevailing land use practice is changing. With higher summer temperatures, a marked rise in the survival of small and medium-sized individuals of *D. lapponica* should increasingly compensate the reduced individual growth and fecundity caused by mowing. While the current regime, mowing every second year, appears to reduce population growth under the average climate of the latest 30 years, it is likely to become more beneficial in a warmer climate. Moreover, as community succession ensues, the abundance of shrubs and tall graminoids will increase in unmanaged areas (Moen *et al.*, 1999), and the disparity of temperature effects in managed and unmanaged plots is likely to increase. This highlights the importance of integrating climate change effects into conservation planning. The persistence of an increasing number of species depends on management actions that might become out of tune with prevailing climate in the near future.

The ability to adjust and adapt practices will thus be critical for successful conservation.

Our results also demonstrated that the effects of climatic variation differed markedly between regions, suggesting that the local effects of large-scale changes in climate might vary over relatively small spatial scales. Also in other systems, the effect of climate has been found to depend on region and local habitat conditions. In a climate change experiment, Bütöf *et al.* (2012) found no effects of warming on survival of six grassland herbs in the wettest region, whereas significant reductions were detected at two drier sites. In the alpine herb *Dracocephalum austriacum*, negative effects of summer temperature were stronger among populations growing on steep slopes compared to those on gentle slopes (Nicolè *et al.*, 2011), and Peery *et al.* (2012) found contrasting responses to climate change among populations of spotted owls. Taken together, these results suggest that interactions between climate and local conditions are common. Species that are broadly distributed are thus likely to experience substantial among-population variation in the effects of climate change, and it will be essential to include such variation when resources for management and conservation are allocated.

The question of how climate change will influence biodiversity and individual species is often addressed at large spatial scales. Our results suggest that such large-scale generalizations may be misleading even for single species, because the climatic effects on species performance might differ qualitatively among local habitats that differ in abiotic conditions or management. We therefore need to explicitly account for regional and local habitat heterogeneity and differences in management practices when downscaling the effects of climate change. In addition, development of tools to assess both the direct and indirect effects of climate change should be a general priority for conservation and management. Demographic approaches that link variation in vital rates to variation in climate and management across a relevant spatial scale constitute a particularly powerful method to design flexible conservation plans that mitigate negative effects of climate change. Although such approaches are labour-intensive and can be applied only to a subset of species of conservation concern, detailed examples are important to deepen our general understanding of the complex relationship between climate and species performances.

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References

- Adler PB, Dalgleish HJ, Ellner SP (2012) Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology*, **100**, 478–487.
- Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using Eigen and R syntax. R package version 0.999375-42. <http://CRAN.R-project.org/package=lme4>
- Brook BW, Akcakaya HR, Keith DA, Mace GM, Pearson RG, Araujo MB (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters*, **5**, 723–725.
- Brooker RW (2006) Plant-plant interactions and environmental change. *New Phytologist*, **171**, 271–284.
- Bucharová A, Brabec J, Münzbergová Z (2012) Effect of land use and climate change on the future fate of populations of an endemic species in central Europe. *Biological Conservation*, **145**, 39–47.
- Bütöf A, von Riedmatten LR, Dormann CF, Scherer-Lorenzen M, Welk E, Bruelheide H (2012) The responses of grassland plants to experimentally simulated climate change depend on land use and region. *Global Change Biology*, **18**, 127–137.
- Caswell H (2001) *Matrix Population Models: Construction, Analysis and Interpretation*, 2nd edn. Sinauer, Sunderland.
- Crawford RMM (2000) Ecological hazards of oceanic environments. *New Phytologist*, **147**, 257–281.
- Crone EE, Menges ES, Ellis MM *et al.* (2011) How do plant ecologists use matrix population models? *Ecology Letters*, **14**, 1–8.
- Dahlgren JP, Ehrlén J (2009) Linking environmental variation to population dynamics of a forest herb. *Journal of Ecology*, **97**, 666–674.
- Dahlgren JP, Ehrlén J (2011) Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos*, **120**, 1183–1190.
- Dalgleish HJ, Koons DN, Hooten MB, Moffet CA, Adler PB (2011) Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, **92**, 75–85.
- Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Delforge P, Harrap S (2006) *Orchids of Europe, North Africa and the Middle East*. A&C Black, London.
- Ehrlén J, Syrjänen K, Leimu R, Garcia MB, Lehtilä K (2005) Land use and population growth of *Primula veris*: an experimental demographic approach. *Journal of Applied Ecology*, **42**, 317–326.
- Fox LR, Ribeiro SP, Brown VK, Masters GJ, Clarke IP (1999) Direct and indirect effects of climate change on St John's wort, *Hypericum perforatum* L. (Hypericaceae). *Oecologia*, **120**, 113–122.
- Gillespie DR, Nasreen A, Moffat CE, Clarke P, Roitberg BD (2012) Effects of simulated heat waves on an experimental community of pepper plants, green peach aphids and two parasitoid species. *Oikos*, **121**, 149–159.
- Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution*, **25**, 325–331.
- Gregg KB (2011) Recovery from bud disappearance explains prolonged dormancy in *Cleistes bifaria* (Orchidaceae). *American Journal of Botany*, **98**, 326–330.
- Hutchings MJ (2010) The population biology of the early spider orchid *Ophrys sphegodes* Mill. III. Demography over three decades. *Journal of Ecology*, **98**, 867–878.
- Inouye DW, Morales MA, Dodge GJ (2002) Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia*, **130**, 543–550.
- Jenouvrier S, Holland M, Stroeve J, Barbraud C, Weimerskirch H, Serreze M, Caswell H (2012) Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. *Global Change Biology*, **18**, 2756–2770.
- Jongejans E, de Kroon H, Tuljapourkar S, Shea K (2010) Plant populations track rather than buffer climate fluctuations. *Ecology Letters*, **13**, 736–743.
- Kotowski W, van Andel J, van Diggelen R, Hogendorf J (2001) Responses of fen plant species to groundwater level and light intensity. *Plant Ecology*, **155**, 147–156.

- Kytöviita MM, Ruotsalainen AL (2007) Mycorrhizal benefit in two low arctic herbs increases with increasing temperature. *American Journal of Botany*, **94**, 1309–1315.
- Laaksonen K (1979) Effective temperature sums and durations of the vegetative period in Fennoscandia (1920–1950). *Fennia*, **157**, 171–197.
- Levine JM, McEachern AK, Cowan C (2008) Rainfall effects on rare annual plants. *Journal of Ecology*, **96**, 795–806.
- Levine JM, McEachern AK, Cowan C (2010) Do competitors modulate rare plant response to precipitation change? *Ecology*, **91**, 130–140.
- Lucas RW, Forseth IN, Casper BB (2008) Using rainout shelters to evaluate climate change effects on the demography of *Cryptantha flava*. *Journal of Ecology*, **96**, 514–522.
- Moen A (1990) The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands. *Gunnar*, **63**, 1–451.
- Moen A (1999) *National Atlas of Norway: Vegetation*. Norwegian Mapping Authority, Hønefoss.
- Moen A, Nilsen LS, Øien D-I, Arnesen T (1999) Outlying haymaking lands at Sølendet, central Norway: effects of scything and grazing. *Norwegian Geographical Journal*, **53**, 93–102.
- Moen A, Lyngstad A, Øien D-I (2012) Boreal rich fen vegetation formerly used for haymaking. *Nordic Journal of Botany*, **30**, 226–240.
- Morris WF, Pfister CA, Tuljapurkar S *et al.* (2008) Longevity can buffer plant and animal populations against climatic variability. *Ecology*, **89**, 19–25.
- Nicolé F, Dahlgren JP, Vivat A, Till-Bottraud I, Ehrlén J (2011) Interdependent effects of habitat quality and climate on population growth of an endangered plant. *Journal of Ecology*, **99**, 1211–1218.
- Øien D-I, Moen A (2002) Flowering and survival of *Dactylorhiza lapponica* and *Gymnadenia conopsea* in the Sølendet nature reserve, Central Norway. In: *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations* (eds Kindlmann P, Willems JH, Whigham DF), pp. 3–22. Backhuys Publishers, Leiden.
- Øien D-I, Pedersen B (2005) Seasonal pattern of dry matter allocation in *Dactylorhiza lapponica* (Orchidaceae) and the relation between tuber size and flowering. *Nordic Journal of Botany*, **23**, 441–451.
- Øien D-I, O'Neill JP, Whigham DF, McCormick MK (2008) Germination ecology of the boreal-alpine terrestrial orchid *Dactylorhiza lapponica* (Orchidaceae). *Annales Botanici Fennici*, **45**, 161–172.
- Pedersen HÆ (2010) Inadequate morphometric analyses have contributed to oversplitting in European orchids: a case study in *Dactylorhiza* (Orchidaceae). In: *Diversity, Phylogeny, and Evolution in the Monocotyledons* (eds Seberg O, Petersen G, Barfod AS, Davies JJ), pp. 193–212. Aarhus University Press, Denmark.
- Peery MZ, Gutiérrez RJ, Kirby R, LeDee OE, LaHaye W (2012) Climate change and spotted owls: potentially contrasting responses in the Southwestern United States. *Global Change Biology*, **18**, 865–880.
- Pereira HM, Leadley PW, Proença V *et al.* (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496–1501.
- Pfeifer M, Heinrich W, Jetschke G (2006a) Climate, size and flowering history determine flowering pattern of an orchid. *Botanical Journal of the Linnean Society*, **151**, 511–526.
- Pfeifer M, Wiegand K, Heinrich W, Jetschke G (2006b) Long-term demographic fluctuations in an orchid species driven by weather: implications for conservation planning. *Journal of Applied Ecology*, **43**, 313–324.
- van de Pol M, Vindenes Y, Sæther B-E, Engen S, Ens BJ, Oosterbeek K, Tinbergen JM (2010) Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology*, **91**, 1192–1204.
- R Development Core Team (2011) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at: <http://www.R-project.org>
- Riba M, Picó FX, Mayol M (2002) Effects of regional climate and small-scale habitat quality on performance in the relict species *Ramonda myconi*. *Journal of Vegetation Science*, **13**, 259–268.
- Salguero-Gómez R, Siewert W, Casper BB, Tielbörger K (2012) A demographic approach to study effects of climate change in desert plants. *Philosophical Transactions of the Royal Society B*, **367**, 3100–114.
- Shefferson RP (2011) The evolutionary ecology of vegetative dormancy in mature herbaceous perennial plants. *Journal of Ecology*, **97**, 1000–1009.
- Simons AM, Goulet JM, Bellehumeur KF (2010) The effect of snow depth on overwinter survival in *Lobelia inflata*. *Oikos*, **119**, 1685–1689.
- Sletvold N, Øien D-I, Moen A (2010) Long-term influence of mowing on population dynamics in the rare orchid *Dactylorhiza lapponica*: the importance of recruitment and seed production. *Biological Conservation*, **143**, 747–755.
- Suttle K, Thomsen M, Power M (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.
- Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Toräng P, Ehrlén J, Ågren J (2010) Linking environmental and demographic data to predict future population viability of a perennial herb. *Oecologia*, **163**, 99–109.
- Tveite OE, Bjørndal I, Skjelvåg A, Aune B (2005) A GIS-based agro-ecological decision system based on gridded climatology. *Meteorological Applications*, **12**, 57–68.
- Ulván EM, Finstad AG, Ugedal O, Berg OK (2012) Direct and indirect climatic drivers of biotic interactions: ice-cover and carbon runoff shaping Arctic char *Salvelinus alpinus* and brown trout *Salmo trutta* competitive asymmetries. *Oecologia*, **168**, 277–287.

Supporting Information

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

Table S1. Characteristics of the two study areas. Climatic data are mean \pm SD for the period 1980–2010.

Appendix S1. R code giving environment-dependent transition matrices for the two populations of *Dactylorhiza lapponica*.