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Research

The roles of shifting and filtering in generating community-level flowering phenology

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Plant phenologies are key components of community assembly and ecosystem function, yet we know little about how phenological patterns differ among ecosystems. Community-level phenological patterns may be driven by the filtering of species into communities based on their phenology or by intraspecific responses to local conditions that shift when species flower. To understand the relative roles of filtering and shifting on community-level phenological patterns we compared patterns of first flowering dates (FFD) for herbaceous species at Konza Prairie, KS, USA with those from the colder Fargo, ND, USA area and from Chinnor, England, which has a less continental climate. Comparing patterns of FFD supports that Konza's flowering patterns are potentially influenced both by filtering species that flower early in the growing season and by phenological shifting. Konza species flowering dates were earlier in the spring and later in the fall compared to Fargo, but were not shifted compared to Chinnor, which had a unique suite of early-flowering species. In all, comparing flowering phenology among three sites reveals that intraspecific responses to climate can generate phenological shifts that compress or stretch community-level phenological patterns, while novel niches in phenological space can also alter community-level patterns. Community flowering patterns related to climate suggest that climatic warming has the potential to further distribute flowering of the Konza flora over a longer period, but also could further open it to introductions of non-native species that have evolved to flower early in the season.

Plant phenology, the timing of life history events such as leaf production and flowering, is an important component controlling diverse ecosystem services (Cleland et al. 2007) and contributing to how communities assemble through time (Stubbs and Wilson 2004). Because phenology is tied strongly to plant resource use and competition (e.g. for nutrients and pollinators) species with greater overlap in their phenology should also face stronger competition, possibly driving phenological partitioning (Parrish and Bazzaz 1979, Ollerton and Lack 1992). However, sharp climatic limits, which define the growing seasons in many habitats, place an upper-limit on the diversity of plant phenologies possible in any one location (Morin et al. 2009, Chuine 2010), while interannual variability in climate selects for plasticity in phenology as species time growth to avoid death or tissue loss while taking advantage of favorable conditions (Larcher 2003). Community-level patterns of phenology should thus vary across habitats based on local climate conditions and the phenologies (timing and plasticity) of the regional species pool (Kembel and Cahill 2005).

Comparing the flowering phenology of communities in different ecosystems could shed light on the role of flowering in community assembly, particularly on the relative roles of interspecific (environmental filtering) or intraspecific (phenotypic 'shifting') mechanisms driving differences in community-level flowering patterns (Kebart and Anderson 1987, Sargent and Vamosi 2008). For example, if low temperatures early in the growing season inhibit flowering, species in colder habitats should flower later in the growing season (Schwartz and Reiter 2000). Yet, this could happen through two separate mechanisms. First, climate can select for genotypes that differ in their flowering cues (Wilczek et al. 2009) and assemblages could contain species that differ in their timing of flowering as a consequence of environmental filtering (Keddy 1992) that selects for species that flower later in the growing season. Alternatively, climate can also directly influence flowering (Sherry et al. 2007) causing the same species to consistently flower earlier or later at different sites. This could be due either to direct physiological responses to environmental cues or to selection for different genotypes. At the community level, the same set of species flowering over a longer period, i.e. 'phenological stretching', or over a shorter period, i.e. 'phenological compression', is a likely outcome of the aggregate of individual responses to a longer or shorter growing season.

Questions about the roles of climate in community assembly and in generating community-level phenological patterns come into focus for Konza Prairie, a humid North

American prairie in Kansas. At Konza, first flowering dates for the diverse herbaceous flora extend over more than 180 d, beginning in late March and ending in October (Craine et al. in press). Interspecific phenological patterns within the growing season seem to track environmental stress at Konza. The number of species flowering for the first time peaks in early June when soils are both warm and wet. The number of species flowering for the first time declines thereafter and reaches a minimum in early August when soils are typically the driest, before increasing again. However, we have little understanding of how inter- or intra-specific mechanisms have potentially contributed to these patterns.

To further our understanding of flowering phenology at Konza and begin to better understand the inter- and intra-specific mechanisms generating community-level phenology, we compared community-level flowering patterns between Konza and two other sites. The first site was a northern prairie and surrounding areas near Fargo, North Dakota (Dunnell and Travers 2011), which share many of the same species as Konza, but have a mean annual temperature that is approximately 8°C lower. The second site was a temperate grassland in Chinnor, England (Fitter and Fitter 2002), which has a similar mean annual temperature as Konza, but a less continental climate with warmer winters and cooler summers than Konza. In comparing the flowering patterns of all species present at Konza with the same patterns in the other two sites, we tested for differences when first flowering began, peaked, and ended between sites. We then tested whether differences could be explained by inter- or intra-specific differences. For example, the flowering season at Fargo would likely be narrower than at Konza, but there are competing hypotheses as to how narrower ranges in flowering phenology would be generated. It is uncertain whether the differences could be ascribed to early-flowering species flowering later at Fargo and late-flowering species flowering earlier, or whether species with extreme flowering times were absent from Fargo.

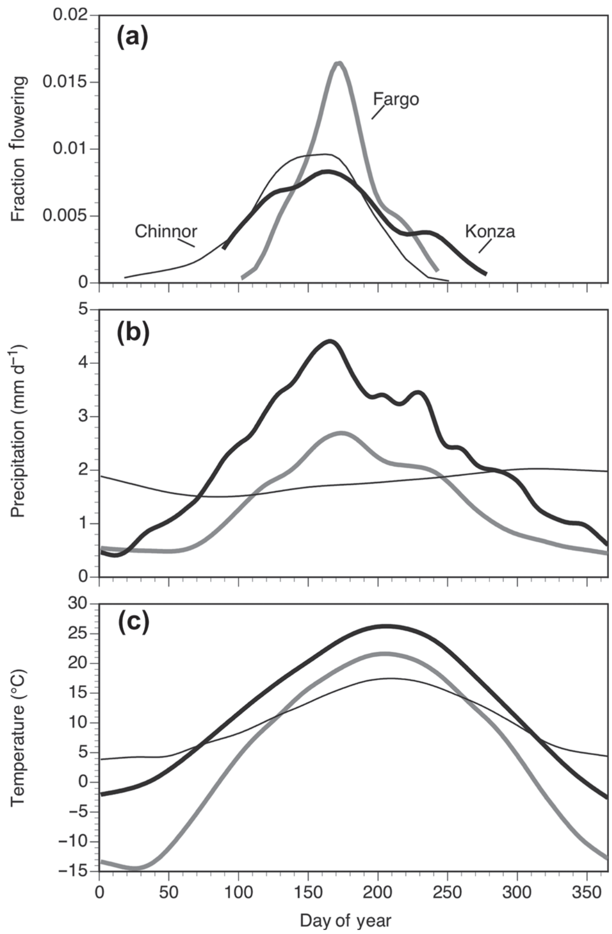

Figure 1. Annual patterns of first flowering dates for herbaceous flora at Konza (thick black line), Chinnor (thin black line), and Fargo (grey line) expressed as a fraction of flora flowering each day (a) and for precipitation (b) and temperature (c).

Methods

The study was conducted at Konza Prairie Biological Station, a 3487-ha native tallgrass prairie located in northeastern Kansas, USA (39.08°N, 96.56°W) (Knapp et al. 1998). Mean annual temperature is 13°C, with mean minimum and maximum monthly temperatures ranging from −3°C in January to 27°C in July (Fig. 1). Annual precipitation for Konza Prairie averaged 844 mm from 1983 to 2009, with approximately 75% falling in the April through September growing season and peak precipitation in June. The vegetation at Konza is primarily unplowed native tallgrass prairie. Woody species form gallery forests in riparian areas, and can be abundant in specific watersheds, depending upon fire frequency (Briggs et al. 2002). The known vascular flora of Konza Prairie is comprised of 597 species, of which 59 are woody. Of the 539 herbaceous species, 122 are graminoids, 411 are eudicots, and 6 are ferns. Graminoid species consist of C_4 Poaceae (51 species), C_3 Poaceae (38 species), C_3 Cyperaceae (26 species), and C_4 Cyperaceae (7 species). Of the herbaceous eudicots, 397 species utilize the C_3 photosynthetic pathway and 14 have the C_4 photosynthetic pathway. At Konza, grazing, burning, and landscape position are the main environmental contrasts that affect plant communities other than climate (Knapp et al. 1998, Craine et al. in press).

Herbaceous species on Konza were surveyed for first flower appearance over a large portion of Konza with surveys conducted almost daily across the majority of Konza over 129 d between 30 March to 5 October, 2010 with additional surveys outside of this range not finding species (Craine et al. 2012). When a species was found to be flowering for the first time, the date was recorded and the plant collected. We assessed first flowering dates (FFD) for a total of 430 herbaceous species.

Phenology comparisons between flora

To further understand the influence of climate on flowering patterns, first flowering patterns at Konza were compared with those at Fargo, ND, USA and Chinnor, England. Compared to Konza, Fargo's climate is colder (mean annual temperature [MAT] = 5.0°C, mean annual precipitation [MAP] = 482 mm), but still highly seasonal, while Chinnor's climate has a similar mean annual temperature as Konza (MAT = 10.2°C, MAP = 649 mm), but is less seasonal (Fig. 1). Data on FFD for Fargo were recorded for 269 herbaceous species (Travers and Dunnell 2009). Flowering for these species were observed on the campus of the Univ. of North Dakota and nearby areas. Data on first flowering for Chinnor and its surrounding areas (Fitter and Fitter 2002) were recorded for 343 herbaceous species.

For each of these two sites, seasonal patterns of FFD were constructed in a similar manner as for Konza. Data are expressed in terms of the fraction of all species flowering each day and the fraction of all species in a given functional group flowering each day. Relationships between the flowering dates at Konza and the two other sites were tested with orthogonal regression, which tests for linear relationships between two variables without assuming causality. To further understand some of the determinants of differences in community-level FFD, we also compared patterns of precipitation and temperature between Konza and the other two sites. Climate data for Fargo and Chinnor were acquired from the GHCN-D dataset from NCDC/NOAA and accessed through < http://climexp.knmi.nl >. Climate data for Fargo were taken from a weather station in nearby Moorhead, MN for the period of 1910–1952. Climate data for Chinnor were taken from a weather station in Oxford for the period of 1954–1999.

Results

Comparisons among flora from different regions

The general patterns of first flowering dates at each of the three sites were distinctively different from one another (Fig. 2). Flowering at Chinnor occurred earlier than at Konza as a result of the presence of species with earlier flowering times as opposed to a given species flowering earlier at Chinnor than Konza. The average flowering time for Chinnor species was 22 d before Konza (26 May vs 17 June) with peak flowering times differing only by 3 d (11 June vs 14 June, respectively). At Chinnor, the first species flowered on 18 January and 9% of Chinnor herbaceous flora (31 of 343) flowered before the first Konza herbaceous species flowered. Yet, 99.5% of the Chinnor flora flowered by 8 August, whereas only 82.3% (355 of 431) of the Konza flora flowered by that date. These differences in timing between the two sites were not associated with a shifting in FFD for the 28 species found at both sites. Although FFD between the two sites did not statistically differ, species tended to flower later at Chinnor than Konza ($FFD_{Chinnor}$–FFD_{Konza} = 6.3, $p = 0.14$ with paired t-test). On average, C_3 eudicots flowered earlier at Chinnor than Konza (146.1 ± 2.5 vs 167.5 ± 2.4, respectively; $p < 0.001$), while the C_3 graminoids flowered on average at similar times ($p = 0.22$) (Fig. 2).

Whereas flowering in the Chinnor flora was earlier than Konza as a result of the presence of early-flowering species and absence of late-flowering species, the Fargo flora had a narrower range of dates due to phenological compression rather than filtering of species with extreme FFDs. Species at Fargo flowered on average at a similar time as Konza species (22 June vs 17 June, respectively, $p = 0.25$) with peak

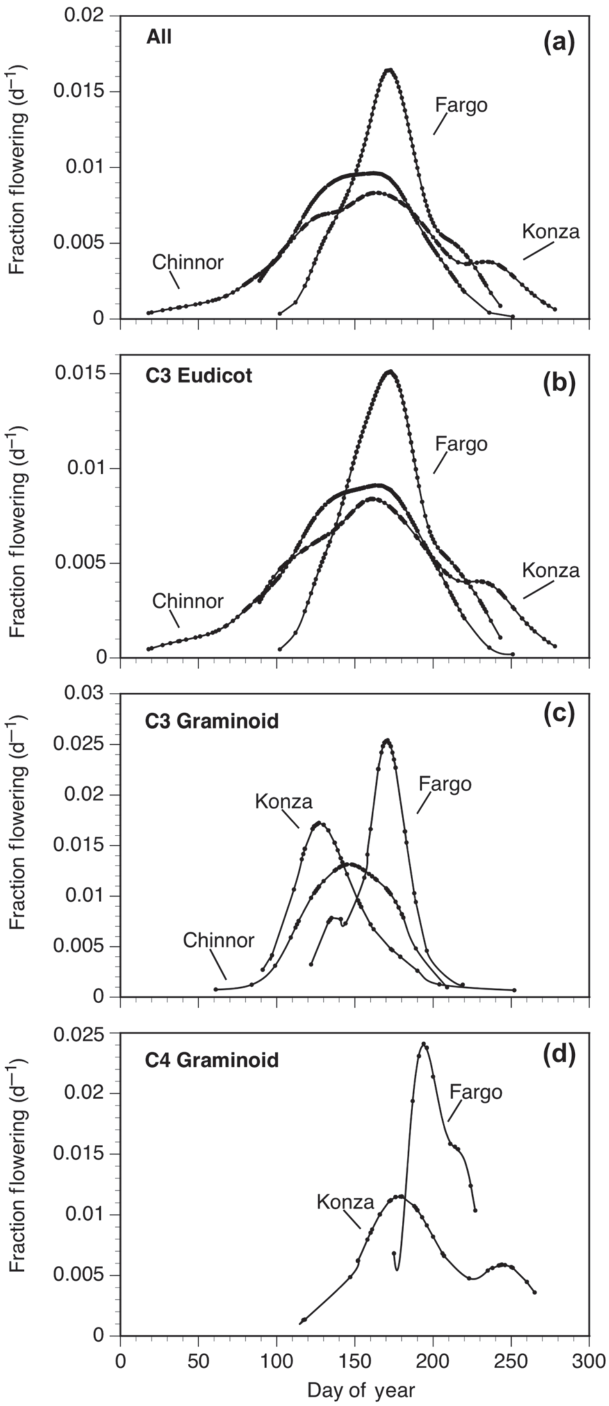

Figure 2. Annual patterns of first flowering dates (FFD) expressed as a fraction of each functional group for a site flowering each day. Data shown for (a) all species, (b) C_3 Eudicots, (c) C_3 Graminoids, and (d) C_4 Graminoids.

flowering times at Fargo also on 22 June. Although peak FFD for species were similar between the two sites, flowering at Fargo occurred over a narrower range of dates. For example, 95% of the species at Konza flowered within a 166-d range (4 April–17 September), while at Fargo the window was only 106 d (4 May–18 August). The standard deviation for FFD for all species at a site was 67% greater at Konza than Fargo (45 vs 27 d). The first Fargo flowering date was on 12 April (*Crocus vernus*, an introduced perennial forb), which on average had a mean daily temperature of 4.3°C. The first native species to flower at Fargo was the perennial forb *Sanguinaria canadensis*, which first flowered on 27 April. Mean temperature on that day was 9.5°C. The last species to begin flowering was the biennial forb *Artemisia biennis*, with a FFD on 31 August, when mean temperature was 19.1°C. The phenological shifting of the community at Fargo relative to Konza was consistent across functional groups (Fig. 3).

The role of phenological shifting at Fargo was apparent from comparing the flowering dates of species that were common between Fargo and Konza (Fig. 4). Early-flowering species flowered later at Fargo than Konza (paired t-test, $p < 0.001$) – up to 45 d later for the earliest flowering species. Late-flowering species flowered earlier at Fargo than Konza (paired t-test, $p < 0.001$) – up to 30 d earlier for the latest-flowering species shared between the two sites. Species that flowered on 14 July at Konza flowered on the same date between the two sites. These general patterns held for the C_3 eudicots when analyzed separately (Fig. 4). C_3 and C_4 Poaceae were too restricted in their flowering time to test these patterns conclusively, yet C_3 grasses flowered earlier at Konza than Fargo and C_4 grasses at similar times (Fig. 4).

Discussion

To place the flowering patterns at Konza into context and test processes that underlie community-level phenology at Konza, we compared patterns of first flowering dates with two other grasslands that differed in their mean annual temperature and seasonality of temperature. Comparing the flowering patterns at these sites revealed two factors that likely contribute to the general patterns of flowering at Konza. Intraspecific responses to climate can generate phenological shifts that compress or stretch community-level phenological patterns. The phenological pattern at Fargo was compressed compared to Konza across multiple functional groups with early-flowering species flowering later and late-flowering species flowering earlier at Fargo than at Konza. With many of Konza's species extending into warmer regions to the south of Konza as well as colder regions to the north (Craine et al. 2011), part of the seasonal pattern of flowering at Konza is likely due to individualistic responses of species adjusting phenotypically and genotypically to the general patterns of temperature. For example, the early-season C_3 forb *Viola pedatifida* flowered 40 d earlier at Konza than Fargo, while the late-season C_4 forb *Bassia scoparia* flowered 55 d later.

Although the seasonal pattern of flowering is in part associated with how individual species adjust through phenotypic and genotypic mechanisms to the climate at Konza, the flowering patterns at Konza compared to Chinnor also show evidence of novel niches (Craine et al. 2006, Moles et al. 2008) in phenological space that alter community-level patterns. At Chinnor, almost 10% of the site's species flowered before the first Konza species flowered. Although some of this pattern could potentially be ascribed to the milder winter temperatures at Chinnor, of the 28 species common to both sites, there was no difference in average flowering times between the two sites ($p > 0.1$). As such, it is likely that the Chinnor flora contains species that occupy early phenological niches that are not viable in most years

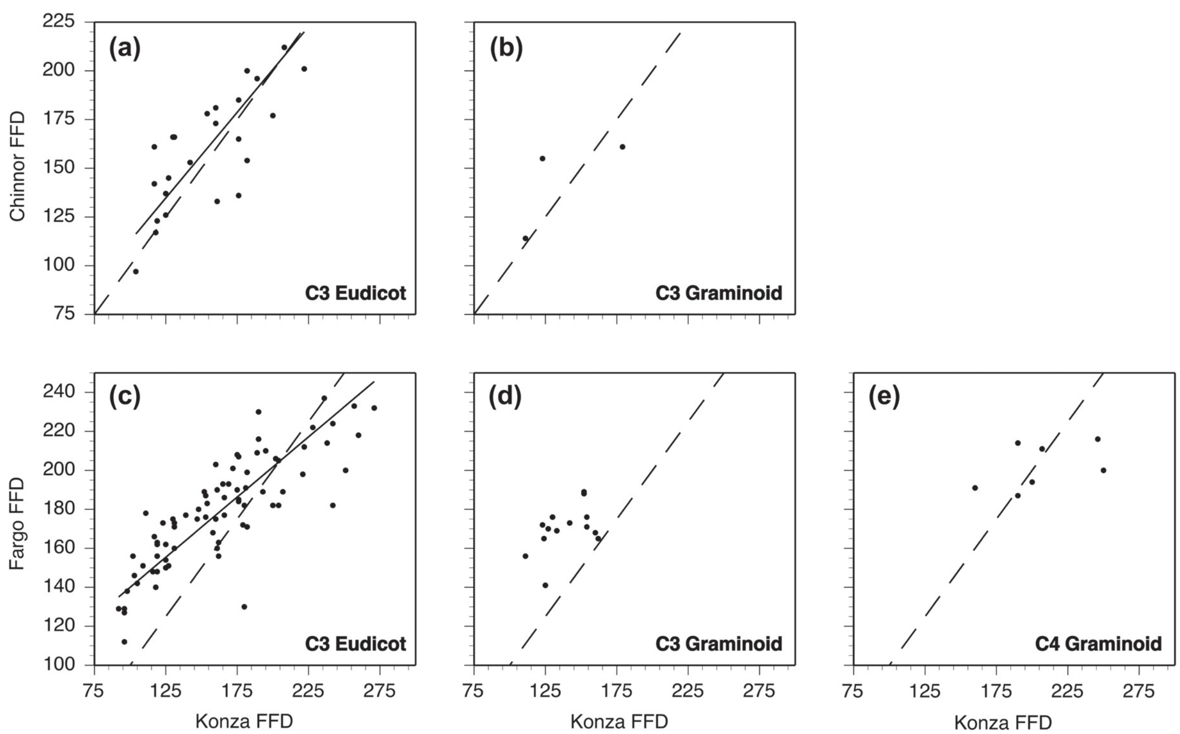

Figure 3. Comparison of first flowering dates (FFD) for those species common between Konza and (a, b) Chinnor or (c–e) Fargo. Relationships shown for three functional groups: (a, c) C_3 eudicots, (b, d) C_3 graminoids, and (e) C_3 graminoids.

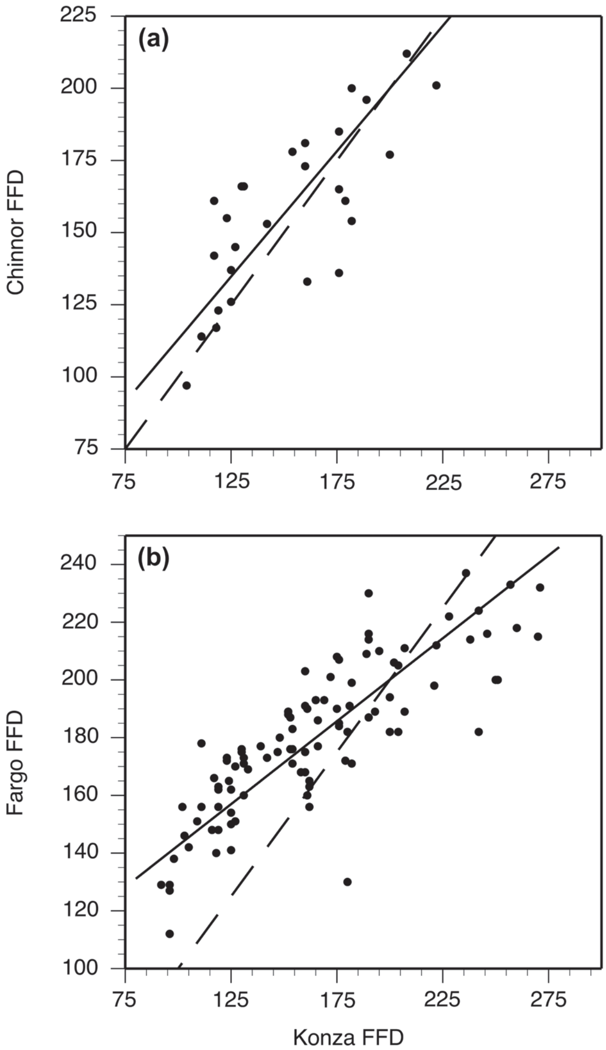

Figure 4. Comparison of first flowering dates (FFD) for those species common between Konza and (a) Chinnor and (b) Fargo. Dashed line is 1:1 line with species falling below this line flowering later at Konza than the other site and species falling above this line flowering earlier. Solid line is the orthogonal regression line.

at Konza. The earliest first flowering date at Konza for a species found at both sites was 14 April (*Alliaria petiolata*, which is native to Europe). No other species that flowered before *A. petiolata* at Chinnor can be found at Konza.

By the same token, Konza seems to have phenological niches that are apparently absent at Chinnor. The numerous species that begin flowering late in the growing season at Konza are absent at Chinnor. Although some of these are C_4 grasses, there are many C_3 eudicots that flower late that are neither present nor have analogs in the Chinnor flora. Although the pattern is clear, why Chinnor would not have species that begin to flower late in the growing season is uncertain as its mild climate certainly supports vegetative growth during this period. The presence of species at Konza that begin flowering late in the growing season such as *Gentiana puberulenta* are unlikely to be associated with the harshness of the winter, which would select against species beginning to flower close to environmentally stressful periods. The continental climate of Konza could promote late-flowering species that would benefit from waiting to flower until after the stressful midsummer dry periods. Testing this would likely require common garden experiments with climatic manipulations.

Comparing the patterns of flowering between Konza and Chinnor and the pattern of flowering for Konza's native and non-native species suggests a potential link between the climate of a donor flora and the pattern of non-native establishment in a recipient flora (Godoy et al. 2009). At Konza, non-native species tend to flower, early in the growing season with very few non-natives starting to flower after the mid-season drought (Craine et al. 2012). Furthermore, the overlap with Chinnor species did not include any species that flower before the Konza growing season begins, with shared species flowering dates agreeing almost exactly. This suggests some pre-existing agreement to the phenology of the native flora is necessary for non-natives to successfully establish (Craine et al. 2006, Moles et al. 2008). That said, the absence of a species from a site does not necessarily imply that its absence was caused by environmental filtering as some species might never have been introduced to the site. Hence, future predictions of the invasion potential of species will likely have to incorporate the interactions between species' phenology and the phenologically-relevant environmental factors that restrict species occurrence.

Predicting future community composition

Based on how closely Konza community flowering tracks environmental conditions (Craine et al. 2012) and its predictable differences from other floras, informed predictions about how future climate change may alter plant communities are possible. In Konza, where regional climate models consistently predict warmer future temperatures along with a more variable precipitation regime (Christensen et al. 2007), a series of changes may alter general flowering patterns. First, as found with many floras globally, early-season species may shift earlier as thermal sums required to trigger flowering are met earlier. Second, species invasions from donor floras may increase (Wolkovich and Cleland 2010) as the Konza season expands to increase overlap in phenological climatic space with floras such as those of Europe like Chinnor. Third, as the mid-growing season drought may become more pronounced – possibly reducing the number of species flowering mid-season – evidence of a such a shift towards a novel mid-season gap (or decrease) in flowering has already been suggested in other floras observationally (Aldridge et al. 2011) and via experiments (Sherry et al. 2007). Comparing the responses of flowering phenology to experimental warming and the differences in flowering between Konza and Fargo suggest that the response to changes in temperature varies according to the flowering time of species, i.e. depending on whether they are earlier or later than a common inflection point. In an Oklahoma grassland experiment, warming caused early-flowering species to flower earlier and late-flowering species to flower later with an inflection point near mid- to late-July. This date range is similar to the 14 July inflection point for changes in flowering dates between Konza and Fargo. The universality of this mid-July date remains to be seen, but it appears to serve as a consistent benchmark for predicting the responses of flowering phenology to warming (Sherry et al. 2007).

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