

Climate Change: Flowering Time May Be Shifting in Surprising Ways

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A new study examined how flowering phenology has changed over the past three decades along an elevational gradient. These findings indicate that climate change is shifting flowering time in complex ways, even across local spatial gradients.

The timing of seasonal biological events, such as the first flowers appearing across the landscape in spring, have fascinated scientists and non-scientists alike for generations. The study of these cyclical events in the natural world is called phenology. Shifting phenological patterns are some of the most easily observable and well-documented biological responses to climate change [1–3]. Phenological responses to changes in climate have been studied extensively in temperate ecosystems, where biological processes are primarily limited by cold temperatures (e.g., [4,5]). However, phenological changes in drier ecosystems that are primarily limited by water have received relatively less attention [6,7]. Additionally, there have been a number of meta-analyses examining phenological responses to climate change at the global scale (e.g., [5,8,9]), but there is less information on how phenology is changing across local environmental gradients over long time scales. In a new study in this issue of *Current Biology*, Rafferty *et al.* address these gaps in knowledge by examining how flowering observations of hundreds of plant species along an elevational gradient in a dry ecosystem in the southwestern USA have changed over the last 33 years [10].

In this study, the authors analyze flowering observations of 590 species of plants in five communities along an elevational gradient to see if flowering is shifting in the same ways in the plant communities over time, and whether changes in phenology can be linked to directional changes in temperature or precipitation over the last three decades. There have been many observed linkages between temperature and phenology in

colder ecosystems; however, in drier, water-limited ecosystems, the interactive effects of both temperature and precipitation on phenological changes are less well understood. The observed plant species in this study include a mix of herbaceous plants, cacti, a vine, shrubs, and tree species (Figure 1), ranging from riparian specialists, to desert scrub vegetation, to higher-altitude tree species, growing along and across an elevational gradient that spans 1,267 meters. Thus, the observations in this study capture a diversity of plant life forms, as well as a large range of variation in environmental conditions over a relatively small spatial scale.

One interesting aspect of flowering in this warm, semi-arid ecosystem is that many of the plant species flower multiple times throughout the year [7]. This contrasts with flowering seasons in cooler, temperature-limited ecosystems, where there is a well-defined seasonality to most phenological events, with plants becoming dormant while there are freezing temperatures over winter, and then coming out of dormancy to flower for one distinct time period when temperatures warm in spring or summer. In temperature-limited ecosystems, one can measure the direction and magnitude of phenological changes by counting the number of days earlier or later in the calendar year that a phenological event, such as first flowering date or peak flowering date, has occurred. However, the multiple periods of flowering of desert plant species pose a challenge for statistically analyzing how plant phenology is shifting over space and time. In this study, the authors used a novel circular statistics method to address this issue. Circular statistics have been

previously used in ecological studies for analyzing directional data, such as the flight directions of birds, but the statistical method has relevant applications for phenological studies as well [11]. Circular statistics circumvent the need to identify distinct phenological events occurring along a linear time-scale. Instead, the technique allows for comparing the concentration of flowering dates along a circle of calendar dates to identify and compare the mean, mode, and median flowering times for different sites or years, even when there are multiple flowering seasons spread sporadically over the calendar year.

Using this circular statistics approach, the authors showed that flowering phenology had shifted in different, and non-linear, ways along the elevational gradient over the past 33 years. Overall, the lowest elevation plant communities shifted flowering dates earlier, whereas there were no significant shifts in flowering times for the highest elevation community. The mid-elevation communities experienced delayed flowering in the most recent decade of measurements (2007–2016) compared with the earliest decade (1984–1993), and this has led to a divergence in community-level flowering times between the lowest and middle elevation communities of almost a month in recent years. Flowering times also became more spread out between plants within the low and mid-elevation communities. Importantly, these diverging phenological changes between and within sites are not detectable if data are pooled across the elevational gradient, illustrating that phenological responses to climate change may differ greatly across small spatial scales.





Figure 1. Flowers of Southwestern Arizona.

Four of the 590 species of plants analyzed in the study, from top left to bottom right: *Passiflora mexicana*, *Castilleja tenuiflora*, *Echinocereus coccineus*, and *Funastrum heterophyllum*. (Photo credits: C. David Bertelsen.)

Temperatures increased and precipitation decreased across all elevations over the 33-year study period, with slightly higher increases in temperature at higher elevations. When looking at yearly fluctuations in temperature and precipitation, the authors found that across all communities, increases in temperature were associated with earlier flowering times, and decreased precipitation was associated with later-flowering times. These findings demonstrate that precipitation is an important driver of phenological changes in desert ecosystems, and future changes in precipitation may negate or even counteract the directionality of phenological responses to temperature in water-limited systems such as this one. These results also highlight the idiosyncratic responses of individual species and plant communities to environmental change, and demonstrate that phenological shifts with climate change will be complex, even over local spatial scales [6,12]. This study shows that it will continue to be important to observe and measure changes over local as well as global scales to understand impacts of climate change on biological processes.

This study is an important contribution to the phenological literature because it

examines phenology in an understudied ecosystem, it includes a relatively long time period of phenological observations, and it shows that changes in phenology may differ greatly between populations even at small spatial scales. The authors found that phenological responses to changes in temperature and precipitation varied non-linearly by elevation and within subpopulations. Interestingly, this finding of a divergence in phenology across an environmental gradient, and within plant communities, in this semi-arid ecosystem differs from studies in colder ecosystems. Other studies in temperate and tundra ecosystems have found a linear convergence in phenological timing across latitudinal and elevational gradients [13,14], and within plant communities [15]. In water-limited ecosystems such as those in the mountains of southern Arizona, variation in precipitation may lead to divergence of flowering times over the season [16]. Even on local scales, differences in water availability between sites along the elevational gradient may influence dates of flowering, with later or delayed flowering in drier years and on drier sites. These non-linear shifts between local populations could alter plant reproductive success and fitness across small spatial scales, change when floral resources are available for pollinators, and thus have

cascading impacts across the ecosystem [17–19]. Important next steps following this study will be to identify how temperature and precipitation, along with local-scale environmental variation, mechanistically interact to cause the non-linear shifts in flowering times between and among plant communities in water-limited ecosystems [20] to accurately predict how climate change will continue to influence flowering phenology in dry ecosystems in the future.

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Bacterial Division: Journey to the Center of the Cell

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Most bacteria divide by corraling the tubulin-like FtsZ protein to mid-cell, where it assembles into a ring of treadmilling membrane-tethered oligomers. A study in this issue reveals new details about how FtsZ finds its way to the ring.

Most bacterial cells use the tubulin-like FtsZ protein as an essential cytoskeletal element to orchestrate their binary fission. As *Escherichia coli* cells prepare to divide, one of the first essential steps is the coalescence of FtsZ into a single ring-like zone, approximately 100 nm wide, at the future site of division precisely at mid-cell [1]. However, only about a third of cellular FtsZ is in the mid-cell ring, and FtsZ also forms dynamic structures elsewhere in the cell that seem to interchange with FtsZ within the ring. This non-ring FtsZ often forms highly mobile helix-like clusters [2,3] that probably serve as pools of FtsZ to be recruited to the FtsZ ring as the time for cell division approaches. In *E. coli*, a visible portion of this non-ring FtsZ also migrates periodically from one cell pole to the opposite cell pole in counter-oscillation with the oscillating Min inhibitory system [2,4],

one of several spatial regulators that restrict the FtsZ ring to mid-cell [5]. Despite these and other advances, the assembly states of non-ring FtsZ pools and how they transition to the mid-cell ring remained uncharted until now. A new study by Walker *et al.* published in this issue of *Current Biology* [6] uses advanced super-resolution light microscopy methods with live cells to provide new quantitative insights into how FtsZ first organizes itself in peripheral locations in the cell and then makes the journey to the central cytokinetic ring.

Thanks to recent imaging breakthroughs, we now know that FtsZ polymers within the ring exist in several discrete subcomplexes that move, often processively, around the ring's circumference by treadmilling [7,8]. Similar to actin filaments, a single filament of FtsZ treadmill by adding

monomers to one end and releasing them from the opposite end, resulting in directional movement. This net movement of FtsZ polymers, along with connections to transmembrane proteins involved in peptidoglycan synthesis, is crucial for coordinating membrane invagination with the synthesis of the septal wall required for cytokinesis. Each of these FtsZ complexes acts independently and locally to stimulate constriction of the cell envelope. In support of this, membrane-attached oligomers of FtsZ have been shown to drive localized, asymmetric envelope constriction in various bacterial species [9].

Assembly of FtsZ polymers within a restricted zone at mid-cell, as well as their mostly processive circumferential motion, depend on their strong interaction with the inner surface of the cytoplasmic

