

Phenology and climate

by
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The Department of Ecology,
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Cover: The butterfly *Anthocharis cardamines* and its hostplant *Cardamine pratensis*,
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Summary

Within the last 20 years, it has been documented that human caused climate change occurs on all continents having major influences on ecosystems. Knowledge on how individuals respond to climate change is of high importance for understanding the effects of climate change on ecosystems. A common way of assessing how individuals respond to climate change is by studying changes in phenology (timing of life-history events). This is done by studying reaction norms. Reaction norms are functions showing trait values of a genotype over an environmental gradient. Phenological changes across a large number of organisms have been reported from a range of geographic locations around the world as a result of climatic changes. Studies on birds, mammals, insects and plants show how individuals can differ in trait response to environmental factors both within and among species. So far, only few studies have been investigating whether observed responses to climate change represent phenotypic plasticity or genetic changes.

Sammanfattning

Under de senaste 20 åren har det dokumenterats att klimatförändringar orsakade av människan förekommer på alla kontinenter, och att dessa klimatförändringar påverkar ekosystem i stor utsträckning. Kunskap angående hur individer svarar på klimatförändringar är mycket viktig för att skapa förståelse för de effekter som klimatförändringar har på ekosystem. Vanligvis uppskattas individers respons på klimatförändringar genom att studera förändringar i fenologi (tiden på året då livshistorieevent inträffar). Detta görs genom att studera reaktionsnormer. Reaktionsnormer är funktioner som visar karaktärsvärden hos en genotyp över en miljögradient. Förändringar i fenologi som orsakats av klimatförändringar har rapporterats i ett stort antal områden världen över. Studier av fåglar, däggdjur, insekter och växter visar hur karaktärsrespons till olika miljöfaktorer kan skilja sig åt mellan individer inom, så väl som mellan, arter. Hitintills har endast ett fåtal studier undersökt om den observerade responsen till klimatförändringar representerar fenotypisk plasticitet eller genetiska förändringar.

Introduction

Within the last 20 years, the scientific view has changed from a general understanding of climate change as having minor impact on the world's ecosystems, to today's documentation of human caused climate change on every continent (Parmesan 2006). It is by now well documented that the climate is changing due to human influence, largely due to the emission of greenhouse gasses such as CO₂ (IPCC 2007). One of the key climatic changes that we see is an increase in global average temperature. Since 1990, when the IPCC published their first report on climate change, we have observed an average temperature increase of 0.2°C per decade worldwide (IPCC 2007), and with predictions from the IPCC (2007) of an increase in temperature of up to 4°C by 2090-2099 compared to 1980-1999, it is clear, that a challenging future is ahead for the world's ecosystems.

The seriousness of climate change is already felt and global predictions show that 20-30% of plants and animals will be in danger of extinction in less than 100 years due to climate change (IPCC 2007). Knowledge on how individuals respond to changes in climate is of high importance if we are going to understand the effects of climate change on ecosystems and the mechanisms involved (Bale et al. 2002). A common way of assessing how individuals respond to recent climate change is by studying changes in phenology (timing of life-history events). So far, phenological changes across a large number of organisms have been reported from a range of geographic locations around the world (Walther et al. 2002). One of the most common findings is advanced spring activities, such as earlier breeding in birds and earlier initiation of growth for plants (Walther et al. 2002). In recent years it has become clear that it is important to study not only how one species respond to climate change but also to look at the ecological context of a given species (Visser & Both 2005). This can for example be by studying more than one trophic level since different species can react in different ways (Visser & Both 2005; Durant et al. 2007) or by including several environmental factors since the outcome might be different for e.g. temperature and precipitation (Bale et al. 2002).

This review will focus on how climate change can affect phenology, how individuals respond to changes in phenology, how such changes can lead to changes in species interactions and if observed responses represent phenotypic plasticity or microevolution.

What is phenology and how is it connected to climate

‘Phenology is the study of the timing of recurrent biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species’ (Lieth et al. 1974). Phenology and climate are very tightly linked. It is for example well known how phenology can be directly linked to temperature and precipitation (Cleland et al. 2007; Pau et al. 2011). An example of this is that if spring temperatures are rising, organisms might react by faster or earlier development. Timing of phenological events is easy to monitor, making the response of phenology to climatic factors a convenient and common object of studies in relation to how individuals respond to climate change. It is important however to consider that other factors such as photoperiod or light intensity can influence the strength of the connection between phenology and climate (Visser & Both 2005) making it difficult to draw general conclusions in relation to phenology and climate change.

How do individuals respond to a variable environment, i.e. what are the reaction norms?

Organisms have responded to different climatic patterns throughout their evolutionary history (Harris 1993). Response to climate change can happen through phenotypic plasticity or genetic changes. Phenotypic plasticity is when a genotype generates different phenotypes in different environments in terms of behavioral, morphological or physiological changes (Pigliucci 2001). This means that traits can vary through the lifetime of an organism as a result of the climatic conditions that it is exposed to (Nussey et al. 2005a). Phenotypic plasticity is often described as reaction norms, which are functions showing phenotypic trait values over an environmental gradient (Pigliucci 2001). Phenotypic plasticity is thus when phenotypic changes occur along a reaction norm while microevolution is when the reaction norm change. The slope of the reaction norm represents to what degree the trait reacts to a given climatic variable, whereas the elevation represents the expected phenological event in an average environment (Brommer et al. 2005). Figure 1 gives an example of how the reaction norms for two genotypes might look. Each genotype is represented by a line; this line is the reaction norm for the genotype. Since both reaction norms are sloping, the genotypes are plastic. Since the reaction norms are non-parallel there is a genotype-environment interaction effect (Fig. 1). This means that the genotype and the environment are both affecting the phenotype; there is genetic variation for the slope.

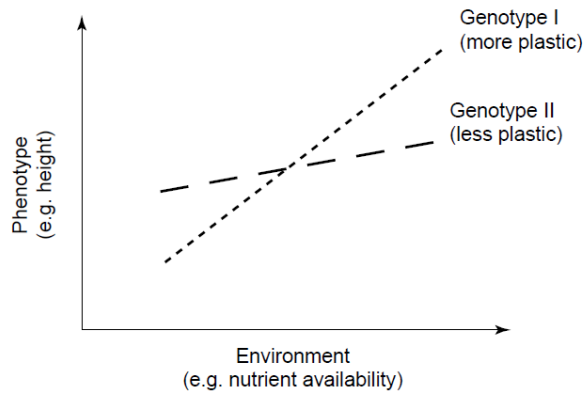


Figure 1. Reaction norms for two genotypes. Both lines are sloping which means that they are plastic. There is also an genotype x environment interaction since the reaction norms are non-parallel (From Pigliucci 2005).

Observed phenotypic changes in phenology as a result of variation in climate

Since the realisation that human induced climate change is happening, many phenological studies have been conducted. The studies have focused on temperate regions of the world with long term observations missing from e.g. the tropics (Cleland et al. 2007; Bertin 2008) and the studies do so far only cover a low number of taxa (Root et al. 2003). The most common phenological traits that have been studied are first leaf emergence and timing of flowering in plants together with insect emergence, bird migration patterns (Bertin 2008) and breeding times for birds and mammals (Clements et al. 2011). Those studies have focused on phenotypic plasticity, and the literature shows extensive evidence of phenotypic plasticity responding to environmental factors for both birds (Brommer et al. 2003; Bearhop et al. 2005), mammals (Réale et al. 2003; Nussey et al. 2005a), insects and plants (Franks et al. 2007; Parmesan 2007) both among and within species. The general trend is that climate change lead to advanced phenological events (Parmesan & Yohe 2003; Visser & Both 2005; Parmesan 2006). A meta-analysis on phenotypic data from 143 data series of more than 10 years data including plants, invertebrates, amphibians, birds and mammals revealed that more than 80% of the investigated species showed phenological shift as a consequence of global warming, and that during the last 50 years, phenology of many species has advanced their springtime development with an average of 5.1 days (Root et al. 2003). Parmesan and Yohe (2003) examined more than 1700 species including plants, birds, butterflies and amphibians through meta-analysis. They reported an average of 2.3 day earlier spring occurrence of phenological events. Menzel et al. (2006) compared 125,000 phenological datasets of both plant and animal species from 1971-2000. Their results showed that 78% of all the

observational data on plants showed advanced leafing, flowering and fruiting. The most recent large scale study comparing temporal phenological events compared more than 100,000 recordings of first flowering and leafing from 1950-2009 for more than 50 taxa (Cook et al. 2012a). They found that most species showed earlier occurrence of phenological events during springtime.

From the results above, it is clear that many springtime events occur earlier in the season as a result of climate change. This correlates with the predictions of spring time warming (Menzel et al. 2006). In relation to autumn time phenological events, the results are much more diverse (Cleland et al. 2007). For example, data on autumn events from the International Phenological Gardens from 1959-1996 showed that around half of the species showed earlier onset of autumn and the other half showed later onset of autumn (Menzel 2000). Bertin (2008) reviewed why a large number of species show advanced phenological events during springtime compared to the more mixed picture in relation to autumn phenology. He found the main reasons to be that research seems to have focused more on spring time changes than on autumn changes and that winter and early spring temperatures have increased more than summer and autumn temperatures in many regions of the world (Bertin 2008).

Although recent research in relation to climate change and phenology has proven that many species respond to climate change, a large proportion of species does not show any response. An example is the work by Parmesan & Yohe (2003) who compared the results from a number of studies on phenology and climate change. They showed that out of 677 species, 27% did not show any change in phenology as a response to climate change. Cook et al. (2012b) investigated why some species seem to have no phenological response to the warming climate. They related data from 490 species to temperature data and found that what at first is understood to be a non-response often is a result of insufficient vernalization. If the vernalization period is becoming warmer, this can lead to insufficient chilling for a given plant species, which can lead to late flowering. This means that if the vernalization period had been colder the result could have been an earlier onset of spring development but what is actually seen is no response due to insufficient vernalization. If this is a general trend for non-responding plant species it would add to the complexity of how phenology is influenced by climate change.

It is by now clear that shifts in phenological events are occurring as a result of variation in climate. However, Visser (2008) points out that phenotypic plasticity in itself is not enough to

ensure sufficient adaptation. Instead, microevolution is needed (Visser 2008). Although many scientists find it a reasonable assumption that climatic changes can lead to microevolution, fossil records demonstrate limited evolution within species despite climatic changes that were larger than what we witness today (Parmesan 2006). So far, only few studies have been investigating whether reaction norms can respond to selection - in other words, whether there is genetic variation in reaction norms and thus potential for microevolution. Brommer et al. (2005) studied how reaction norms of laying date of collared flycatchers (*Ficedula albicollis*) in relation to climate variables varied between individuals and found some evidence of additive genetic factors having an impact on the laying date. They did not however see any signs that the individual reaction norm of laying date was heritable, and their study therefore did not suggest any evolution of phenotypic plasticity. In contrast, Nussey et al. (2005b) found that the reaction norms in relation to laying dates for great tits (*Parus major*) were heritable, but they could not find indications that there was selection on reaction norms. Reed et al. (2009) found that up until 1989 selection favored early breeding and earlier laying dates for common guillemots (*Uria aalge*), but that between 1989 and 2005 there was no clear pattern in relation to breeding or laying dates. The patterns were caused by environmental factors and phenotypic plasticity, not genetic, so this study also showed no evolutionary effect.

Differences in phenological response to climate change at different trophic levels

During the first years of climate change related research, most studies on phenology were carried out by studying one life history event for of a species in comparison to one environmental factor (Harrington 1999). Since then, the importance of studying several trophic levels has become evident (Tylianakis et al. 2008; Visser 2008; Visser et al. 2010; Yang & Rudolf 2010). It has also become clear that it is important to study species interactions at different times in the life cycles of the organisms, because depending on when phenological changes occur, it can have different consequences. Some herbivores can for example cause damage to their host plants at an early life stage, but when they reach later stages of their development they become pollinators of the same host plants (Yang & Rudolf 2010). The response to climatic variation often varies between organisms and if there is a difference in response between interacting organisms this can lead to asynchrony. Asynchrony can have major consequences for ecosystem processes, and those consequences can often be caused by only small changes in synchrony (Parmesan 2007).

Differences in response to climatic changes can either be in the degree of change or the direction of change and it can be influenced by which cues that influences the phenology of a species or by a difference in response to the same cue (Visser & Both 2005). Flowering in plants are for example often triggered by photoperiod (Glover 2007), but also temperature and moisture can be important cues affecting flowering (Neil & Wu 2006). Seasonality often affects which cues the phenology of plants is affected by (Gilman et al. 2012), and often several cues act together creating a combined effect. For insects, phenology is most often linked to temperature (Tauber et al. 1986). Insect development is often controlled by degree-days, which refers to a number of days with temperatures over a given threshold (van Asch & Visser 2007).

Despite the importance of studying the response to climate change for interacting species, not much research has been done. Harrington et al. (1999) reviewed some of the first studies on insects and host plant phenology in relation to recent climatic changes, and found a general trend of different phenological response for insects and host plants in relation to climate variation. Visser & Both (2005) reviewed the literature and found 11 studies investigating changes in phenology between species. Out of those 11 studies, seven showed different levels of change in reaction norms for interacting species. Parmesan (2007) showed that butterfly and bird phenology advanced more than three times as much during spring times in comparison to plants, and Doi et al. (2008) found that *Prunus* tree species and their pollinator *Pieris rapae* both respond to temperature, but at different rates. It has also been shown that organisms from lower tropic levels often react more strongly to climate change in comparison to consumer level (Both et al. 2009) and several studies have reported how higher tropic levels such as bird species have altered their laying dates in order to match the shifts in phenology of their food (e.g. Brown et al. 1999; Crick & Sparks 1999).

Understanding the response of species to variation in climate

Although it is clear that interacting species can respond differently to climatic changes, not much is known about the fitness consequences. Many approaches have been suggested in order to find out what consequences climatic changes have for a given species (Tylianakis et al. 2008; Visser 2008; Miller-Rushing 2010; Yang & Rudolf 2010). Suggestions are to gain greater knowledge of the processes controlling shifts in phenology (Wilczek 2010) or by agreeing on how studies on phenology and climate variation should ideally be conducted (Visser & Both 2005; Parmesan 2007; Yang & Rudolf 2010).

Visser (2008) finds it important to investigate whether a given species can respond sufficiently in order to ensure the species survival. He suggests determining the highest amount of adaptation possible for a given species since this will determine how high a temperature increase can be before the species will suffer. This can for example be done by studying microevolution and by using long data series at the individual level. Salamin et al. (2010) suggests the use of population genetics based on phylogenetics which gives knowledge on the amount of response possible for an organism.

Visser & Both (2005) suggest that studies should focus on the time of reproduction or development when an organism requires the highest level of available food. They were able to find 15 studies where both the phenology of a species and its food source were investigated. The approach of focusing on time of maximum food availability is supported by Durant et al. (2005) who use a model in order to determine how much food a given predator has at a given time in its development. Jonzén et al. (2007) however, finds that Visser and Both (2005) did not take into consideration that climate change has a different impact on temperature over different seasons. The time where food is at its highest might for example advance, but e.g. the period where breeding time is decided might show no advancement. Yang & Rudolf (2010) suggests plotting life history events of several species against each other to observe pair wise interactions e.g. over the duration of a season. In this way both interacting species and the whole length of the interaction is taken into consideration. This type of data can then be used in models to investigate population change and evolution for different phenological shifts. There is so far no evidence of one organism being able to follow the physiology of another species (Harrington et al. 1999). Instead it is hypothesised that host switching can be a potential consequence of asynchrony, and Parmesan (2006) suggests more focus on investigating host switching. Miller-Rushing et al. (2010) suggests adding phenological observations to already existing data on species interactions. They suggest focusing on individuals in contrast to observing a population as whole and to monitor whole networks of species. In addition, they see a large potential in using a combination of observation, experiments and predictive models.

Other methods that have been suggested to gain information on phenological responses to climate change include the use of Bayesian methods in order to study phenological changes over time, such as whether flowering has advanced as a result of climatic variations (Parmesan 2007). Johansson & Jonsén (2012) suggests using game theory models which can be used to study how e.g. birds select for early arrival due to a factor such as competition.

From this essay it is clear that much knowledge is still needed if we are to understand to what extent changes in phenology induced by climate change are the results of phenotypic plasticity or microevolution. A key aspect for future research is to also look at how changes in phenology influence species interactions.

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