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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

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Introduction

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

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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

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

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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

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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

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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

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(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

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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

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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

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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.

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