Global Change Biology

Global Change Biology (2011) **17**, 3633–3643, doi: 10.1111/j.1365-2486.2011.02515.x

REVIEW

Predicting phenology by integrating ecology, evolution and climate science

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Abstract

Forecasting how species and ecosystems will respond to climate change has been a major aim of ecology in recent years. Much of this research has focused on phenology – the timing of life-history events. Phenology has well-demonstrated links to climate, from genetic to landscape scales; yet our ability to explain and predict variation in phenology across species, habitats and time remains poor. Here, we outline how merging approaches from ecology, climate science and evolutionary biology can advance research on phenological responses to climate variability. Using insight into seasonal and interannual climate variability combined with niche theory and community phylogenetics, we develop a predictive approach for species' reponses to changing climate. Our approach predicts that species occupying higher latitudes or the early growing season should be most sensitive to climate and have the most phylogenetically conserved phenologies. We further predict that temperate species will respond to climate change by shifting in time, while tropical species will respond by shifting space, or by evolving. Although we focus here on plant phenology, our approach is broadly applicable to ecological research of plant responses to climate variability.

Keywords: environmental filtering, growing-degree day models, niche conservatism, photoperiod, temperature sensitivity, temporal niche

Received 29 March 2011; revised version received 11 July 2011 and accepted 21 July 2011

Introduction

Accurate forecasting of how species will respond to climate change requires perspectives fr'om the fields of ecology, climatology and evolutionary biology (Jackson *et al*., 2009). Synthesizing these perspectives, however, requires reconciling both fundamental differences in the temporal and spatial scales at which ecological and evolutionary processes can operate, as well as divergent views of the principal drivers underlying responses (Benton, 2009). This tension between research fields is particularly evident in the study of plant phenology, defined as the timing of periodic life-history events such as leaf budburst or first flower.

Phenology is strongly linked to climate – which, for the purpose of this article, we define as the composite of generally prevailing weather conditions (e.g. temperature and precipitation) at a site or over a region, for some defined period of time (e.g. months, seasons and years). The magnitude and direction of plant species' phenological responses to climate cues have widespread consequences for trophic interactions, ecosystem services, and our ability to predict the shape of future communities, which feed back into important biosphere–atmosphere interactions (Cleland *et al*., 2007; Parmesan, 2007). Accurately forecasting phenology is thus a current objective in many fields, but these fields have widely divergent perspectives. Community ecologists have focused on localized, short-term (generally 1–3 years) studies that emphasize pairwise species interactions, trophic mismatches or competition for resources (Sargent & Ackerly, 2008; Miller-Rushing *et al*., 2010; Thackeray *et al*., 2010). Climate-focused

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studies rely on long-term (i.e. decades) and synoptic-scale (ecosystems to biomes) observations to identify shared climatic signals in phenology (Menzel *et al.*, 2006; Schwartz *et al.*, 2006), or they use phenology as a constraint on biogeochemical feedbacks between the biosphere and atmosphere (Peñuelas *et al.*, 2009; Richardson *et al.*, 2009). Species-specific phenological studies have been scaled-up in the context of spatial and temporal shifts in range sizes through process-based models (Chuine & Beaubien, 2001; Morin *et al.*, 2009), but these models still lack a community context.

Demonstrating how community-level processes influence the larger-scale functional roles of ecosystems remains a challenge. Trait-based approaches that consider how the traits of organisms turn over along abiotic gradients provide a bridge between processes at the community level and global change predictions (McGill *et al.*, 2006; Ackerly & Cornwell, 2007; Suding *et al.*, 2008). Phenological traits, such as flowering time and plant sensitivities to climate (e.g. degree of shift in phenology with shift in temperature), can be mapped onto phylogenetic trees. Phylogenetic methods provide an integrated approach to predicting the phenology of many species, and will allow us to address critical questions on how constrained or variable phenology may be across species, sites, and time in response to climate variability (Ollerton & Lack, 1992; Willis *et al.*, 2008).

Here we briefly review how climatology and ecology have traditionally approached phenological research, and in particular where these fields diverge. We consider how different scales and paradigms have shaped findings, including which environmental cues govern phenology – especially the widely studied events of leaf-burst and flowering. We propose that a more integrative approach drawing on niche theory and community phylogenetics could use site- and species-specific plant responses to make broad-scale predictions for many species. We further emphasize how shifting abiotic and biotic forces, which vary with seasonal and interannual climate variability, should shape phenologies across space and time. Our framework provides predictions for current patterns of plant sensitivities to climate, has direct ties to how species, communities, and ecosystems will respond to future climate change, and should be testable with current climate and phenology data.

Environmental cues: linking climate to phenology across scales

For phenology, as with many fields of ecology today, the holy grail is to unify our understanding of variation across scales, linking genetic studies to the expansive spatial and temporal scales of natural systems (Fig. 1). At any scale, a fundamental challenge is identifying the suite of environmental cues that initiate biological processes. But different fields of study have divergent findings regarding the relative importance among phenological cues such as irradiance, temperature or precipitation. This disparity is potentially due to inherent differences in the way that researchers from different fields approach the study of phenology. For

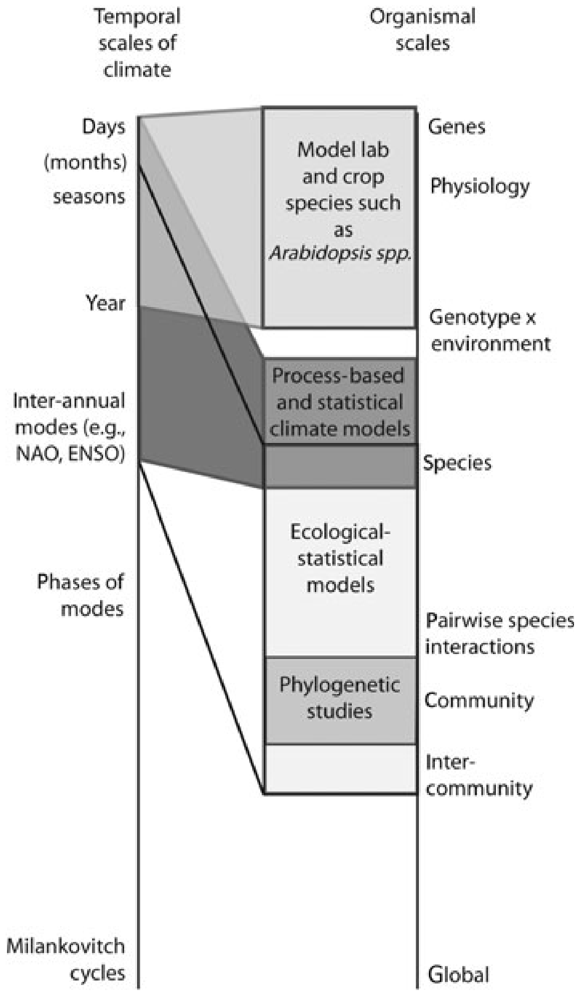

Fig. 1 Predicting how species respond to climate requires a merging of perspectives and matching climate data to relevant biological scales. While genetic-physiological studies have provided detailed information for several species on daily to seasonal scales, they are not easily applied to other species. Process-based and integrative climate models have linked field phenology to daily, seasonal and large-scale climate metrics. There is a wide range of ecological-statistical models, however studies on larger spatial scales tend to ignore community-level variation where phylogenetic studies may offer insight into community structure. Almost no efforts have examined how plant phenology has responded to previous long-term shifts in environmental cues. (Shading is meant to delineate overlapping boxes representing model types and the scales they typically address).

example, we reviewed studies that sought to identify environmental cues for flowering or budburst and found that at the genetic and physiological levels, approximately half of all studies (51%, see Appendix S1) identify photoperiod or irradiance cues, with temperature following closely behind (32%). In contrast, ecological (field or plot-scale) and climatological studies overwhelmingly find temperature cues across species and latitudes (86%) while <3% cite photoperiod or irradiance. All fields, however, find approximately the same proportion of cues due to precipitation, at about 10%. Resolving these differences is key to predicting biological responses to climate change because accurately forecasting phenology depends on identifying the correct cues.

Climatologists (or more specifically, biometereologists or bioclimatologists) have viewed phenology largely as an adaptation to avoid environmental stress, especially cold and drought. By assuming that the phenological response is broadly synchronous and correlated to climate, climatologists have treated plant species effectively as permuted meteorological stations, where one or two event dates (e.g. leafing and flowering) represent an integrated metric of climate over the preceding days and seasons. With this perspective climate-focused studies have been able to work on large spatial scales, matching regional and continental-scale climate patterns to phenology. In particular, 'growing-degree day' models have proved highly accurate at predicting start-of-season ('spring') phenology. These statistical models typically use daily temperature data to capture chilling requirements and heat accumulations over the course of a season (Schwartz *et al.*, 2006). However, such models may not detect when multiple environmental cues are required to initiate a phenological event, nor detect cues that are relatively static across space, such as photoperiod. Process-based models (Chuine & Beaubien, 2001) attempt to work around these issues by combining species or population-level information on thresholds and dormancy, usually derived from growth-chamber experiments, using time-series approaches. These more complex models have provided insight into how phenology may determine ranges of several northern temperate tree species (Morin *et al.*, 2008) and thus offer promise for scaling from physiological processes to patterns of species composition over the landscape. In addition, climate indices such as the NAO (North Atlantic Oscillation)

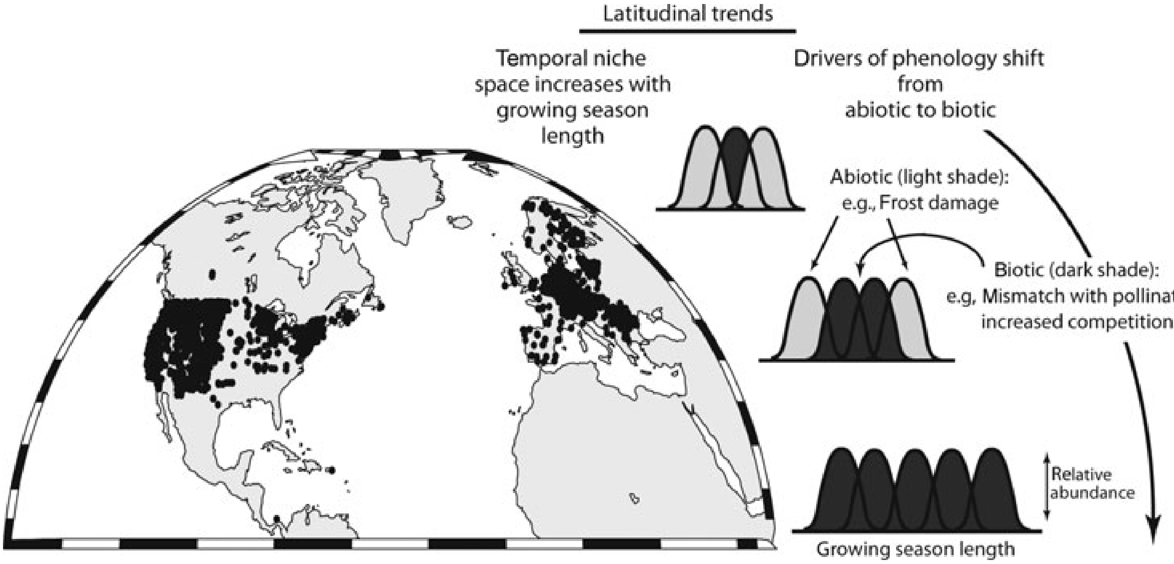

Fig. 2 Growing season length scales inversely with latitude. Thus, compared to northern areas, lower latitudes provide a longer period of time each year for species to be active (i.e. greater temporal niche axis, curves represent idealized species niches for simple communities). Alongside this, we predict that the relative importance of biotic vs. abiotic drivers varies with latitude such that aseasonal tropical communities have mainly biotic drivers of phenology because mis-timing would likely lead to mis-match with pollinators or competitors, not highly unfavorable abiotic conditions (but see Prediction 3 and Fig. 5). In contrast, the phenology of arctic communities is driven mainly by abiotic forces, and species should be highly sensitive to climate to avoid heavy abiotic costs associated with mis-timed phenological events. Additionally, for seasonal systems the relative role of abiotic and biotic forces would vary such that abiotic selective forces predominate for species active at the start or end of growing seasons, when the costs of small mis-calculations should promote high sensitivity to climate. In contrast, species that leaf or bloom during periods of lower abiotic stress may have less sensitive climate cues but track strongly to other cues which allow them to map onto periods of low competition for soil or pollinator resources. Carefully testing these predictions, however, requires far more long-term tropical data than currently available, because phenological records are generally focused on temperate latitudes (black points, references given in Appendix S2).

may have greater power to predict phenology than single climate variables (e.g. temperature and precipitation) because they integrate many weather variables that influence phenology over seasons and interannual timescales (Beaubien & Freeland, 2000; Stenseth & Mysterud, 2005; Vicente-Serrano *et al*., 2006) and can capture abrupt shifts in climate (Cayan *et al*. 2001).

A major limitation of these climatological modeling approaches is their reliance on an underlying assumption of both temporal and spatial stationarity – i.e. phenological responses to climate that are stable and consistent through time and across space. Phenological models have largely relied on data from temperate mid-latitudes (Fig. 2) and on analyses from networks of cultivated and clonal species (Schwartz & Reiter, 2000; Menzel *et al*., 2006). However, phenology–climate relationships derived from these clonal studies may not scale easily to natural populations where species' sensitivities to climate can vary across individuals, sites, communities, and climate gradients (Olsson & Agren, 2002; Jentsch *et al*., 2009). Assessing the validity of the stationarity assumption will be critical for models to accurately predict ecological responses to climate change globally.

Climatologists have generally de-emphasized intra- and inter-specific variation in phenology, in part due to the lack of long-term, spatially distributed data for all but a few species. Such de-emphasis has advantages, allowing climate-focused studies to infer patterns across broad spatial and temporal scales, but with the implicit assumption that variation among and within species do not scale up in a meaningful way to affect ecosystem functions that influence climate processes. Where broad-scale climatological studies may fall short – by ignoring inter- and intra-specific differences – physiological research into phenology has excelled for a handful of model species. While a number of crop and lab model species have been studied (see Appendix S2), such as *Arabidopsis thalina* (Mouradov *et al*., 2002), enormous efforts are required to produce a model for a single species (Wilczek *et al*., 2009). Scaling up from lab and crop species to natural systems is currently impossible. Thus even with carefully mapped physiological pathways, a community context is still crucial to predicting phenology in natural communities.

Ecological research emphasizes how interspecific interactions and variation can drive phenology. In particular, phenology provides a mechanism by which co-occuring species can reduce competition by partitioning resources through time – the temporal niche (Gotelli & Graves, 1996) – hence the community context of phenology becomes important. This prediction is supported by work showing that a species' phenology may be sensitive to local community composition (Lack, 1982). Ecologists have typically regarded climate as a source of cues underlying phenological events upon which selection acts, for example, to maximize germination rates, match pollinators, or reduce resource competition (van Schaik *et al*., 1993). Because selection might act independently upon multiple life-history traits, phenology may be correlated with, or constrained by, a number of reproductive characters, including pollination mode (Rabinowitz *et al*., 1981), seed set and seed dispersal (Mazer, 1990; Oberrath & Böhning-Gaese, 2002; Bolmgren & Cowan, 2008).

In order to make significant progress from documenting change to predicting and forecasting phenology, researchers must draw on the strengths of ecological and climatological perspectives, while embracing new approaches that incorporate evolutionary change. Selection and adaptation are critical to understanding differential and non-stationary species responses to climate change (Hoffman & Sgrò, 2011), but a framework for mapping phenological variation across species and sites is first needed.

A multi-species approach: integrating phylogeny and traits into phenological research

Evolutionary trees and mapping phenological traits

An evolutionary perspective provides a multi-species approach for plant phenology research. Because physiological pathways and responses are likely to be evolutionary conserved (i.e. close relatives share similar traits), it is possible to generate predictive models using information on the evolutionary relationships among species – their phylogeny. Phylogeny may be an especially powerful approach for understanding phenology because it provides a simple method to integrate species differences across multiple traits, which may have complex underlying physiological pathways. Phylogenetic approaches can map both raw observational phenology data, such as flowering dates, as well as model estimates of how strongly species cue to different environmental variables such as temperature (Bolmgren & Cowan, 2008; Willis *et al*., 2008; Davis *et al*., 2010). In addition, because phylogeny allows us to infer the evolutionary dynamics of trait changes it can also help address questions regarding the underlying physiological pathways that determine phenology, as well as the ecological and evolutionary pressures that structure communities and drive variation in the timing of events. Importantly, by placing phenology within an historical evolutionary framework, we can also project forward to predict adaptive potential in response to future climate change (Hoffman & Sgrò, 2011).

The accuracy with which phylogeny predicts phenology can be assessed by evaluating the strength of evolutionary niche conservatism in phenological responses (as a proxy for the conservatism of the underlying traits that determine responses). While evolutionary niche conservatism is increasingly recognized as a pervasive phenomenon with broad ecological implications (Wiens *et al.*, 2010), there has been some debate as to its definition (Losos, 2008). For purposes here, we partition niche conservatism into two components: first, the strength of the covariance between the evolutionary distances between taxa and their difference in trait values, referred to as phylogenetic signal (Blomberg *et al.*, 2003). Second, an evolutionary rate component, describing the velocity of change along the branches of the evolutionary tree (Ackerly, 2009). Importantly, strength of phylogenetic signal for unconstrained traits (e.g. traits that have not yet approached the bounds of evolutionary limits) is independent from evolutionary rates (Revell *et al.*, 2008). Therefore phenology might map closely onto phylogeny (strong phylogenetic signal), so that evolutionary divergence is a good predictor of difference in phenology, but species differences may be large or small depending upon the evolutionary rate of change. Accurately tracing the evolution of phenology requires information on both signal and rates – to date, we have little information on either (but see Willis *et al.*, 2008).

Phylogenetic approaches also provide a means to test for temporal niche differentiation in communities. For example, if closely related species share similar phenological traits, then at local spatial scales species may partition themselves through time to reduce competition, producing a phylogenetically over-dispersed pattern (species less related than expected) (Webb, 2000; Cavender-Bares *et al.*, 2004). In contrast, at larger spatial scales, environmental filtering, defined as abiotic limitations on growth and/or establishment (van der Valk, 1981; Cavender-Bares *et al.* 2009), may produce communities of species that share similar traits related to environmental tolerance (e.g. traits that optimize phenology to the growing season) and therefore would produce under-dispersed assemblages (Webb *et al.*, 2002; Kraft *et al.*, 2007). Importantly, predictions are senstive to the mode of trait evolution, for example, phylogenetic community structure might be absent if phylogentic signal in phenology is weak or if phenological traits are evolutionarily convergent (Webb *et al.*, 2002). Therefore, it is critical to construct robust phylogenetic hypotheses of trait change.

While integrating phylogeny into phenological research provides important information on constraints and flexibility across species, studies using contemporary methods are uncommon and have only been conducted at the single community or sub-community level (Fig. 1). However such studies, might prove particularly powerful for detecting evolutionary trends because members of a community share a common environment, and hence experience the same suite of environmental cues. Currently, weight-of-evidence suggests that flowering time shows strong phylogenetic signal and is highly conserved within species. In the largest analysis to date, including data on >5000 species, Kochmer & Handel (1986) found strong congruence in flowering times for species shared between the floras of North Carolina and Japan. Evidence for evolutionary niche conservatism has been found in several species-rich floras, including the Cape of South Africa (Johnson, 1993) and some tropical forests (Wright & Calderon, 1995). In a recent study of one northern US plant community, Willis *et al.* (2008) found species' phenological sensitivities to spring temperatures and extinction risk were evolutionarily conserved. If such patterns generalize widely, phylogeny will be a useful tool for predicting species sensitivities in less well-studied communities. However, using a long-term record of UK flora, Davis *et al.* (2010) found evidence for phylogenetic signal in climate tracking only when some clades were excluded, indicating community context might be important. Further research across diverse systems is therefore vital.

Predictions across space and time

Synthesizing perspectives from ecology and evolutionary biology with climate science should advance research towards developing a framework for predicting phenological responses to climate. The predictive framework we present here is based on evolutionary relationships between coexisting species and exploring the temporal niche as a reflection of latitudinal variation in the growing season, the seasonal transition length and interannual variability. Our predictions of plant phenology consider fitness costs to mis-timing, and specifically we suggest that the relative importance of abiotic forces, such as environmental filtering, and biotic forces, especially niche-based processes (e.g. competition), will variably shape species and community phenologies across growing seasons and latitudes (Fig. 2).

Major drivers of plant phenology: abiotic vs. biotic drivers

Species are under continuous selective pressure to match their phenologies to favorable environmental conditions and positive biotic interactions to reduce fitness costs associated with mis-timing. Costs of mistimed phenology associated with abiotic drivers should be high (Schwartz *et al.*, 2006): blooming too early or late can lead to death or extensive tissue loss due to frost in temperate climates (Inouye, 2008) or drought in semi-arid systems. In contrast, costs associated with biotic drivers may be lower over short-time scales (Ollerton & Lack, 1992). For example, if a species flowers during the growing season but at the wrong period it may face increased competition for soil resources or reduced pollination, which may reduce growth and reproductive output. The relative strength and proportion of species within a community governed by these drivers should vary according to local environmental conditions and species' ecologies: in particular we suggest three metrics of climate variability may be important.

How growing season, seasonal transition length, and interannual variability may shape the phenologies of species and communities

Prediction 1: Early season species' phenologies should be more sensitive to abiotic forces, whereas mid-growing season species' phenologies should be governed by biotic forces. As growing season length increases towards the tropics the relative within-season weight of abiotic vs. biotic forces on plant phenology should decrease.

The growing season defines the window of time in which plant growth is possible, i.e. the fundamental temporal niche. While some tropical wet forests have year-round seasons (i.e. they are aseasonal), with arguably many temporal niches for species to occupy (Mittelbach *et al.*, 2007), most habitats, including many tropical forests, are seasonal. Therefore most species must time their growth carefully to capture optimal conditions of sufficient warmth, irradiance and soil moisture (Larcher, 2003), but also to minimize competition for limited resourses. In seasonal environments, phenology determines a species' ability to establish and persist within the local temporal niche (i.e. environmental filtering in relation to phenology, Fig. 3a). The phenology of a species relative to other members of the community should have important ramifications for species interactions, such as competition for resources (favoring temporal displacement) or facilitation via shared pollinators (favoring temporal convergence) (Fig. 3b).

The period within the growing season that a species occupies should additionally determine the relative strength of abiotic vs. biotic forces driving phenology and thus the types of cues used to time events (Fig. 2). The strength of abiotic forces often varies within a growing season: for example, there should be strong abiotic forces at the beginning of the growing season in temperate environments and the mid-growing season for environments characterized by mid-summer droughts because mis-timing has large fitness costs. For species with temporal niches occupying these portions of the growing season, the heavy costs of small mis-calculations should promote high sensitivity to climate (producing a flexible phenology) because the calendar day of these abiotic forces varies dynamically in most systems from year to year.

In contrast, species occupying other portions of the growing season may be less sensitive to climate and

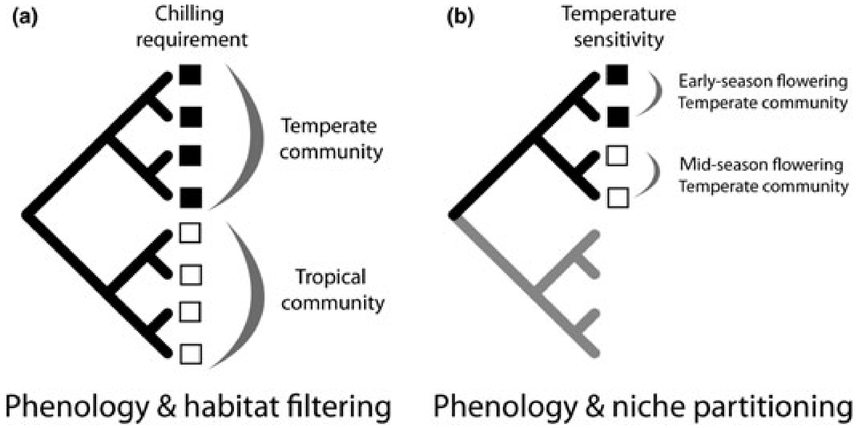

Fig. 3 Phylogenetic patterns within communities may reflect both broad scale environmental filtering (a) as well as local-scale partitioning of time in response to community context (b). For example, in temperate systems species filling the same general ecological niche (or guild) may sort into environments using common chilling requirements (e.g. a habitat filter, a), resulting in a phylogenetically clustered pattern if chilling requirements are phylogenetically conserved. However, at smaller spatial scales within a community (b), species may subdivide temporal niche space using more subtle environmental cues, such as varying temperature or precipitation triggers.

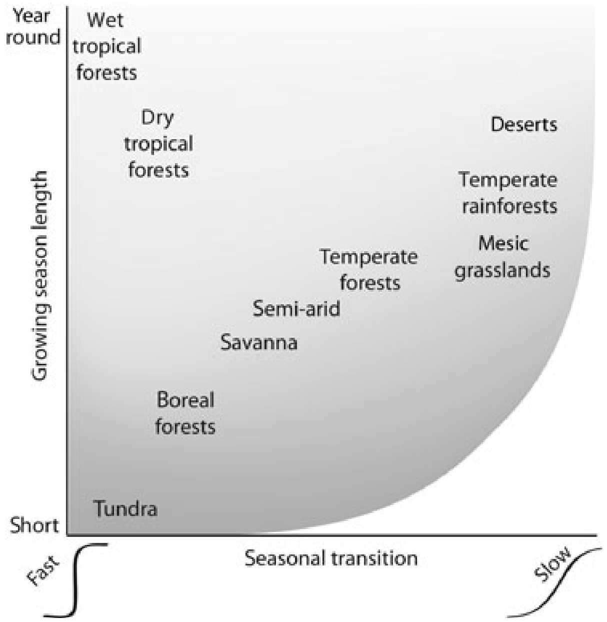

Fig. 4 The speed of transition into the growing season (x-axis) may fundamentally affect the phenologies of species within biomes. Species, especially those that are active during rapid transitions, should be most plastic with climate in areas with the shortest seasons (represented by darker shading, e.g. tundra).

could use more static cues such as photoperiod. For example, in many mesic temperate systems, early season species should attune to abiotic cues so as to prevent growth during the winter or very early spring. However, mid-growing season species should be governed by biotic forces, such as competition for resources (Morales *et al*., 2005), because potential for species phenological overlap is highest in the mid-season (i.e. mid-domain effect) and the risk of encountering adverse growing conditions is lowest. Thus, selection pressure for climate sensitivity may be low and static cues such as photoperiod might dominate (Calle *et al*., 2010), allowing for consistent partitioning of the temporal niche from year-to-year. Evidence that early season species are most sensitive to climate supports this hypothesis (Menzel *et al*., 2006), but there is little work that we are aware of testing how cues vary along a growing season (Ollerton & Lack, 1992) and no general predictions for which cues species may use to time their growth to reduce competition (further discussion below). We predict that as growing seasons lengthen towards the tropics the relative within-season weight of abiotic vs. biotic forces on plant phenology should decrease, such that in high latitude systems almost all species must be sensitive to climate to capture the shorter growing season, while in tropical systems the majority of species may use static cues (Fig. 2).

Prediction 2: Species phenologies occupying relatively long gradual seasonal transition periods should be sensitive to climate. Species timed to rapid transitions may be less sensitive to climate because of high competition.

For many environments the temporal niche space may additionally be defined by the seasonal transition length (the absolute time it takes for a system to transition into and out of its growing season). In most environments, the majority of the growing season is defined by a period of relative climatic stability when most species grow and flower. Some systems have extremely rapid, consistent transition periods such as tropical monsoon forests (Elliott *et al*., 2006; Williams *et al*., 2008), while many habitats have longer transitions, such as in most temperate biomes (Fig. 4). Fewer species often grow and flower during the transitional period in seasonal environments as compared to the mid-season (van Schaik *et al*., 1993; Morales *et al*., 2005), thus we predict that transitional species face lower competition for resources. Yet, these species should experience high costs if they mis-time their growth (in conditions too cold or dry for tissue growth). Thus species occupying gradual seasonal transition periods should cue to climate and flexibly shift their phenologies between years, even within biomes where the total growing season is long. In contrast, wet tropical biomes, especially monsoon systems, often have very short transitions, during which many species begin their growth and reproduction rapidly. In such systems cuing to photoperiod or other non-climate cues may be more advantageous to avoid competition (Elliott *et al*., 2006) and could result in low variation in early season timing. Across biomes, the intersection of growing season length (see Prediction 1) and the seasonal transition length may shape how plants respond to climate variation (Fig. 4).

Prediction 3: Species phenologies in environments with low interannual variability should respond more strongly to biotic forces, whereas species in environments experiencing high interannual variability should be more sensitive to abiotic forces.

Interannual variability in temperature or moisture should also affect the relative importance of abiotic vs. biotic drivers by influencing the optimal bet-hedging strategy, a strategy that describes plant responses in the face of environmental uncertainty (Fig. 5). In areas with long growing seasons and relatively low interannual variability, such as many low latitude regions (Fig. 6), costs associated with mis-timing are low and biotic forces are therefore expected to drive phenology. In systems with high interannual variability however,

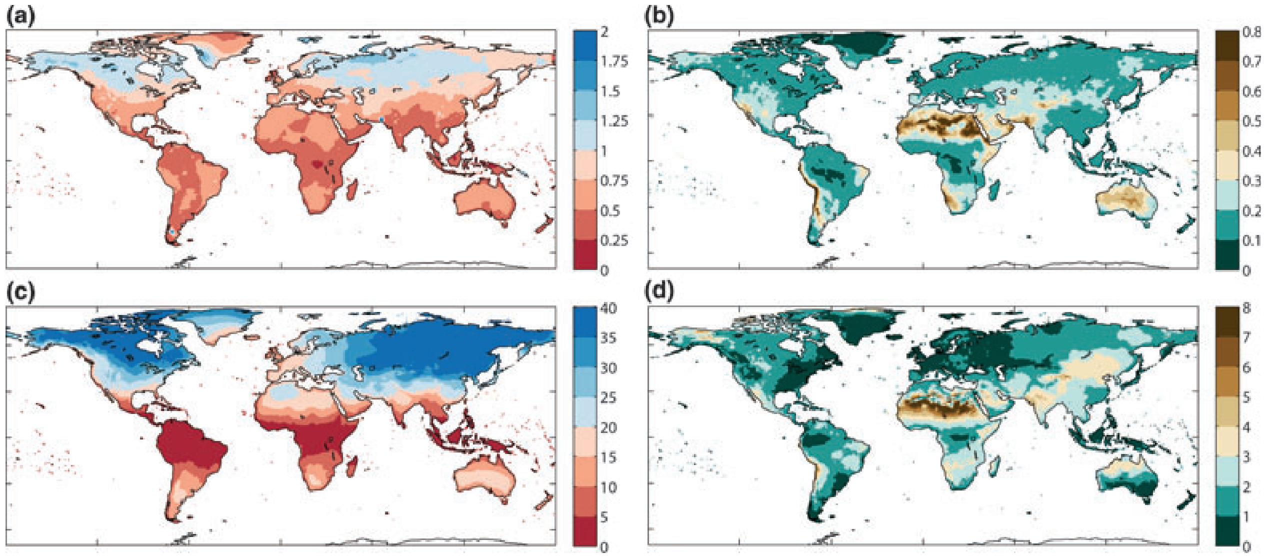

Fig. 5 Interannual variability in the mean temperature (a, standard deviation in °C) and precipitation (b, coefficient of variation – unitless) combined with seasonality of temperature (c, in °C) and precipitation (d, unitless) varies across the globe and should predict the strength of different phenological cues. Plant species in tropical regions of the Americas and some parts of Asia and Africa experience relatively low interannual variability and seasonality and thus may use distinctly different cues than species in regions of high seasonality and variability in rainfall (Mediterranean regions, parts of Asia and Australia). Across temperate and arctic regions – where the majority of phenology work has been conducted – high seasonality and variability in temperature dominates. This makes extrapolating from these regions to other areas of the globe, which have distinctly different patterns of interannual variability and seasonality, difficult. Note that seasonality scales inversely with growing season length, such that aseasonal systems have year-round growing seasons and highly seasonal habitats (in temperature or precipitation) have comparatively short seasons for plant growth and reproduction. Data sources and complete methods are given in Appendix S2.

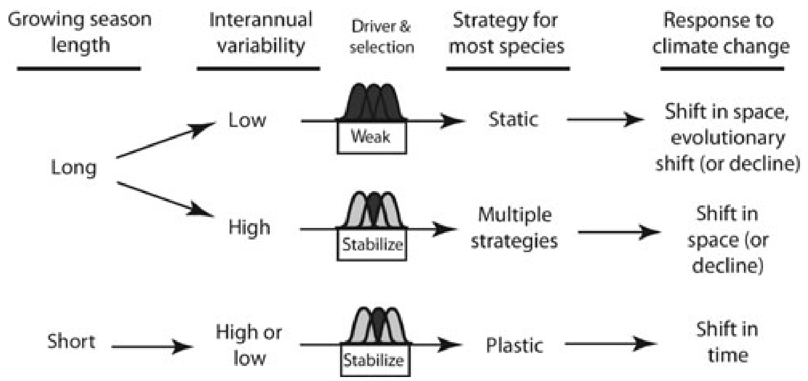

Fig. 6 Growing season length and interannual variability in climate may predict the most common phenological strategy for most species in a habitat. Abiotic forces (light shading) should restrict membership in a community to species with minimal cues, and thus where stabilizing selection should be strong. In contrast other environments may be dominantly governed by biotic forces (dark shading) and thus there would be comparatively weak selection on phenological cues.

climate sensitivity may be more important. Temperature and precipitation cues may then interact with or mask photoperiod cues to help species optimally time growth and reproduction. In such systems multiple strategies that vary with the frequency of life-history events may occur: species that bloom often (e.g. annually) would place consistent but smaller bets, while other species may bloom supra-annually, avoiding years of sub-optimal climate and expending high resources in optimal years (Venable, 2007). Such strategies appear to underlie many semi-arid systems (Venable, 2007) and monsoon tropical forests (Sakai, 2001), and should be further dependent on the generation time of species (Chesson, 2000). In addition, species placing larger bets to cue to optimal conditions that occur less frequently may rely upon multiple cues, whereas species placing smaller bets might converge on single cues that are only good predictors on average.

Variation in evolutionary rates in phenological traits

Prediction 4: Phenological traits responding to cues associated with temporal niche-partitioning, such as photoperiod, should exhibit faster evolutionary rates, whereas responses to temperature and precipitation should exhibit slower evolutionary rates.

Our framework, based on the three climate metrics described above, assumes variation in the costs of mis-timed phenology associated with different cues. A difference in costs associated with mis-timed phenology might translate into variation in evolutionary rates – the rate at which species' phenotypes diverge over time. Specifically, if photoperiod is associated with temporal niche partitioning to avoid competition for resources, the costs of mis-timing may be relatively low. We therefore predict greater evolutionary lability in plant responses to photoperiod cues, which may translate into faster evolutionary rates. In contrast, responses to temperature or precipitation cues might evolve slowly (Fig. 6) because they are associated with abiotic drivers of selection and thus likely under strong stabilizing selection (Levin, 2006). Where strategies are mixed, we predict responses to cues might also be mixed. For example, while we predict some lability around the timing of annual blooming species, responses to cues for supra-annual species should evolve slowly since blooming in sub-optimal years would impose high costs. To date there have been almost no studies exploring variation in evolutionary rates of traits associated with response to phenological cues (see Martin *et al*., 2009). Because responses should be apparent directly as variation in phenology, it should be possible to evaluate predictions with current data given reasonable estimates of phylogeny.

Predicting the cues and their conservatism across species and biomes has clear relevance to forecasting plant responses to climate change (Fig. 6). Species that track climate variables closely should be most able to adjust their phenologies with climate change and face minimal population changes (Visser, 2008). This suggests species in high latitudes (Fig. 5) should cope well with climate change. However, because we predict that such plasticity is under strong stabilizing selection there may be little genotypic variation underlying this plasticity. Thus, if climate shifts beyond conditions for which species are adapted and cues or cue sequences break down, rapid evolutionary shifts might not be possible. In contrast, species that occupy less variable habitats such as the aseasonal tropics may have little ability to track climate, and thus should instead shift their ranges or face population declines. However, if biotic forces structure species' phenologies in such communities (see Predictions 1–3), then they may also have high variation in phenology, suggesting that some species may be optimally timed for new climate regimes, but we risk losing species at both the trailing and leading edges of the climate window. Cues underlying tropical phenology have allowed most species in the past to remain extant by shifting their ranges in response to global shifts in photoperiod and climate associated with variations in the earth's orbit and tilt (Jansson & Dynesius, 2002). Research is needed, however, to test how species will respond to rapidly changing cues independent from photoperiod (Fig. 1), and to assess the risk that climate change might disrupt cascading cues (both biotic and abiotic).

Current opportunities in testing predictions

Testing these predictions certainly requires more field and lab-based studies. However, we can make large advances using current long-term records of species phenology by integrating frameworks from climatology and ecology. Ecological predictions may improve by matching organismal scales with climate variables (Fig. 1). While ecologists have used a wide variety of different climate variables and models (Diekmann, 1996; Post & Stenseth, 1999), recent work has often used monthly and annual means, which operate on human calendar scales, instead of on biological scales (Yang & Rudolf, 2010). With the increased availability of daily climate data (Peterson & Vose, 1997) future ecological research should use daily models that have clear ties to plants' circadian timescales (Dodd *et al*., 2005) and to how climate change has influenced daily minima and maxima disproportionately (Vose *et al*., 2005). In turn, climate science could benefit from greater focus on intra- and inter-specific variation, resulting in more accurate predictions of biological responses to climate change. For example Dynamic Global Vegetation Models as components of coupled climate-carbon models are being evolved to realistically represent biodiversity and competition among individual forest species, rather than assume some average forest phenology (Lichstein *et al*., 2010).

Clearly, more research is needed across tropical and semi-arid systems (Fig. 2), and across time at the middle and end of growing seasons. In addition, while we have focused here on photoperiod, precipitation and temperature, a number of other cues may modulate phenology, and these might be more important in non-temperate systems. For example, in some parts of the tropics phenology may be most sensitive to variation in solar insolation produced by changes in cloud cover and drought (Huete *et al.*, 2006; Asner & Alencar, 2010), or tree water potential, which is not always easily related to recent precipitation (Reich & Borchert, 1984). Our predictions also point toward the need for a far better understanding of which cues species use to partition themselves in temporal niches within a community. We have assumed that photoperiod may be important to temporal niche partitioning, because it should allow species to consistently partition the growing season between years, and because evidence suggests it is a dominant cue for species with lower abiotic stress (Calle *et al.*, 2010). Other research however, suggests species may use a variety of mechanisms (Borchert *et al.*, 2004; Calle *et al.*, 2010). Additionally, environmental cues underlying end of growing season phenology (e.g. leaf coloring, leaf abscission, etc.) are poorly understood (Menzel *et al.*, 2006), but appear to be less variable from year to year and less sensitive to temperature cues, especially when compared to start of growing season metrics (Barr *et al.*, 2004). Our poor understanding is especially disconcerting, given the importance of end of growing season timing for ecosystem functioning, including net ecosystem productivity (Angert *et al.*, 2005). Thus, even within the highly sampled temperate midlatitudes (Fig. 2), there are still large gaps in our understanding of phenology-climate connections.

Acknowledgements

This work was conducted as part of the Forecasting Phenology working group supported by the National Center for Ecological Analysis and Synthesis (NCEAS), a Center funded by NSF (Grant #EF-0553768), the University of California, Santa Barbara, and the State of California, and was supported by the USA National Phenology Network and its NSF RCN grant (IOS-0639794) and conducted while EMW was an NSF Postdoctoral Research Fellow in Biology (DBI-0905806), SP was an NCEAS postdoctoral associate and while NJBK was supported by the NSERC CREATE training program in biodiversity research. Please see Appendix S3 for author contributions. We thank A. Rogstad and J. Weltzin for assistance in reviewing cues across fields, H. Kharouba, S. Mazer, C. Parmesan, K. Gerst, and J. Morisette for comments on an earlier draft, and thank all members of the working group for discussion and perspectives across fields.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Literature review description and references.
Appendix S2. References and methods for Figs 2 and 5.
Appendix S3. Author contributions.