Demographic responses to climate variation depend on spatial- and life history-differentiation at multiple scales

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Running head: Linking demography and climate

Abstract

Long-term demographic data are needed for detailed viability analyses of populations threatened by climate change, but the infeasibility of obtaining such data makes it urgent to assess whether demographic responses to climatic variation can be generalized across populations and species. We used 32 years of demographic data on four species of closely related orchids (genera *Dactylorhiza* and *Gymnadenia*), replicated in a coastal and an inland region in central Norway, to test how demographic responses to climate varied among geographical regions and species. We fit generalized linear mixed models (GLMMs) to study climate effects on vital rates and included GLMMs as components in matrix models to examine climate effects on population dynamics. We found that, overall, vital rates and population growth rates of the eight populations responded independently to variation in both temperature and rainfall. Only probability of flowering showed expected regional differentiation in response to climate, despite notable regional climatic differences. Other vital rate – climate relationships were structured by species or a combination of both region and species. The weak clustering of demographic responses to climate variation by species and region demonstrates that effects of climatic variation can strongly depend on variation in local habitat and life history, even among closely related populations occupying similar niches. This highlights the difficulty in transferring data from ~~similar~~ closely related and/or located populations for viability analyses and for models predicting range shifts, and a general need to account for among-population variation in demographic responses to develop successful conservation and management plans.

Key words: climate change, demography, life history differences, orchids, population dynamics, spatial variation

Introduction

Linking populations' performance, in terms of demographic rates, to environmental variation is essential to understand and predict changes in population viability, abundance and geographical ranges (Ehrlén and Morris 2015). However, although the number of studies that link environmental factors to demographic change is growing, few have assessed such links in multiple populations using long-term data (Ehrlén et al. 2016). Thus, little is known about the generality of population responses to changes in environmental factors. This knowledge gap is particularly urgent to bridge regarding climatic factors, given that climate change already caused species range shifts (Chen et al. 2011) and community changes (Devictor et al. 2012).

Potential global impacts of climate change on population, community, and ecosystem dynamics have led to an increasing amount of studies attempting to generalize effects of climatic variation across large spatial and taxonomic scales (Parmesan 2006; Bellard et al. 2012). Such large-scale approaches are necessary for developing cohesive management and mitigation strategies, and predicting future range shifts and species distributions. However, recent analyses of demographic data from hundreds of plant species point to low predictability both across species and geography (Coutts et al. 2016; Che-Castaldo et al. 2018). Population and community responses to environmental drivers such as climate can greatly depend on local habitat conditions, due to regional or more small-scale variation in abiotic factors (Nicolè et al. 2011; Mclaughlin and Zavaleta 2012), biotic interactions (Brodie et al. 2012), and/or management practices (Sletvold et al. 2013). Moreover, the specific climatic factor associated with among-population differentiation in demographic response can depend on spatial scale (Villellas et al. 2013). Studies that compare populations of the same species in different regions or habitats are thus needed to understand how effects of large-scale climatic variation interact with more small-scale habitat heterogeneity.

Climatic factors may most strongly affect one portion of a lifecycle (Scheuerell and Williams 2005; Prior et al. 2010), have broad and consistent effects on the whole lifecycle (Irwin and Lee 2000) or have opposing effects on different vital rates or induce life history tradeoffs (Bond and Midgley 1995; Siemens et al. 2012). Accordingly, population-level effects of climate should be closely linked to an organism's life history, and variation in response to climate should be associated with life history differentiation. For example, variation in traits such as reproductive effort, life expectancy or flowering frequency may lead to marked differences in population-level responses to environmental drivers (Kolb and Diekmann 2005; Morris et al. 2008), and the relative importance of a specific vital rate for population growth may change across a species' distributional range (e.g. Jongejans et al. 2010)). Life history differentiation can also be associated with variation in habitat preferences, and habitats may vary in how they are affected by climate change. To elucidate the effects of life history variation on the link between climate and population dynamics, we need spatially replicated long-term demographic and climatic data for species that vary in degree of life history differentiation.

We studied responses of four species of long-lived orchids (*Dactylorhiza incarnata s.l., Dactylorhiza lapponica, Dactylorhiza maculata,* and *Gymnadenia conopesa*), in two regions in central Norway (Nordmarka and Sølendet), to variation in climatic conditions across 32 years. This allows us to compare long-term differences in climatic response both between regions and among species within region. The coastal Nordmarka region experiences a wetter and warmer oceanic climate, relative to the more continental climate at the inland Sølendet region. The study species are closely related with similar life history strategies, but vary in life expectancy, reproductive effort, and local habitat. Although they all occur in rich fens, *D. incarnata s.l.* tends to favour the wet end of the water level gradient (Sjörs 1948) while *D. lapponica* and *D. maculata* occur in a broader range of plant communities. *G. conopsea* has the broadest range and also occurs in grasslands (Øien and Moen 2002; Moen et al. 2012). In the fen habitat of the studied species, water is likely to be available throughout the growing season, and higher summer temperatures should increase resource acquisition whereas higher rainfall could lead to water-logging of roots. Previous work on *D. lapponica* suggests a positive relationship between population growth rate and previous year summer temperature in both study regions, a negative effect of spring temperature in the inland region and a negative effect of previous year precipitation in the coastal region (Sletvold et al. 2013). Here, we examine to what degree these relationships can be generalized across related species, or whether modest differences in life history and habitat lead to variation in response to climate.

For each species and study region, we created generalized linear mixed models for vital rates and used fitted parameter values to construct climate-dependent stage-based matrix models. Based on the strong regional difference in climate, we predicted that (i) differences between study regions (regional climate) would drive the strongest differentiation in vital rate responses to climate variation, (ii) smaller variation in vital rate responses would be observed within regions driven by differences in species habitat and life history, and consequently, (iii) the link between climatic variation and population growth rate would be more similar within region than within species. Finally, we predicted that (iv) higher summer temperature would increase population growth rates and be more important in the colder inland region, while higher precipitation would reduce population growth rates and be more important in the wetter coastal region.

Methods

Study regions and species

Data were collected at Nordmarka (63°03′N, 9°05′E), located at 440-470 m a.s.l. near the coast of Central Norway, and Sølendet (62°40′N, 11°50′E), located approximately 145 km inland and at a higher elevation (710-750 m a.s.l.). Nordmarka has an oceanic climate while Sølendet has a more continental climate (Sletvold et al. 2010), and both study regions are situated at the transition between the middle and northern boreal vegetation zones (Moen 1999). The growing season is short, usually lasting from late May until late August. Annual precipitation is 1601±269 mm at Nordmarka and 644±84 mm at Sølendet, and effective temperature sum (day degrees, see definition below) is 654±123 and 590±95, respectively (mean ± SD for the period 1980-2010). Both regions were formerly used for haymaking. They are dominated by sloping fen communities with similar soil properties and management histories (Moen et al. 2012), and hold large populations of many orchid taxa. The orchid populations are studied in permanent plots laid out in calcareous, species-rich fen vegetation and wooded grassland vegetation where traditional hay-cutting was abandoned around 1950. The plots included in the present study have received no management since, and have been part of a long-term monitoring program since the 1970s.

We included data on three species in the genus *Dactylorhiza* (*D. incarnata s.l., D. lapponica, D. maculata*) and one in the genus *Gymnadenia* (*G. conopsea*). All species are tuberous and non-clonal, and all produce a single inflorescence with multiple flowers during reproductive years and a vegetative stage with several basal leaves during non-reproductive years. The *Dactylorhiza* species flower in early to mid-summer (June-July) and *Gymnadenia* *conopsea* flowers in mid to late summer (July-August). Species in the genus *Dactylorhiza* are deceptive and rely primarily on naïve bumblebee pollination, while *G. conopsea* is a nectar-producing species pollinated primarily by butterflies and hawkmoths (Sletvold and Ågren 2010). Pollen limitation is strong in *Dactylorhiza* populations, with fruit set typically ranging from 13% to 36%, while *Gymnadenia* experiences weaker pollen limitation, with 55% to 70% fruit set (Table S1). Additionally, all species experience vegetative dormancy in some years. See Supplementary material for more information about each species.

Sampling Design

Demographic data was collected annually from 1981 to 2013 at Nordmarka and Sølendet. Individuals were monitored and tagged within 5 m × 2.5 m permanent plots established in localities with one to several plots per locality with new individuals being monitored beginning at time of first flowering (cf. ~~(~~Sletvold et al. 2010). In total, we included 2929 individuals of orchids (Table S1) in up to 14 plots from each site, including a total of 25540 observations. In each annual survey we recorded survival and stage (dormant, small vegetative (total leaf area <2 cm^2), medium vegetative (total leaf area 2-6 cm^2), large vegetative (total leaf area >6 cm^2), reproductive) for all individuals. Leaf area was estimated from leaf counts and measurements of maximum leaf length and width. Dormant individuals were classified as those that reappeared after having been missing in a given census. The long-term data shows that dormancy lasts one or two years, and individuals missing three consecutive years were considered dead, and mortality was assumed to occur in the first year of disappearance. Inflorescence height and flower number were recorded for reproductive individuals. Monthly climatic data are available for the entire sampling period from nearby weather stations. We used spatially interpolated estimates of temperature and precipitation for both regions provided by the Norwegian

Meteorological Institute (cf. Sletvold et al. 2013). We calculated four climatic variables: Spring temperature (monthly effective temperature sum (defined as the summation of the mean daily temperature subtracted by 5°C of the snow free period; (Laaksonen 1979; Sletvold et al. 2013) for May and June), spring precipitation (summed May and June precipitation), summer temperature (monthly effective temperature sum for July and August in the previous year), and summer precipitation (summed July and August precipitation in the previous year). These variables were selected based on information from previous studies in this system (Sletvold et al. 2013). The distribution of the four climatic variables in each site during the study period is shown in Fig. S1. Total sample sizes were unequal for the eight populations, with lowest numbers for *Dactylorhiza maculata* (82 and 154 individuals in Sølendet and Nordmarka, respectively) and *Gymnadenia conopsea* at Nordmarka (64 individuals; with 666 observations). The other five populations included more than 290 individuals each (Table S1).

Vital Rates

We modelled the effect of climatic variables on individual vital rates using generalized linear mixed models (Bolker et al. 2015). For each species and study region, we constructed vital rate models for survival, transition probabilities between the five stages (dormant, small vegetative, medium vegetative, large vegetative and reproductive) and fecundity (flower number). We used separate models for each species and site because we wanted to estimate an independent set of vital rates and population growth rates for each individual population. Survival and transition variables were assessed by logistic regression and flower production (number of flowers per individual) by Poisson regression. For each vital rate model (survival, stage transitions, and fecundity) the four climatic variables were used as fixed factors. We also included life stage (small, medium, large) as a fixed factor, and year, locality and plot as random factors. To limit model complexity, we excluded interactions among climatic variables and between climate and other factors. This implies that we assume that all life stages respond similarly to climatic variation. We initially explored models including interactions between significant climatic factors and life stage, but very few cases were significant, and those that were showed minor differences in strength of response rather than in direction. Due to weak effects and problems of model convergence we decided to exclude interactions in all final models. Quadratic effects were also excluded as visual inspection of model residuals revealed poor fits. To increase interpretability of vital rate comparisons among species and regions, data used to fit fixed effects of the model were standardized by subtracting the mean from each value and dividing by the standard deviation.

To compare responses of all populations to climatic variation we used hierarchical clustering. Cluster analyses on effects of the four standardized climate parameters were performed for survival, dormancy, probability of flowering and flower production using R package gplots and Ward's minimum variance method, which minimizes total within-cluster variance (Ward 1963). To visualize the results, we constructed heat maps based on the same data. Due to the large number of tests linking climatic variables to vital rates, we also used Fisher's combined probability test (Fisher 1925) to evaluate the distribution of *P*-values resulting from these models. The test was done for all climatic variables combined as well as for each climatic variable separately.

Population growth rates

We constructed separate stage-based matrix models for each population using fixed effects coefficients of each vital rate model to estimate values of each cell in a stage-based Lefkovitch matrix. The models included the classes: dormant plants (1), small vegetative plants (2), medium vegetative plants (3), large vegetative plants (4), and flowering plants (5)~~, and seedlings (6)~~ (Fig. S2). There is an invisible seedling stage which includes all belowground phases (protocorm, mycorhizome), and we assume that germinated seeds spend a year underground as seedlings and emerge as small vegetative individuals. There is no indication of a seed or protocorm bank in the included species. Per-capita seedling recruitment rate was estimated as number of new individuals in year t+1 divided by number of reproductive individuals in year t. To ensure that all possible transition probabilities sum to one we scaled total matrix column sums including mortality to be equal to one. To visualize interactions between two climatic factors, we estimated the climatic variable effects by alternatively fixing two variables at their median values and interactively assessing the other two variables at 100 separate levels comprising the entire range of observed values. At each level, we parameterized a new matrix and assessed asymptotic population growth rate (λ). To visualize the effect of each climatic factor independetly, we also estimated effects of each climatic variable in the same way, but keeping each of the other three variables constant at their median value. We repeated the matrix column scaling procedure for each parameter combination in these runs.

Results

Vital Rates

The regression analyses suggested variable effects of climatic factors among vital rates, both in terms of the direction of the effect and effect size (Fig. 1, Table S2). Standard errors of regression coefficients also varied and were often relatively large, but each climatic factor was significantly correlated (at $P < 0.05$) with at least one vital rate. However, only 9% of the tested relationships were statistically significant at $P < 0.05$, with relationships being particularly weak for some of the populations (i.e., *Dactylorhiza maculata* and *Gymnadenia conopsea* at

Nordmarka, Fig. 1; DMN, GCN). Fisher's combined probability test was significant for the overall model ($P = 0.017$), and for summer precipitation ($P = 0.0044$) and summer temperature ($P = 0.044$) separately, but not for spring precipitation or temperature (both $P > 0.44$). Cluster analysis based on effect size revealed some clustering of relationships between vital rates and climatic factors by region or by species, depending on the vital rate (Fig. 1).

Relationships between climatic factors and survival varied widely among the eight populations, and variation was pronounced both among species and between study regions (Fig. 1A). Climate-survival relationships for *D. incarnata s.l.* and *D. lapponica* were similar in both regions (DIN vs. DIS and DLN vs. DLS), whereas they differed markedly between regions for *D. maculata* (DMN vs. DMS) and *G. conopsea* (GCN vs. GCS). High spring precipitation was strongly associated with low survival in DMN, but was weakly positive or showed no relationships with survival in other populations. In contrast, high previous summer rainfall was associated with low survival in most populations, with the exception of GCN and DMS, where the relationship was weakly positive. Spring temperature was positively or not related to survival in inland (Sølendet) populations, whereas in two coastal populations (GCN and DMN) the relationships with survival were strongly negative. In both regions, higher summer temperature in the previous year was associated with high survival in *G. conopsea* and *D. lapponica* and low survival in *D. incarnata s.l.* and *D. maculata*.

Among-population variation in dormancy response to climate was largely structured by species. The cluster analysis revealed two distinct groups, one containing *D. lapponica* and *D. maculata* and the other containing *D. incarnata s.l.* and *G. conopsea* (Fig. 1B). The clustering by species was mainly driven by a similar response of DL and DM to summer temperature and rainfall in the previous year, where high rainfall was associated with increased dormancy and high temperature was strongly related to reduced dormancy. In DI and GC, the association with summer climate was weaker and population-specific (Fig. 1B). Higher spring precipitation decreased dormancy in inland (Sølendet) populations of DM and GC, and increased dormancy or was unrelated to dormancy rate in other populations. Higher spring temperature was associated with increased dormancy in *D. lapponica* populations in both regions (DLN and DLS) and reduced dormancy or showed no relationship in all other populations.

The relationships between climatic variation and probability of flowering differed more between study regions than among species. Cluster analysis showed two distinct groups split mainly by region, with the exception of the inland (Sølendet) population of *D. maculata*, which fell into the coastal group (Fig. 1C, DMS). The clustering by region was driven by contrasting responses to summer temperature and rainfall in the previous year. High summer precipitation was associated with increased probability of flowering in all coastal populations as well as DMS, but with strongly reduced probability of flowering in all other inland (Sølendet) populations. In contrast, increasing summer temperature had negative relationships with probability of flowering in all coastal populations and DMS, and positive or no effects in all other inland populations. Probability of flowering was reduced or unaffected by spring precipitation in all populations. Relationships tended to be weaker in the coastal region, with the exception of DIN. Increasing spring temperature similarly reduced probability of flowering in all populations except for DIS. Climatic variation had no effect on probability of flowering in GCN.

Among-population variation in flower production in response to climate was mainly structured by species, and the hierarchal clustering showed distinct separation between the two *Gymnadenia* populations and all *Dactylorhiza* populations (Fig. 1D). All climatic variables were positively associated with flower production in both populations of *G. conopsea*, whereas only summer temperature tended to have a positive relationship with flower production in the *Dactylorhiza* populations. In contrast, higher spring temperature, spring precipitation and previous summer precipitation had negative or no relationship with flower production in the *Dactylorhiza* populations, with particularly strong negative relationships with spring rain in *D. incarnata s.l.*

Population growth rate

In general, the modelled effects on population growth rate of previous summer climate were stronger than the effects of spring climate, with the exception of DIS and GCN (Figs. 2-4). The overall effects of previous summer temperature were stronger than of previous summer precipitation, and spring temperature was more important than spring precipitation. Variation in lambda tended to be greater among species within region than between populations of the same species in different regions, although variation was high in both (Figs. 2-4).

Previous summer precipitation was associated with lower or unchanged population growth rate (Fig. 2). The strength of the association varied considerably by both region and species, with stronger effects in the inland (Sølendet) region, except for *D. maculata.* Previous summer temperature was positively correlated with population growth or had no association in inland populations, except for *D. maculata*, and negative or no effects in coastal populations, the sole exception to this being once again DMS. There were also notable interactions between these two factors due to opposing effects of underlying vital rates in both DMS and DLN. Higher spring precipitation increased growth rate of inland (Sølendet) populations of *D. incarnata* and *G. conopsea*, and had negative or no association with growth rate of all other populations (Fig. 3). Higher spring temperature increased growth rate of two populations (DIS and DMS), decreased growth rate in four (DLS, DIN, GCN, DMN) and had no association in two populations (DLN and GCS).

Discussion

Individual populations showed considerable variability in relationships with climatic factors, both regarding specific vital rates and overall population growth rate. In contrast to our predictions, the results suggest that responses to climate variation were not consistently differentiated by region. Only probability of flowering showed a pattern suggesting strong regional effects, whereas the link between climate and other vital rates depended more on species. These findings indicate that among-population variation in life history and local habitat may override the impact of regional climatic differences, even for closely taxonomically and ecologically related species. Similar insights have emerged from recent studies that have used comparative demographic approaches including hundreds of plant species, and found low predictability both across species and geography (Coutts et al. 2016; Che-Castaldo et al. 2018). This has important implications for predicting species distributions, population viability and developing targeted management actions for species in changing environments, and suggests that ecological models that are based on large-scale geographical differences can yield misleading predictions.

Several previous studies have shown that effects of climate on plant population dynamics depend on other environmental characteristics (Maschinski et al. 2006; Nicolè et al. 2011; Diez et al. 2012), indicating that climatic factors interact, or that climate interacts with other abiotic or biotic factors. In the present study, there was a marked difference between regions in the relationship between probability of flowering and climate variation (Fig. 1C), suggesting such an interaction. The observed differences were mainly driven by contrasting responses to summer temperature and rainfall in the previous year. While we predicted flowering to be negatively associated with rainfall and positively with temperature throughout, the opposite pattern was seen in the coastal region. It is possible that the mechanisms for determining suitable climates for reproduction are based on local adaptation (Matías and Jump 2012), with wetter coastal populations being more tolerant to high summer precipitation and low temperatures. For example, in American ginseng, populations from disparate climates responded differently to temperature variation, indicating local thermal adaptation (Souther et al. 2012). Regional differences in the relationship between climate and flowering could also indicate biotic effects, so that e.g. competing plants in the coastal region benefitted more from the favourable growing conditions in good years (cf. Sletvold et al. 2013). It is likely that a combination of direct climatic effects and indirect effects due to altered biotic interactions contribute to the regional differentiation (Matías and Jump 2012). Whatever the underlying mechanism, site-specific relationships between climate and vital rates means that e.g. climate envelope approaches to climate change responses may erroneously predict population persistence (Souther et al. 2012), and, given the prevalence of local adaptation detected in reciprocal transplant studies (Hereford 2009), the climatic niche at the local population level should often differ from that at the species level, reiterating the caution against large-scale modelling.

For all vital rates apart from flowering probability, regional differentiation was surprisingly weak. The design of our study does not allow a true separation of life history and habitat effects, but the results suggest that the variable responses to climate were influenced by both. Species-specific patterns in the association between climate and vital rates were most evident for flower production, with a clear division between the rewarding *Gymnadenia* populations and the deceptive *Dactylorhiza* populations (Fig. 1D). Rewarding populations have a considerably higher flower and fruit production than deceptive ones, suggesting that differentiation in reproductive investment may largely determine climatic responses. Additionally, costs of reproduction have been shown to be climate-dependent for both *Dactylorhiza* and *Gymnadenia* populations, with declining survival and fecundity costs with increasing summer temperature and length of the growing season (Sletvold and Ågren 2015). This may create an investment-specific climatic response, where populations with a higher initial investment in reproduction are more likely to increase allocation to maximize reproduction in favourable years. Support for this investment-specific response also extends to within the group of deceptive species, where populations of *D. incarnata s.l.*, with the highest flower production and weakest pollen limitation, fall out in a separate cluster from the more pollen limited *D. lapponica*. In contrast, the relationship between survival probability and climate showed no clear differentiation based on life history (Fig 1A). There was some support for population responses being associated with habitat differentiation, and more specifically the wet-dry (water level) gradient, which is considered one of the major structuring factors of mire communities (Sjörs 1948; Wheeler and Proctor 2000). Species at the dry end of the gradient (*D. maculata* and *G. conopsea*) exhibited contrasting responses to both spring temperature and summer precipitation between regions, whereas species at the wet end had similar responses in both regions. In general, ecological conditions are more variable at the dry end, where 10 m^2 plots contains twice as many species compared to the wet end, and with less species overlap between regions (cf. (Moen et al. 2012). This could explain why regional differentiation in survival was observed only for the dry-end species. Dormancy responses fell out in two distinct species pairs (*D. incarnata* and *G. conopsea* vs. *D. maculata* and *D. lapponica*) related to reproductive investment but not to overall dormancy rate (Fig. 1B). However, the relatively low occurrence of dormancy also means that the estimated differences between populations are based on only a few instances of dormancy. These results suggest that complex interactions with both life history and habitat variation may override geographical differences in responses.

The way model predictions of population dynamics were affected by climate was mostly consistent with our hypotheses. Previous summer climate was generally correlated to stronger changes in overall population growth rate than climate in spring of the focal year (cf. Fisher's test), and temperature was more influential than both previous summer and spring precipitation (Fig. 4b) This is in line with a recent meta-analysis including 132 long-term studies covering a large taxonomic and geographic range, where temperature tended to have a greater overall impact on population responses than precipitation (Pearce-Higgins et al. 2015). In contrast, a higher temperature was not consistently associated with higher vital rates, as we hypothesized, particularly in the coastal region where it was associated with decreased probability of flowering. One cause of this deviation from expected findings may be that the impact of different climatic factors varies at different spatial scales. In *Plantago coronopus*, among-population variation in vital rate contributions within regions was correlated with precipitation, whereas correlations with temperature were seen at continental scale (Villellas et al. 2013). Likewise, among-population variation in performance of *Stipa capillata* was correlated with climate in central areas and with soil conditions in edge areas (Wagner et al. 2011). The substantial variation in responses to climatic variation observed in the current and previous studies suggest that linking a specific climatic variable and population growth rate across a range of spatial scales will be particularly valuable (Jongejans et al. 2010). For understanding climate effects on demography, the large number of temporal replicates needed in single-site studies may potentially also be replaced by a combination of spatial and temporal replication (Ehrlén et al. 2016).

It is important to note that the number of vital rate – climatic predictor variable relationships that were statistically significant were only marginally higher than what would be expected due to chance. Still, the overall statistical test of environmental factors was significant at the α = 0.05 level (*P* = 0.017). There are several factors that might be at play to produce ~~this large variation~~the low number of statistically significant relationships. Survival and dormancy had more significant climatic associations compared to probability of reproduction and flower number. This is consistent with the generally low elasticity of fecundity compared to survival and growth in long~~-~~-lived plants in general (Silvertown et al. 1993). Additionally, fecundity in long-lived plants tends to be only weakly affected by climatic variables (Salguero-Gómez et al. 2012). ~~Another possibility is that the climatic associations need even longer time series, more variation in climate, or more individuals to be accurately assessed. However, this seems unlikely given that strong climatic effects on demography have been found in other systems with shorter timespans or lower sample sizes (Salguero-Gómez et al. 2012; Dahlgren et al. 2016).~~ Moreover, o~~O~~ur decision to compare the same climatic variables for all vital rates and populations may have led to a lower rate of significant associations than if we had allowed the climatic windows for each vital rate and population to shift (e.g., van de Pol and Cockburn 2011). However, this decision also made comparisons straightforward, and comparative analyses were based on effect sizes and not P-values. Variation in effect sizes did not seem to be affected by variation in data-availability across populations. ~~Moreover, f~~For all climatic variables, the observed range was larger at the coastal site (Fig. S1), but this larger variation was not associated with a consistently stronger response of population growth rate (Fig. 4). For example, summer precipitation exhibits a considerably higher range at the coastal site, but the variation in population growth rate associated with variation in summer rain was equally large at the inland site (and even larger for GC and DM; Fig. 4). We also had fewest observations per year in the *Gymnadenia* population at the coastal site (GCN), but this population was as likely as the others to have strongly negative (Fig. 1A) or positive effects of climate on vital rates (Fig. 1D). Strong climatic effects on demography have been found in other systems with shorter timespans or lower sample sizes (Salguero-Gómez et al. 2012; Dahlgren et al. 2016), also suggesting that availability of data did not severely limit the asessment of climatic associations in the present study.~~Our decision to compare the same climatic variables for all vital rates and populations may have led to a lower rate of significant associations than if we had allowed the climatic windows for each vital rate and population to shift (e.g. van de Pol and Cockburn 2011). However, this decision also made comparisons straightforward, and comparative analyses were based on effect sizes and not P-values.~~

In conclusion, this study demonstrated variation in the effects of climate on vital rates and population dynamics, both between populations of the same species located in different regions and among similar species within region. Demographic projection models allow for detailed understanding of how environmental drivers produce changes in population dynamics via effects on vital rates, which is needed to understand changes in species distributions and abundancies resulting from climate change, and decide specific management actions for threatened populations. The documented high diversity in climate effects suggests caution when basing management actions on generalizations of climate effects across even moderate spatial, temporal or taxonomic scales.

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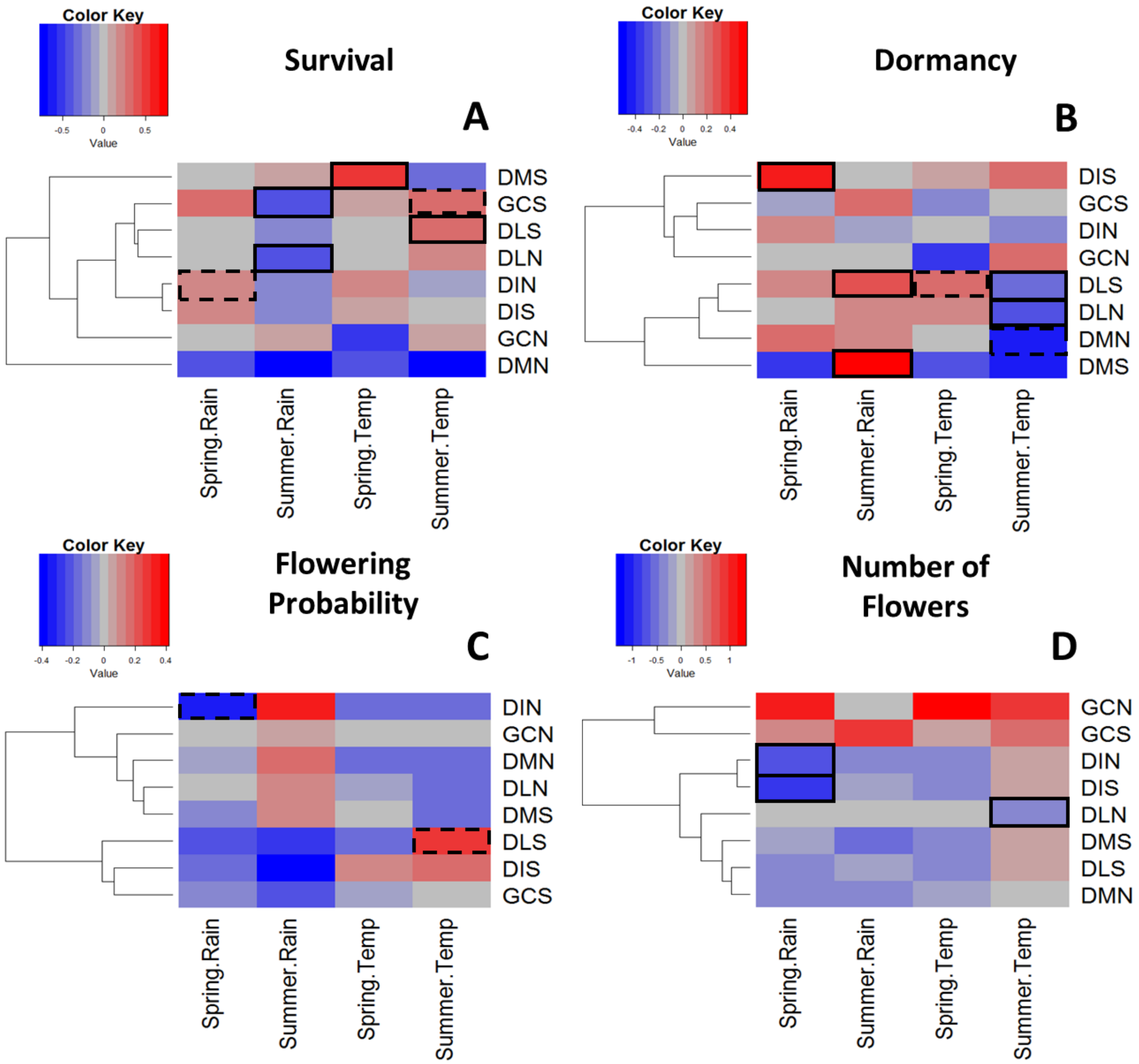
Figure 1. Heatmaps of scaled GLMM-estimated slopes for four climatic variables (rows) on (a) survival, (b) dormancy, (c) probability of flowering, and (d) number of flowers for each population (columns). Dendrograms represent results of a hierarchical cluster analysis. Cells framed in black indicate $p<0.05$ and cells framed in dashed black indicate $0.05<p<0.1$. Population abbreviations: DLS= *D. lapponica* Sølendet, DLN= *D. lapponica* Nordmarka, DIN=*D. incarnata* Nordmarka, DIS=*D. incarnata* Sølendet, DMN=*D. maculata* Nordmarka, DMS=*D. maculata* Sølendet, GCN= *G. conopsea* Nordmarka, GCS= *G. conopsea* Sølendet

Figure 2. Population growth rates at different combinations of summer temperature and precipitation in the previous year. Values on x and y axes represent scaled variables with 100

being the maximum observed value, 0 being the minimum observed value and 50 being the median. Populations in the coastal Nordmarka site are presented in the top row (panel A-D) and populations in the inland Sølendet site in the bottom row (panel E-F).

Figure 3. Population growth rates at different combinations of spring temperature and precipitation. Values on x and y axes represent scaled variables with 100 being the maximum observed value, 0 being the minimum observed value and 50 being the median. Populations in the coastal Nordmarka site are presented in the top row (panel A-D) and populations in the inland Sølendet site in the bottom row (panel E-F).

Figure 4. The range of predicted asymptotic population growth rates across observed values of each climatic variable for each population.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Summer.Rain
Spring.Temp
Summer.Temp
Color Key
-0.4
-0.2
0
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Figure 1.

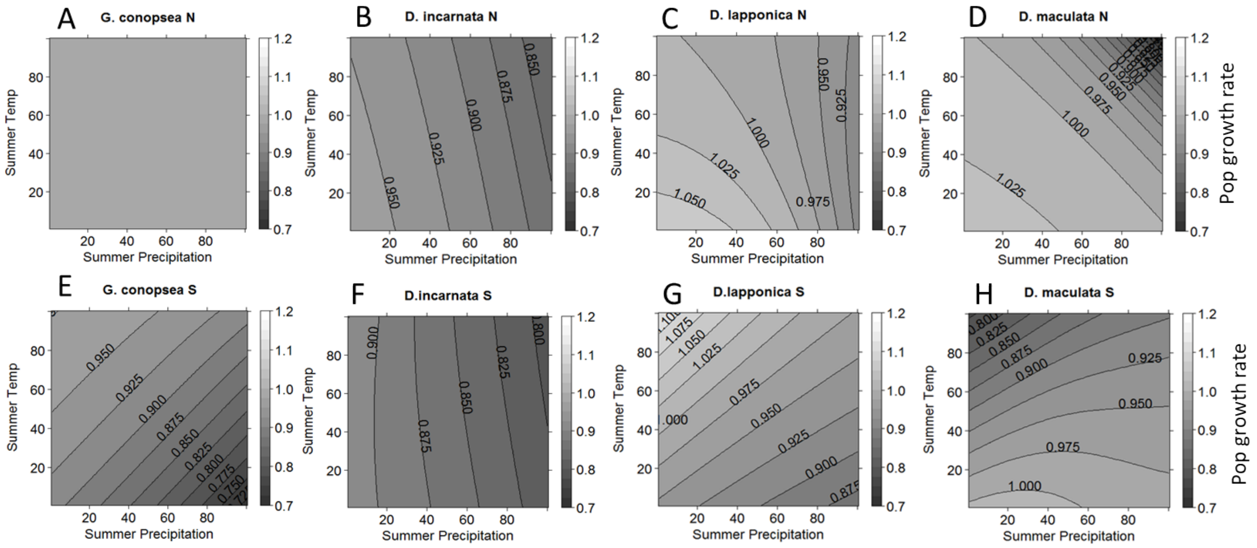


Figure 2.

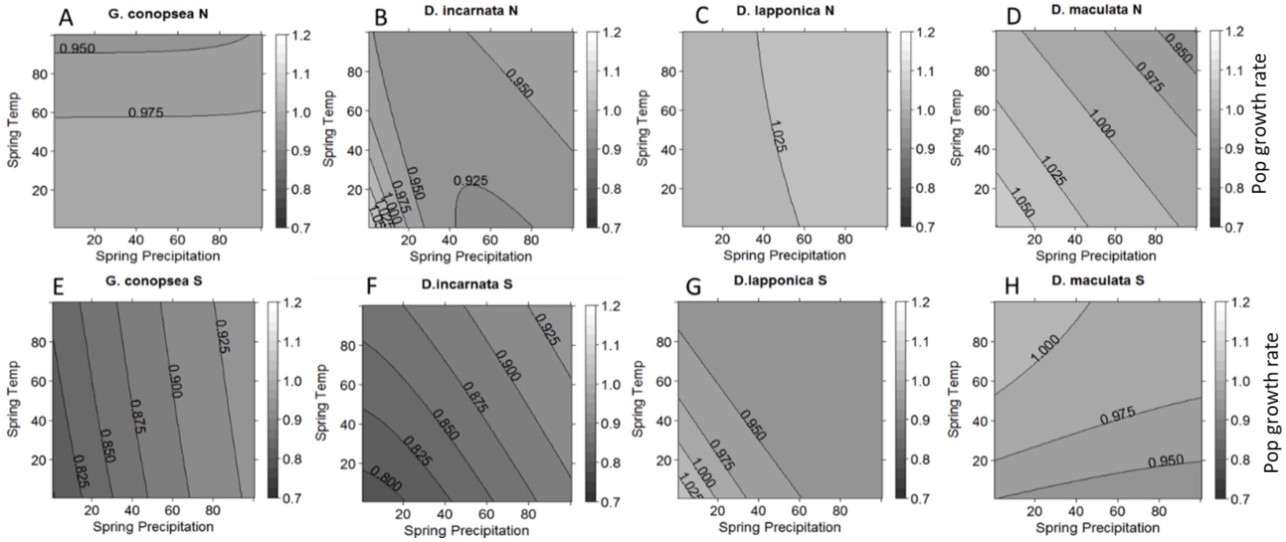
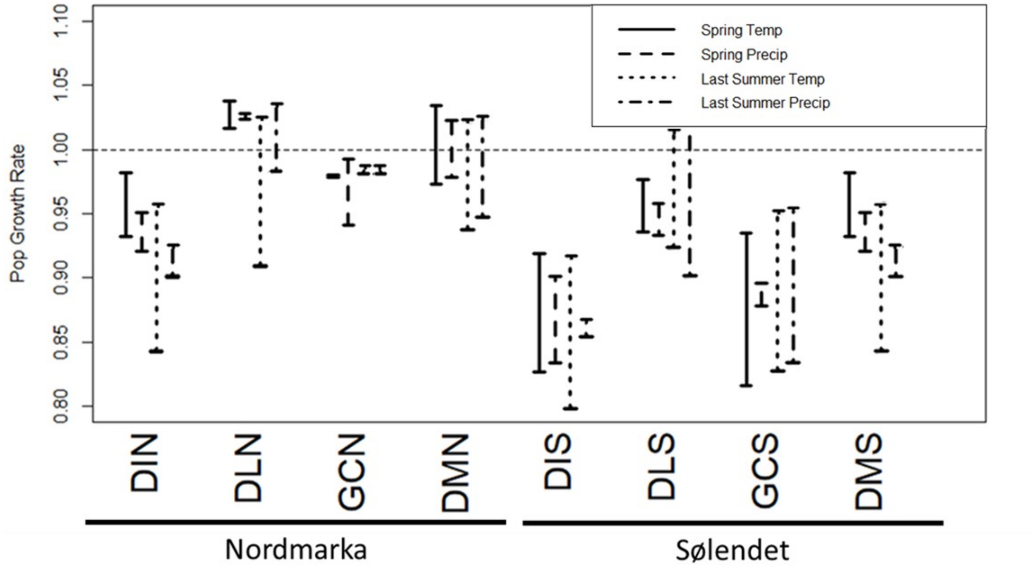


Figure 3


Pop Growth Rate
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1.10
Spring Temp
Spring Precip
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DMN
DIS
DLS
GCS
DMS
Nordmarka
Sølendet

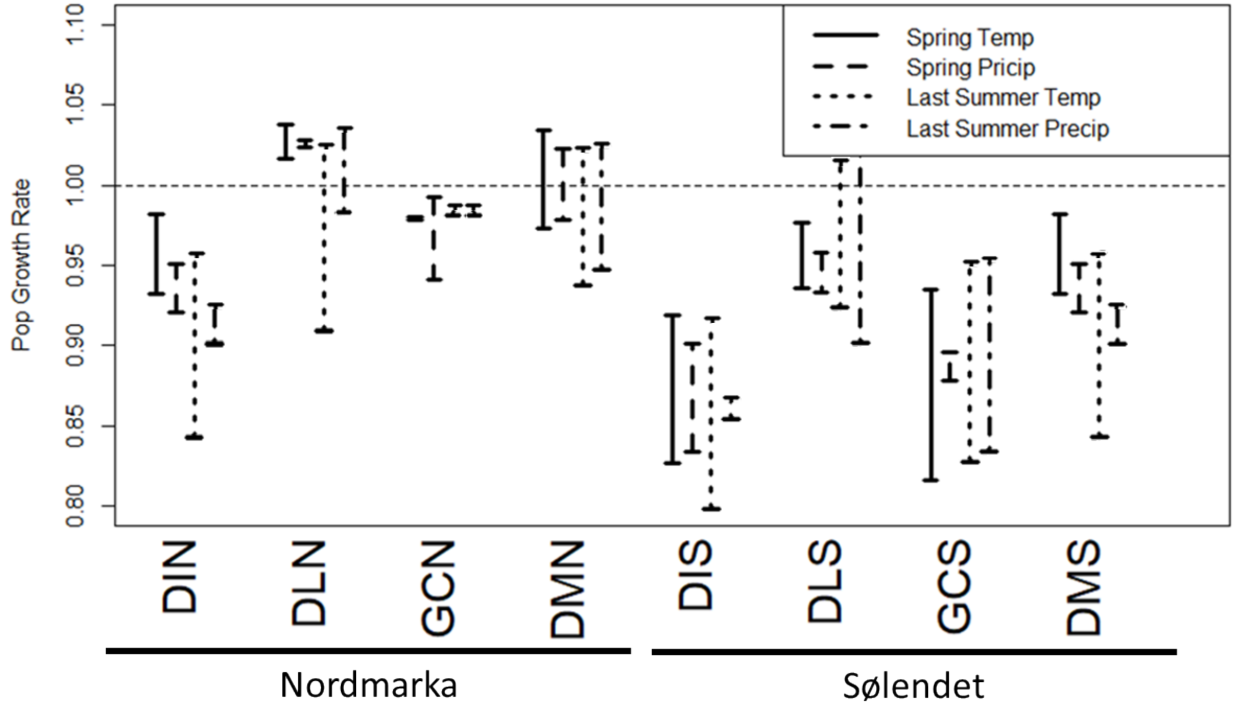
Pop Growth Rate
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Figure 4.