

Shifting plant phenology in response to global change

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Plants are finely tuned to the seasonality of their environment, and shifts in the timing of plant activity (i.e. phenology) provide some of the most compelling evidence that species and ecosystems are being influenced by global environmental change. Researchers across disciplines have observed shifting phenology at multiple scales, including earlier spring flowering in individual plants and an earlier spring green-up of the land surface revealed in satellite images. Experimental and modeling approaches have sought to identify the mechanisms causing these shifts, as well as to make predictions regarding the consequences. Here, we discuss recent advances in several fields that have enabled scaling between species responses to recent climatic changes and shifts in ecosystem productivity, with implications for global carbon cycling.

Introduction

Researchers have used numerous techniques to observe how phenology (see Glossary) has shifted in recent decades, including species-level observations [1–5], satellite remote-sensing of ecosystem production [6,7] and atmospheric monitoring of carbon dioxide (CO₂) concentrations as an indication of the timing of carbon uptake through photosynthesis [8,9]. Many of these studies have documented a correlation between earlier spring phenology and rising temperatures in recent years, but have found differing effects on the end of the growing season [10,11]. Global change experiments have also documented the influence of increasing temperature, shifting precipitation and other aspects of global change, such as rising CO₂ concentrations on the timing of species and ecosystem-level phenology [12–15]. Finally, recent advances in species-specific phenological models now enable researchers to scale from local to regional shifts in phenology [16], as well as to predict shifts in species ranges in response to changing environmental conditions [17], and use historical records of harvest dates to reconstruct past climate [18].

Here, we focus on the response of terrestrial plant phenology to global environmental changes, drawing on

recent advances across the disciplines that contribute to phenology research. Comparing the findings of multiple approaches is necessary to understand how phenology will shift in response to different aspects of global change, and to identify the processes that scale between species and ecosystem phenology.

Phenology and climate are intimately linked

Phenology is a dominant and often overlooked aspect of plant ecology, from the scale of individuals to whole ecosystems. The timing of the switch between vegetative and reproductive phases that occurs in concert with flowering is crucial to optimal seed set for individuals and populations [19]; variation among species in their phenology is an important mechanism for maintaining species coexistence in diverse plant communities, by reducing competition for pollinators and other resources [20]; the timing of growth onset and senescence also determine growing season length, thus driving annual carbon uptake in terrestrial ecosystems [21].

Global climate change could significantly alter plant phenology because temperature influences the timing of development, both alone and through interactions with other cues, such as photoperiod [19,22]. Thermometer records show that, over the past 30 years, global average surface temperatures increased by 0.2°C per decade [23]. In addition, numerous studies examining frost dates, growing

Glossary

Degree day: number of degrees above a particular temperature threshold that can be calculated by many methods and accumulated to provide a sum of (growing) degree days over a period; for example, using the simplest method, with a temperature threshold of 10 °C, the growing degree days over a three-day period with daily mean temperatures of 19 °C, 22 °C and 18 °C is 9 + 12 + 8 = 29 °C.

Phenoclimatic measures: indices of temperature that integrate over important time periods for plant growth and development; examples include degree days, number of frost-free days, as well as calculations of Spring Indices.

Phenology: the study of periodic events in the life cycles of animals or plants, as influenced by the environment (especially seasonal variations in temperature and precipitation).

Phenophase: a particular stage of development, such as bud burst, flowering, fruiting, leaf-out, or senescence (equivalent to phenological event used in some publications).

Photoperiod: the length of time that an organism is exposed to sunlight each day, generally equivalent to day length.

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season length, growing degree totals, or more complex indices, have found changes that are consistent with climate warming [24,25]. These phenoclimatic measures represent changes in temperature that are relevant for different phases of plant development. The Spring Indices (SI), a suite of such phenoclimatic measures, found that first leaf dates and last frost dates were 1.2 days and 1.5 per decade earlier, respectively, for Northern Hemisphere temperate land areas from 1955 to 2002 [26]. This acceleration of spring has led to a longer growing season, predominantly via warming of the coldest days in late winter and early spring as opposed to consistent warming throughout the year [27]. These phenoclimatic measures have important applications for agriculture [28], as well as for parameterizing leaf phenology in global climate models [29,30].

In tropical ecosystems, phenology might be less sensitive to temperature and photoperiod, and more tuned to seasonal shifts in precipitation [31–33]. Such shifts are expected to occur in concert with rising global temperatures, but both the direction and magnitude of change vary regionally [34]. For areas where precipitation patterns are strongly influenced by the El Niño-Southern Oscillation, the frequency and intensity of El Niño events are expected to increase, which has already begun to affect tropical forest phenology in Brazil [35].

Species-level phenology: observational networks

Phenological networks rely on volunteers to collect observations of various phenophases of wild plants, fruit trees and agricultural crops at numerous stations. The longest and best known phenological records come from the Far East and Europe, including a 5000-year record of phenological events, weather and farming activities in China (reviewed in Ref. [36]), the 1300+-year Kyoto cherry blossom time series [37], 670+ years of grape harvest dates in Central Europe [18], and the 200+-year Marham record of plant and avian phenology in the UK [2]. These long-term historical records can serve as proxies for temperature where thermometer data are unavailable. More recently, shifting phenology from the mid-20th century onwards is evident from numerous phenological observation networks in the Far East [38], North America [39] and Europe (reviewed in Ref. [1]). A meta-database (<http://www.pik-potsdam.de/~rachimow/eppn/html/frameok.html>) of existing networks shows that most observation networks are located in temperate ecosystems and that long-term phenological observations in the tropics are lacking (but see Refs in Ref. [32]).

Two recent meta-analyses of observational data have found that spring has advanced globally at a rate of 2.3 days per decade [3] and 5.1 days per decade [4], respectively. The second study excluded records exhibiting no trend. The most comprehensive analysis of observed trends in phenological data has been carried out for Europe. This study included >125 000 observational series of 542 plant and 19 animal species in 21 European countries (1971–2000) [1] and found a coherent signal of earlier spring (leaf unfolding and flowering) and summer (fruit ripening) of 2.5 and 2.4 days per decade, respectively. More than 75% of the species had accelerated phenology over this time period (the acceleration was statistically significant for one third

of the total species). Variation among species in their phenological trends has been attributed to pollination type, life form [40] and time of year. Early-season species exhibit the greatest acceleration [11,40,41], possibly because their phenology is cued by melting snowpack [42]. Interestingly, farmers' decisions about which crops to plant in a given year have resulted in the phenology of agricultural species changing less than those in the wild and, as a consequence, farmers' activities in Europe have only advanced by 0.4 days per decade [43].

The ground-observational signal of leaf coloring and leaf fall in autumn is more variable than is leaf unfolding in spring; some areas show acceleration whereas others show delay [10]; by contrast, remotely sensed and phenoclimatic measures consistently find that the onset of autumn has been delayed in recent years [6,7,24]. Ground-observation data averaged across continental Europe suggest a delayed autumn of 1.3 days per decade [1], whereas results for some regions within Europe show little change [11].

Analyses to detect temporal trends in phenology have traditionally relied on regressions or correlations between observed events and variables, such as year or temperature and, less frequently, have utilized time-series analysis. These traditional methods cannot detect abrupt phenological changes that can accompany rapid shifts in climate; however, new techniques based on change point analysis [44], and Bayesian techniques [45] enable a quantitative representation of non-linear phenological responses and associated rates of change.

Ecosystem- and global-scale phenology: remote sensing

Satellite observations are increasingly important for studies of phenological and ecological responses to environmental changes over space and time [46]. Although specific phenophases such as flowering and fruiting cannot be discerned in satellite images, their combination of comprehensive ground coverage and regularly repeated observations offer the opportunity for global phenological monitoring that is not possible with any other source. Several phenological metrics derived from satellite data are available, and represent different phenomena. The Normalized Difference Vegetation Index (NDVI) is a measure of greenness that is often used as a proxy for plant production, as is the Enhanced Vegetation Index (EVI), which improves discrimination of bare soil from vegetation over NDVI (e.g. Ref. [47]). The MODIS sensor provides a measure of Leaf Area Index (LAI) (e.g. Ref. [48]), similar to the fractional leaf cover calculated through spectral mixture analysis (SMA) of satellite reflectance data [49]. Despite their promise, interpretation of these metrics is still a challenge [50,51]. Two major issues have impeded progress in the development and application of satellite-derived phenological metrics [52,53]: atmospheric interference and a lack of biome-scale ground phenological data.

Surface reflectance in the visible and near-infrared portions of the electromagnetic spectrum are sensitive to plant growth and development, but can be partially or completely attenuated by atmospheric haze and clouds. Thus, although many satellite systems collect daily

reflectance information, the raw data must be processed through filtering to detect signal from noise. Filtering techniques vary, but all include compositing, smoothing, or screening, such that the processed data integrate over several days and mask rapid phenological changes occurring on the ground [53]. This has hampered progress in cloudy tropical areas in particular, although a re-examination of filtering techniques [35] and use of newly developed metrics [50] have enabled recent studies of variation in phenology and productivity of Brazilian tropical forests.

New approaches seek to overcome the limitations imposed by filtering. The pixels-above-threshold (PAT) technique abandons smoothing and individual pixel analyses in favor of an area-based probabilistic approach [54]. Satellite time-series data are now also being fitted to logistic (growth-simulating) curves, to replicate expected vegetation responses more closely [47,49]. New applications have also emerged, such as the quantification of urban–rural phenological differences [55], approaches to disaggregate satellite-derived phenology into temperature-driven components versus genetic variance within populations of widely studied species [56], and the development of phenoregions (areas of coherent phenological response that are essentially free from non-climatic forcing) to be used for global change detection [57].

The second major issue is a lack of biome-scale ground phenological data that could be effectively compared with satellite measurements using a common scale. Even where ground phenology data exist, they are usually point values from a single location, which are inappropriate for comparison to remote sensors that integrate across pixel areas 250 m² or larger [52,53]. Recent advances in remote-sensing technology that enable finer temporal and spatial resolution show promise in scaling phenological observations from local to regional scales. For instance, Fisher *et al.* [49] have shown that Landsat measures of spring leaf-out correlate well with photographs taken on the ground, and that small-scale topography resulting in cold-air drainages drives local variation in phenology (Figure 1). This study highlights the need to incorporate local processes when scaling up from ground-based to regional observations of phenology.

Implications for the global carbon cycle: atmospheric monitoring networks

A major goal of global change research is to understand whether plant responses to global changes will dampen or accelerate the current rise in atmospheric CO₂ concentrations ([CO₂]). Several sampling methodologies are used to monitor atmospheric [CO₂], including weekly flask

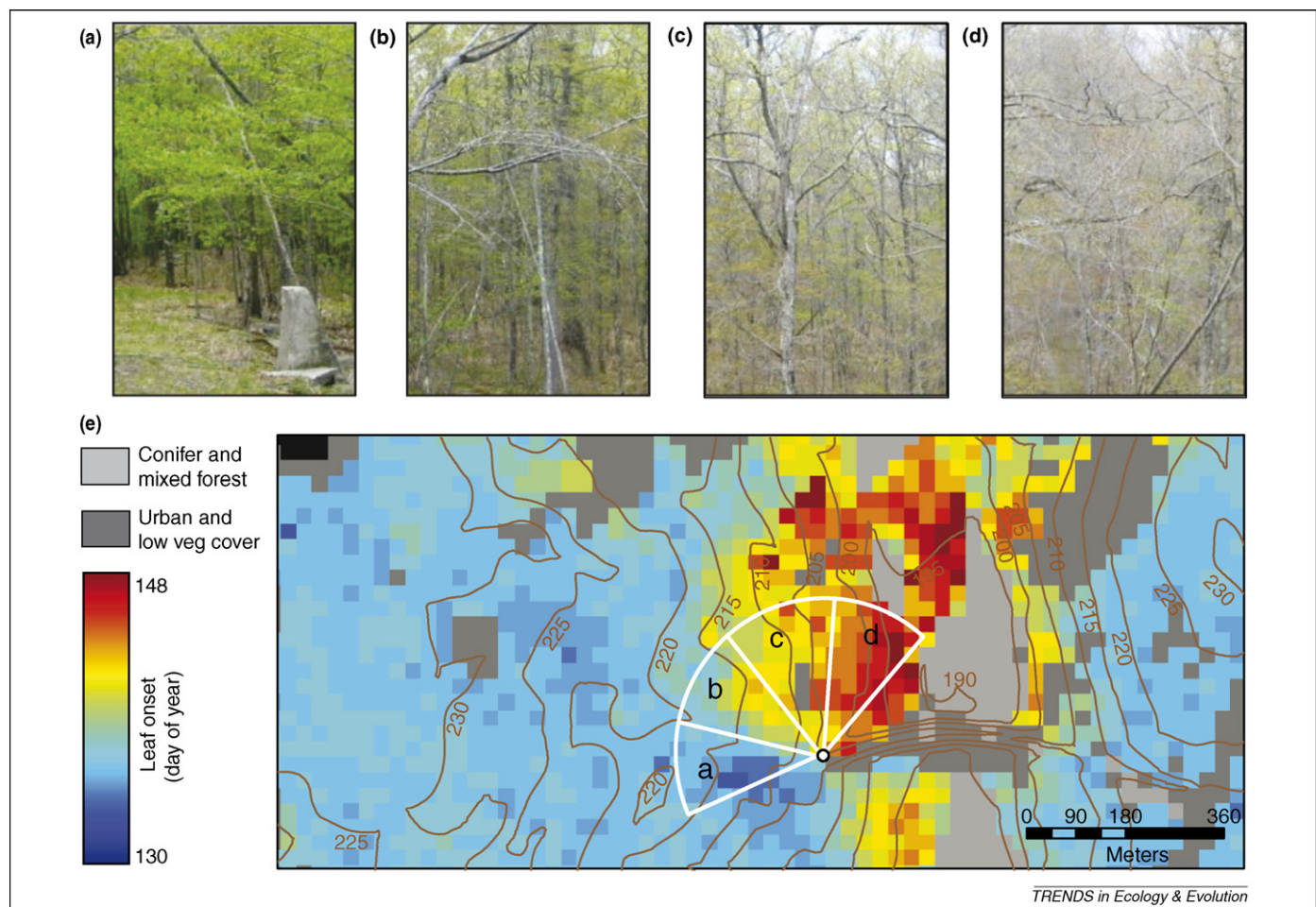


Figure 1. Linking ground-based and remotely sensed observations of spring leaf-out. Topography is closely tied to leaf-out observed from Landsat satellite imagery and in photographs taken on the ground in the Douglas Forest, Rhode Island USA. (a–d) were taken in four forest quadrants dominated by deciduous trees on 18 May 2005. The two-week difference in leaf-onset time among the quadrants is shown in the photographs and in the Landsat imagery (e), and is correlated with a microgradient created by cold-air drainage in low-lying areas. Redrawn with permission from Ref. [49].

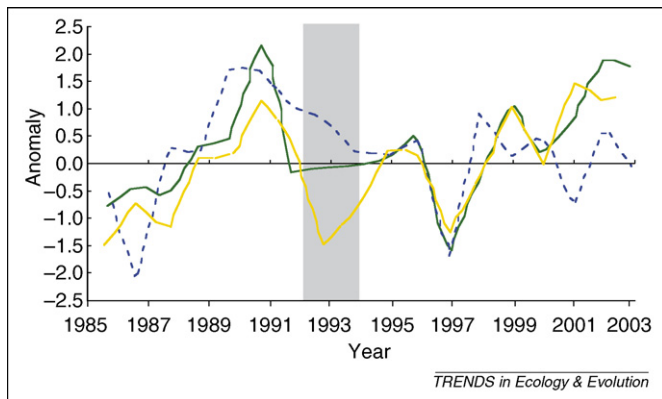


Figure 2. Interannual variation in spring and total growing season carbon uptake. The mean normalized anomalies in CO₂ uptake by Northern Hemisphere (>20° latitude) vegetation were calculated for 1985–2003; net spring uptake during June is shown in green, net growing season uptake from March to August is shown in blue and anomalies in average growing season temperatures are shown in orange. The grey area indicates the years influenced by the Mount Pinatubo eruption in 1991, which injected large amounts of aerosols into the stratosphere and decreased global temperatures. In the years before this volcanic event, temperatures and CO₂ uptake showed an increasing trend over time, both during spring and across the growing season. Since 1994, net growing season CO₂ uptake has not risen in concert with rising temperatures, possibly indicating that warmer, drier summers are dampening the expected increase in net ecosystem productivity that would result from an earlier onset of spring. Redrawn with permission from Ref. [59].

collection, discrete aircraft sampling transects and continuous eddy-covariance flux monitoring towers. The Cooperative Atmospheric Data Integration Project compiles and standardizes atmospheric CO₂ measurements taken at a network of locations around the globe, and also integrates across multiple sampling methodologies*. This high-quality global data set has led to several recent advances in our understanding of how vegetation phenology influences the global carbon balance.

Flask collections show that atmospheric [CO₂] oscillates on an annual cycle, dipping during the Northern Hemisphere summer, when the largest area of terrestrial vegetation is actively fixing carbon through photosynthesis. Along with the mean increase in atmospheric CO₂ concentrations in recent decades, the amplitude of the seasonal cycle has also significantly increased and shifted earlier [9]. In high latitude ecosystems, in particular, the advancement of spring and concurrent uptake of CO₂ is tightly linked to the timing of thaw, as a recent analysis combining atmospheric [CO₂] monitoring with satellite microwave remote sensing has shown [58]. Interannual variation in the onset and length of the growing season influences the magnitude of ecosystem primary production [8], but warmer, drier summers in recent years appear to be suppressing production, potentially offsetting the increase in terrestrial production that is expected with longer growing seasons (Figure 2 [59]).

Eddy-covariance flux towers continuously measure [CO₂] in upward- and downward-moving air components and the data can be used to separate carbon fluxes into uptake through growth and release through respiration [60]. The ability to collect fine temporal-scale data and separate flux components are advantages of eddy-flux

measurements over flask sampling. For instance, a synthesis of eddy-flux tower sites in Europe (EuroFlux) found that increases in production with warmer temperatures (consistent with longer growing seasons) tended to offset concurrent increases in soil respiration [61]. It remains to be seen whether the increased plant growth and carbon uptake associated with earlier and longer growing seasons will be offset by greater carbon losses through decomposition, either because of warmer overall temperatures or shorter winter seasons (reviewed in Ref. [62]).

Disentangling the influences of multiple global changes: experiments

To date, most observational studies have attributed the acceleration of spring events in recent decades to the warming trend over that same time period, but less attention has focused on the role of other co-occurring global changes, such as increasing atmospheric [CO₂] and shifts in precipitation. By controlling for variation in underlying environmental gradients and manipulating environmental factors separately, global change experiments can determine the relative influence of individual global changes on various components of the plant community.

Consistent with the findings of observational studies, experimental warming studies have documented an acceleration of growth and flowering [13,15,63], and have shown that early-spring flowering species are the most accelerated by warming [13]. Interestingly, species that are active later in the growing season can either be unresponsive [13] or even have delayed phenology [64], particularly if temperatures rise above their physiological tolerances.

In the future, shifts in precipitation are expected to occur in concert with increasing temperatures, but the direction and intensity of these shifts will vary regionally [34]. Despite the importance of water availability for plant growth, researchers have generally found no [12,65] or species-specific responses to rainfall manipulations [14]. For example, in the Mediterranean region, where conditions are expected to become warmer and drier over the next century, rainfall reduction experiments have found mixed results, sometimes delaying the onset of flowering and senescence [66].

The increase in atmospheric [CO₂] is a key driver of changes in temperature and precipitation, but could also alter phenology directly. Researchers investigating the responses of crop species to elevated CO₂ have found predominantly accelerated phenological development [67]. By contrast, few generalizations can be made regarding the responses of wild species to experimentally elevated CO₂; budburst was delayed in some trees [68,69] and annual grasses [12], flowering in nitrogen-fixing clover was accelerated [70] and development of other herbaceous dicots was either accelerated or delayed (reviewed in Ref. [12]); however, most studies have found no significant effects of elevated CO₂ on phenology (reviewed in Ref. [71]). However, crop species respond more to elevated CO₂ than do wild species for several other reproductive traits, such as flower number [72], perhaps because their growth is not limited by other resources, such as nutrients, water and light.

Temporal dispersion (or complementarity) in phenology is an important factor promoting co-existence among

* GLOBALVIEW-CO2 (2006) GLOBALVIEW-CO2: Cooperative Atmospheric Data Integration Project – Carbon Dioxide. CD-ROM, NOAA GMD, Boulder, Colorado [Also available via anonymous FTP to <ftp.cmdl.noaa.gov>, Path: <cgg/co2/GLOBALVIEW>].

species in plant communities [20]. Phenological complementarity can also influence ecosystem processes, such as nutrient capture and productivity [73]. Thus, asynchronous responses among species to environmental changes could lead to altered community structure or ecosystem processes; however, researchers seldom monitor the phenology of all species in a community, limiting research progress at the community scale. Two recent experiments show species-level shifts in phenology can alter community interactions. Cleland *et al.* [12] found that elevated CO₂ accelerated flowering in forbs but delayed it in grasses, which decreased phenological complementarity, and probably contributed to a decline in productivity by the later-active forbs. Sherry *et al.* [64] found that warming accelerated development in early-season species but delayed development in later-active species, resulting in an open phenological niche that could facilitate future invasions by non-native species.

From observation to prediction: modeling phenology

Predicting species phenology for the 21st century has become a major issue for several fundamental as well as applied scientific questions. Accurate phenology predictions would: (i) increase the accuracy of the predictions of ecosystems productivity and gas exchanges with the atmosphere and thereby the predictions of our future climate; (ii) enable a better understanding of population dynamics in multi-species interactions systems (especially between plants and animals); and (iii) help farmers and foresters select provenances or varieties that will be best adapted to the new climatic conditions.

The relationship between temperature or degree days and phenophases, especially flowering and leaf unfolding, is well known and has been widely reviewed [74]. The evidence for the role of the photoperiod in tree phenology is conflicting, depending on species and location [22,75]. Further experimental work on the impact of the interaction of photoperiod and temperature on leaf unfolding and flowering dates is required so that photoperiod can be used appropriately in phenological models. One recent model estimated the importance of temperature, photoperiod and water availability in predicting the phenology of NDVI, and found that the relative importance of these three factors varied both seasonally and regionally [30].

Three main types of phenological model have been used to predict the timing of particular phenophases: theoretical models, statistical models and process-based models (reviewed in Ref. [76]). Theoretical models are based on the cost–benefit tradeoff of producing leaves to optimize resource acquisition [77] and have been designed primarily to understand the evolution of leaf lifespan strategies in trees. Statistical models relate empirical observations of phenological events and climatic factors with various mathematical linear equations (reviewed in Refs [44,74]). Process-based models formally describe known or assumed cause–effect relationships between biological processes and driving environmental factors.

Traditionally, process-based models only consider what happens during quiescence, when dormancy has been broken and development and cell growth are triggered by external factors (usually temperature). Dormancy refers

to the physiological state during which development and cell growth are prevented by internal factors despite favorable external conditions. The Thermal Time model is a commonly used example of a model focused solely on quiescence [78,79]. More recently, experiments have shown that the phase of dormancy is important in plant development, and several phenological process models have been developed to incorporate dormancy (reviewed in Ref. [76]). These newer process-based models differ mainly in the type of response to temperature used during the phases of quiescence and dormancy, and in the relationships between these phases.

Recently, process-based and statistical plant phenology models have been used in the reconstruction of past climate variations using historical phenological series, such as grape harvest dates since 1370 [18,80]. Another important application of phenology models is in predicting species distribution with future climatic change [17]. As a major adaptive trait to climate, phenology determines the reproductive success of a population each year, the growth and the survival probability of individuals, and thereby the fitness and probability of occurrence of the species under particular climatic conditions (Figure 3).

Integrating multiple techniques for measuring phenological responses to global change

Efforts to scale from site-specific, species-level observations to predict regional phenological patterns are at the forefront of current phenological research. The POSITIVE project (Phenological Observations and Satellite Data: Trends in the Vegetation Cycle in Europe) used phenological models to make regional predictions of spring leaf-out based on ground-level observations of birch leaf unfolding, and compared these projections to satellite observations of spring green-up (Figure 4)[†]. Both methods found an acceleration of spring, but poor correlations for particular regions, highlighting the difficulty of scaling from species- to ecosystem-level phenology [52].

Several studies have sought to integrate remote sensing and atmospheric [CO₂] monitoring metrics of phenology. For instance, comparison of the timing of ecosystem production as measured by the satellite MODIS sensor versus ground-based eddy-covariance metrics from a network of North America sites (AmeriFlux), showed generally good correlations [81]. However, the MODIS data were averaged over an eight-day period (as are many products derived from satellite observations) and, hence, did not accurately capture spring leaf-out or the onset of other rapid phenological events captured by the eddy-covariance measures [81]. Eddy-covariance and remotely sensed data can also be utilized in simulation models; one such simulation study suggested that a five–ten day lengthening of the growing season could increase net primary production in forest ecosystems by as much as one third [82].

Future directions: challenges and opportunities

The approaches reviewed here each make important contributions to our understanding of how global changes

[†] Menzel, A., ed (2002) Final Report (Feb. 2000–June 2002) of the EU project POSITIVE (EVK2-CT-1999-0012). Technical University of Munich (<http://www.forst.tu-muenchen.de/EXT/LST/METEO/positive/>).

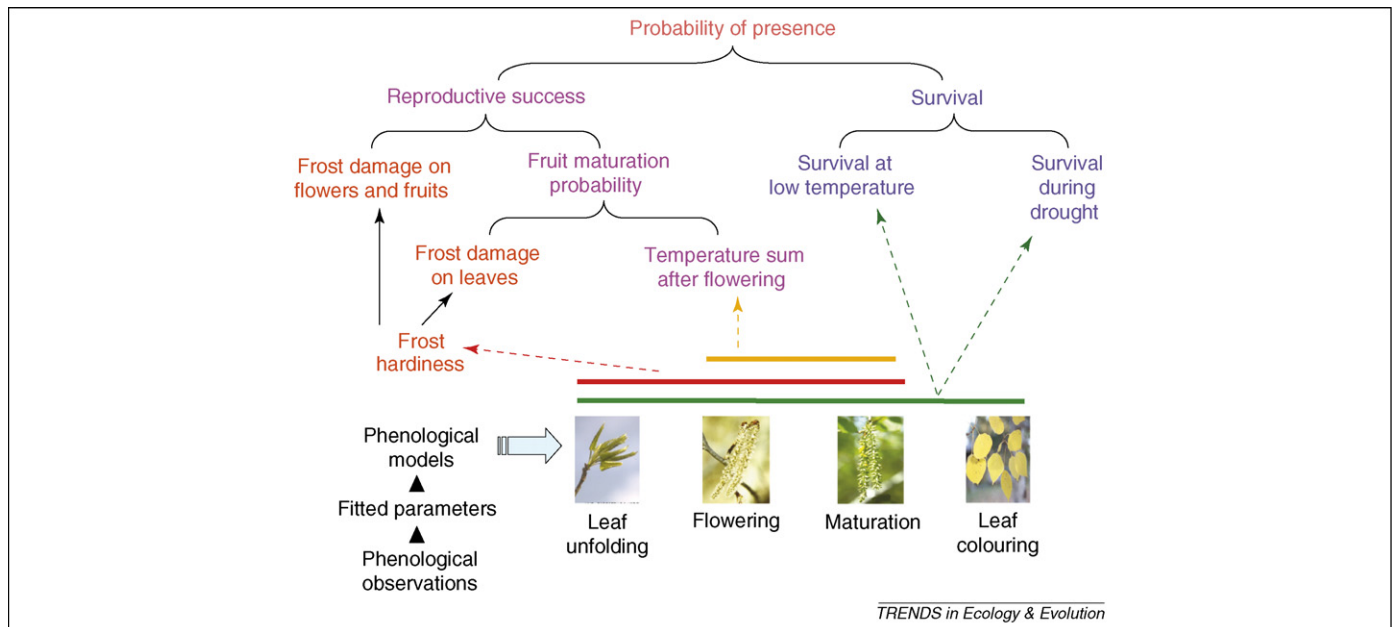


Figure 3. The PHENOFIT model used to predict changes in species ranges with future climate change scenarios. The likelihood of species presence depends on the predicted outcome of survival and reproduction, which are both influenced by species phenology. Dashed arrows represent the direct influence of phenology on some of the fitness components. Horizontal bars symbolize some key periods during which integrated abiotic conditions determine fitness components such as survival (green bar, the growing season from leaf onset to leaf senescence), reproductive success (red bar and yellow bar, the period during which fruit maturation can be compromised by frost damage on leaves, flowers or fruits; or by a lack of thermal energy necessary for fruit carbohydrate accumulation, respectively). The annual phenological cycle is simulated with process-based phenological models fitted on species-level observations using daily climatic conditions. Redrawn with permission from Ref. [17].

are altering terrestrial plant phenology, but each are suited to a particular scale (Table 1). A challenge lies in synthesizing across these different scales of inference to make predictions about future global change impacts. For instance,

how often do observations of species-level phenology scale up to predict the timing and magnitude of ecosystem-level fluxes of carbon, water or nutrients? Eddy-covariance flux sites, in particular, provide an untapped opportunity to link ecosystem function with species-level phenology. The few attempts to link ground-based and satellite-derived observations have often yielded poor correlations, probably because the unit of measurement in remotely sensed images encompasses many individuals and species, which can vary in their phenology [52].

In addition to shifting phenology, species have begun to adapt to recent climatic changes via altered species ranges [83]. It will be important to address whether the combination of physiological shifts within species and range shifts among species will alter community-level patterns of phenology. Species within communities are often remarkably varied in their phenology, and we are just beginning to understand how potential shifts in phenological complementarity might feedback to influence ecosystem structure and function. Aerobiology, or the study of pollen composition, is a promising new approach for studying the phenology of whole communities, although it is taxonomically limited in scope (dominated by trees) and resolution (identified at the genus or family level), and there is uncertainty around the degree of long-distance pollen transport [16,84].

Shifts in the synchrony of plant–animal interactions could also negatively impact particular plant populations, and re-order communities. The best studies of disrupted synchrony involve trophic interactions (reviewed in Ref. [83]). For instance, in some migrating birds, the timing of egg hatching has become asynchronous with the availability of insects that are an essential food source for hatchlings (reviewed in Ref. [85]) and, in marine ecosystems, the timing

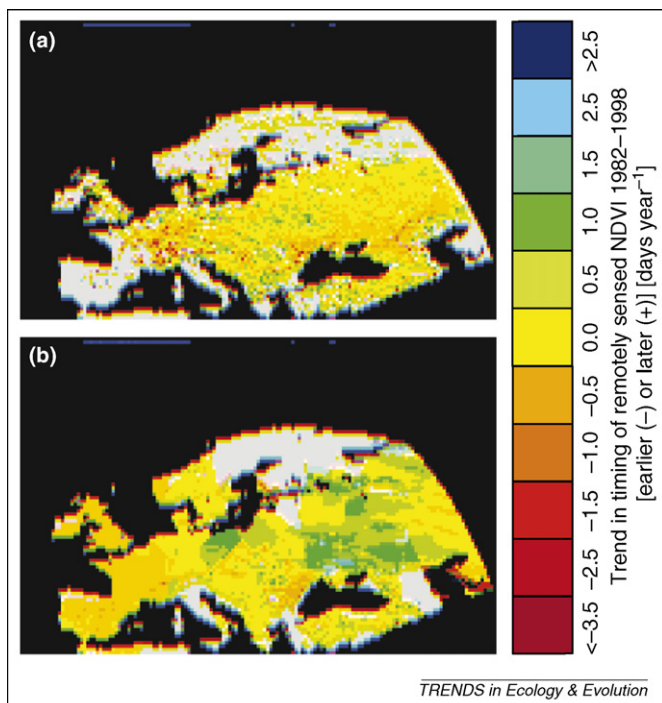

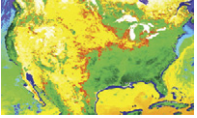




Figure 4. Changes in the start of spring in Europe. The POSITIVE project compared linear trends [days year⁻¹] over the period 1982–1998 in the timing of remotely sensed NDVI, a measure of greenness, based on yearly crossings of 50% of the annual amplitude (a) with birch leaf-out (b), simulated with a process-based phenological model parameterized with species-level observations. Although there is a generally good correlation between NDVI (a) and modeled leaf-out (b), there was poor agreement in some regions, highlighting the difficulty of scaling between methodologies. Redrawn with permission from A. Menzel[†].

Table 1. The utility, limitations and temporal and spatial resolution of methods used to investigate the influence of global change on terrestrial plant and ecosystem phenology

Approach ^a	Utility	Limitations	Temporal and spatial scale	Refs
(i) Species-level observation networks 	Various phenological stages of different plant species at numerous sites are observed	Data quality and availability depends on observational effort and labor of human observers	A few long-term records begin during the 8th century; national networks in Europe in existence since the 19th century and in North America and Far Asia since the mid-20th century	[1–5,10,11, 36–41]
(ii) Remote sensing 	Collects data on spectral reflectance for locations worldwide	Older satellites collect data on large grid cells; newer satellites have limited time-series data; cloudy areas have patchy temporal resolution	First Landsat satellite launched in 1972; newer satellites that collect images with higher spatial resolution have been steadily developed	[6,7,24,35, 46–57]
(iii) Eddy-covariance monitoring of carbon fluxes 	Measures carbon and other biogeochemical fluxes in and out of vegetation and soils	Data are site specific and expensive to collect; they do not relate directly to species-level observations	Developed during the 1980s; now, an international network of >200 towers collects information for a footprint of 1–100 km ² at each location*	[60,61,81]
(iv) Phenology modeling y such as $S_f(y) = \sum_{t_1}^y R_f(x_t) = F^*,$ $F^* = ae^{bSc} \text{ with}$ $Sc = \sum_{t_0}^{t_1} R_c[x_t],$ $R_f(x_t) = \begin{cases} 0 & x_t \leq 0 \\ \frac{28.4}{1 + e^{-0.185(xt-18.4)}} & x_t > 0 \end{cases}$	Scales past, present and future phenology of species or ecosystems across space and time	Models represent a limited number of physiological processes; numerous phenological data are required to fit their parameters	Models can accommodate multiple temporal and spatial timescales and are the only method that can project into the future or reconstruct the past when actual phenology data are lacking	[16–18,30, 44,74,76–80]
(v) Global change experiments 	Intensive observation of many species in response to controlled environmental changes enables mechanistic investigations	Results are limited to the location and species present; experiments vary in their methods and few incorporate multiple aspects of global change	Plot sizes are usually small (1–10 m ²) and experiments seldom run for more than ten years	[12–15,42, 63–72]

*Photographs highlight: (i) flowering of individual species monitored by observers (reproduced with permission from M.D.S.); (ii) MODIS satellite image of NDVI; (iii) an AmeriFlux eddy-covariance flux tower at the University of Michigan Biological Station (reproduced with permission from Alan Hogg); (iv) Equations from the PHENOFIT model [17]; and (v) an experimental plot in the Jasper Ridge Global Change Experiment [12] (reproduced with permission from Nona Chiariello).

of phytoplankton availability has cascaded up the food chain to impact fish predators [86]. These observations have been largely attributed to rising temperatures over the same time period, but a review of experimental studies shows that elevated CO₂ can also change the phenology of plants and insect herbivores in opposing directions [87]. The study of synchrony between plant and animal mutualists is an area of much needed research. For instance, if pollinators were cued to temperature and plants to photoperiod, this could lead to asynchrony in pollinator mutualisms.

In areas that lack long-term ground-based phenological observations, robust phenological models could be used to simulate past, present and future species phenology over wide areas, and these predictions could be compared with remotely sensed data (e.g. Figure 1). It would be particularly desirable to advance the ability of phenological models to predict leaf senescence, which is not yet possible [10]. End-of-season senescence is more variable than springtime phenology [41], and has enormous potential to influence the carbon balance via influences on growing season length. Furthermore, despite a long history of research into the physiological pathways that underlie

plant phenology (e.g. Ref. [19]), we are still learning how multiple environmental influences interact with endogenous cues to predict events such as flowering [88]. By incorporating newly understood physiological pathways, phenological models could be used to explain why we find consistent phenological advances in response to warming, but widely varied responses to other global changes, such as elevated CO₂ and altered precipitation regimes.

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