Climate influences flowering time but not natural selection in a perennial herb

*Introduction*

Climate change has important effects on the abundance and distribution of species, as well as on ecosystem functioning (REF). It also affects the seasonal timing of life cycle events, and differential effects might lead to mismatches between interacting species (REF). While such short-term, plastic, responses are relatively well documented, we know less about how climate change influences natural selection, the covariation between traits and fitness, and to what extent populations are able to respond evolutionary to altered selection (e.g. MacColl 20xx, REF; reviewer + Soay sheep). In particular, we know little about to what extent observed patterns of trait changes in response to climate change, are the result of changes in trait expression (plasticity) vs. evolutionary responses to changes natural selection.

In many environments the effects of climate change on the timing of life cycle events are crucial to the survival of organisms. Timing constitutes the main way in which an organism can modify its interactions with the surrounding abiotic environment as well as with other species. For example, in plants resource availability and abiotic conditions, like temperature, humidity and light availability, are important determinants of optimal timing of flowering, but also interactions with pollinators and herbivores constitute important sources of selection. Abiotic and biotic factors can influence both the timing of a given genotype in a given year (ref …), and natural selection on timing. For example, higher temperatures and a longer growing season might lead both to a plastic response in terms of an earlier start of growth, and to selection for a lower sensitivity to temperature increases in spring (changes in thermal reaction norms), i.e., counter-gradient responses. … While studies with many types of organisms have documented strong effects of climate on the timing of different life cycle events (REF), the effects on natural selection on timing, and how these are related to plasticity, are much less known (but see ….).

To examine how climate simultaneously influences phenotypic responses and selection, we need not only temporally well replicated estimates of trait values and potential drivers, but also yearly estimates of phenotypic selection. In this study we use a long-term (22 years) data set for a population of the perennial herb *Lathyrus vernus* to explore how trait expression and phenotypic selection on flowering time in a vary among years. Because the study species is long-lived and the turn-over of individuals within the study population is very low, changes in flowering phenology can be assumed to the result of phenotypic plasticity. Previous studies with this species … Ehrlén and Munzbergova 2009 … We recorded flowering times and fitness of xx-xxx individuals in each of 22 years and estimated selection gradients for flowering phenology. We addressed the following questions: (1) Does flowering time vary among years in response to spring temperature, (2) Does the direction and strength of phenotypic selection on flowering time vary among years? (How much? Is there a trend? Are patterns equal for indirect (selection differentials) and direct (selection gradients) selection?), and (3) Is variation in phenotypic selection among years related to spring temperatures or mean flowering phenology?

*Methods*

Study system

The study was carried out in a population of *Lathyrus vernus* … Tullgarn area, SE Sweden coordinates, in a deciduous forest … from 1987 to 2017. …

*Lathyrus vernus* is a long-lived forest herb. The average conditional life span of flowering individuals has been estimated to 44.3 years and the age at which individuals start to reproduce in this population is more than 10 years (REF). *Lathyrus vernus* flowers early in the season before the canopy of deciduous trees develops. Flowering phenology is closely correlated with vegetative phenology (REF), and the shoots emerge from a subterranean rhizome a few weeks before flowering. Timing of flowering has been shown to be correlated with differences in fruit set and this pattern seem to be influenced by both resource and pollen availability (REF). Timing of flowering is also associated with differences in antagonistic interactions with pre-dispersal seed predators and ungulate herbivores (REF).

… Heritability of flowering time …?

Seed production … dispersal … germination … growth … reproduction … dormancy … frequency of flowering … Individuals do not flower in all years but frequently skip flowering

The long life span of *L. vernus* and an observed low turnover of individuals in the study population means that in spite of the long duration of the study, observed variation in trait distributions among years is likely to mostly be the result of phenotypic plasticity while changes in the genetic structure of the population are likely to have played a minor role.

Data collection

Data was collected in 22 years, 1987 – 1996 and 2006 – 2017. … Study plot … new plot and new individuals in 2006, adjacent to the old plot, i.e., new individuals but similar environmental conditions … permanent markings of all flowering individuals using … flags, individuals followed through years … recordings starting early in the season … every fourth to fifth day – bud size, flower opening … flower number … fitness, vegetative size. … In some of the years, first flowering day (FFD) was assigned to each individual by recording the state of the most advanced bud or flower at each recording. For just open flowers, FFD was set to the day of recording. For buds, FFD was estimated to occur one or several days later based on the size and shape of the largest bud. For open flowers, FFD was estimated to have occurred one or several days earlier based on the color and degree of wilting. For flowers that were not considered to have opened recording days, we used the mean of the estimated FFD before and after flower opening. In other years, … Daily recordings of a subset of flowers in some of the study years shows that this method often assigns the correct FFD and that the estimate never differs with more than one day from the actual date. … non-flowering …

Weather data was … mean of two stations?

Data management

Imputation (note only in cases where bud size was not recorded) … Flowering time for individuals that were grazed before flower opening .. the invisible fraction

Weather parameters … “Spring temperature” .. other parameters (do we need to mention all?)

Data analysis

Plant ID …

Selection differentials (estimates of phenology and flower number (size?))

… A main caveat with phenotypic selection gradients based on correlations between traits and fitness is that they may not reflect causal relationships. Environmental heterogeneity may confound estimates of selection in terms of a covariance between focal traits and fitness. To decrease this problem, we will include condition variables in all analyses….

Selection gradients (including flower number as a measure of resource state and reduce biases due to environmental covariance)

Link among-year variation in selection gradients to climatic conditions, summarized by (a) position of flowering season (in terms of mean (10/20%, 80/90%) FFD, MFD and LFD) (perhaps it is worthwhile to also use SD and skewness to characterize the spring climate!?), and (b) duration of flowering season (e.g. in terms the mean duration of individual flowering times (not available for all years) or population estimates such as 90% FFD – 10% FFD)\*.

Mean temperature during April and May … motivation … other measures tested but none provided a better fit (how much about this?) …

Using mean FFD within the population as a measure of yearly environmental conditions …

Trends in mean values of FFD and selection estimates over the study period!? – Detrended values?

*Results*

First flowering date was significantly earlier in years higher spring temperatures (Table 1, Fig. 1: Mean FFD vs. spring temperature). The predicted difference in mean yearly FFD between the warmest and coldest springs during the study period was x days, y vs. z, respectively (or give it for the predicted change in temperature during the study period (from a regression of observed values on year)). … Effects on other aspects of the distribution of FFD-values … Other potential drivers examined …

Selection gradients for FFD differed significantly among years, from xxx to xxx (Table 2, Fig. 2: Selection gradients for FFD in 22 different years). … selection differentials …

Among-year variation in selection gradients for FFD was not correlated with mean spring temperature or with yearly mean FFD (Table 3, Fig. 3: Selection gradients vs. mean FFD/spring temperature). … Other potential drivers examined …

Spring temperatures xxx over the study period (Fig. 4 or in appendix: Changes in spring temperatures during the study years, or in an extended set of years).

*Discussion*

Our results show that flowering phenology in terms of first flowering date in this forest herb is strongly correlated with spring temperature, flowering being xx days earlier with a one-degree increase in mean temperature during April-May (or min vs. max). Phenotypic selection gradients varied significantly among years, from strongly favoring (?) early flowering in some years to … in other years. This variation in selection was, however, not linked to spring temperatures or mean flowering time within the population. Our results thus show that while spring temperature had strong effects on trait expression, it had no detectable effect on phenotypic selection on flowering time. … Provide no support for that we should expect evolutionary responses to changes in temperatures … other factors causing variation in selection on flowering time than those influencing phenotypic plasticity of the trait …

… flowering phenology in terms of first flowering date was strongly correlated with spring temperature, flowering being xx days earlier with a one-degree increase in mean temperature during April-May. … Other potential drivers examined … Explanatory power … Causal mechanisms … Other studies … Concluding remark

… Phenotypic selection gradients varied significantly among years, from strongly favoring (?) early flowering in some years to … in other years. … Other results for selection on flowering time … direction … among-year variation … Among-year variation in selection gradients in general … methodological concerns … implications … [Temporal variation in selection is important because it determines the overall direction and magnitude of selection, and because it may constrain adaptive evolution. Both the direction and strength of selection has been shown to vary geographically and among years, and in some systems temporal variation can be linked to climatic variation (e.g. Thompson 2005; Siepielski, DiBattista & Carlsson 2009).] … Empirical evidence suggest that selection estimates vary both spatially and over time within populations (cf. reviews)… Yet, the prevalence of temporal variation in selection have been questioned based on … Hadfield et al 2xxx). We also know very little about the causes of temporal variation in natural selection (but see Charmantier et al. 2008, …).]

… This variation in selection was, however, not linked to spring temperatures or mean flowering time within the population. … Implications … Consequences … Causes … Other selective agents – Not strongly linked to spring temperatures … Other studies … General about effects of (climatic) drivers on trait expression, selection on thermal reaction norms (can not be excluded – further studies needed), counter- and co-gradient patterns, other types of potential relationships .. Concluding remark

We conclude … CC vs. plasticity and selection …