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Phenology

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Phenology is the study of the seasonal timing of events in nature: when flowers bloom, trees leaf out, birds migrate, animals hibernate, fish spawn, phytoplankton blooms, lakes freeze and the like. Phenology is not concerned with events such as the solstices and equinoxes that are determined by astrophysical laws -- these vary only slowly and predictably over millennia. Events that are influenced by climatic factors on the other hand are far more variable and less predictable from year to year. Organisms able to survive in a given climate must respond effectively to the vagaries of day to day weather during the seasonal cycle. The advance of spring-warming is an expected and normal part of high-latitude climates, but no one expects the end of winter to begin on a particular date year after year or to follow a specific sequence of ever-warmer days until summer arrives. Phenological records thus can provide an integrative index of weather through the seasons, a capability that is becoming increasingly valuable in gauging trends indicative of changing climate.

Long before scientific interest in phenology arose in the 19th Century, people had paid close attention to the seasonal timing of natural events. Some phenological events associated with cultural and religious festivals have been recorded for a very long time; annual records for the flowering of cherry trees in Kyoto, Japan date back to the 9th century. Before weather records and weather forecasting existed, the everyday lives of people depended on closely observing the timing of natural events. The return of migratory birds or the leafing of a particular species of forest tree could provide a reliable signal of when best to plant a frost-sensitive crop. "Calendars of the seasons" collating this sort of folk knowledge began to appear in the 18th century and at about the same time, individuals and governments began to formally observe and record phenological events. The Marsham family recorded daily phenological observations at their estate in Norfolk, England from 1736 through 1925! Many, shorter series of phenological records are available, especially for sites in the north temperate zone.

The scientific study of phenology initially focussed on the relationship between weather and the timing of events. Can we predict the timing of events from our knowledge of the response of an organism to a progression of weather conditions? Yes, to a considerable degree we can, usually with an accuracy of a few days. For example it is possible to predict the timing of leafing out or flowering in most trees within 2-5 days from place to place and year to year. We also have some understanding of the reasons why different species in the same locality do not all have exactly the same phenology. Because of differences in functional organization conserved in evolution, each species at a locality responds to changing climatic conditions somewhat distinctly.

More recently, the scientific study of phenology has shifted to questions of how phenology will be affected by global change, and what consequences any changes may have for species distribution and ecosystem function. An important impetus to this shift was the recent discovery that modest changes in the length of the season when plants are actively photosynthesizing can significantly *alter the storage of carbon. A forest at high latitudes can be a net sink or a net source of atmospheric carbon dioxide by virtue of a week more or less in the length of the growing season. In other words, there are feedbacks between phenology and factors affecting the global carbon balance that may act to accelerate or decelerate rates of climate change. The study of phenology therefore has taken on new urgency and scientific significance as we struggle to understand the nature and consequences of climate change.*

Brief history of phenology

The modern roots of phenology as a science are in the careful observations of naturalists in the 18th and 19th centuries, Gilbert White and Henry David Thoreau being perhaps the best known among them. In these times in fact many people engaged in regular observation of phenological events. The daily records of the Marsham family, noting the seasonal activity of birds and plants in central England (Sparks and Carey 1995), span the period between 1736 and 1925. Thomas Mikesell, a farmer in Ohio, made meticulous, twice-daily records of weather and phenology between 1883 and 1912 (Lechowicz 1995). Fairly many long-term data sets of this sort exist, usually for only single localities. Naturalists have continued a tradition of phenological observation into this century (Fitter et al 1995; Bradley et al 1999), and their efforts have been augmented by the collection of phenological data in various scientific and government networks with greater spatial coverage (Ahas 1999; Bruns 1996). For example, the Royal Meteorological Society (UK) published phenology data regularly for at least 75 years, terminating about 1945.

Factors affecting phenology

The precise timing of events in the natural cycle of the seasons often determines the success or failure of individual plants or animals. Many migratory birds must lay eggs in advance of the availability of ample food for their young, but neither so early that hatchlings want for caterpillars nor so late that the young are not ready to migrate in advance of winter. Deciduous trees burst bud only when the risk of late frost is low, but not so long into summer that their annual period of photosynthetic activity is much diminished. In the seasonal tropics, many trees flower during the dry season with their fruits maturing in time for seedlings to establish themselves with the onset of the rains. In all these instances, the timing of phenological events must respond to environmental cues that presage future conditions, usually with allowance for the costs and benefits of alternative timing of an event. An exception is in events such as blooms of oceanic phytoplankton, which have very short life cycles and simply respond rapidly to periods of high irradiance in less cloudy weather when water temperatures are adequate (Townsend et al 1994).

Although the diversity and complexity of phenological responses are impressively great, the environmental cues on which phenological events depend are relatively few. Phenological cues fall into two basic classes: photoperiodic and climatic. Temperature influences predominate among the climatic cues, although precipitation and irradiance regimes sometimes also play a role. The photoperiodic and climatic signals differ in their nature and in their utility for gauging environmental conditions later in the annual cycle.

Photoperiod, the length of the day relative to the night, changes at different latitudes in a very predictable cycle through the year. The tilt of the Earth's axis of rotation and its orbital path around the sun determine the seasonal progression of photoperiod. As a consequence photoperiodic cues in a locality are essentially invariant from year to year. Daylength will begin to increase after the winter solstice, reaching 12 hours on the vernal equinox and getting steadily longer until the summer solstice; then the cycle reverses with shortening days until the winter solstice passing through a 12 hour day on the autumnal equinox. The annual amplitude of variation in photoperiod does vary from place to place, being near zero in equatorial regions and increasingly greater toward the poles. Organisms in a given locality thus can use photoperiod to reliably gauge the time of year.

The problem with photoperiod alone as a phenological cue is that climate is nowhere entirely predictable within or among years. Just knowing the time of the year is insufficient to evaluate the likely environmental conditions in the weeks or months ahead. Lengthening days can cue the onset of spring, but not whether the spring will advance quickly or slowly, or be especially warm or cool. Organisms thus use temperature, and sometimes water, regimes to better estimate the progression of seasons in a given year and locality. These climatic signals are useful cues for phenological events, but also not entirely reliable. Changes in atmospheric circulation may indeed bring an earlier than usual onset to spring-warming, but not necessarily preclude a late freeze. Nonetheless, there is enough coherence in weather over weeks and months in a given year that recent events can help anticipate future conditions.

Many organisms outside the tropics seem to depend on short-term (2-12 week) temperature trends as the most reliable aspect of climate for assessing seasonal changes and triggering phenological responses. Phenological events in spring, for example, often can be predicted from heat sums, which are a measure of the accumulation of warmth above a base temperature. Phenological events occur when a certain heat sum is attained. Thermal summation may begin after some requisite degree of chilling obtains, or when a photoperiodic cue is satisfied. In some instances the heat sum required to trigger the event is contingent on the degree of prior chilling or the length of the photoperiod. For example, longer chilling of trees can reduce the heat sum required for flowering. Similarly, some oak trees will leaf out at a lower heat sum as the days become longer. Photoperiod becomes a more dominant cue later in the season but some influence of warming or chilling trends persists. The formation of flower buds is often set by quite precise photoperiodic signals, but flowering itself depends on the temperature regime (Fitter et al 1995). Similarly, egg-laying by birds is set by a combination of photoperiodic and climatic cues, including indirect effects of temperature regime on the availability of insects to feed hatchlings (Visser et al 1998). The physiological means by which organisms actually monitor and respond to these sorts of direct and indirect influences of chilling, warming and photoperiod are poorly known. We can use photoperiod and weather data to predict phenological events, but without any sure understanding of underlying mechanisms (Hunter and Lechowicz 1992; Chuine et al 1999).

In tropical regions seasonal variations in photoperiod and temperature are less marked than at higher latitudes, but precipitation can be strongly seasonal in some regions (Corlett and LaFrankie 1998). Although most tropical trees have consistent and fairly well-defined flowering times during the year, the environmental cues that trigger flowering are not well known. Some trees flower and fruit when there is a recharge of tissue water either through the onset of rains or when the dropping of leaves in the dry season places less transpirational demand on the tree, but this is not a universal phenomenon (Wright and Calderon 1995). Flowering and fruiting typically occur throughout the year on one species or another in tropical ecosystems, with the adaptive value of timing of flowering for each species obscure. The phenology of tropical species is too little studied to support broad generalizations (Corlett and LaFrankie 1998).

Phenological variation within communities

Species of generally similar organisms in a locality do not usually share exactly the same phenology. This is because phenology is only one element in each species suite of adaptations to the local environment. Take as an example, the warm- versus cool-season grasses that co-occur throughout the North American Great Plains (White et al 1997). The cool-season grasses are green and actively growing in the cool and moist weather of fall and spring, but brown and dormant in summer. The warm-season grasses conversely only begin greening up in later spring and are actively growing during the warm, dry summer months. The warm-season grasses have C_4 photosynthetic metabolism well-suited to warm, dry conditions but sensitive to chilling. The cool-season grasses have C_3 photosynthetic metabolism well-suited to cool, moist conditions but sensitive to drought. The contrasting phenology of the warm- and cool-season grasses is part of an integrated suite of traits that defines their functional ecology. There are, of course, also phenological differences among species within each functional group, but these are relatively minor variations within the basic dichotomy. The two groups of grasses together lengthen the effective period for photosynthetic production in the prairie ecosystem.

The phenological differences among co-occurring species sometimes can become more diverse and less easy to characterize by simple dichotomies. Consider, for example, the situation in a mixed-wood at mid-latitudes where two functional groups of trees share dominance in the community. Deciduous species are leafless over winter, with individual leaves having longevity measured in months. Evergreen species keep leaves over the winter, with individual leaves having longevity measured in years. The two groups are apparently well-defined by the sharp distinction in their overwintering leaf habit, but in fact they fall along a continuum of variation in leaf longevity that organizes their production ecology (Reich et al 1997). Evergreen and deciduous species overlap in their timing of production of new leaves in spring and early summer, both within and between the two apparent functional groups. Such differences in foliar phenology among co-occurring tree species are linked to evolutionary and paleo-ecological as well as functional considerations unique to each individual species (Lechowicz 1984). This individualistic nature of species phenology complicates the analysis of the impact of changing climate on community composition and ecosystem function. As climate shifts, we can expect that relationships among species differing in phenology may also shift, both in terms of competitive and trophic interactions (Harrington et al 1999).

Predicting the effects of changing phenology

We can imagine three basic responses of species to a reasonably gradual climate change. First, species may migrate to remain in climatic regimes to which they are phenologically well adapted. There is good evidence that such migrations have occurred during deglaciation. As glaciers retreat and climatic zonation shifts to higher latitudes, the formerly glaciated landscape has been colonized by species better suited to north temperate, boreal and arctic regions that have migrated from glacial refugia now subject to increasingly warm and less strongly seasonal climates. Second, species subject to a changing climate may not migrate to track their favored climatic regime, but rather stay in place and adjust to changing conditions. In terms of phenology, there is always a certain degree of variation among individuals within populations in their responses to environmental cues for seasonality. From an evolutionary point of view, we expect the maintenance of such variability among individuals as a form of bet-hedging against normal patterns of year to year climatic variability. We therefore can expect the average timing of a phenological event in a particular species to track climate change provided the ongoing changes do not exceed the previous range of climatic variability. A simple shift in the balance of phenologically early or late individuals in a population can then accommodate the shift in climate; over sufficient time the shifting advantage of different phenological variants within the population may affect a genetically determined adaptive shift in the phenology of the species. Finally, species may simply fail to accommodate effectively to changing climate, perhaps becoming much less dominant in a locality or even going locally extinct. It is difficult to know with any certainty what effects these diverse changes at the species-level may have at the community and ecosystem levels.

Recent shifts in phenology associated with changing climate

Since phenology is so closely linked to weather conditions, trends in phenology may serve as natural indicators of an ongoing climate change. Where we have suitable records over reasonably long periods of time, we can directly evaluate the degree to which recent climatic trends have influenced phenological events. Various phenological observations do suggest a climatic warming trend in recent decades in some parts of the world. This is the case for leafing of trees, timing of flowering, and egg-laying by birds, and spring migration by both birds and butterflies. Modelling (White et al 1999), ground (Menzel and Fabian 1999) and satellite observations (Myeni et al 1997) all support a recent increase of about 8-10 days in the period when mid-latitude forests of Europe and North America are in leaf. This lengthening of the growing season results primarily from earlier springs, but also a later onset of winter. The increasing earliness of spring has also been manifest in advances in the leafing and flowering of many individual plant species (Fitter et al 1995; Sparks and Carey 1995; Bradley et al 1999). Egg-laying in 36 species of birds in the United Kingdom has become earlier in recent decades (Crick and Sparks 1999) as has the spring arrival of migrant species (Sparks and Carey 1995; Sparks 1999). These results suggest that recent climate warming may be having widespread impact on the phenology of many species, which can potentially alter biotic interactions at the community and ecosystem levels. While there are some observable changes in ecosystem function (Myeni et al 1997; Menzel and Fabian 1999) and some butterfly species have shifted their ranges poleward (Parmesan et al 1999), there is no evidence at this time that global systems are being disrupted by widespread species migration or extinction associated with climate change. The real question is whether or not climate change has begun that in time will lead to such reorganization of biota and major shifts in global ecosystems.

Predicting long-term phenological responses to climate change

Climate may change in two respects, quantitatively in its regional expression or qualitatively in its basic seasonal structure. Each has quite different potential consequences for species and ecosystems. A quantitative shift in local climate, provided it is neither too rapid nor too great, may have only negligible influence on species distribution and ecosystem function. Species may simply respond to their usual cues, perhaps prospering by a longer growing season or shifting their range to track their preferred climatic regime. It is unlikely that modest quantitative shifts in climate will dramatically alter community composition or ecosystem function. This sort of modest quantitative change seems to characterize our present situation. On the other hand, qualitative shifts in the nature of the seasonal cycle have greater potential to disrupt phenological responses in a community in ways that more rapidly disrupt ecosystem function. If the basic nature or stability of the seasonal cycle is altered by climate change, then cues evolved in an earlier climatic regime may no longer lead to effective phenological responses. Or even should the cues remain consistent with evolved phenological responses, any increase in the variance of climatic regimes poses a serious risk. Extreme events such as an early winter storm can extirpate populations adapted to a reliable progression of fall weather. There is evidence that global patterns of seasonality are reasonably stable from year to year, at least at the coarse temporal resolution afforded by satellite data (Potter and Brooks 1998). We do not know whether more precise data would reveal trends in seasonality with adverse implication for the adaptive value of contemporary phenological responses. The greatest challenge of global change to contemporary biological systems may not be a gradual shift in average climate over time, but rather the possibility of qualitative shifts in the nature and stability of seasonality.

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