

Phenological responsiveness to climate differs among four species of *Quercus* in North America

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Summary

1. The timing of the seasonal activity of organisms is a tractable indicator of climate change. Many studies in North America have investigated the role of temperature on the onset date of phenological transitions in temperate deciduous trees and found that the onset of leafing and flowering in numerous species has occurred earlier in recent years, apparently in response to higher temperatures in winter and spring.

2. Few studies have examined the climatic and biogeographic drivers of phenological responses in water-limited ecosystems or explored interspecific variation in responses of phenological metrics other than the timing of onset, such as the periodicity or duration of phenological activity.

3. This study used phenological observations of four species of *Quercus* contributed to the USA National Phenology Network database from 2009 to 2014 to investigate how responses to climate (temperature and precipitation) and geographic location (latitude, longitude and elevation) varied among two western North American species (*Q. agrifolia* and *Q. lobata*) and two eastern and central North American species (*Q. alba* and *Q. rubra*).

4. Within years, in species in the western, water-limited ecosystems, the phenological phases observed here (bud break, flowers or flower buds) tend to occur intermittently throughout the growing season, and each event is of longer duration than the same phenophases of the temperate-zone species, rendering a single onset date an incomplete metric with which to track responsiveness or to compare species. By contrast, the eastern/central U.S. species were phenologically more responsive than the western species to spatial and temporal variation in winter, spring, and fall precipitation and maximum temperature.

5. Synthesis. Within and between regions these congeners exhibited a diversity of responses to seasonal temperature and precipitation. This indicates that for predictive model development it is critical to understand how each underlying driver influences species that are adapted to different climatic regimes. These results underscore the value of studying a range of phenological metrics and species from a variety of ecosystems to better predict phenological responses to short-term variation and to long-term change in climate.

Key-words: breaking leaf buds, citizen science data, flowering, phenology, phenophase onset, plant-climate interactions, *Quercus*, USA National Phenology Network

Introduction

Phenology, the study of the timing of the seasonal activity of plants and animals, is a valuable indicator of the ecological responses to climate change (IPCC 2014). Phenological variation associated with climatic conditions within and between sites can be used as an indicator of the degree to which the timing of species' phenological events (including their

duration and within-season periodicity) are sensitive, or responsive, to climatic drivers (Pau *et al.* 2011; Cook, Wolkovich & Parmesan 2012a). Phenological responsiveness to spatial variation in climate may correspond to the ability of a species to track climate change, and greater sensitivities to climate have been linked to increased species performance (e.g. population growth) in the context of ongoing climate change (Cleland *et al.* 2012).

Numerous studies have found a shift in recent years towards an earlier spring and a longer growing season (e.g.

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Parmesan & Yohe 2003; Inouye 2008). However, there is variation among species in both the direction and the magnitude of change through time within communities (Davis *et al.* 2010; Cleland *et al.* 2012; Cook, Wolkovich & Parmesan 2012a; Wolkovich *et al.* 2012; Mazer *et al.* 2013). Several studies have found that species that initiate budbreak or flowering relatively early in the growing season have higher sensitivity to winter temperatures than those that initiate growth and reproduction later in the growing season (Sparks & Carey 1995; Fitter & Fitter 2002; Menzel *et al.* 2006; Miller-Rushing & Primack 2008; Cook *et al.* 2012b; Wolkovich *et al.* 2012; Mazer *et al.* 2013; Shen *et al.* 2014). However, these patterns are not consistent among ecosystems and species.

The majority of studies that have elucidated the relationships between phenology and climate have focused on woody species in temperate ecosystems, including the Midwest and Northeastern United States as well as Europe, where it is generally assumed that temperature and/or photoperiod are the primary driver(s) of phenology (Schaber & Badeck 2003; Basler & Körner 2012; Zohner & Renner 2014, 2015; Pletsers *et al.* 2015; Primack *et al.* 2015; Way & Montgomery 2015). However, researchers are paying increasing attention to species and ecosystems that may be influenced by multiple drivers and by interactions between them, including seasonal temperature and precipitation (Crimmins, Crimmins & Bertelsen 2010, 2011; Gordo & Sanz 2010; Dunnell & Travers 2011; Matthews & Mazer 2015; de Oliveira *et al.* 2015). In the arid and semi-arid ecosystems of the western United States, seasonal moisture can play either an interactive or a primary role in triggering vegetative and reproductive activity in plants (Beatley 1974; Kemp 1983). For example, recent work by Mazer *et al.* (2015) in semi-arid regions of California found that, for some species and phenophases, precipitation played a primary role in predicting the onset of vegetative growth or flowering; however, this study also detected complex monthly interactions between temperature and precipitation that influenced the onset of phenological transitions.

Climatic cues that cause phenological transitions in water limited systems can be challenging to detect using modelling frameworks that focus on onset events and that assume a well-defined beginning and end of the season, as many species in these ecosystems exhibit multiple onset events within a year or within a season. While the onset date of phenological activity is an intuitive and meaningful measure to use when tracking how species respond to climatic drivers and to capture long-term phenological trends, characterizing the drivers of other phenological metrics such as the duration, peak, and periodicity of specific phenophases is crucial for detecting the full spectrum of ways in which climatic change will affect populations and communities (Miller-Rushing, Inouye & Primack 2008; Rawal *et al.* 2015). Within species, for example, the duration and periodicity of vegetative phenophases have a strong influence on the carbon cycle (Richardson *et al.* 2013), while the duration, intensity, and frequency of pollen-releasing phenophases enables us to anticipate exposure and concentration of allergens (Fairley & Batchelder 1986; Galán

et al. 2005; Garcia-Mozo *et al.* 2006). Identifying the timing of peak abundance or the duration of reproductive phenophases within or among years could capture the dynamics of fruit availability for animals, or nectar and pollen availability for pollinators. At the level of the community, the study of such metrics could detect temporal change within or among years in the taxonomic composition and diversity of fruit, nectar and pollen availability (Miller-Rushing *et al.* 2010). These metrics also provide a way to track the intensity of antagonistic relationships by examining the timing of competitive interactions between natives and invasive species (Engelhardt & Anderson 2011; Wolkovich & Cleland 2011; Wolkovich *et al.* 2013), herbivores and their plant hosts (Murali & Sukumar 1993; Asch & Visser 2007; Pearse *et al.* 2015), or disease vectors and their hosts (Hard, Bradshaw & Holzapfel 1993; Krugner *et al.* 2012).

Robust predictions of the future phenological behaviour of a given species require knowledge of both its plastic responses to inter-annual variation in climate and its genetically based, adaptive responses to spatial variation in climate and other factors that may influence its phenological evolution. For example, a population's phenological behaviour at a given location may represent the outcome of natural selection in response to the availability of its local fruit dispersers, pollinators, herbivores, and competitors (Cleland *et al.* 2012). In the absence of a very long observational record (i.e., hundreds of years) for a particular species, the analysis of its responses to climatic variation across its geographic range, but over relatively short (multi-year) periods, can detect the climatic cues to which it is most sensitive as well as the phenophases that are most likely to change (and their direction of change), at least in the short term, in response to such cues. Thus, when there is not a deep temporal record available, phenological data from regions that encompass broad climatic envelopes experienced by a species and where individuals are tracked over multiple years can be informative for predicting the degree to which a species may be sensitive to climate change (Mäkelä 2013).

With phenological data recorded from individual plants across a species' range, we can quantify the extent to which members of the species respond to their local climate in a consistent manner. For species that respond similarly to changes in climatic parameters across their geographic range, spatial variation in climate and phenological parameters can be used as a proxy for temporal variation in order to generate predictions of their phenological responses to future climatic conditions. By contrast, for species whose phenology is influenced by interactions between climate and geographic location (e.g., latitude, longitude or elevation), or by effects of geographic location that are associated with local biotic or abiotic attributes *other* than climate that may impose selection on (or induce plasticity of) phenological behaviour phenological responses to climate change may be location-specific. In the current study, we constructed models specifically to detect such independent effects of geographic location as well as the effects of interactions between climatic variables and geographic location.

Species within the genus *Quercus* are a promising group in which to detect the influence of climatic cues and geographic location on phenological patterns in temperate and water-limited environments. Investigations of the climatic drivers of phenology in *Quercus* have focused largely on the influence of temperature on the vegetative phenology, particularly bud break, of temperate species. The majority of studies report that temperature is strongly correlated with the onset date of bud break; warmer temperatures advance bud break in a variety of species (Kramer 1995; Menzel 2000; Askeyev *et al.* 2005; Morin *et al.* 2009; Vitasse *et al.* 2009; Basler & Körner 2012). Studies have reported conflicting results, however, concerning the importance of precipitation as a climatic driver in *Quercus*. Samtani, Appleby & Masiunas (2015) found that increased cumulative precipitation delayed bud break of two North American *Quercus* species, while Morin *et al.* (2010) found that bud break of three European *Quercus* species did not respond to variation in precipitation. In California, Fairley & Batchelder (1986) reported that precipitation positively affected the magnitude, rather than the timing, of pollen release from oak species.

Photoperiod, for which latitude is often used as a proxy, may also influence the phenology of *Quercus* species. Some studies report that photoperiod is an important driver of bud break (Schaber & Badeck 2003; Samtani, Appleby & Masiunas 2015), while others report that including photoperiod in temperature-based models used to predict bud break does not improve the fit of the models (Hunter & Lechowicz 1992; Kramer 1995). Even within a single species and phenophase, there is conflicting evidence as to whether photoperiod is an important driver of bud break. For example, Samtani, Appleby & Masiunas (2015) found a strong correlation between the timing of bud development and photoperiod in *Q. rubra*, while Laube *et al.* (2014) reported that this species is insensitive to photoperiod. To our knowledge, no study to date has simultaneously evaluated the roles of geographic location, temperature and precipitation in determining the onset, periodicity, or duration of vegetative and reproductive phenophases in water-limited ecosystems. Moreover, none have compared congeners adapted to contrasting climates with respect to their phenological behaviour or the climatic cues that influence it. The research presented here was designed to begin to fill this gap.

In the face of predicted increases in spring temperatures (continent-wide) and potentially intensifying drought conditions in the western U.S. (Westerling *et al.* 2006; MacDonald 2010; Diffenbaugh, Swain & Touma 2015), we sought to detect how responsiveness to climatic (temperature and precipitation) and geographic (latitude, longitude and elevation) drivers differs among four *Quercus* tree species. In particular, by focusing on two species in the western U.S. and two species distributed in the central and eastern U.S., we aimed to determine whether the drivers of phenological onset dates differed between taxa adapted to a Mediterranean climate relative to those occupying a more temperate climate. Within this small group of species, we could also assess whether

geographic overlap and climatic similarities between species were more important than taxonomic relatedness in determining their patterns of responsiveness. We predicted that western U.S. species would be more responsive to recent seasonal precipitation than the eastern/central U.S. species, and that the former would have shorter phenophase durations, including both the number of days of individual episodes and the total number of days that a phenophase is visible. Given the periodic and intermittent nature of rainfall events in the western U.S., we also predicted that the western taxa would exhibit greater periodicity of phenological activity than the eastern taxa.

Materials and methods

STUDY SPECIES

Species were selected based on the availability of phenological data across large geographic areas, and on the opportunity to compare species adapted to water-limited habitats to those in more temperate conditions. *Quercus agrifolia* (Coast live oak) is an evergreen oak with a distribution spanning the coastal region of California and northern Baja California. It is a dominant tree in the coast live oak woodland and is found on slopes with well-drained soils. *Quercus lobata* (Valley oak) is a large, deciduous oak species endemic to California and found in rich deep soils in valleys. *Quercus alba* (White oak) is a deciduous tree that ranges throughout eastern and central North America in a variety of habitats. The geographic range of *Q. rubra* (Northern red oak) overlaps with *Q. alba*, and is often found in well drained soils near streams (Fig. 1). Bivariate plots of climatic conditions at study sites for each species during the study period demonstrate a clear difference between the climatic ranges experienced by the two western species compared to the two eastern/central species (Fig. 2); the western taxa occupy warmer and drier sites. The wider range of climatic conditions experienced by *Q. alba* and *Q. rubra* relative to *Q. agrifolia* and *Q. lobata* reflects the greater range of latitude, longitude and elevation represented by the sampled sites (Table 1).

The four oak species are members of two different sections in the genus *Quercus*. *Quercus lobata* and *Q. alba* are in the white oak section (*Quercus*) while *Q. rubra* and *Q. agrifolia* are red oaks (*Lobatae*). In other words, *Q. lobata*, a western species, and *Q. alba*, a central/eastern species, are more closely related to each other than to *Q. agrifolia* and *Q. rubra* (Manos, Doyle & Nixon 1999; Hipp *et al.* 2014).

PHENOLOGICAL DATA

For this study, we used a geographically extensive phenological dataset comprising *Quercus* observation records from 2009 to 2014 that were contributed to the USA National Phenology Network database (USA National Phenology Network 2015, Gerst, Rossington & Mazer 2017). The sites from which data were available are distributed across much of each species' geographic range (Fig. 1). The majority of the data for the two western species (*Q. agrifolia* and *Q. lobata*) was collected at sites established by the California Phenology Project: a monitoring program designed to characterize phenological variation across gradients within and beyond California National Parks (www.usanpn.org/cpp; Haggerty *et al.* 2013; Matthews *et al.* 2013; Mazer *et al.* 2015).

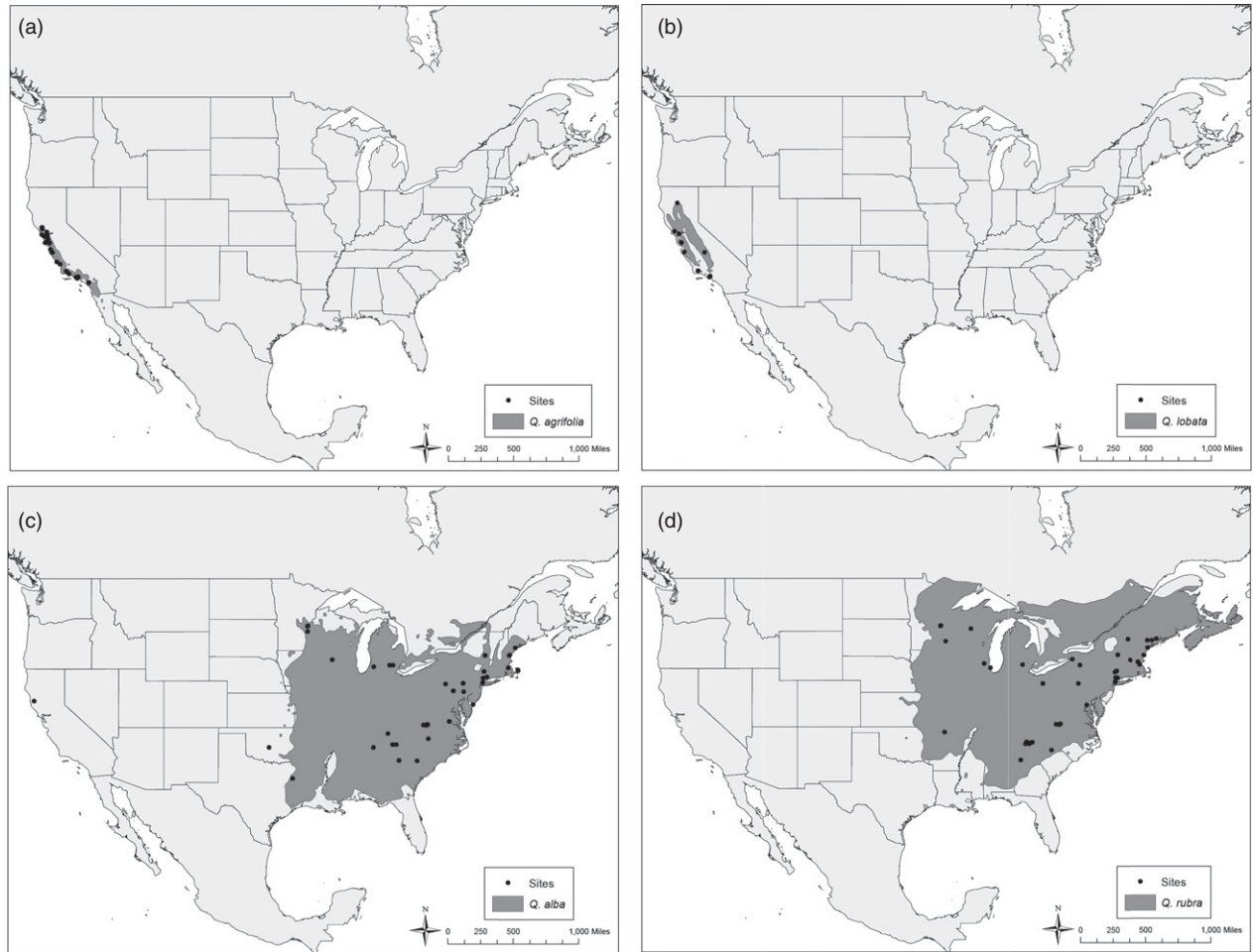


Fig. 1. Geographic range and the location of the USA-NPN sites included in this study for (a) *Quercus agrifolia*, (b) *Q. lobata*, (c) *Q. alba* and (d) *Q. rubra*.

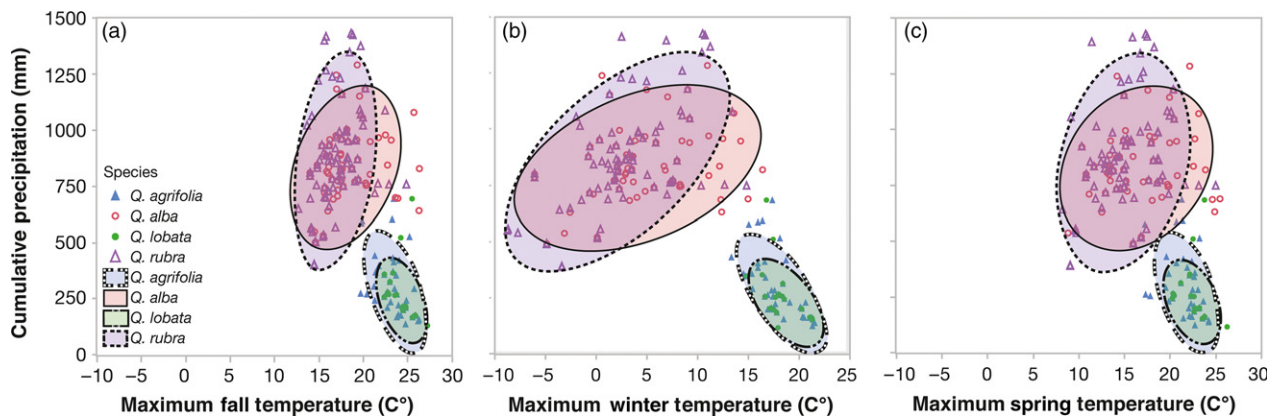


Fig. 2. Bivariate plots of cumulative precipitation and Tmax for Fall (a), Winter (b) and Spring (c) representing the breadth of climate conditions experienced by the four species at the sites used in the study. Data used are from the sites where the ‘breaking leaf bud’ phenophase was monitored, recorded and contributed to the USA-NPN database. Shaded ellipses represent the 95% confidence interval for each species.

Two phenophases that were regularly monitored in all four species from 2009 to 2014 were selected for analysis: ‘breaking leaf buds’ and ‘flowers or flower buds’ (Denny *et al.* 2014). We downloaded summarized data, which, for each monitored individual, provides its

latitude, longitude, and elevation, as well as the day of year (DOY) of the first and last positive observation records of each phenophase in each calendar year. Onset DOY was filtered to include only positive observation dates that were recorded ≤ 7 days after a negative

Table 1. Latitudinal, longitudinal, and elevation ranges of focal *Quercus* species

Species	Latitude range	Longitude range	Elevation range (m)
<i>Q. agrifolia</i>	33.6°–38.6°	–122.7° to –117.6°	16–593
<i>Q. alba</i>	32.4°–45.4°	–123.4° to –69.9°	0–696
<i>Q. lobata</i>	34.1°–40.6°	–122.6° to –118.7°	61–536
<i>Q. rubra</i>	34.0°–45.4°	–93.2° to –69.3°	12–696

observation (defined as a day on which the targeted phenophase was unambiguously identified as not being visible) (Denny *et al.* 2014; Gerst *et al.* 2016). The resulting onset date was therefore accurate with a maximum error of 7 days. In order to calculate *first* onset dates within a calendar year, we constrained our query to the earliest onset dates per individual between DOY 1–182 (January 1 to July 1), as it is possible for an individual tree to have multiple periods of activity and we excluded onset events that were only detected in the later part of the year in order to identify drivers of the onset of spring phenological activity. Where multiple individuals were monitored at the same location, we used the site mean for the *first* onset DOY; each site was represented by a single DOY, regardless of the number of individuals located there. There were data available for a total of 89 individual trees in 34 sites for *Q. agrifolia* (96 site × year records); 83 trees in 43 sites for *Q. alba* (93 site × year records); 59 trees in 18 sites for *Q. lobata* (61 site × year records); and 92 trees in 49 sites for *Q. rubra* (129 site × year records). The numbers of sites and individuals that contributed data for each phenophase and year are shown in Table 2.

The number of activity periods per individual was identified as an informative metric because many individuals in the dataset exhibited multiple phenological onset dates during each of one or more years; that is, within a given year, a positive observation of a given phenophase was followed by a negative observation, which was then followed by a positive observation at a later date. For some individuals and phenophases, this sequence was repeated several times, indicating multiple episodes of the initiation and cessation of either vegetative bud break or flowering. To characterize episodic phenological behaviour, we calculated the number of periods of activity for each individual and phenophase, determined by the number of onset events captured within 7 days of a previous negative observation throughout the entire calendar year (DOY 1–366). We then summarized these data at the site level by calculating the mean number of periods of activity among co-occurring individuals for each site for each species and phenophase.

Table 2. Number of sites and individual trees contributing to the analyses of each *Quercus* species, phenophase and year. BLB = breaking leaf buds, flowers = flowers and flower buds

Species	Phenophase	2009		2010		2011		2012		2013		2014		
		Sites	Trees	Sites	Trees	Sites	Trees	Sites	Trees	Sites	Trees	Sites	Trees	
<i>Q. agrifolia</i>	BLB							11	20	14	22	26	49	
<i>Q. agrifolia</i>	Flowers							10	19	12	17	23	43	
<i>Q. alba</i>	BLB	5	5	4	5	7	8	15	25	15	22	17	23	
<i>Q. alba</i>	Flowers					4	4	6	15	6	8	14	24	
<i>Q. lobata</i>	BLB							3	9	20	10	25	16	35
<i>Q. lobata</i>	Flowers							7	18	7	20	12	25	
<i>Q. rubra</i>	BLB	4	4	16	22	12	14	11	15	18	23	23	30	
<i>Q. rubra</i>	Flowers					7	8	7	7	12	14	19	26	

Finally, we calculated the number of days (duration) that each individual was observed in a phenophase at a given site for each episode of activity within the span of the calendar year (DOY 1–366), limited to episodes when the onset and end dates were both captured within 7 days, respectively, of a prior or subsequent negative observation record. These data were summarized at the site level by taking the mean number of days in each phenophase during each episode of activity among co-occurring individuals for each species at a site, as well as the mean *total* number of days in phenophase within the calendar year. For example, an individual that exhibited 3- to 7-day periods with open flowers would have a mean duration/episode of 7 days and a total number of 21 days in this phenophase.

CLIMATE DATA

Climate data originated from Daymet (Thornton *et al.* 2015) and was obtained via the USA-NPN Data Output Tool (USA National Phenology Network 2015). The USA-NPN tool provides seasonal averages of minimum and maximum daily temperature (Tmin and Tmax) and seasonal accumulated precipitation (total mm) for each site and year (Fall = Sept, Oct, Nov of prior year; Winter = Dec of prior year, Jan, Feb; Spring = Mar, Apr, May; Summer = Jun, Jul, Aug). We created an additional derived precipitation variable that was the sum of Fall, Winter, and Spring precipitation.

STATISTICAL ANALYSES

We calculated mean onset DOY, mean duration (two metrics: total number of days in a phenophase and mean number of days in a phenophase per episode) and mean number of episodes (a metric of periodicity, or pulsing) per individual at each site and compared these site mean values among species using Tukey-Kramer tests.

We performed principal components analyses (PCA) to identify the climatic variables contributing significantly to variation among all site × year combinations used in this study and to assess the relationships between the first onset dates of each phenophase and the primary principal component. We first used climate data from all sites within the entire dataset to determine how the climate space varied and overlapped among all four species. We then calculated separate PCAs for the western and eastern species to identify the region-specific principal components (referred to below as the Western or Eastern PC). For each species and phenophase, we then conducted a linear regression of the onset DOY on PC1 (using the Western or the Eastern PC, as appropriate), using site mean values, to determine the extent to

which an integrative metric of climate can predict phenological metrics.

To further detect the effects of climate and geographic variables and their interactions on the onset DOY for each phenophase and species, we carried out ANOVAs on the seasonal temperature variables that were determined to be the best predictors for each species. We initially ran six separate multivariate models using each seasonal set of conditions (Tmin or Tmax for Fall, Winter, or Spring) to determine which season's temperature best predicted the DOY of each phenophase for each species. Only one temperature variable — the one that was the best predictor for each species and phenophase in model comparisons (Tmin or Tmax from one of the three seasons) — was then used in a step-wise model selection process. For the step-wise modelling, we used the minimum Akaike's Information Criterion to select variables using a forward selection process.

We carried out step-wise model selection for each species-phenophase combination to determine the strongest predictor variables for the first onset dates of bud break and flowering. These models included the following variables: the single seasonal temperature variable that provided the best fit; accumulated precipitation from October to May; and latitude, longitude, and elevation. We then carried out General Linear Models (GLMs) using only the relevant climate and geographic variables selected by the step-wise analysis, along with their interactions (all as fixed effects) to detect their significance. Finally, we re-ran these GLMs without the geographic variables in order to determine the degree to which their inclusion improved the models.

All statistical analyses were performed in JMP Pro 11 (SAS Institute Inc., Cary, NC, USA, 1989–2007).

Results

VARIATION IN PHENOPHASES AMONG SPECIES

For breaking leaf buds, *Q. agrifolia* and *Q. lobata*, the two western species, had earlier onsets with more activity periods per year and more total days in phenophase than *Q. alba* and *Q. rubra*. *Quercus lobata* had a mean duration per activity period that was longer than the other three species; individuals exhibited breaking leaf buds about twice as many days as the other focal species. *Quercus lobata* had an earlier onset date for bud break than *Q. agrifolia* (Table 3).

Similarly, *Q. agrifolia* and *Q. lobata* had earlier onsets of flowers or flower buds, with more activity periods per year

and more total days in this phenophase than *Q. alba* and *Q. rubra*. *Quercus lobata*'s mean duration per activity period was longer than that of the other species, while *Q. agrifolia* had a mean duration per activity period that was longer than *Q. rubra* but not *Q. alba*. *Quercus lobata* had an earlier onset of this phenophase than *Q. agrifolia* (Table 3).

RESPONSIVENESS TO GEOGRAPHY AND CLIMATE

Principal components analysis

Principal components analysis using all sites for which 'breaking leaf buds' was captured, and all four species, revealed that the Fall, Winter, and Spring climate variables were the primary component of variation in the PC1 axis whereas the summer variables dominated the PC2 axis (Table 4). Region and phenophase-specific PC axes were consistent with this pattern. Higher temperature conditions were generally correlated with lower precipitation across all sites and years, with the western species experiencing warmer and drier conditions than the eastern/central species. The distribution of sites within these climate spaces showed distinct separation along both PC axes for the western versus the eastern/central species (Fig. 3).

The western species were generally less responsive to the climatic gradient represented by the region-specific PC1 than the eastern/central species. The Western PC1 was a good predictor of onset DOY for flowering in *Q. agrifolia* and for budbreak in *Q. lobata* (Fig. 4), although the R^2 values for these relationships were less than 17%. By contrast, in both of the eastern/central species, the region-specific PC1 was a strong predictor of the onset dates of both phenophases, with the R^2 values for these relationships ranging from 36% to 63% (Fig. 5).

Analysis of variance

In the initial selection of seasonal variables, the first onset DOYs for the two eastern/central species (*Q. alba* and *Q. rubra*) were best predicted by Spring Tmax, whereas the two western species (*Q. agrifolia* and *Q. lobata*) were best

Table 3. Mean onset, duration and periodicity for each *Quercus* species and phenophase. Within each phenophase and metric, mean values associated with distinct superscripts signify significant differences between species using Tukey-Kramer tests. W = Western USA, E/C = Eastern/Central USA, BLB = breaking leaf buds, flowers = flowers and flower buds, DOY = day of year

Species	Region	Phenophase	N (individual-years)	Mean first onset DOY	Mean no. of episodes per year	Total duration of phenophase per year (days)	Mean phenophase duration per episode (days)
<i>Q. agrifolia</i>	W	BLB	160	93.81 ± 5.52 ^B	2.63 ± 0.18 ^A	25.21 ± 1.88 ^B	12.36 ± 1.07 ^B
<i>Q. alba</i>	E/C	BLB	112	115.88 ± 2.53 ^C	1.18 ± 0.04 ^B	14.05 ± 1.65 ^C	13.00 ± 1.62 ^B
<i>Q. lobata</i>	W	BLB	131	73.07 ± 5.07 ^A	3.02 ± 0.28 ^A	34.04 ± 2.33 ^A	21.02 ± 2.05 ^A
<i>Q. rubra</i>	E/C	BLB	136	118.96 ± 2.74 ^C	1.22 ± 0.89 ^B	14.05 ± 1.53 ^C	12.76 ± 1.45 ^B
<i>Q. agrifolia</i>	W	Flowers	122	99.39 ± 5.58 ^B	1.89 ± 0.15 ^B	24.88 ± 2.14 ^B	15.98 ± 1.62 ^B
<i>Q. alba</i>	E/C	Flowers	64	114.20 ± 2.69 ^{BC}	1.28 ± 0.09 ^B	11.22 ± 1.31 ^C	10.20 ± 1.25 ^{BC}
<i>Q. lobata</i>	W	Flowers	115	74.78 ± 4.83 ^A	3.40 ± 0.35 ^A	46.90 ± 2.49 ^A	29.18 ± 2.57 ^A
<i>Q. rubra</i>	E/C	Flowers	84	122.94 ± 3.23 ^C	1.19 ± 0.06 ^B	9.22 ± 1.09 ^C	8.52 ± 1.05 ^C

Table 4. Principal components analysis of seasonal climate variables for all species of *Quercus*, and PC1 values presented separately for each phenophase and regional pair of species. Also presented is the percent variation among the climate variables explained by each PC1. Data used for the PCA with all four species are from sites where the ‘breaking leaf bud’ phenophase was monitored, recorded and contributed to the USA-NPN database. BLB = breaking leaf buds, flowers = flowers and flower buds. Bolded values represent values over 0.5

Variable	All species BLB PC1	All species BLB PC2	All species BLB PC3	Eastern species BLB PC1	Eastern species Flowers PC1	Western species BLB PC1	Western species Flowers PC1
% variation	64.4	15.9	8.96	51.8	49.2	54.0	51.0
Tmax Winter	0.94	0.08	0.29	0.91	0.92	0.80	0.81
Tmax Summer	0.22	0.77	-0.45	0.78	0.56	0.47	0.57
Tmax Spring	0.89	0.31	0.11	0.89	0.91	0.73	0.73
Tmax Fall	0.94	0.22	0.12	0.95	0.95	0.83	0.84
Tmin Winter	0.94	0.11	0.27	0.91	0.90	0.86	0.83
Tmin Summer	0.02	0.83	-0.41	0.82	0.64	0.79	0.83
Tmin Spring	0.93	0.29	0.08	0.95	0.97	0.91	0.91
Tmin Fall	0.92	0.23	0.04	0.91	0.85	0.82	0.78
Precip Winter	-0.47	0.49	0.65	0.43	0.53	-0.47	-0.47
Precip Summer	-0.89	0.23	-0.02	-0.32	-0.18	-0.15	-0.26
Precip Spring	-0.83	0.29	0.04	-0.03	0.05	-0.73	-0.66
Precip Fall	-0.75	0.38	0.18	0.16	0.24	-0.76	-0.78
Precip Fall + Winter + Spring	-0.82	0.45	0.33	0.31	0.49	-0.84	-0.89

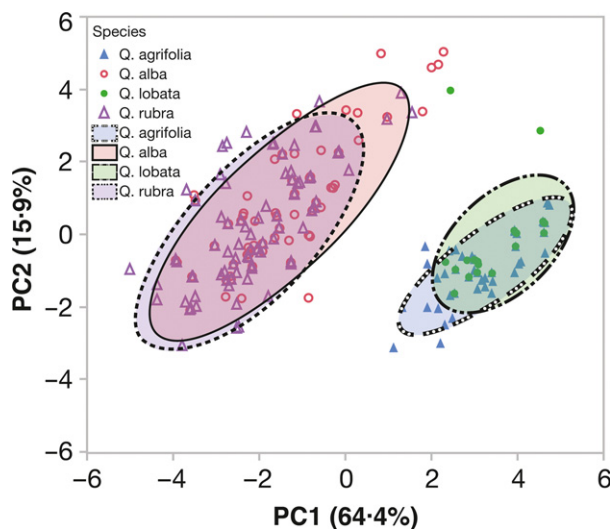


Fig. 3. PC1 plotted against PC2 for the four species, showing the distribution of climate space occupied by the sites where each species was monitored. Shaded ellipses represent the 95% confidence interval for each species.

predicted by Winter Tmin and Tmax, and Spring Tmin (Table 5). In *Q. lobata*, the timing of breaking leaf buds and flowers were both influenced by precipitation (in interaction terms with latitude, longitude and elevation), and in *Q. alba*, high precipitation promoted the early appearance of flowers or flower buds (Tables 5 and S4, Supporting Information). For flowering in *Q. rubra*, precipitation was found to have an interactive effect with Spring Tmax (Tables 5 and S8). Precipitation did not influence the DOY of either phenophase in *Q. agrifolia* or in breaking leaf buds of *Q. rubra*. Generally, the first DOY of phenophases for *Q. agrifolia* was not easily predicted by either climate or geographic variables, possibly due to its high periodicity.

When geographic location was included in the models, latitude, longitude and elevation were more likely to be selected as main effects for both phenophases in the two western taxa (*Q. agrifolia* and *Q. lobata*) than in the eastern taxa, with the exception of elevation for breaking leaf buds of *Q. alba*, and latitude for breaking leaf buds of *Q. rubra* (Table 5). For both phenophases, the model R^2 was considerably increased when geographic variables were included for the two western taxa (R^2 increased by ~ 0.3 – 0.5 with geographic variables included) whereas the eastern taxa had relatively small changes (within ~ 0.1 increase in R^2) in the model R^2 (Table 5).

Discussion

INTERSPECIFIC VARIATION IN PHENOLOGICAL RESPONSES TO CLIMATIC AND GEOGRAPHIC DRIVERS

We detected species-specific responsiveness to climate drivers, both within and between ecoregions. While maximum spring temperatures overall were more useful for predicting the onset of phenophases in the eastern taxa, winter and/or minimum temperatures tended to be more important for the western taxa. Interestingly, we did not find strong evidence for precipitation as a major driver in triggering the onset of phenophases in the western taxa compared to the eastern taxa. However, it is possible that the timing and variability in this driver may play a role in determining the duration and number of episodes exhibited by a species at a given site. Among species that have been well monitored, species-specific responses to specific drivers (such as winter or spring Tmax or Tmin) can be used to predict how these species will be affected by future climate change, particularly in temperate ecosystems, where ongoing change is expected to continue to advance spring conditions and result in greater variability and uncertainty in the timing of precipitation (Gherardi & Sala

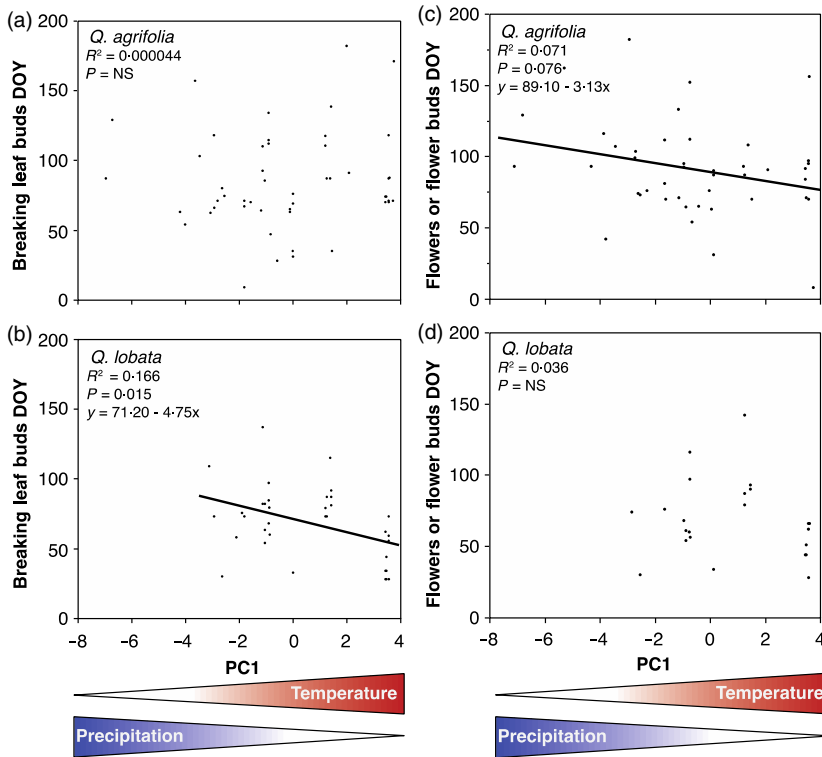


Fig. 4. Linear regressions of the onset day of year (DOY) for breaking leaf buds (a, b) and flowers or flower buds (c, d) versus the region-specific PC1 for *Quercus agrifolia* and *Q. lobata*. Regression lines shown only for linear relationships for which the slope differs significantly from zero.

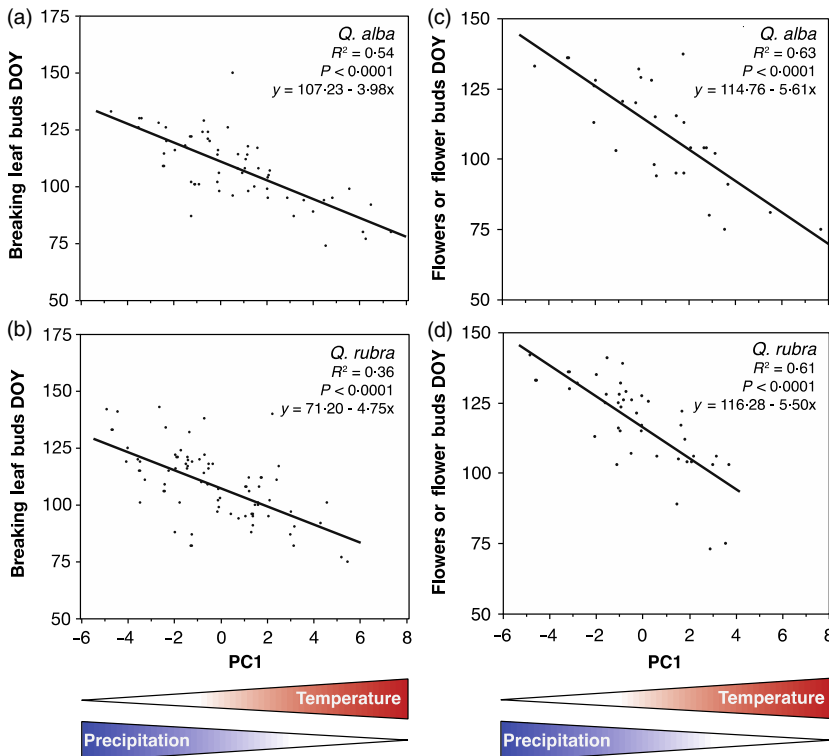


Fig. 5. Linear regressions of the onset day of year (DOY) for breaking leaf buds (a, b) and flowers or flower buds (c, d) versus the region-specific PC1 for *Quercus alba* and *Q. rubra*.

2015; Chen *et al.* 2016). Predictions concerning how entire communities are likely to change phenologically, however, will require the monitoring and analysis of their component species.

The species-specific nature of phenological sensitivity applies to all of the metrics examined here, including onset, intra-annual episodic tendency, and duration. Specifically, the

western taxa (*Q. agrifolia* and *Q. lobata*) exhibited a greater number of episodes per year, and longer durations, of both breaking leaf buds and flowering, compared to their temperate zone congeners distributed in the eastern and central U.S. (*Q. alba* and *Q. rubra*). This type of episodic behaviour suggests that onset date alone is not always the most informative metric for tracking phenological change, particularly in

Table 5. Climatic and geographic factors influencing onset DOY ($P < 0.1$) in four species of *Quercus*. Factors were considered influential if they were identified as a significant main effect or interaction term in the best GLM constructed using both climatic and geographic variables. Full GLM results are found in Table S1–S8. W = Western USA, E/C = Eastern/Central USA, BLB = breaking leaf buds, flowers = flowers or flower buds. ‘M’ indicates that a factor was identified as a significant main effect, and ‘I’ indicates if it was identified as part of a significant interaction term

Species	Region	Phenophase	Best model R^2						
			Best model R^2 Climate only	Climate + Geography	Temperature variable	Accum Precip	Latitude	Longitude	Elevation
<i>Q. agrifolia</i>	W	BLB	0.017	0.310	Tmin Spring (I)	–	I	M	
		Flowers	0.144	0.584	Tmin Winter (I)	–	M	M	M
<i>Q. alba</i>	E/C	BLB	0.588	0.692	Tmax Spring (M)	–	I	–	M
		Flowers	0.736	0.829	–	M	–	–	–
<i>Q. lobata</i>	W	BLB	0.286	0.726	Tmin Winter (M)	I	I	M	M
		Flowers	0.392	0.709	Tmax Winter (M)	I	M	I	I
<i>Q. rubra</i>	E/C	BLB	0.400	0.425	Tmax Spring (M)	–	M	–	–
		Flowers	0.492	0.433	Tmax Spring (M)	I	–	I	–

species and phenophases that may be triggered by precipitation events or other periodic conditions and that do not exhibit a single, uninterrupted period of seasonal activity.

INTERSPECIFIC AND REGIONAL VARIATION IN NUMBER AND DURATION OF EPISODES PER PHENOPHASE

While the California species have more episodes per year of both breaking leaf buds and flowering than *Q. alba* and *Q. rubra*, as well as longer durations of each phenophase over the course of entire growing seasons (Table 3), it is not known whether the intensity of these phenophases (i.e., the proportion of an individual’s total leaf or flower production that is displayed at any given time) also differs between the California versus Central/Eastern U.S. taxa. One explanation for the tendency of the Western taxa to exhibit a higher number of phenophase episodes and longer durations is that this pattern may be an adaptive response to unpredictable and variable water availability; in other words, trees may respond to intermittent resource pulses with short episodes of leaf or flower production (Childs, Metcalf & Rees 2010; Berger & Ludwig 2014).

Alternatively, the periodicity of these phenophases in the western taxa may reflect constraints imposed by variable environmental conditions. For example, where water availability is episodic and limits new growth or reproduction, longer leafing and flowering durations may necessitate a reduction in leaf or flower production at any given time (Nord & Lynch 2009; Kuster *et al.* 2014). We are aware of no study to date that has reported a trade-off (expressed among individuals or among species) between the duration and the intensity of any phenophase. While we found limited evidence that precipitation influences the onset of leaf and flower production, future work is needed to better understand its effects on phenophase duration and intensity.

THE INDEPENDENT EFFECTS OF GEOGRAPHIC LOCATION AND CLIMATIC FACTORS ON ONSET DATES

We found that, independent of climatic variables, geographic variables had a strong influence on the DOY of both

phenophases, particularly in the two western species (Tables S1–S8). Additionally, integrative metrics of climate (PC1) were more strongly correlated with the onset DOY of both phenophases in the eastern than in the western species (Figs 4 and 5). The significant effects of latitude, longitude and elevation (independent of climatic variation) indicate that factors other than temperature and precipitation at local sites, such as biotic interactions, soil moisture and type, and humidity, are likely to be important in triggering phenological transitions. In particular, genetic variation contributing to local adaptation needs to be considered when untangling the drivers of phenological variation at large-scale spatial and temporal patterns. Thus, researchers should be cautious in applying space for time substitutions as a path towards predictive phenological, particularly in taxa where geographic factors independent of climate are likely to influence phenological behaviour (Wittich & Liedtke 2015).

The relationships among sites between climatic variables and mean DOY detected in this study probably reflect a combination of plastic and genetically based (evolutionary) responses, as data were pooled across years, with many sites monitored multiple times in the timeframe of the study. Parsing the relevant contribution of phenotypic plasticity and genetically based adaptation to the observed site means is beyond the scope of this particular study. However, distinguishing between plasticity and genetically based variation in phenological onset dates will be feasible and valuable to investigate in the future as the spatial and temporal extent of the National Phenology Database continues to grow.

GEOGRAPHIC OVERLAP IS MORE IMPORTANT THAN PHYLOGENETIC RELATEDNESS IN PREDICTING PHENOLOGICAL RESPONSIVENESS OF CONGENERS

Interestingly, we found that the sensitivities of each of the *Quercus* species studied here were more similar to the taxon that occupied a similar geographic range (e.g., *Q. agrifolia* and *Q. lobata*) than to the taxon with which they shared phylogenetic history. For example, although *Q. agrifolia* and *Q. rubra* are more closely related to each other than to

Q. lobata and *Q. alba*, respectively, they were each more similar to the species with which their geographic range overlapped (Table 3); the same pattern was true for *Q. alba* and *Q. lobata* (Manos, Doyle & Nixon 1999; Hipp *et al.* 2014). Despite the smaller geographic area (Table 1; Fig. 1) and climate space (Fig. 3) occupied by the two western taxa, geographic location was critical in identifying the best predictive models in the western taxa, potentially due to greater habitat variability or community structure variability occupied by the focal sites within the species ranges.

In California, geographic attributes such as longitude and elevation strongly influence plant community composition (Bakker 1984; Cornwell & Ackerly 2009; Fernandez-Going *et al.* 2013), which in turn might influence the environmentally induced or genetically based onset dates of local bud break or flowering. For example, if the species composition and competitive interactions among sympatric taxa change with elevation, latitude, or longitude, then site-specific DOY for bud break or flowering may evolve (at least in part) independently of temperature or precipitation. Our results support this hypothesis, as longitude and elevation were more likely to affect DOY in our models for the California species than for the eastern and central U.S. species (Table 5). This evaluation is further supported by the considerable improvement in model R^2 when geographic variables were included for the western taxa compared to the eastern taxa (Tables S1, S2, S5 and S6). Alternatively, the western oak species may be adapted to greater inter- and intra-annual climate variability and thus have more complex multi-driver responses to phenology related to the resource status and prior conditions experienced by individual trees. Thus, more research is needed to identify the mechanistic drivers and genetic components of phenology, particularly in the context of factors other than temperature and precipitation.

COMPARISON WITH OTHER OAK STUDIES

Our results agree to some extent with previous models that have been developed to describe and predict phenological activity in oaks. Previous studies have detected a strong role of photoperiod for multiple *Quercus* species, which may have been reflected in our models in which latitude had a significant effect on DOY independent of temperature (Table 5). Specifically, *Q. alba* has been found to respond to photoperiod whereas *Q. rubra* does not (Way & Montgomery 2015). However, for breaking leaf buds, latitude was determined to be a main effect in our *Q. rubra* model and to interact with elevation in *Q. alba*.

Similar to recent studies, we found that in three of the four focal species (*Q. alba*, *Q. lobata*, and *Q. rubra*), temperature had a significant accelerating effect on onset DOY (Tables S3, S5, S6, S7 and S8) (Menzel 2000; Askeyev *et al.* 2005; Cleland *et al.* 2012; Marchin *et al.* 2015; Medvigy *et al.* 2015; Wittich & Liedtke 2015; Yu *et al.* 2016). Surprisingly, however, we did not find support for a stronger role of precipitation in predicting the DOY of phenophases in the western taxa than in the temperate taxa, in contrast to patterns

reported by Fairley & Batchelder (1986). The deep taproots of *Q. agrifolia* and *Q. lobata* may buffer them against the effects of inter-annual variation in precipitation, reducing their sensitivity to seasonal or annual rainfall. By contrast, precipitation was the sole factor predicting the onset of flowering in *Q. alba*, an eastern/central U.S. species, and was important in an interaction term in *Q. lobata* and *Q. rubra*. *Quercus agrifolia*, the western species that exhibited the greatest number of intra-annual phenological episodes, did not respond predictably to either climatic driver, suggesting that first onset DOY is not a meaningful metric by which to track or to predict the phenology of this species (at least in response to temperature and rainfall).

POTENTIAL CONSEQUENCES OF SPECIES-SPECIFIC SENSITIVITIES TO CLIMATE

Given variable responsiveness within and between species related to local conditions, the impacts of changing conditions and phenologies on population dynamics is likely to vary regionally. If interacting pairs or networks of species differ in their response to local climatic shifts, so may the nature of their relationships. Mutualistic relationships may break down, reducing fruit and seed set in plants whose seed dispersers and pollinators are no longer as abundant or as effective during the height of flower and fruit production. In the case of *Quercus*, which is wind-pollinated, the timing of acorn availability could have considerable consequences for populations of insect herbivores, birds and mammals that depend on acorns, as oaks often act as keystone species within their habitats, providing a primary food source for many animals. Additionally, plants whose flowering times currently overlap may experience decreased fertilization if they flower asynchronously and, collectively, attract fewer pollinators. Phenological shifts of plant populations could also expose them to herbivores from which they previously escaped in time; in this case, new antagonist relationships could develop. Finally, if co-occurring species respond differently to a given climatic change, then the community-wide distribution of vegetative growth and flowering times will change, potentially becoming more peaked, multi-peaked, or broader; flowering distributions could change to yield floral 'droughts' during the flowering period.

These results highlight the value of studying a range of phenological metrics, including episodic behaviour and duration, to better characterize phenological behaviour and to generate more holistic predictions of phenological responses to short-term variation and to long-term change. Future work will investigate how peak phenological activity varies across species and time, and how this relates to resource availability, species interactions, and drought. In addition, it is essential to collect and analyse phenological data from a variety of species and ecosystems, as even closely related species respond in distinct and sometimes idiosyncratic ways to a broad spectrum of potential climatic drivers. Finally, the strong role of geographic location, independent of climate, provides evidence for additional cues, interspecific interactions,

phenotypic plasticity, and local adaptation that merit further study in order to generate robust phenological predictions.

Authors' contributions

K.G. and S.M. conceived the ideas and designed methodology; K.G. compiled the dataset; K.G., N.R. and S.M. analysed the data; K.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qb70g> (Gerst, Rossington & Mazer 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Best-fit GLM model for the DOY of *Quercus agrifolia* breaking leaf buds.

Table S2. Best-fit GLM model for the DOY of *Quercus agrifolia* flowers and flowers buds.

Table S3. Best-fit GLM model for the DOY of *Quercus alba* breaking leaf buds.

Table S4. Best-fit GLM model for the DOY of *Quercus alba* flowers and flower buds.

Table S5. Best-fit GLM model for the DOY of *Quercus lobata* breaking leaf buds.

Table S6. Best-fit GLM model for the DOY of *Quercus lobata* flowers and flower buds.

Table S7. Best-fit GLM model for the DOY of *Quercus rubra* breaking leaf buds.

Table S8. Best-fit GLM model for the DOY of *Quercus rubra* flowers and flower buds.