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Biologically-Relevant Trends in Springtime Temperatures Across the United States

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Key Points:
- Trends in multiple heat accumulation thresholds better reflect long-term changes in conditions that are biologically relevant.
- Within-spring heat accumulation thresholds show clear advancements over the past 70 years, especially in Northeast, Western United States.
- The span between when a single threshold is met across latitude is decreasing in the Eastern United States and expanded in the West.

Supporting Information:
- Supporting Information S1

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Abstract Long-term trends in temperature—a primary driver of phenology—are typically evaluated using monthly or seasonal averages. However, accumulated warmth, rather than average temperature, cues phenological events; further, the amount of heat necessary to trigger activity is species-specific. We evaluated trends in the timing of three heat accumulation thresholds encompassing spring-season biological activity in the conterminous United States over a 70-year period to document changes from a biologically relevant perspective. The Southwest, Northeast, and Northwest regions exhibit the strongest advancements. Rates of change vary among thresholds within many regions, resulting in temporal compression and lengthening within the season. Further, in the Eastern United States, the days between when a single threshold is met in the south and north are decreasing; in the West, the opposite pattern is occurring. These trends generally match long-term observations of species' phenology, underscoring the value of this approach for documenting biologically relevant changes in temperature.

Plain Language Summary Studies that document changes in the timing of leaf-out, flowering, and other springtime activity typically use monthly or seasonal temperatures. However, the amount of springtime warmth that is necessary to trigger a species to initiate activity is unique to each species. For this reason, evaluating trends in various amounts of spring heat accumulation, which are reached at different times within the season, can yield a richer understanding of how conditions specific to different species are changing. We evaluated long-term trends in three heat sums in the spring season across the United States to better understand how biologically relevant springtime temperature is changing. In several parts of the United States—including the Southwest, Northeast, and Northwest—the timing of these springtime heat accumulation thresholds is advancing rapidly. Further, within many regions, the thresholds are not advancing at the same rate, resulting in compressions or lengthening of the in the span of time between the thresholds being met. Our results generally match long-term observations of species' activity. Our findings demonstrate the value of this approach for documenting biologically relevant changes in temperature. These results reveal how species interactions might be expected to be affected into the future with continued warming.

1. Introduction

Over the past century, winter and spring-season temperatures in the Northern Hemisphere have increased steadily and significantly (Barichivich et al., 2012; U.S. Environmental Protection Agency, 2016; Vose et al., 2017). In response, spring-season phenological events such as leaf-out, flowering, migration, and breeding have advanced in many species, though not uniformly (e.g., Chambers et al., 2013; Cohen et al., 2018; Cook et al., 2008; Thackeray et al., 2010). Reported changes vary taxonomically as well as by geography. First, advancements have been greater for species undergoing phenological transitions earlier in the season than those active later in the season (e.g., Fitter & Fitter, 2002; Hepper, 2003; Mo et al., 2017; Park et al., 2018). Species also show varying rates of change in different locations, with a general pattern of more rapid rates of advancement occurring at higher latitudes and elevations (Asse et al., 2018; Post et al., 2018; Vitasse et al., 2018; Waller et al., 2018; Zohner & Renner, 2014). Finally, locations with higher mean temperatures tend to harbor fewer species demonstrating advancements (Cook, Wolkovich, Davies, et al., 2012). Uneven changes in phenology among species can have dramatic consequences for community structure and functioning, including increasing or decreasing competition among species (Yang & Rudolf, 2010), decoupling existing phenological synchronies (Iler et al., 2013), and species invasions as novel temporal niches emerge (Wolkovich & Cleland, 2011).

Long-term phenological records that can be used to demonstrate species responses to changing climate conditions are rare. Synthetic studies (e.g., Parmesan & Yohe, 2003; Wolkovich et al., 2012) reveal broad and significant changes to phenology across many taxonomic groups; however, we lack a detailed understanding of how phenology is changing—among individual species and across geography. An alternative approach for understanding how species are advancing or delaying their phenology in various regions, as well as how they may be expected to change in the future, is to evaluate trends in the variables that drive phenological events. For many spring-season phenological events in temperate and boreal systems, temperature is a primary forcing variable and therefore the logical variable to examine (Basler, 2016; Cook, Wolkovich, & Parmesan, 2012; Hunter & Lechowicz, 1992; Linkosalo et al., 2006).

Studies that document changes in temperature, or phenological shifts driven by changes in temperature, typically use a single, synthetic measurement such as monthly or seasonal average temperatures (e.g., Crimmins et al., 2010; Miller-Rushing & Primack, 2008). However, the amount of heat required to initiate activity is species-specific (Basler, 2016; Hunter & Lechowicz, 1992; Panchen, 2016), and as a result, individual plant and animal species commence activity over the course of the season, rather than all at once (Panchen et al., 2014; Park, 2016; Wang et al., 2016). For many species, the amount of accumulated warmth necessary to trigger the transition from one state (such as leaf buds not broken) to another (leaf buds broken) has been quantified in the form of thermal constants or growing degree day (GDD) thresholds. These measures can serve as a suitable proxy for the timing of spring-season activity in many plant and insect species in temperate and boreal systems (e.g., Arnold, 1959; Campbell et al., 1974; Herms, 2004; Murray, 2008). Evaluating trends in GDD thresholds across geography yields a more complete picture of how conditions that drive the timing of springtime biological events are changing, filling gaps where long-term observational data are sparse. Further, evaluating trends in multiple GDD thresholds within the spring season yields a richer understanding of whether conditions within different segments of the season—when different species are undergoing phenological transitions—exhibit changes of similar direction and magnitude. Trends of varying magnitude result in a lengthening or compression of the span of time between the thresholds being achieved, with varying consequences to species undergoing transitions on or around those thresholds.

In this study, we evaluated the magnitude of trends in the timing of three heat accumulation thresholds encompassing initiation of spring-season activity in the conterminous United States using a long-term record of gridded daily temperature measurements. Our aim was to better understand changes in springtime conditions from a biologically relevant perspective. Specifically, we evaluated patterns in these three thresholds within regions across geography and across latitude and elevation gradients.

2. Materials and Methods

To evaluate long-term trends in the spring development period in plants and animals, we examined three thresholds in spring-season heat accumulation: 50, 250, and 450 GDDs calculated in Celsius, based on a January 1 start date and base temperature 10 °C. The base temperature is the temperature below which accumulated heat units are biologically irrelevant to species and phenological event of interest. These heat accumulation thresholds encompass the initiation of spring-season activity including budburst, leaf-out, flowering, and hatch in the majority of plant and insect species in the United States (Cornell Cooperative Extension, 2010; Herms, 2004 ; Murray, 2008 ; University of California Statewide Integrated Pest Management Program, 2019), as these events are generally strongly driven by temperature (Basler, 2016; Cook, Wolkovich, & Parmesan, 2012; Linkosalo et al., 2006; Melaas et al., 2016; Polgar et al., 2014). When calculated using 10 °C base temperature, 50GDD represents some of the earliest-season activities in plants (Herms, 2004). The 250GDD threshold represents a very active point in the season, around which many plants and insects are initiating spring activity, and 450 GDD represents a point several weeks later in the season, around which many plant species are exhibiting flowering activity (Herms, 2004; Murray, 2008; University of California Statewide Integrated Pest Management Program, 2019).

We calculated cumulative GDDs for each grid cell in each year (1948–2016) using the TopoWx gridded climatic dataset resampled from 800 m to a nominal resolution of 3 km (Oyler et al., 2014). The TopoWx dataset is well-suited for evaluating temporal trends, as it is generated using homogenized station data, thereby minimizing non-climatic trends arising from missing or erroneous station data (Oyler et al., 2015; Walton & Hall, 2018). Daily total GDDs above 10 °C were calculated using the simple average method, {GDD = [(minimum temperature + maximum temperature)/2] − base temperature}; McMaster & Wilhelm, 1997). The day of year (DOY) that the 50GDD, 250GDD, and 450GDD thresholds were met were then determined from the daily cumulative growing degree grids. Locations higher than 2,750 m in elevation failed to consistently reach 450 GDDs; these areas were masked from subsequent analysis. To determine yearly anomalies for each of the thresholds, we calculated the mean DOY; each threshold was met over the climate normal period of 1981–2010 and then differenced this DOY layer from each yearly threshold DOY layer. All analyses were undertaken using R v3.6.0.

Our aim was to evaluate and compare trends in multiple heat accumulation thresholds representing various points in the spring season across the continental United States. Spring-season heat accumulation does not happen at a constant rate; warmth accumulates rapidly during warm spells and stalls out during cold periods (Crimmins & Crimmins, 2019). Geographic patterns in the variability in heat accumulation at a location are a function of latitude, elevation, topography, sun angle, and atmospheric circulation (James & Arguez, 2015; McKinnon et al., 2016; Stine & Huybers, 2012). As such, the variability in when a threshold is met shows distinct patterns across geography (Figure S1). In the Eastern United States, broad regions frequently exhibit coherent patterns in GDD threshold anomalies, organizing along the latitudinal gradient (Figure S1). In contrast, in the West, GDD threshold anomalies tend to organize around topography, where topography dictates when and where thermal time accumulates (Figure S1). We capitalized on these emergent geographic patterns to produce GDD time series from coherent regions that could be assessed for trend and compared across the continental Unites States.

To generate these regions, we used a nonhierarchical clustering technique (k-means clustering) to identify areas with coherent, within-season variability in the DOY; the three GDD thresholds were met among the three thresholds over the study period of record. We generated clusters using the standardized (z-score) anomalies for each year and each threshold. Anomaly z-scores were calculated by subtracting the population mean from each individual anomaly and then dividing by the population standard deviation. Clustering approaches have been used widely to identify regions sharing similar variability in temperature and precipitation patterns (e.g., Bernard et al., 2013; Carreau et al., 2016; McKinnon et al., 2016; Sanderson et al., 2019). We used the "unsuperClass" function in the RSToolbox to identify the optimal cluster number (k) and the classification error for all values of k from 2 to 20. We used the difference in within-group sum of squares (DiffWSS) and difference in minimum within-group sum of squares (DiffMinWSS) to guide selection of the number of clusters to retain for further analysis (Zhang et al., 2016). DiffWSS values plateaued just past $k = 10$, while DiffMinWSS decreased to a local minimum at $k = 12$, indicating diminishing returns on error minimization with additional clusters.

Within each cluster, we calculated a time series of mean DOY for each of the GDD thresholds in each year. This yielded a time series of the regional average day of year; each GDD threshold was met for each year from 1948 to 2016. Ordinary least squares regression was used to assess trends within each GDD threshold time series in each cluster. To assess the degree to which periods within the spring season have lengthened or become compressed, we differenced the slope values for the three thresholds within each region.

3. Results

Using the clustering results from $k = 12$ yielded broad regions of similar size oriented along latitudinal gradients in the Central and Eastern United States. Regions in the Western United States were organized around a combination of latitude and topography (Figure 1). When calculated for the entire conterminous United States, all three thresholds show significant negative trends (GDD50: −0.80 day/decade; GDD250: −0.71 day/decade; GDD450: −0.85 day/decade; $p < 0.01$).

3.1. Within-Region Trends in GDD Thresholds

Within regions, trends in GDD thresholds generally are either all significant ($p < 0.05$) or show no significance (Table 1, Figure 1). Trends toward earlier DOYs thresholds are met were significant in most regions in the Western zone (Southwest, Pacific Northwest, Northern Rockies, and Southern Rockies) as well as

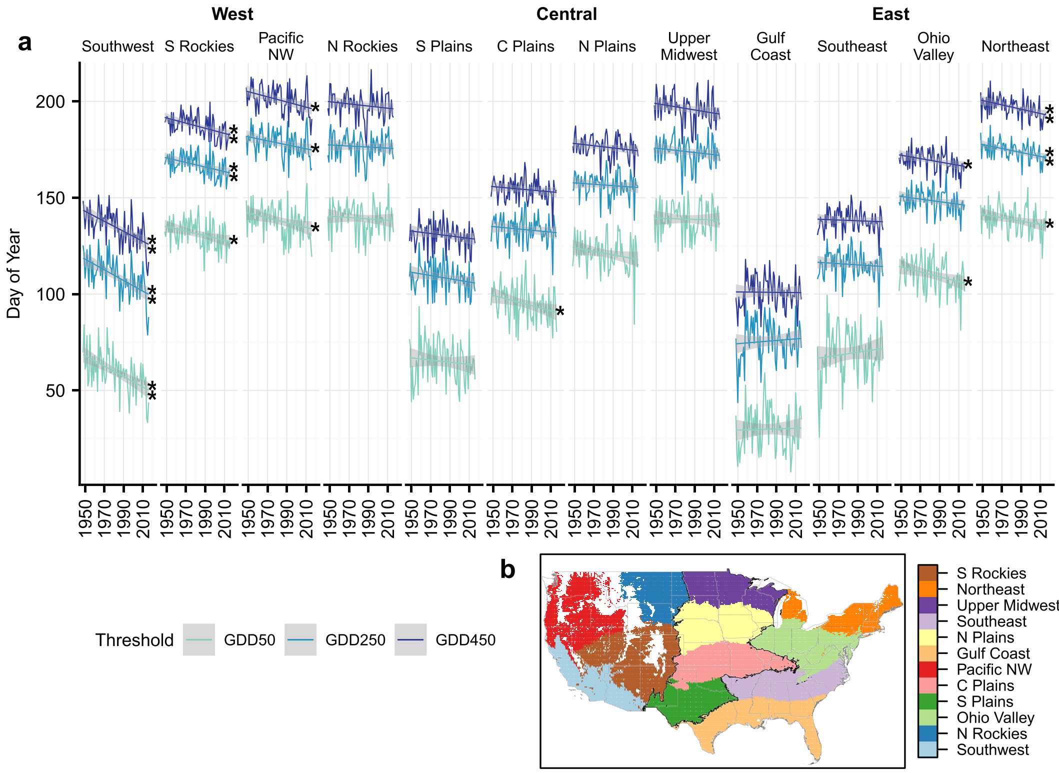

Figure 1. (a) Mean day of year 50 growing degree day (GDD), 250GDD, and 450GDD thresholds were met (1948–2016) within 12 geographic regions in the conterminous United States. Trend lines (grey shading depicts 95% confidence interval) are shown with significant trends denoted as $*p < 0.05$; $**p < 0.01$. (b) The 12 regions are situated within Eastern, Central, and Western zones.

higher latitude regions in the Eastern zone (Ohio Valley and Northeast; Figure 2). Additionally, the 50GDD threshold in the Central Plains region shows a significantly advancing trend.

Except for the Southwest, significant trends in the DOY, the thresholds are met in these regions advanced 0.9 to 1.4 day/decade over the past 70 years (Table 1). Trends in the Southwest region are more than twice that of many other regions, ranging from −2.6 to −2.8 day/decade.

Thresholds exhibited varying rates of change within regions, leading to lengthened or compressed segments of the spring season. In the Central Plains and Ohio Valley regions, the 50GDD threshold is advancing more rapidly than one or more of the other thresholds, resulting in a lengthening of the leading portion of the season (Figures 2a and 2b; Table 1). This pattern is also apparent in the Northern Plains, though trends in GDD thresholds are not statistically significant in this region. In the Ohio Valley and Pacific Northwest regions, trends in 50GDD and 450GDD are of greater magnitude than 250GDD, leading to lengthening of the leading portion of the season and a temporal compression in the later part of the spring season (Figures 2a and 2c). This pattern is also apparent in the Northern Plains and Gulf Coast regions, though trends in thresholds are not significant. The opposite pattern—where trends in 50GDD and 450GDD are of a lesser magnitude than 250GDD, leading to a compression in the earlier portion of the season and a compression in the later part of the season—is occurring in the Southeast and Southern Plains regions, though trends in these regions are not significant. Finally, a pattern of a compression occurring later in the season due to a more rapid rate of change in 450GDD than the other two thresholds is also apparent in several regions including the Southern Rockies and the Northeast, where trends are significant, as well as in the Southeast and Upper Midwest (Figures 2b and 2c).

3.2. Patterns in GDD Threshold Trends Along Latitudinal Gradients

Across regions in the Eastern zone, individual thresholds are advancing more rapidly in the north than in the south, leading to a compression in when thresholds are met across this gradient. The opposite pattern is apparent in the Western zone; rates of change in thresholds are much greater in lower latitude regions

Table 1
Slopes (day/decade) for DOY 50GDD, 250GDD, and 450GDD are met in 12 regions of the conterminous United States (1948–2016)

Region	Cluster	Threshold	Slope (day/decade)	p	Mean DOY	SD DOY	Difference in slope from 250GDD (day/decade)	Difference in slope from 450GDD (day/decade)
East	Northeast	50	−0.89	**0.039***	138.3	8.8	−0.14	−0.24
East	Northeast	250	−1.03	**0.000****	173.9	8.7	—	−0.10
East	Northeast	450	−1.13	**0.000****	196.4	10.3	—	—
East	Ohio Valley	50	−1.28	**0.014***	108.8	9.4	0.60	0.40
East	Ohio Valley	250	−0.68	0.061	148.3	8.4	—	−0.20
East	Ohio Valley	450	−0.88	**0.008****	168.7	8.5	—	—
East	Southeast	50	0.75	0.362	69.4	11.5	−1.07	−0.95
East	Southeast	250	−0.32	0.448	115.5	8.8	—	0.12
East	Southeast	450	−0.20	0.574	138.5	8.3	—	—
East	Gulf Coast	50	0.17	0.814	29.1	12.1	0.25	−0.23
East	Gulf Coast	250	0.42	0.522	75.86	18.0	—	−0.48
East	Gulf Coast	450	−0.06	0.910	100.9	18.1	—	—
Central	U. Midwest	50	−0.16	0.755	138.4	6.3	−0.4	-0.67
Central	U. Midwest	250	−0.56	0.180	173.5	7.3	—	−0.27
Central	U. Midwest	450	−0.83	0.064	195.6	9.2	—	—
Central	N Plains	50	−0.93	0.081	120.6	6.1	0.57	0.36
Central	N Plains	250	−0.36	0.347	156.4	5.6	—	−0.21
Central	N Plains	450	−0.57	0.100	176.0	5.7	—	—
Central	C Plains	50	−1.35	**0.014***	93.6	8.6	0.87	0.89
Central	C Plains	250	−0.48	0.256	133.5	6.9	—	0.02
Central	C Plains	450	−0.46	0.191	154.3	6.4	—	—
Central	S Plains	50	−0.56	0.391	63.9	14.4	−0.28	−0.07
Central	S Plains	250	−0.84	0.063	108.0	11.9	—	0.21
Central	S Plains	450	−0.63	0.115	130.2	10.8	—	—
West	N Rockies	50	−0.36	0.460	138.2	5.1	0.09	−0.2
West	N Rockies	250	−0.27	0.507	176.1	6.4	—	−0.29
West	N Rockies	450	−0.56	0.177	197.5	7.9	—	—
West	Pacific NW	50	−1.25	**0.014***	140.7	12.9	0.21	−0.09
West	Pacific NW	250	−1.04	**0.013***	181.7	13.0	—	−0.3
West	Pacific NW	450	−1.34	**0.001****	202.8	14.6	—	—
West	S Rockies	50	−1.19	**0.007***	131.6	16.2	0.01	−0.14
West	S Rockies	250	−1.18	**0.000****	167.3	15.9	—	−0.15
West	S Rockies	450	−1.33	**0.000****	187.6	17.0	—	—
West	Southwest	50	−2.72	**0.000****	56.6	24.7	−0.05	0.12
West	Southwest	250	−2.77	**0.000****	106.7	26.5	—	0.17
West	Southwest	450	−2.60	**0.000****	132.0	26.1	—	—

Note. Slope values are differenced in final columns; in these columns, a negative (positive) value indicates a shortening (lengthening) of the duration between the two thresholds being met.
Abbreviations: DOY, day of year; GDD, growing degree day; SD, standard deviation.
*$p < 0.05$. **$p < 0.01$.

(Table 1). The more rapid advancement at low latitudes is resulting in a lengthening of the duration from when spring begins in the Southwest to when it is reached in the Northwest. Finally, very few thresholds in regions in the Central zone exhibit trends in the timing of the thresholds evaluated.

4. Discussion

We evaluated trends in three heat accumulation thresholds encompassing initiation of spring-season activity in the conterminous United States to more fully characterize how the timing of these thresholds has changed over the past seven decades. These patterns offer insight into how the timing of phenological events driven by accumulated temperature may have also changed over this period. Our choice of thresholds evaluated in this study encompasses the portion of the season when many species are initiating springtime activity (Herms, 2004) and thereby reveals long-term changes that are biologically relevant.

Our results generally agree with trends in average temperatures and indicators of spring onset documented elsewhere (e.g., Ault et al., 2015; Mehdipoor et al., 2018; Schwartz et al., 2006; Schwartz & Reiter, 2000; U.S. Environmental Protection Agency, 2016; Vose et al., 2017). We observed advancement in threshold timing in

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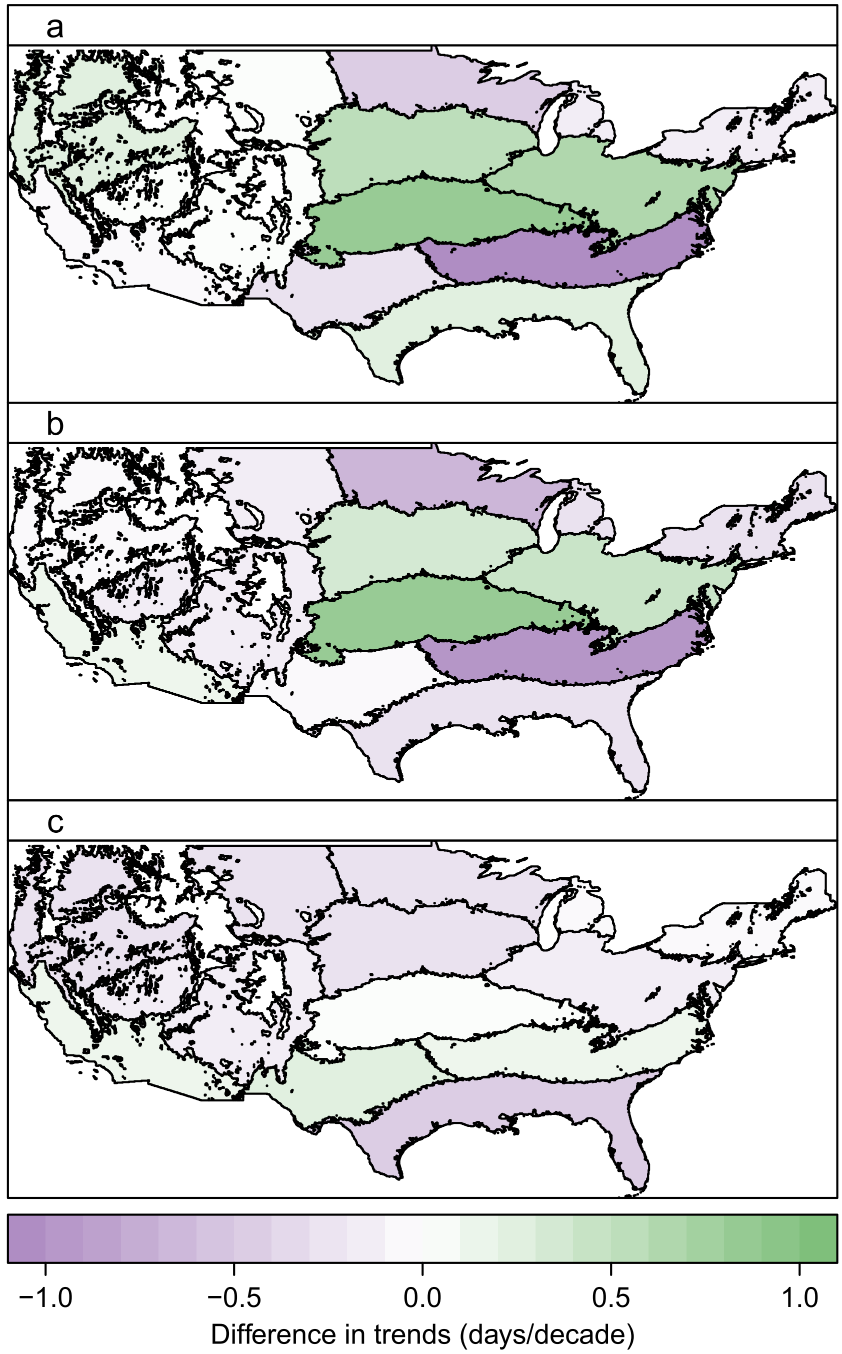

Figure 2. Difference in trends in day of year 50 growing degree day (GDD), 250GDD, and 450GDD thresholds were met (1948–2016) within 12 geographic regions in the conterminous United States (day/decade). (a) 250GDD trend–50GDD trend; (b) 450GDD trend–50GDD trend; (c) 450GDD trend–250GDD trend. Green shades indicate the earlier threshold is advancing at a greater rate than the later threshold, leading to a lengthening of time between the two thresholds being met; purple shades indicate the earlier threshold is advancing at a lesser rate than the later threshold, leading to a compression between the two thresholds being met.

the Southwest, Southern Rockies, and Northeast, and a lack of strong advancement in the Southeast, consistent with other studies. However, we also report advancements in the Ohio Valley and Central plains—regions not highlighted as exhibiting dramatic trends in other studies—as well as more rapid rates of warming in the Southwest. Further, the rates of change documented on a continental scale are slightly less than those reported in studies calculating trends in start of season metrics (Schwartz et al., 2006; Schwartz & Reiter, 2000), though the measures reported in these studies represent the leading edge of spring and occur earlier in the season than those presented here.

4.1. Trends in GDD Thresholds Match Reported Phenological Advancements

As long-term phenological records, especially those that match the span of years evaluated in this study, are rare in the United States; our ability to compare these trends to observations of the timing of seasonal events in plant and animals—events that may be affected by changes in temperature—is limited. However, in several cases, the strength of the trends in the GDD thresholds evaluated in this study is consistent with trends documented in long-term observational records of spring-season phenological events, lending support for the use of GDD thresholds as a proxy for the timing of phenological events. For example, Cook et al. (2008) reported an advancing trend in flowering of mountain laurel (*Kalmia latifolia*) over the period 1931–2002 in New York, a region showing strongly advancing trends in the present study. Mountain laurel initiates flowering around 650GDD (10 °C base temp; Herms, 2004). Though this threshold is later in the season than those evaluated in the present study, this trend matches those seen in the Northeast in the other thresholds evaluated in this study. In the same study, Cook et al. (2008) report a marginally significant trend in shadbush (*Amelanchier* spp.); shadbush typically exhibits first bloom around 50GDD (10 °C base temp; Cornell Cooperative Extension, 2010). We similarly observe a significantly advancing trend in 50GDD in the Northeast region (Figure 1).

Bradley et al. (1999) reported significant advancements for several phenological events in southern Wisconsin over the period 1936–1998. Notably, in the earliest months of the year (February, March), Bradley et al. (1999) reported more events advancing significantly than events not advancing. Later in the season, this pattern reversed; in June, more than twice as many events showed no trend than those exhibiting significant trends. These results align closely with our findings for the Northern Plains region in which Bradley et al.'s (1999) study was situated, where 50GDD shows a marginally significantly ($p = 0.08$) advancing trend and the other two thresholds do not (Table 1). In an evaluation of herbarium data in Ohio, Calinger et al. (2013) documented stronger phenological responsiveness in spring-flowering species, which align generally with 50GDD, than did summer flowering species, which align generally with the later GDD thresholds. This pattern matches the trends observed in the Ohio Valley region, where the trend in 50GDD is significant and nearly twice that of 250GDD. Finally, the strong trends observed in the Northeast cluster in the present study are in agreement with the strongly advancing trends documented in several long-term studies in this region (e.g., Bertin, 2015; Miller-Rushing & Primack, 2008; Wolfe et al., 2005).

The nonsignificant trends observed in the Central portion of the United States in this study are similarly supported by reports of observational data. In their evaluation of long-term records from eastern North Dakota, Dunnell and Travers (2011) reported that compared with other studies, “the proportion of species significantly changing phenology is low,” indicating that of the dozens of plant species evaluated, few showed clear advancements in their phenology since the early 20th century. We similarly document no significant trends in the Upper Midwest region, which encompasses eastern North Dakota.

4.2. Differential Rates of Change Among Thresholds Within Regions Leads to Compression and Lengthening Within the Spring Season

Several regions exhibit noticeably different rates of change among heat accumulation thresholds, both in magnitude and direction. For example, The Ohio Valley region shows a clear pattern of lengthening in the leading portion of the season, due to a strong advancement in 50GDD relative to 250GDD, and a compression of the latter portion of the season, due to more rapid advance in 450GDD relative to 250GDD. The Northern Plains region exhibits similar changes in season length (Table 1). Such differential rates of change in thresholds can lead to increasing or decreasing competition among species (Yang & Rudolf, 2010), decoupling existing phenological synchronies (Iler et al., 2013), and species invasions as novel temporal niches emerge (Wolkovich & Cleland, 2011).

All three thresholds exhibit strong advancements in the Northeast region, with 450GDD showing the most rapid rate of change and 50GDD showing the slowest rate of advancement. Several studies from this region have reported the greatest advancement in springtime phenology among species undergoing transitions earlier in the year (Bertin, 2015; Miller-Rushing & Primack, 2008; Park et al., 2018). Our findings, in direct contrast with these results, suggest that heat accumulation is not the sole variable influencing the timing of species activity in these regions.

4.3. Timing of Thresholds Across Latitude and Elevation is Being Compressed in the East and Expanded in the West

In the East, the pattern of advancing thresholds occurring at higher latitudes and not at lower latitudes is consistent with other studies reporting an increasing "speed of spring," where the span of time between when a single threshold is met at lower latitudes or elevations and when it is met at higher latitudes or elevations is decreasing (Asse et al., 2018; Post et al., 2018; Vitasse et al., 2018). Attributed primarily to a slower rate of warming in the Southeastern United States (Ault et al., 2015; Meehl et al., 2012; Pan et al., 2004; Schwartz et al., 2006; Waller et al., 2018), the pattern observed in this study is anticipated to persist into the future (Jeong et al., 2013; Wuebbles et al., 2017).

In the West, the opposite pattern is apparent, where the timing of all three thresholds are advancing very rapidly in the Southwest region and at slower rates in higher latitude and elevation regions. The very rapid rate of change seen in the Southwest is consistent with similar recent analyses (MacDonald, 2010; Mehdipoor et al., 2018; Wang et al., 2017). However, even excluding the strongly advancing thresholds in the Southwest, this pattern of a decrease in the "speed of spring" in the West across latitude and elevation in the thresholds evaluated persists. In a similar evaluation of changes in the start of the spring season, Waller et al. (2018) reported no trends across latitude in the Western United States; however, the temporal extent of the study encompassed the entire 20th century, and the metric used, the Spring Leaf Index (Schwartz et al., 2006), represented the leading edge of the spring season. The varying rates of change observed across latitudes have implications for migratory birds and insects seeking resources across the gradient (Armstrong et al., 2016; Waller et al., 2018). These patterns suggest that species migrating north in the spring in the East may need to speed up their rates of migration to keep pace with food resources, whereas species in the West may need to slow down their migrations to keep pace with resource availability.

The notably rapid advances in threshold timing in the Southwest may have comparatively small impacts on the timing of phenological events in natural systems in this region, where events such as leaf-out and flowering are governed to a greater extent by moisture availability than temperature (Cook, Wolkovich, Davies, et al., 2012; Crimmins et al., 2010, 2011). Consequences of rapid increases in temperature are more likely to manifest in species range changes (Crimmins et al., 2009) and increased water stress, potentially leading to large-scale die-offs (Breshears et al., 2013). Further, irrigated agricultural systems across the Southwest would be expected to be impacted by these rapid advancements, with shifts in growing season timing and length and the loss of chill hours necessary for some crops (Baldocchi & Wong, 2008; Pathak et al., 2018).

4.4. Limitations and Opportunities

The trends and patterns documented in heat accumulation thresholds in this study are a coarse approximation of advancements or delays in the timing of seasonal events in plants and animals. The base temperature used in this study is commonly used in agriculture, turf management, and integrated pest management applications (e.g., Alessi & Power, 1971; Cardina et al., 2011; Herms, 2004). However, individual species respond to a wide range of base temperatures—the temperature below which accumulated heat units are biologically irrelevant—and heat sums. To more fully characterize biologically relevant changes in seasonal temperature, this analysis should be extended to additional base temperatures, start dates, and GDD thresholds. Further, many phenological events are cued by additional variables such as vernal chilling, daylength, and soil moisture (Flynn & Wolkovich, 2018; Polgar et al., 2014). The trends documented here may not reflect changes in the phenology of species cued by multiple environmental variables.

5. Conclusions

We evaluated long-term, biologically relevant trends spring-season thermal time. The Southwest, Northeast, and Northwest regions show the strongest advancements, consistent with other studies, with rates of advancement among thresholds varying within many regions. These uneven changes are resulting in temporal compression and lengthening in various segments of the season; these temporal changes in the seasons are not uniform across geography. We found that in many regions, the trends in growing degree thresholds matched trends documented using long-term records of phenology observations. Further, as in other recent studies, we document a shortening in the span of time between when a single threshold is met in the south and north in the Eastern United States; in the West, the opposite pattern is occurring. Our approach of regionalizing patterns in GDD anomalies and focusing on multiple thresholds in the portion of the season most relevant to species cued by accumulated warmth reveals nuance regarding how within-spring conditions are changing. These results have direct relevance to interactions among species cued by heat accumulation in the spring. These findings also suggest how spring-season heat accumulation thresholds—and species that undergo transitions on or around those thresholds—may change into the future, with continued global warming.

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