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

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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 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.

1. 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.

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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.

2. Methods

2.1. 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.

2.2. 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 25,540 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

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