PHENOLOGICAL LITERACY

UNDERSTANDING THROUGH SCIENCE & STEWARDSHIP

Seminar Module 1

Synthetic Studies Of Phenology: Reviews And Meta-Analyses

Alisa Hove, Brian Haggerty, and Susan Mazer
University of California, Santa Barbara

Goals For Student Learning

This module was created to help students:

- Use peer-reviewed literature to familiarize themselves with phenological research
- Understand the biotic and abiotic causes of phenological variation in populations
- Understand how species biogeographic ranges are predicted to shift in response to climate change
- Describe the predicted and observed phenological responses of different taxa/functional groups to climate change

Use of synthetic research to understand how biological systems are responding to global climate change

Ecological, biogeographic, and evolutionary changes in the phenology of many plant and animal species have been documented in terrestrial, marine, and freshwater ecosystems. The **peer-reviewed scientific literature** includes thousands of **primary articles** describing field and laboratory studies that concentrate on one (or a few) species for periods of time ranging from one season to several decades. **Review articles** generally synthesize and integrate the findings of many primary research articles, thus providing both a broad overview of a given field, including the hypotheses and predictions on which it focuses, and a qualitative presentation of overarching trends.

The three review articles presented here provide an excellent entry point into field of phenological research. In a widely cited article, Parmesan (2006) reviews numerous long-term studies of phenology and discusses how phenological shifts have influenced different functional groups of species, the **synchrony** of interacting species' **life-history** stages, different types of organisms, and different global regions. More recently, Forrest and Miller-Rushing (2010) discuss the potential of life history theory to inform our understanding of phenology; explore phenological research's potential to inform our understanding of evolutionary and ecological processes; and suggest key areas for future research. To evaluate the genetic and environmental causes of phenological variation in wild plant species, Wilczek et al. (2010) review extensive research on the widespread model plant species, *Arabidopsis thaliana* to evaluate relationships between genetic variation in flowering time pathways and the expression of phenological traits.

Meta-analysis is a statistical approach that synthesizes the quantitative results of multiple, similar, independent studies in order to detect trends that may operate on a broad scale. Parmesan (2007) conducted a meta-analysis evaluating the phenological responses of 203 species to determine whether some species are more sensitive to climate change than others and whether phenological responses to climate change depend on geographic latitude.

In this module, we use Parmesan (2007) to illustrate the utility of meta-analyses when attempting to detect broad-scale biological trends.

Articles To Read

Forrest, J., and A. J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B-Biological Sciences 365:3101-3112.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37:637-669.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13:1860-1872.

Wilczek, A. M., L. T. Burghardt, A. R. Cobb, M. D. Cooper, S. M. Welch, and J. Schmitt. 2010. Genetic and physiological bases for phenological responses to current and predicted climates. Philosophical Transactions of the Royal Society B-Biological Sciences 365:3129-3147.

Suggested Discussion Questions

1. What are the differences and similarities between phenology and life history? How might life history theory contribute to our understanding of phenological responses to climate change? (Forrest and Miller-Rushing 2010)

2. What is the difference between an evolutionary response and a plastic phenological response to climate change? Are these two categories of responses mutually exclusive? (Forrest and Miller-Rushing 2010, Parmesan 2006, 2007, Wilczek et al. 2010)

3. What are some environmental causes of variation among individuals in their phenological schedules? What are some genetic causes of variation among individuals in phenological schedules? (Forrest and Miller-Rushing 2010, Wilczek et al. 2010)

4. How are species' elevational ranges predicted to change in response to climate change? What are some examples of documented shifts in elevation? (Parmesan 2006)

5. How are species' latitudinal ranges predicted to change in response to climate change? What are some examples of documented latitudinal shifts? (Parmesan 2006)

6. Which taxa are most likely to show strong phenological responses to climate change? Why might these taxa be especially vulnerable? What specific example from any of the four articles that we've read supports your answer? (Paremesan 2007)

7. What are the relative benefits and drawbacks of using meta-analysis to evaluate broad scale phenological trends? (Paremesan 2007)

8. Two meta-analyses discussed by Parmesan (2007), came to different conclusions regarding phenological responses to climate change (Figure 3, Parmesan 2003). Briefly discuss the differences between the "P and Y" and "Retal" studies that Parmesan (2007) compares. Why might these studies have differed so dramatically in their findings?

9. There may be cases where exposure of a certain phenophase to a changing climate may kill an organism or limit its potential to survive and/or reproduce. Choose a plant or animal species that you encounter in your hometown. Which of this species' phenophases would you predict to be most vulnerable to climate change? Outline 2-3 potential ecological or evolutionary phenological responses that this species could reasonably by predicted to exhibit. Use information from today's reading to support your reasoning for each phenological response.

Glossary

- **Life-history:** the sequence and timing of an organism's progression from birth to death. Life history events include the transition from juvenile to adult stages and reproduction.

- **Meta-analysis**: a statistical analysis designed to synthesize quantitative results from similar and independent experiments

- **Peer-reviewed literature**: scholarly work that has been generally accepted by academic/professional peers prior to publication in a journal. Also known as "refereed publications".

- **Primary source (primary article)**: in the sciences, this term refers to articles publishing new information, ideas, analyses, or experimental or observational findings for the first time.

- **Secondary source (secondary article)**: in the sciences, this term refers to articles that present a broad overview of a given topic by synthesizing and/or reviewing the ideas, observations, and results of many people, surveys, and experiments. A review article is an example of secondary literature. Note: secondary sources often contain tables and figures that have been reproduced from a primary source that published the original results.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2010) **365**, 3101–3112
doi:10.1098/rstb.2010.0145

Introduction

Toward a synthetic understanding of the role of phenology in ecology and evolution

Jessica Forrest[1,2,*] **and Abraham J. Miller-Rushing**[3,4,5]

[1]*Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada M5S 3G5*
[2]*Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA*
[3]*USA National Phenology Network, Tucson, AZ 85719-5224, USA*
[4]*The Wildlife Society, Bethesda, MD 20814-2197, USA*
[5]*National Park Service, Acadia National Park, Schoodic Education and Research Center, Bar Harbor, ME 04609, USA*

Phenology affects nearly all aspects of ecology and evolution. Virtually all biological phenomena—from individual physiology to interspecific relationships to global nutrient fluxes—have annual cycles and are influenced by the timing of abiotic events. Recent years have seen a surge of interest in this topic, as an increasing number of studies document phenological responses to climate change. Much recent research has addressed the genetic controls on phenology, modelling techniques and ecosystem-level and evolutionary consequences of phenological change. To date, however, these efforts have tended to proceed independently. Here, we bring together some of these disparate lines of inquiry to clarify vocabulary, facilitate comparisons among habitat types and promote the integration of ideas and methodologies across different disciplines and scales. We discuss the relationship between phenology and life history, the distinction between organismal- and population-level perspectives on phenology and the influence of phenology on evolutionary processes, communities and ecosystems. Future work should focus on linking ecological and physiological aspects of phenology, understanding the demographic effects of phenological change and explicitly accounting for seasonality and phenology in forecasts of ecological and evolutionary responses to climate change.

Keywords: climate change; life history; natural selection; phenology; synchrony

1. INTRODUCTION

The word 'phenology' has the same Greek root, *phainomai* ('to appear'), as the words 'phenomenon' and 'phenotype'. Although the latter two words may be more familiar, phenology—the study of the timing of recurring seasonal biological events—has existed as a field of scientific inquiry for centuries. Whether for agricultural or religious reasons, or simply as a way of marking the passage of the seasons, humans have long had an interest in documenting the more-or-less regular appearances of such things as the first flower blossoms of spring, the first migrating birds or the first frost-damaged leaves of fall (Hopkins 1918; Sparks & Menzel 2002; Aono & Kazui 2008). The ancient Greeks themselves recognized the value of phenology—a more reliable indicator of local weather than the movement of the constellations—and used the timing of leaf fall as a guide for when to sow winter crops (Bostock & Riley 1855).

At its simplest, phenology is merely the temporal dimension of natural history. However, this temporal dimension is critical, because it determines the stage of development reached by an organism or population at the time when it intersects with particular components of its environment. Phenology is therefore a major structuring element in nearly all areas of ecology and evolution. Historically, because of its practical importance for plant cultivation, much phenological research has focused on agricultural applications such as pest management, agricultural meteorology and horticulture (Hopkins 1918; Garner & Allard 1920; Schwartz *et al.* 1997). Ecological and evolutionary studies with a focus on phenology also have a long history (e.g. Robertson 1924; Leopold & Jones 1947); however, many studies with important phenological components did not refer to these as phenology *per se* (e.g. Clausen *et al.* 1941; Corbet 1954; Janzen 1967).

In the last two decades, growing concern with documenting and forecasting the impacts of climate change has driven increased interest in the role of phenology in ecology and evolution. Phenological shifts have been among the most obvious and thoroughly documented biological responses to the climate warming of the last 150 years (Beebee 1995; Myneni *et al.* 1997; Crick & Sparks 1999; Fitter & Fitter 2002; Parmesan & Yohe 2003). At the same time, progress in elucidating the genetic basis of flowering time in plants (Ausín *et al.* 2005; Buckler *et al.* 2009; Wang *et al.* 2009), diapause induction in insects (Tauber *et al.* 2007) and offspring hatching date in birds (Liedvogel *et al.* 2009) is bringing a more

---

[*] Author for correspondence (jessica.forrest@utoronto.ca).

One contribution of 11 to a Theme Issue 'The role of phenology in ecology and evolution'.

mechanistic understanding of phenology within reach. Advances in the fields of molecular and developmental biology, quantitative genetics, phylogenetics and ecosystem ecology have also contributed to the recent growth of phenological research.

To date, these various strands of phenology research have tended to proceed independently and have employed different terminologies. In convening this themed issue, we aim to bring together some of these disparate lines of inquiry to clarify vocabulary, facilitate comparisons among habitat types and, most of all, promote the integration of ideas and methodologies across different disciplines and scales. This issue also emphasizes the importance of phenology in nearly all aspects of ecology and evolution.

In this introduction, we start by clarifying the relationship between phenology and life history, and by briefly reviewing the physiological processes and environmental cues governing phenology in different taxa. We then move from the individual organism to the level of the population, and discuss how the shape of the population-level phenological distribution can be characterized—and why it matters. Finally, we provide an overview of the role of phenology in the ecology of communities and ecosystems, and in the evolution of adaptation (or, sometimes, maladaptation). Along the way, we outline some of the main challenges and areas for further work in this field.

2. PHENOLOGY AND LIFE HISTORY

Historical observations of phenology, as well as many recent ecological studies, have mainly concerned patterns at the population level. These studies ask questions such as: how does a plant population's timing of leaf unfolding vary with respect to temperature? Or, has the date of the first frog call advanced over a period of decades? At the individual level, in contrast, the question of interest might be: why does an individual of a particular size or sex begin growth or reproduction at a given time of year? Individual-level patterns are less often equated with phenology (Visser *et al.* 2010), but understanding them is essential for making sense of many population-level patterns, which, after all, represent the integrated activity schedules of many individuals.

The term phenology is sometimes used interchangeably with life history because both incorporate the timing of growth, reproduction and senescence. Of course, phenology does not encompass such non-temporal aspects of life history as size at reproductive maturity and brood size. However, interpreting phenology in the context of life history allows us to integrate phenological investigations with the existing theory and experiments that describe life-history evolution—e.g. the trade-offs that underlie why, in an ultimate sense, annual plants flower at a particular time or why tadpoles metamorphose when they do. Unfortunately, life-history theory and the implications of relevant trade-offs are rarely included in studies exploring variation among species in recent shifts in phenology (Fitter *et al.* 1995; Bradley *et al.* 1999; Miller-Rushing & Primack 2008).

One such trade-off occurs between optimal age (young) and size (large) at maturity. The realized life-history strategy of an individual is expected to reflect some balance between these, with the exact point of compromise influenced by factors such as sex of the individual (Morbey & Ydenberg 2001; Nève & Singer 2008) or relative risk of mortality in larval and adult habitats (Werner 1986; Abrams & Rowe 1996). Environmental factors can obscure the trade-off: individuals growing in a high-quality environment can both be large at maturity and reach maturity early (van Noordwijk & de Jong 1986). Nevertheless, the age–size compromise may influence the type or magnitude of evolutionary change in phenology that would be expected in response to a warming climate (Etterson & Shaw 2001). In annual plants, for example, there is frequently a positive genetic correlation between age and size at flowering (Mitchell-Olds 1996; Franks & Weis 2008); in insects, many of which are likewise annuals, later metamorphosis to adulthood means more time for growth (Masaki 1967). In both cases, the optimal phenological response to an extended growing season depends on the relative benefits of reaching reproductive maturity earlier in the season or growing larger before reproducing.

The utility of this basic life-history framework depends on how a species' lifespan and schedule of reproduction fit within the annual cycle. The expected trade-off between optimal timing and size at reproduction is modified in iteroparous species, which can use resources acquired in a previous growing season for reproduction in the current year. For this reason, in temperate-zone perennials, large plants frequently flower earlier than smaller individuals in the same populations (Forrest & Thomson 2010 and references therein). Similarly, birds in good condition generally lay eggs earlier in a given season than those in poor condition (Price *et al.* 1988; Rowe *et al.* 1994). In red squirrels (*Tamiasciurus hudsonicus*), variation in breeding date is also influenced by maternal condition, itself a response to food availability in the previous year (Réale *et al.* 2003). Thus, both iteroparity and environmental variation in resource availability obscure the time–size trade-off because the resources available for reproduction are not solely determined by the individual's ability to acquire resources in a particular growing season.

In addition, many species do not reproduce on an annual schedule. The phenology of flowering and fruiting in southeast Asian rain forests, in which community-wide mass-flowering events take place at irregular intervals of more than 1 year (Medway 1972; Brearley *et al.* 2007), has little to do with the life history of individual trees and much to do with the factors favouring population- and community-level synchrony among individuals. In short-lived taxa with several generations per year, the link between life history and phenology may likewise not be immediately apparent. However, life-history theory can still be useful; for example, the expected number of generations per year in multi-voltine insects—and, therefore, the times of year when particular life stages will be abundant—is the outcome of the same age–size optimization problem described above (Roff 1980). In general, integrating life-history theory into ecological studies should help both in forecasting changes in phenology and in understanding whether the changes observed so far are likely to be adaptive responses to new conditions.

3. THE MECHANISTIC BASIS OF PHENOLOGY

Just as it is important to understand the life-history trade-offs that are the ultimate causes of many phenological patterns, understanding the proximate drivers of phenology is critical if we wish to predict phenological responses to environmental change. Forecasts of evolutionary change in phenology based on simple optimality models could well be modified by an understanding of the genetics and physiology involved, including the pleiotropic effects of alleles affecting phenological traits (Metcalf & Mitchell-Olds 2009). The timing of many phenological events (e.g. onset of reproduction, entry into or emergence from a dormant stage) results proximately from a complex interplay among an organism's genes and several external environmental factors. These environmental factors, such as temperature or precipitation (see below), may directly control the timing of biological events, or they may act instead as cues that set the organism's internal 'biological clock' (Gwinner 1996; Ausín *et al.* 2005). For most species, however, we do not know (i) the specific environmental factors that are most important in determining phenology, (ii) the precise molecular and physiological processes that regulate phenology, and (iii) whether variation in phenology over time or among individuals reflects genetic differences or simply plastic responses to environmental heterogeneity. Rapid progress is being made to address these uncertainties about the mechanisms regulating phenology (e.g. Visser *et al.* 2010; Wilczek *et al.* 2010), but for now, they substantially limit our ability to anticipate future responses to changes in a variety of climate variables. Here, we review some of the best-studied factors that are known to affect the phenology of plants and animals.

(a) *Genes*

Some of the variation in phenological traits between individuals and populations clearly has a genetic basis. This conclusion is supported by heritability estimates (reviewed by Mazer & LeBuhn 1999; Geber & Griffen 2003; Hendry & Day 2005) as well as empirical demonstrations of evolution in phenological traits (Paterniani 1969; Réale *et al.* 2003; Bradshaw & Holzapfel 2006; Franks *et al.* 2007). Genes may confer a propensity for earlier growth or reproduction regardless of environmental conditions, or they may affect an individual's sensitivity to the environmental conditions that affect timing. For example, in *Arabidopsis thaliana*, plants carrying different alleles at the *FRIGIDA* or *PHYC* loci differ in their sensitivity to vernalization or photoperiod, respectively, and therefore in the relationship between flowering time and environment (Stinchcombe *et al.* 2004; Balasubramanian *et al.* 2006). Similarly, variants of the *timeless* gene differentially affect sensitivity to diapause cues in certain European populations of *Drosophila melanogaster* (Tauber *et al.* 2007).

(b) *Photoperiod*

In several cases where the genetic basis of phenological traits has been confirmed, the alleles involved confer different levels of responsiveness to photoperiod cues (Bradshaw & Holzapfel 2001; Sandrelli *et al.* 2007; Van Dijk & Hautekèete 2007). The predictability of the seasonal change in the light–dark cycle at a given latitude makes photoperiod a reliable indicator of the time of year, at least away from the equator; accordingly, many organisms use changing daylength as a cue for the initiation of reproduction, hibernation, migration, diapause or moult. Photoperiod plays a role in regulating seasonal patterns in such distantly related organisms as mustards (Ausín *et al.* 2005), mollusks (Wayne 2001) and mammals (Goldman 2001). Changing daylength influences the timing of sexual reproduction in some freshwater zooplankton (Stross & Hill 1968; Gilbert 1974), the timing of spore germination in marine diatoms (Eilertsen *et al.* 1995) and the induction and termination of diapause in freshwater copepods (Williams-Howze 1997). Seasonal variation in insolation may even influence the timing of leaf flush in 'aseasonal' tropical forests (van Schaik *et al.* 1993). In many insects, diapause initiation and—perhaps less commonly—termination are controlled by photoperiod, although the resumption of activity following diapause is likely to depend on other factors, such as temperature, as well (Mazaki 1980; Tauber *et al.* 1986).

(c) *Temperature*

Dependence on photoperiod cues alone would render organisms vulnerable to mistiming their activities in years with unusual weather conditions, or in the event of rapid climate change. However, the photoperiod response is often modified or even overridden by other, more directly relevant environmental factors, of which the most commonly used, at least in temperate climates, is temperature. The interaction between long days and warm temperatures has been well characterized in the flowering pathway of *A. thaliana* (Ausín *et al.* 2005; Wilczek *et al.* 2009). Certain migrating birds also integrate information on temperature and photoperiod (Bauer *et al.* 2008).

Although endotherms such as birds may use temperature, like photoperiod, simply as a cue informing them of the likely future availability of food, in other organisms, temperature affects phenology directly by influencing the rates of biochemical processes (cf. Gillooly *et al.* 2002). As a consequence, the accumulation of a certain number of heating units (e.g. degree-days) often predicts well the date of flowering in plants (e.g. Jackson 1966; Diekmann 1996), and flowering phenology commonly tracks interannual variation in air temperatures (Fitter *et al.* 1995; Sparks *et al.* 2000; Miller-Rushing *et al.* 2007). Heat accumulation similarly affects development rate and, hence, the timing of appearance of adults, in many economically important insect species (Embree 1970; Kemp & Onsager 1986; Kemp *et al.* 1986; Régnière *et al.* 2007). In multi-voltine insects (those with multiple generations in a year), shortening days late in the year commonly induce diapause regardless of temperature; but the number of generations achieved prior to this will depend on temperatures experienced, and hence the rate of development, up to that point (Tobin *et al.* 2008).

However, there is often more to the temperature effect than simple heat accumulation. Many plants have a chilling requirement, such that subsequent development is delayed or prevented if they have not experienced cold winter temperatures (Murray *et al.* 1989; Morin *et al.* 2009). This requirement is referred to as vernalization when applied to flowering (Henderson *et al.* 2003). The need for cool temperatures has the counterintuitive effect of delaying phenology in warm years (Zhang *et al.* 2007). A similar phenomenon has been documented in insects: in several temperate-zone species, a longer overwintering period reduces the heat requirement for springtime emergence of adults (Kimberling & Miller 1988; Bosch & Kemp 2003, 2004). Other factors that complicate the relationship between temperature and phenology are differences between species in their lower threshold temperatures for development (Kemp & Dennis 1989) or in their abilities to behaviourally thermoregulate by moving into patches of sunlight or shade (van Nouhuys & Lei 2004).

(d) *Precipitation*

In the tropics and arid environments, variation in precipitation is more likely than temperature to drive phenological patterns. In different types of tropical forests, either rain or drought can induce flowering (Medway 1972; van Schaik *et al.* 1993; Brearley *et al.* 2007); often, this does not occur on an annual cycle. Many desert plants germinate (annuals) or resume growth (perennials) in response to rainfall (Beatley 1974; Zhang *et al.* 2006; Kimball *et al.* 2010). Desert animals often emerge from diapause or aestivation in response to moisture (Cloudsley-Thompson 1991; Danforth 1999).

At high altitudes and latitudes, flowering time and insect activity can be strongly, and apparently linearly, correlated with timing of snowmelt (Ellebjerg *et al.* 2008; Høye & Forchhammer 2008; Forrest *et al.* 2010). However, it is not clear that snowmelt is itself a cue to which organisms respond. Instead, disappearance of snowpack may set a lower bound on the date at which heat units can begin to accumulate (Thórhallsdóttir 1998). Thus, extremely early snowmelt unaccompanied by warm early-spring temperatures—a conjunction of circumstances that can occur if there is little snowfall the previous winter—may fail to advance phenology. This can look like an accelerating relationship between phenology and snowmelt date (Inouye 2008; Steltzer *et al.* 2009), but a simple, uniform response to accumulated degree-days in a given year may be a more parsimonious interpretation.

Often it is not possible to compare alternative environmental predictors of phenology (e.g. temperature versus snowmelt) because detailed weather records are not available. This illustrates a common limitation of descriptive phenological studies: it is relatively easy to detect a correlation between some climate variable and a particular phenological response; but this in itself does not demonstrate that the climate variable in question is the proximate cue regulating phenology. This is simply another case of correlation not equalling causation: multiple climate factors are likely to covary, and standard experimental designs (such as snow removal or warming structures), while valuable in their own right, may be inadequate for separating these variables. More tightly controlled experiments are necessary to determine unequivocally which environmental factors regulate phenology (e.g. Cleland *et al.* 2006; Sherry *et al.* 2007). Where experiments are impossible, statistical modelling to compare the effectiveness of different predictors can at least provide clues about which cues are most likely involved (e.g. Dunne *et al.* 2003; Hülber *et al.* 2010). Similar responses to recent climate change among groups of related species (i.e. phylogenetic conservatism in phenological shifts; Davis *et al.* 2010) suggest common drivers of phenology within clades; this may permit inferences about mechanism in taxa that have not yet been studied. A better mechanistic understanding is necessary if we are to make predictions about phenological responses to future, novel climates, and the chances of phenological decoupling among interacting species (see below; Araújo & Luoto 2007).

4. CHARACTERIZING PHENOLOGIES AT THE POPULATION LEVEL

The ultimate and proximate factors that regulate the phenologies of individual organisms contribute in turn to phenological patterns at the level of the population or community. Phenology, as a characteristic of the population, has the components of any statistical distribution. In the case of flowering phenology, these include the mean flowering date, duration (range) of flowering and the higher moments such as variance and skewness. Importantly, population-level distributions can be inferred from the traits of individuals, but not always vice versa: a skewed flowering distribution could result from individuals having skewed flowering curves, or from individuals with symmetrical flowering curves having a skewed distribution of first flowering dates. The positions of phenological distributions (i.e. first dates, means or peaks) have received the most attention from population and community ecologists, because of the consequences for overlap with other temporally varying components of the environment (see below; Araújo & Luoto 2007). However, the distributions as a whole, and precisely how they relate to individual-level phenology, have received less attention to date (though see Laaksonen *et al.* 2006; Elzinga *et al.* 2007). This lack of attention—caused in part by the rarity of adequate datasets—limits our ability to understand the ecological and evolutionary consequences of population-level phenology, including the availability of temporal niches for non-native species (Wolkovich & Cleland in press) and the form of selection on phenological traits. Here, we outline some aspects of phenological distributions that are often overlooked.

Variance and kurtosis ('peakedness') in phenology reflect within-population synchrony. Synchrony in reproduction can improve chances of mate-finding

(Augspurger 1981; Reed *et al.* 2009) and offspring survival (Ims 1990; Kelly & Sork 2002), but it also increases competition for resources. Less obviously, decreased variance in phenology at one trophic level can affect higher trophic levels, which may depend on the food supply being more evenly distributed in time—that is, having higher among-individual or among-plot variability in phenological events (Post *et al.* 2008). Changes in population and community-level synchrony in response to warming temperatures are worth monitoring because of these potential effects on demography and ecosystem processes (Miller-Rushing *et al.* 2010).

Skewness is common in phenological distributions, and it determines the extent to which the population mean is an adequate reflection of central tendency: in strongly skewed distributions, shifts in the mean, rather than the median, poorly represent trends experienced by most individuals. Timing of germination and flowering in plant populations is often positively skewed (Rabinowitz *et al.* 1981; Rathcke & Lacey 1985; Brown & Mayer 1988), as are timing of emergence in insects (Danks 2006) and arrival and laying dates in migratory birds (Sparks *et al.* 2005; Laaksonen *et al.* 2006). This pattern may arise because most individuals respond rapidly and similarly to the relevant environmental cues, while a smaller number experience problems in development or migration that delay phenology to varying extents (Rathcke & Lacey 1985; Danks 2006). Intriguingly, skewness often increases in warm years, with populations developing a longer tail at the end of the season (Roy & Sparks 2000; Sparks *et al.* 2005; Forrest & Thomson 2010). Skewness also determines the extent to which an individual's timing of activity covaries with population density. This makes directional selection on temporal traits difficult to distinguish from stabilizing selection: given a positively skewed distribution, selection for earliness resembles selection for synchrony.

Although recognition of the full shape of phenological distributions is important for many ecological and evolutionary questions, a framework based on a simple, unimodal trait distribution will be inadequate for characterizing some cyclical phenomena. Primary production in many aquatic habitats, for example, does not have a clearly defined duration or even, in some cases, an obvious seasonal peak. Simply demonstrating the frequency and consistency of population or community cycles—a prerequisite for documenting effects of climate change on phenology—can be a challenge in such systems. Winder & Cloern (2010) overcome this challenge with an innovative approach: wavelet analysis applied to time series of phytoplankton biomass. Elsewhere, Altermatt (2010) has used a kernel-density estimation function to describe the multi-modal distributions produced by multi-voltine insects. Techniques like these could have broad applicability to systems where analysing temporal trends in phenology would otherwise be problematic.

5. ECOLOGICAL EFFECTS OF PHENOLOGY

There has been much attention in recent literature to the likely ecological consequences of shifts in phenological distributions in response to climate change. Because phenology is involved in nearly all ecological relationships, there is clearly potential for important effects. Here, we highlight a few of the consequences of changing phenology for population dynamics, species interactions and ecosystems.

One often-discussed possible result of climate change is that species will differ in the degree to which their phenologies shift, with potentially dire consequences for interacting species (e.g. Harrington *et al.* 1999; Durant *et al.* 2007; Both *et al.* 2009; Hegland *et al.* 2009). In principle, these shifts could have positive or negative consequences for the populations involved, depending on whether the interaction in question is mutually beneficial (i.e. a mutualism), mutually detrimental (i.e. competition) or unilaterally beneficial (e.g. predation), and whether differential changes in phenology drive species closer together or further apart in time. Such shifts in interactions seem inevitable, insofar as species use different cues to regulate phenology (still something of an unanswered question; Aono & Kazui 2008; see above). In practice, however, there are still few examples of such shifts having detectable demographic consequences. Reasons for this persistent gap, and possible solutions, are discussed by Miller-Rushing *et al.* (2010). A convincing demonstration requires showing that a change in interaction strength or frequency has occurred, that this change is the result of climate change and that the change has altered the vital rates of one or more of the species involved. In this issue, Thomson (2010) provides one of the few examples of an important species interaction that has been documented over the long term, showing that pollen limitation in a subalpine wildflower has increased over the last 17 years, and suggesting that plant–pollinator decoupling may be occurring. This is a phenomenon that has been predicted by many (e.g. Dunne *et al.* 2003; Memmott *et al.* 2007), but not previously demonstrated. However, the data are inconclusive as to whether climate change is responsible, and population declines have yet to be observed: the plant is a perennial, and we do not know whether population size is limited by seed supply. This illustrates the difficulties inherent in this type of work and suggests where further efforts are required.

Shifts in the timing of reproduction, in particular, have possible consequences beyond changing species interactions. The need to fit at least one reproductive episode into the annual cycle can be the factor limiting a species' geographical range (e.g. Jönsson *et al.* 2009), such that longer growing seasons can allow species establishment beyond the current range limit. This is the rationale behind process-based models such as PHENOFIT, described in this issue by Chuine (2010). Such approaches promise more mechanistically grounded forecasts of species range changes with climate warming than have been provided by purely correlation-based 'climate envelope' techniques. Furthermore, for some species, early completion of a first bout of reproduction may permit a second breeding attempt in the same season. This is particularly likely if the tail end of the growing season is being extended as well. Several temperate-zone birds and other taxa are capable of double-brooding if there is time (Verhulst *et al.* 1997 and references therein; Saino *et al.* 2004), provided food resources are also sufficient (cf. Husby *et al.* 2009). In short-lived species, warmer temperatures and longer growing seasons may allow additional generations per year (e.g. Tobin *et al.* 2008; Jönsson *et al.* 2009; Altermatt 2010). Both of these possibilities have major implications for population growth. However, because not all species are capable of multiple broods or generations in a year, even when growing season length is adequate, some species will benefit more than others from warming. In particular, there is concern that outbreaks of certain insect pests will increase in frequency (Logan *et al.* 2003). Interestingly, this is not only an ecological advantage; in principle, having more generations in a given time span could allow more rapid adaptation, provided selection pressures experienced by the different generations are sufficiently similar.

Finally, length of the growing season has ecosystem-level consequences for water, nutrient and carbon cycling. For carbon in particular, it is not obvious whether changes in the length of the growing season will lead to a net increase or decrease in carbon fixation, because of the opposing effects of increases in photosynthesis and respiration. Phenology determines the time period over which photosynthesis can occur, and the increase in primary productivity resulting from this temporal effect can exceed the direct effect of temperature on photosynthetic rate (Piao *et al.* 2007). In this issue, Richardson *et al.* (2010) investigate how this phenological effect on ecosystem productivity varies across temperate forest types and between spring and autumn seasons, showing that an extended growing season can increase net productivity despite increased carbon loss at high temperatures.

Thus, forecasting growing season length under future climate change in various ecosystems is immensely important. However, forecasts of community-level changes in phenology are problematic, given both the rarity of comprehensive long-term datasets and the variability in phenological responses among different species and sites. Ibáñez *et al.* (2010) outline a hierarchical Bayesian approach to this problem that circumvents some of the limitations of more conventional statistical techniques.

As for the consequences of future changes in growing season length, Richardson *et al.* (2010) point out that both spatial proxies and historical conditions are imperfect predictors: changes in species' distributions will interact with phenological changes to affect ecosystem processes (cf. Cleland *et al.* 2007). Indirect effects of growing season length are also possible if, for instance, pest insect outbreaks in longer summers cause severe plant mortality. This suggests a need for incorporating more of the direct and indirect effects of phenology into forecasts of ecosystem change. This entails, in part, knowing the proximate factors regulating phenology and the ultimate factors responsible for current life-history strategies—as discussed earlier. Clearly, this is an enormous challenge, but one that is critical to forecasting the ecological consequences of climate change.

6. EVOLUTION OF PHENOLOGY

Phenology at the population or ecosystem level is ultimately a product of selection acting on variation among individuals. Interest in the evolution of phenological traits such as timing of reproduction or migrations is hardly new, but it has been reinvigorated by recent climate change (e.g. Visser 2008). Even so, our ability to predict how phenologies will evolve in response to recent climate change remains limited. Numerous studies have shown evidence of selection on timing of various biological processes, especially in plants (e.g. Kingsolver *et al.* 2001; Gienapp *et al.* 2006; Elzinga *et al.* 2007; Reed *et al.* 2009), but documented responses to selection in natural environments are rare (Gienapp *et al.* 2008; but see Franks *et al.* 2007). Even in some cases where evolutionary change is expected, based on trait heritabilities and selection pressures, adaptation is not observed (Gienapp *et al.* 2006; van Asch *et al.* 2007), suggesting that we must improve our understanding of the form of selection and constraints on its operation.

In particular, there are some peculiarities to *timing* as a trait that make its evolution especially interesting and challenging to investigate. Adaptive change is facilitated when the trait under selection is also the trait according to which individuals choose mates (Doebeli & Dieckmann 2000; but see Fox 2003). For a trait such as timing of breeding, some level of assortative mating between individuals with similar trait values is inevitable (Fox 2003; Weis & Kossler 2004; Weis 2005), and the resulting inflation of genetic variance can hasten evolutionary change in breeding time (Hendry & Day 2005; Devaux & Lande 2008).

In contrast, the evolutionary lability of phenology can be limited because life-history traits are subject to certain unavoidable constraints. The evidence for genetic correlations limiting the short-term rate of adaptive change is so far surprisingly mixed (Agrawal & Stinchcombe 2009); but basic life-history trade-offs are inescapable, and constraints on the evolution of phenological traits may be relatively widespread (cf. Diggle 1999). In fact, this might explain observations of apparent 'maladaptation' in populations that seem to be frequently mistimed to the phenology of their food sources or mutualists (e.g. Zimmerman *et al.* 1989). As Singer & Parmesan (2010) discuss, such persistent asynchrony may be the result of trade-offs with other, perhaps unmeasured, life-history components (see also Ejsmond *et al.* 2010). Clearly, recognizing the existence of trade-offs and developmental constraints is essential for determining whether current asynchrony in fact represents a negative impact of current climate change—as well as for understanding possible evolutionary responses to future environmental change.

Inherently time-dependent processes such as learning can also influence the evolution of phenology: consumers may take time to learn about the existence or location of a food source, and therefore may ignore individuals of the prey species that appear or reproduce early relative to the population mean. This selective advantage (or disadvantage, if the relationship is mutualistic) to early individuals imposes selection on the relative timing of reproduction, regardless of the absolute date. At least in theory, this can produce phenological patterns that seem maladaptive at the population level (Forrest & Thomson 2009). In addition, males and females within a population may differ in the optimal timing of emergence or reproduction, because precedence is often favoured in mate competition between males but is less strongly selected in females (Wiklund & Fagerström 1977; Bawa & Beach 1981; Morbey & Ydenberg 2001). This could, in principle, drive sexual conflict over timing (Møller *et al.* 2009), something that could again produce apparently maladaptive features in the population as a whole. Similarly, it has been suggested that protandry could produce negative demographic consequences, and possible 'evolutionary suicide', simply by causing mate-limitation in females when population densities are low (Calabrese & Fagan 2004). These sometimes counterintuitive evolutionary dynamics specific to temporal traits deserve more attention.

There may also be interesting interactions between plasticity and selection on phenological traits. The frequent occurrence of a genetic correlation between the mean value of life-history traits and plasticity in those same traits (Scheiner 1993) complicates the interpretation of selection on phenology (e.g. Nussey *et al.* 2005). In addition, phenotypic plasticity can reduce the strength of selection on the underlying traits, but it can also facilitate adaptation by allowing populations to persist long enough to undergo evolutionary change, or by exposing novel traits on which selection can act (Price *et al.* 2003). Plasticity in the timing of particular life-history stages influences the environmental conditions experienced by, and therefore the nature of selection on, these or later developmental stages (Donohue 2005). So, for example, plastic shifts to earlier flowering or leaf budburst in response to warming temperatures could result in selection for later phenology if early development exposes plants to frost damage. Alternatively, plastic shifts to earlier reproduction in an insect could lead to selection against obligate diapause in offspring if this allowed completion of a second generation per year. Similar ideas about opposing effects of selection and environment on phenotypes have been explored in studies of local adaptation along elevational or latitudinal gradients. For example, high-altitude populations have delayed phenologies relative to their low-elevation counterparts but have been selected for faster development (a phenomenon known as countergradient variation; Conover & Schultz 1995). However, interactions between plastic and genetic changes in phenology have received little study in the context of climate change (though see Crozier *et al.* 2008).

Finally, organisms may have means to 'escape'—either behaviourally or evolutionarily—apparent selection on phenology. For example, seasonal declines in a particular food item might select for increased diet breadth, diet switching or increased dispersal distance instead of earlier phenology. A full, multi-dimensional characterization of the adaptive landscape that would reveal these alternative trajectories will remain an unattainable ideal for most systems. Nevertheless, acknowledging these evolutionary options, as well as the constraints mentioned above, should better allow us to understand apparent failures to respond to selection on phenology.

7. FUTURE DIRECTIONS

In this introduction, we have tried to give a broad overview of the mechanisms governing phenology and the reasons why phenology is an important factor in evolutionary and ecological research. The articles in this special issue develop many of these topics further, and we hope the issue as a whole will stimulate more synthetic work in this field.

In particular, we perceive some key areas where future research could usefully be focused: first, stronger linkages are needed between the ecology and physiology of phenology. As Visser *et al.* (2010) show, a large body of physiological and chronobiological work relevant to eco-evolutionary studies of phenology has gone largely unnoticed by ecologists and evolutionary biologists because we consult different journals and use different terminologies. Awareness of the linkages between these fields should improve the mechanistic understanding of phenology and forecasts of climate change impacts. The articles by Wilczek *et al.* (2010) and Chuine (2010) illustrate the utility of taking a mechanistic approach to fundamental ecological questions (see also de Senerpont Domis *et al.* (2007) for an application in a different system). Furthermore, deeper knowledge of the developmental and physiological aspects of phenology should improve our understanding of the prospects for evolutionary change in phenological traits (cf. Metcalf & Mitchell-Olds 2009; Singer & Parmesan 2010). This too will be an important component of forecasts of climate change impacts on communities.

Second, there is a need for more information about population-level consequences of phenological variation. An increasing number of documented instances of apparent asynchrony between interacting species leads to obvious questions about the impacts of this asynchrony on the vital rates of the populations involved. Too often, it is impossible to answer these questions because we do not know the baseline degree of synchrony—weather conditions were variable even before recent accelerated climate change, and occasional mismatches must have arisen—and because we do not know how the specific interaction affects population growth rates (the work of Both *et al.* (2006) is a notable exception). It is possible that 'mismatched' species or individuals can often switch to other food sources or move elsewhere. As discussed by Miller-Rushing *et al.* (2010), the population biology of phenology is an area where much work remains to be done.

Third, we argue that an explicit recognition of phenology and seasonality will make for more realistic models of community and ecosystem processes and the ecological impacts of climate change. It is not enough to know the effects of mean annual temperatures and precipitation; we must also know the effects of timing of temperature anomalies and precipitation events. For instance, warming restricted to the cold season may have little impact on populations compared with summer warming, provided winter temperatures remain below a certain threshold (e.g. Yamanaka *et al.* 2008). Models that incorporate seasonal changes in conditions can reach qualitatively different conclusions than those that assume constant, equilibrium conditions (Steiner *et al.* 2009). Although this may seem an obvious point, most models of community dynamics still operate on the assumption of invariant, or randomly varying, environmental conditions. Similarly, many forecasts of climate-driven changes in species ranges ignore phenology (but see Chuine 2010). Forecasts that incorporate ecological information, particularly niche-based models (e.g. Araújo & Luoto 2007; Wiens *et al.* 2009), tend to focus on whether interacting species will occur in the same place, but neglect to consider whether the temporal aspect of their interactions will be disrupted. Including phenology in these forecasts could yield important insights into future species distributions and interactions.

Because of the interdisciplinary nature of phenology, and the ubiquity of phenological responses to climate change, there are many opportunities for novel synthetic research. Furthermore, timing, as a biological phenomenon, is unique. Unlike other variables, time is not only directional but completely asymmetric: early events can affect later ones, but not vice versa. A plant that germinates and bolts early in a season can change light conditions for its later neighbours, potentially yielding a competitive advantage. As climate conditions and season lengths continue to change, these temporal relationships will also evolve. We expect that the articles collected here will advance our understanding of these changes and point the way for future research.

We thank James Thomson and Elizabeth Wolkovich for their thoughtful comments on the manuscript. J.F. was supported by a scholarship from IODE, Canada.

REFERENCES

Abrams, P. A. & Rowe, L. 1996 The effects of predation on the age and size of maturity of prey. *Evolution* **50**, 1052–1061. (doi:10.2307/2410646)

Agrawal, A. F. & Stinchcombe, J. R. 2009 How much do genetic covariances alter the rate of adaptation? *Proc. R. Soc. B* **276**, 1183–1191. (doi:10.1098/rspb.2008.1671)

Altermatt, F. 2010 Climatic warming increases voltinism in European butterflies and moths. *Proc. R. Soc. B* **277**, 1281–1287. (doi:10.1098/rspb.2009.1910)

Aono, Y. & Kazui, K. 2008 Phenological data series of cherry tree flowering in Kyoto, Japan, and its application to reconstruction of springtime temperatures since the 9th century. *Int. J. Climatol.* **28**, 905–914. (doi:10.1002/joc.1594)

Araújo, M. B. & Luoto, M. 2007 The importance of biotic interactions for modelling species distributions under climate change. *Global Ecol. Biogeogr.* **16**, 743–753. (doi:10.1111/j.1466-8238.2007.00359.x)

Augspurger, C. K. 1981 Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators in *Hybanthus prunifolius* (Violaceae). *Ecology* **62**, 775–788. (doi:10.2307/1937745)

Ausín, I., Alonso-Blanco, C. & Martínez-Zapater, M. 2005 Environmental regulation of flowering. *Int. J. Dev. Biol.* **49**, 689–705. (doi:10.1387/ijdb.052022ia)

Balasubramanian, S. *et al.* 2006 The PHYTOCHROME C photoreceptor gene mediates natural variation in flowering and growth responses of *Arabidopsis thaliana*. *Nat. Genet.* **38**, 711–715. (doi:10.1038/ng1818)

Bauer, S., Gienapp, P. & Madsen, J. 2008 The relevance of environmental conditions for departure decision changes en route in migrating geese. *Ecology* **89**, 1953–1960. (doi:10.1890/07-1101.1)

Bawa, K. S. & Beach, J. H. 1981 Evolution of sexual systems in flowering plants. *Ann. MO Bot. Gard.* **68**, 254–274. (doi:10.2307/2398798)

Beatley, J. C. 1974 Phenological events and their environmental triggers in Mojave desert ecosystems. *Ecology* **55**, 856–863. (doi:10.2307/1934421)

Beebee, T. J. C. 1995 Amphibian breeding and climate. *Nature* **374**, 219–220. (doi:10.1038/374219a0)

Bosch, J. & Kemp, W. P. 2003 Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environ. Entomol.* **32**, 711–716. (doi:10.1603/0046-225X-32.4.711)

Bosch, J. & Kemp, W. P. 2004 Effect of pre-wintering and wintering temperature regimes on weight loss, survival, and emergence time in the mason bee *Osmia cornuta* (Hymenoptera: Megachilidae). *Apidologie* **35**, 469–479. (doi:10.1051/apido:2004035)

Bostock, J. & Riley, H. T. (eds) 1855 *The natural history of Pliny*. London, UK: H.G. Bohn.

Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006 Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81–83. (doi:10.1038/nature04539)

Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. & Visser, M. E. 2009 Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J. Anim. Ecol.* **78**, 73–83. (doi:10.1111/j.1365-2656.2008.01458.x)

Bradley, N. L., Leopold, A. C., Ross, J. & Huffaker, W. 1999 Phenological changes reflect climate change in Wisconsin. *Proc. Natl Acad. Sci. USA* **96**, 9701–9704. (doi:10.1073/pnas.96.17.9701)

Bradshaw, W. E. & Holzapfel, C. M. 2001 Genetic shift in photoperiod response correlated with global warming. *Proc. Natl Acad. Sci. USA* **98**, 14 509–14 511. (doi:10.1073/pnas.241391498)

Bradshaw, W. E. & Holzapfel, C. M. 2006 Evolutionary response to rapid climate change. *Science* **312**, 1477–1478. (doi:10.1126/science.1127000)

Brearley, F. Q., Proctor, J., Suriantata, Nagy, L., Dalrymple, G. & Voysey, B. C. 2007 Reproductive phenology over a 10-year period in a lowland evergreen rain forest of central Borneo. *J. Ecol.* **95**, 828–839. (doi:10.1111/j.1365-2745.2007.01258.x)

Brown, R. F. & Mayer, D. G. 1988 Representing cumulative germination. 2. The use of the Weibull function and other empirically derived curves. *Ann. Bot.* **61**, 127–138.

Buckler, E. S. *et al.* 2009 The genetic architecture of maize flowering time. *Science* **325**, 714–718. (doi:10.1126/science.1174276)

Calabrese, J. M. & Fagan, W. F. 2004 Lost in time, lonely, and single: reproductive asynchrony and the Allee effect. *Am. Nat.* **164**, 25–37.

Chuine, I. 2010 Why does phenology drive species distribution? *Phil. Trans. R. Soc. B* **365**, 3149–3160. (doi:10.1098/rstb.2010.0142)

Clausen, J., Keck, D. D. & Hiesey, W. M. 1941 Regional differentiation in plant species. *Am. Nat.* **75**, 231–250.

Cleland, E. E., Chiariello, N. R., Loarie, S. R., Mooney, H. A. & Field, C. B. 2006 Diverse responses of phenology to global changes in a grassland ecosystem. *Proc. Natl Acad.*

Sci. USA **103**, 13 740–13 744. (doi:10.1073/pnas.0600815103)

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A. & Schwartz, M. D. 2007 Shifting plant phenology in response to global change. *Trends Ecol. Evol.* **22**, 357–365. (doi:10.1016/j.tree.2007.04.003)

Cloudsley-Thompson, J. L. 1991 *Ecophysiology of desert arthropods and reptiles*. Berlin, Germany: Springer-Verlag.

Conover, D. O. & Schultz, E. T. 1995 Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends Ecol. Evol.* **10**, 248–252. (doi:10.1016/S0169-5347(00)89081-3)

Corbet, P. S. 1954 Seasonal regulation in British dragonflies. *Nature* **174**, 655–655. (doi:10.1038/174655a0)

Crick, H. Q. P. & Sparks, T. H. 1999 Climate change related to egg-laying trends. *Nature* **399**, 423–424. (doi:10.1038/20839)

Crozier, L. G., Hendry, A. P., Lawson, P. W., Quinn, T. P., Mantua, N. J., Battin, J., Shaw, R. G. & Huey, R. B. 2008 Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. *Evol. Appl.* **1**, 252–270. (doi:10.1111/j.1752-4571.2008.00033.x)

Danforth, B. N. 1999 Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proc. R. Soc. Lond. B* **266**, 1985–1994. (doi:10.1098/rspb.1999.0876)

Danks, H. V. 2006 Key themes in the study of seasonal adaptations in insects. II. Life-cycle patterns. *Appl. Entomol. Zool.* **41**, 1–13. (doi:10.1303/aez.2006.1)

Davis, C. C., Willis, C. G., Primack, R. B. & Miller-Rushing, A. J. 2010 The importance of phylogeny to the study of phenological response to global climate change. *Phil. Trans. R. Soc. B* **365**, 3201–3213. (doi:10.1098/rstb.2010.0130)

de Senerpont Domis, L. N., Mooij, W. M., Hülsmann, S., van Nes, E. H. & Scheffer, M. 2007 Can overwintering versus diapausing strategy in *Daphnia* determine match-mismatch events in zooplankton–algae interactions? *Oecologia* **150**, 682–698. (doi:10.1007/s00442-006-0549-2)

Devaux, C. & Lande, R. 2008 Incipient allochronic speciation due to non-selective assortative mating by flowering time, mutation and genetic drift. *Proc. R. Soc. B* **275**, 2723–2732. (doi:10.1098/rspb.2008.0882)

Diekmann, M. 1996 Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests of Sweden. *Can. J. Bot.* **74**, 528–537.

Diggle, P. K. 1999 Heteroblasty and the evolution of flowering phenologies. *Int. J. Plant Sci.* **160**(Suppl.), S123–S134.

Doebeli, M. & Dieckmann, U. 2000 Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am. Nat.* **156**, S77–S101.

Donohue, K. 2005 Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytol.* **166**, 83–92. (doi:10.1111/j.1469-8137.2005.01357.x)

Dunne, J. A., Harte, J. & Taylor, K. J. 2003 Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecol. Monogr.* **73**, 69–86. (doi:10.1890/0012-9615(2003)073[0069:SMFPRT]2.0.CO;2)

Durant, J. M., Hjermann, D. Ø, Ottersen, G. & Stenseth, N. C. 2007 Climate and the match or mismatch between predator requirements and resource availability. *Climate Res.* **33**, 271–283. (doi:10.3354/cr033271)

Eilertsen, H. C., Sandberg, S. & Tøllefsen, H. 1995 Photoperiodic control of diatom spore growth: a theory to explain the onset of phytoplankton blooms. *Mar. Ecol. Prog. Ser.* **116**, 303–307. (doi:10.3354/meps116303)

Ejsmond, M. J., Czarnołęski, M., Kapustka, F. & Kozłowski, J. 2010 How to time growth and reproduction during the vegetative season: an evolutionary choice for indeterminate growers in seasonal environments. *Am. Nat.* **175**, 551–563. (doi:10.1086/651589)

Ellebjerg, S. M., Tamstorf, M. P., Illeris, L., Michelsen, A. & Hansen, B. U. 2008 Inter-annual variability and controls of plant phenology and productivity at Zackenberg. *Adv. Ecol. Res.* **40**, 249–273. (doi:10.1016/S0065-2504(07)00011-6)

Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E. & Bernasconi, G. 2007 Time after time: flowering phenology and biotic interactions. *Trends Ecol. Evol.* **22**, 432–439. (doi:10.1016/j.tree.2007.05.006)

Embree, D. G. 1970 The diurnal and seasonal pattern of hatching of winter moth eggs, *Operophtera brumata* (Geometridae: Lepidoptera). *Can. Entomol.* **102**, 759–768. (doi:10.4039/Ent102759-6)

Etterson, J. R. & Shaw, R. G. 2001 Constraint to adaptive evolution in response to global warming. *Science* **294**, 151–154. (doi:10.1126/science.1063656)

Fitter, A. H. & Fitter, R. S. R. 2002 Rapid changes in flowering time in British plants. *Science* **296**, 1689–1691. (doi:10.1126/science.1071617)

Fitter, A. H., Fitter, R. S. R., Harris, I. T. B. & Williamson, M. H. 1995 Relationships between first flowering date and temperature in the flora of a locality in central England. *Funct. Ecol.* **9**, 55–60. (doi:10.2307/2390090)

Forrest, J. & Thomson, J. D. 2009 Pollinator experience, neophobia and the evolution of flowering time. *Proc. R. Soc. B* **276**, 935–943. (doi:10.1098/rspb.2008.1434)

Forrest, J. & Thomson, J. D. 2010 Consequences of variation in flowering time within and among individuals of *Mertensia fusiformis* (Boraginaceae), an early spring wildflower. *Am. J. Bot.* **97**, 38–48. (doi:10.3732/ajb.0900083)

Forrest, J., Inouye, D. W. & Thomson, J. D. 2010 Flowering phenology in subalpine meadows: does climate variation influence community co-flowering patterns? *Ecology* **91**, 431–440. (doi:10.1890/09-0099.1)

Fox, G. A. 2003 Assortative mating and plant phenology: evolutionary and practical consequences. *Evol. Ecol. Res.* **5**, 1–18.

Franks, S. J. & Weis, A. E. 2008 A change in climate causes rapid evolution of multiple life-history traits and their interactions in an annual plant. *J. Evol. Biol.* **21**, 1321–1334. (doi:10.1111/j.1420-9101.2008.01566.x)

Franks, S. J., Sim, S. & Weis, A. E. 2007 Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl Acad. Sci. USA* **104**, 1278–1282. (doi:10.1073/pnas.0608379104)

Garner, W. W. & Allard, H. A. 1920 Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *J. Agric. Res.* **18**, 553–606.

Geber, M. A. & Griffen, L. R. 2003 Inheritance and natural selection on functional traits. *Int. J. Plant Sci.* **164**, S21–S42. (doi:10.1086/368233)

Gienapp, P., Postma, E. & Visser, M. E. 2006 Why breeding time has not responded to selection for earlier breeding in a songbird population. *Evolution* **6**, 2381–2388.

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merilä, J. 2008 Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* **17**, 167–178. (doi:10.1111/j.1365-294X.2007.03413.x)

Gilbert, J. J. 1974 Dormancy in rotifers. *Trans. Am. Microsc. Soc.* **93**, 490–513. (doi:10.2307/3225154)

Gillooly, J. F., Charnov, E. L., West, G. B., Savage, V. M. & Brown, J. H. 2002 Effects of size and temperature on developmental time. *Nature* **417**, 70–73. (doi:10.1038/417070a)

Goldman, B. D. 2001 Mammalian photoperiodic system: formal properties and neuroendocrine mechanisms of photoperiodic time measurement. *J. Biol. Rhythms* **16**, 283–301. (doi:10.1177/074873001129001980)

Gwinner, E. 1996 Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199**, 39–48.

Harrington, R., Woiwod, I. & Sparks, T. 1999 Climate change and trophic interactions. *Trends Ecol. Evol.* **14**, 146–150. (doi:10.1016/S0169-5347(99)01604-3)

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. 2009 How does climate warming affect plant–pollinator interactions? *Ecol. Lett.* **12**, 184–195. (doi:10.1111/j.1461-0248.2008.01269.x)

Henderson, I. R., Shindo, C. & Dean, C. 2003 The need for winter in the switch to flowering. *Annu. Rev. Genet.* **37**, 371–392. (doi:10.1146/annurev.genet.37.110801.142640)

Hendry, A. P. & Day, T. 2005 Population structure attributable to reproductive time: isolation by time and adaptation by time. *Mol. Ecol.* **14**, 901–916. (doi:10.1111/j.1365-294X.2005.02480.x)

Hopkins, A. D. 1918 Periodical events and natural law as guides to agricultural research and practice. *Monthly Weather Rev.* Suppl. 9, 1–42.

Høye, T. T. & Forchhammer, M. C. 2008 Phenology of high-arctic arthropods: effects of climate on spatial, seasonal, and inter-annual variation. *Adv. Ecol. Res.* **40**, 299–324. (doi:10.1016/S0065-2504(07)00013-X)

Hülber, K., Winkler, M. & Grabherr, G. 2010 Intraseasonal climate and habitat-specific variability controls the flowering phenology of high-alpine plant species. *Funct. Ecol.* **24**, 245–252. (doi:10.1111/j.1365-2435.2009.01645.x)

Husby, A., Kruuk, L. E. B. & Visser, M. E. 2009 Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. *Proc. R. Soc. B* **276**, 1845–1854. (doi:10.1098/rspb.2008.1937)

Ibáñez, I., Primack, R. B., Miller-Rushing, A. J., Ellwood, E., Higuchi, H., Lee, S. D., Kobori, H. & Silander, J. A. 2010 Forecasting phenology under global warming. *Phil. Trans. R. Soc. B* **365**, 3247–3260. (doi:10.1098/rstb.2010.0120)

Ims, R. A. 1990 The ecology and evolution of reproductive synchrony. *Trends Ecol. Evol.* **5**, 135–140. (doi:10.1016/0169-5347(90)90218-3)

Inouye, D. W. 2008 Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* **89**, 353–362. (doi:10.1890/06-2128.1)

Jackson, M. T. 1966 Effects of microclimate on spring flowering phenology. *Ecology* **47**, 407–415. (doi:10.2307/1932980)

Janzen, D. H. 1967 Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* **21**, 620–637. (doi:10.2307/2406621)

Jönsson, A. M., Appelberg, G., Harding, S. & Bärring, L. 2009 Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle *Ips typographus*. *Global Change Biol.* **15**, 486–499. (doi:10.1111/j.1365-2486.2008.01742.x)

Kelly, D. & Sork, V. L. 2002 Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* **33**, 427–447. (doi:10.1146/annurev.ecolsys.33.020602.095433)

Kemp, W. P. & Dennis, B. 1989 Development of two rangeland grasshoppers at constant temperatures: development thresholds revisited. *Can. Entomol.* **121**, 363–371. (doi:10.4039/Ent121363-4)

Kemp, W. P. & Onsager, J. A. 1986 Rangeland grasshoppers (Orthoptera: Acrididae): modeling phenology of natural populations of six species. *Environ. Entomol.* **15**, 924–930.

Kemp, W. P., Dennis, B. & Beckwith, R. C. 1986 Stochastic phenology model for the western spruce budworm (Lepidoptera: Tortricidae). *Environ. Entomol.* **15**, 547–554.

Kimball, S., Angert, A. L., Huxman, T. E. & Venable, D. L. 2010 Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Global Change Biol.* **16**, 1555–1565. (doi:10.1111/j.1365-2486.2009.02106.x)

Kimberling, D. N. & Miller, J. C. 1988 Effects of temperature on larval eclosion of the winter moth, *Operophtera brumata*. *Entomol. Exp. Appl.* **47**, 249–254. (doi:10.1007/BF00352211)

Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P. & Beerli, P. 2001 The strength of phenotypic selection in natural populations. *Am. Nat.* **157**, 245–261.

Laaksonen, T., Ahola, M., Eeva, T., Väisänen, R. A. & Lehikoinen, E. 2006 Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. *Oikos* **114**, 277–290. (doi:10.1111/j.2006.0030-1299.14652.x)

Leopold, A. & Jones, S. E. 1947 A phenological record for Sauk and Dane Counties, Wisconsin, 1935–1945. *Ecol. Monogr.* **17**, 81–122. (doi:10.2307/1948614)

Liedvogel, M., Szulkin, M., Knowles, S. C. L., Wood, M. J. & Sheldon, B. C. 2009 Phenotypic correlates of *Clock* gene variation in a wild blue tit population: evidence for a role in seasonal timing of reproduction. *Mol. Ecol.* **18**, 2444–2456. (doi:10.1111/j.1365-294X.2009.04204.x)

Logan, J. A., Régnière, J. & Powell, J. A. 2003 Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* **1**, 130–137. (doi:10.1890/1540-9295(2003)001[0130:ATIOGW]2.0.CO;2)

Masaki, S. 1967 Geographic variation and climatic adaptation in a field cricket (Orthoptera: Gryllidae). *Evolution* **21**, 725–741. (doi:10.2307/2406770)

Mazaki, S. 1980 Summer diapause. *Annu. Rev. Entomol.* **25**, 1–25.

Mazer, S. J. & LeBuhn, G. 1999 Genetic variation in life-history traits: heritability estimates within and genetic differentiation among populations. In *Life history evolution in plants* (eds T. O. Vuorisalo & P. K. Mutikainen), pp. 85–171. Dordrecht, The Netherlands: Kluwer Academic.

Medway, L. 1972 Phenology of a tropical rain forest in Malaya. *Biol. J. Linn. Soc.* **4**, 117–146. (doi:10.1111/j.1095-8312.1972.tb00692.x)

Memmott, J., Craze, P. G., Waser, N. M. & Price, M. V. 2007 Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* **10**, 710–717. (doi:10.1111/j.1461-0248.2007.01061.x)

Metcalf, C. J. E. & Mitchell-Olds, T. 2009 Life history in a model system: opening the black box with *Arabidopsis thaliana*. *Ecol. Lett.* **12**, 593–600. (doi:10.1111/j.1461-0248.2009.01320.x)

Miller-Rushing, A. J. & Primack, R. B. 2008 Global warming and flowering times in Thoreau's Concord: a community perspective. *Ecology* **89**, 332–341. (doi:10.1890/07-0068.1)

Miller-Rushing, A. J., Katsuki, T., Primack, R. B., Ishii, Y., Lee, S. D. & Higuchi, H. 2007 Impact of global warming on a group of related species and their hybrids: cherry tree (Rosaceae) flowering at Mt. Takao, Japan. *Am. J. Bot.* **94**, 1470–1478. (doi:10.3732/ajb.94.9.1470)

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. & Post, E. 2010 The effects of phenological mismatches on demography. *Phil. Trans. R. Soc. B* **365**, 3177–3186. (doi:10.1098/rstb.2010.0148)

Mitchell-Olds, T. 1996 Genetic constraints on life-history evolution: quantitative-trait loci influencing growth and flowering in *Arabidopsis thaliana*. *Evolution* **50**, 140–145. (doi:10.2307/2410788)

Møller, A. P., Balbontín, J., Cuervo, J. J., Hermosell, I. G. & de Lope, F. 2009 Individual differences in protandry, sexual selection, and fitness. *Behav. Ecol.* **20**, 433–440. (doi:10.1093/beheco/arn142)

Morbey, Y. E. & Ydenberg, R. C. 2001 Protandrous arrival timing to breeding areas: a review. *Ecol. Lett.* **4**, 663–673. (doi:10.1046/j.1461-0248.2001.00265.x)

Morin, X., Lechowicz, M. J., Augspurger, C., O'Keefe, J., Viner, D. & Chuine, I. 2009 Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biol.* **15**, 961–975. (doi:10.1111/j.1365-2486.2008.01735.x)

Murray, M. B., Cannell, M. G. R. & Smith, R. I. 1989 Date of budburst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* **26**, 693–700.

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G. & Nemani, R. R. 1997 Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**, 698–702. (doi:10.1038/386698a0)

Nève, G. & Singer, M. C. 2008 Protandry and postandry in two related butterflies: conflicting evidence about sex-specific trade-offs between adult size and emergence time. *Evol. Ecol.* **22**, 701–709.

Nussey, D. H., Postma, E., Gienapp, P. & Visser, M. E. 2005 Selection on heritable phenotypic plasticity in a wild bird population. *Science* **310**, 304–306. (doi:10.1126/science.1117004)

Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)

Paterniani, E. 1969 Selection for reproductive isolation between two populations of maize, *Zea mays* L. *Evolution* **23**, 534–547. (doi:10.2307/2406851)

Piao, S., Friedlingstein, P., Ciais, P., Viovy, N. & Demarty, J. 2007 Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Global Biogeochem. Cycles* **21**, GB3018. (doi:10.1029/2006GB002888)

Post, E., Pedersen, C., Wilmers, C. C. & Forchhammer, M. C. 2008 Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proc. R. Soc. B* **275**, 2005–2013. (doi:10.1098/rspb.2008.0463)

Price, T., Kirkpatrick, M. & Arnold, S. J. 1988 Directional selection and the evolution of breeding date in birds. *Science* **240**, 798–799. (doi:10.1126/science.3363360)

Price, T. D., Qvarnström, A. & Irwin, D. E. 2003 The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. B* **270**, 1433–1440. (doi:10.1098/rspb.2003.2372)

Rabinowitz, D., Rapp, J. K., Sork, V. L., Rathcke, B. J., Reese, G. A. & Weaver, J. C. 1981 Phenological properties of wind- and insect-pollinated prairie plants. *Ecology* **62**, 49–56. (doi:10.2307/1936667)

Rathcke, B. & Lacey, E. P. 1985 Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* **16**, 179–214. (doi:10.1146/annurev.es.16.110185.001143)

Réale, D., McAdam, A. G., Boutin, S. & Berteaux, D. 2003 Genetic and plastic responses of a northern mammal to climate change. *Proc. R. Soc. Lond. B* **270**, 591–596. (doi:10.1098/rspb.2002.2224)

Reed, T. E., Warzybok, P., Wilson, A. J., Bradley, R. W., Wanless, S. & Sydeman, W. J. 2009 Timing is everything: flexible phenology and shifting selection in a colonial seabird. *J. Anim. Ecol.* **78**, 376–387. (doi:10.1111/j.1365-2656.2008.01503.x)

Régnière, J., Lavigne, D., Dupont, A. & Carter, N. 2007 Predicting the seasonal development of the yellowheaded spruce sawfly (Hymenoptera: Tenthredinidae) in eastern Canada. *Can. Entomol.* **139**, 365–377. (doi:10.4039/N06-054)

Richardson, A. D. *et al.* 2010 Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Phil. Trans. R. Soc. B* **365**, 3227–3246. (doi:10.1098/rstb.2010.0102)

Robertson, C. 1924 Phenology of entomophilous flowers. *Ecology* **5**, 393–407. (doi:10.2307/1929302)

Roff, D. A. 1980 Optimizing development time in a seasonal environment: the 'ups and downs' of clinal variation. *Oecologia* **45**, 202–208. (doi:10.1007/BF00346461)

Rowe, L., Ludwig, D. & Schluter, D. 1994 Time, condition, and the seasonal decline of avian clutch size. *Am. Nat.* **143**, 698–772.

Roy, D. B. & Sparks, T. H. 2000 Phenology of British butterflies and climate change. *Global Change Biol.* **6**, 407–416. (doi:10.1046/j.1365-2486.2000.00322.x)

Saino, N., Szép, T., Romano, M., Rubolini, D., Spina, F. & Møller, A. P. 2004 Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol. Lett.* **7**, 21–25. (doi:10.1046/j.1461-0248.2003.00553.x)

Sandrelli, F. *et al.* 2007 A molecular basis for natural selection at the *timeless* locus in *Drosophila melanogaster*. *Science* **316**, 1898–1900. (doi:10.1126/science.1138426)

Scheiner, S. M. 1993 Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* **24**, 35–68. (doi:10.1146/annurev.es.24.110193.000343)

Schwartz, M. D., Carbone, G. J., Reighard, G. L. & Okie, W. R. 1997 A model to predict peach phenology and maturity using meteorological variables. *Hortscience* **32**, 213–216.

Sherry, R. A., Zhou, X. H., Gu, S. L., Arnone, J. A., Schimel, D. S., Verburg, P. S., Wallace, L. L. & Luo, Y. Q. 2007 Divergence of reproductive phenology under climate warming. *Proc. Natl Acad. Sci. USA* **104**, 198–202. (doi:10.1073/pnas.0605642104)

Singer, M. C. & Parmesan, C. 2010 Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Phil. Trans. R. Soc. B* **365**, 3161–3176. (doi:10.1098/rstb.2010.0144)

Sparks, T. H. & Menzel, A. 2002 Observed changes in seasons: an overview. *Int. J. Climatol.* **22**, 1715–1725. (doi:10.1002/joc.821)

Sparks, T. H., Jeffree, E. P. & Jeffree, C. E. 2000 An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *Int. J. Biometeorol.* **44**, 82–87. (doi:10.1007/s004840000049)

Sparks, T. H., Bairlein, F., Bojarinova, J. G., Hüppop, O., Lehikoinen, E. A., Rainio, K., Sokolov, L. V. & Walker, D. 2005 Examining the total arrival distribution of migratory birds. *Global Change Biol.* **11**, 22–30. (doi:10.1111/j.1365-2486.2004.00887.x)

Steiner, C. F., Schwaderer, A. S., Huber, V., Klausmeier, C. A. & Litchman, E. 2009 Periodically forced food-chain dynamics: model predictions and experimental validation. *Ecology* **90**, 3099–3107. (doi:10.1890/08-2377.1)

Steltzer, H., Landry, C., Painter, T. H., Anderson, J. & Ayres, E. 2009 Biological consequences of earlier snowmelt from desert dust deposition in alpine landscapes. *Proc. Natl Acad. Sci. USA* **106**, 11 629–11 634. (doi:10.1073/pnas.0900758106)

Stinchcombe, J. R., Weinig, C., Ungerer, M., Olsen, K. M., Mays, C., Halldorsdottir, S. S., Purugganan, M. D. & Schmitt, J. 2004 A latitudinal cline in flowering time in *Arabidopsis thaliana* modulated by the flowering time gene *FRIGIDA*. *Proc. Natl Acad. Sci. USA* **101**, 4712–4717. (doi:10.1073/pnas.0306401101)

Stross, R. G. & Hill, J. C. 1968 Photoperiod control of winter diapause in the fresh-water crustacean, *Daphnia*. *Biol. Bull.* **134**, 176–198. (doi:10.2307/1539976)

Tauber, M. J., Tauber, C. A. & Masaki, S. 1986 *Seasonal adaptations of insects*. New York, NY: Oxford University Press.

Tauber, E. *et al.* 2007 Natural selection favors a newly derived *timeless* allele in *Drosophila melanogaster*. *Science* **316**, 1895–1898. (doi:10.1126/science.1138412)

Thomson, J. D. 2010 Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Phil. Trans. R. Soc. B* **365**, 3187–3199. (doi:10.1098/rstb.2010.0115)

Thórhallsdóttir, T. E. 1998 Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia* **114**, 43–49.

Tobin, P. C., Nagarkatti, S., Loeb, G. & Saunders, M. C. 2008 Historical projected interactions between climate change insect voltinism in a multivoltine species. *Global Change Biol.* **14**, 951–957. (doi:10.1111/j.1365-2486.2008.01561.x)

van Asch, M., van Tienderen, P. H., Holleman, L. J. M. & Visser, M. E. 2007 Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biol.* **13**, 1596–1604. (doi:10.1111/j.1365-2486.2007.01400.x)

Van Dijk, H. & Hautekèete, N. 2007 Long day plants and the response to global warming: rapid evolutionary change in day length sensitivity is possible in wild beet. *J. Evol. Biol.* **20**, 349–357. (doi:10.1111/j.1420-9101.2006.01192.x)

van Noordwijk, A. J. & de Jong, G. 1986 Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* **128**, 137–142.

van Nouhuys, S. & Lei, G. C. 2004 Parasitoid–host metapopulation dynamics: the causes and consequences of phenological asynchrony. *J. Anim. Ecol.* **73**, 526–535. (doi:10.1111/j.0021-8790.2004.00827.x)

van Schaik, C. P., Terborgh, J. W. & Wright, S. J. 1993 The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* **24**, 353–377. (doi:10.1146/annurev.es.24.110193.002033)

Verhulst, S., Tinbergen, J. M. & Daan, S. 1997 Multiple breeding in the great tit. A trade-off between successive reproductive attempts? *Funct. Ecol.* **11**, 714–722. (doi:10.1046/j.1365-2435.1997.00145.x)

Visser, M. E. 2008 Keeping up with a warming world: assessing the rate of adaptation to climate change. *Proc. R. Soc. B* **275**, 649–659. (doi:10.1098/rspb.2007.0997)

Visser, M. E., Caro, S. P., van Oers, K., Schaper, S. V. & Helm, B. 2010 Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Phil. Trans. R. Soc. B* **365**, 3113–3127. (doi:10.1098/rstb.2010.0111)

Wang, R., Farrona, S., Vincent, C., Joecker, A., Schoof, H., Turck, F., Alonso-Blanco, C., Coupland, G. & Albani, M. C. 2009 *PEP1* regulates perennial flowering in *Arabis alpina*. *Nature* **459**, 423–427. (doi:10.1038/nature07988)

Wayne, N. L. 2001 Regulation of seasonal reproduction in mollusks. *J. Biol. Rhythms* **16**, 391–402. (doi:10.1177/074873001129002097)

Weis, A. E. 2005 Direct and indirect assortative mating: a multivariate approach to plant flowering schedules. *J. Evol. Biol.* **18**, 536–546. (doi:10.1111/j.1420-9101.2005.00891.x)

Weis, A. E. & Kossler, T. M. 2004 Genetic variation in flowering time induces phenological assortative mating: quantitative genetic methods applied to *Brassica rapa*. *Am. J. Bot.* **91**, 825–836. (doi:10.3732/ajb.91.6.825)

Werner, E. E. 1986 Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *Am. Nat.* **128**, 319–341.

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A. & Snyder, M. A. 2009 Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl Acad. Sci. USA* **106**, 19 729–19 736. (doi:10.1073/pnas.0901639106)

Wiklund, C. & Fagerström, T. 1977 Why do males emerge before females? *Oecologia* **31**, 153–158. (doi:10.1007/BF00346917)

Wilczek, A. M. *et al.* 2009 Effects of genetic perturbation on seasonal life history plasticity. *Science* **323**, 930–934. (doi:10.1126/science.1165826)

Wilczek, A. M., Burghardt, L. T., Cobb, A. R., Cooper, M. D., Welch, S. M. & Schmitt, J. 2010 Genetic and physiological bases for phenological responses to current and predicted climates. *Phil. Trans. R. Soc. B* **365**, 3129–3147. (doi:10.1098/rstb.2010.0128)

Williams-Howze, J. 1997 Dormancy in the free-living copepod orders Cyclopoida, Calanoida, and Harpacticoida. *Oceanogr. Mar. Biol. Annu. Rev.* **35**, 257–321.

Winder, M. & Cloern, J. E. 2010 The annual cycles of phytoplankton biomass. *Phil. Trans. R. Soc. B* **365**, 3215–3226. (doi:10.1098/rstb.2010.0125)

Wolkovich, E. M. & Cleland, E. E. In press. The phenology of plant invasions: a community ecology perspective. *Front. Ecol. Environ.*

Yamanaka, T., Tatsuki, S. & Shimada, M. 2008 Adaptation to the new land or effect of global warming? An age-structured model for rapid voltinism change in an alien lepidopteran pest. *J. Anim. Ecol.* **77**, 585–596. (doi:10.1111/j.1365-2656.2008.01367.x)

Zhang, X., Friedl, M. A. & Schaaf, C. B. 2006 Global vegetation phenology from Moderate Resolution Imaging Spectroradiometer (MODIS): evaluation of global patterns and comparison with *in situ* measurements. *J. Geophys. Res.* **111**, G04017. (doi:10.1029/2006JG000217)

Zhang, X., Tarpley, D. & Sullivan, J. T. 2007 Diverse responses of vegetation phenology to a warming climate. *Geophys. Res. Lett.* **34**, L19405. (doi:10.1029/2007GL031447)

Zimmerman, J. K., Roubik, D. W. & Ackerman, J. D. 1989 Asynchronous phenologies of a neotropical orchid and its euglossine bee pollinator. *Ecology* **70**, 1192–1195. (doi:10.2307/1941389)

Ecological and Evolutionary Responses to Recent Climate Change

Camille Parmesan

Section of Integrative Biology, University of Texas, Austin, Texas 78712;
email: parmesan@mail.utexas.edu

Annu. Rev. Ecol. Evol. Syst. 2006. 37:637–69

The *Annual Review of Ecology, Evolution, and Systematics* is online at
http://ecolsys.annualreviews.org

This article's doi:
10.1146/annurev.ecolsys.37.091305.110100

1543-592X/06/1201-0637$20.00

Key Words

aquatic, global warming, phenology, range shift, terrestrial, trophic asynchrony

Abstract

Ecological changes in the phenology and distribution of plants and animals are occurring in all well-studied marine, freshwater, and terrestrial groups. These observed changes are heavily biased in the directions predicted from global warming and have been linked to local or regional climate change through correlations between climate and biological variation, field and laboratory experiments, and physiological research. Range-restricted species, particularly polar and mountaintop species, show severe range contractions and have been the first groups in which entire species have gone extinct due to recent climate change. Tropical coral reefs and amphibians have been most negatively affected. Predator-prey and plant-insect interactions have been disrupted when interacting species have responded differently to warming. Evolutionary adaptations to warmer conditions have occurred in the interiors of species' ranges, and resource use and dispersal have evolved rapidly at expanding range margins. Observed genetic shifts modulate local effects of climate change, but there is little evidence that they will mitigate negative effects at the species level.

INTRODUCTION

Historical Perspective

Climate change is not a new topic in biology. The study of biological impacts of climate change has a rich history in the scientific literature, since long before there were political ramifications. Grinnell (1917) first elucidated the role of climatic thresholds in constraining the geographic boundaries of many species, followed by major works by Andrewartha & Birch (1954) and MacArthur (1972). Observations of range shifts in parallel with climate change have been particularly rich in northern European countries, where observational records for many birds, butterflies, herbs, and trees date back to the mid-1700s. Since the early part of the twentieth century, researchers have documented the sensitivity of insects to spring and summer temperatures (Bale et al. 2002, Dennis 1993, Uvarov 1931). Ford (1945) described northward range shifts of several butterflies in England, attributing these shifts to a summer warming trend that began around 1915 in Britain. Ford noted that one of these species, *Limenitis camilla*, expanded to occupy an area where attempted introductions prior to the warming had failed. Kaisila (1962) independently documented range shifts of Lepidoptera (primarily moths) in Finland, using historical data on range boundaries dating back to 1760. He showed repeated instances of southward contractions during decades of "harsh" climatic conditions (cold wet summers), followed by northward range expansion during decades with climate "amelioration" (warm summers and lack of extreme cold in winter). Further corroboration came from the strong correlations between summer temperatures and the northern range boundaries for many butterflies (Dennis 1993).

Similar databases exist for northern European birds. A burst of papers documented changed abundances and northerly range shifts of birds in Iceland, Finland, and Britain associated with the 1930s–1940s warming period (Gudmundsson 1951; Harris 1964; Kalela 1949, 1952; Salomonsen 1948). A second wave of papers in the 1970s described the subsequent retreats of many of these temperate bird and butterfly species following the cool, wet period of the 1950s–1960s (Burton 1975, Heath 1974, Severnty 1977, Williamson 1975).

Complementing this rich observational database is more than 100 years of basic research on the processes by which climate and extreme weather events affect plants and animals. As early as the 1890s, Bumpus (1899) noted the differential effects of an extreme winter storm on the introduced house sparrow (*Parus domesticus)*, resulting in stabilizing selection for intermediate body size in females and directional selection for large body size in males (Johnston et al. 1972). The first extensive studies of climate variability as a powerful driver of population evolution date back to the 1940s, when Dobzhansky (1943, 1947) discovered repeated cycles of seasonal evolution of temperature-associated chromosomal inversions within *Drosophila pseudoobscura* populations in response to temperature changes from spring through summer.

In summary, the history of biological research is rich in both mechanistic and observational studies of the impacts of extreme weather and climate change on wild species: Research encompasses impacts of single extreme weather events; experimental studies of physiological tolerances; snapshot correlations between climatic variables and species' distributions; and correlations through time between climatic trends and changes in distributions, phenologies, genetics, and behaviors of wild plants and animals.

Anthropogenic Climate Change

In spite of this wealth of literature on the fundamental importance of climate to wild biota, biologists have been reluctant to believe that modern (greenhouse gas-driven) climate change is a cause of concern for biodiversity. In his introduction to the 1992 *Annual Review of Ecology, Evolution, and Systematics* volume on "Global Environmental Change," Vitousek wrote, "ultimately, climate change probably has the greatest potential to alter the functioning of the Earth system . . . . nevertheless, the major effects of climate change are mostly in the future while most of the others are already with us." Individual authors in that volume tended to agree—papers were predominantly concerned with other global change factors: land use change, nitrogen fertilization, and the direct effects of increased atmospheric CO_2 on plant ecophysiology.

Just 14 years later, the direct impacts of anthropogenic climate change have been documented on every continent, in every ocean, and in most major taxonomic groups (reviewed in Badeck et al. 2004; Hoegh-Guldberg 1999, 2005b; Hughes 2000; IPCC 2001a; Parmesan 2005b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Sparks & Menzel 2002; Thomas 2005; Walther et al. 2002, 2005). The issue of whether observed biological changes can be conclusively linked to anthropogenic climate change has been analyzed and discussed at length in a plethora of syntheses, including those listed above. Similarly, complexity surrounding methodological issues of detection (correctly detecting a real trend) and attribution (assigning causation) has been explored in depth (Ahmad et al. 2001; Dose & Menzel 2004; Parmesan 2002, 2005a,b; Parmesan & Yohe 2003; Parmesan et al. 2000; Root et al. 2003, Root & Hughes 2005, Schwartz 1998, 1999; Shoo et al. 2006). The consensus is that, with proper attention to sampling and other statistical issues and through the use of scientific inference, studies of observed biological changes can provide rigorous tests of climate-change hypotheses. In particular, independent syntheses of studies worldwide have provided a clear, globally coherent conclusion: Twentieth-century anthropogenic global warming has already affected Earth's biota.

Detection: ability to discern long-term trends above yearly variability and real changes from apparent changes brought about by changes in sampling methodology and/or sampling intensity

Attribution: teasing out climate change as the causal driver of an observed biological change amid a backdrop of potential confounding factors

Globally coherent: a common term in economics, a process or event is globally coherent when it has similar effect across multiple systems spread across different locations throughout the world

Scope of This Review

This review concentrates on studies of particularly long time series and/or particularly good mechanistic understanding of causes of observed changes. It deals exclusively with observed responses of wild biological species and systems to recent, anthropogenic climate change. In particular, agricultural impacts, human health, and ecosystem-level responses (e.g., carbon cycling) are not discussed. Because they have been extensively dealt with in previous publications, this review does not repeat discussions of detection and attribution, nor of the conservation implications of climate change. Rather, some of the best-understood cases are presented to illustrate the complex ways in which various facets of climatic change impact wild biota. The choice of studies for illustration attempts to draw attention to the taxonomic and geographic breadth of climate-change impacts and to the most-recent literature not already represented in prior reviews.

Researchers have frequently associated biological processes with indices of ocean-atmosphere dynamics, such as the El Niño Southern Oscillation and the North Atlantic Oscillation (Blenckner & Hillebrand 2002, Holmgren et al. 2001, Ottersen et al. 2001). However, the nature of the relationship between atmospheric dynamics, ocean circulation, and temperature is changing (Alley et al. 2003, IPCC 2001b, Karl & Trenberth 2003, Meehl et al. 2000). Therefore, there is large uncertainty as to how past relationships between biological systems and ocean indices reflect responses to ongoing anthropogenic climate change. Although I use individual examples where appropriate, this complex topic is not fully reviewed here.

OVERVIEW OF IMPACTS LITERATURE

An extensive, but not exhaustive, literature search revealed 866 peer-reviewed papers that documented changes through time in species or systems that could, in whole or in part, be attributed to climate change. Some interesting broad patterns are revealed. Notably, the publication rate of climate-change responses increases sharply each year. The number of publications between 1899 and January 2003 (the date of two major syntheses) was 528. Therefore, approximately 40% of the 866 papers compiled for this review were published in the past three years (January 2003 to January 2006).

The studies are spread broadly across taxonomic groups. Whereas distributional studies concentrated on animals rather than plants, the reverse is true of phenological time series. This may simply be because historical data on species range boundaries have higher resolution for animals than for plants. Conversely, local records of spring events are much more numerous for plants (e.g., flowering and leaf out) than for animals (e.g., nesting).

Although there is still a terrestrial bias, studies in marine and freshwater environments are increasing in proportional representation. The largest gaps are geographic rather than taxonomic. In absolute numbers, most biological impact studies are from North America, northern Europe and Russia. Few biological studies have come from South America, and there are large holes in Africa and Asia, with most of the studies from these two continents coming from just two countries: South Africa and Japan. In past decades, Australia's impact studies have stemmed predominantly from the coral reef community, but in recent years scientists have dug deep to find historical data, and terrestrial impact studies are now emerging. Similarly, the Mediterranean/North African region (Spain, France, Italy, and Israel) has recently spawned a spate of studies. Antarctica stands out as a region where impacts (or lack of impacts) on most species and systems have been documented, even though data often have large geographic or temporal gaps.

Few studies have been conducted at a scale that encompasses an entire species' range (i.e., a continental scale), with only a moderate number at the regional scale (e.g., the United Kingdom or Germany). Most have been conducted at local scales, typically at a research station or preserve. Continental-scale studies usually cover most or all of a species' range in terrestrial systems (Both et al. 2004, Burton 1998a,b, Dunn & Winkler 1999, Menzel & Fabian 1999, Parmesan 1996, Parmesan et al. 1999). However, even a continental scale cannot encompass the entire ranges of many oceanic species (Ainley & Divoky 1998, Ainley et al. 2003, Beaugrand et al. 2002, Croxall et al. 2002, Hoegh-Gulberg 1999, McGowan et al. 1998, Reid et al. 1998, Spear & Ainley 1999). Terrestrial endemics, in contrast, can have such small ranges that regional, or even local, studies may represent impacts on entire species (Pounds et al. 1999, 2006).

Meta-analysis: set of statistical techniques designed to synthesize quantitative results from similar and independent experiments

Meta-Analyses and Syntheses: Globally Coherent Signals of Climate-Change Impacts

A handful of studies have conducted statistical meta-analyses of species' responses or have synthesized independent studies to reveal emergent patterns. The clear conclusion across global syntheses is that twentieth-century anthropogenic global warming has already affected the Earth's biota (IPCC 2001a; Parmesan 2005a,b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Thomas 2005; Walther et al. 2002, 2005).

One study estimated that more than half (59%) of 1598 species exhibited measurable changes in their phenologies and/or distributions over the past 20 to 140 years (Parmesan & Yohe 2003). Analyses restricted to species that exhibited change documented that these changes were not random: They were systematically and predominantly in the direction expected from regional changes in the climate (Parmesan & Yohe 2003, Root et al. 2003). Responding species are spread across diverse ecosystems (from temperate grasslands to marine intertidal zones and tropical cloud forests) and come from a wide variety of taxonomic and functional groups, including birds, butterflies, alpine flowers, and coral reefs.

A meta-analysis of range boundary changes in the Northern Hemisphere estimated that northern and upper elevational boundaries had moved, on average, 6.1 km per decade northward or 6.1 m per decade upward ($P < 0.02$) (Parmesan & Yohe 2003). Quantitative analyses of phenological responses gave estimates of advancement of 2.3 days per decade across all species (Parmesan & Yohe 2003) and 5.1 days per decade for the subset of species showing substantive change (>1 day per decade) (Root et al. 2003).

A surprising result is the high proportion of species responding to recent, relatively mild climate change (global average warming of 0.6°C). The proportion of wild species impacted by climate change was estimated at 41% of all species (655 of 1598) (Parmesan & Yohe 2003). This estimate was derived by focusing on multispecies studies that reported stable as well as responding species. Because responders and stable species were often sympatric, variation of response is not merely a consequence of differential magnitudes of climate change experienced.

PHENOLOGICAL CHANGES

By far, most observations of climate-change responses have involved alterations of species' phenologies. This is partly a result of the tight links between the seasons and agriculture: Planting and harvest dates (and associated climatic events such as day of last frost) have been well recorded, dating back hundreds of years for some crops. But the plethora of records also stems from the strong sociological significance of the change of the seasons, particularly in high-latitude countries. Peoples of Great Britain, the Netherlands, Sweden, and Finland have been keen on (some might say even obsessed with) recording the first signs of spring—the first leaf on an oak, the first peacock butterfly seen flying, the first crocus in bloom—as a mark that the long, dark winter is finally over. Fall has not captured as much enthusiasm as spring, but some good records exist, for example, for the turning of leaf color for trees.

The longest records of direct phenological observations are for flowering of cherry trees *Prunus jamasakura* and for grape harvests. Menzel & Dose (2005) show that timing of cherry blossom in Japan was highly variable among years, but no clear trends were discerned from 1400 to 1900. A statistically significant change point is first seen in the early 1900s, with steady advancement since 1952. Recent advancement exceeds observed variation of the previous 600 years. Menzel (2005) analyzed grape-harvest dates across Europe, for which April-August temperatures explain 84% of the variation. She found that the 2003 European heat wave stands out as an extreme early harvest (i.e., the warmest summer) going back 500 years. Although such lengthy observational records are extremely rare, these two unrelated plants on opposite sides of the world add an important historical perspective to results from shorter time series.

Several lines of evidence indicate a lengthening of vegetative growing season in the Northern Hemisphere, particularly at higher latitudes where temperature rise has been greatest. Summer photosynthetic activity (normalized difference vegetation index estimates from satellite data) increased from 1981–1991 (Myneni et al. 1997), concurrent with an advance and increase in amplitude of the annual CO_2 cycle (Keeling et al. 1996). White et al. (1999) modeled meteorological and satellite data to estimate actual growing season length each year from 1900–1987 in the United States. Growing season was unusually long during the warm period of the 1940s at all 12 sites. However, patterns have recently diverged. Since 1966, growing season length has increased only in four of the coldest, most-northerly zones (42°–45° latitude), not in the three warmest zones (32°–37° latitude). Across the European Phenological Gardens (experimental clones of 16 species of shrubs and trees at sites across Europe), a lengthening of the growing season by 10.8 days occurred from 1959–1993 (Menzel 2000, Menzel & Fabian 1999). Analysis of climatological variables (e.g., last frost date of spring and first frost date of fall) mirrors this finding, with an estimated lengthening of the growing season of 1.1–4.9 days per decade since 1951 (Menzel et al. 2003).

Bradley et al. (1999) built on Aldo Leopold's observations from the 1930s and 1940s on the timing of spring events on a Wisconsin farm. Of 55 species resurveyed in the 1980s and 1990s, 18 (35%) showed advancement of spring events, whereas the rest showed no change in timing (with the exception of cowbirds arriving later). On average, spring events occurred 7.3 days earlier by the 1990s compared with 61 years before, coinciding with March temperatures being 2.8°C warmer.

Another long-term (100-year) study by Gibbs & Breisch (2001) compared recent records (1990–1999) of the calling phenology of six frog species in Ithaca, New York, with a turn-of-the-century study (1900–1912). They showed a 10–13-day advance associated with a 1.0–2.3°C rise in temperature during critical months. Amphibian breeding has also advanced in England, by 1–3 weeks per decade (Beebee 1995). Ecophysiological studies in frogs have shown that reproduction is closely linked to both nighttime and daytime temperatures (Beebee 1995).

In the United Kingdom, Crick et al. (1997), analyzing more than 74,000 nest records from 65 bird species between 1971 and 1995, found that the mean laying dates of first clutches for 20 species had advanced by an average 8.8 days. Brown et al. (1999) found a similar result for the Mexican jay (*Aphelocoma ultramarina*) in the mountains of southern Arizona. In the North Sea, migrant birds have advanced their passage dates by 0.5–2.8 days per decade since 1960, with no significant difference between short- and long-distance migrants (Hüppop & Hüppop 2003). In contrast, Gordo et al. (2005) found that three of six long-distance migrant birds had significantly delayed arrival to breeding grounds in Spain, with arrival date highly correlated with climatic conditions in their overwintering grounds in the southern Sahara.

Butterflies frequently show a high correlation between dates of first appearance and spring temperatures, so it is not surprising that their first appearance has advanced for 26 of 35 species in the United Kingdom (Roy & Sparks 2000) and for all 17 species analyzed in Spain (Stefanescu et al. 2003). Seventy percent of 23 species of butterfly in central California have advanced their first flight date over 31 years, by an average of 24 days (Forister & Shapiro 2003). Climate variables explained 85% of variation in flight date in the California study, with warmer, drier winters driving early flight.

There are only two continental-scale studies of bird phenology. Dunn & Winkler (1999) analyzed changes in breeding for tree swallows (*Tachycineta bicolor*) from 1959 to 1991 over the entire breeding range in the contiguous United States and Canada. Laying date was significantly correlated with mean May temperature and had advanced by an average of nine days over the 32-year period. In a complementary study, Both et al. (2004) analyzed the pied flycatcher (*Ficedula hypoleuca*) at 23 sites across Europe and found a significant advance in laying date for nine of the populations, which also tended to be those with the strongest warming trends. Continental-scale studies of both lilac (*Syringa vulgaris*) and honeysuckle (*Lonicera tatarica* and *L. korolkowii*) in the western United States have shown an advance in mean flowering dates of 2 and 3.8 days per decade, respectively (Cayan et al. 2001).

Aquatic systems exhibit similar trends to those of terrestrial systems. In a lake in the northwestern United States, phytoplankton bloom has advanced by 19 days from

1962 to 2002, whereas zooplankton peak is more varied, with some species showing advance and others remaining stable (Winder & Schindler 2004). The Arctic seabird Brunnich's guillemot, *Uria lomvia*, has advanced its egg-laying date at its southern boundary (Hudson Bay) with no change at its northern boundary (Prince Leopold Island); both trends are closely correlated with changes in sea-ice cover (Gaston et al. 2005).

Roetzer et al. (2000) explicitly quantified the additional impacts of urban warming by comparing phenological trends between urban and rural sites from 1951 to 1995. Urban sites showed significantly stronger shifts toward earlier spring timing than nearby rural sites, by 2–4 days. An analysis of greening across the United States via satellite imagery also concluded that urban areas have experienced an earlier onset of spring compared with rural areas (White et al. 2002).

Researchers generally report phenological changes as a separate category from changes in species' distributions, but these two phenomena interplay with each other and with other factors, such as photoperiod, to ultimately determine how climate change affects each species (Bale et al. 2002, Chuine & Beaubien 2001).

INTERACTIONS ACROSS TROPHIC LEVELS: MATCHES AND MISMATCHES

Species differ in their physiological tolerances, life-history strategies, probabilities of population extinctions and colonizations, and dispersal abilities. These individualistic traits likely underlie the high variability in strength of climate response across wild species, even among those subjected to similar climatic trends (Parmesan & Yohe 2003). For many species, the primary impact of climate change may be mediated through effects on synchrony with that species' food and habitat resources. More crucial than any absolute change in timing of a single species is the potential disruption of coordination in timing between the life cycles of predators and their prey, herbivorous insects and their host plants, parasitoids and their host insects, and insect pollinators with flowering plants (Harrington et al. 1999, Visser & Both 2005). In Britain, the butterfly *Anthocharis cardamines* has accurately tracked phenological shifts of its host plant, even when bud formation came two to three weeks early (Sparks & Yates 1997). However, this may be the exception rather than the rule.

Visser & Both (2005) reviewed the literature and found only 11 species' interactions in which sufficient information existed to address the question of altered synchrony. Nine of these were predator-prey interactions, and two were insect–host plant interactions. In spite of small sample size, an important trend emerged from this review: In the majority of cases (7 of 11), interacting species responded differently enough to climate warming that they are more out of synchrony now than at the start of the studies. In many cases, evidence for negative fitness consequences of the increasing asynchrony has been either observed directly or predicted from associated studies (Visser & Both 2005).

In one example, Inouye et al. (2000) reported results of monitoring between 1975 and 1999 at Rocky Mountain Biological Laboratory in Colorado, where there has been a 1.4°C rise in local temperature. The annual date of snowmelt and plant flowering did not change during the study period, but yellow-bellied marmots (*Marmota flaviventris*) advanced their emergence from hibernation by 23 days, changing the relative phenology of marmots and their food plants. In a similar vein, Winder & Schindler (2004) documented a growing asynchrony between peak phytoplankton bloom and peak zooplankton abundances in a freshwater lake.

More complex phenomena resulting from trophic mismatches have also been documented. For example, phenological asynchrony has been linked to a range shift in the butterfly *Euphydryas editha*. Warm and/or dry years alter insect emergence time relative to both the senescence times of annual hosts and the time of blooming of nectar sources (Singer 1972, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996, Weiss et al. 1988). Field studies have documented that butterfly-host asynchrony has resulted directly in population crashes and extinctions. Long-term censuses revealed that population extinctions occurred during extreme droughts and low snowpack years (Ehrlich et al. 1980, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996), and these extinctions have been highly skewed with respect to both latitude and elevation, shifting mean location of extant populations northward and upward (Parmesan 1996, 2003, 2005a).

Van Nouhuys & Lei (2004) showed that host-parasitoid synchrony was influenced signficantly by early spring temperatures. Warmer springs favored the parasitoid wasp *Cotesia melitaearum* by bringing it more in synchrony with its host, the butterfly *Melitaea cinxia*. Furthermore, they argue that because most butterfly populations are protandrous (i.e., males pupating earlier than females), temperature-driven shifts in synchrony with parasitoids may affect butterfly sex ratios.

Intergovernmental Panel on Climate Change: a scientific panel formed under the auspices of the United Nations and the World Meteorological Organization for the purpose of synthesizing literature and forming scientific consensus on climate change and its impacts

OBSERVED RANGE SHIFTS AND TRENDS IN LOCAL ABUNDANCE

Expected distributional shifts in warming regions are poleward and upward range shifts. Studies on these shifts fall mainly into two types: (*a*) those that infer large-scale range shifts from small-scale observations across sections of a range boundary (with the total study area often determined by a political boundary such as state, province, or country lines) and (*b*) those that infer range shifts from changes in species' composition (abundances) in a local community. Studies encompassing the entire range of a species, or at least the northern and southern (or lower and upper) extremes, are few and have been concentrated on amphibians (Pounds et al. 1999, 2006), a mammal (Beever et al. 2003), and butterflies (Parmesan 1996, Parmesan et al. 1999). The paucity of whole-range studies likely stems from the difficulties of gathering data on the scale of a species' range—often covering much of a continent.

Shifts at Polar Latitudes

Broad impacts of climate change in polar regions—from range shifts to community restructuring and ecosystem functioning—have been reviewed by the Intergovernmental Panel on Climate Change (Anisimov et al. 2001), the Arctic Climate Impact Assessment (2004) and the Millenium Ecosystem Assessment (Chapin et al. 2006).

SST: sea surface temperature

Antarctic. Plant, bird, and marine life of Antarctica have exhibited pronounced responses to anthropogenic climate change. These responses have been largely attributed to extensive changes (mostly declines) in sea-ice extent, which in turn appears to have stimulated a trophic cascade effect in biological systems. Declines in sea-ice extent and duration since 1976 have apparently reduced abundances of ice algae, in turn leading to declines in krill (from 38%–75% per decade) in a large region where they have been historically concentrated, the southwest Atlantic (Atkinson et al. 2004). Krill (*Euphausia superba*) is a primary food resource for many fish, seabirds, and marine mammals. Interestingly, McMurdo Dry Valleys, which actually cooled between 1990 and 2000, also showed declines in lake phytoplankton abundances and in soil invertebrate abundances (Doran et al. 2002).

Penguins and other seabirds in Antarctica have shown dramatic responses to changes in sea-ice extent over the past century (Ainley et al. 2003, Croxall et al. 2002, Smith et al. 1999). The sea-ice dependent Adélie and emperor penguins (*Pygoscelis adeliae* and *Aptenodytes forsteri*, respectively) have nearly disappeared from their northernmost sites around Antarctica since 1970. Emperors have declined from 300 breeding pairs down to just 9 in the western Antarctic Peninsula (Gross 2005), with less severe declines at Terre Adélie (66° S), where they are now at 50% of pre-1970s abundances (Barbraud & Weimerskirch 2001). Adélies have declined by 70% on Anvers Island (64°–65° S along the Antarctic peninsula (Emslie et al. 1998, Fraser et al. 1992), whereas they are thriving at the more-southerly Ross Island at 77° S (Wilson et al. 2001)—effectively shifting this species poleward. In the long-term, sea-ice-dependent birds will suffer a general reduction of habitat as ice shelves contract [e.g., as has already occured in the Ross Sea (IPCC 2001b)] or collapse [e.g., as did the Larsen Ice Shelves along the Antarctic Peninsula in 2002 (Alley et al. 2005)].

In contrast, open-ocean feeding penguins—the chinstrap and gentoo—invaded southward along the Antarctic Peninsula between 20 and 50 years ago, with paleological evidence that gentoo had been absent from the Palmer region for 800 years previously (Emslie et al. 1998, Fraser et al. 1992). Plants have also benefited from warming conditions. Two Antarctic vascular plants (a grass, *Deschampsia antarctica*, and a cushion plant, *Colobanthus quitensis*) have increased in abundance and begun to colonize novel areas over a 27-year period (Smith 1994).

Arctic. Nearly every Arctic ecosystem shows marked shifts. Diatom and invertebrate assemblages in Arctic lakes have shown huge species' turnover, shifting away from benthic species toward more planktonic and warm-water-associated communities (Smol et al. 2005). Across northern Alaska, Canada, and parts of Russia, shrubs have been expanding into the tundra (Sturm et al. 2005). Field studies, experimentation, and modeling link this major community shift to warming air temperatures, increased snow cover, and increased soil microbial activity (Chapin et al. 1995; Sturm et al. 2001, 2005). Populations of a pole-pole migrant, the sooty shearwater (*Puffinus griseus*), have shifted their migration routes by hundreds of kilometers in concert with altered sea surface temperature (SST) in the Pacific (Spear & Ainley 1999).

Sea-ice decline in the Arctic has been more evenly distributed than in the Antarctic. Because of differing geology, with an ocean at the pole rather than land, Arctic species that are sea-ice dependent are effectively losing habitat at all range boundaries. Polar bears have suffered significant population declines at opposite geographic boundaries. At their southern range boundary (Hudson Bay), polar bears are declining both in numbers and in mean body weight (Stirling et al. 1999). Climate change has caused a lengthening of ice-free periods on Hudson Bay, periods during which the bears starve and live on their reserves because an ice shelf is necessary for feeding. Furthermore, researchers have also linked warming trends to reductions of the bears' main food, the ringed seal (Derocher et al. 2004, Ferguson et al. 2005). At the bears' northern range boundaries off Norway and Alaska, sea ice has also been reduced, but poorer records make it is less clear whether observed declines in body size and the number of cubs per female are linked to climate trends or to more basic density-dependent processes (Derocher 2005, Stirling 2002).

Shifts in Northern-Hemisphere Temperate Species

On a regional scale, a study of the 59 breeding bird species in Great Britain showed both expansions and contractions of northern range boundaries, but the average boundary change for 12 species that had not experienced overall changes in density was a mean northward shift of 18.9 km over a 20-year period (Thomas & Lennon 1999). For a few well-documented bird species, their northern U.K. boundaries have tracked winter temperatures for over 130 years (Williamson 1975). Physiological studies indicate that the northern boundaries of North American songbirds may generally be limited by winter nighttime temperatures (Burger 1998, Root 1988).

Analogous studies exist for Lepidoptera (butterflies and moths), which have undergone an expansion of northern boundaries situated in Finland (Marttila et al. 1990, Mikkola 1997), Great Britain (Hill et al. 2002, Pollard 1979, Pollard & Eversham 1995, Warren 1992), and across Europe (Parmesan et al. 1999). Depending on the study, some 30% to 75% of northern boundary sections had expanded north; a smaller portion (<20%) had contracted southward; and the remainder were classified as stable. In a study of 57 nonmigratory European butterflies, data were obtained from both northern and southern range boundaries for 35 species (Parmesan et al. 1999). Nearly two thirds (63%) had shifted their ranges to the north by 35–240 km, and only two species had shifted to the south (Parmesan et al. 1999). In the most-extreme cases, the southern edge contracted concurrent with northern edge expansion. For example, the sooty copper (*Heodes tityrus*) was common in the Montseny region of central Catalonia in the 1920s, but modern sightings are only from the Pyrenees, 50 km to the north. Symmetrically, *H. tityrus* entered Estonia for the first time in 1998, by 1999 had established several successful breeding populations, and by 2006 had reached the Baltic Sea (Parmesan et al. 1999; T. Tammaru, personal communication).

Another charismatic insect group with good historical records is Odonata (dragonflies and damselflies). In a study of all 37 species of resident odonates in the United Kingdom, Hickling et al. (2005) documented that 23 of the 24 temperate species had expanded their northern range limit between 1960–1995, with mean northward shift of 88 km.

Nondiapausing (i.e., active year-round) butterfly species are also moving northward with warmer winters. The northern boundary of the sachem skipper butterfly has expanded from California to Washington State (420 miles) in just 35 years (Crozier 2003, 2004). During a single year—the warmest on record (1998)—it moved 75 miles northward. Laboratory and field manipulations showed that individuals are killed by a single, short exposure to extreme low temperatures (–10°C) or repeated exposures to –4°C, indicating winter cold extremes dictate the northern range limit (Crozier 2003, 2004). The desert orange tip (*Colotis evagore*), which historically was confined to northern Africa, has established resident populations in Spain while maintaining the same ecological niche. Detailed ecological and physiological studies confirm that *C. evagore* has remained a specialist of hot microclimates, needing more than 164 days at greater than 12°C to mature. It has not undergone a host switch in its new habitat, and it has not evolved a diapause stage (Jordano et al. 1991).

In the Netherlands between 1979 and 2001, 77 new epiphytic lichens colonized from the south, nearly doubling the total number of species for that community (van Herk et al. 2002). Combined numbers of terrestrial and epiphytic lichen species increased from an average of 7.5 per site to 18.9 per site. An alternate approach to documenting colonizations is to document extinction patterns. Comparing recent censuses across North America (1993–1996) with historical records (1860–1986), Parmesan (1996) documented that high proportions of population extinctions along the southern range boundary of Edith's checkerspot butterfly (*E. editha*) had shifted the mean location of living populations 92 km farther north (Parmesan 1996, 2003, 2005a).

Shifts of Tropical Species Ranges

Warming trends at lower latitudes are associated with movements of tropical species into more-temperate areas. The rufous hummingbird has undergone a dramatic shift in its winter range (Hill et al. 1998). Thirty years ago it wintered mainly in Mexico, and between 1900 and 1990, there were never more than 30 winter sightings per year along the Gulf Coast of the United States. In the early 1990s, sightings increased to more than 100 per year in the southern United States. The number of sightings has increased steadily since then—up to 1,643 by 1996, with evidence that, by 1998, resident populations had colonized 400 km inland (Howell 2002). Over this same period, winter temperatures rose by approximately 1°C (IPCC 2001b). In Florida, five new species of tropical dragonfly established themselves in 2000, an apparently natural invasion from Cuba and the Bahamas (Paulson 2001).

Similarly, North African species are moving into Spain and France, and Mediterranean species are moving up into the continental interior. The African plain tiger butterfly (*Danaus chrysippus*) established its first population in southern Spain in 1980 and by the 1990s had established multiple, large metapopulations (Haeger 1999).

Elevational Shifts

Montane studies have generally been scarcer and less well documented (lower sampling resolution), but a few good data sets show a general movement of species upward in elevation. By comparing species compositions in fixed plots along an elevational gradient in Monteverde National Park, Costa Rica, Pounds et al. (1999, 2005) documented that lowland birds have begun breeding in montane cloud-forest habitat over the past 20 years. A similar study across 26 mountains in Switzerland documented that alpine flora have expanded toward the summits since the plots were first censused in the 1940s (Grabherr et al. 1994, Pauli et al. 1996). Upward movement of treelines has been observed in Siberia (Moiseev & Shiyatov 2003) and in the Canadian Rocky Mountains, where temperatures have risen by 1.5°C (Luckman & Kavanagh 2000).

The few studies of lower elevational limits show concurrent contractions upward of these warm range boundaries. Because warm boundaries generally have data gaps through time, these studies have conducted recensuses of historically recorded (sedentary) populations and looked for nonrandom patterns of long-term population extinctions.

A 1993–1996 recensus of Edith's checkerspot butterfly (*E. editha*) populations recorded 1860–1986 throughout its range (Mexico to Canada) documented that more than 40% of populations from 0–2400 m were extinct (in spite of having suitable habitat), whereas less than 15% were extinct at the highest elevations (2400–3500 m) (Parmesan 1996). Over the past 50–100 years, snowpack below 2400 m has become lighter by 14% and melts 7 days earlier, whereas higher elevations (2400–3500 m) have 8% heavier snowpack and no change in melt date (Johnson et al. 1999). In concert with altered snow dynamics, the mean location of *E. editha* populations has shifted upward by 105 m (Parmesan 1996, 2003, 2005a).

In southern France, metapopulations of the cool-adapted Apollo butterfly (*Parnassius apollo*) have gone extinct over the past 40 years on plateaus less than 850 m high but have remained healthy where plateaus were greater than 900 m high (Descimon et al. 2006). The data suggest that dispersal limitation was important, and this strong flyer can persist when nearby higher elevation habitats exist to colonize. In Spain, the lower elevational limits of 16 species of butterfly have risen an average of 212 m in 30 years, concurrent with a 1.3°C rise in mean annual temperatures (Wilson et al. 2005).

In the Great Basin of the western United States, 7 out of 25 recensused populations of the pika (*Ochotona princeps*, Lagomorpha) were extinct since being recorded in the 1930s (Beever et al. 2003). Human disturbance is minimal because pika habitat is high-elevation talus (scree) slopes, which are not suitable for ranching or recreational activities. Extinct populations were at significantly lower elevations than those still present (Parmesan & Galbraith 2004). Field observations by Smith (1974) documented that adult pika stopped foraging in the midday heat in August at low elevation sites. Subsequent experiments showed that adults were killed within a half hour at more than 31°C (Smith 1974).

Marine Community Shifts

Decades of ecological and physiological research document that climatic variables are primary drivers of distributions and dynamics of marine plankton and fish (Hays et al. 2005, Roessig et al. 2004). Globally distributed planktonic records show strong shifts of phytoplankton and zooplankton communities in concert with regional oceanic climate regime shifts, as well as expected poleward range shifts and changes in timing of peak biomass (Beaugrand et al. 2002, deYoung et al. 2004, Hays et al. 2005, Richardson & Schoeman 2004). Some copepod communities have shifted as much as 1000 km northward (Beaugrand et al. 2002). Shifts in marine fish and invertebrate communities have been been particularly well documented off the coasts of western North America and the United Kingdom. These two systems make an interesting contrast (see below) because the west coast of North America has experienced a 60-year period of significant warming in nearshore sea temperatures, whereas much of the U.K. coast experienced substantial cooling in the 1950s and 1960s, with warming only beginning in the 1970s (Holbrook et al. 1997, Sagarin et al. 1999, Southward et al. 2005).

Sagarin et al. (1999) related a 2°C rise of SST in Monterey Bay, California, between 1931 and 1996 to a significant increase in southern-ranged species and decrease of northern-ranged species. Holbrook et al. (1997) found similar shifts over the past 25 years in fish communities in kelp habitat off California.

Much of the data from the North Atlantic, North Sea, and coastal United Kingdom have exceptionally high resolution and long time series, so they provide detailed information on annual variability, as well as long-term trends. Over 90 years, the timing of animal migration (e.g., veined squid, *Loligo forbesi*, and flounder *Platichthys flesus*) followed decadal trends in ocean temperature, being later in cool decades and up to 1–2 months earlier in warm years (Southward et al. 2005).

In the English Channel, cold-adapted fish (e.g., herring *Clupea harengus*) declined during both warming periods (1924 to the 1940s, and post-1979), whereas warm-adapted fish did the opposite (Southward et al. 1995, 2005). For example, pilchard *Sardina pilchardus* increased egg abundances by two to three orders of magnitude during recent warming. In the North Sea, warm-adapted species (e.g., anchovy *Engraulis encrasicolus* and pilchard) have increased in abundances since 1925 (Beare et al. 2004), and seven out of eight have shifted their ranges northward (e.g., bib, *Trisopterus luscus*) by as much as 100 km per decade (Perry et al. 2005). Records dating back to 1934 for intertidal invertebrates show equivalent shifts between warm- and cold-adapted species (e.g., the barnacles *Semibalanus balanoides* and *Chthamalus* spp., respectively), mirroring decadal shifts in coastal temperatures (Southward et al. 1995, 2005).

Pest and Disease Shifts

Pest species are also moving poleward and upward. Over the past 32 years, the pine processionary moth (*Thaumetopoea pityocampa*) has expanded 87 km at its northern range boundary in France and 110–230 m at its upper altitudinal boundary in Italy (Battisti et al. 2005). Laboratory and field experiments have linked the feeding behavior and survival of this moth to minimum nighttime temperatures, and its expansion has been associated with warmer winters. In the Rocky Mountain range of the United States, mountain pine beetle (*Dendroctonus ponderosae*) has responded to warmer temperatures by altering its life cycle. It now only takes one year per generation rather than its previous two years, allowing large increases in population abundances, which, in turn, have increased incidences of a fungus they transmit (pine blister rust, *Cronartium ribicola*) (Logan et al. 2003). Increased abundance of a nemotode parasite has also occurred as its life cycle shortened in response to warming trends. This has had associated negative impacts on its wild musk oxen host, causing decreased survival and fecundity (Kutz et al. 2005).

In a single year (1991), the oyster parasite *Perkinsus marinus* extended its range northward from Chesapeake Bay to Maine—a 500 km shift. Censuses from 1949 to 1990 showed a stable distribution of the parasite from the Gulf of Mexico to its northern boundary at Chesapeake Bay. The rapid expansion in 1991 has been linked to above-average winter temperatures rather than human-driven introduction or genetic change (Ford 1996). A kidney disease has been implicated in low-elevation trout declines in Switzerland. High mortality from infection occurs above 15°–16°C, and water temperatures have risen in recent decades. High infection rates (27% of fish at 73% of sites) at sites below 400 m have been associated with a 67% decline in catch; mid-elevation sites had lower disease incidence and only moderate declines in catch; and the highest sites (800–3029 m) had no disease present and relatively stable catch rates (Hari et al. 2006).

Changes in the wild also affect human disease incidence and transmission through alterations in disease ecology and in distributions of their wild vectors (Parmesan & Martens 2006). For example, in Sweden, researchers have documented marked increases in abundances of the disease-transmitting tick *Ixodes ricinus* along its northernmost range limit (Lindgren & Gustafson 2001). Between the early 1980s and 1994, numbers of ticks found on domestic cats and dogs increased by 22%–44% along the tick's northern range boundary across central Sweden. In the same time period, this region had a marked decrease in the number of extremely cold days (<-12°C) in winter and a marked increase in warm days (>10°C) during the spring, summer, and fall. Previous studies on temperature developmental and activity thresholds indicated the observed warmer temperatures cause decreased tick mortality and longer growing seasons (Lindgren & Gustafson 2001).

Trees and Treelines: Complex Responses

A complex of interacting factors determines treeline, often causing difficulties in interpretation of twentieth-century trends. Some species are "well behaved" in that they show similar patterns of increased growth at treeline during the early warming in the 1930s and 1940s as during the recent warming of the past 20 years. In recent decades, treelines have shifted northward in Sweden (Kullman 2001) and eastern Canada (Lescop-Sinclair & Payette 1995), and upward in Russia (Meshinev et al. 2000, Moiseev & Shiyatov 2003) and New Zealand (Wardle & Coleman 1992).

However, in other studies, researchers saw a strong response to warming in the late 1930s and 1940s but a weaker (or absent) response in recent warm decades (Innes 1991, Jacoby & D'Arrigo 1995, Lescop-Sinclair & Payette 1995, Briffa et al. 1998a,b), possibly resulting from differences in rainfall between the two warm periods. In Alaska, recent decades have been relatively dry, which may have prevented trees from responding to current warming as they did before (Barber et al. 2000, Briffa et al. 1998b). In contrast, treelines in the arid southwest United States, which has had increased rainfall, have shown unprecedented increased tree-ring growth at high elevations (Swetnam & Betancourt 1998).

An impressive study across all of northern Russia from 1953–2002 showed a shift in tree allometries. In areas where summer temperatures and precipitation have both increased, a general increase in biomass (up 9%) is primarily a result of increased greenery (33% more carbon in leaves and needles), rather than woody parts (roots and stem). In areas that have experienced warming and drying trends, greenery has decreased, and both roots and stems have increased (Lapenis et al. 2005).

EXTINCTIONS

Amphibians

Documented rapid loss of habitable climate space makes it no surprise that the first extinctions of entire species attributed to global warming are mountain-restricted species. Many cloud-forest-dependent amphibians have declined or gone extinct on a mountain in Costa Rica (Pounds et al. 1999, 2005). Among harlequin frogs in Central and South American tropics, an astounding 67% have disappeared over the past 20–30 years. Pounds et al. (2006) hypothesised that recent trends toward warmer nights and increased daytime cloud cover have shifted mid-elevation sites (1000–2400 m), where the preponderance of extinctions have occurred, into thermally optimum conditions for the chytrid fungus, *Batrachochytrium dendrobatidis.*

Tropical Coral Reefs

Elevated sea temperatures as small as 1°C above long-term summer averages lead to bleaching (loss of coral algal symbiont), and global SST has risen an average of 0.1°–0.2°C since 1976 (Hoegh-Guldberg 1999, IPCC 2001b). A more acute problem for coral reefs is the increase in extreme temperature events. El Niño events have been increasing in frequency and severity since records began in the early 1900s, and researchers expect this trend to continue over coming decades (Easterling et al. 2000, IPCC 2001b, Meehl et al. 2000). A particularly strong El Niño in 1997–1998 caused bleaching in every ocean (up to 95% of corals bleached in the Indian Ocean), ultimately resulting in 16% of corals rendered extinct globally (Hoegh-Guldberg 1999, 2005b; Wilkinson 2000).

Recent evidence for genetic variation among the obligate algal symbiont in temperature thresholds suggests that some evolutionary response to higher water temperatures may be possible (Baker 2001, Rowan 2004). Changes in genotype frequencies toward increased frequency of high-temperature-tolerant symbiont appear to have occurred within some coral populations between the mass bleaching events of 1997–1998 and 2000–2001 (Baker et al. 2004). However, other studies indicate that many entire reefs are already at their thermal tolerance limits (Hoegh-Guldberg 1999). Coupled with poor dispersal of symbiont between reefs, this has led several researchers to conclude that local evolutionary responses are unlikely to mitigate the negative impacts of future temperature rises (Donner et al. 2005, Hoegh-Guldberg et al. 2002).

One optimistic result suggests that corals, to some extent, may be able to mirror terrestrial range shifts. Two particularly cold-sensitive species (staghorn coral, *Acropora ceervicornis*, and elkhorn coral, *Acropora palmata*) have recently expanded their ranges into the northern Gulf of Mexico (first observation in 1998), concurrent with rising SST (Precht & Aronson 2004). Although continued poleward shift will be limited by light availability at some point (Hoegh-Guldberg 1999), small range shifts may aid in developing new refugia against extreme SST events in future.

Although impacts have not yet been observed, the fate of coral reefs may be as, or more, affected in coming decades by the direct effects of CO_2 rather than temperature rise. Increased atmospheric CO_2 since industrialization has significantly lowered ocean pH by 0.1. The more dire projections (a doubling to tripling of current CO_2 levels) suggest that, by 2050, oceans may be too acidic for corals to calcify (Caldeira & Wickett 2003, Hoegh-Guldberg 2005a, Orr et al. 2005).

Population Extinctions Leading to Range Contractions

Many species have suffered reduced habitable area due to recent climate change. For those species that have already been driven extinct at their equatorial or lower range boundaries, some have either failed to expand poleward or are unable to expand due to geographic barriers. Such species have suffered absolute reductions in range size, putting them at greater risk of extinction in the near future.

This is particularly evident in polar species, as these are already pushed against a geographical limit. Researchers have seen large reductions in population abundances and general health along the extreme southern populations of Arctic polar bears (Derocher 2005, Derocher et al. 2004, Stirling et al. 1999) and the extreme northern populations of Antarctic Adélie and emperor penguins (Ainley et al. 2003, Croxall et al. 2002, Emslie et al. 1998, Fraser et al. 1992, Smith et al. 1999, Taylor & Wilson 1990, Wilson et al. 2001). In the United Kingdom, four boreal odonates have contracted northward by an average of 44 km over 40 years (Hickling et al. 2005).

Similarly, high numbers of population extinctions have occurred along the lower elevational boundaries of mountaintop species, such as pikas in the western United States (Beever et al. 2003) and the Apollo butterfly in France (Descimon et al. 2006). For 16 mountain-restricted butterflies in Spain, warming has already reduced their habitat by one third in just 30 years (Wilson et al. 2005). Warming and drying trends on Mt. Kiliminjaro have increased fire impacts, which have caused a 400-m downward contraction of closed (cloud) forest, now replaced by an open, dry alpine system (Hemp 2005). Temperate low-elevation species are not immune: Twenty-five percent of temperate butterflies in Europe contracted northward by 35–50 km over a 30–70-year period. For one of these, its northern range boundary had not expanded, so it suffered an overall contraction of range size (Parmesan et al. 1999).

EVOLUTION AND PLASTICITY

Species ranges are dynamic. Historically, ecologists have viewed species' niches as static and range shifts over time as passive responses to major environmental changes (global climate shifts or geological changes in corridors and barriers).

There is no doubt that climate plays a major role in limiting terrestrial species' ranges (Andrewartha & Birch 1954; Bale et al. 2002; Parmesan et al. 2000, 2005; Precht et al. 1973; Webb & Bartlein 1992; Weiser 1973; Woodward 1987). Recent physiological and biogeographic studies in marine systems also implicate temperature as a primary driver of species' ranges (Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg & Pearse 1995).

However, evolutionary processes clearly can substantially influence the patterns and rates of response to climate change. Theoretically, evolution can also drive range shifts in the absence of environmental change (Holt 2003). A prime example of this is the hybridization of two species of Australian fruit fly that led to novel adaptations, allowing range expansion with no concomitant environmental change (Lewontin & Birch 1966).

The problem of estimating the relative roles of evolution and plasticity is tractable with extensive, long-term ecological and genetic data. For example, genetic analysis of a population of red squirrels in the Arctic indicated that 62% of the change in breeding dates occurring over a 10-year period was a result of phenotypic plasticity, and 13% was a result of genetic change in the population (Berteaux et al. 2004, Réale et al. 2003).

Geneticists in the 1940s noticed that certain chromosomal inversions in fruit flies (*Drosophila*) were associated with heat tolerance (Dobzhansky 1943, 1947). These "hot" genotypes were more frequent in southern than in northern populations and increased within a population during each season, as temperatures rose from early spring through late summer. Increases in the frequencies of warm-adapted genotypes have occurred in wild populations of *Drosophila ssp* in Spain between 1976 and 1991 (Rodríguez-Trelles & Rodriguez 1998, Rodríguez-Trelles et al. 1996, 1998), as well as in the United States between 1946 and 2002 (Levitan 2003). The change in the United States was so great that populations in New York in 2002 were converging on genotype frequencies found in Missouri in 1946.

In contrast, red deer in Norway show completely plastic responses. Their body size responds rapidly to yearly variability of winter temperatures. Warmer winters cause developing males to become larger while females become smaller (Post et al. 1999). In consequence, the end result of a gradual winter warming trend has been an increase in sexual dimorphism.

A surprising twist is that species whose phenology is under photoperiodic control have also responded to temperature-driven selection for spring advancement or fall delay. Bradshaw & Holzapfel (2001) showed that the pitcher plant mosquito, *Wyeomyia smithii*, has evolved a shorter critical photoperiod in association with a longer growing season. Northern populations of this mosquito now use a shorter day-length cue to enter winter diapause, doing so later in the fall than they did 24 years ago.

The Role of Evolution in Shaping Species' Impacts

Increasing numbers of researchers use analyses of current intraspecific genetic variation for climate tolerance to argue for a substantive role of evolution in mitigating negative impacts of future climate change (Baker 2001, Baker et al. 2004, Davis & Shaw 2001, Rowan 2004). However, in spite of a plethora of data indicating local adaptation to climate change at specific sites, the fossil record shows little evidence for the evolution of novel phenotypes across a species as a whole. Pleistocene glaciations represent shifts 5–10 times the magnitude of twentieth-century global warming. These did not result in major evolution at the species level (i.e., appearance of new forms outside the bounds of known variation for that species), nor in major extinction or speciation events. Existing species appeared to shift their geographical distributions as though tracking the changing climate, rather than remaining stationary and evolving new forms (Coope 1994, Davis & Zabinski 1992, Huntley 1991).

Most of the empirical evidence for rapid adaptation to climate change comes from examples of evolution in the interiors of species' ranges toward higher frequencies of already existing heat-tolerant genotypes. In studies that focus on dynamics at the edge of a species' range or across an entire range, a different picture emerges. Several studies suggest that the effects of both genetic constraints and asymmetrical gene flow are intensified close to species' borders (Antonovics 1976, Garcia-Ramos & Kirkpatrick 1997, Hoffmann & Blows 1994). It is expected that a warming climate strengthens climate stress at equatorial range boundaries and reduces it at poleward boundaries. Equatorial boundary populations are often under natural selection for increased tolerance to extreme climate in the absence of climate change, but may be unable to respond due to lack of necessary genetic variance. Furthermore, gene flow from interior populations may stifle response to selection at the range limits, even when sufficient genetic variation exists (Kirkpatrick & Barton 1997).

Because of strong trade-offs between climate tolerance and resource/habitat preferences, a relaxation of selection on climate tolerance at northern boundaries may cause rapid evolution of these correlated traits. This process has been investigated in the European butterfly *Aricia agestis*, in which populations near the northern range boundary had previously adapted to cool conditions by specializing on the host genus, *Helianthemum*, which grows in hot microclimates and hence supports fast larval growth. Climate warming did not initially cause range expansion because *Helianthemum* was absent to the immediate north of the range limit. However, warming did permit rapid evolution of a broader diet at the range limit, to a host used in more southern populations, *Geranium*, which grows in cooler microclimates. Once this local diet evolution occurred, the boundary expanded northward across the band from which *Helianthemum* was absent but *Geranium* was present (Thomas et al. 2001).

This example shows how a complex interplay may occur between evolutionary processes and ecological responses to extreme climates and climate change. However, these evolutionary events did not constitute alternatives to ecological responses to climate change; they modulated those changes. Adaptive evolution of host preference occurred at the northern range boundary in response to temperature rise, but genetic variation for host use already existed within the *A. agestis* butterfly. In this case, evolutionary processes are not an alternative to range movement, but instead modulate the magnitude and dynamics of the range shift. This is not likely to be an isolated example because populations of other species near poleward boundaries are known to specialize on resources that mitigate the effects of cool climate. Such resources either support rapid growth or occur in the hottest available microclimates (Nylin 1988, Scriber & Lederhouse 1992, Thomas et al. 2001).

In addition to resource choice, dispersal tendency evolves at range margins in response to climate change. In nonmigratory species, the simplest explanation of northward range expansions is that individuals have always crossed the species' boundary, and with climate warming, some of these emigrants are successful at founding new populations outside the former range. When dispersal tendency is heritable, these new populations contain dispersive individuals and higher rates of dispersal will soon evolve at the expanding boundary.

Evolution toward greater dispersal has indeed been documented in several species of insect. Two species of wing-dimorphic bush crickets in the United Kingdom have evolved longer wings at their northern range boundary, as mostly long-winged forms participated in the range expansion and short-winged forms were left behind (Thomas et al. 2001). Adults of newly colonized populations of the speckled wood butterfly (*Pararge aegeria*) in the United Kingdom have larger thoraces and greater flight capability than historical populations just to the south (Hill et al. 1999). Variation in dispersal abilities can be cryptic. Newly founded populations of the butterfly *M. cinxia* contained females that were genetically superior dispersers due to increased production of ATP (Hanski et al. 2004).

Overall, empirical evidence suggests that evolution can complement, rather than supplant, projected ecological changes. However, there is little theoretical or experimental support to suggest that climate warming will cause absolute climatic tolerances of a species to evolve sufficiently to allow it to conserve its geographic distribution in the face of climate change and thereby inhabit previously unsuitable climatic regimes (Donner et al. 2005; Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg et al. 2002; Jump & Peñuelas 2005).

CONCLUDING THOUGHTS ON EVOLUTION AND CLIMATE CHANGE

For species-level evolution to occur, either appropriate novel mutations or novel genetic architecture (new gene complexes) would have to emerge to allow a response to selection. Lynch & Lande (1993) used a genetic model to infer rates of environmental change that would allow populations to respond adaptively. However, Travis & Futuyma (1993)—discussing the same question from broad paleontological, population, genetic, and ecological perspectives—highlighted the complexity of predicting future responses from currently known processes. Fifteen years later, answers still lie very much in empirical observations. These observations indicate that, although local evolutionary responses to climate change have occurred with high frequency, there is no evidence for change in the absolute climate tolerances of a species. This view is supported by the disproportionate number of population extinctions documented along southern and low-elevation range edges in response to recent climate warming, resulting in contraction of species' ranges at these warm boundaries, as well as by extinctions of many species.

SUMMARY POINTS

1. The advance of spring events (bud burst, flowering, breaking hibernation, migrating, breeding) has been documented on all but one continent and in all major oceans for all well-studied marine, freshwater, and terrestrial groups.
2. Variation in phenological response between interacting species has already resulted in increasing asynchrony in predator-prey and insect-plant systems, with mostly negative consequences.
3. Poleward range shifts have been documented for individual species, as have expansions of warm-adapted communities, on all continents and in most of the major oceans for all well-studied plant and animal groups.
4. These observed changes have been mechanistically linked to local or regional climate change through long-term correlations between climate and biological variation, experimental manipulations in the field and laboratory, and basic physiological research.
5. Shifts in abundances and ranges of parasites and their vectors are beginning to influence human disease dynamics.
6. Range-restricted species, particularly polar and mountaintop species, show more-severe range contractions than other groups and have been the first groups in which whole species have gone extinct due to recent climate change. Tropical coral reefs and amphibians are the taxonomic groups most negatively impacted.
7. Although evolutionary responses have been documented (mainly in insects), there is little evidence that observed genetic shifts are of the type or magnitude to prevent predicted species extinctions.

FUTURE ISSUES

1. Ocean-atmosphere processes are dynamically changing in response to anthropogenic forcings. Indices such as the El Niño Southern Oscillation and the North Atlantic Oscillation may be a poor basis for projecting future biological impacts.
2. Projections of impacts will be aided by a better mechanistic understanding of ecological, behavioral, and evolutionary responses to complex patterns of climate change, and in particular to impacts of extreme weather and climate events.

ACKNOWLEDGMENTS

I would like to give many thanks to C. Britt, M. Butcher, J. Mathews, C. Metz, and P. van der Meer for help with the literature search and to D. Simberloff and D. Futuyma for helpful comments on earlier versions. I also want to give special appreciation to M.C. Singer for his critique and editorial assistance.

LITERATURE CITED

Ahmad QK, Warrick RA, Downing TE, Nishioka S, Parikh KS, et al. 2001. Methods and tools. See IPCC 2001a, pp. 105–43

Ainley DG, Ballard G, Emslie SD, Fraser WR, Wilson PR, Woehler EJ. 2003. Adelie penguins and environmental change. *Science* 300:429–30

Ainley DG, Divoky GJ. 1998. Climate change and seabirds: a review of trends in the eastern portion of the Pacific Basin. *Pac. Seab.* 25:20

Alley RB, Clark PU, Huybrechts P, Joughin I. 2005. Ice-sheet and sea-level changes. *Science* 310:456–60

Alley RB, Marotzke J, Nordhaus WD, Overpeck JT, Peteet DM, et al. 2003. Abrupt climate change. *Science* 299:2005–10

Andrewartha HG, Birch LC. 1954. *The Distribution and Abundance of Animals*. Chicago, IL: Univ. Chicago Press

Anisimov O, Fitzharris B, Hagen JO, Jefferies R, Marchant H, et al. 2001. Polar regions (Arctic and Antarctic). See IPCC 2001a, pp. 801–47

Antonovics J. 1976. The nature of limits to natural selection. *Ann. Mo. Bot. Gard.* 63:224–47

Arctic Climate Impact Assessment. 2004. *Impacts of a Warming Arctic*. Cambridge, UK: Cambridge Univ. Press

Atkinson A, Siegel V, Pakhomov E, Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–3

Badeck FW, Bondeau A, Böttcher K, Doktor D, Lucht W, et al. 2004. Responses of spring phenology to climate change. *New Phytol.* 162:295–309

Baker AC. 2001. Reef corals bleach to survive change. *Nature* 411:765–66

Baker AC, Starger CJ, McClanahan TR, Glynn PW. 2004. Coral reefs: corals' adaptive response to climate change. *Nature* 430:741

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.* 8:1–16

Barber VA, Juday GP, Finney BP. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405:668–73

Barbraud C, Weimerskirch H. 2001. Emperor penguins and climate change. *Nature* 411:183–86

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, et al. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Appl.* 15:2084–96

Beare DJ, Burns F, Greig A, Jones EG, Peach K, et al. 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. *Mar. Ecol. Prog. Ser.* 284:269–78

Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–94

Beebee TJC. 1995. Amphibian breeding and climate. *Nature* 374:219–20

Beever EA, Brussard PF, Berger J. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *J. Mammal.* 84:37–54

Berteaux D, Reale D, McAdam AG, Boutin S. 2004. Keeping pace with fast climate change: Can Arctic life count on evolution? *Integr. Comp. Biol.* 44:140–51

Blenckner T, Hillebrand H. 2002. North Atlantic Oscillation signatures in aquatic and terrestrial ecosystems: a meta-analysis. *Glob. Change Biol.* 8:203–12

Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, et al. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc. R. Soc. London Ser. B* 271:1657–62

Bradley NL, Leopold AC, Ross J, Wellington H. 1999. Phenological changes reflect climate change in Wisconsin. *Proc. Natl. Acad. Sci. USA* 96:9701–4

Bradshaw WE, Holzapfel CM. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci. USA* 98:14509–11

Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Harris IC, et al. 1998a. Trees tell of past climates, but are they speaking less clearly today? *Philos. Trans. R. Soc. London Ser. B* 353:65–73

Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA. 1998b. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* 391:678–82

Brown JL, Li SH, Bhagabati N. 1999. Long-tem trend toward earlier breeding in an American bird: a response to global warming? *Proc. Natl. Acad. Sci. USA* 96:5565–69

Bumpus HC. 1899. The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesicus*. In *Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl*, 1896–97, pp. 209–26. Boston: Ginn & Co

Burger M. 1998. *Physiological mechanisms limiting the northern boundary of the winter range of the northern cardinal* (Cardinalis cardinalis). PhD diss. Univ. Mich., Ann Arbor

Burton J. 1975. The effects of recent climatic change on British insects. *Bird Study* 22:203–4

Burton JF. 1998a. The apparent effects of climatic changes since 1850 on European lepidoptera. *Mém. Soc. R. Belge Entomol.* 38:125–44

Burton JF. 1998b. The apparent responses of European lepidottera to the climate changes of the past hundred years. *Atropos* 5:24–30

Caldeira K, Wickett ME. 2003. Anthropogenic carbon and ocean pH. *Nature* 425:365

Cayan DR, Kammerdiener SA, Dettinger MD, Caprio JM, Peterson DH. 2001. Changes in the onset of spring in the western United States. *Bull. Am. Meteorol. Soc.* 82:399–415

Chapin FS III, Berman M, Callaghan TV, Convey P, Crepin AS, et al. 2006. Polar systems. In *Millennium Ecosystem Assessment, Ecosystems and Human Well-Being, Volume 1: Current State and Trends*, ed. R Hassan, R Scholes, N Ash, pp. 717–43. Washington, DC: Island Press

Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KG, Laundre JA. 1995. Response of Arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711

Chuine I, Beaubien E. 2001. Phenology is a major determinant of tree species range. *Ecol. Lett.* 4:500–10

Coope GR. 1994. The response of insect faunas to glacial-interglacial climatic fluctuations. *Philos. Trans. R. Soc. London Ser. B.* 344:19–26

Crick HQ, Dudley C, Glue DE. 1997. UK birds are laying eggs earlier. *Nature* 388:526

Croxall JP, Trathan PN, Murphy EJ. 2002. Environmental change and Antarctic seabird populations. *Science* 297:1510–14

Crozier L. 2003. Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia* 135:648–56

Crozier L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* 85:231–41

Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* 292:673–79

Davis MB, Zabinski C. 1992. Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. In *Global Warming and Biological Diversity*, ed. TEL Peters, R Lovejoy, pp. 297–308. New Haven, CT: Yale Univ. Press

Dennis RLH. 1993. *Butterflies and Climate Change*. Manchester, UK: Manchester Univ. Press

Derocher AE. 2005. Population ecology of polar bears at Svarlbad, Norway. *Popul. Ecol.* 47:267–75

Derocher AE, Lunn NJ, Stirling I. 2004. Polar bears in a warming climate. *Integr. Comp. Biol.* 44:163–76

Descimon H, Bachelard P, Boitier E, Pierrat V. 2006. Decline and extinction of *Parnassius apollo* populations in France—continued. In *Studies on the Ecology and Conservation of Butterflies in Europe (EBIE)*, ed. E Kühn, R Feldmann, J Settele. Bulgaria: PENSOFT. In press

deYoung B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L. 2004. Detecting regime shifts in the ocean: data considerations. *Prog. Oceanogr.* 60:143–64

Dobzhansky TH. 1943. Genetics of natural populations. IX. Temporal changes in the composition of populations of *Drosophila pseudoobscura*. *Genetics* 28:162–86

Dobzhansky TH. 1947. A response of certain gene arrangements in the third chromosome of *Drosophila pseudoobscura* to natural selection. *Genetics* 32:142–60

Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob. Change Biol.* 11:2251–65

Doran PT, Priscu JC, Lyons WB, Walsh JE, Fountain AG, et al. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415:517–22

Dose V, Menzel A. 2004. Bayesian analysis of climate change impacts in phenology. *Glob. Change Biol.* 10:259–72

Dunn PO, Winkler DW. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proc. R. Soc. London Ser. B* 266:2487–90

Easterling DR, Meehl J, Parmesan C, Chagnon S, Karl TR, Mearns LO. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–74

Ehrlich PR, Murphy DD, Singer MC, Sherwood CB, White RR, Brown IL. 1980. Extinction, reduction, stability and increase: the responses of checkerspot butterfly populations to the California drought. *Oecologia* 46:101–5

Emslie SD, Fraser W, Smith RC, Walker W. 1998. Abandoned penguin colonies and environmental change in the Palmer Station area, Anvers Island, Anatarctic Peninsula. *Antarct. Sci.* 10:257–68

Ferguson SH, Stirling I, McLoughlin P. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Mar. Mamm. Sci.* 21:121–35

Ford EB. 1945. *Butterflies*. London: Collins

Ford SE. 1996. Range extension by the oyster parasite *Perkinsus marinus* into the northeastern United States: response to climate change? *J. Shellfish Res.* 15:45–56

Forister ML, Shapiro AM. 2003. Climatic trends and advancing spring flight of butterflies in lowland California. *Glob. Change Biol.* 9:1130–35

Fraser WR, Trivelpiece WZ, Ainley DC, Trivelpiece SG. 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol.* 11:525–31

Garcia-Ramos G, Kirkpatrick M. 1997. Genetic models of adaptation and gene flow in peripheral populations. *Evolution* 51:21–28

Gaston AJ, Gilchrist HG, Hipfner M. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). *J. Anim. Ecol.* 74:832–41

Gibbs JP, Breisch AR. 2001. Climate warming and calling phenology of frogs near Ithaca, New York, 1900–1999. *Conserv. Biol.* 15:1175–78

Gordo O, Brotons L, Rerrer X, Comass P. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Glob. Change Biol.* 11:12–21

Grabherr G, Gottfried M, Pauli H. 1994. Climate effects on mountain plants. *Nature* 369:448

Grinnell J. 1917. Field tests of theories concerning distributional control. *Am. Nat.* 51:115–28

Gross L. 2005. As the Antarctic ice pack recedes, a fragile ecosystem hangs in the balance. *PLoS Biol.* 3(4):e127

Gudmundsson F. 1951. The effects of the recent climatic changes on the bird life of Iceland. *Proc. 10th Int. Ornithol. Congr.*, *Uppsala*, *June 1950*, pp. 502–14

Gurevitch J, Hedges LV. 1999. Statistical issues in ecological meta-analyses. *Ecology* 80:1142–49

Haeger JF. 1999. *Danaus chrysippus* (Linnaeus 1758) en la Península Ibérica: migraciones o dinámica de metapoblaciones? *Shilap* 27:423–30

Hanski I, Erälahti C, Kankare M, Ovaskainen O, Sirén H. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecol. Lett.* 7:958–66

Hari RE, Livingstone DM, Siber R, Burkhardt-Holm P, Güttinger H. 2006. Consequences of climatic change for water temperature and brown trout population in Alpine rivers and streams. *Glob. Change Biol.* 12:10–26

Harrington R, Woiwod I, Sparks T. 1999. Climate change and trophic interactions. *Trends Ecol. Evol.* 14:146–50

Harris G. 1964. Climatic changes since 1860 affecting European birds. *Weather* 19:70–79

Hays GC, Richardson AJ, Robinson C. 2005. Climate change and marine plankton. *Trends Ecol. Evol.* 20:337–44

Heath J. 1974. A century of changes in the lepidoptera. In *The Changing Flora and Fauna of Britain*, ed. DL Hawkesworth, 6:275–92. London: Syst. Assoc.

Hemp A. 2005. Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. *Glob. Change Biol.* 11:1013–23

Hickling R, Roy DB, Hill JK, Thomas CD. 2005. A northward shift of range margins in British Odonata. *Glob. Change Biol.* 11:502–6

Hill GE, Sargent RR, Sargent MB. 1998. Recent change in the winter distribution of Rufous Hummingbirds. *Auk* 115:240–45

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, et al. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proc. R. Soc. London Ser. B* 269:2163–71

Hill JK, Thomas CD, Lewis OT. 1999. Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*. *Biol. Conserv.* 87:277–84

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* 50:839–66

Hoegh-Guldberg O. 2005a. Low coral cover in a high-CO_2 world. *J. Geophys. Res.* 110:C09S06

Hoegh-Guldberg O. 2005b. Marine ecosystems and climate change. See Lovejoy & Hannah 2005, pp. 256–71

Hoegh-Guldberg O, Jones RJ, Ward S, Loh WK. 2002. Is coral bleaching really adaptive? *Nature* 415:601–2

Hoegh-Guldberg O, Pearse JS. 1995. Temperature, food availability, and the development of marine invertebrate larvae. *Am. Zool.* 35:415–25

Hoffmann AA, Blows MW. 1994. Species borders: ecological and evolutionary perspectives. *Trends Ecol. Evol.* 9:223–27

Holbrook SJ, Schmitt RJ, Stephens JS Jr. 1997. Changes in an assemblage of temperate reef fishes associated with a climatic shift. *Ecol. Appl.* 7:1299–310

Holmgren M, Scheffer M, Ezcurra E, Gutierrez JR, Mohren GMJ. 2001. El Niño effects on the dynamics of terresrial ecosystems. *Trends Ecol. Evol.* 16:89–94

Holt RD. 2003. On the evolution ecology of species' ranges. *Evol. Ecol. Res.* 5:159–78

Howell SNG. 2002. *Hummingbirds of North America*. San Diego, CA: Academic

Hughes L. 2000. Biological consequences of global warming: Is the signal already apparent? *Trends Ecol. Evol.* 15:56–61

Huntley B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for the plant communities. *J. Bot.* 67:15–22

Hüppop O, Hüppop K. 2003. North Atlantic Oscillation and timing of spring migration in birds. *Proc. R. Soc. London Ser. B* 270:233–40

Innes JL. 1991. High-altitude and high-latitude tree growth in relation to past, present, and future global climate change. *Holocene* 1:168–73

Inouye DW, Barr B, Armitage KB, Inouye BD. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl. Acad. Sci. USA* 97:1630–33

IPCC (Intergovernmental Panel Climate Change). 2001a. *Climate Change 2001: Impacts, Adaptation, and Vulnerability, Contribution of Working Group II to the Intergovernmental Panel on Climate Change Third Assessment Report*, ed. JJ McCarthy, OF Canziani, NA Leary, DJ Dokken, KS White. Cambridge, UK: Cambridge Univ. Press

IPCC (Intergovernmental Panel Climate Change). 2001b. *Climate Change 2001: The Science of Climate Change, Contribution of Working Group I to the Intergovernmental Panel on Climate Change Third Assessment Report*, ed. JT Houghton, Y Ding, DJ Griggs, M Noguer, PJ van der Linden, X Dai, K Maskell, CA Johnson. Cambridge, UK: Cambridge Univ. Press

Jacoby GC, D'Arrigo RD. 1995. Tree ring width and density evidence of climatic and potential forest change in Alaska. *Glob. Biogeochem. Cycles* 9:227–34

Johnson T, Dozier J, Michaelsen J. 1999. Climate change and Sierra Nevada snowpack. *IAHS Publ.* 256:63–70

Johnston RF, Niles DM, Rohwer SA. 1972. Hermon Bumpus and natural selection in the house sparrow *Passer domesticus*. *Evolution* 26:20–31

Jordano D, Retamosa EC, Fernandez H. 1991. Factors facilitating the continued presence of *Colotis evagore* (Klug 1829) in southern Spain. *J. Biogeogr.* 18:637–46

Jump AS, Peñuelas J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8:1010–20

Kaisila J. 1962. Immigration und Expansion der Lepidopteren in Finnland in den Jahren 1869–1960. *Acta Entomol. Fenn.* 18:1–452

Kalela O. 1949. Changes in geographic ranges in the avifauna of northern and central Europe in response to recent changes in climate. *Bird-Band.* 20:77–103

Kalela O. 1952. Changes in the geographic distribution of Finnish birds and mammals in relation to recent changes in climate. In *The Recent Climatic Fluctuation in Finland and its Consequences: A Symposium*, ed. I Hustichi, pp. 38–51. Helsinki: Fennia

Karieva PM, Kingsolver JG, Huey RB, eds. 1993. *Biotic Interactions and Global Change*. Sunderland, MA: Sinauer

Karl TR, Trenberth KE. 2003. Modern global climate change. *Science* 302:1719–23

Keeling CD, Chin JFS, Whorf TP. 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. *Nature* 382:146–49

Kirkpatrick M, Barton NH. 1997. Evolution of a species' range. *Am. Nat.* 150:1–23

Kullman L. 2001. 20th century climate warming and tree-limit rise in the southern Scandes of Sweden. *Ambio* 30:72–80

Kutz SJ, Hoberg EP, Polley L, Jenkins EJ. 2005. Global warming is changing the dynamics of Arctic host-parasite systems. *Proc. R. Soc. London Ser. B* 272:2571–76

Lapenis A, Shvidenko A, Shepaschenko D, Nilsson S, Aiyyer A. 2005. Acclimation of Russian forests to recent changes in climate. *Glob. Change Biol.* 11:2090–102

Lescop-Sinclair K, Payette S. 1995. Recent advance of the Arctic treeline along the eastern coast of Hudson Bay. *J. Ecol.* 83:929–36

Levitan M. 2003. Climatic factors and increased frequencies of 'southern' chromosome forms in natural populations of *Drosophila robusta*. *Evol. Ecol. Res.* 5:597–604

Lewontin RC, Birch LC. 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* 20:315–36

Lindgren E, Gustafson R. 2001. Tick-borne encephalitis in Sweden and climate change. *Lancet* 358:16–18

Logan JA, Regniere J, Powell JA. 2003. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* 1:130–37

Lovejoy T, Hannah L, eds. 2005. In *Climate Change and Biodiversity*. New Haven, CT: Yale Univ. Press

Luckman B, Kavanagh T. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio* 29:371–80

Lynch M, Lande R. 1993. Evolution and extinction in response to environmental change. See Karieva et al. 1993, pp. 234–50

MacArthur RM. 1972. *Geographical Ecology*. New York: Harper & Row

Marttila O, Haahtela T, Aarnio H, Ojalainen P. 1990. *Suomen Päiväperhoset*. Helsinki: Kirjayhtymä

McGowan JA, Cayan DR, Dorman LM. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281:210–17

Meehl GA, Zwiers F, Evans J, Knutson T, Mearns LO, Whetton P. 2000. Trends in extreme weather and climate events: issues related to modeling extremes in projections of future climate change. *Bull. Am. Meteorol. Soc.* 81:427–36

Menzel A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *Int. J. Biometeorol.* 44:76–81

Menzel A. 2005. A 500 year pheno-climatological view on the 2003 heatwave in Europe assessed by grape harvest dates. *Meteorol. Z.* 14:75–77

Menzel A, Dose V. 2005. Analysis of long-term time-series of beginning of flowering by Bayesian function estimation. *Meteorol. Z.* 14:429–34

Menzel A, Fabian P. 1999. Growing season extended in Europe. *Nature* 397:659

Menzel A, Jakobi G, Ahas R, Scheifinger H, Estrella N. 2003. Variations of the climatological growing season (1951–2000) in Germany compared with other countries. *Int. J. Climatol.* 23:793–812

Meshinev T, Apostolova I, Koleva E. 2000. Influence of warming on timberline rising: a case study on *Pinus peuce* Griseb. in Bulgaria. *Phytocoenologia* 30:431–38

Mikkola K. 1997. Population trends of Finnish Lepidoptera during 1961–1996. *Entomol. Fenn.* 3:121–43

Moiseev PA, Shiyatov SG. 2003. The use of old landscape photographs for studying vegetation dynamics at the treeline ecotone in the Ural Highlands, Russia. In *Alpine Biodiversity in Europe*, ed. L Nagy, G Grabherr, C Körner, DBA Thompson, pp. 423–36. Berlin: Springer-Verlag

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702

Nylin S. 1988. Host plant specialization and seasonality in a phytophagous butterfly, *Polygonia c-album* (Nymphalidae). *Oikos* 53:381–86

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–86

Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia* 128:1–14

Parmesan C. 1996. Climate and species' range. *Nature* 382:765–66

Parmesan C. 2002. Detection of range shifts: general methodological issues and case studies using butterflies. In *Fingerprints of Climate Change: Adapted Behaviour and Shifting Species' Ranges*, ed. G-R Walther, CA Burga, PJ Edwards, pp. 57–76. Dordrecht, Netherlands: Kluwer Acad./Plenum

Parmesan C. 2003. Butterflies as bio-indicators of climate change impacts. In *Evolution and Ecology Taking Flight: Butterflies as Model Systems*, ed. CL Boggs, WB Watt, PR Ehrlich, pp. 541–60. Chicago: Univ. Chicago Press

Parmesan C. 2005a. Detection at multiple levels: *Euphydryas editha* and climate change. Case study. See Lovejoy & Hannah 2005, pp. 56–60

Parmesan C. 2005b. Range and abundance changes. See Lovejoy & Hannah 2005, pp. 41–55

Parmesan C, Gaines S, Gonzalez L, Kaufman DM, Kingsolver J, et al. 2005. Empirical perspectives on species' borders: environmental change as challenge and opportunity. *Oikos* 108:58–75

Parmesan C, Galbraith H. 2004. *Observed Ecological Impacts of Climate Change in North America*. Arlington, VA: Pew Cent. Glob. Clim. Change

Parmesan C, Martens P. 2006. Climate change. In *Biodiversity, Health and the Environment: SCOPE/Diversitas Rapid Assessment Project*, ed. O Sala, L Meyerson, C Parmesan. Washington, DC: Island Press. In press

Parmesan C, Root TL, Willig MR. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bull. Am. Meteorol. Soc.* 81:443–50

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–83

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42

Pauli H, Gottfried M, Grabherr G. 1996. Effects of climate change on mountain ecosystems: upward shifting of mountain plants. *World Res. Rev.* 8:382–90

Paulson DR. 2001. Recent odonata records from southern Florida: effects of global warming? *Int. J. Odonatol.* 4:57–69

Peñuelas J, Filella I. 2001. Responses to a warming world. *Science* 294:793–94

Perry AL, Low PJ, Ellis JR, Reynolds JD. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–15

Pollard E. 1979. Population ecology and change in range of the white admiral butterfly *Ladoga camilla* L. in England. *Ecol. Entomol.* 4:61–74

Pollard E, Eversham BC. 1995. Butterfly monitoring 2: interpreting the changes. In *Ecology and Conservation of Butterflies*, ed. AS Pullin, pp. 23–36. London: Chapman & Hall

Post E, Langvatn R, Forchhammer MC, Stenseth NC. 1999. Environmental variation shapes sexual dimorhism in red deer. *Proc. Natl. Acad. Sci. USA* 96:4467–71

Pounds JA, Bustamente MR, Coloma LA, Consuegra JA, Fogden MPL, et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161–67

Pounds JA, Fogden MPL, Campbell JH. 1999. Biological response to climate change on a tropical mountain. *Nature* 398:611–15

Pounds JA, Fogden MPL, Masters KL. 2005. Responses of natural communities to climate change in a highland tropical forest. Case study. See Lovejoy & Hannah 2005, pp. 70–74

Precht H, Christophersen J, Hensel H, Larcher W. 1973. *Temperature and Life*. New York: Springer-Verlag

Precht WF, Aronson RB. 2004. Climate flickers and range shifts of reef corals. *Front. Ecol. Environ*. 2:307–14

Réale D, McAdam A, Outin G, Berteaux S. 2003. Genetic and plastic response of a northern mammal to climate change. *Proc. R. Soc. London Ser. B* 270:591–96

Reid PC, Edwards M, Hunt HG, Warner AJ. 1998. Phytoplankton change in the North Atlantic. *Nature* 391:546

Richardson AJ, Schoeman DS. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305:1609–12

Rodríguez-Trelles F, Álvarez G, Zapata C. 1996. Time-series analysis of seasonal changes of the O inversion polymorphism of *Drosophila subobscura*. *Genetics* 142:179–87

Rodríguez-Trelles F, Rodriguez MA. 1998. Rapid micro-evolution and loss of chromosomal diversity in *Drosophila* in response to climate warming. *Evol. Ecol.* 12:829–38

Rodríguez-Trelles F, Rodriguez MA, Scheiner SM. 1998. Tracking the genetic effects of global warming: *Drosophila* and other model systems. *Conserv. Ecol*. 2:2

Roessig JM, Woodley CM, Cech JJ, Hansen LJ. 2004. Effects of global climate change on marine and estuarine fishes. *Rev. Fish Biol. Fish*. 14:215–75

Roetzer T, Wittenzeller M, Haeckel H, Nekovar J. 2000. Phenology in central Europe: difference and trends of spring phenophases in urban and rural areas. *Int. J. Biometeorol*. 44:60–66

Root TL. 1988. Energy constraints on avian distributions and abundances. *Ecology* 69:330–39

Root TL, Hughes L. 2005. Present and future phenological changes in wild plants and animals. See Lovejoy & Hannah 2005, pp. 61–69

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60

Rowan R. 2004. Thermal adaptation in reef coral symbionts. *Nature* 430:742

Roy DB, Sparks TH. 2000. Phenology of British butterflies and climate change. *Glob. Change Biol*. 6:407–16

Sagarin RD, Barry JP, Gilman SE, Baxter CH. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecol. Monogr*. 69:465–90

Salomonsen F. 1948. The distribution of birds and the recent climatic change in the North Atlantic area. *Dansk. Orn. Foren. Tidsskr*. 42:85–99

Schwartz MD. 1998. Green-wave phenology. *Nature* 394:839–40

Schwartz MD. 1999. Advancing to full bloom: planning phenological research for the 21st century. *Int. J. Biometeorol*. 42:113–18

Scriber JM, Lederhouse RC. 1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbinores. In *Effects of Resource Distribution on Plant-Animal Interactions*, ed. MR Hunter, T Ohgushi, PW Price, pp 429–66. New York: Academic

Severnty DL. 1977. The use of data on the distribution of birds to monitor climatic changes. *Emu* 77:162–66

Shoo LP, Williams SE, Hero JM. 2006. Detecting climate change induces range shifts: Where and how should we be looking? *Aust. Ecol*. 31:22–29

Singer MC. 1972. Complex components of habitat suitability within a butterfly colony. *Science* 176:75–77

Singer MC, Ehrlich PR. 1979. Population dynamics of the checkerspot butterfly *Euphydryas editha*. *Fortschr. Zool*. 25:53–60

Singer MC, Thomas CD. 1996. Evolutionary responses of a butterfly metapopulation to human and climate-caused environmental variation. *Am. Nat*. 148:S9–39

Smith AT. 1974. The distribution and dispersal of pikas: influences of behavior and climate. *Ecology* 55:1368–76

Smith RC, Ainley D, Kaber K, Domack E, Emslie S, et al. 1999. Marine ecosystem sensitivity to historical climate change in the Antarctic Peninsula. *BioScience* 49:393–404

Smith RIL. 1994. Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia* 99:322–28

Smol JP, Wolfe AP, Birks HJB, Douglas MSV, Jones VJ, et al. 2005. Climate-driven regime shifts in the biological communities of Arctic lakes. *Proc. Natl. Acad. Sci. USA* 102:4397–402

Southward AJ, Hawkins SJ, Burrows MT. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *J. Therm. Biol*. 20:127–55

Southward AJ, Langmead O, Hardman-Mountford NJ, Aiken J, Boalch GT, et al. 2005. Long-term oceanographic and ecological research in the western English Channel. *Adv. Mar. Biol*. 47:1–105

Sparks TH, Menzel A. 2002. Observed changes in seasons, an overview. *Int. J. Climatol*. 22:1715–26

Sparks TH, Yates TJ. 1997. The effect of spring temperature on the appearance dates of British butterflies 1883–1993. *Ecography* 20:368–74

Spear LB, Ainley DG. 1999. Migration routes of sooty shearwaters in the Pacific Ocean. *Condor* 101:205–18

Stefanescu C, Peñuelas J, Filella I. 2003. Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Glob. Change Biol*. 9:1494

Stirling I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. *Arctic* 55:59–76

Stirling I, Lunn NJ, Iacozza J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* 52:294–306

Sturm M, Racine C, Tape K. 2001. Increasing shrub abundance in the Arctic. *Nature* 411:546–47

Sturm M, Schimel J, Mechaelson G, Welker JM, Oberbauer SF, et al. 2005. Winter biological processes could help convert Arctic tundra to shrubland. *BioScience* 55:17–26

Swetnam TW, Betancourt JL. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Clim.* 11:3128–47

Taylor RH, Wilson PR. 1990. Recent increase and southern expansion of Adelie penguin populations in the Ross Sea, Antarctica, related to climatic warming. *N.Z. J. Ecol.* 14:25–29

Thomas C. 2005. Recent evolutionary effects of climate change. See Lovejoy & Hannah 2005, pp. 75–90

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, et al. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–81

Thomas CD, Lennon JJ. 1999. Birds extend their ranges northwards. *Nature* 399:213

Thomas CD, Singer MC, Boughton D. 1996. Catastrophic extinction of population sources in a butterfly metapopulation. *Am. Nat.* 148:957–75

Travis J, Futuyma DJ. 1993. Global change: lessons from and for evolutionary biology. See Karieva et al. 1993, pp. 234–50

Uvarov BP. 1931. Insects and climate. *R. Entomol. Soc. London* 79:174–86

van Herk CM, Aptroot A, van Dobben HF. 2002. Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist* 34:141–54

Van Nouhuys S, Lei G. 2004. Parasitoid-host metapopulation dynamics: the causes and consequences of phenological asynchrony. *J. Anim. Ecol.* 73:526–35

Visser ME, Both C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B* 272:2561–69

Walther GR, Hughes L, Vitousek P, Stenseth NC. 2005. Consensus on climate change. *Trends Ecol. Evol.* 20:648–49

Walther GR, Post E, Convery P, Menzel A, Parmesan C, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–95

Wardle P, Coleman MC. 1992. Evidence for rising upper limits of four native New Zealand forest trees. *N.Z. J. Bot.* 30:303–14

Warren MS. 1992. The conservation of British butterflies. In *The Ecology of Butterflies in Britain*, ed. RLH Dennis, pp. 246–74. Oxford, UK: Oxford Univ. Press

Webb T III, Bartlein PJ. 1992. Global changes during the last 3 million years: climatic controls and biotic responses. *Annu. Rev. Ecol. Syst.* 23:141–73

Weiser W, ed. 1973. *Effects of Temperature on Ectothermic Organisms*. New York: Springer-Verlag

Weiss SB, Murphy DD, White RR. 1988. Sun, slope and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology* 69:1486–96

White MA, Nemani RR, Thornton PE, Running SW. 2002. Satellite evidence of phenological differences between urbanized and rural areas of the eastern United States deciduous broadleaf forest. *Ecosystems* 5:260–73

White MA, Running SW, Thornton PE. 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *Int. J. Biometeorol.* 42:139–45

Wilkinson CR, ed. 2000. *Global Coral Reef Monitoring Network: Status of Coral Reefs of the World in 2000*. Townsville, Qld: Aust. Inst. Mar. Sci.

Williamson K. 1975. Birds and climatic change. *Bird Study* 22:143–64

Wilson JW, Gutiérrez D, Martinez D, Agudo R, Monserrat VJ. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* 8:1138–46

Wilson PR, Ainley DG, Nur N, Jacobs SS, Barton KJ, et al. 2001. Adélie penguin population change in the pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. *Mar. Ecol. Prog. Ser.* 213:301–9

Winder M, Schindler DE. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85:2100–6

Woodward FI. 1987. *Climate and Plant Distribution*. Cambridge, UK: Cambridge Univ. Press

---

RELATED RESOURCES

Alford, RA, Richards SJ. 1999. Global amphibian declines: a problem in applied ecology. *Annu. Rev. Ecol. Syst.* 30:133–65

Glynn PW. 1988. El Niño-Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. *Annu. Rev. Ecol. Syst.* 19:309–45

Ludwig D, Marc M, Haddad B. 2001. Ecology, conservation, and public policy. *Annu. Rev. Ecol. Syst.* 32:481–517

Smith SV, Buddemeier RW. 1992. Global change and coral reef ecosystems. *Annu. Rev. Ecol. Syst.* 23:89–118

Stevens GC, Fox JF. 1991. The causes of treeline. *Annu. Rev. Ecol. Syst.* 22:177–91

Global Change Biology (2007) **13,** 1860–1872, doi: 10.1111/j.1365-2486.2007.01404.x

Influences of species, latitudes and methodologies on estimates of phenological response to global warming

CAMILLE PARMESAN

Section of Integrative Biology, University of Texas, Austin, TX 78712, USA

Abstract

New analyses are presented addressing the global impacts of recent climate change on phenology of plant and animal species. A meta-analysis spanning 203 species was conducted on published datasets from the northern hemisphere. Phenological response was examined with respect to two factors: distribution of species across latitudes and taxonomic affiliation or functional grouping of target species. Amphibians had a significantly stronger shift toward earlier breeding than all other taxonomic/functional groups, advancing more than twice as fast as trees, birds and butterflies. In turn, butterfly emergence or migratory arrival showed three times stronger advancement than the first flowering of herbs, perhaps portending increasing asynchrony in insect–plant interactions. Response was significantly stronger at higher latitudes where warming has been stronger, but latitude explained $<4\%$ of the variation. Despite expectation, latitude was not yet an important predictor of climate change impacts on phenology. The only two previously published estimates of the magnitude of global response are quite different: 2.3 and 5.1 days decade^{-1} advancement. The scientific community has assumed this difference to be real and has attempted to explain it in terms of biologically relevant phenomena: specifically, differences in distribution of data across latitudes, taxa or time periods. Here, these and other possibilities are explored. All analyses indicate that the difference in estimated response is primarily due to differences between the studies in criteria for incorporating data. It is a clear and automatic consequence of the exclusion by one study of data on 'stable' (nonresponsive) species. Once this is accounted for, the two studies support each other, generating similar conclusions despite analyzing substantially nonoverlapping datasets. Analyses here on a new expanded dataset estimate an overall spring advancement across the northern hemisphere of 2.8 days decade^{-1}. This is the first quantitative analysis showing that data-sampling methodologies significantly impact global (synthetic) estimates of magnitude of global warming response.

Keywords: animal, climate change, global warming, insect–plant interactions, latitude, meta-analysis, phenology, plant, temperature, trophic interactions

Received 22 June 2006; revised version received 19 January 2007 and accepted 6 February 2007

Introduction

Increasing levels of greenhouse gases began to have a major impact on global climate only a few decades ago, yet there are already hundreds of studies documenting responses of wild species to that relatively small level of global warming (reviewed by IPCC, 2001a, b; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006). However, these responses are far from uniform. There are only a few species, which differ from the majority in direction of response, such as breeding later in spite of warming temperatures, but the strength of response in the expected direction varies by an order of magnitude across species. For example, multispecies studies have documented large differences in responses within given communities on a farm in the USA (among birds, butterflies, herbs and trees), in Britain (birds and butterflies) and across the whole of Europe (butterflies, trees and shrubs) (Bradley *et al.*, 1999; Menzel & Fabian, 1999; Parmesan *et al.*, 1999; Sparks, 1999; Menzel, 2000; Roy & Sparks, 2000). Further, many species (from 20% to 70% of species at a given location) have shown no response at all, exhibiting stable phenological patterns

Correspondence: Dr Camille Parmesan, tel. +1 512 232 1860, fax +1 512 232 3402, e-mail: parmesan@mail.utexas.edu

across years despite living in environments experiencing warming trends (Parmesan & Yohe, 2003).

Estimates of phenological response have the potential to be substantially influenced by the choice of study design and statistical methodology. However, because phenological data have been gathered and compiled in a diversity of ways over a diversity of time periods, their analysis is not straightforward, and there are as yet, no generally agreed methods. Several authors have identified particular problem areas and suggested refinements to deal with them. Sagarin (2001) pointed out a subtle source of bias present in virtually all analyses of temporal trends in phenology. He showed that analyses, which did not adjust event dates through time to account for long-term change in the calendar date of the vernal equinox had a bias toward stronger estimates of spring advancement. For example, the estimate of advancement of first bloom of *Rudbeckia hirta* (black-eyed Susan) from 1935 to 2000 was 5% stronger than the actual advancement. For all biological datasets analyzed, this resulted in a small but persistent overestimate of the magnitude of response to warming (Sagarin, 2001).

Sampling methodology, both within and across studies, could also have a large impact on estimates of response. One concern which has cropped up in several studies is that increases either in numbers of observers (particularly for databases derived mostly from amateur records) or real increase in population abundances could cause apparent expansions of ranges (Thomas & Lennon, 1999) or apparent earlier migrant arrival (Tryjanowski, 2001). Thus, what appears to be a change over time could, in reality, be due solely to statistical artifact stemming from a change in the absolute probability of sighting an individual at a particular place or time, with no real change in the species' range or phenology.

A suggested methodological refinement is use of Bayesian techniques for estimating response through time. For example, Bayseian methods can take into account changes in sampling density over time, by incorporating variability of sampling intensity into error terms across space and time for the desired estimate (Wikle, 2003). Dose & Menzel (2004) showed that Bayesian techniques for estimating changes in flowering time provided a means of asking quantitatively whether the rates of change were themselves changing. This technique enabled them to show a recent and significant increase in rate of phenological advance, thereby supporting previous, more qualitative claims that responses have become stronger in more recent (warmer) decades.

More general discussions of how differing methodologies might affect estimates of climate change impacts include concerns about effects of publication bias, differences across studies in time periods analyzed, nonrandom sampling within a species and nonrandom selection of species (Ahmad *et al*., 2001; Parmesan & Yohe, 2003; Badeck *et al*., 2004; Parmesan, 2004, 2005; Parmesan *et al*., 2005). However, to date, no study has explicitly explored the impact of these effects on quantitative estimates of species' responses.

There are, as yet, only two quantitative, globally comprehensive datasets on phenological responses to recent climate warming: Root *et al*. (2003) and Parmesan & Yohe (2003) hereafter abbreviated as Retal and P&Y. Quantitative comparisons across broad taxonomic and functional groups have been limited to a single study (Root *et al*., 2003). Because the criteria for data selection differed strongly between Retal and P&Y, the two resulting datasets were largely nonoverlapping. Therefore, a comparison between these studies has the potential to reveal the effects of differing data-selection techniques on overall conclusions.

Since the publication of Retal and P&Y, new data have been accumulating at an increasing rate (Parmesan, 2006), so these questions should ideally be tackled using all the accumulated information. However, before this can be achieved in a definitive manner, it would behoove the entire community to reach agreement on sampling and statistical methodology. Such agreement is still missing, in spite of the discussions referenced above showing that differences across studies in methodology have the potential to profoundly influence results. Before devoting efforts to new analyses of an ever-expanding database, priority should be given to developing consensus on how to best compile and interpret data across disparate studies to derive general conclusions. This paper attempts to inform such a future consensus by presenting new analyses of the existing datasets and by discussing the influence of the different approaches on the nature of the conclusions.

Specifically, I investigate the underlying causes of a more than two-fold difference in estimates of the mean magnitude of advance in timing of spring events between the two studies: 2.3 days decade^{-1} advance found by P&Y, and 5.1 days decade^{-1} advance found by Retal. Badeck *et al*. (2004) suggested that the difference between these two studies could be due to data being from different latitudes, different taxa, or different time periods. However, they did not investigate these possibilities analytically.

The two synthetic papers were both confined to data published in peer-reviewed literature, but differed in their criteria for data inclusion. This largely reflected differing aims of the two studies. Retal were focused on estimating the pervasiveness of a positive correlation between temperature trends and phenological trends for species *that were changing* through time. P&Y

focused on estimating *total response* to climate change by analyzing the overall strength and consistency of response across all species, whether or not they showed phenological change. Further, P&Y attempted to control for publication bias by taking data only from multispecies studies (which included stable as well as responding species), while Retal used data from both single species and multispecies studies.

Here, I compare the two datasets to explicitly explore possible drivers of the difference in estimated strength of phenological responses between P&Y and Retal. A series of comparisons and analyses of the two datasets attempts to ascertain whether the differences in estimated responses represent biologically important phenomena or simply departures of methodology. A related question is: 'do the available data accurately reflect trends in natural systems, or are they biased?' One obvious source of bias would stem from positive (significant) results being more likely to be published than negative (nonsignificant) results. What are the effects of positive publishing bias on apparent strengths and patterns of overall global responses of wild species?

Further, I conduct new analyses across a substantially larger dataset than has previously been analyzed to explore effects on phenological advance of latitude and taxonomic/functional group affiliation. Because mean annual temperature rise has been much stronger at higher latitudes, there has been an expectation among biologists that magnitude of response in wild species would also be stronger at higher latitudes (IPCC, 2001a, b; Root *et al*., 2003; Arctic Climate Impact Assessment, 2004; Badeck *et al*., 2004).

Specifically, I address the following questions: What is the mean rate of response of wild species? Are some taxonomic groups more sensitive than others? Are species responding differently in geographic regions subject to different rates or patterns of climate change? In particular, is the magnitude of response stronger at higher latitudes, as expected from larger temperature increases toward the North Pole?

Materials and methods

Full lists of species and published studies included in this study are given in P&Y and in Appendix 3 of supplemental materials in Retal which is available from *Nature's* website.

Responses across taxonomic groups and with latitude

Patterns of association between strength of response and taxonomic grouping or latitude were conducted for a new combined dataset compiled from studies conducted in the Northern hemisphere. The single southern hemisphere species, the little penguin, *Eudyptula minor*, from Retal was eliminated from analyses. Where necessary, corrections were made for data errors in the Retal dataset as posted on *Nature*'s website (see 'Modifications of datasets'). All statistical analyses were conducted with STATVIEW statistical software. Earlier timing was indicated with negative values, later timing with positive values. Analysis of effect of latitude on response (change in days decade^{-1}) was by linear regression. Analysis of differences among taxonomic groups was by one-way ANOVA followed by Fisher's least significant difference (LSD) tests for multiple comparisons. Significance of effects was set at $\alpha = 0.05$ throughout.

Study designs: the two approaches

There were distinctly different methodologies for inclusion of species and studies between P&Y and Retal. Criteria for inclusion by Retal were: (1) Time series had to have at least 10 years of data from recent decades (1951–2001). (2) Study had to include an analysis of the association between temperature trends and phenological trends. (3) An observed change was only included if it showed more than 1 day decade^{-1} of change, regardless of whether the change was significant.

Criteria for inclusion by P&Y were: (1) time series had to contain 20 years or more of data, starting from the past decade and working backward. (2) Single-species studies were excluded. Data were restricted to studies of suites of multiple species in the same area, with both responding and nonresponding species reported. This was done to minimize expected positive publishing bias from single-species studies, since a study of one species that fails to show effects of climate change is unlikely to be published. (3) An analysis of temperature trends over time had to have been published for the study region, but not necessarily in the same paper as the biological analysis (although most did coincide).

Both syntheses allowed minor deviations from their stated criteria: Retal included a few multispecies studies where only the mean response was known, hence nonresponding species likely contributed to the estimate of magnitude of response. P&Y included one amphibian study (six species) with only 17 years of data, because of rarity of nonbird vertebrate studies and because this UK study nicely complemented North American studies of 10 other amphibian species.

Despite this partial relaxing of the different criteria, there were only 59 species in common between the two synthetic studies, out of a total of 172 distinct species in P&Y and 87 distinct species in Retal. Retal included many single-species, single-location studies not included in P&Y. P&Y included some multispecies studies that had long biological time series and data on mean temperature change, but were excluded by Retal because they had not conducted an explicit statistical analysis of the strength of association between temperature trends and biological trends.

Modifications of datasets

The P&Y dataset was used without modification. Base analyses were conducted on the Retal dataset from Appendix 3, supplemental material posted on Nature's website without modification. The same set of analyses conducted on the unmodified (base) dataset was repeated with modified datasets: with and without the composite (mean) values from studies where species were not separated, and with and without replication of individual species in different studies. Finally, a combined dataset was compiled in which each datapoint represented one unique species (no replicate estimates for the same species and no means for multiple species were included), and in which some errors in original datasets were corrected. Details of the modifications are given below.

One reason for using only a single datapoint per species is that responses of conspecific populations are not likely to be independent, for two reasons. First, there may be migration that homogenizes responses across geographical regions; second, conspecific populations may respond similarly because of biological similarity. At the next taxonomic level up, responses of closely related species are also not independent, but for only one of these reasons, biological similarity derived from common ancestry. This can cause bias in any attempt to derive an overall mean biological response. For example, an overall mean derived from a dataset that overrepresented amphibians, which are responding particularly strongly to climate warming (see 'Results'), would overestimate the overall mean response. Ideally, to get an overall mean response, all the different taxonomic groups that exist should be represented in the dataset in the proportions in which they occur in nature. At present, the data do not exist to even approximate this. It is, however, possible to calculate an overall mean response for the data that do exist and then to examine them for differences among taxa or functional groups, as was first done by Retal.

There are very few species for which there is sufficient information across the species' range for detailed analysis of within-species variation of phenological trends. The rare exceptions include trees and shrubs in the European phenological gardens (Menzel & Fabian, 1999; Menzel, 2000), the tree swallow, *Tachycineta bicolor* (Dunn & Winkler, 1999) and the pied flycatcher, *Ficedula hypoleuca* (Both *et al*., 2004). Therefore, most analyses have been conducted at the species level or above. This reality of data limitation was reflected in the guidelines laid down by IPCC (2001b) for use of the species as the smallest unit.

Reduction of the Retal dataset to a single point per species was carried out because the inclusion of the same species more than once occurred in two ways. First, the same species was sometimes explicitly reported in different studies. Examples are apple trees (*Malus domesticus*) in Estonia (Ahas, 1999) and in Germany (Menzel *et al*., 2001), and the pied flycatcher (*F. hypoleuca*) in Wales (Slater, 1999), the Netherlands (Both & Visser, 2001) and in Finnish Lapland (Jarvinen, 1989). By this means eight species contributed 21 points to the Retal data. The modification used here was to randomly choose one datapoint per species.

The second means by which a species was represented more than once was that some studies that only reported a mean value for many species included species that were in common with studies that reported each species separately. Thus, the same species may show up in two different datapoints. For example, Myneni *et al*. (1997) reported a mean change in 'green up' of all plants in northern latitudes estimated from satellite data, and Schwartz (1998) reported a change in 'green up' of plants in eastern North America estimated from a phenological model based on observed climate data. The studies overlap – the Schwartz study encompasses a subset of the Myneni *et al*. geographic area – and so are not independent. Thirteen datapoints in Retal each represented mean values across a suite of species. Not all studies listed the species used to obtain these means. For studies that did list species, there was considerable overlap with studies that listed individual values for each species. A further modification of the dataset was created without this subset of composite, mean values, as well as without replicate values for individual species (eliminated by the first modification).

In compiling the combined dataset, only datapoints representing individual species were included (means across multiple species were excluded). Where there were multiple studies of the same species, one study was chosen at random for inclusion so that there was only one datapoint per species. In addition, the combined dataset corrected some errors present in the original Retal dataset. In particular, from the Beebee (1995) amphibian study, Retal mistakenly used values from the correlation coefficients ($r \times 10$) rather than from the slope of the regression line to estimate change through time. Finally, the Retal dataset only provided data for one out of the four amphibian species presented in Blaustein *et al*. (2001). The combined dataset here added in data for the three additional species of amphibian reported in that study.

Results

Differences across latitudes

A significant trend ($P < 0.01$) toward stronger advancement at higher latitudes was found in the combined dataset ($N = 203$, Fig. 1), but this association explains <4% of the variation in response across species ($R^2 = 0.035$). To test whether a few extreme species might have been responsible for the significant association, the analysis was repeated eliminating four of the most extreme shifts toward earlier spring phenology (three amphibians and one bird at 52°–54°N latitude). A significant trend ($P < 0.01$) remained.

Differences among taxonomic/functional groups

For the combined dataset, there were significant differences across taxonomic groups in strength of response ($N = 203$, one-way ANOVA, $F = 4.4$, df = 8, 194, $P < 0.0001$). *Post-hoc* multiple comparisons for fish, flies and mammals were not made due to small sample sizes ($n < 3$ for each group). Amphibians showed a two to four times stronger spring advancement when compared with any or all other taxonomic groups ($P < 0.001$ for all comparisons of amphibians with other groups). The only other significant differences were that butterflies and birds showed a significantly stronger advancement than herbs ($P < 0.01$). (Table 1, Fig. 2).

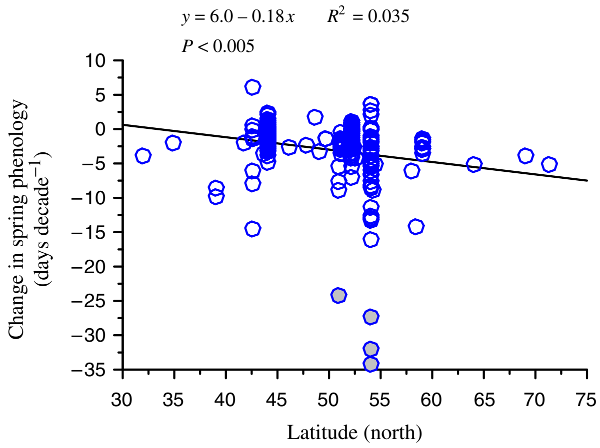

Fig. 1 Response in terms of days of change per decade for individual species by latitude in the combined dataset, $N = 203$. Data were analyzed both with and without the four most extreme species in terms of response (shaded circles). Line drawn is from linear regression.

Table 1 Comparisons across taxonomic groups in strength of response using the combined datasets with mean change in timing standardized to days decade^{-1}, $N_{\text{total}} = 203$

	Spring advancement in days decade^{-1}	
Taxon	Mean ± SE	(n)
Overall	−2.8 ± 0.35	(203)
Amphibian	−7.6 ± 3.09^{a}	(16)
Bird	−3.7 ± 0.70^{b}	(41)
Butterfly	−3.7 ± 0.78^{b}	(35)
Herb and grass	−1.1 ± 0.16^{c}	(85)
Shrub	−1.1 ± 0.68^{b,c}	(6)
Tree	−3.3 ± 0.87^{b,c}	(16)
Fish	−1.3 ± 0.20*	(2)
Fly	−5.0*	(1)
Mammal	−9.6*	(1)

Each datapoint here represents a single species. A negative sign indicates advancement of spring events. Analysis was by one-way ANOVA, with *post-hoc* pairwise comparisons by Fisher's LSD. Significant differences between taxonomic groups are indicated by different letters (for each significant comparison, calculated probabilities came out to <0.01).

*Groups with less than three species not included in the pairwise comparisons analyses.

Differences across studies – effects of sampling methodology

The three potential sources of sampling difference outlined in Badeck *et al.* (2004) are considered first (Table 2). Inspection reveals no substantial differences between the two datasets in mean latitude or taxonomic profiles. In contrast, mean time period of observation in Retal is about half that of P&Y, with medians showing even larger difference. Half the studies in Retal recorded changes only during the strong warming trend of the 1980s and 1990s, whereas half the studies in P&Y extended further back than the 1950s, into much cooler decades.

A pivotal difference between the two studies that has not been considered in prior discussions is whether or not the analyses included apparently 'stable' species. In P&Y, these represented 33% of all species (Fig. 3b). The remainder of the analyses here estimate the impact of this methodological divergence.

There are two ways in which the stable category was missing from the Retal dataset. The first way is very straightforward. Species reported as showing no change or <1 day decade^{-1} change were explicitly eliminated by Retal before analysis. This procedure directly excluded from their analysis a large number of 'zeros' and very small changes. Changes of >1 day decade^{-1} were included, regardless of whether the trend was significant over time (Fig. 3a).

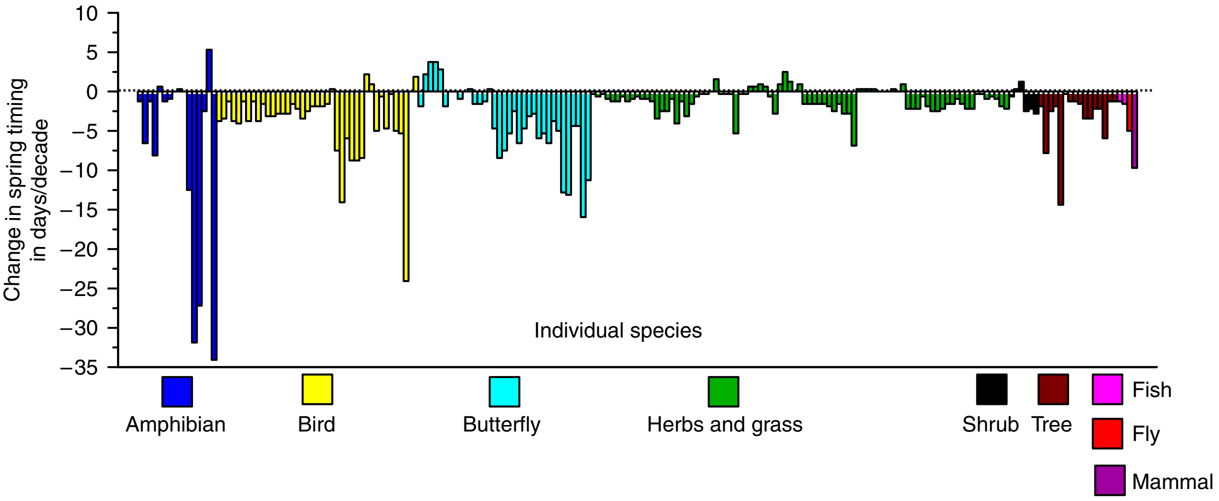

Fig. 2 Changes in timing of spring events in days decade^{-1} for individual species grouped by taxonomy or functional type for the combined dataset. Each bar represents a separate, independent species. Negative values indicate advancement (earlier phenology through time) while positive values indicate delay (later phenology through time).

Table 2 Comparison of datasets between the two meta-analyses of global phenological changes

Study	Data profile	Latitude of data*	Taxonomic representation: *n*	Length of time series (years)
Parmesan & Yohe (2003)	172 individual species	Range: 42.5–59° Mean: 49.8° Median: 52	Birds: 21 Butterflies: 35 Amphibians: 12 Fish: 2 Trees: 12 Herbs&grass: 85 Shrub: 5	Range: 17–99 Mean: 46.2 Median: 46
Root *et al.* (2003)	87 individual species 13 replicates of species 13 composite means	Range: 31.9–71.2° Mean: 51.7° Median: 52.5°	Birds: 24 Butterflies: 30 Fly: 1 Moth: 1 Amphibians: 7 Fish: 2 Zooplankton: 1 Mammal: 1 Trees: 15 Herbs&grass: 3 Shrub: 2	Range: 10–54 Mean: 28.9 Median: 23.5

*Latitudes are all northern hemisphere. Single southern-hemisphere data point in Root *et al.* (2003) excluded from latitude statistics.

The second way in which stable species were not represented is more subtle. It comes from the inclusion by Retal of single-species, single-location studies that do not report on other species at the same location. One-hundred percent of these studies show significant change, while in multispecies studies, on average only 67% of species are reported as changing phenologically (Parmesan & Yohe, 2003). The complete absence of single-species studies that report lack of response results from one type of publication bias: positive results from single species are much more likely to be published than neutral results (i.e. significant change over time is more likely to be published than no change). If we assume that the proportion of responding species is the same in habitats where multi- and single-species studies have been based, we can use the multi-species phenological studies reported by P&Y to deduce that the published single-species studies mask the ex-

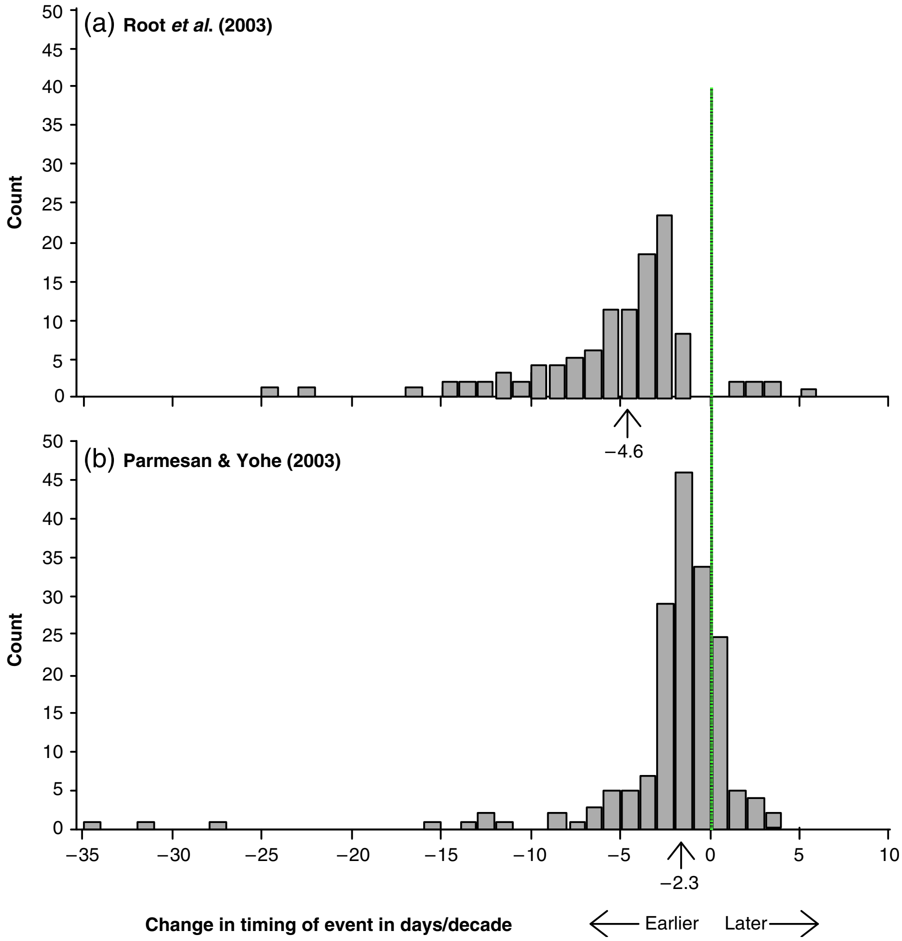

Fig. 3 Histograms of phenological trends across species from unaltered datasets from (a) Root *et al.* (2003) and (b) Parmesan & Yohe (2003). Arrows show estimated mean responses from (a) analyzing data from Root *et al.* (2003) as posted on *Nature's* website, without modification and (b) analyzing data from Parmesan & Yohe (2003) without modification. Zero line is indicated by dashed line.

istence of an additional 33% of unreported species living in the same habitats that would have shown little or no change.

In order to compare the two studies (P&Y and Retal) quantitatively, three analyses were conducted. First, a baseline analysis used the original unmodified Retal datset provided in Appendix 3 of the supplemental material for Retal posted on *Nature's* website. The resulting estimate of mean advancement, before any manipulation of the data, was 4.6 days decade^{-1}. This is inexplicably lower than the 5.1 days decade^{-1} reported by Retal. However, the 4.6 days decade^{-1} estimate is still significantly higher than P&Y's estimate of 2.3 days decade^{-1} (Table 3, *t*-test, df = 283, $P < 0.001$).

Second, the Retal dataset was modified to allow for unrecorded or unreported stable species by retrospectively adding 56 dummy 'zero' values to the analysis (33% of the total) corresponding to 56 'phantom' stable species excluded by Retal by the mechanisms listed above. The new analysis gives an estimate of mean advance in spring timing of 3.1 days decade^{-1}, which is not significantly different from P&Y's estimate of 2.3 days decade^{-1} (Table 3, *t*-test, df = 339, $P = 0.11$).

Third, stable species were deleted from the P&Y dataset (those with <1 day decade^{-1} change). This drives the P&Y estimate up to 3.4 days decade^{-1}, which is not significantly different from the unmodified Retal estimate of 4.6 days decade^{-1} (Table 3, *t*-test, df = 226, $P = 0.06$).

Discussion

Latitudinal effects

Boreal regions have warmed by as much as 4 °C over the 20th century while much of the tropics has shown little change (IPCC, 2001a). Therefore, there is a clear expectation of stronger phenological response at higher latitudes. P&Y did not analyze their data for latitudinal trends. Retal did so and found an effect of latitude in the

Table 3 Results of reanalyses of datasets from Parmesan & Yohe (2003) and Root *et al.* (2003) to look for effects of study design on estimates of response

	Unaltered datasets		Adding dummy stable species (zeros) to Root *et al.* (2003)		Deleting stable species (<1 day decade^{-1} change) from Parmesan & Yohe (2003)	
Statistic	Parmesan & Yohe (2003)	Root *et al.* (2003)	Parmesan & Yohe (2003)	Root *et al.* (2003)	Parmesan & Yohe (2003)	Root *et al.* (2003)
Mean*	−2.3	−4.6	−2.3	−3.1	−3.4	−4.6
± SE	−0.36	0.43	0.36	0.33	0.51	0.43
Median	−1.4	−3.4	−1.4	−2.1	−2.1	−3.4
Mode	0.0	−2.4	0.0	0.0	−1.5	−2.4
n	172	113	172	169	115	113
P (mean difference)	<0.001		ns		ns	

*Mean is mean change in timing of event, standardized to days decade^{-1}.

expected direction, with mean advance reported for species between 32° and 49.9° latitude of −4.2 days decade^{-1} and mean advance between 50° and 72° latitude of −5.5 day decade^{-1} (Kruskal–Wallis rank test for two means $P<0.0001$). However, Retal's data, if plotted, show no visible trend with latitude and their result does not appear in reanalysis of their original published (unmodified) dataset, either when analyzed with an equivalent rank test (Mann–Whitney *U*-test for two means, $N=112$, $P=0.36$), or when analyzed by linear regression (slope of regression line $=-0.008$, $P=0.91$).

New analysis of the combined datasets does show a significant increase in strength of spring advancement as one goes northward in the northern hemisphere, but this trend explains $<4\%$ of the overall variance in phenological change (Fig. 1, $P<0.005$, $R^2<0.04$). Such a small latitudinal trend might stem from a few very strongly responding species, specifically the four species with >20 days decade^{-1} advancement (three amphibians and one bird). Surprisingly though, high significance of the trend persisted even when these four most extreme responders were taken out (Fig. 1, shaded circles taken out, $P<0.002$). However, while an effect of latitude is present and significant, it is not yet an important predictor of the magnitude of phenological response to climate change.

These results from phenology are in contrast to those from analyses of species' distributions. The very limited data available from population and range dynamics suggest that, in this respect, the expected latitudinal differences in response strength are already appearing. Poleward range shifts have occurred at most latitudes (Parmesan & Yohe, 2003). However, in one study which looked at responses over the entire ranges of 35 butterfly species, a significantly greater proportion of populations at high latitudes had undergone abundance or distributional change compared with more equatorial populations of the same set of species. Sixty-seven percent of northern range boundaries shifted northward (in Finland, Sweden, Great Britain, France and Estonia) compared with only 30% of southern range boundaries contracting northward for the same individual butterfly species (in northern Africa, Spain and France; Parmesan *et al.*, 1999). Further, overall range contractions and population declines appear to be more pronounced, as well as more consistent across species in polar communities, as compared with temperate communities (Parmesan, 2006).

Taxonomic/functional group effects

In contrast to a weak latitudinal effect, differences among broad taxonomic/functional groups in strength of response were both significant and substantial (analysis of the combined dataset Table 1, Fig. 2). This is not surprising. More than a 100 years of experimentation on temperature tolerances and developmental thresholds, plus field studies in behavioral ecology, have demonstrated strong differences in response to climate and extreme temperatures, both among related species and across broad taxonomic groups (Andrewartha & Birch, 1954; Precht *et al.*, 1973; Weiser, 1973; Woodward, 1987; Parmesan *et al.*, 2000).

Amphibian advance was more than twice as rapid as that of trees, birds and butterflies, and nearly eight times as strong as that for herbs, grasses and shrubs. Failure to find faster change by amphibians in the prior analysis by Retal likely stemmed from errors in incorporating the amphibian data into their database. Data from three out of the four species in Blaustein *et al.* (2001) were omitted by Retal, while their data from Beebee (1995) listed *Rana kl. esculenta*, *Triturus cristatus*,

Table 4 Temperature trends from Moonsenee climate station, near Long Point field site for *Bufo fowleri* in Ontario, Canada

	Trend mean		
Month	Minimum temperature (°C)	Maximum temperature (°C)	Precipitation (mm)
February	−3.4	−2.4	−3.8
March	−1.2	−0.49	6.6
April	2.0	1.8	−34.7

Data all begin at 1980. Data are not available for all years for all months. Data for temperature goes through 1997 for February, through 1993 for March, and through 1991 for April. Data for precipitation goes through 1998 for February and March, and through 1985 for April. No trends were significant at the $\alpha = 0.05$ level.

Triturus helveticus and *Triturus vulgaris* as having advanced their breeding dates by 5.8, 5.9, 6.0 and 7.8 days decade^{-1} (respectively), when the correct values are 12.4, 27.1, 31.8 and 34.1 days decade^{-1} (see 'Materials and methods' for an explanation of the discrepancy).

Amphibian responses were particularly diverse as well as particularly strong. The most extreme advancement (about a month advancement of breeding per decade) was shown by three congeneric amphibians (*Triturus*) studied over 17 years in England (Beebee, 1995). However, amphibians also provide one of the strongest opposing trends – delayed breeding by 5.3 days decade^{-1} for *Bufo fowleri* (Blaustein *et al*., 2001). This observation of phenological delay may stem simply from the fact that both minimum and maximum temperatures have shown a (nonsignificant) trend toward cooling during the time period over which the *B. fowleri* data were taken. Table 4 shows a slight cooling trend from climate station data in the same general areas as the *B. fowleri* field site for key months for amphibian breeding (February and March), although there is also a (nonsignificant) warming trend for later in spring (April). Further, amphibian breeding is likely as sensitive to changes in precipitation as in temperature. The region of the *B. fowleri* study exhibits (nonsignificant) trends in precipitation that are as strong as trends in temperature (Table 4).

In most regions, precipitation has become more extreme. Total precipitation has generally increased globally, but large regions (e.g. northern Africa) have become drier (IPCC, 2001a). For biological systems, as important as mean changes in precipitation is a significant shift in *patterns* of precipitation: rain and snow are falling in fewer, more intense events, causing significant increases in both flood events and in duration of dry periods (Karl *et al*., 1996; Karl & Knight, 1998; Kunkel *et al*., 1999; Easterling *et al*., 2000a, b; IPCC, 2001a; Trenberth *et al*., 2003). Therefore, it may not be surprising that amphibians, a group likely to be particularly sensitive to changes in pond depth, duration and temperature – all of which would be affected by recent climatic trends – showed a very strong departure from other groups, as well as from each other. Because sample sizes are still very low (only 16 species of amphibian from five geographic locations), it is unclear to what extent these results reflect amphibian responses globally.

More generally, one possible source of the high level of variation found here among species within each taxonomic group, is resource-associated differences in strength of response. There is some evidence for this effect among insects. A recent study of 16 butterfly species in Spain documented that strength of phenological advancement was related to both family affiliation and to functional grouping of the species' host plant. Species that specialized on grasses had a stronger advancement than did butterflies whose larvae fed on herbs (Stefanescu *et al*., 2003).

Changes in trophic synchrony

In the present new analysis, butterfly and bird emergence or migratory arrival show more than three times greater phenological advancement than does the first flowering of herbs. This difference in strength of response may be important because butterflies mostly feed on herbs (both as larval hosts and as adult nectar sources), and differential responses of insect vs. host, or of pollinator vs. flowering plant, could either draw these interactions closer into synchrony or further out of synchrony, depending on the starting point. Datasets which would allow analysis of long-term alteration in synchrony between interacting species at a given location are sparse (Harrington *et al*., 1999). In a recent review, Visser & Both (2005) found that for seven species pairs out of 11 total (two of which were insect–plant), interacting species are currently more out of synchrony than they were at the start of the studies, but that this did not always correspond to fitness loss.

If insects are well adapted to their habitats, we might expect that the historical 'starting point' should be good synchrony. However, this expectation is frequently not met. Before the recent bout of climate warming, Feeny (1970) showed that winter moth (*Opheroptera brumata*) routinely suffered high mortality in the field (up to 90%) because of phenological mismatches between egg hatch and budburst on the oak trees that served as larval hosts. Likewise, Singer (1972), also working in the 1960s, showed that Edith's checkerspot butterfly (*Euphydryas editha*) routinely suffered $>98\%$ mortality in the field because of phenological mismatches between larval development and senescence of their annual hosts (*Plantago erecta*). When mismatches such as these form the 'starting point,' insects may be highly vulnerable to small changes in synchrony with their hosts, and flowering plants may be highly vulnerable to small changes in synchrony with their pollinators. Below, I briefly discuss the evidence for historical and current mismatches observed in host relationships of *O. brumata* and *E. editha*.

With respect to the winter moth (*O. brumata*) and climate change, only indirect estimates of changes in synchrony with oak budburst have been possible, due to lack of long-term field data on moth egg-hatch which would complement existing long-term data on oak budburst (Harrington *et al*., 1999). An experimental study in the United Kingdom indicated that both moth and oak accelerate development in concert with warming, suggesting that timing has advanced in both species, but that synchrony has not been affected (Buse & Good, 1996). Conversely, a Dutch study which derived estimates from phenological models indicated that moth hatching should have advanced faster than oak budburst, suggesting an increasing asynchrony through time (Visser & Holleman, 2001). Without hard empirical data, definitive conclusions about the effects of climate change on oak/moth interactions are elusive (Watt & McFarlane, 2002).

For the second example, Edith's checkerspot butterfly, there is evidence of a climate-change driven range shift in both latitude and elevation (Parmesan, 1996) across an area where the mean temperature had increased by 0.7 °C (Karl *et al*., 1996). It has been suggested that increasing butterfly–plant asynchrony contributed to this shift (Parmesan, 2003), as well as to the extinctions of populations which had been shown to be phenologically mismatched under historical (1960s) conditions (McLaughlin *et al*., 2002). We cannot ask directly whether asynchrony has increased, because the populations in which asynchrony was measured in the field nearly 40 years ago are now extinct. However, through field and greenhouse manipulations as well as through analysis of spatial and temporal climate and vegetational variability in multiple populations, it has been documented that higher temperatures or drier conditions than normal speed up host plant senescence faster than caterpillar development (Singer, 1972; Weiss *et al*., 1988; Hellmann, 2002). This asymmetry of response causes a shortening of the time window available for insect feeding, a type of asynchrony that causes deaths of those individuals unable to fit their life cycles into the shortened period. Increasing air temperatures by 2 °C, which shortens the window of food availability by about 2 days, can cause 'normal' caterpillar starvation rates of 80–98% to jump to 100% (Weiss *et al*., 1988). Observed population extinctions of this species have historically occurred immediately following severe droughts and extreme weather events (Singer & Ehrlich, 1979; Ehrlich *et al*., 1980; Singer & Thomas, 1996; Thomas *et al*., 1996; McLaughlin *et al*., 2002). The documented northward and upward range shift of this species in the 20th century (Parmesan, 1996) was comprised of a disproportionately high rate of population extinctions among low-elevation and low-latitude populations, a high proportion of which fed on annual hosts and were subject to the phenological mismatches described here.

Effects of data-sampling methodologies

Effects of excluding stable species. Once we take into account the differences resulting solely from the criteria for study selection used by P&Y and Retal, the two meta-analyses give estimates of mean spring advancement that are not significantly different from each other. Reanalyses of the two datasets here indicate that the apparently stronger spring advancement shown by the Retal study can be explained solely as a consequence of their exclusion of stable (nonresponsive) species from their analysis.

Even after differences in methodologies of P&Y and Retal are accounted for, there remained a nonsignificant tendency for the Retal dataset to display a stronger spring advancement than the P&Y dataset (by a bit $<1\,\mathrm{day\,decade}^{-1}$). If it is real, this remnant tendency toward stronger spring advancement in Retal could be due to two factors that merit further investigation.

Effects of time period. As suggested by Badeck *et al*. (2004), a stronger estimate of advancement would be expected from the greater concentration of the Retal data in more recent, strongly warming decades. A meta-analysis of long-term (48–132 years) datasets showed that for 100% of 44 species, biological trends through time – either in spring phenologies or in geographic location of their northern range boundaries – mirrored decadal temperature trends over the 20th century (Parmesan & Yohe, 2003). For example, with data going back to 1947, McCleery & Perrins (1998) documented that nesting times for the great tit (*Parus major*) in England did not start advancing until the current warming trend began in 1970. In another study, the skylark (*Alauda arvensis*) and the white wagtail (*Motacilla alba*) advanced their arrival to Estonia during the warming trend of the 1930s and 1940s, delayed arrival during the cooling trends of the 1950s and 1960s, and again started arriving earlier as the current warming trend began in the early 1970s (Ahas, 1999). Repeated instances of these patterns across diverse species, in and of themselves, were used to diagnose a climate 'fingerprint' in biological changes that provided a causal link between anthropogenic global warming and biological impacts (Parmesan & Yohe, 2003).

Studies published subsequently continue to support this pattern, although it is not universal across all species. A shift toward stronger spring advancement starting in the mid-1980s was documented for snowdrops (*Galanthus nivalis*), sweet cherry (*Prunus avium*) and lime tree (*Tilia platyphyllos*) (Dose & Menzel, 2004). Similarly, out of 10 plants in a German study, all showed spring advancement since 1984, and eight of these had shown opposite responses (delayed budburst or blooming) during the cool period of 1951–1984 (Schaber & Badeck, 2005).

Effects of publishing bias. A stronger estimate of spring advancement would also be expected from the inclusion by Retal of a substantial number of single species, single location studies. Individual species tend to be chosen *a posteriori* as being 'interesting' from a climate change angle. Further, single-species studies that fail to show effects usually remain unpublished. Thus, single-species data are susceptible to a positive publishing bias and likely to be skewed toward stronger effects. The potential for single-species studies to skew estimated response was the reasoning behind P&Y's criterion for studies to be multispecies, with data presented for all species in the category studied irrespective of any observed degree of change.

Indeed, a comparison of the two histograms for responsive species (>1 day decade^{-1} change) shows the pattern expected from this potential effect. In P&Y, a very high proportion of responsive species (40%) show weak response (1–2 days decade^{-1} advancement), as compared with only 15% in Retal (Fig. 3). In the Retal dataset, only 12.5% of weak responders (1–2 days decade^{-1} advancement, $n = 16$ total) are from single-species studies, compared with 33% of strong responders (≥ 2 days decade^{-1} advancement, $n = 90$ total). The difference in strength of response between single-species and multispecies studies was not quite significant (Contingency table test, $G = 3.21$, df $= 1$, $P = 0.07$). It nonetheless suggests that inclusion of single-species, single-location studies could skew estimates of overall responses of wild species toward a stronger response to climate warming, compared with estimates derived only from multispecies studies.

Conclusions

At first sight, there appear to be large differences in estimates of phenological response between between two major global meta-analyses: Retal and P&Y. These studies had differing criteria for data selection and in consequence used moderately nonoverlapping datasets. However, once the use of different methodologies for data inclusion is taken into account, there is remarkable consistency between these studies in the estimated strength of response by wild species to warming temperatures of the past several decades. New analyses here indicate a consensus estimate of mean response between 2.3 and 2.8 days decade^{-1} advancement of spring events across all taxa globally (Tables 1 and 3).

Analyses presented here fail to show any important latitudinal trend in responses (Fig. 1). This contrasts with earlier published conclusions (Root *et al*., 2003). A significant increase in strength of response at higher latitudes *was* found in the current analyses of 203 species reported here, but explained very little of the variation in response. Thus, latitude is not yet an important explanatory variable.

Multispecies studies have documented an enormous variation of response among species within taxonomic groups and across broad taxonomic/functional groups exposed to the same type and intensity of climate change (i.e. emerging from a single study in the same region; Parmesan & Yohe, 2003). Variation among species at a given site is as great (or greater) than variation across geographic regions. This explains why latitude, in itself, is not strongly associated with strength of response, even though latitude *is* associated with strength of warming trends. These two patterns indicate that the absolute strength of warming trend at any given location is a poor predictor of community-wide responses.

There were significant differences in mean response across taxonomic groups, but the largest differences – between amphibians and all other taxa – stem from extremely strong spring advancements of just a few amphibian species, and so may not be generalizable (Table 1, Fig. 2). Stronger advancement of butterflies compared with herbs may portend an increasing asynchrony in insect–plant interactions (Table 1, Fig. 2).

Observed high variation of response among species experiencing similar climatic trends – within latitudes, within regions, within communities and within taxonomic groupings – suggests that projections of impacts will continue to be a challenge. In particular, projections of response across interacting trophic levels will be hampered without an increased investment in empirical data. Only long-term field observations can reveal complex interdependencies between species, an essential component to estimating future responses to global warming.

Acknowledgements

Many thanks to G. Yohe and M. C. Singer for intellectual stimulation and insightful comments. Thanks also to T. L. Root, J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig and J. A. Pounds for placing their database in accessible form on the web. The original analyses in P&Y were facilitated by the Centre National de la Recherche Scientifique (CEFE, Montpellier).

References

Ahas R (1999) Long-term phyto-, ornitho- and ichthyophenological time-series analyses in Estonia. *International Journal of Biometeorology*, **42**, 119–123.

Ahmad QK, Warrick RA, Downing TE *et al*. (2001) Methods and tools. In: *Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Panel on Climate Change Third Assessment Report* (eds McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS), pp. 105–143. Cambridge University Press, Cambridge, UK.

Andrewartha HG, Birch LC (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.

Arctic Climate Impact Assessment (2004) *Impacts of a Warming Arctic* (Chair Corell RW). Cambridge University Press, Cambridge, UK.

Badeck FW, Bondeau A, Böttcher K, Doktor D, Lucht W, Schaber J, Sitch S (2004) Responses of spring phenology to climate change. *New Phytologist*, **162**, 295–309.

Beebee TJC (1995) Amphibian breeding and climate. *Nature*, **374**, 219.

Blaustein AR, Belden LK, Olson DH, Green DM, Root TL, Kiesecker JM (2001) Amphibian breeding and climate change. *Conservation Biology*, **15**, 1804–1809.

Both C, Artemyev AV, Blaauw B *et al*. (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London Series B – Biological Sciences*, **271**, 1657–1662.

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296–298.

Bradley NL, Leopold AC, Ross J, Wellington H (1999) Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences USA*, **96**, 9701–9704.

Buse A, Good JEG (1996) Synchronization of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change. *Ecological Entomology*, **21**, 335–343.

Dose V, Menzel A (2004) Bayesian analysis of climate change impacts in phenology. *Global Change Biology*, **10**, 259–272.

Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London Series B – Biological Sciences*, **266**, 2487–2490.

Easterling DR, Evans JL, Groisman PY, Karl TR, Kunkel KE, Ambenje P (2000a) Observed variability and trends in extreme climate events: a brief review. *Bulletin of the American Meteorological Society*, **81**, 417–425.

Easterling DR, Meehl GA, Parmesan C, Chagnon S, Karl TR, Mearns L (2000b) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Ehrlich PR, Murphy DD, Singer MC, Sherwood CB, White RR, Brown IL (1980) Extinction, reduction, stability and increase: the responses of checkerspot butterfly populations to the California drought. *Oecologia*, **46**, 101–105.

Feeny PP (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51**, 565–581.

Harrington R, Woiwod I, Sparks T (1999) Climate change and trophic interactions. *Trends in Ecology and Evolution*, **14**, 146–150.

Hellmann JJ (2002) The effect of an environmental change on mobile butterfly larvae and the nutritional quality of their hosts. *Journal of Animal Ecology*, **70**, 925–936.

Intergovernmental Panel on Climate Change Third Assessment Report (2001a) *Climate Change 2001: The Science of Climate Change* (eds Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA), Cambridge University Press, Cambridge, UK.

Intergovernmental Panel on Climate Change Third Assessment Report (2001b) *Climate Change 2001: Impacts, Adaptation, and Vulnerability* (eds McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS), Cambridge University Press, Cambridge, UK.

Jarvinen A (1989) Patterns and causes of long-term variation in reproductive traits of the Pied Flycatcher *Ficedula hypoleuca* in Finnish Lapland. *Ornis Fennica*, **66**, 24–31.

Karl TR, Knight RW (1998) Secular trends of precipitation amount, frequency, and intensity in the United States. *Bulletin of the American Meteorological Society*, **79**, 231–242.

Karl TR, Knight RW, Easterling DR, Quayle RG (1996) Indices of climate change for the United States. *Bulletin of the American Meteorological Society*, **77**, 279–292.

Kunkel KE, Andsager K, Easterling DR (1999) Long-term trends in extreme precipitation events over the conterminous United States and Canada. *Journal of Climate*, **12**, 2515–2527.

McCleery RH, Perrins CM (1998) Temperature and egg-laying trends. *Nature*, **391**, 30–31.

McLaughlin JF, Hellman J, Boggs CL, Ehrlich PR (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences USA*, **99**, 6070–6074.

Menzel A (2000) Trends in phenological phases in Europe between 1951 and 1996. *International Journal of Biometeorology*, **44**, 76–81.

Menzel A, Estrella N, Fabian P (2001) Spatial and temporal variability of the phenological seasons in Germany from 1951 to 1996. *Global Change Biology*, **7**, 657–666.

Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature*, **397**, 659.

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.

Parmesan C (1996) Climate and species range. *Nature*, **382**, 765–766.

Parmesan C (2003) Butterflies as bio-indicators of climate change impacts. Chapter 24. In: *Evolution and Ecology Taking Flight: Butterflies as Model Systems* (eds Boggs CL, Watt WB, Ehrlich PR), pp. 541–560. University of Chicago Press, Chicago.

Parmesan C (2004) Uncertainty in estimating biological impacts of climate change: sources of error and methods of quantifying uncertainty. In: *Intergovernmental Panel on Climate Change Workshop on Describing Scientific Uncertainties in Climate Change to Support Analysis of Risk and of Options* (eds Manning M, Petit M, Easterling D, Murphy J, Patwardhan A, Rogner H, Swart R, Yohe G), pp. 99–101. Intergovernmental Panel on Climate Change, Boulder, CO.

Parmesan C (2005) Range and abundance changes. Chapter 12. In: *Climate Change and Biodiversity* (eds Lovejoy T, Hannah L), pp. 41–55. Yale University Press.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Reviews of Ecology, Evolution and Systematics*, **37**, 637–669.

Parmesan C, Gaines S, Gonzalez L, Kaufman DM, Kingsolver J, Peterson AT, Sagarin R (2005) Empirical perspectives on species' borders: environmental change as challenge and opportunity. *Oikos*, **108**, 58–75.

Parmesan C, Root TL, Willig M (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, **81**, 443–450.

Parmesan C, Ryrholm N, Stefanescu C *et al*. (1999) Poleward shift of butterfly species' ranges associated with regional warming. *Nature*, **399**, 579–583.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Precht H, Christophersen J, Hensel H, Larcher W (1973) *Temperature and Life*. Springer-Verlag, New York.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.

Sagarin R (2001) False estimates of advance of spring. *Nature*, **414**, 600.

Schaber J, Badeck F-W (2005) Plant phenology in Germany over the 20th century. *Regional Environmental Change*, **5**, 37–46.

Schwartz MD (1998) Green-wave phenology. *Nature*, **394**, 839–840.

Singer MC (1972) Complex components of habitat suitability within a butterfly colony. *Science*, **173**, 75–77.

Singer MC, Ehrlich PR (1979) Population dynamics of the checkerspot butterfly *Euphydryas editha*. *Fortschritte Zoologie*, **25**, 53–60.

Singer MC, Thomas CD (1996) Evolutionary responses of a butterfly metapopulation to human and climate-caused environmental variation. *American Naturalist*, **148**, S9–S39.

Slater FM (1999) First-egg date fluctuations for the Pied Flycatcher *Ficedula hypoleuca* in the woodlands of mid-Wales in the twentieth century. *Ibis*, **141**, 497–499.

Sparks TH (1999) Phenology and the changing pattern of bird migration in Britain. *International Journal of Biometeorology*, **42**, 134–138.

Stefanescu C, Peñuelas J, Fillela I (2003) Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology*, **9**, 1494–1506.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, **399**, 213.

Thomas CD, Singer MC, Boughton D (1996) Catastrophic extinction of population sources in a butterfly metapopulation. *American Naturalist*, **148**, 957–975.

Trenberth KE, Dai AD, Parsons DB (2003) The changing character of precipitation. *Bulletin of the American Meteorological Society*, **84**, 1205–1217.

Tryjanowski PSTH (2001) Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*. *International Journal of Biometeorology*, **45**, 217–219.

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London Series B – Biological Sciences*, **272**, 2561–2569.

Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B – Biological Sciences*, **268**, 289–294.

Walther GR, Post E, Convery P *et al*. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Watt AD, McFarlane AM (2002) Will climate change have a different impact on different trophic levels? Phenological development of winter moth *Operophtera brumata* and its host plants. *Ecological Entomology*, **27**, 254–256.

Weiser W (ed.) (1973) *Effects of Temperature on Ectothermic Organisms*. Springer-Verlag, New York.

Weiss SB, Murphy DD, White RR (1988) Sun, slope and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology*, **69**, 1486–1496.

Wikle CK (2003) Hierarchical Bayesian models for predicting the spread of ecological processes. *Ecology*, **84**, 1382–1394.

Woodward FI (1987) *Climate and Plant Distribution*. Cambridge University Press, Cambridge.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2010) **365**, 3129–3147
doi:10.1098/rstb.2010.0128

Genetic and physiological bases for phenological responses to current and predicted climates

A. M. Wilczek[1,*], **L. T. Burghardt**[1], **A. R. Cobb**[2], **M. D. Cooper**[1], **S. M. Welch**[3] **and J. Schmitt**[1]

[1] *Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA*
[2] *Center for Environmental Sensing and Modeling, Singapore-MIT Alliance for Research and Technology, Singapore 117543, Republic of Singapore*
[3] *Department of Agronomy, Kansas State University, Manhattan, KS 66506, USA*

We are now reaching the stage at which specific genetic factors with known physiological effects can be tied directly and quantitatively to variation in phenology. With such a mechanistic understanding, scientists can better predict phenological responses to novel seasonal climates. Using the widespread model species *Arabidopsis thaliana*, we explore how variation in different genetic pathways can be linked to phenology and life-history variation across geographical regions and seasons. We show that the expression of phenological traits including flowering depends critically on the growth season, and we outline an integrated life-history approach to phenology in which the timing of later life-history events can be contingent on the environmental cues regulating earlier life stages. As flowering time in many plants is determined by the integration of multiple environmentally sensitive gene pathways, the novel combinations of important seasonal cues in projected future climates will alter how phenology responds to variation in the flowering time gene network with important consequences for plant life history. We discuss how phenology models in other systems—both natural and agricultural—could employ a similar framework to explore the potential contribution of genetic variation to the physiological integration of cues determining phenology.

Keywords: phenology; genetic architecture; life-history evolution; seasonal timing; local adaptation

1. INTRODUCTION

Within the last 50 years, drastic, directional shifts have occurred in the seasonal timing of many natural events including bud burst, flowering and migration (Fitter & Fitter 2002; Walther *et al.* 2002; Parmesan & Yohe 2003; Lehikoinen *et al.* 2004; Parmesan 2006; Bertin 2008; van Buskirk *et al.* 2009). The observed changes correspond in general to patterns of human-induced climate change (Rosenzweig *et al.* 2008). Advancing timing of spring events, alteration of range limits and clines and changing phenology in urban versus rural areas have all been demonstrated to mirror recent changes in temperature and growing season length (Roetzer *et al.* 2000; Bradshaw & Holzapfel 2001; Parmesan & Yohe 2003; Primack *et al.* 2004; Menzel *et al.* 2006*a*; Miller-Rushing *et al.* 2006; Miller-Rushing & Primack 2008). Shifts in seasonal timing are obvious indicators of climate change not only to scientists but also to the general public, and farming practices have already begun to adapt to altered climate patterns (Menzel *et al.* 2006*a*,*b*). As a result, the changing timing of biotic and abiotic indicators of season has recently received widespread popular and scientific coverage (e.g. Post *et al.* 2009).

Nonetheless, organisms' patterns of response are neither uniform nor universal, and the underlying causes of some common patterns remain mysterious. For example, in temperate environments, spring phenological events have advanced far further and more consistently than autumn events (Lehikoinen *et al.* 2004; Bertin 2008; van Buskirk *et al.* 2009; but see Ibáñez *et al.* 2010). Even within a given community, different species have shown contrasting long-term responses to directional climate change as well as to inter-annual variation in climate (Miller-Rushing & Primack 2008; Willis *et al.* 2008; Primack *et al.* 2009).

Under changing climates, the magnitude and flexibility of species phenological responses have many important consequences. Species responsiveness to year-to-year climate variation has been linked to long-term persistence versus local extinction in both bird and plant communities (Moller *et al.* 2008; Willis *et al.* 2008; Davis *et al.* 2010). Timing mismatches that are attributed to climate change have resulted in disrupted trophic interactions and altered competitive dynamics within community assemblages (Durant *et al.* 2005; Post & Forchhammer 2008; van der Jeugd *et al.* 2009; Singer & Parmesan 2010). Emphasis has been placed on understanding species tolerances to novel combinations of environmental factors (Williams & Jackson 2007), but the basis of this

---

[*] Author for correspondence (amity_wilczek@brown.edu).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rstb.2010.0128 or via http://rstb.royalsocietypublishing.org.

One contribution of 11 to a Theme Issue 'The role of phenology in ecology and evolution'.

tolerance will probably depend on the way in which species respond phenologically to different environmental variables individually and in combination. Thus, to understand the basis of observed changes (or stasis) in phenological timing, and to make predictions for future responses, it will be necessary to have an understanding of the mechanisms underlying phenological response.

Plants serve as ideal model organisms in which to examine the mechanistic bases of seasonal response and adaptation. Plants come in many different life forms and inhabit a broad variety of geographical and seasonal habitats. And yet, plants are (for the most part) sessile and ectothermic, so they must cope with the climatic conditions into which they are dispersed. Nonetheless, plants can control the climatic conditions they experience during critical life stages through phenological control of dormancy, quiescence and/or the timing of developmental transitions. Several phenological traits in plants are of great economic importance and have been the object of extensive study; for instance, the timing of flowering and fruiting in cereals has been studied intensively because these plants supply the majority of food calories to the human population. Accumulated understanding of genetic and environmental influences on development, multiple seasonal traits and a rich history of manipulative experiments make plants prime candidates for studying how evolution has shaped phenology as a function of different external cues.

Understanding the genetic and physiological mechanisms that plants use for the timing of seasonal responses may allow us to predict phenological responses to no-analogue climates that will become increasingly common with anthropogenic climate change (Williams *et al.* 2007), as well as the capacity for adaptation under these scenarios. Such an understanding will also inform breeding strategies by highlighting signalling pathways and conditions under which sensitivities to different environmental factors are exposed. Thus, a more mechanistic understanding of phenology has become of major interest within the fields of conservation, ecology, evolution and agronomy, among others.

Here, we examine what is known about the seasonal cues to which plants respond, and the importance of these cues for appropriate timing of plant life-history events. Focusing on recent advances in uncovering the genetic mechanisms underlying seasonal traits, we elaborate on common themes and genetic architectures of plant responses. Finally, we explore genetically informed models of plant development and life history that link genetic architecture and sensitivity to differences in phenological response with geographical and temporal variation in climate.

2. SEASONAL CUES REGULATING PLANT PHENOLOGY

Timing developmental events to coincide with favourable seasonal conditions is critical for plant growth, survival and reproduction. Spring, summer and autumn are characterized by different combinations of environmental cues (figure 1), and plant traits expressed in these seasons are subjected to distinct selection pressures. For example, early establishment in spring can provide competitive advantages, but not if it exposes delicate growing tissues to late frosts (Howe *et al.* 2003). Cues that precede or anticipate seasonal changes are particularly important because plant responses involve cellular, metabolic, morphological or developmental changes that require time to complete. Plants make use of several cues that serve as reliable indicators of season and thus resource availability, of which light and temperature are usually most important in temperate plant species. The environmental sensitivity of many plant life cycles reflects these different life-history strategies in both natural and agricultural settings.

Temperature is a seasonal cue that cycles annually in temperate climates following patterns of day length and insolation (figure 1*b*). Ambient temperature also directly affects growth and development rates. Such rates typically increase with ambient temperatures up to some optimum or maximum, and then decline as warming continues. In temperate environments, however, optimum ambient temperatures for growth are rarely exceeded (e.g. Schaber & Badeck 2002). Many plants also respond to cold temperature cues, typically referred to as chilling or vernalization effects. For sensitive traits, passage through a cold season accelerates the subsequent pace of development (Henderson *et al.* 2003). For traits that respond to chilling, changes in seasonal temperature can have complex effects on phenology when the generally promotive effects of increasing temperature oppose the influence of reduced vernalization (see below). Plant life-cycle events that occur in spring often rely on vernalization as well as photoperiod and/or warming temperature cues. In these traits, response to increasing day length (or ambient temperature) is greatly amplified following prolonged exposure to cold that serves as an indication that winter has passed (Harrington *et al.* 2010).

Light quantity contributes to plant growth and development, but day length can also serve as an important developmental cue. Decreasing day lengths are reliable cues of the impending end of the growing season and winter onset for many temperate biomes; increasing day length indicates the arrival of spring (figure 1*a*). Bud-set timing is more influenced by declining day lengths that indicate the approach of autumn than by low temperatures *per se* (Bohlenius *et al.* 2006; Savolainen *et al.* 2007), most probably because declining photoperiods are a more reliable indicator of the end of the growing season. Day length can also serve as an important cue for the appropriate timing of flowering and fruiting with respect to seasonal patterns of temperature and precipitation. Spring-flowering, Mediterranean-adapted plants (e.g. barley, wheat) often accelerate development in response to lengthening days, which allows them to complete their life cycle before the hot, dry conditions of summer. In tropical plants such as sorghum, the shortening days of late summer can serve as a cue signalling the end of summer and the onset of the autumn monsoon rains, which are favourable for grain filling (Dingkuhn *et al.* 2008). Owing to its

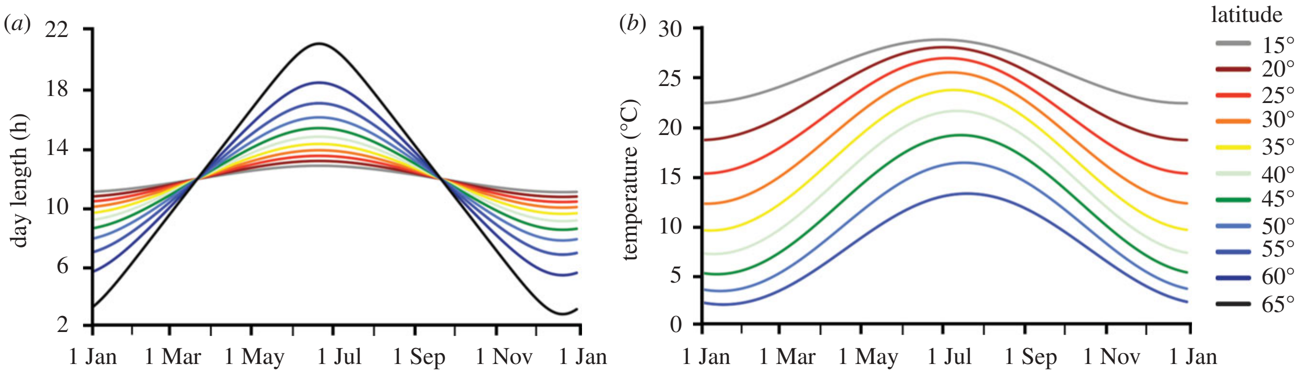

Figure 1. (*a*) Seasonal variation in photoperiod (from Ham 2004) from 15° to 65° latitude and (*b*) daily average temperatures (from Charles-Edwards *et al.* 1986) from 15° to 55° latitude. The yearly range in photoperiod increases with latitude, and the amplitude of photoperiod increases more rapidly towards the poles. In general, the lag between daily temperature and photoperiod cycles increases with latitude.

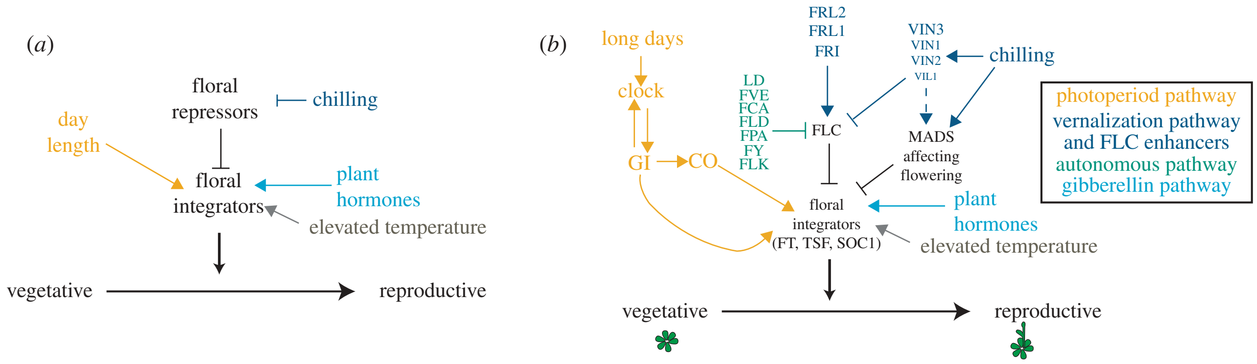

Figure 2. (*a*) General diagram of environmentally sensitive flowering time pathways in plants. (*b*) Simplified diagram of the network of the environmentally sensitive flowering time pathways in *Arabidopsis thaliana*. See text for details.

Table 1. General, large-scale patterns in the seasonal distribution of temperatures. (Compiled from information in Landsberg (1941), Sellers (1965), Akin (1990) and Linacre (1992).)

	winter temperature	summer temperature	yearly temperature range	diurnal temperature range	seasonal lag
proximity to equator	significantly warmer	slightly warmer	reduced	reduced	reduced
proximity to ocean	significantly warmer	slightly warmer	reduced	reduced	increased
northern versus southern hemisphere	slightly cooler	significantly warmer	increased		
proximity to forest	slightly cooler	significantly cooler	reduced	reduced	
increase in altitude	slightly cooler	significantly cooler	variable, generally reduced	variable	reduced

dependable annual cycle, plants use day length as an important cue of season, and the genes involved in response to photoperiodic events are anciently conserved (see below).

Precipitation affects both plant survival and growth and can also show strong seasonal patterns. In seasonally dry communities, the initiation of seasonal growth (as measured by greenness at a landscape scale) closely tracks the onset of rains (Zhang *et al.* 2006). It is unclear whether moisture in itself serves as an anticipatory cue, or whether plants use other seasonal cues to become competent to respond to precipitation once it arrives. Pre-formation of leaves or other organs whose emergence depends on permissive moisture conditions may allow plants to get a 'jump start' when favourable conditions arrive (Damascos *et al.* 2005). Whether or not precipitation serves as a cue, water availability may determine the length of the growing season and thus can have important effects on the relationship between phenology and fitness (Franks *et al.* 2007).

Day length and temperature can serve as reliable cues of seasonal conditions across a broad range of temperate climates and geographical scales, and plants use both cues to appropriately time important life-cycle events; however, the temperatures and photoperiods indicative of season vary. Even under current climate conditions, the appropriate cue of a favourable seasonal environment in one location may not be the same in another (figure 1 and table 1). For instance, the characteristic day length three weeks prior to autumn frost falls precipitously with latitude. The underlying geographical distribution of relevant seasonal environmental cues and resources can serve as an important driver of locally adapted phenological responses. That is, given geographical variation in the seasonal availability of different resources, plants might be expected to and often do show distinct phenologies in different habitats. And yet, many plant species have broad distributions. How do species adapt to this variation within their range? When is it advantageous to have populations with rigid seasonal responses, and when is it advantageous to respond plastically to environmental cues? Understanding the physiological and genetic basis of phenology can help to answer these questions.

3. GENETIC BASIS OF PHENOLOGICAL RESPONSE

(a) *Flowering time gene network in* **Arabidopsis thaliana**

The converging genetic signalling pathways mediating environmental response of flowering time have been particularly well studied in the model annual plant *Arabidopsis thaliana* (figure 2). *Arabidopsis thaliana* integrates the environmental signals of long days, growing degree days and winter chilling, all of which speed the rate of development towards flowering. Under long days, the photoperiod pathway promotes flowering via the transcriptional regulator *CONSTANS* (*CO*; Koornneef *et al.* 1991; Lee & Amasino 1995) and its upstream activator *GIGANTEA* (*GI*; Mizoguchi *et al.* 2005). These signals activate floral integrator genes including *FLOWERING LOCUS T* (*FT*), *TWIN SISTER OF FT* (*TSF*) and *SUPPRESSOR OF OVEREXPRESSION OF CO 1* (*SOC1*; Kim *et al.* 2005; Yamaguchi *et al.* 2005; Kobayashi & Weigel 2007), which in turn promotes the transition from vegetative to reproductive development. Higher ambient temperatures speed the accumulation of growing degree days and also promote flowering (Granier *et al.* 2002; Blazquez *et al.* 2003; Welch *et al.* 2003; Lempe *et al.* 2005; Balasubramanian *et al.* 2006*b*).

The ability of floral integrator genes to respond to inductive signals is mediated by a suite of repressor genes, notably the MADS-box transcription factor *FLOWERING LOCUS C* (*FLC*) and related MADS-box genes such as *SHORT VEGETATIVE PHASE* (*SVP*), *FLOWERING LOCUS M* (*FLM or MAF1*) and *MADS AFFECTING FLOWERING 2–5* (*MAF2-5*; Alexandre & Hennig 2008). *FLC* is activated by genes such as *FRIGIDA* (*FRI*; Geraldo *et al.* 2009) and its relatives *FRIGIDA-LIKE1* and *2* (*FRL1, FRL2*; Michaels *et al.* 2004; Schlappi 2006), and is repressed by genes in the 'autonomous' or 'endogenous' pathway (Baurle & Dean 2006). Autonomous pathway genes are identified as those that affect flowering regardless of the environment (or in all environments), and this pathway is thought to be sensitive to internal or endogenous signals of developmental stage. Attenuation of floral repressors can also be achieved through prolonged winter chilling (vernalization) that induces expression of *VERNALIZATION-INSENSITIVE-3* (*VIN3*), which initiates stable epigenetic repression of FLC via the vernalization pathway (Sung & Amasino 2004; Finnegan & Dennis 2007). Deficiencies in *FLC* activators such as *FRI* remove the vernalization requirement for flowering, and under laboratory conditions result in a 'rapid-cycling' life history (Johanson *et al.* 2000; Michaels *et al.* 2003; Boss *et al.* 2004; Lempe *et al.* 2005; Moon *et al.* 2005; Shindo *et al.* 2005; Searle *et al.* 2006; Schmitz *et al.* 2008). Through this complex network of converging pathways, *Arabidopsis* plants balance different seasonal cues in order to time flowering appropriately (Boss *et al.* 2004; Wilczek *et al.* 2009; see below).

Historically, *A. thaliana* genes underlying variation in flowering time have been discovered and described from forward genetic screens carried out in controlled conditions using a combination of mutagenized and transformed lines, recombinant inbred lines (RILs) and naturally occurring variation in wild-collected accessions (Alonso-Blanco *et al.* 2005, 2009; Engelmann & Purugganan 2006). The genetic basis of flowering time has received a great deal of attention both because of its agronomic relevance and also because there is enormous variation in flowering time exhibited in the laboratory and in natural populations (Koornneef *et al.* 2004). Explicit genetic models based on gene expression profiles and interactions have successfully modelled behaviour and feedback integration of the *Arabidopsis* circadian clock (Locke *et al.* 2005, 2006; Zeilinger *et al.* 2006; Salazar *et al.* 2009) and time to flowering as a function of temperature and day length in various mutant lines (Dong 2003; Welch *et al.* 2003, 2005). Much interest has been focused on working out the signalling pathways involved using both experimental and modelling approaches, but understanding the synthesis by floral integrator genes of signals from these pathways and their relative importance in different environments has proved more difficult.

The contributions of the different flowering time candidate genes and pathways under complex combinations of environmental factors have begun to be explored only recently. Field studies have largely validated the described roles of these flowering time genes, but several studies in natural conditions or with natural populations have highlighted the conditions (both environmental and genetic) in which variation in these signalling pathways is expressed. For instance, studies with field-sown RILs have demonstrated both site- and season-specific quantitative trait loci (QTLs) (Weinig *et al.* 2002; Malmberg *et al.* 2005). Recent controlled environment studies have included more complex temperature and photoperiod interactions, and perhaps as a result have uncovered more subtle environment-dependent pleiotropic, epistatic and dominance effects of known flowering time genes (Li *et al.* 2006; Scarcelli *et al.* 2007; Scarcelli & Kover 2009). Together, these studies have highlighted how a combination of field and controlled environment studies can be used to explore genetic determination of phenological traits and their role in adaptation to environment.

(b) *Genetic architecture of seasonal sensitivity in plants*

Among important plant seasonal responses, the timing of flowering, fruit or grain production, bud burst and bud set have all been extensively studied in crop and forestry species (Cooper & Hammer 1996). The genetic basis of these traits is important for plant breeding and improvement strategies (Cooper & Hammer 1996; Hammer *et al.* 2006) as well as for predicting responses to changing climates (Davis *et al.* 2005; Aitken *et al.* 2008). Extensive quantitative genetic studies have demonstrated that most of these phenological traits have a heritable genetic basis (reviewed in Cooper & Hammer 1996; Howe *et al.* 2003; Savolainen *et al.* 2007). In temperate species, the loci involved appear to respond to one or more of a combination of factors including endogenous developmental status, day length and chilling (figure 2; Colasanti & Coneva 2009). We focus here on phenology in temperate regions because of the greater seasonality in these areas, and the greater amount of data available. Since the timing of seasonal events in plant life cycles has important fitness consequences in natural habitats, the genetic architecture of response bears the signature of past evolution and depends on habitat, type of signal and life history of species considered. Seasonal traits in many plant species have a similar architecture of underlying sensitivity to environmental factors involving integration of temperature, day length and chilling cues (see above; Howe *et al.* 2003; Cockram *et al.* 2007*b*; Savolainen *et al.* 2007).

More recently, specific genes involved in phenology and seasonal traits have been described in several plant species (see review in Alonso-Blanco *et al.* 2009). These genes have been characterized through complementary approaches that include identifying the causal loci of QTL through positional cloning as well as identification and characterization of orthologues of known flowering-time genes from model species, particularly *Arabidopsis*. The genetic module involved in photoperiod integration is remarkably ancient, which may have advantages for understanding the functional basis and manipulation of day length responses across a wide range of important plant species. Several photoperiod genes identified initially through quantitative genetic studies have since been revealed to be orthologous to genes in the photoperiod pathway in *Arabidopsis* (e.g. from rice, barley, wheat). The *CONSTANS* gene family in particular is involved in photoperiodic response in all plants studied, including the bryophyte *Physcomitrella* (Zobell *et al.* 2005), and is even implicated in the photoperiodic response of growth and starch accumulation in the green alga *Chlamydomonas* (Serrano *et al.* 2009). However, expression of *CO in planta* has different effects on phenology depending on the downstream targets. In both *Oryza sativa* (rice) and *A. thaliana*, *CO* and its rice orthologue *Hd1* combine signals from the diurnal clock oscillator with the outputs of photoreceptors to measure day length as per the external coincidence model (Hayama & Coupland 2004). However, whereas high levels of *CO* upregulate the floral integrator *FT* in *A. thaliana*, expression of rice *Hd1* represses the *FT* rice orthologue *Hd3a*, thus producing a short-day flowering response (Hayama *et al.* 2003).

Meristem identity (i.e. vegetative versus floral) and floral integrator genes are also highly conserved, particularly *FT*, which has been shown to act as a mobile signal acting in the manner of ‘florigen’ in rice (Tamaki *et al.* 2007), tomato (Lifschitz *et al.* 2006) and *Arabidopsis* (Corbesier *et al.* 2007), with similar roles suggested in several other plant species including grasses, sunflowers, poplar and morning glory (Turck *et al.* 2008; Kikuchi *et al.* 2009; Blackman *et al.* 2010). Related genes that, like *FT*, carry a phosphatidyl ethanolamine-binding protein domain appear to be involved in the determination of phenological traits and/or onset of reproduction over evolutionary time dating all the way to bryophytes (Hedman *et al.* 2009) and spruce (Gyllenstrand *et al.* 2007). Despite conservation of involvement, the details of the environmental sensitivity of these integrator genes and their interaction with other floral/seasonal trait network genes may differ by species (Nemoto *et al.* 2003).

There appears to be greater variation in the genes underlying the response to chilling, although lifting of repression following chilling is a common response among temperate plants. While nonetheless variably involved, MIKC^{C}-type MADS box genes including *FLC* orthologues are implicated in integrating vernalization cues and repressing flowering or growth prechilling across a broad range of plant taxa including sugar beet, citrus and peach (Kim *et al.* 2007; Reeves *et al.* 2007; Li *et al.* 2009; Zhang *et al.* 2009). In cereals, however, not all genes involved in vernalization sensitivity fall in this family (Trevaskis *et al.* 2007; Greenup *et al.* 2009). *PEP1*, an *FLC* orthologue in the perennial species *Arabidopsis alpine*, is involved in both flowering time as well as the resumption of vegetative growth after chilling, which is accompanied by a ‘resetting’ of the epigenetic state of this gene (Wang *et al.* 2009). *Arabidopsis alpina* is one of the few species for which we understand how genes involved in non-circadian environmental sensing reversibly shift their sensitivity within a single individual plant. (In the annual *A. thaliana*, the epigenetic resetting of *FLC* occurs during embryo development; Sheldon *et al.* 2008.) Understanding these resetting processes will be critical to determining the mechanistic bases of annually recurring traits in perennial species as well as in different traits that use the same genes as environmental reporters.

Plant traits that are expressed in different seasonal environments appear to have distinct genetic bases, which might provide greater response flexibility (both in short and evolutionary time frames) if they are responding to different cues. On the other hand, genes involved in diverse developmental events that occur in the same season may be jointly regulated, as has been recently described for cold tolerance and vernalization responses in cereals (Galiba *et al.* 2009).

Autumn traits in trees such as timing of bud set and cold hardening also appear to be genetically correlated, but there is little relationship between these traits and bud burst in the spring (Howe *et al.* 2003; Savolainen *et al.* 2007). Additionally, in tree species such as poplar, autumn traits may have greater heritability and greater standing genetic variation than spring traits, which respond more plastically to local environmental conditions (e.g. Hall *et al.* 2007; Luquez *et al.* 2008). Oddly, results of those quantitative genetic studies that find little correlation between different seasonal traits often contrast with functional studies of individual loci that are implicated in several seasonal responses. For example, the poplar orthologue of *FT* is involved in both bud set (autumn) and flowering (spring) and shows a strong north–south cline in the timing and environmental sensitivity of activity (Bohlenius *et al.* 2006). This seeming paradox remains to be resolved, but may involve shifting upstream or downstream interactions, with the relevant genetic variation identified in quantitative genetic studies located in these interacting genes (Ingvarsson *et al.* 2006, 2008).

To summarize, many plant species and traits show similar genetic architecture of seasonal response, as might be expected given the commonality of cues indicating season. We are still in the early stages of identifying and characterizing the individual genes underlying sensitivity to photoperiod, temperature and developmental state in most plant species. Work to date has shown that many of these environmental-sensing modules involve orthologous genes or similar gene family members even across deep evolutionary divides, which suggests that a unified understanding of the genetic basis of phenology may be a tractable goal.

(c) *Intraspecific variation in sensitivity to environmental cues*

Where phenology contributes to local adaptation, we might expect to see genetic differentiation in response across the native range of species. Combinations of light and temperature that correspond to the beginning and end of the growing season vary geographically (table 1 and figure 1), and clinal patterns in environmental sensitivity may allow species to respond appropriately to local seasonal cues (see also Chuine 2010). For example, autumn frosts arrive earlier in the north where day lengths before the equinox are also longer. Most probably reflecting this latitudinal trend, many tree species show marked clines in the critical short-day length that induces bud set at both the phenotypic and allelic level, resulting in bud set at earlier calendar dates and longer days in more northern populations (Bohlenius *et al.* 2006; Hall *et al.* 2007; Luquez *et al.* 2008). Within species or genera, chilling cues may become subordinate to photoperiod cues in the timing of bud burst closer to the tropics and/or the temperatures required to fulfil chilling requirements may rise (Borchert *et al.* 2005; Wilkie *et al.* 2008; Colasanti & Coneva 2009). In *Arabidopsis*, clines in vernalization response (Lempe *et al.* 2005; Shindo *et al.* 2005; Stinchcombe *et al.* 2005), light sensitivity (Maloof *et al.* 2001; Stenoien *et al.* 2002), circadian clock period (Michael *et al.* 2003) and day length sensitivity (Balasubramanian *et al.* 2006*a*; but see Samis *et al.* 2008) have all been identified. Overall developmental rates or response to endogenous cues may also shift with climate. A broad survey of *Arabidopsis* accessions revealed that lines from cooler native climates were more responsive to warmer temperatures (Hoffmann *et al.* 2005); more rapid flowering under warmer temperatures might reflect the need to complete growth in a shorter growing season (cf. Bradshaw & Holzapfel 2008). In the northeast USA, there is apparent community-level, landscape-scale differentiation in the environmental cues influencing bud burst, although this may involve both changes in intraspecific variation and species-level shifts in plant assemblage composition (Fisher *et al.* 2007). The elucidation of clines or lack of clines in phenological traits and in the genes underlying these traits can give important information about the past selective history of species (Joost *et al.* 2007) as well as their ability to respond to changing environments (Aitken *et al.* 2008).

The selection of varieties within crop species provides an interesting counterpoint to the natural clines set up over evolutionary time through natural selective events. Many crop plants including wheat and barley have both ‘spring’ and ‘winter’ varieties. At a phenotypic level, these are distinguished by a loss of vernalization sensitivity in spring-sown varieties. More recent work has revealed that this change typically involves only a few loci and alleles in wheat and barley (Cockram *et al.* 2007*a*,*b*, 2009; Jones *et al.* 2008). Photoperiod sensitivity also plays an important role in the seasonal timing of grain production, but this usually marks differences in varieties sown in the same season but in different geographical regions. As one moves north, sensitivity to photoperiod results in yield losses in the Mediterranean-adapted winter wheat (Worland *et al.* 1998; Cockram *et al.* 2007*a*). In the south, flowering and heading under lengthening days allow plants to avoid the dry conditions of summer, but in the north, the lower temperatures and wetter summers mean that early flowering induced by lengthening days results in flowering at smaller size and with less productivity. Land races of both barley and wheat show strong south-to-north clines of declining photoperiod sensitivity and allele frequency of the major mutation that causes this insensitivity (Turner *et al.* 2005; Cockram *et al.* 2007*a*; Lister *et al.* 2009). Soybean, a short-day plant, exhibits a similar cline in which the flowering time of northern landraces is relatively insensitive to day length, but also—in contrast to wheat and barley—uniformly rapid (Zhang *et al.* 2008). Interestingly, this pattern of decreased photoperiod sensitivity in northern populations in agricultural settings is in direct contrast to the common pattern of many natural species such as *Arabidopsis* that show increased photoperiod sensitivity and more extreme critical day lengths in northern populations (see also above; Ray & Alexander 1966; Griffith & Watson 2006). The factors that drive selection of ideally suited local crop varieties and how these might differ from natural seasonal selection pressures remain an interesting topic to explore further.

4. PHENOLOGY AND LIFE-HISTORY VARIATION IN *ARABIDOPSIS THALIANA*

(a) *Linking genetic sensitivity to the timing of flowering*

Arabidopsis thaliana's well understood flowering time network and extensive natural variation in flowering time genes make it an ideal model in which to explore the link between genetic factors and phenological response. Moreover, this weedy annual species inhabits a wide range of climates across its native range in Europe and central Asia and exhibits distinct geographical patterns in its seasonal life history. According to field observations, at high latitudes, *A. thaliana* behaves as a winter annual, germinating in autumn, overwintering as a rosette and flowering in the spring soon after snowmelt (Petipas *et al.* in preparation). Similarly, in Mediterranean climates close to its southern range limit, *Arabidopsis* overwhelmingly germinates in autumn and flowers in spring (Montesinos *et al.* 2009). However, these two winter annual life histories differ dramatically in total length. Populations in Oulu, Finland, near the Arctic Circle germinate in September and flower in May (Petipas *et al.* in preparation), while those near the Mediterranean coast in Spain germinate in November and flower in February (Wilczek *et al.* 2009). In northwestern European locations including the UK and Germany, autumn germinants display diverse flowering times spanning from later autumn to mid-spring (Thompson 1994; Wilczek *et al.* 2009). In these climates, rapid-cycling life histories have also been observed in which individuals germinate in spring or summer and flower within one to two months of emergence (Thompson 1994; Wilczek *et al.* 2009). Field studies have demonstrated that both the germination timing of *A. thaliana* (reviewed in Donohue 2009) and genetic differences in integration of environmental signals after germination can contribute to spatial and temporal variability of life-history expression; however, the complex interplay of environmental and genetic factors underlying life-history variation in natural populations has remained largely unexplored.

Studies that sample geographical and seasonal variation in climate can help inform the relative contribution of environmental inputs and genetic sensitivity that underlies the observed diversity of natural responses. Using climate and phenology data from *Arabidopsis* lines grown in a multinational European field study, we created a genetically informed photothermal model of development that successfully explained over 90 per cent of the variation in the timing of flowering in wild-type plants and mutant lines carrying disruptions to the gene pathways involved in environmental sensing (Wilczek *et al.* 2009). This model, the first to predict quantitatively the integration of these pathways in a field setting, thus provides a powerful tool for examining the balance of genetic and environmental factors in determining life history in complex natural environments. We focus here specifically on four genotypes harbouring mutations affecting day length and vernalization response. The Columbia ecotype (Col, wild-type) is a widely studied accession from northwest Europe that is rapid-cycling in laboratory studies and carries a natural lesion in the locus *FRI* that mediates the strength of the vernalization response (figure 2*b*). We also studied a line in the Col background into which a natural functional *FRI* allele from the Spanish ecotype Sf-2 had been introgressed (Col *FRI*), resulting in greater initial floral repression and a more pronounced vernalization response (Lee & Amasino 1995). Comparisons between Col and Col *FRI* revealed the effects of vernalization sensitivity on the pre-flowering vegetative interval. Understanding the allelic effect of *FRI* is of special interest because both null and functional alleles at the *FRI* locus are found in natural populations, and chamber studies have suggested that *FRI* is involved in determining life-history variation in the wild (Johanson *et al.* 2000; Boss *et al.* 2004; Lempe *et al.* 2005; Shindo *et al.* 2005). We also considered a mutant line (Col *FRI vin3*) that does not respond developmentally to winter chilling, and by comparing this line with its control (Col *FRI*), we were able to assess the contribution of vernalization signals to developmental rate and timing of flowering. Finally, we grew a mutant in the day-length-sensing photoperiod pathway (Col *gi*), with which it was possible to quantify the importance of long-day signals.

Plantings of these lines in five European common gardens revealed important differences in the sensitivity of flowering time to genetic perturbation depending on site and season of growth, with most of this variation in response captured by our photothermal model. For example, in the mild oceanic climate of Norwich, UK, where wild *Arabidopsis* cohorts germinate naturally throughout much of the year, a wide range of genotypes are expected to flower rapidly when they germinate in spring and summer (Wilczek *et al.* 2009). Using 2 years of on-site weather data to simulate reaction norms of life history with our developmental model, we predicted that later autumn germinants would overwinter in the vegetative state and transition to reproductive growth (bolt) at similar times in the spring. Thus, in a narrow germination window in the early autumn, bolting time was exceptionally sensitive to both small changes in genetic background and germination timing. Outside of this window, the effects of genotype on bolting time were muted and no single allelic change resulted in a major life-history conversion. The predicted sensitivity window was observed in field plantings of Col and Col *FRI*, where the presence of a functional *FRI* allele caused a life-history conversion only during a limited portion of the year, with the exact timing depending on the climate at the growth site (Wilczek *et al.* 2009). Thus, genetically informed developmental modelling approaches can be used to highlight the environmental signals that influence life history in different environments, and the sensitivity of life-history variation to genetic variation in signalling pathways.

Because the photothermal model uses detailed plant-level measurements of temperature, initial explorations of life history were limited to the five sites and 2 years for which we had such data (Wilczek *et al.* 2009). In order to generalize the photothermal model to other years and locations, we needed to

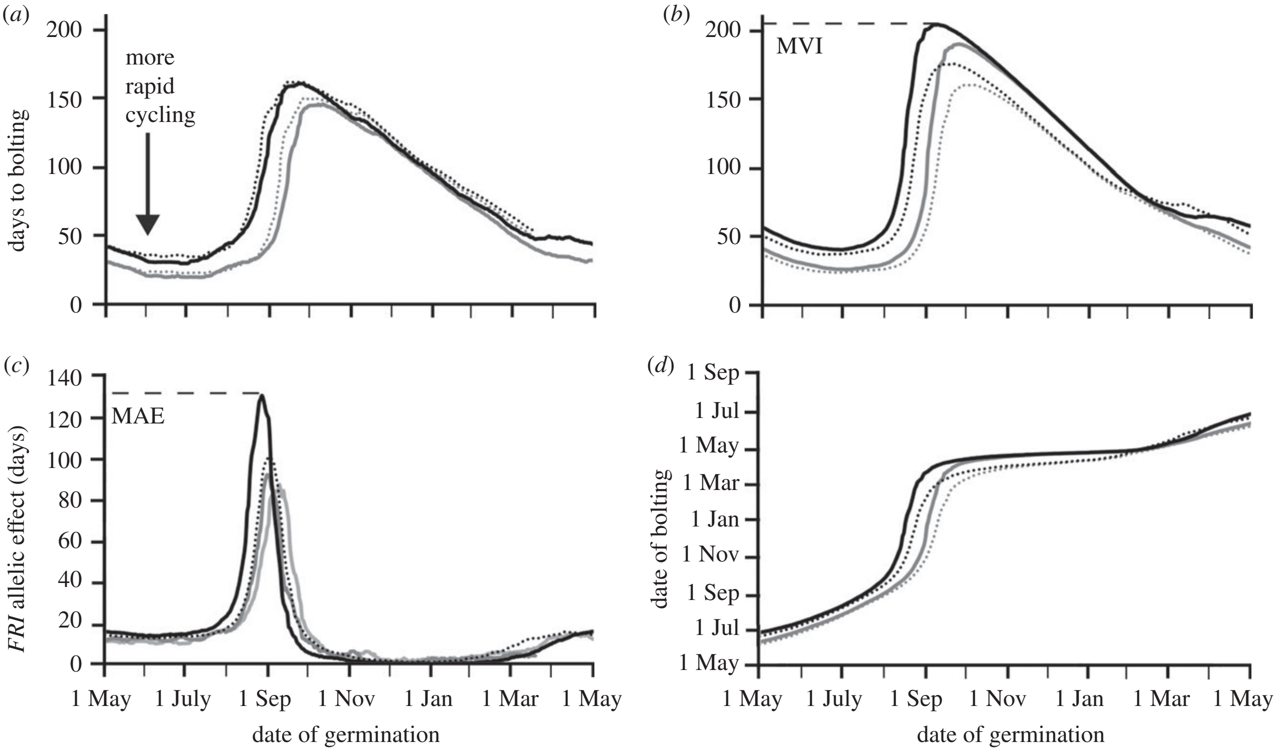

Figure 3. (*a*) Days to bolting as a function of germination date from May 2006 to May 2007 and May 2007 to May 2008 for genotypes (Col, Col *FRI*) differing in vernalization sensitivity. Predicted development time calculated using on-site plant-level measurements of temperature in Norwich, UK. Data for 2006–2007 reproduced from Wilczek *et al.* (2009). Solid grey line, Col 2006; dotted grey line, Col 2007; solid black line, *FRI* 2006; dotted black line, *FRI* 2007. (*b*) Days to bolting as a function of germination date in projected current (average for 2004–2009) and future (2094–2099) climates for genotypes (Col, Col *FRI*) differing in vernalization sensitivity. A dashed line shows the maximum vegetative interval (MVI) for Col *FRI* under current conditions. Predicted development time was based on 6 year average time to bolting using simulated 2004–2009 temperatures and for 6 year average using simulated 2094–2099 temperatures in Norwich, UK. Temperature projections from the A1B scenario. Solid grey line, Col present; dotted grey line, Col future; solid black line, *FRI* present; dotted black line, *FRI* future. (*c*) The effect of functional *FRI* on flowering time under current measured climates, as well as projected current and future climates, using data from (*a*) and (*b*). A dashed line shows the maximum allelic effect (MAE) of *FRI* under current conditions. Solid light grey line, 2006; solid dark grey line, 2007; solid black line, present; dotted black line, future.(*d*) Date of bolting as a function of germination date in projected current (average for 2004–2009) and future (2094–2099) climates for genotypes (Col, Col *FRI*) differing in vernalization sensitivity. Data replotted from (*b*). Key to plots as for (*b*).

convert the widely available temperature data (daily maxima and mimima at 1.5 m) to hourly, ground-level temperatures. Therefore, we developed a set of simple conversions that captured over 99 per cent of the variation in bolting-time-relevant temperatures across our five sites (appendix A). Clearly, the exact correspondence of simulated life-history data to finer-scale geographical patterns will depend largely on the accuracy and precision of the underlying climate models (for future climate scenarios) and the grain of recorded air temperature data (for spatial extrapolation). Our simulations of the timing of reproduction using available climate models nevertheless broadly reproduce the patterns we observed in our European field plantings (see below). Here, we expand our analysis temporally via projected future climate scenarios and spatially across the native range in order to illustrate large-scale patterns of *Arabidopsis* life history under changing climates.

(b) *Contributions of vernalization sensitivity to life history of* Arabidopsis thaliana *under changing climates*

Our first example is a temporal analysis of patterns of life-history variation under current and projected climates in Norwich, UK, where natural *A. thaliana* cohorts are seen throughout the year. Comparing on-site temperature data from Norwich in 2006–2008 against projected temperatures for current and end-of-century future climates under the A1B scenario (NOAA GFDL 2004; Delworth *et al.* 2006) revealed some startling differences. We found that while real and simulated minimum temperatures were in general agreement for the current time period, real air temperature maxima were consistently higher than even simulated future maxima. The years 2006–2008 were all considerably warmer than the 1961–2000 regional average (UK National Weather Service 2009); an alternate explanation for our high measured temperatures is that the microclimate at our site is warmer than that of the 2.5° × 2.5° geographical grid cell that includes Norwich. Owing to the warm temperature maxima experienced by field plants in 2006–2008, bolting responses of those plants mimic more closely the responses of plants to projected future climates (figure 3).

Simulations of bolting as a function of germination date under warmer future climates at this site indicated that the impact of *FRIGIDA*-mediated vernalization sensitivity will remain qualitatively similar to its life-history effect in cooler climates. A functional *FRI* allele increased the amount of time elapsed between germination and flowering (figure 3*a*) or the predicted maximum vegetative interval (MVI) both in current and future climates. Further, the predicted magnitude of the *FRI* allele effect was not much altered in future climates for late spring and late summer germinants (figure 3*c*). In contrast, for *FRI* functional plants germinating from late January through early April, a decrease in late winter chilling actually delayed bolting in warmer, as compared with cooler, climates (figure 3*b*). However, climate change did cause quantitative shifts in both the seasonal timing and magnitude of life-history transitions. For cohorts germinating throughout much of the late autumn and winter, *FRI* had no allelic effect on flowering time, yet under projected future climates, the flowering of late autumn germinants occurred earlier in the spring for both Col and Col *FRI* genotypes (figure 3*d*). Additionally, we observed a shift in the timing of the sensitivity window, where the change from rapid-cycling, autumn-flowering behaviour to spring-flowering behaviour occurred at a later germination date in warmer climates and with loss of *FRIGIDA* function (figure 3*b*).

The maximum allelic effect (MAE) of *FRI* on flowering time (figure 3*c*) is a measure of the largest potential effect on the life history of a given perturbation of gene function. The MAE of *FRI* not only decreased in magnitude under warmer climates, but also the germination dates on which the MAE occurred shifted later in the autumn season. The attenuation of the influence of *FRI* under climates with less winter chilling may seem counterintuitive, given that prior to chilling *FRI* functional plants develop more slowly and that *FRI* has the strongest effect in constant warm conditions in controlled environment studies (Lempe *et al.* 2005; Balasubramanian *et al.* 2006*b*; Shindo *et al.* 2006). The weakening of chilling cues that would equalize the developmental rates of the two genotypes was counterbalanced as warmer temperatures accelerated overall development, leading to decreased MVI in both genetic backgrounds. Thus, regardless of the maintenance or even exaggeration of relative differences in developmental rates between the two genotypes with warming climates, in most cases (with the exception of some spring germinants, figure 3*b*), their difference in flowering time as measured in days decreased (figure 3*c*).

Based on our projections in Norwich, we find that *FRIGIDA* genotype alone is grossly insufficient to explain life-history variation at this site in both current and future climates. We would not expect variation in *FRI* status to account completely for rapid-cycling versus winter annual life histories in co-occurring populations that have been observed in the UK, despite the fact that *FRI* has a measurable effect on flowering time throughout most of the year (figure 3*c*). Instead, the length of time spent as a vegetative individual prior to flowering depended largely on the timing of germination (figure 3*b*), with genotype playing a major role in flowering phenology only for a subset of autumn-germination cohorts (figure 3*c*). What emerges in this analysis of response to climate change at a single location is a complex set of relationships between genetic sensitivity, seasonal distribution of environmental cues and the timing of reproduction that can nonetheless be precisely predicted and mapped when the physiological bases of these developmental processes are understood.

(c) *Genetic sensitivity and life-history variation across the native range of* **Arabidopsis thaliana**

What then drives variation in life history in this species? What is the effect of the candidate locus *FRIGIDA* on life-history expression across a range of different seasonal climates? How conserved is the pattern of sensitivity of life-cycle length to germination timing under different climates? To address these questions, we expanded our phenological analysis of *FRI* to a broader geographical scale encompassing much of the species's native range in Europe and central Asia. From simulations of time to bolting (length of vegetative interval) as a function of germination date under current and future projected climates, we found that early summer germinants of both Col and Col *FRI* showed very little variation in life-cycle length (appendix A; electronic supplementary material, movies S1 and S2). These rapid-cycling cohorts transitioned from vegetative to reproductive growth within two months of germination regardless of geographical location or genotype, although *FRI* functional plants generally required about 10 more days to reach bolting. As our simulations progressed through summer and into autumn-germination cohorts, the seasonal transition from rapid-cycling to spring-flowering life history as a function of germination date occurred in a wave from north to south, with the onset of this wave coming earlier in *FRI* functional plants and in current (versus future) climates.

To characterize geographical patterns in life-cycle variation, we determined the MVI between germination and bolting for each genotype, and the date of germination on which life-cycle length was maximized (figures 3*b* and 4). Since the minimum life-history length achieved by summer germinants was similar everywhere, the MVI is representative of the magnitude of seasonal variation in life history at a given location; the date on which this transition to spring-flowering occurs gives an indication of the germination season in which the window of life-history sensitivity occurs. We found that more northern populations had the greatest variation in life-cycle length (figure 4*a*,*b*). Depending on location (and genetic background to a lesser extent), the MVI varied from less than 3 months to over a year. Despite transitioning to spring-flowering behaviour in earlier germination cohorts (figure 4*c*,*d*), autumn germinants in northern populations flowered later in the spring (electronic supplementary material, movies S1 and S2) so that both the length of the life cycle and the seasonal timing of flowering showed geographical structure. Under projected future climates, these patterns were largely maintained but shifted slightly northwards (electronic supplementary material, figure S1).

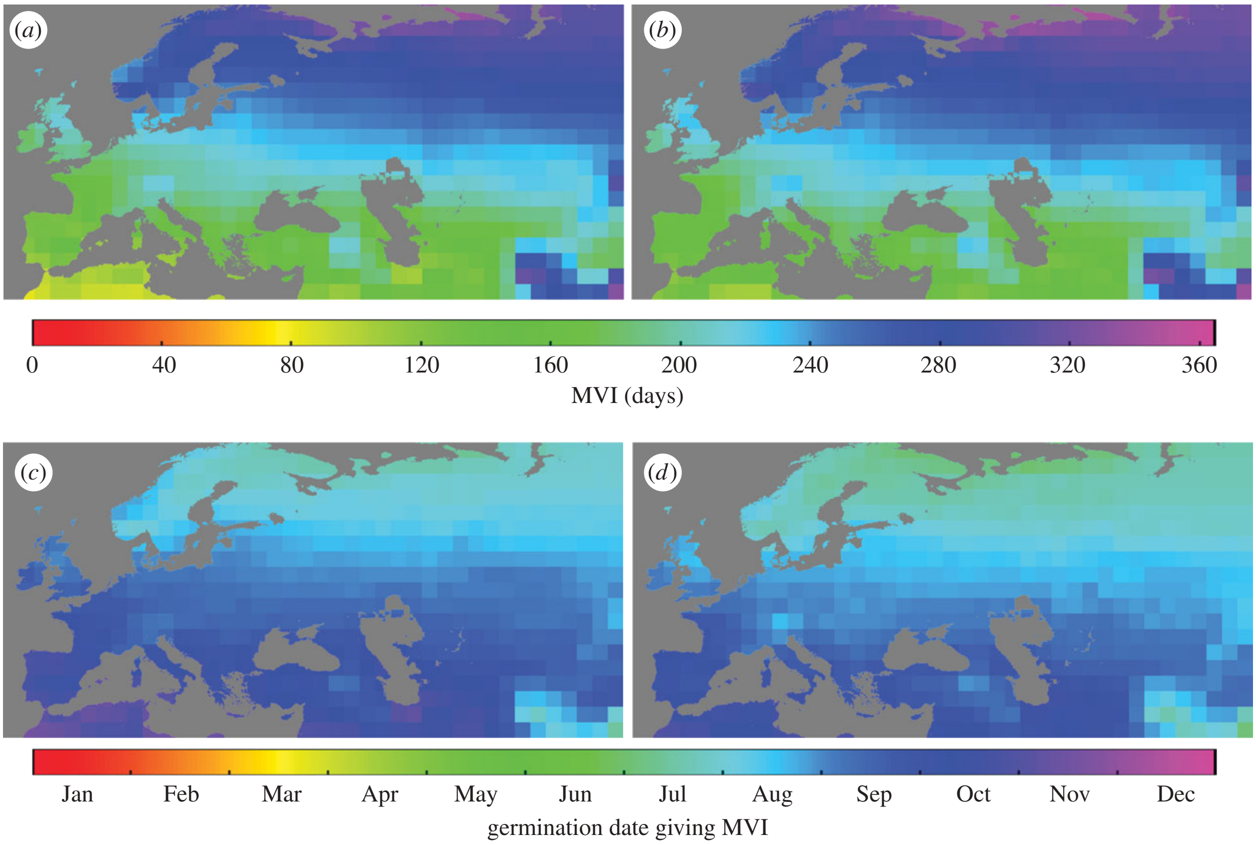

Figure 4. Current geographical patterns of (*a*,*b*) the maximum vegetation interval (MVI) between germination and bolting, and (*c*,*d*) the germination date on which the MVI occurs in *A. thaliana* accessions that differ in vernalization sensitivity. (*a*,*c*) Col ecotype (Col) and (*b*,*d*) Col ecotype with functional *FRIGIDA* (Col *FRI*). Estimates of bolting time are based on a 6 year average from 2004 to 2009 under the A1B projection scenario.

In order to better understand the effect of *FRI* on life history in current and future climates, we looked at the maximum life-history effect owing to allelic variation in *FRI* and the germination date on which this MAE is achieved. We used these values to assess the magnitude and timing of the life-history transition caused by changes in the strength of vernalization response. The magnitude of the difference in life-cycle length between ecotypes that differ in *FRI* functionality, and thus vernalization response, decreased with latitude (figure 5*a*) and, generally, with warming climates within sites (figure 5*b*).

Other perturbations to the environmentally sensitive flowering pathways in *A. thaliana* revealed distinct geographical and temporal patterns of life history. Complete genetic insensitivity to vernalization signals, such as that found in Col *FRI vin3* plants, resulted in transition to spring-flowering behaviour at even earlier summer and autumn germination dates accompanied by greater increases in the MVI (electronic supplementary material, figure S2 and movie S3). The maximum effect of the *VIN3* locus was in general smaller than at the *FRI* locus and showed a stronger oceanic to continental gradient, even while the timing of this life-history transition showed a clear latitudinal pattern (electronic supplementary material, figure S4). Col and Col *FRI* plants differed in developmental rate prior to exposure to chilling cues, while Col *FRI* and Col *FRI vin3* plants diverged after chilling had occurred. Thus, changes in vernalization sensitivity can have disparate effects on life-history expression depending on details of the response mechanism (i.e. genetic basis), seasonal timing of germination and geographical location.

The effects of the photoperiod-sensing pathway on flowering time also varied strikingly with site and season. At lower latitudes, both plants that are insensitive to the accelerating effects of long days (Col *gi*) and plants with the sensitive wild-type background transitioned to spring-flowering at similar germination dates (electronic supplementary material, figure S3). As a result, life history of autumn-germinating cohorts was more sensitive to variation in vernalization pathways than in photoperiod-response pathways. At more northern latitudes, however, photoperiod-insensitive individuals had a longer MVI that was reached in earlier germinating cohorts (electronic supplementary material, figure S3 and movie S4). The MAE of the *GI* mutation was small towards the more southern (but extratropical, approx. 35–40° N) latitudes we explored (electronic supplementary material, figure S5). Thus, as might have been expected *a priori*, we found a greater overall importance of photoperiod sensitivity for life history in the north; however, the seasonal timing of the photoperiod sensitivity effect was less expected. One might predict the MAE of complete photoperiod insensitivity to occur in spring- or early summer-germinating cohorts, which would experience the longest days. This was true only at our southernmost locations, where the MAE, maximum day length and number of days per year above the critical long-day length were also

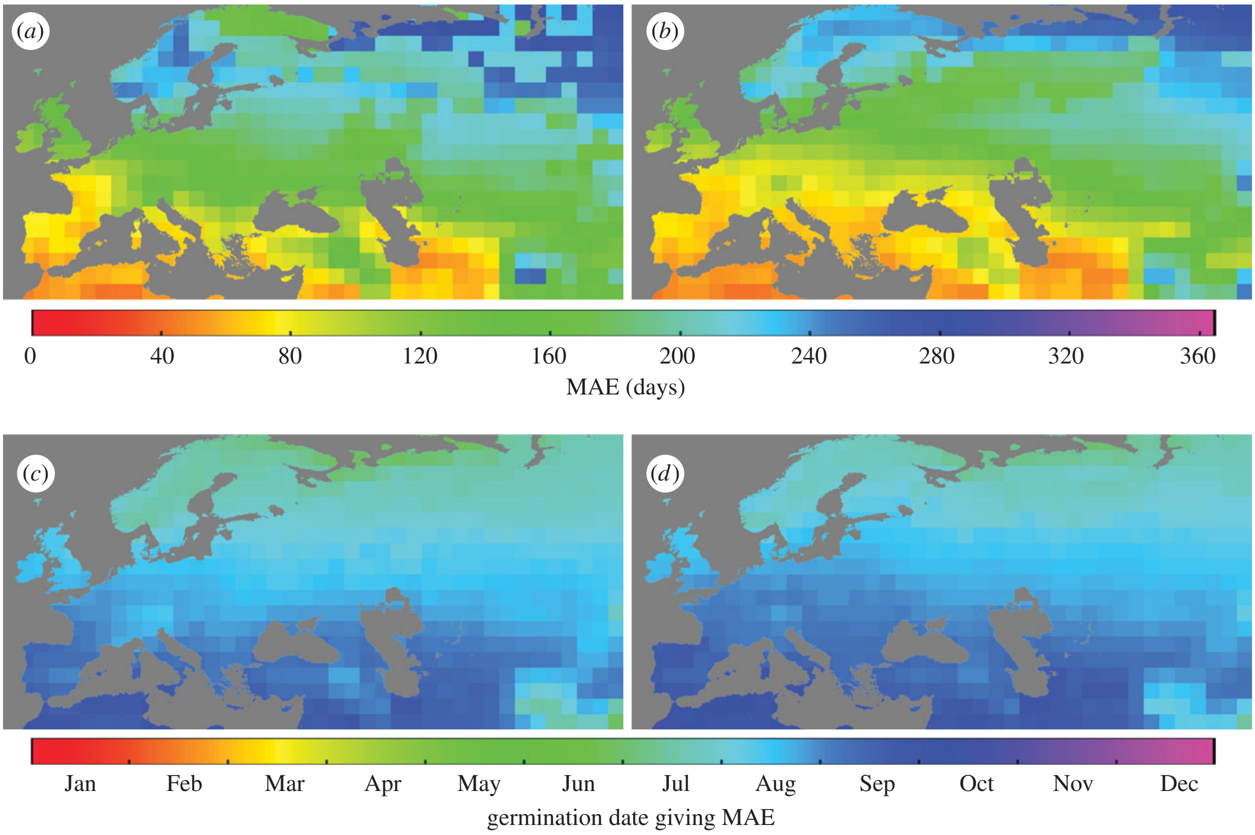

Figure 5. Geographical patterns in the maximum difference in bolting time (maximum allelic effect, MAE) between *A. thaliana* ecotypes that differ at the *FRIGIDA* locus under (*a*) current (2004–2009) and (*b*) projected (2094–2099) climates. The time of year at which this life-history transition window occurred also showed geographical variation in both (*c*) current and (*d*) projected climates across the native range of the species.

smallest. Moving north into the regions where the maximum life-history effect of *GI* increased (to levels comparable to that of *FRI*), the timing of the MAE shifted to later autumn-germinating cohorts. At northern latitudes, longer days occur earlier in the spring and contribute more to the importance of photoperiod effects in the flowering behaviour of winter annuals. The unexpected influence of photoperiod pathway disruption for seedlings germinating in shortening, non-inductive days would be difficult to understand without a detailed photothermal model of development.

(d) *Model limitations and future extensions*

This photothermal model of *Arabidopsis* development can be used to describe seasonal and geographical patterns of genetic sensitivity in flowering time and to project these patterns into predicted climates. Nonetheless, there are several clear extensions to the model presented here that would further enhance our understanding of phenological response to novel climates in *Arabidopsis*.

Our model demonstrates the exquisite sensitivity of life history to seasonal timing, and yet for most habitats, we know little about the factors determining the season in which natural *Arabidopsis* cohorts occur. For instance, our model of *Arabidopsis* phenology is at present silent about the factors that influence the timing of germination, even though recent studies have shown that certain genes in the flowering time network are also involved in seed dormancy and germination behaviour (Heschel *et al.* 2008; Chiang *et al.* 2009). Both maternal environmental factors such as temperature (Schmuths *et al.* 2006) and genetic factors (Alonso-Blanco *et al.* 2003; Holdsworth *et al.* 2008; Chiang *et al.* 2009) affect germination behaviour in this species. Despite such advances, we still know relatively little about the natural seasonal and climatic conditions that are permissive for germination (see also review in Donohue 2009). For instance, the warmer temperatures at the southern range limit confer a longer window in which summer and early autumn germinants could complete their life cycle prior to winter; however, drier summers at these sites (in concert with warmer temperatures, which can induce secondary dormancy in this species) may mean that germination during this window is impossible despite the permissive photothermal conditions for vegetative development (Montesinos *et al.* 2009). Without a detailed understanding of these factors, we cannot know what portion of the possible life-history variation predicted by the model will be expressed in nature.

The genetic and physiological bases of several later life-history stages, and their effects on the coordination of the complete life cycle, likewise remain to be explored. Our model estimates the timing of bolting, which is the appearance of the floral meristem that signals the switch from vegetative to reproductive growth. Although bolting time is used interchangeably with flowering time in much of the *Arabidopsis* developmental literature, the two events do not coincide and may respond to different environmental cues or be under distinct selection pressures. Elucidating the physiological and developmental responses of each life stage may lead to a better understanding of how and why some habitats support multiple natural cohorts of *Arabidopsis* per year while others have only a winter annual generation. For example, studies of insect life cycles have shown that the combination of seasonally distributed environmental signals and life-history stages with distinct sensitivities can be sufficient to generate multiple cohorts and synchronize the life cycles of individuals within a population across years (Jenkins *et al.* 2001; Powell & Logan 2005). Future models that explore the sensitivity, phenology and coordination of distinct life stages in *A. thaliana* will contribute further to the goal of creating a complete life-history map (cf. Donohue 2009).

Finally, we must understand the relationship between seasonal expression of phenology and fitness. Such information is necessary to explore how selection will act on the environmental sensitivity of phenological traits in changing environments (cf. Davis *et al.* 2005; Aitken *et al.* 2008). Phenological transitions can have direct fitness consequences, but selection for timing traits may vary with the environment. In *Arabidopsis*, inappropriate early bolting in winter annuals can lead to decreased fitness, but earlier bolting is advantageous in spring germinants under field conditions (Korves *et al.* 2007). Selection experiments under contrasting CO_2 or simulated seasonal conditions have identified distinct genetic responses in *Arabidopsis* that account for evolutionary changes in flowering time depending on the selection environment (Springer *et al.* 2008; Scarcelli & Kover 2009). The fitness consequences of dormancy characteristics differ between seeds dispersed in autumn and those in spring, and seasonal QTL involved in dormancy response and fitness can also be identified (Donohue *et al.* 2005; Huang *et al.* 2010). Thus, knowledge at the genetic level of the basis of phenological traits, the amount of natural variation in these traits, the effect of season on expression of these traits and their fitness consequences in seasonal environments will be necessary to achieve more accurate predictions of the integrated life-history responses of plants to novel environments.

5. PROSPECTS FOR UNDERSTANDING PHENOLOGY IN CHANGING CLIMATES

Process-based phenology models that link mechanism to responsiveness provide an important step forward in predicting plant behaviour and life history under future climate scenarios (cf. Chuine & Beaubien 2001; Morin *et al.* 2007). In particular, models that integrate and balance the importance of different environmental cues should obviate some of the problems associated with predictions of behaviour under no-analogue climates of the future (Williams & Jackson 2007; Williams *et al.* 2007). In *Arabidopsis*, even a simple model using only day length and thermal inputs can explain a great deal of the observed phenological behaviour in a variety of genetic backgrounds, seasons and geographical locations (Wilczek *et al.* 2009).

Despite a wide diversity of physiologically motivated thermal, photothermal and hydrothermal models of development for various plant species and phenological traits, most existing approaches have focused on generating separate and separately parametrized models for every species and variety considered (Cooper *et al.* 1995; Cooper & Hammer 1996). The environmentally driven response of plant timing traits modelled using these approaches can be thought of as simulated reaction norms. The *Arabidopsis* model presented here represents a step forward in understanding the genetic influence on phenology because it both ties parameters that mediate environmental response to known genes in environmental-sensing pathways and also scales developmental rates according to pathway sensitivity. Models of phenology that are sensitive to changes in allele strength at candidate loci or changes in pathway strength in genetic networks can be used to understand the magnitude of phenotypic response as a function of both environmental conditions and the genetic variation sampled. With this approach, we can also generate reaction norms in phenology space along axes of genetic pathway sensitivity. For instance, the predicted timing of life-history sensitivity as a function of genetic pathway function can inform strategies to optimize flowering to specific times in different geographical areas, as well as illustrating how planting dates and ploughing schedules should be shifted to expose genetic variation in sensitivity to different environmental variables. Thus, such trajectories in genetic sensitivity can inform plant breeding strategies for novel climates and will also be critical to understanding potential evolutionary responses to changing climates.

At the moment, there are few other plant species or traits for which the genetic basis of phenology is so well understood at the molecular level. Nonetheless, the approach of modelling general pathway sensitivity, balance and integration should be possible in any species where the basic genetic architecture of environmental response is known (figure 2)—a category that already includes several crop and forestry species. Numerous plant studies provide a rich source of phenological data from complex (and semi-natural) field environments (e.g. Betancourt & Schwartz 2005), in which individuals experience a range of temperature and photoperiod cues in combination. Building on well-developed traditions in crop research that quantify influences of different environmental variables even when they covary (Cooper & Hammer 1996), future work would benefit from considering how perturbation in the sensitivities to environmental variables singly and in concert would affect phenology. Genetic research and screens can also be used to explore the loci and pathways that underlie these environmental sensitivities (Cooper *et al.* 2005; Welch *et al.* 2005; Hammer *et al.* 2006). From work to date, we can predict that for any particular network architecture, the exact balance of converging gene pathways in determining phenology will depend on genetic sensitivity to environmental cues, the input of relevant environmental factors and the seasonal timing of life history.

6. CONCLUSIONS

Even simple process-based models can be sufficient to explain a great deal of variation in phenology at a broad scale. Given the growing interest in phenology under changing climates and the relative paucity of detailed physiological data for many plant species, it may be valuable to explore a more general approach to physiological sensitivity of different seasonal environmental inputs with models that are more heuristic and tractable. Agronomy, forestry and other applied fields are rich in data and well-developed methods for exploring the physiological basis of phenology that can be directly transferred to natural systems. To date, a great deal of effort has been focused on understanding plasticity of response to environmental factors, and as a result, the basic seasonal cues to which most plant species and traits respond are fairly well understood. Examination of intraspecific variation in phenology within the framework of models that balance response to different environmental cues may help elucidate the genetic pathways involved as well as the amount of genetic variation in this sensitivity (see also Laurie *et al.* 2004; Welch *et al.* 2005). The magnitude and distribution of natural intraspecific variation in environmental response will inform whether adaptation to new climatic regimes will be genetically constrained or how it might be facilitated through natural or assisted migration. Future challenges that will help complete our understanding of phenology in changing environments include further explorations of the genetic basis of phenological traits, the integration of seasonal timing across different life stages and the resetting of developmental time in recurring seasonal traits.

Unlike many indicators of global change that are only detectable to scientists with specialized equipment, many seasonal shifts in abiotic and biotic phenological events are immediately obvious to a large audience. The timing of leafing out in deciduous forests, onset of different pollen seasons, date of first and last frost, bloom time of showy wildflowers, timing of migration of songbirds and butterflies and bird nesting are all undergoing rapid and obvious changes detectable on the scale of a human lifetime. In exploring the mechanistic basis of phenology, evolutionary biologists, ecologists and geneticists have the opportunity to prove the explanatory power of physiological and genetic models in both recreating observed responses and projecting responses to novel environments.

We thank R. Early for assistance with GIS data formats and J. Roe for helpful discussions about the structure of flowering time networks. We are grateful to members of the Brown University Autumn 2009 Graduate Seminar for many interesting discussions about phenology in changing climates. This work was supported by an NSF Frontiers in Integrative Biological Research programme grant EF-0425759.

APPENDIX A

A.1. *Modified photothermal unit calculation*

The model used to calculate photothermal unit accumulation, and thus the progression of development to bolting, was that described in Wilczek *et al.* (2009). The modified photothermal time u_j of genotype j at time t, $u_j(t)$, was calculated from the hourly instantaneous rate $u_j'(t)$ at which genotype j accumulated modified photothermal (developmental) time. This instantaneous rate was calculated as the product of temperature above threshold Θ, a photoperiod factor p and a vernalization effectiveness e,

$$u_j'(t) = \Theta(T)p(d)e(v_j). \tag{A 1}$$

All inputs were calculated from temperature and photoperiod information by site, S. Temperature $T(S;\ t)$, day length $d(S;\ t)$ and chilling duration $v(S;\ t)$ were all site-dependent functions of time representing the growth environment to which plants were exposed. The four genotypes in our simulations were isogenic for floral integrator genes (as well as other background loci), and thus all genotypes were assumed to bolt at a common threshold of modified photothermal time. However, the rate at which any given genotype accumulated developmental time depended both on environmental inputs (day length, temperature) and on its genetically determined sensitivity to these environmental factors. Full calculation details and genotype-specific parameters for day length and vernalization sensitivity can be found in Wilczek *et al.* (2009).

A.2. *Converting daily maxima and minima to hourly air temperatures*

The photothermal accumulation model depended on hourly plant-level temperature profiles, but only daily maxima and minima were available for most climate projection datasets. We therefore simulated hourly temperature profiles from daily maxima and minima based on equations modified from Cesaraccio *et al.* (2001)

$$T = \begin{cases} c + \dfrac{a}{2}\cos\left(\pi + \dfrac{t - H_\mathrm{n}}{H_\mathrm{m} - H_\mathrm{n}}\pi\right), & H_\mathrm{n} \le t \le H_\mathrm{m} \\ T_\mathrm{s} + k\log_j L, & H_\mathrm{m} \le t \le H_\mathrm{s} \\ T_\mathrm{s} + b\sqrt{t - H_\mathrm{s}} & H_\mathrm{s} \le t \le H_\mathrm{p} \end{cases}, \tag{A 2}$$

where H_n, H_m and H_s are the time of dawn, daily maximum and dusk of that day, and t the hour. Local times of dawn and dusk were calculated using equations from Ham (2004). Additional intermediates were as follows: temperature at sunset T_s is estimated as $T_\mathrm{s} = T_\mathrm{m} - s(T_\mathrm{m} - T_\mathrm{p})$, where T_n is the day's minimum temperature, T_m the day's maximum temperature, T_p the next day's minimum temperature, and s is a parameter; the average daily increase c is the arithmetic mean of T_m and T_n, i.e. $c = (T_\mathrm{m} + T_\mathrm{n})/2$; a is the amplitude of the increase $T_\mathrm{m} - T_\mathrm{n}$; k is $T_\mathrm{m} - T_\mathrm{s}$; the logarithmic base j is $1 + H_\mathrm{s} - H_\mathrm{m}$, $L = j - (t - H_\mathrm{m})$ and

$$b = \frac{T_\mathrm{p} - T_\mathrm{s}}{\sqrt{H_\mathrm{p} - H_\mathrm{s}}},$$

where $H_\mathrm{p} - H_\mathrm{s}$ is the interval from sunset until the next dawn. H_m, the time of daily maximum temperature, is simulated as

$$H_m = H_n + x \sin\left(\frac{2\pi(w-y)}{365}\right) + z, \tag{A 3}$$

where w is the day of year (doy) and x, y, z and s are parameters. Equation (A 2) differed from that in Cesaraccio *et al.* (2001) with respect to the calculation of temperature from the time of maximum until sunset, as inspection of data from weather stations at five field sites in Europe revealed a systematic bias in the estimation of temperature decline that could be better approximated using a log function (L. Burghardt 2010, unpublished data). Parameters were fit using real data from five European weather stations, spanning from 38° N to 65° N, at which we gathered real hourly air temperature profiles for at least 1 year at each site and compared these with hourly profiles simulated using measured daily maxima and minima (Wilczek *et al.* 2009). Final parameter values were set to $x = 2.036391$, $y = 79.22015$, $z = 9.285504$ and $s = 0.227538$.

A.3. *Simulation of ground temperature from air temperature*

Surface temperature T_g in kelvins was simulated based on Kelvin air temperature T_a as

$$T_g = aW + cT_a + e\sin\left(\frac{2\pi t}{365} + f\right) + d, \tag{A 4}$$

where a, c, d, e and f are parameters, W (hour, doy) is clear sky irradiance as calculated in Ham (2004) and t is (fractional) time since midnight on 1 January in days. Values of parameters were fit empirically using data from the same five European weather stations to $a = 0.004099$, $c = 0.920493$, $d = 22.466179$, $e = -1.861643$, and $f = 1.549941$.

A.4. *Accuracy of hourly ground temperature simulations from daily air temperature*

Using the photothermal unit accumulation model, days to bolting (DTB) for the Col wild-type genotype was estimated for between 346 and 815 (average 644, median 662) germination dates from 2006 to 2008 at each of the five sites. DTB was calculated using either real hourly ground temperatures measured from on-site weather stations (Wilczek *et al.* 2009) or measured daily air temperature maxima and minima from these same stations and equations (A 2), (A 3) and (A 4), from which hourly ground temperature profiles were simulated. The correlation between DTB calculated from real hourly ground temperature data and from simulated hourly ground temperature profiles was greater than 0.99 in each of the sites. The slope of DTB predicted from real hourly ground versus simulated hourly ground temperatures was on average 1.00 between the five sites, with a range of 0.98–1.05. Thus, these hourly profile simulations can capture much of the flowering-relevant temperature variation across a broad geographical and seasonal range.

A.5. *Estimating phenology in projected climate scenarios*

We chose to explore flowering behaviour in an area of Europe and central Asia (11–86° E and 35–71° N) that encompasses much of *A. thaliana*'s native contiguous range. The northern and eastern borders of this grid were set by the extreme locations of recent *A. thaliana* sampling efforts and range descriptions as well as online available herbaria records (Hoffmann 2002; Schmid *et al.* 2006; Beck *et al.* 2008; GBIF). However, even within this grid, there are probably large areas from which natural populations of *A. thaliana* are absent, particularly in northern Scandinavia and much of Siberia (Hoffmann 2002; Koornneef *et al.* 2004). In fact, the described northern range limit closely follows the pattern described by our model predictions of MVI for *FRI* populations under current climates. *Arabidopsis* is largely absent from areas in which the MVI exceeds 320 days (figure 4), suggesting that the inability to complete a winter annual life cycle may limit the maintenance of populations in these areas. Described populations of *A. thaliana* that occur outside (particularly south) of this grid occur largely at high elevations (e.g. in the Himalayas and northern Africa) or on oceanic islands, where the microclimate is not likely to be captured at the scale of available climate projections.

For the simulations of flowering time across the native range (approximated here by the area from 11° to 86° E and 35° to 71° N), we used data from the NOAA GFDL CM2.1 A1B_X1 climate scenario for 2001–2100 (NOAA GFDL 2004; Delworth *et al.* 2006). This scenario, which simulates temperatures under increasing CO_2 concentrations up to 720 ppm in the year 2100, projects global daily temperature maxima and minima at a spatial resolution of $2.5° \times 2.5°$. For each day and geographical grid cell, hourly temperature profiles were simulated from the projected daily maxima and minima using equations (A 2), (A 3) and (A 4). We chose two 6 year time intervals, 2004–2009 and 2094–2099, inclusive, to represent current and future projected climates, respectively. For germination on each successive calendar day of the year, the required number of days to reach the developmental threshold for bolting as a function of simulated local temperature and photoperiod conditions was calculated for the Col, Col *FRI*, Col *FRI vin3* and Col *gi* genotypes according to the model in Wilczek *et al.* (2009). For the two 6 year intervals, the average time to bolting (in days) and standard deviation of time to bolting were then calculated for each genotype for each germination day.

REFERENCES

Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T. L. & Curtis-Mclane, S. 2008 Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* **1**, 95–111. (doi:10.1111/j.1752-4571.2007.00013.x)

Akin, W. E. 1990 *Global patterns: climate, vegetation and soils.* Norman, OK: University of Oklahoma Press.

Alexandre, C. M. & Hennig, L. 2008 FLC or not FLC: the other side of vernalization. *J. Exp. Bot.* **59**, 1127–1135. (doi:10.1093/jxb/ern070)

Alonso-Blanco, C., Bentsink, L., Hanhart, C. J., Blankestijn-de Vries, H. & Koornneef, M. 2003 Analysis of natural allelic variation at seed dormancy loci of *Arabidopsis thaliana*. *Genetics* **164**, 711–729.

Alonso-Blanco, C., Mendez-Vigo, B. & Koornneef, M. 2005 From phenotypic to molecular polymorphisms involved in naturally occurring variation of plant development. *Int. J. Dev. Biol.* **49**, 717–732. (doi:10.1387/ijdb.051994ca)

Alonso-Blanco, C., Aarts, M. G. M., Bentsink, L., Keurentjes, J. J. B., Reymond, M., Vreugdenhil, D. & Koornneef, M. 2009 what has natural variation taught us about plant development, physiology, and adaptation? *Plant Cell* **21**, 1877–1896. (doi:10.1105/tpc.109.068114)

Balasubramanian, S. *et al.* 2006*a* The PHYTOCHROME C photoreceptor gene mediates natural variation in flowering and growth responses of *Arabidopsis thaliana*. *Nat. Genet.* **38**, 711–715. (doi:10.1038/ng1818)

Balasubramanian, S., Sureshkumar, S., Lempe, J. & Weigel, D. 2006*b* Potent induction of *Arabidopsis thaliana* flowering by elevated growth temperature. *PLoS Genet.* **2**, 980–989.

Baurle, I. & Dean, C. 2006 The timing of developmental transitions in plants. *Cell* **125**, 655–664. (doi:10.1016/j.cell.2006.05.005)

Beck, J. B., Schmuths, H. & Schaal, B. A. 2008 Native range genetic variation in *Arabidopsis thaliana* is strongly geographically structured and reflects Pleistocene glacial dynamics. *Mol. Ecol.* **17**, 902–915.

Bertin, R. I. 2008 Plant phenology and distribution in relation to recent climate change. *J. Torrey Bot. Soc.* **135**, 126–146.

Betancourt, J. L. & Schwartz, M. 2005 Implementing a U.S. national phenology network. *EOS Trans. AGU* **86**, 539–541.

Blackman, B., Strasburg, J. L., Raduski, A., Michaels, S. & Rieseberg, L. 2010 The role of recently derived FT paralogs in sunflower domestication. *Curr. Biol.* **20**, 629–635. (doi:10.1016/j.cub.2010.01.059)

Blazquez, M. A., Ahn, J. H. & Weigel, D. 2003 A thermosensory pathway controlling flowering time in *Arabidopsis thaliana*. *Nat. Genet.* **33**, 168–171. (doi:10.1038/ng1085)

Bohlenius, H., Huang, T., Charbonnel-Campaa, L., Brunner, A. M., Jansson, S., Strauss, S. H. & Nilsson, O. 2006 CO/FT regulatory module controls timing of flowering and seasonal growth cessation in trees. *Science* **312**, 1040–1043. (doi:10.1126/science.1126038)

Borchert, R., Robertson, K., Schwartz, M. D. & Williams-Linera, G. 2005 Phenology of temperate trees in tropical climates. *Int. J. Biometeorol.* **50**, 57–65. (doi:10.1007/s00484-005-0261-7)

Boss, P. K., Bastow, R. M., Mylne, J. S. & Dean, C. 2004 Multiple pathways in the decision to flower: enabling, promoting, and resetting. *Plant Cell* **16**, S18–S31. (doi:10.1105/tpc.015958)

Bradshaw, W. E. & Holzapfel, C. M. 2001 Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl Acad. Sci. USA* **98**, 14 509–14 511. (doi:10.1073/pnas.241391498)

Bradshaw, W. E. & Holzapfel, C. M. 2008 Genetic response to rapid climate change: it's seasonal timing that matters. *Mol. Ecol.* **17**, 157–166. (doi:10.1111/j.1365-294X.2007.03509.x)

Cesaraccio, C., Spano, D., Duce, P. & Snyder, R. L. 2001 An improved model for determining degree-day values from daily temperature data. *Int. J. Biometeorol.* **45**, 161–169.

Charles-Edwards, D. A., Doley, D. & Rimmington, G. M. 1986 *Modelling plant growth and development*. North Ryde, Australia: Academic Press.

Chiang, G. C. K., Barua, D., Kramer, E. M., Amasino, R. M. & Donohue, K. 2009 Major flowering time gene, *FLOWERING LOCUS C*, regulates seed germination in *Arabidopsis thaliana*. *Proc. Natl Acad. Sci. USA* **106**, 11 661–11 666. (doi:10.1073/pnas.0901367106)

Chuine, I. 2010 Why does phenology drive species distribution? *Phil. Trans. R. Soc. B* **365**, 3149–3160. (doi:10.1098/rstb.2010.0142)

Chuine, I. & Beaubien, E. G. 2001 Phenology is a major determinant of tree species range. *Ecol. Lett.* **4**, 500–510. (doi:10.1046/j.1461-0248.2001.00261.x)

Cockram, J., Chiapparino, E., Taylor, S. A., Stamati, K., Donini, P., Laurie, D. A. & O'Sullivan, D. M. 2007*a* Haplotype analysis of vernalization loci in European barley germplasm reveals novel VRN-H1 alleles and a predominant winter VRN-H1/VRN-H2 multi-locus haplotype. *Theor. Appl. Genet.* **115**, 993–1001. (doi:10.1007/s00122-007-0626-x)

Cockram, J., Jones, H., Leigh, F. J., O'Sullivan, D., Powell, W., Laurie, D. A. & Greenland, A. J. 2007*b* Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity. *J. Exp. Bot.* **58**, 1231–1244. (doi:10.1093/jxb/erm042)

Cockram, J., Norris, C. & O'Sullivan, D. M. 2009 PCR-based markers diagnostic for spring and winter seasonal growth habit in barley. *Crop Sci.* **49**, 403–410. (doi:10.2135/cropsci2008.07.0398)

Colasanti, J. & Coneva, V. 2009 Mechanisms of floral induction in grasses: something borrowed, something new. *Plant Physiol.* **149**, 56–62. (doi:10.1104/pp.108.130500)

Cooper, M. & Hammer, G. (eds) 1996 *Plant adaptation and crop improvement*. Wallingford, CT: CAB International.

Cooper, M., Podlich, D. W. & Smith, O. S. 2005. Gene-to-phenotype models and complex trait genetics. *Aust. J. Agric. Res.* **56**, 895–918. (doi:10.1071/AR05154)

Corbesier, L. *et al.* 2007 FT protein movement contributes to long-distance signaling in floral induction in *Arabidopsis*. *Science* **316**, 1030–1033. (doi:10.1126/science.1141752)

Damascos, M. A., Prado, C. & Ronquim, C. C. 2005 Bud composition, branching patterns and leaf phenology in Cerrado woody species. *Ann. Bot.* **96**, 1075–1084. (doi:10.1093/aob/mci258)

Davis, M. B., Shaw, R. G. & Etterson, J. R. 2005 Evolutionary responses to changing climate. *Ecology* **86**, 1704–1714. (doi:10.1890/03-0788)

Davis, C. C., Willis, C. G., Primack, R. B. & Miller-Rushing, A. J. 2010 The importance of phylogeny to the study of phenological response to global climate change. *Phil. Trans. R. Soc. B* **365**, 3201–3213. (doi:10.1098/rstb.2010.0130)

Delworth, T. L. *et al.* 2006 GFDL's CM2 global coupled climate models. Part I: formulation and simulation characteristics. *J. Climate* **19**, 643–674. (doi:10.1175/JCLI3629.1)

Dingkuhn, M., Kouressy, M., Vaksmann, M., Clerget, B. & Chantereau, J. 2008 A model of sorghum photoperiodism using the concept of threshold-lowering during prolonged appetence. *Eur. J. Agron.* **28**, 74–89. (doi:10.1016/j.eja.2007.05.005)

Dong, Z. S. 2003 *Incorporation of genomic information into the simulation of flowering time in* Arabidopsis thaliana. Manhattan, KS: Kansas State University.

Donohue, K. 2009 Completing the cycle: maternal effects as the missing link in plant life histories. *Phil. Trans. R. Soc. B* **364**, 1059–1074. (doi:10.1098/rstb.2008.0291)

Donohue, K., Dorn, L., Griffith, C., Kim, E., Aguilera, A., Polisetty, C. R. & Schmitt, J. 2005 The evolutionary ecology of seed germination of *Arabidopsis thaliana*: variable natural selection on germination timing. *Evolution* **59**, 758–770.

Durant, J. M., Hjermann, D. O., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. & Stenseth, N. C. 2005 Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol. Lett.* **8**, 952–958. (doi:10.1111/j.1461-0248.2005.00798.x)

Engelmann, K. & Purugganan, M. 2006 The molecular evolutionary ecology of plant development: flowering time in *Arabidopsis thaliana*. *Adv. Bot. Res.* **44**, 507–526. (doi:10.1016/S0065-2296(06)44013-1)

Finnegan, E. J. & Dennis, E. S. 2007 Vernalization-induced trimethylation of histone H3 lysine 27 at FLC is not maintained in mitotically quiescent cells. *Curr. Biol.* **17**, 1978–1983. (doi:10.1016/j.cub.2007.10.026)

Fisher, J. I., Richardson, A. D. & Mustard, J. F. 2007 Phenology model from surface meteorology does not capture satellite-based greenup estimations. *Global Change Biol.* **13**, 707–721. (doi:10.1111/j.1365-2486.2006.01311.x)

Fitter, A. H. & Fitter, R. S. R. 2002 Rapid changes in flowering time in British plants. *Science* **296**, 1689–1691. (doi:10.1126/science.1071617)

Franks, S. J., Sim, S. & Weis, A. E. 2007 Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl Acad. Sci. USA* **104**, 1278–1282. (doi:10.1073/pnas.0608379104)

Galiba, G., Vagujfalvi, A., Li, C. X., Soltesz, A. & Dubcovsky, J. 2009 Regulatory genes involved in the determination of frost tolerance in temperate cereals. *Plant Sci.* **176**, 12–19. (doi:10.1016/j.plantsci.2008.09.016)

GBIF Data Portal, data.gbif.org. Accessed 2009-07-01.

Geraldo, N., Baurle, I., Kidou, S., Hu, X. Y. & Dean, C. 2009 FRIGIDA delays flowering in *Arabidopsis* via a cotranscriptional mechanism involving direct interaction with the nuclear cap-binding complex. *Plant Physiol.* **150**, 1611–1618. (doi:10.1104/pp.109.137448)

Granier, C., Massonnet, C., Turc, O., Muller, B., Chenu, K. & Tardieu, F. 2002 Individual leaf development in *Arabidopsis thaliana*: a stable thermal-time-based programme. *Ann. Bot.* **89**, 595–604. (doi:10.1093/aob/mcf085)

Greenup, A., Peacock, W. J., Dennis, E. S. & Trevaskis, B. 2009 The molecular biology of seasonal flowering-responses in *Arabidopsis* and the cereals. *Ann. Bot.* **103**, 1165–1172. (doi:10.1093/aob/mcp063)

Griffith, T. M. & Watson, M. A. 2006 Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. *Am. Nat.* **167**, 153–164.

Gyllenstrand, N., Clapham, D., Kallman, T. & Lagercrantz, U. 2007 A Norway spruce *FLOWERING LOCUS T* homolog is implicated in control of growth rhythm in conifers. *Plant Physiol.* **144**, 248–257. (doi:10.1104/pp.107.095802)

Hall, D., Luquez, V., Garcia, V. M., St Onge, K. R., Jansson, S. & Ingvarsson, P. K. 2007 Adaptive population differentiation in phenology across a latitudinal gradient in European aspen (*Populus tremula*, L.): a comparison of neutral markers, candidate genes and phenotypic traits. *Evolution* **61**, 2849–2860. (doi:10.1111/j.1558-5646.2007.00230.x)

Ham, J. M. 2004 Useful equations in micrometeorology. In *Micrometeorology of agricultural systems* (eds J. L. Hatfield & J. M. Baker). Madison, WI: ASA-CSSA-SSSA.

Hammer, G. L., Cooper, M., Tardieu, F., Welch, S. M., Walsh, B., van Eeuwijk, F., Chapman, S. & Podlich, D. 2006 Models for navigating biological complexity in breeding improved crop plants. *Trends Plant Sci.* **11**, 587–593. (doi:10.1016/j.tplants.2006.10.006)

Harrington, C. A., Gould, P. J. & St. Clair, J. B. 2010 Modeling the effects of winter environment on dormancy release of Douglas-fir. *For. Ecol. Manage.* **259**, 798–808. (doi:10.1016/j.foreco.2009.06.018)

Hayama, R. & Coupland, G. 2004 The molecular basis of diversity in the photoperiodic flowering responses of *Arabidopsis* and rice. *Plant Physiol.* **135**, 677–684. (doi:10.1104/pp.104.042614)

Hayama, R., Yokoi, S., Tamaki, S., Yano, M. & Shimamoto, K. 2003 Adaptation of photoperiodic control pathways produces short-day flowering in rice. *Nature* **422**, 719–722. (doi:10.1038/nature01549)

Hedman, H., Kallman, T. & Lagercrantz, U. 2009 Early evolution of the MFT-like gene family in plants. *Plant Mol. Biol.* **70**, 359–369. (doi:10.1007/s11103-009-9478-x)

Henderson, I. R., Shindo, C. & Dean, C. 2003 The need for winter in the switch to flowering. *Annu. Rev. Genet.* **37**, 371–392. (doi:10.1146/annurev.genet.37.110801.142640)

Heschel, M. S., Butler, C. M., Barua, D., Chiang, G. C. K., Wheeler, A., Sharrock, R. A., Whitelam, G. C. & Donohue, K. 2008 New roles of phytochromes during seed germination. *Int. J. Plant Sci.* **169**, 531–540. (doi:10.1086/528753)

Hoffmann, M. H. 2002 Biogeography of *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae). *J. Biogeog.* **29**, 125–134. (doi:10.1046/j.1365-2699.2002.00647.x)

Hoffmann, M. H., Tomiuk, E., Schmuths, H., Koch, C. & Bachmann, K. 2005 Phenological and morphological responses to different temperature treatments differ among a world-wide sample of accessions of *Arabidopsis thaliana*. *Acta Oecol. Int. J. Ecol.* **28**, 181–187. (doi:10.1016/j.actao.2005.03.010)

Holdsworth, M. J., Bentsink, L. & Soppe, W. J. J. 2008 Molecular networks regulating Arabidopsis seed maturation, after-ripening, dormancy and germination. *New Phytol.* **179**, 33–54. (doi:10.1111/j.1469-8137.2008.02437.x)

Howe, G. T., Aitken, S. N., Neale, D. B., Jermstad, K. D., Wheeler, N. C. & Chen, T. H. H. 2003 From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Can. J. Bot. Rev.* **81**, 1247–1266. (doi:10.1139/b03-141)

Huang, X., Schmitt, J., Dorn, L., Griffith, C., Effgen, S., Takao, S., Koornneef, M. & Donohue, K. 2010 The earliest stages of adaptation in an experimental plant population: strong selection on QTLS for seed dormancy. *Mol. Ecol.* **19**, 1335–1351. (doi:10.1111/j.1365-294x.2010.04557.x)

Ibáñez, I., Primack, R. B., Miller-Rushing, A. J., Ellwood, E., Higuchi, H., Lee, S. D., Kobori, H. & Silander, J. A. 2010 Forecasting phenology under global warming. *Phil. Trans. R. Soc. B* **365**, 3247–3260. (doi:10.1098/rstb.2010.0120)

Ingvarsson, P. K., Garcia, M. V., Hall, D., Luquez, V. & Jansson, S. 2006 Clinal variation in phyB2, a candidate gene for day-length-induced growth cessation and bud set, across a latitudinal gradient in European aspen (*Populus tremula*). *Genetics* **172**, 1845–1853. (doi:10.1534/genetics.105.047522)

Ingvarsson, P. K., Garcia, M. V., Luquez, V., Hall, D. & Jansson, S. 2008 Nucleotide polymorphism and phenotypic associations within and around the phytochrome B2 locus in European aspen (*Populus tremula*, Salicaceae). *Genetics* **178**, 2217–2226. (doi:10.1534/genetics.107.082354)

Jenkins, J. L., Powell, J. A., Logan, J. A. & Bentz, B. J. 2001 Low seasonal temperatures promote life cycle synchronization. *Bull. Math. Biol.* **63**, 573–595. (doi:10.1006/bulm.2001.0237)

Johanson, U., West, J., Lister, C., Michaels, S., Amasino, R. & Dean, C. 2000 Molecular analysis of FRIGIDA, a major determinant of natural variation in *Arabidopsis* flowering time. *Science* **290**, 344–347. (doi:10.1126/science.290.5490.344)

Jones, H. *et al.* 2008 Population-based resequencing reveals that the flowering time adaptation of cultivated barley originated east of the fertile crescent. *Mol. Biol. Evol.* **25**, 2211–2219. (doi:10.1093/molbev/msn167)

Joost, S., Bonin, A., Bruford, M., Després, L., Conord, C., Erhardt, G. & Taberlet, P. 2007 A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. *Mol. Ecol.* **16**, 3955–3969. (doi:10.1111/j.1365-294X.2007.03442.x)

Kikuchi, R., Kawahigashi, H., Ando, T., Tonooka, T. & Handa, H. 2009 Molecular and functional characterization of *PEBP* genes in barley reveal the diversification of their roles in flowering. *Plant Physiol.* **149**, 1341–1353. (doi:10.1104/pp.108.132134)

Kim, S. Y., He, Y. H., Jacob, Y., Noh, Y. S., Michaels, S. & Amasino, R. 2005 Establishment of the vernalization-responsive, winter-annual habit in *Arabidopsis* requires a putative histone H3 methyl transferase. *Plant Cell* **17**, 3301–3310. (doi:10.1105/tpc.105.034645)

Kim, S. Y. *et al.* 2007 Delayed flowering time in *Arabidopsis* and *Brassica rapa* by the overexpression of *FLOWERING LOCUS C* (*FLC*) homologs isolated from Chinese cabbage (*Brassica rapa* L. ssp *pekinensis*). *Plant Cell Rep.* **26**, 327–336. (doi:10.1007/s00299-006-0243-1)

Kobayashi, Y. & Weigel, D. 2007 Move on up, it's time for change—mobile signals controlling photoperiod-dependent flowering. *Gen. Dev* **21**, 2371–2384.

Koornneef, M., Hanhart, C. J. & Vanderveen, J. H. 1991 A genetic and physiological analysis of late flowering mutants in *Arabidopsis thaliana*. *Mol. Gen. Genet.* **229**, 57–66.

Koornneef, M., Alonso-Blanco, C. & Vreugdenhil, D. 2004 Naturally occurring genetic variation in *Arabidopsis thaliana*. *Annu. Rev. Plant Biol.* **55**, 141–172. (doi:10.1146/annurev.arplant.55.031903.141605)

Korves, T. M., Schmid, K. J., Caicedo, A. L., Mays, C., Stinchcombe, J. R., Purugganan, M. D. & Schmitt, J. 2007 Fitness effects associated with the major flowering time gene *FRIGIDA* in *Arabidopsis thaliana* in the field. *Am. Nat.* **169**, E141–E157.

Landsberg, H. 1941 *Physical climatology.* State College, PA: Gray Printing Company.

Laurie, D. A., Griffiths, S., Dunford, R. P., Christodoulou, V., Taylor, S. A., Cockram, J., Beales, J. & Turner, A. 2004 Comparative genetic approaches to the identification of flowering time genes in temperate cereals. *Field Crops Res.* **90**, 87–99. (doi:10.1016/j.fcr.2004.07.007)

Lee, I. & Amasino, R. M. 1995 Effect of vernalization, photoperiod, and light quality on the flowering phenotype of *Arabidopsis* plants containing the *Frigida* gene. *Plant Physiol.* **108**, 157–162.

Lehikoinen, E., Sparks, T. H. & Zalakevicius, M. 2004 Arrival and departure dates. In *The effects of climate change on birds* (eds A. P. Moller, W. Fielder & P. Berthold), pp. 1–31. New York, NY: Academic Press Ltd.

Lempe, J., Balasubramanian, S., Sureshkumar, S., Singh, A., Schmid, M. & Weigel, D. 2005 Diversity of flowering responses in wild *Arabidopsis thaliana* strains. *PLoS Genet.* **1**, 109–118.

Li, Y., Roycewicz, P., Smith, E. & Borevitz, J. O. 2006 Genetics of local adaptation in the laboratory: flowering time quantitative trait loci under geographic and seasonal conditions in *Arabidopsis*. *PLoS ONE* **1**, e105. (doi:10.1371/journal.pone.0000105)

Li, Z. G., Reighard, G. L., Abbott, A. G. & Bielenberg, D. G. 2009 Dormancy-associated MADS genes from the *EVG* locus of peach *Prunus persica* (L.) Batsch have distinct seasonal and photoperiodic expression patterns. *J. Exp. Bot.* **60**, 3521–3530. (doi:10.1093/jxb/erp195)

Lifschitz, E., Eviatar, T., Rozman, A., Shalit, A., Goldshmidt, A., Amsellem, Z., Alvarez, J. P. & Eshed, Y. 2006 The tomato *FT* ortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli. *Proc. Natl Acad. Sci. USA* **103**, 6398–6403. (doi:10.1073/pnas.0601620103)

Linacre, E. 1992 *Climate, data and resources: a reference and guide*. New York, NY: Routledge.

Lister, D. L. *et al.* 2009 Latitudinal variation in a photoperiod response gene in European barley: insight into the dynamics of agricultural spread from 'historic' specimens. *J. Archaeol. Sci.* **36**, 1092–1098. (doi:10.1016/j.jas.2008.12.012)

Locke, J. C. W., Southern, M. M., Kozma-Bognar, L., Hibberd, V., Brown, P. E., Turner, M. S. & Millar, A. J. 2005 Extension of a genetic network model by iterative experimentation and mathematical analysis. *Mol. Syst. Biol.* **1**. (doi:10.1038/msb4100018)

Locke, J. C. W., Kozma-Bognar, L., Gould, P. D., Feher, B., Kevei, E., Nagy, F., Turner, M. S., Hall, A. & Millar, A. J. 2006 Experimental validation of a predicted feedback loop in the multi-oscillator clock of *Arabidopsis thaliana*. *Mol. Syst. Biol.* **2**, 6.

Luquez, V., Hall, D., Albrectsen, B. R., Karlsson, J., Ingvarsson, P. & Jansson, S. 2008 Natural phenological variation in aspen (*Populus tremula*): the SwAsp collection. *Tree Genet. Genomes* **4**, 279–292. (doi:10.1007/s11295-007-0108-y)

Malmberg, R. L., Held, S., Waits, A. & Mauricio, R. 2005 Epistasis for fitness-related quantitative traits in *Arabidopsis thaliana* grown in the field and in the greenhouse. *Genetics* **171**, 2013–2027. (doi:10.1534/genetics.105.046078)

Maloof, J. N. *et al.* 2001 Natural variation in light sensitivity of *Arabidopsis*. *Nat. Genet.* **29**, 441–446. (doi:10.1038/ng777)

Menzel, A. *et al.* 2006*a* European phenological response to climate change matches the warming pattern. *Global Change Biol.* **12**, 1969–1976. (doi:10.1111/j.1365-2486.2006.01193.x)

Menzel, A., Von Vopelius, J., Estrella, N., Schleip, C. & Dose, V. 2006*b* Farmers' annual activities are not tracking the speed of climate change. *Climate Res.* **32**, 201–207.

Michael, T. P., Salome, P. A. & McClung, C. R. 2003 Two *Arabidopsis* circadian oscillators can be distinguished by differential temperature sensitivity. *Proc. Natl Acad. Sci. USA* **100**, 6878–6883. (doi:10.1073/pnas.1131995100)

Michaels, S. D., He, Y. H., Scortecci, K. C. & Amasino, R. M. 2003 Attenuation of FLOWERING LOCUS C activity as a mechanism for the evolution of summer-annual flowering behavior in *Arabidopsis*. *Proc. Natl Acad. Sci. USA* **100**, 10 102–10 107. (doi:10.1073/pnas.1531467100)

Michaels, S. D., Bezerra, I. C. & Amasino, R. M. 2004 FRIGIDA-related genes are required for the winter-annual habit in *Arabidopsis*. *Proc. Natl Acad. Sci. USA* **101**, 3281–3285. (doi:10.1073/pnas.0306778101)

Miller-Rushing, A. J. & Primack, R. B. 2008 Global warming and flowering times in Thoreau's concord: a community perspective. *Ecology* **89**, 332–341. (doi:10.1890/07-0068.1)

Miller-Rushing, A. J., Primack, R. B., Primack, D. & Mukunda, S. 2006 Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *Am. J. Bot.* **93**, 1667–1674. (doi:10.3732/ajb.93.11.1667)

Mizoguchi, T. *et al.* 2005 Distinct roles of *GIGANTEA* in promoting flowering and regulating circadian rhythms in *Arabidopsis*. *Plant Cell* **17**, 2255–2270. (doi:10.1105/tpc.105.033464)

Moller, A. P., Rubolini, D. & Lehikoinen, E. 2008 Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Natl Acad. Sci. USA* **105**, 16 195–16 200. (doi:10.1073/pnas.0803825105)

Montesinos, A., Tonsor, S. J., Alonso-Blanco, C. & Xavier Pico, F. 2009 Demographic and genetic patterns of variation among populations of *Arabidopsis thaliana* from contrasting native environments. *PLoS ONE* **4**, no. e7213. (doi:10.1371/journal.pone.0007213)

Moon, J., Lee, H., Kim, M. & Lee, I. 2005 Analysis of flowering pathway integrators in *Arabidopsis*. *Plant Cell Physiol.* **46**, 292–299. (doi:10.1093/pcp/pci024)

Morin, X., Augspurger, C. & Chuine, I. 2007 Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology* **88**, 2280–2291. (doi:10.1890/06-1591.1)

Nemoto, Y., Kisaka, M., Fuse, T., Yano, M. & Ogihara, Y. 2003 Characterization and functional analysis of three wheat genes with homology to the *CONSTANS* flowering time gene in transgenic rice. *Plant J.* **36**, 82–93. (doi:10.1046/j.1365-313X.2003.01859.x)

NOAA GFDL (US Department of Commerce/NOAA/Geophysical Fluid Dynamics Laboratory) 2004 *IPCC Fourth Assessment and US CCSP Projects*. Princeton, NJ, USA. See http://data1.gfdl.noaa.gov/CM2.X/references/ (Accessed).

Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)

Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)

Petipas, R. H., Wilczek, A. M., Schmitt, J. & Savolainen, O. In preparation. Demography of *Arabidopsis thaliana* at its northern range limit in Finland.

Post, E. & Forchhammer, M. C. 2008 Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Phil. Trans. R. Soc. B* **363**, 2369–2375. (doi:10.1098/rstb.2007.2207)

Post, E. *et al.* 2009 Ecological dynamics across the Arctic associated with recent climate change. *Science* **325**, 1355–1358. (doi:10.1126/science.1173113)

Powell, J. A. & Logan, J. A. 2005 Insect seasonality: circle map analysis of temperature-driven life cycles. *Theor. Popul. Biol.* **67**, 161–179. (doi:10.1016/j.tpb.2004.10.001)

Primack, D., Imbres, C., Primack, R. B., Miller-Rushing, A. J. & Del Tredici, P. 2004 Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *Am. J. Bot.* **91**, 1260–1264. (doi:10.3732/ajb.91.8.1260)

Primack, R. B., Ibanez, I., Higuchi, H., Lee, S. D., Miller-Rushing, A. J., Wilson, A. M. & Silander, J. A. 2009 Spatial and interspecific variability in phenological responses to warming temperatures. *Biol. Conserv.* **142**, 2569–2577. (doi:10.1016/j.biocon.2009.06.003)

Ray, P. M. & Alexander, W. E. 1966 Photoperiodic adaptation to latitude in *Xanthium strumarium*. *Am. J. Bot.* **53**, 806–816. (doi:10.2307/2440183)

Reeves, P. A., He, Y. H., Schmitz, R. J., Amasino, R. M., Panella, L. W. & Richards, C. M. 2007 Evolutionary conservation of the *FLOWERING LOCUS C*-mediated vernalization response: evidence from the sugar beet (*Beta vulgaris*). *Genetics* **176**, 295–307. (doi:10.1534/genetics.106.069336)

Roetzer, T., Wittenzeller, M., Haeckel, H. & Nekovar, J. 2000 Phenology in central Europe—differences and trends of spring phenophases in urban and rural areas. *Int. J. Biometeorol.* **44**, 60–66. (doi:10.1007/s004840000062)

Rosenzweig, C. *et al.* 2008 Attributing physical and biological impacts to anthropogenic climate change. *Nature* **453**, 353–357. (doi:10.1038/nature06937)

Salazar, J. D., Saithong, T., Brown, P. E., Foreman, J., Locke, J. C. W., Halliday, K. J., Carre, I. A., Rand, D. A. & Millar, A. J. 2009 Prediction of photoperiodic regulators from quantitative gene circuit models. *Cell* **139**, 1170–1179. (doi:10.1016/j.cell.2009.11.029)

Samis, K. E., Heath, K. D. & Stinchcombe, J. R. 2008 Discordant longitudinal clines in flowering time and phytochrome c in *Arabidopsis thaliana*. *Evolution* **62**, 2971–2983. (doi:10.1111/j.1558-5646.2008.00484.x)

Savolainen, O., Pyhajarvi, T. & Knurr, T. 2007 Gene flow and local adaptation in trees. *Annu. Rev. Ecol. Evol. Syst.* **38**, 595–619. (doi:10.1146/annurev.ecolsys.38.091206.095646)

Scarcelli, N. & Kover, P. X. 2009 Standing genetic variation in FRIGIDA mediates experimental evolution of flowering time in *Arabidopsis*. *Mol. Ecol.* **18**, 2039–2049. (doi:10.1111/j.1365-294X.2009.04145.x)

Scarcelli, N., Cheverud, J. M., Schaal, B. A. & Kover, P. X. 2007 Antagonistic pleiotropic effects reduce the potential adaptive value of the FRIGIDA locus. *Proc. Natl Acad. Sci. USA* **104**, 16 986–16 991. (doi:10.1073/pnas.0708209104)

Schaber, J. & Badeck, F. W. 2002 Evaluation of methods for the combination of phenological time series and outlier detection. *Tree Physiol.* **22**, 973–982.

Schlappi, M. R. 2006 *FRIGIDA LIKE 2* is a functional allele in *Landsberg erecta* and compensates for a nonsense allele of *FRIGIDA LIKE 1*. *Plant Physiol.* **142**, 1728–1738. (doi:10.1104/pp.106.085571)

Schmid, K., Torjek, O., Meyer, R., Schmuths, H., Hoffmann, M. H. & Altmann, T. 2006 Evidence for a large-scale population structure of *Arabidopsis thaliana* from genome-wide single nucleotide polymorphism markers. *Theor. Appl. Genet.* **112**, 1104–1114. (doi:10.1007/s00122-006-0212-7)

Schmitz, R. J., Sung, S. & Amasino, R. M. 2008 Histone arginine methylation is required for vernalization-induced epigenetic silencing of FLC in winter-annual *Arabidopsis thaliana*. *Proc. Natl Acad. Sci. USA* **105**, 411–416. (doi:10.1073/pnas.0710423104)

Schmuths, H., Bachmann, K., Weber, W. E., Horres, R. & Hoffmann, M. H. 2006 Effects of preconditioning and temperature during germination of 73 natural accessions of *Arabidopsis thaliana*. *Ann. Bot.* **97**, 623–634. (doi:10.1093/aob/mcl012)

Searle, I., He, Y. H., Turck, F., Vincent, C., Fornara, F., Krober, S., Amasino, R. A. & Coupland, G. 2006 The transcription factor FLC confers a flowering response to vernalization by repressing meristem competence and systemic signaling in *Arabidopsis*. *Genes Dev.* **20**, 898–912. (doi:10.1101/gad.373506)

Sellers, W. D. 1965 *Physical climatology.* Chicago, IL: University of Chicago Press.

Serrano, G., Herrera-Palau, R., Romero, J. M., Serrano, A., Coupland, G. & Valverde, F. 2009 *Chlamydomonas CONSTANS* and the evolution of plant photoperiodic signaling. *Curr. Biol.* **19**, 359–368. (doi:10.1016/j.cub.2009.01.044)

Sheldon, C. C., Hills, M. J., Lister, C., Dean, C., Dennis, E. S. & Peacock, W. J. 2008 Resetting of *FLOWERING LOCUS C* expression after epigenetic repression by vernalization. *Proc. Natl Acad. Sci. USA* **105**, 2214–2219. (doi:10.1073/pnas.0711453105)

Shindo, C., Aranzana, M. J., Lister, C., Baxter, C., Nicholls, C., Nordborg, M. & Dean, C. 2005 Role of *FRIGIDA* and *FLOWERING LOCUS C* in determining variation in flowering time of *Arabidopsis*. *Plant Physiol.* **138**, 1163–1173. (doi:10.1104/pp.105.061309)

Shindo, C., Lister, C., Crevillen, P., Nordborg, M. & Dean, C. 2006 Variation in the epigenetic silencing of FLC contributes to natural variation in *Arabidopsis* vernalization response. *Genes Dev.* **20**, 3079–3083. (doi:10.1101/gad.405306)

Singer, M. C. & Parmesan, C. 2010 Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Phil. Trans. R. Soc. B* **365**, 3161–3176. (doi:10.1098/rstb.2010.0144)

Springer, C. J., Orozco, R. A., Kelly, J. K. & Ward, J. K. 2008 Elevated CO_2 influences the expression of floral-initiation genes in *Arabidopsis thaliana*. *New Phytol.* **178**, 63–67. (doi:10.1111/j.1469-8137.2008.02387.x)

Stenoien, H. K., Fenster, C. B., Kuittinen, H. & Savolainen, O. 2002 Quantifying latitudinal clines to light responses in natural populations of *Arabidopsis thaliana* (Brassicaceae). *Am. J. Bot.* **89**, 1604–1608. (doi:10.3732/ajb.89.10.1604)

Stinchcombe, J. R., Caicedo, A. L., Hopkins, R., Mays, C., Boyd, E. W., Purugganan, M. D. & Schmitt, J. 2005 Vernalization sensitivity in *Arabidopsis thaliana* (Brassicaceae): the effects of latitude and FLC variation. *Am. J. Bot.* **92**, 1701–1707. (doi:10.3732/ajb.92.10.1701)

Sung, S. B. & Amasino, R. M. 2004 Vernalization in *Arabidopsis thaliana* is mediated by the PHD finger protein VIN3. *Nature* **427**, 159–164. (doi:10.1038/nature02195)

Tamaki, S., Matsuo, S., Wong, H. L., Yokoi, S. & Shimamoto, K. 2007 Hd3a protein is a mobile flowering signal in rice. *Science* **316**, 1033–1036. (doi:10.1126/science.1141753)

Thompson, L. 1994 The spatiotemporal effects of nitrogen and litter on the population-dynamics of *Arabidopsis thaliana*. *J. Ecol.* **82**, 63–68.

Trevaskis, B., Hemming, M. N., Dennis, E. S. & Peacock, W. J. 2007 The molecular basis of vernalization-induced flowering in cereals. *Trends Plant Sci.* **12**, 352–357. (doi:10.1016/j.tplants.2007.06.010)

Turck, F., Fornara, F. & Coupland, G. 2008 Regulation and identity of florigen: FLOWERING LOCUS T moves center stage. *Annu. Rev. Plant Biol.* **59**, 573–594. (doi:10.1146/annurev.arplant.59.032607.092755)

Turner, A., Beales, J., Faure, S., Dunford, R. P. & Laurie, D. A. 2005 The pseudo-response regulator Ppd-H1 provides adaptation to photoperiod in barley. *Science* **310**, 1031–1034. (doi:10.1126/science.1117619)

UK National Weather Service 2009 See http://www.metoffice.gov.uk/climate/uk/. (Accessed 10 January 2009)

van Buskirk, J., Mulvihill, R. S. & Leberman, R. C. 2009 Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Global Change Biol.* **15**, 760–771. (doi:10.1111/j.1365-2486.2008.01751.x)

van der Jeugd, H. P., Eichhorn, G., Litvin, K. E., Stahl, J., Larsson, K., van der Graaf, A. J. & Drent, R. H. 2009 Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biol.* **15**, 1057–1071. (doi:10.1111/j.1365-2486.2008.01804.x)

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)

Wang, R. H., Farrona, S., Vincent, C., Joecker, A., Schoof, H., Turck, F., Alonso-Blanco, C., Coupland, G. & Albani, M. C. 2009 PEP1 regulates perennial flowering in *Arabis alpina*. *Nature* **459**, 423–427. (doi:10.1038/nature07988)

Weinig, C., Ungerer, M. C., Dorn, L. A., Kane, N. C., Toyonaga, Y., Halldorsdottir, S. S., Mackay, T. F. C., Purugganan, M. D. & Schmitt, J. 2002 Novel loci control variation in reproductive timing in *Arabidopsis thaliana* in natural environments. *Genetics* **162**, 1875–1884.

Welch, S. M., Roe, J. L. & Dong, Z. S. 2003 A genetic neural network model of flowering time control in *Arabidopsis thaliana*. *Agron. J.* **95**, 71–81.

Welch, S. M., Dong, Z. S., Roe, J. L. & Das, S. 2005 Flowering time control: gene network modelling and the link to quantitative genetics. *Aust. J. Agric. Res.* **56**, 919–936. (doi:10.1071/AR05155)

Wilczek, A. M. *et al.* 2009 Effects of genetic perturbation on seasonal life-history plasticity. *Science* **323**, 930–934. (doi:10.1126/science.1165826)

Wilkie, J. D., Sedgley, M. & Olesen, T. 2008 Regulation of floral initiation in horticultural trees. *J. Exp. Bot.* **59**, 3215–3228. (doi:10.1093/jxb/ern188)

Williams, J. W. & Jackson, S. T. 2007 Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5**, 475–482. (doi:10.1890/070037)

Williams, J. W., Jackson, S. T. & Kutzbacht, J. E. 2007 Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl Acad. Sci. USA* **104**, 5738–5742. (doi:10.1073/pnas.0606292104)

Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J. & Davis, C. C. 2008 Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proc. Natl Acad. Sci. USA* **105**, 17 029–17 033. (doi:10.1073/pnas.0806446105)

Worland, A. J., Borner, A., Korzun, V., Li, W. M., Petrovic, S. & Sayers, E. J. 1998 The influence of photoperiod genes on the adaptability of European winter wheats (Reprinted from Wheat: Prospects for global improvement, 1998). *Euphytica* **100**, 385–394. (doi:10.1023/A:1018327700985)

Yamaguchi, A., Kobayashi, Y., Goto, K., Abe, M. & Araki, T. 2005 *TWIN SISTER OF FT* (*TSF*) acts as a floral pathway integrator redundantly with *FT*. *Plant Cell Physiol.* **46**, 1175–1189. (doi:10.1093/pcp/pci151)

Zeilinger, M. N., Farre, E. M., Taylor, S. R., Kay, S. A. & Doyle, F. J. 2006 A novel computational model of the circadian clock in *Arabidopsis* that incorporates PRR7 and PRR9. *Mol. Syst. Biol.* **2**, 13.

Zhang, X. Y., Friedl, M. A. & Schaaf, C. B. 2006 Global vegetation phenology from moderate resolution imaging spectroradiometer (MODIS): evaluation of global patterns and comparison with *in situ* measurements. *J. Geophys. Res. Biogeosci.* **111**, G04017.

Zhang, Q. Z. *et al.* 2008 Association of the circadian rhythmic expression of GmCRY1a with a latitudinal cline in photoperiodic flowering of soybean. *Proc. Natl Acad. Sci. USA* **105**, 21 028–21 033. (doi:10.1073/pnas.0810585105)

Zhang, J. Z., Li, Z. M., Mei, L., Yao, J. L. & Hu, C. G. 2009 *PtFLC* homolog from trifoliate orange (*Poncirus trifoliata*) is regulated by alternative splicing and experiences seasonal fluctuation in expression level. *Planta* **229**, 847–859. (doi:10.1007/s00425-008-0885-z)

Zobell, O., Coupland, G. & Reiss, B. 2005 The family of CONSTANS-like genes in *Physcomitrella patens*. *Plant Biol.* **7**, 266–275. (doi:10.1055/s-2005-865621)