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Extreme winter warm event causes exceptionally early bud break for many woody species

LAURA M. LADWIG,† JENNIFER L. CHANDLER, PETER W. GUIDEN, AND JONATHAN J. HENN

Department of Integrative Biology, University of Wisconsin—Madison, 250 N. Mills Street, Madison, Wisconsin 53706 USA

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Abstract. In many ecosystems, climate is changing faster during winter compared to other seasons. However, we lack basic information about the responses of many species to winter climate change, including extreme warm events. Extreme warm events may have particularly strong influences at the end of winter, when some species begin to break dormancy while the risk of freezing remains high. Here, we monitored bud burst of 101 temperate woody species following an extreme warm event during winter to investigate species responses to this anomalous event and determine whether functional traits predicted species responses. Following six consecutive days of extreme warm temperatures in winter, nearly half the surveyed tree and shrub species had an advanced stage of bud phenology. Responding species were most likely to be shade-intolerant, phylogenetically related, and have weaker dormancy requirements. Based on established species response thresholds to spring temperatures in the region, species were expected to be unresponsive to warm temperatures this early in the year, yet many species broke dormancy. Species responses to this extreme winter warm event highlighted how climate change can alter well-established species–climate associations. In an era of increasing climate change creating novel winter conditions, continued monitoring both long-term and following extreme events is needed to understand new species–climate dynamics.

Key words: bud break; climate change; deciduous; extreme weather event; phenology; winter ecology.

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† **E-mail:** lmladwig@wisc.edu

INTRODUCTION

In an era of global change, climate may change faster than many species can respond (Zhu et al. 2012, Fu et al. 2013), and determining how species respond to climate change is critical to maintaining biodiversity and healthy functioning ecosystems. Moreover, rapid anthropogenic climate change may create highly novel environmental conditions when temperature or precipitation differs greatly from historical averages (Williams et al. 2007, Williams and Jackson 2007, Radeloff et al. 2015). While the causes and consequences of novelty and global change are often measured in terms of annual or seasonal means (Williams et al. 2007), an increase in the frequency, duration, or intensity of extreme events (Jentsch et al. 2007) may also provide an often-overlooked dimension of novelty. This rapid environmental change and increase in extreme events are especially concerning for species that rely on evolutionary adaptations to cope with normal variation in climate (e.g., deciduous leaf habit), because adaptations that historically enhanced fitness may be maladaptive in the Anthropocene (Sih et al. 2011). For example, in temperate systems, cumulative growing degree days historically provided a reliable and adaptive indicator for the arrival of the growing season (Zohner et al. 2016), but warmer-than-average winter temperatures could lead to an early initiation of bud burst followed by damaging below-freezing temperatures (Gu et al. 2008, Hufkens et al. 2012, Augspurger 2013).

For terrestrial plants, the timing of spring phenology has long interested researchers (Sparks and Carey 1995), with natural temporal variation in leaf emergence visually apparent across the temperate landscape (Panchen et al. 2014). The timing of bud break varies among species (Lechowicz 1984, Vitasse et al. 2008), geographic locations (Lechowicz 1984, Morin et al. 2009), and climatic history and interannual variation (Vitasse et al. 2009, Polgar and Primack 2011, Fahey 2016, Muffler et al. 2016, Zohner et al. 2017). Early leaf out confers a competitive advantage to individuals by advancing, and often extending, the growing season, but also potentially exposes expanding buds and young tissues, the most temperature-sensitive phenological stage (Vitasse et al. 2014), to damaging late spring cold events (Gu et al. 2008, Augspurger 2013, Muffler et al. 2016). Woody species with the earliest bud burst in spring often have diffuse wood porosity with smaller vessel elements that are less prone to freeze damage (Lechowicz 1984, Michelot et al. 2012, Panchen et al. 2014) and are often shade-intolerant, early-successional species (Caffarra and Donnelly 2011, Basler and Körner 2012).

In recent decades, altered timing of phenological events (Tang et al. 2016) particularly associated with the beginning (Chmielewski and Rötzer 2002, Badeck et al. 2004, Menzel et al. 2006, Schwartz et al. 2006) and end of the growing season (Vaganov et al. 1999, Bertin 2008, Fu et al. 2018) are some of the most noticeable biotic responses to climate change. Warmer springs have advanced the start of growing seasons by days to weeks (Ellwood et al. 2013, Fahey 2016), often with cascading consequences to ecosystem and community processes (Inouye 2008, Polgar and Primack 2011). However, species responses to warmer springtime temperatures are variable (Murray et al. 1989) and may depend on species traits (e.g., shade tolerance, wood anatomy, and home range; Panchen et al. 2014) and dormancy requirements (Cannell 1996, Chmielewski and Rötzer 2002, Richardson et al. 2006, Caffarra and Donnelly 2011, Basler and Körner 2012, Fu et al. 2013, Way and Montgomery 2015). As temperatures begin rising faster than plant response rates (Fu et al. 2015), it remains unclear just how early into dormancy plants can respond to warm temperatures.

In many temperate systems, climate change in winter is outpacing changes in other seasons (Notaro et al. 2014), and this includes an increase in extreme events that often have different, sometimes more severe, ecological consequences than gradual changes in mean climatic conditions (Smith 2011). Both magnitude and timing of extreme events shape ecological response, as an extreme cold event during spring can cause significant damage (Muffler et al. 2016) while equally extreme cold temperatures in winter may have minimal impact on woody species (Vitra et al. 2017). Extreme warm events in spring can trigger a false spring—an erroneous detection of the end of winter—(Parmesan and Hanley 2015) and an earlier start to the growing season (Fahey 2016) but it is unclear whether and how plants respond to extreme warm events during winter. Warm events during winter may come too early to elicit a biotic response. For example, across a 20-yr bud break record in a temperate forest, Augspurger (2013) documented earlier bud break associated with warmer temperatures from March onward, but plants were not responsive to warm temperatures before 17 March. Alternatively, a long-duration extreme warm event may overwhelm and override chilling, heat, or photoperiod dormancy requirements, causing plants to respond unexpectedly early (Fahey 2016). If this happens during winter, newly established young tissues are likely to be damaged when the typical cold temperatures of winter return. Early warm events are predicted to increase in frequency (Schwartz et al. 2006) yet we have a poor understanding of plant response to winter warm events in temperate systems.

Here, we surveyed bud break of woody species following an extreme warm event during winter (17–22 February 2017). Our study is unique in that we examine the response of 101 species to an extreme warm spell during winter, which occurred at a date when cold temperatures were nearly certain to return. This study builds upon work showing that warming spring temperatures can initiate early bud break in eastern deciduous species (Ellwood et al. 2013, Fahey 2016) and also allows us to examine which species may be most susceptible to novel extreme events occurring well before the typical arrival of spring. This warm event, therefore, provided a natural experiment to (1) test whether woody plant species will break dormancy and (2) identify predictive characteristics of species more at risk of erroneously responding to a winter warming event. We hypothesized that species' responses would be minimal given the early timing of the warm event. Although, if species were responsive to the unseasonably warm winter temperatures, we expected that species with traits associated with early spring phenology (e.g., early successional, diffuse-porous wood anatomy, and shrub growth habit) would have a higher probability of breaking bud. Additionally, the climate under which species evolved can influence the timing of spring phenology and responsiveness to false springs (Morin et al. 2009, Muffler et al. 2016, Zohner et al. 2017). Therefore, we predicted that species from colder regions would be more likely to break bud because they have more cold-tolerant tissues, thus decreasing the damage risk of making an erroneous response to warm temperatures. Furthermore, we predicted that species from climates with less variable spring temperatures would also respond because the climate under which they evolved did not prepare them for false springs (Zohner et al. 2017).

METHODS

Study site

Surveys of bud break were conducted in Madison, Wisconsin, USA, in the Longenecker Horticultural Garden at the University of Wisconsin-Madison Arboretum (UW Arboretum; 43.043135, −89.429459). Arboretums and Botanical Gardens provide excellent locations for studying interspecific responses of bud break to climate change as they contain many species growing together in a common environment (Primack and Miller-Rushing 2009, Jalili et al. 2010, Panchen et al. 2014, Zohner and Renner 2014, Fahey 2016, Muffler et al. 2016). In Madison, Wisconsin, monthly average $T_{\max}$ and $T_{\min}$ during winter (December, January, February) are −0.5°C and −11.6°C, respectively, with an average annual snowfall of 129 cm (Midwestern Regional Climate Center 2018).

Weather data

Weather data were gathered from the Dane County Regional Airport, 12.55 km from the sample location, and closely align with temperatures at the UW Arboretum (Appendix S1). To quantify whether the warm temperature event during February 2017 was an extreme event, weather conditions during the event had to either fall below the 5th percentile or above the 95th percentile based on the 50-yr climate record to be considered extreme (Smith 2011, Hoover et al. 2014). Many aspects of a weather event can be extreme, including the magnitude, duration, or timing; therefore, we evaluated the extremity of this warm event in several ways. First, to test whether the magnitude of the daily temperatures was extreme, we compared the daily $T_{\max}$ during our study to the 50-yr average $T_{\max}$ for 15–28 February. Second, to test whether the duration of the event was extreme, we first defined the duration of the event as the number of consecutive days with temperatures above the 95th percentile and then examined the distribution of extreme event durations over the past 50 winters. Lastly, to test whether the timing of the event was extreme, we evaluated the timing of both magnitude (absolute temperature) and duration (consecutive days of with extreme magnitude temperatures). For timing of magnitude, we examined the long-term distribution of the first day of year (DOY) when $T_{\max} \geq 20°C$ (the maximum temperature observed during the 2017 warm event). For timing of duration, we examined the long-term distribution of DOY when climate of similar magnitude and duration to the 2017 warm event ($T_{\max} \geq 15°C$ for six consecutive days) first occurs each year. We also examined cumulative growing degree days (GDD; >10°C, Raulier and Bernier 2000) occurring during the month of February over the past 50 yr to examine how 2017 compared to prior years.

Field surveys

Our ecological response variable was the phenological phase of deciduous tree and shrub buds after a week of warm temperatures. All measurements were recorded on a single day—the day after the warm event ended (23 February 2017). We examined canopy buds, using binoculars when necessary, to determine phenological phase based on major classifications of Augspurger (2009), which included five stages: (1) buds dormant and closed; (2) buds swollen with scales parted revealing underlying tissues; (3) shoot emerging from bud scales and elongating, green present, but no major leaf expansion; (4) undergoing major leaf expansion; and (5) flower undergoing major expansion. The last three stages did not necessarily represent increasingly advanced phenological stages, as flowering occurs before leaf expansion for some species. The most abundant phenological phase was recorded as well as the most advanced phenological phase that occurred on at least three branches. Six people conducted the field surveys, and to ensure consistent classification of bud phases among observers, all observers first surveyed a subset of trees, after which groups of two observers completed further surveys.

Species traits

Many factors influence the timing of bud break, and we examined the influence of several traits related to biogeography, ecological strategy, and evolutionary history on the probability of bud break (Table 1). First, the timing of bud burst can relate to the climate of a species' native range (Vitasse et al. 2014, Zohner et al. 2017). We extracted species native ranges from occurrence records from the GBIF database (Global Biodiversity Information Facility; GBIF 2017) using the rgbif package (Chamberlain 2017), limiting occurrence records to those of vouchered specimens with known sources and a spatial uncertainty of <10,000 m. To match species ranges with climate data, we extracted bioclimatic variables of interest (minimum temperature of the coldest month, spring temperature variation, and isothermality) for all BioClim (Fick and Hijmans 2017) grid cells overlapping with the species' range. To reduce spatial sampling bias, we randomly selected one occurrence record per grid cell of BioClim data (10-arcmin^2 area; Beck et al. 2014). From these cells, we calculated the 10th quantile of minimum temperatures for each species, which provided an estimate of minimum temperatures in each species' native range while reducing the chance that an outlier would bias this metric. We also calculated spring variability within a species range, as species that are accustomed to high variation in spring temperature may be less likely to respond to a winter warm event. Lastly, we calculated the mean isothermality, or seasonality, for each species' native range, which describes how variable monthly temperatures are relative to annual temperature variation—low variation equates to high isothermality.

In addition to climate of the native range, we also evaluated several species characteristics related to timing of bud break, including growth habit, shade tolerance, and wood anatomy. For growth habit, species were categorized as a tree or shrub based on USDA PLANTS distinctions (plants.usda.gov) and the accession list from UW

Table 1. Response variables included in statistical models comparing species characteristics to early bud break following warm temperatures in February 2017.

Parameter	Predicted response to extreme warm event	Variable used	Data source
Shade tolerance	Shade-intolerant species respond more than shade-tolerant species (Augspurger et al. 2005)	Score ranging from 0 (low tolerance) to 5 (high tolerance)	Niinemets and Valladares (2006)
Wood anatomy	Species with diffuse wood respond most strongly, then semi-porous species, and less response from porous species (Panchen et al. 2014, Fahey 2016)	Ring, semi-ring, diffuse	Panchen et al. (2014)
Growth habit	Shrubs respond more than trees (Panchen et al. 2014)	Tree or shrub	United States Department of Agriculture PLANTS database (www.plants.usda.gov)
Seasonality	Stronger response from species from less seasonal habitats (Zohner et al. 2017)	Mean isothermality in native range	BioClim BIO7 (www.worldclim.org/bioclim)
Minimum spring temperature	Strongest response from species from areas with mild spring temperatures (Vitasse et al. 2014)	10th quantile of minimum temperature in native range	BioClim BIO6 (www.worldclim.org/bioclim)
Spring temperature variation	Strongest response from species from stable climates (Zohner et al. 2017)	Standard deviation of mean minimum spring temperature in native range	Zohner et al. (2017)

Arboretum. Shade tolerance data for each species were obtained from Niinemets and Valladares (2006) and were on a scale ranging from no shade tolerance (0) to maximum shade tolerance (5). Wood anatomy (ring-, semi-ring, or diffuse-porous) was extracted from Panchen et al. (2014). To account for non-independent responses based on phenological patterns formed through evolutionary time, we included a phylogeny in our evaluations. Specifically, we used a published tree of 31,749 plant species that is based on GenBank data for seven gene regions for land plants (Zanne et al. 2014, Qian and Jin 2016). We subset the tree to include only species surveyed in this study, resulting in a tree consisting of 86 species.

We also examined whether species response to the warm event was related to the strength of dormancy cues related to chilling, warm forcing, and photoperiod, with the prediction that species with weaker dormancy requirements would break bud and those with stronger dormancy requirements would remain dormant. Dormancy requirements were obtained for a subset of species from Zohner and Renner (2014) where species were placed in broad categories based on factors known to affect their dormancy from experimental evidence. These categories include (1) photoperiod + high chilling + forcing, (2) high chilling + forcing, (3) low chill + forcing, and (4) forcing. Although there is likely variation in the strength of the requirements in each category, these designations allowed us to test the greatest number of species.

Statistical analysis

All statistical analyses were run at the species level, and bud break was treated as a binary variable (dormant/active) with all advanced bud break categories grouped into active bud status. If individuals within a species had different bud stages, the species was categorized as active since some individuals expressed advanced phenology. We tested the phylogenetic signal of early bud break response by calculating *D*, a measure of phylogenetic signal in binary traits (Fritz and Purvis 2010) where a value of 0 indicates random assortment of traits on the phylogeny and a value of 1 corresponds to the Brownian motion expectation. Brownian motion can be used as a model for the development of trait distributions through evolution where small random changes accumulate through time, approximated as a random walk. To test whether early bud break was randomly distributed or clumped within the phylogenetic tree, we randomized the tips of our tree 1000 times under random and Brownian motion conditions and comparing our observed *D* value to these randomizations using the phylo.d function in the geiger package (Harmon et al. 2008). If early bud break was not completely random or there was evidence of Brownian motion evolution (high *D*), we ran both phylogenetic generalized linear models and generalized linear models without phylogenetic corrections to further test the influence of phylogeny on bud response and evaluate the extent to which shared evolutionary history predicts bud break compared to other species traits. Phylogenetic models were fit using the phylolm package (Ho and Ane 2014), and non-phylogenetic models were fit using the glmr function in the lme4 package (Bates et al. 2015). To determine whether species traits were related to their bud breaking ability and to detect relative explanatory value of each predictor variable, we fit single-predictor models for each hypothesized trait as predictor variables. This allowed us to avoid having to consider a large number of models with different combinations of predictors, which inflates the risk of mistakenly identifying a predictor as meaningful when it is not (i.e., Type I error). Information on dormancy requirements was not available for most of our species, which limited our ability to include dormancy requirements in the aforementioned statistical analysis. Instead, for the limited subset of species with data available (25 species), we used a G test of independence using the G.test function in the RVAide-Memoire package (Hervé 2017) to examine whether species responses (dormant vs. active) varied among the four dormancy classes compiled by Zohner et al. (2014). For all statistical tests, alpha = 0.05. All statistical analyses were run in R (R Foundation for Statistical Computing, Vienna, Austria, version 3.2.1).

RESULTS

Weather extremes

The warm event of February 2017 was extreme in magnitude, timing, and duration. For magnitude, the $T_{\max}$ of 20°C that occurred on 22 February 2017 was above the long-term average $T_{\max}$

of 1.47° ± 0.72°C (mean ± SE) and the 95th percentile (9.24°C; Fig. 1A) for 22 February. For duration, over the past 50 winters when temperatures reached >10°C, the minimum growing degree requirement (Raulier and Bernier 2000), the length of the warm event was typically 1 d. The warm event in 2017 lasted 6 d, which was well above the mean (1.8 ± 0.10 d) and 95th percentile (4 d) and only one warm event during the preceding 50 yr exceeded the 2017 event duration (Fig. 1B). Growing degree days in February were historically rare: GDD only accumulated in February during two of the past 50 yr, and the 3.95 GDD that accumulated during February of 2017 exceed all previous 50 yr (Fig. 1C). The timing of an event of such magnitude was also extreme; the first day of the year with a $T_{\max} \geq 20°C$ on average occurs on the 88th day of the year (27 or 28 March), but in 2017, it occurred on day 53 (22 February; Fig. 1D). Furthermore, for timing of duration, the DOY when $T_{\max}$ reaches 15°C for six consecutive days on average occurs at day 105 (14 or 15 April), but in 2017, it occurred nearly 2 months early on day 53 (22 February; Fig. 1D).

Bud break

Of the 101 species evaluated, 45 were in an advanced phenological stage after at the end of the extreme warm event (Table 2). Most of the advanced buds were in the second stage (buds swollen), yet eight species showed some degree of green or expanded floral tissues present. For the univariate generalized linear models (GLMs) which tested whether traits were related to bud break, shade tolerance was the only trait that was significantly related to early bud break where less shade-tolerant species were more likely to have active buds ($P = 0.045$; Table 3, Fig. 2). Mean isotherm and spring variation were marginally significant ($P = 0.055$, $P = 0.077$, respectively) where species from areas with less seasonal temperature variation and less variable springs were more likely to have active buds (Table 3, Fig. 2).

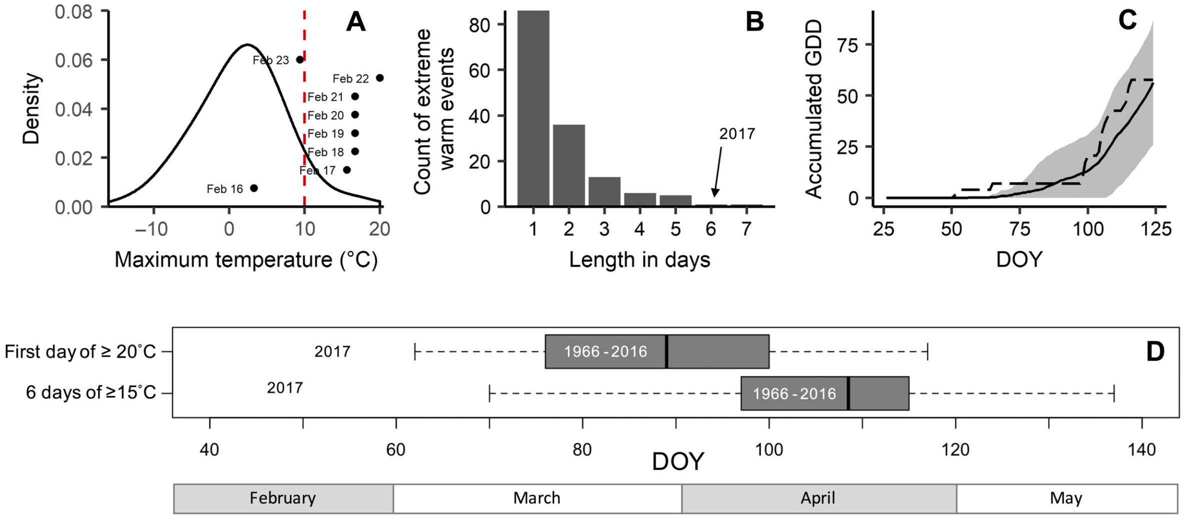

Fig. 1. (A) Density plot of maximum temperatures on 17–22 February during the 50 yr prior to 2017, with a red dashed line representing the 95th percentile of these temperatures. Labeled points represent the daily maximum temperatures (x-axis) for the days immediately before (16 February), during (17–22 February), and after (23 February) the 2017 warm event and are arranged chronologically from bottom to top. (B) Histogram of duration of extreme (95th percentile) warm event during winter for 2017 (indicated with an arrow) and 50 yr prior. (C) Accumulated growing degree days (GDD) at the beginning of the year for 2017 (dashed line) and the 50-yr mean (black line) with standard deviation (gray). (D) The timing (day of year [DOY]) of the first ≥20°C temp of the year and the timing of the first 6-d event of the year when temps reach at least 15°C for all days for 2017 relative to the 50-yr median.

Table 2. Count of species in each phenological stage on 23 February 2017.

Count	Phenological stage				
	(1) Bud closed	(2) Bud swollen	(3) Shoot emerging	(4) Leaf emerged	(5) Flower emerged
Most advanced phenological stage	56	37	3	2	3

Notes: Specifically, stages included (1) buds dormant and closed; (2) buds swollen with scales parted revealing underlying tissues; (3) shoot emerging from bud scales and elongating, green present, but no major leaf expansion; (4) undergoing major leaf expansion; and (5) flower undergoing major expansion.

Table 3. Model results of univariate statistical tests for determining associations between species characteristics and early bud break.

Model	Variable	Estimate	AIC	*P*
GLM	Intercept	−0.278	81.30	0.295
	Mean isotherm	−0.641	78.83	0.055
	Mean spring variability	−0.500	79.99	0.077
	Minimum temperature (10th quartile)	−0.198	82.75	0.461
	Shade tolerance	−0.593	78.88	0.045
	Habit	0.016	83.30	0.977
	Wood anatomy	−0.102	83.26	0.847
Phylogenetic GLM	Intercept	−0.302	72.94	0.33
	Mean isotherm	−0.362	73.33	0.19
	Mean spring variability	−0.199	74.49	0.45
	Minimum temperature (10th quartile)	−0.001	74.93	0.99
	Shade tolerance	−0.379	73.34	0.19
	Wood anatomy	0.000	74.95	0.99
	Habit	0.001	75.03	0.99

Note: AIC, Akaike's information criterion.

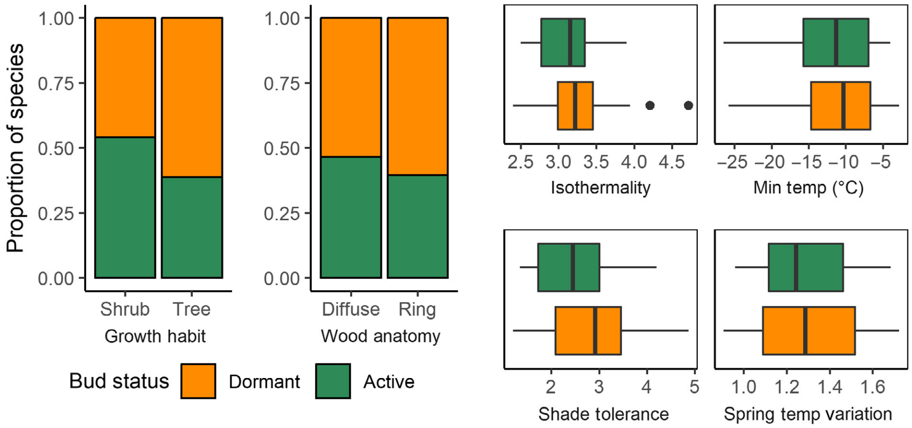

Fig. 2. Bud status (dormant vs. active) of tree and shrub species following the winter warm event in February 2017 based on species traits and climate characteristics from species' native range. Wood anatomy categories are diffuse-porous or ring-porous. Isothermality and spring temp variation are mean values from species' native range while min temp is the 10th percentile from the species' native range.

Phylogenetic signal in early bud break was $D = 0.643$ and was neither randomly distributed ($P < 0.001$) or distributed based on Brownian motion expectations ($P < 0.001$; Fig. 3). For the univariate phylogenetic GLMs which considered phylogenetic relatedness as a predictor of trait and bud break associations, none of the tests were statistically significant ($P \geq 0.19$ for all tests;

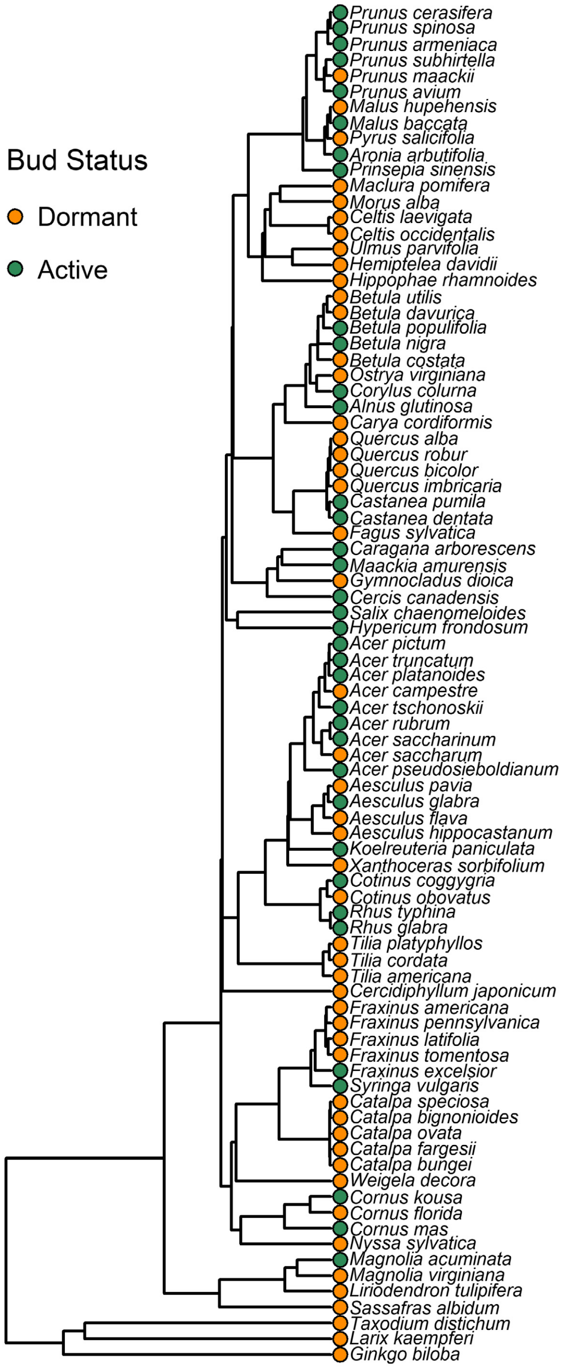

Fig. 3. Phylogenetic tree of trees and shrubs surveyed, with species color-coded by phenological stage (bud dormant vs. active) after the extreme warm winter event in February 2017.

Table 3). For a subset of the species with available data on dormancy requirements, bud break statistically varied based on the intensity of dormancy requirements (P = 0.002, G = 14.819, df = 3), as most species with only warm forcing or low chill requirements broke bud while species with high chilling, heat forcing, and photoperiod requirements remained dormant (Fig. 4).

DISCUSSION

Nearly half the tree and shrub species exhibited advanced phenology following this extreme warm event (Table 2). Given the untimely nature of this event—with warm temperatures occurring nearly two months early—we expected few species to break dormancy. But, the extended duration of the event—six consecutive days of above average temperatures—presumably provided enough heat accumulation to fulfill the forcing dormancy requirements for many species. Although bud burst is advancing as spring temperatures warm (Schwartz et al. 2006, Ellwood et al. 2013), plants cannot keep pace with continually advancing temperatures (Fu et al. 2015) and there are temperature or photoperiod thresholds before which plants do not respond to warm temperatures (Augspurger 2009). For example, at a site 350 km (3°) south of ours in central Illinois, warm temperatures before 17 March did not initiate plant growth (Augspurger 2009). We presumed a slightly later threshold would be evident at our more northern study location, but instead our plants broke dormancy more than three weeks before 17 March (Table 2). The length of this extreme event may explain the difference in response times observed by Augspurger (2009) and our study. This extreme event was longer than any measured by Augspurger (2009), and presumably, these few additional days of warm weather contributed enough to meet forcing dormancy requirements and allow plants to initiate growth much earlier than normal. As winter climate continues changing, we may see increased variability in the timing of new growth.

Despite the common response of many woody species to this extreme warm event, species

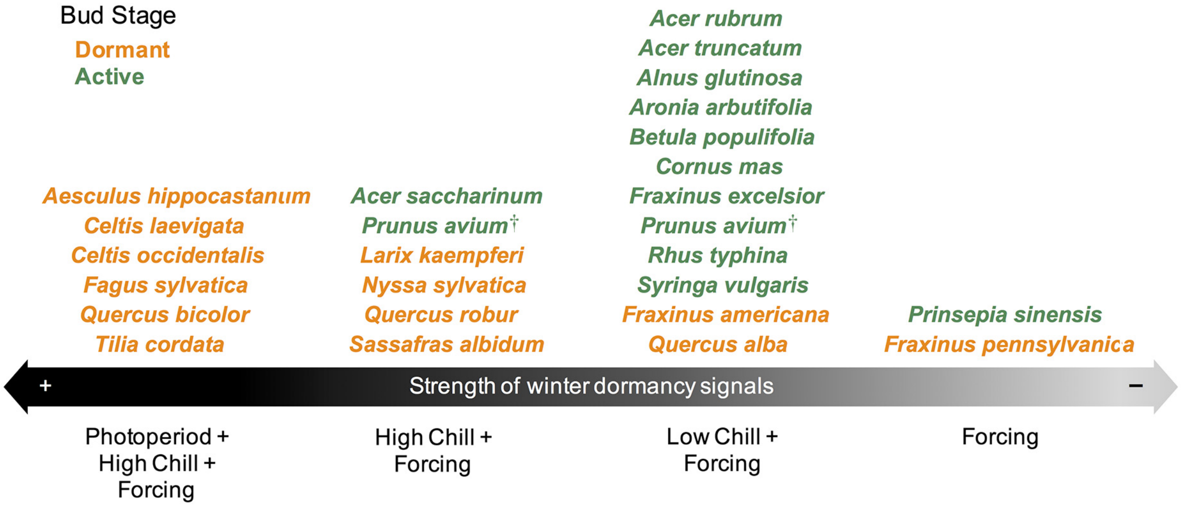

Fig. 4. The external cues for leaf out requirements for a subset of species, ordered from greatest dormancy requirements (left) to least (right). Species are color-coded based on phenological stage on 23 February 2017. Dormancy signals were compiled from Zohner et al. (2014). †*Prunus avium* was listed as having both high and low chill requirements.

characteristics and climate from native ranges could not predict the probability of bud burst. All examined traits have been predictors of spring phenology or responsiveness to false springs for species in other studies (Table 1; Lechowicz 1984, Niinemets and Valladares 2006, Basler and Körner 2012, Panchen et al. 2014, Fahey 2016, Zohner et al. 2017), yet did not relate to species response following this unseasonably warm winter event (Table 3). Although our observations were limited by the number of species present at the arboretum, our sample size falls within previous research on associations between species traits and the timing of breaking dormancy and was unlikely to explain the lack of significant response in our models (23 species in Lechowicz 1984 to 1597 species in Panchen et al. 2014). The strongest factor associated with early bud burst was phylogeny, and some closely related species tended to respond similarly (Fig. 3). Several phylogenetic patterns of bud burst matched the findings of Panchen et al. (2014). For example, many species within Rosaceae have earlier phenology (Panchen et al. 2014) and broke dormancy in our study (Fig. 3), while members of the Fagales and Lamiales, which tend to have later leaf out dates (Panchen et al. 2014), largely remained dormant (Fig. 3). When phylogeny was accounted for in statistical analysis, no other variables were significant, indicating that phylogeny may therefore account for some variation in bud burst. However, phylogeny did not completely explain whether a species broke dormancy or not, as indicated by the lack of conformation to Brownian motion expectations. Since we did not sample species across the phylogeny, we may not have detected all the phylogenetic signal (Revell et al. 2008).

Beyond phylogeny, shade tolerance and dormancy requirements were the only traits predictive of bud break. Shade-intolerant species were more likely to break dormancy than shade-tolerant species (Table 3, Fig. 2). Because shade tolerance is often related to successional stage (i.e., fast-growing, short-lived, and early-successional species are shade-intolerant and break dormancy before slow-growing, long-lived, and late-successional species; Kolářová et al. 2014, Tang et al. 2016), many early-successional species also have dormancy requirements related to accumulation of GDD rather than photoperiod (Caffarra and Donnelly 2011, Basler and Körner 2012, Zohner et al. 2014; Fig. 4), which allows spring phenology of early-successional species to be more variable and responsive to changing temperatures. For a subset of species with documented dormancy requirements (Zohner et al. 2014), the probability of bud burst decreased as dormancy requirements increased (Fig. 4). Species with colder or multiple dormancy requirements, particularly species with photoperiod cues, remained dormant while those with only low chilling and warm forcing controls on dormancy tended to break bud (Fig. 4). For species that do not have dormancy requirements related to photoperiod, breaking dormancy requires first experiencing enough cold weather to fulfill chilling requirements followed by enough warm weather to surpass forcing requirements. Species with chilling requirements that are met early in winter could break dormancy in mid or late winter if warm temperature events provide enough heat to overcome forcing requirements. The strength of dormancy cues (chilling, warm forcing, photoperiod) has been tested in vitro with twigs in growth chambers and greenhouses (Vitra et al. 2017), but twig measurements can misalign with in vivo phenology of trees in nature (Laube et al. 2014), and surveys such as ours can capture just how early species can break dormancy and start spring. The warm event of February 2017 was warm enough and long enough to meet the forcing requirements for half the species surveyed. Activation this early in the season can be problematic, given that after the warm event freezing temperatures returned for several more weeks. As global climate continues warming and extreme events become more frequent, taxa that tend to leaf out early and be responsive to false springs may suffer greater damage following future events. If these species provide key ecological or economic services to the area, increased damage is likely to be a management and conservation concern.

No climate variables were predictive of whether species broke dormancy following the winter warm event (Table 3), yet previous research found species from regions with colder temperatures or low interannual variability in spring temperature responded more often to false or advanced springs (Zohner et al. 2017). Perhaps, the duration of the event overwhelmed species response in that species which typically would not break dormancy did anyway because the event was long enough. Over the past 50 yr, warm events during winter generally lasted a single day, but this event lasted six consecutive days, which might have falsely convinced more species than normal that it was indeed spring even though the timing of the event made it almost inevitable that cold temperatures would return. This lack of predictability between climate data and ecological response may signal troubling changes to underlying associations between climate and plant phenology. As changing climates become less predictable, it may become extremely difficult to anticipate how future events will influence plant communities, given that evolutionary history may not be a good predictor of species' responses to future novel climates (Williams and Jackson 2007).

As extreme events test the persistence of ecological communities, they also test the persistence of underlying relationships and processes that govern these systems. Given that our models for projecting future conditions are based on many of these processes and thresholds, shifting baselines and relationships are troublesome and potentially problematic if not understood. Furthermore, traits associated with species responses to warming temperatures (Lechowicz 1984, Niinemet and Valladares 2006, Basler and Körner 2012, Panchen et al. 2014, Fahey 2016, Zohner et al. 2017) are not necessarily predictive of response to extreme events (Tables 1, 3). As climate warms, it is unclear whether spring phenology can keep pace with rising temperature. In recent years, there have been signs of phenological slowing—plant phenology not keeping pace with rising temperatures (Fu et al. 2015), yet the dormancy of many woody species is not limited by photoperiods (Zohner et al. 2016). The responsiveness of many species to this warm event in winter questions the strength of response thresholds and highlights the different ecological implications of gradual increases in mean conditions and extreme events.

Long-term monitoring is invaluable for understanding ecological impacts of extreme events, but even without a long-term record, tracking phenological response to anomalous weather events, such as the winter warm snap in February 2017, is informative for understanding the limits and thresholds calculated from greenhouse experiments and modeling. As winter continues changing in a variety of ways (Martinuzzi et al. 2016, Rawlins et al. 2016) and extreme events become more frequent (IPCC 2013, Allstadt et al. 2015), monitoring ecological response to climate anomalies, including warm events such as this one, can help us understand the functioning of future systems (Friedl et al. 2014). The combined extremity of several aspects of climate—temperatures

13–20°C above average lasting for 6 d, indicative of climate that typically occurs nearly two months later (Fig. 1)—triggered an equally striking biotic response—bud activation during winter for nearly half of the species surveyed. Early bud expansion has many widespread consequences, as newly exposed tissues are often damaged when cold temperatures return (Hufkens et al. 2012, Augspurger 2013, Muffler et al. 2016) and altered phenology can disrupt ecological networks (Inouye 2008, Deacy et al. 2017). Since we measured trees and shrubs, long-lived, modular organisms with stored energy that can survive organ damage or loss, all individuals survived the return of frost following this warm event. But, the fate of shorter-lived animals is likely more dire, as such organisms are non-modular and may lack key strategies to compensate for severe damage or energy expenditure. Therefore, the full ecological impacts of extreme events such as this one remain largely unknown, and responses of these long-lived trees and shrubs give us only a partial view of an extreme warm event. Given the potential for diverse, cascading, and high magnitude social and ecological consequences of extreme weather events (Felton and Smith 2017), further investigation and long-term monitoring of organisms' responses to extreme events are imperative if there is any hope of management for mitigation.

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DATA AVAILABILITY

All code and data are publicly available at https://osf.io/x3bpu/

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2542/full