

Plant phenological responses to experimental warming—A synthesis

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Abstract

Although there is abundant evidence that plant phenology is shifting with climatic warming, the magnitude and direction of these shifts can depend on the environmental context, plant species, and even the specific phenophase of study. These disparities have resulted in difficulties predicting future phenological shifts, detecting phenological mismatches and identifying other ecological consequences. Experimental warming studies are uniquely poised to help us understand how climate warming will impact plant phenology, and meta-analyses allow us to expose broader trends from individual studies. Here, we review 70 studies comprised 1226 observations of plant phenology under experimental warming. We find that plants are advancing their early-season phenophases (bud break, leaf-out, and flowering) in response to warming while marginally delaying their late-season phenophases (leaf coloration, leaf fall, and senescence). We find consistency in the magnitude of phenological shifts across latitude, elevation, and habitat types, whereas the effect of warming on nonnative annual plants is two times larger than the effect of warming on native perennial plants. Encouragingly for researchers, plant phenological responses were generally consistent across a variety of experimental warming methods. However, we found numerous gaps in the experimental warming literature, limiting our ability to predict the effects of warming on phenological shifts. In particular, studies outside of temperate ecosystems in the Northern Hemisphere, or those that focused on late-season phenophases, annual plants, nonnative plants, or woody plants and grasses, were underrepresented in our data set. Future experimental warming studies could further refine our understanding of phenological responses to warming by setting up experiments outside of traditionally studied biogeographic zones and measuring multiple plant phenophases (especially late-season phenophases) across species of varying origin, growth form, and life cycle.

KEYWORDS

climate change, experimental warming, meta-analysis, phenological sensitivity, phenology, warming

1 | INTRODUCTION

Climate warming is causing substantial shifts in earth's biotic systems (Walther, 2010; Walther et al., 2002) with further change

predicted at an increasing rate for the coming century (Pachauri et al., 2014). Some of the most profound and earliest documented ecological changes associated with global warming have been shifts in phenology—the timing of a species' life history events—with a

notable advancement of the timing of spring events (Chmielewski & Rötzer, 2001; Inouye, 2008; Parmesan & Yohe, 2003). Phenological shifts have been documented across a huge diversity of systems including plants (Fitter & Fitter, 2002) and animals (Cohen et al., 2018) and from the tropics to the arctic (Arft et al., 1999; Bjorkman et al., 2015).

The potential for a species' phenology to track climate change is sometimes referred to as phenological sensitivity, defined as the shift in timing of the phenological event per degree of warming (Cleland et al., 2012). Variability in phenological sensitivity across species can be driven by the fact that phenology is regulated by not only temperature but also other factors, including photoperiod and precipitation (Forrest & Miller-Rushing, 2010; Piao et al., 2019; Way & Montgomery, 2015). As a result, the phenologies of individual species are not advancing in lockstep with one another.

Uneven phenological shifts across species can lead to problematic phenological asynchronies (CaraDonna et al., 2014; Heberling et al., 2019; Sherry et al., 2007; Visser & Both, 2005). Variable phenological sensitivity across species creates two particular challenges for species coping with climate change. First, unequal shifts in phenology across species can lead to phenological mismatches between co-occurring species that may shift at differing rates (Kharouba et al., 2018; Renner & Zohner, 2018). Additionally, failure to advance phenology (or to delay in the case of fall senescence) can put species at a competitive disadvantage if they are unable to lengthen their growing season to the same extent as their competitors (Alexander & Levine, 2019; Willis et al., 2008; Wolkovich & Cleland, 2014). Such an inability to track phenology with climate change had been linked to reduced plant performance (Cleland et al., 2012; Willis et al., 2008). Even within species, juveniles and adults can have variable phenological sensitivities to warming (Mediavilla & Escudero, 2009).

The picture may be further complicated by geographic variability in phenological responses to climate change (Menzel et al., 2006), although there is evidence that this signal may be relatively weak (Ge et al., 2015; Parmesan, 2007). Regardless, climate warming seems to be altering spatial patterns of phenology (Vitasse et al., 2018) and needs to be considered when predicting global trends in shifting phenologies.

In addition to shifts in phenological sensitivity across species and geography, there can be variation in the extent to which different phenological phases, such as budburst, flowering, or fruiting, shift as a result of warming (CaraDonna & Inouye, 2015; Post et al., 2008). Such variability in the capacity of different phenophases to change can have important consequences for plant fitness, demography, and ultimately community composition (Rudolph, 2019; Willis et al., 2008). For example, advances in spring budburst combined with delays in fall leaf or shoot senescence lengthen the growing season (e.g., Norby et al., 2003). Variability in warming-driven advances in flower bud formation relative to seed maturation/fruiting could lengthen or, alternatively, shorten the time a plant has to invest in reproduction (Hoffmann et al., 2010; Post et al., 2008). Experiments elucidating how phenological phases shift in relation to one another will improve our ability to understand how plants may respond to

global climate change. Likewise, species may diverge in phenological sensitivity to warming across the seasons, by delaying their phenological responses if warming occurs in the colder seasons or advancing their phenology if warming occurs in the warmer seasons (Cook et al., 2012).

The impacts of warming are typically studied via one of two methods: experimental climate manipulations or long-term observational monitoring. Although long-term monitoring studies allow us to document changes that have already taken place, experimental manipulations allow us to both exert levels of warming similar to those expected under future climate change scenarios and to examine a broad range of species for which long-term data may not exist. As such, experimental climate manipulations can complement long-term studies by providing a window into how plant species will likely shift their phenology as a result of future global warming. Experiments also allow us to make direct comparisons across biomes, which can be challenging using field data owing to variability in the magnitude of warming across the globe (Arft et al., 1999; Pachauri et al., 2014). Pooling data across studies can allow us to synthesize these results, inferring probable impacts of future warming on patterns of phenology across space, species, and phenological phases.

From a practical standpoint, we have limited understanding of how experimental methods may impact study results and ultimately our interpretation of the extent to which warming shifts phenology. We do know that the specifics of experimental design can drive critical differences in study outcomes for climate change impacts other than phenology (Yuan et al., 2017), although in some cases experimental and observational results map relatively well (Elmendorf et al., 2015; Knapp et al., 2018). For phenology studies, specifically, it is already understood that experimental and observational studies can yield results that differ in magnitude (Wolkovich et al., 2012). Understanding how experimental warming methods may drive the outcomes of phenology experiments is important in helping to interpret the results of such studies.

Here we survey the literature for experimental temperature manipulations that measured phenological shifts in plants. Using a meta-analysis, we explore warming-driven shifts in phenology across multiple phenophases (e.g., germination, leaf emergence, flowering, senescence) for a range of species spanning biomes and latitudes. This is the most comprehensive meta-analysis on the effects of experimental warming on phenology, to date—exploring the magnitude of phenological shifts across latitudinal and elevational gradients, and across species of different origins and life history strategies—for the full range of plant phenophases. Nearly a decade ago, Wolkovich et al. (2012) presented one of the first, and most comprehensive, global syntheses of phenological sensitivities to experimental warming. This is the first global synthesis to explore phenological sensitivities to experimental warming since that groundbreaking work almost a decade ago. Here, we incorporate new empirical data published since Wolkovich et al. (2012) representing an expanded data set that includes two times more studies, two times more plant species, and 1.6 times more individual observations of plant phenological responses to experimental warming than the previous synthesis.

This expanded data set allows us to explore patterns unaddressed in previous syntheses, including how plant phenological response varies by a wider variety of phenophases and plant life forms, as well as across plant origin, plant ontogeny, and season of warming. Like Wolkovich et al. (2012), we not only examine variation in phenological sensitivities across latitudes, mean annual temperatures (MATs), and biomes but also expand our knowledge of phenological variability among plants growing in different habitat types and at different elevations. Results of this meta-analysis improve our understanding of phenological responses to climate change, demonstrating robust support for plant species advancing early-season phenology in response to experimental warming and to a relatively consistent extent across habitats and species around the globe. In addition, we explore how experimental methods may influence results, which will inform future experimental designs, and highlight gaps in our knowledge to direct future research.

2 | METHODS

2.1 | Literature search

To find published literature for this analysis, we searched the Web of Science Core Collection (v. 5.33) using search terms "TS=(phenology) AND TS=(climate change OR warming)" from 1945–2019. This returned 8164 records, of which one quarter were published in the last 2 years of the search (Figure S1a). We screened the titles and abstracts of these publications retaining only those that indicated they experimentally warmed individual plants or plant communities to test plant phenological response, retaining 277 publications for full-text analysis (Figure S1d). Because of our intentionally broad search terms, the vast majority of our initial publications did not meet this first screening criteria (Figure S1b). Briefly, approximately one third of publications focused on animal phenology, especially migrating birds and mammals, and agricultural insect pests. Approximately one third of the initial studies reported observational plant phenology data; of the observational data, about half the studies used remotely sensed data and about half studied plant phenological changes along latitudinal, elevational, or temporal (e.g., herbarium records) gradients. Approximately one tenth of studies were forecasting models, either projecting future agricultural crop species productions or global ecosystem carbon cycling under warming climate scenarios. About 6% of studies excluded at this screening point included reviews and syntheses (<3%) and common garden experiments that used changes in elevation or latitude to simulate, but not directly manipulate, climate warming (<3%). A final one fifth of the studies were not suitable for inclusion in the meta-analysis for a variety of reasons including (but not limited to): (1) seasonal changes in global ice, snowpack and/or soil temperature; (2) impacts of other global change drivers (drought, natural disturbances, animal grazing, etc.) on plant fitness, growth or phenology independent of experimental warming; or (3) horticultural techniques to delay or advance crop phenology. We assessed the full text of the remaining 277 studies

and retained 70 articles that met the following criteria: (1) experimentally manipulated air or soil temperature in a field, growth chamber, or greenhouse experiment using passive or active warming methods; (2) measured species' phenology in ambient temperature controls; (3) reported phenological responses of individual species (i.e., we excluded community-level responses); (4) measured the date of start, peak, or end of at least one phenological response; and (5) reported the mean date and variation around the mean date (e.g., SD, standard error, or 95% confidence intervals [CI]) for a given phenophase in both control and ambient plots. In the full-text assessment, we excluded approximately one third of the publications because they did not report treatment means or variation around the mean. Many of the excluded studies reported means that (1) were aggregated across species, treatments, or sites; (2) estimated model means from linear mixed models or visualized with box plots of medians and inner quartiles; or (3) reported only the mean change in phenological response between warmed and ambient treatments but not each treatment mean alone. We excluded approximately one quarter of these studies because they did not report plant phenological response, instead reporting metrics of plant growth or fitness in response to warming. Approximately one fifth of studies were excluded for other reasons, primarily because they did not meet earlier criteria, which we were unable to assess by only reading the abstract and title (more details on publication sorting is available in Figure S1; full list of articles used in this analysis available in Table S1).

2.2 | Data collection

To assess the effects of climate warming on plant phenology, we collected the day of year for unique phenological occurrences under warmed or ambient treatments (e.g., first day of budbreak or peak-flowering day). Because most studies included in this analysis contained multiple experimental warming treatments (e.g., tested differences in soil warming vs. air warming or levels of warming), measured multiple phenological variables (e.g., leaf emergence, flowering, and fruiting), or measured phenological responses in multiple plant species, we typically collected multiple observations from a single published study. For studies that manipulated additional global change drivers (i.e., precipitation or CO₂), we retained only data related to control and warming-only treatments. Approximately one third ($n = 26$) of the studies manipulated additional global change drivers. Of these, 11 studies manipulated precipitation and warming and eight studies manipulated warming and nitrogen. Fewer than five studies manipulated each of the other global change drivers assessed, including increased winter chilling, CO₂, late frost, photoperiod, shading, or snowpack. If a study reported phenological information on the same species across multiple years, we collected data from each year of study, although we will primarily consider only the final year of observation in the analyses that follow to avoid pseudoreplication. For each observation, we recorded the sample size, mean response value, and SD around the mean for each species' phenological response in warmed and ambient treatments. If

data were presented in figures, we used ImageJ image processing software to digitize and extract relevant statistics (Abramoff et al., 2004). This gave us 1226 observations across the entire data set, or 807 data points when we only consider data collected during the final year of data collection (Supporting Information Data Table).

For each observation, we collected information on the study location, biome, habitat type, experimental design, plant species, and phenological phase measured to account for variation across the data set as well as to address specific questions about the effect of experimental warming on plant phenology. For the study location, we recorded the name of the location, country, continent, elevation, and geographic coordinates (decimal degrees). Nearly all studies had this information available within the text; for those studies that did not include geographic coordinates we used Google Maps (www.maps.google.com) to extract coordinates based on written site descriptions. For those studies that did not include elevation information we extracted elevation from FreeMapTools (www.freemaptools.com) using the study location's geographic coordinates. We also used study coordinates to extract MATs and mean annual precipitation (MAP; for 1970–2000) at the 0.5-min resolution ($\sim 1 \text{ km}^2$) from the WorldClim Database (Fick & Hijmans, 2017). Approximately half of our observations ($n = 480$) reported MAT for their study site within the publication text. For those studies, we found a strong correlation between the study reported MAT and the extracted WorldClim MAT (Pearson's correlation: $r = 0.97$, $t = 95.1$, $df = 578$, $p < 0.0001$) and thus used WorldClim MAT and MAP data for all observations to maintain consistency in data source. We classified plant communities based on their biome (alpine, arctic, subalpine, subarctic, or temperate) and their habitat type (forest, grassland, shrubland, tundra, or wetland), as reported.

Because there are many experimental approaches to simulate climate warming, each with their own limitations and environmental artifacts, we recorded the warming method as growth chamber (in lab), greenhouse (in lab), passive field warming chamber (open-top chamber), active field warming chamber (open-top or closed-top chamber), infrared heaters, heating mats, soil cables (buried or placed on soil surface), snow fence, or vegetation cover curtain or shade cloth. Because some experiments used multiple warming methods for the same plot, we coded each method as a binary variable (0 or 1) to account for multiple warming methods in our models. We further recorded the general type of experiment as field, lab, or common garden, depending on the experimental context. Lab experiments comprised either growth chamber or greenhouse experiments. Multiple warming methods were used in either common garden settings—where plants were transplanted to a single location, typically at or near a researcher's home institution—or field settings—where researchers placed warming devices above existing in situ plant communities. We also recorded the duration of the experiment (number of months), and whether the warming treatment was continuous (all seasons) or pulse (only certain seasons). To record the specific season(s) warmed, we scored whether warming occurred in each of the four major seasons (spring, summer, fall, and winter) as a binary variable (0 for no warming applied or 1

for warming applied during the season). Finally, we noted the average difference in temperature between warmed and ambient treatments for the entire study, as reported by the authors or extracted from figures in the text. The vast majority of observations recorded air temperature (88.5%, $n = 1085$) while a minority of observations (11.5%, $n = 141$) recorded only soil temperature.

Finally, we collected biological information on the study species and phenological phase studied for each species. We recorded the species' name, taxonomic family, biogeographic origin (native or nonnative to the study ecosystem, as reported by the authors), life stage (seed, juvenile [nonreproductive], or adult [reproductive]), growth form (forb, grass, shrub, or tree), and life cycle (annual or perennial). To facilitate comparison among species of different functional groups and across studies, we standardized the phenological state of each observation based on guidelines established by the USA National Phenology Network (Denny et al., 2014). We recorded phenological stages broadly as vegetative (initial growth [seed germination and budbreak of leaves or needles], young leaf or needle growth, mature leaf, or senescing leaf/plant), flowering (flower bud break, open flowers, or pollen release), or fruiting (fruit appearance, fruit maturation, or seed set). See Table S2 for full details on phenophases scoring.

2.3 | Statistical analysis

We calculated the effect of warming on the timing of a plant's phenological response using the Hedges' g effect size metric. Hedges' g is a commonly used effect size metric that standardizes the mean differences between groups, minimizes positive bias, and accounts for dissimilarity in group sizes (Hedges, 1981; Møller & Jennions, 2002; Rosenthal et al., 1994). Hedges' g values are in units of SD, where each value directly corresponds to the number of SDs from the mean for each observation (Ellis, 2010). In this study, a negative Hedges' g value indicates that the date of a phenological event occurred earlier in a warming treatment relative to an ambient treatment. The nature of Hedges' g meant that we were unable to use warming manipulations that failed to report either a measure of error, or provide access to the raw data.

We grouped phenophases into two broad categories: early-season phenophases and late-season phenophases. Broadly, early-season phenophases were those associated with the start of a biotic phase (e.g., budbreak of leaves beginning the growing season), whereas late-season phenophases were those associated with the end of a biotic phase (e.g., leaf senescence ending the growing season). These classifications are similar to previous demarcations of phenophases between “spring” and “fall” season phenophases in temperate ecosystems (Gallinat et al., 2015; Ge et al., 2015). Because our data set includes phenological observations from biomes whose growing seasons are not aligned with temperate climate seasons, we use the terms “early” and “late” season. We found that for late-season phenophases (i.e., senescing leaf/plant and fruit or seed drop, $n = 155$) the effect of warming was, on average,

positive (Hedges' $g = 0.18$, 95% CI = -0.28 to 0.65), whereas for early-season phenophases (i.e., initial growth and budbreak of leaves or needles, young leaf or needle growth, mature leaf, flower bud break, open flowers, pollen release, fruit appearance, and fruit maturation, $n = 1071$) the effect of warming was, on average, negative (Hedges' $g = -0.81$, 95% CI = -1.07 to -0.54 ; Figure 1). As a result of these systematic differences between early- and late-season phenophases ($Q_M = 191.12$, $df = 1$, $p < 0.0001$), combining all phenophase data in the same model could reduce the likelihood of finding a significant effect of warming by averaging early-season phenophases that were generally advancing with late-season phenophases that were generally delayed in response to warming. We therefore opted to split our data set, analyzing early- and late-season phenophases separately to reduce the likelihood of Type I error (Ge et al., 2015).

We used three preliminary analyses to determine how to construct our statistical models. First, we tested whether there was significant variation (residual heterogeneity) among the observed effect sizes within our early- and late-season data sets by constructing a null model and testing the significance of the Cochran's Q statistic from the null model. We found significant residual heterogeneity for both the early-season ($Q = 4524.11$, $df = 1070$, $p < 0.0001$) and late-season data sets ($Q = 602.80$, $df = 154$, $p < 0.0001$), suggesting that the variation in the observed

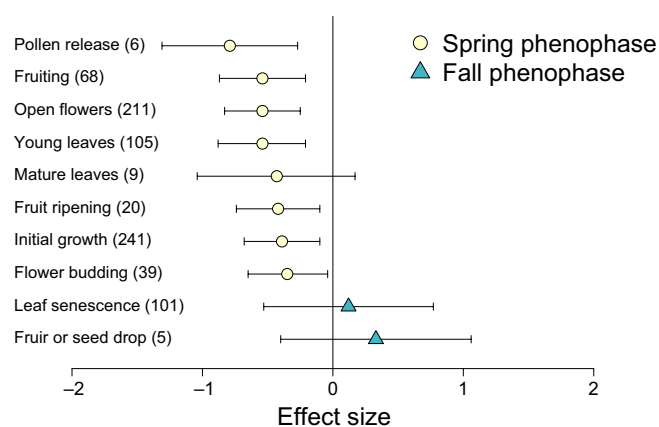


FIGURE 1 Experimental warming advanced early-season phenophases (circles) and delayed late-season phenophases (triangles). Data represent observations of the timing of plant phenology collected from 70 studies around the world that experimentally manipulated temperature under field and/or lab conditions. Values are mean effect sizes (Hedges' g) estimated from mixed-effect meta-analysis models accounting for plant phylogenetic relatedness and the average temperature difference between warmed and ambient treatments. Negative values indicate that the timing of a phenophase was earlier in warmed treatments relative to ambient temperature treatments. Error bars represent 95% confidence intervals calculated from Wald-type tests and numbers in parentheses represent the number of observations for each phenophase. We excluded two late-season data points from the figure (both end of plant growth from Du et al., 2019 because) for visualization purposes, reducing the number of data points from 807 to 805 [Colour figure can be viewed at wileyonlinelibrary.com]

effect sizes is greater than one would expect owing to sampling error. This suggests that other factors are likely contributing to variation in effect sizes. Second, we tested for the presence of a phylogenetic signal in the plant species found in our early- and late-season data sets using the Blomberg's K statistic. We constructed a phylogenetic tree of all species within our data set and constructed a correlation matrix based on tree branch lengths. We found a significant K -value for species in the early- ($K = 1.24$, $p = 0.001$) and late-season ($K = 2.05$, $p = 0.001$) data sets, indicating that we should account for species' phylogenetic relatedness in our meta-analysis models. Finally, there was large variation in the average temperature differences between warmed and ambient experimental treatments among observations in our early-season data set (range: 0.3 – 10.0°C , mean: 2.5°C , median: 2.0°C) and our late-season data set (range: 0.3 – 9.0°C , mean: 2.9°C , median: 3.0°C). For the early-season data set, there was a significant negative relationship between the effect of warming on plant phenology and the temperature difference between warmed and ambient plots ($Q_M = 103.59$, $df = 1$, $p < 0.0001$), which indicated that we should account for the temperature differences between ambient and warmed plots in our early-season meta-analysis models. For late-season data, there was no relationship between the effect of warming and temperature difference between warmed and ambient plots ($Q_M = 0.09$, $df = 1$, $p = 0.76$). We did not find variation in effect sizes across studies reporting air versus soil temperature for early-season ($Q_M = 1.85$, $df = 1$, $p = 0.17$) or late-season ($Q_M = 0.73$, $df = 1$, $p = 0.39$) phenophases. Based on these preliminary analyses, we ran a series of univariate models to test how phenological phase (initial growth and budbreak of leaves or needles, young leaf or needle growth, mature leaf, senescing leaf/plant, flower bud break, open flowers, pollen release, fruit appearance, fruit maturation, or seed set), study characteristics (elevation, latitude, MAT, MAP, biome [arctic, subarctic, alpine, subalpine, temperate], or habitat type [grassland, forest, tundra, shrubland, wetland, snow bed]), plant species' characteristics (biogeographic origin [native or nonnative], life stage [adult, juvenile, or seed], growth habit [forb, grass, shrub, or tree], and life cycle [annual or perennial]), and experimental characteristics (experiment context [lab, field, or common garden], warming method [open-top or closed-top chamber, infrared heaters, growth chamber, greenhouse, heating mats, buried or surface soil cables, snow fence, or vegetation cover curtain], experimental duration [number of months], year of data collection, experimental seasonality [continuously warmed across all seasons or only warmed during certain seasons], and the season(s) warmed) affected Hedges' g values for early- and late-season phenophases. For all models, we only used the last year of data reported from any given study, with the exception of the model testing for the effect of year. We did so to avoid temporal pseudoreplication of studies that included multiple years of data collected on the same plants or in the same plots of the experiment. While this reduced our data set by 419 observations (372 early-season observations and 47 late-season observations), this reduction in data points did not alter our ability

to detect the effect of warming on plant phenology (Table S3). For all models, we included the average temperature difference between ambient and warmed plots as a fixed effect and the following random effects to account for non-independence of data points: study, plant species nested within study, and plant phylogenetic relatedness using the correlation matrix described above. We centered the temperature difference data at 1°C to simplify interpretation of models; thus, model coefficient estimates are the average effect of a given variable at 1°C of warming. For all other continuous predictor variables (latitude, elevation, MAT, MAP), we centered variables at 0 for easier model intercept interpretation. For each model, we report the test of moderator statistic (Q_M) and associated p -value, which indicates whether the effect of warming differed significantly for a given variable. For each significant moderator variable, we calculated the grand mean effect size and 95% CI for each factor. We considered a mean effect size for any given category to be significantly different from zero when its 95% CI did not overlap zero. We tested for pairwise differences between factors using linear contrasts and adjusting our p -values for multiple comparisons using the Holm's correction. Full meta-analysis models and Holm's-corrected pairwise comparisons can be found in the Supporting Information (Tables S4 and S5).

We tested for publication bias in our early-season data set by comparing the absolute effect size to the sample size for each of our data points using Pearson's correlation test as well as funnel plot analysis. We found a negative but significant relationship between absolute effect size and sample size (Pearson's $r = -0.13$, $p < 0.001$), which may indicate that studies with small sample sizes are more likely to be published when they found a larger difference in plant phenology in warmed plots. We also examined plots of the relationship between effect size and standard errors of variance and found a funnel shape distribution of the data as would be expected in the absence of strong publication bias (Figure S2).

We used the following R statistical software (R Development Core Team, 2016) packages for our analyses: the "raster" software package (Hijmans, 2019) to extract climate data from WorldClim data, the "metafor" package (Viechtbauer, 2010) to run our mixed-effect models, and to calculate effect sizes, CI, sampling variation, and publication bias, the "brranching" package (Chamberlain, 2019) to construct our phylogenetic trees and calculate branch lengths, and the "phytools" package (Revell, 2012) to assess the presence of phylogenetic signals.

3 | RESULTS

Synthesizing 70 studies constituting 807 observations of phenological shifts, we found that warming lengthened the growing season by advancing early-season phenologies (Hedges' $g = -0.79$, 95% CI = -1.08 to -0.49 , $n = 699$; Figure 1). Late-season phenophases were understudied ($n = 108$ observations) compared with early-season phenophases ($n = 699$ observations). Because of the low sample sizes for late-season phenophases our ability to robustly

test how biological or geographic variables affect experimental outcomes for late-season phenophases was limited. Although late-season phenophases were often delayed, this effect was not significant (Hedges' $g = 0.15$, 95% CI = -0.44 to 0.73 , $n = 108$; Figure 1). Because of the limited availability of late-season data, the following results are limited to early-season phenology data, but late-season results for all models (phenology as modified by specific environmental, species, and experimental parameters) are available in the supplement (Table S4a–r).

Early-season phenophases included onset of growth, presence of young leaves, presence of mature leaves, flower budding, flower opening, pollen release, fruiting, and fruit ripening. Experimental warming significantly advanced the phenology of all phenophases relative to ambient treatments ($Q_M = 14.98$, $df = 8$, $p = 0.04$; Table S4a) and did so to a similar extent across all phenophases (Holm-corrected pairwise comparisons, $p > 0.05$; Table S5a).

3.1 | Ecosystem characteristics

Warming experiments are predominantly conducted in temperate biomes in the Northern Hemisphere (Figure 2a). Approximately one third of our observations were from experiments conducted in the United States ($n = 288$, 35.7%), and an additional one third of observations were from Europe ($n = 306$, 37.9%). Approximately one tenth of our observations came from Asia ($n = 101$, 12.5%), predominantly China ($n = 77$), and one tenth of our observations came from Australia ($n = 59$, 7.3%). We did not find warming studies conducted in Central America or Africa, and only a single study conducted in South America (Chile; Dudley et al., 2018). Nearly 60% of the observations occurred in temperate biomes ($n = 476$, 59.0%). Almost one fifth of observations were from arctic biomes ($n = 137$, 17.0%), and one tenth of observations were from subalpine ($n = 77$, 9.5%) and alpine ($n = 68$, 8.4%) biomes. Fewer than 5% of the observations came from subarctic ($n = 35$, 4.3%) or subtropical ($n = 14$, 1.7%) biomes. There were no studies conducted in tropical ecosystems. There was similar skew in the habitats studied, with 41% of the observations from grasslands ($n = 330$) and 35% of the observations from forests ($n = 284$). Seventeen percent of observations were from tundra ($n = 137$) and less than 5% of observations were from shrublands ($n = 23$, 2.9%), wetlands ($n = 18$, 2.2%), or snow beds ($n = 15$, 1.9%), respectively.

The effects of warming on early-season plant phenology was not moderated by general ecosystem characteristics. Warming advanced plant phenology to an equal amount across all study biomes ($Q_M = 3.29$, $df = 5$, $p = 0.65$; Table S4f; Holm-corrected $p > 0.05$; Table S5b) and habitats ($Q_M = 3.68$, $df = 5$, $p = 0.60$; Table S4g; Holm-corrected $p > 0.05$; Table S5c). We found no effect of latitude ($Q_M = 0.82$, $df = 1$, $p = 0.36$; Table S4c; Figure 2b), elevation ($Q_M = 0.49$, $df = 1$, $p = 0.49$; Table S4b; Figure 2c), MAT of study location ($Q_M = 0.73$, $df = 1$, $p = 0.39$; Table S4d), or MAP of study location ($Q_M = 0.42$, $df = 2$, $p = 0.52$; Table S4e) on the effect of warming of phenological shifts for early-season phenophases.

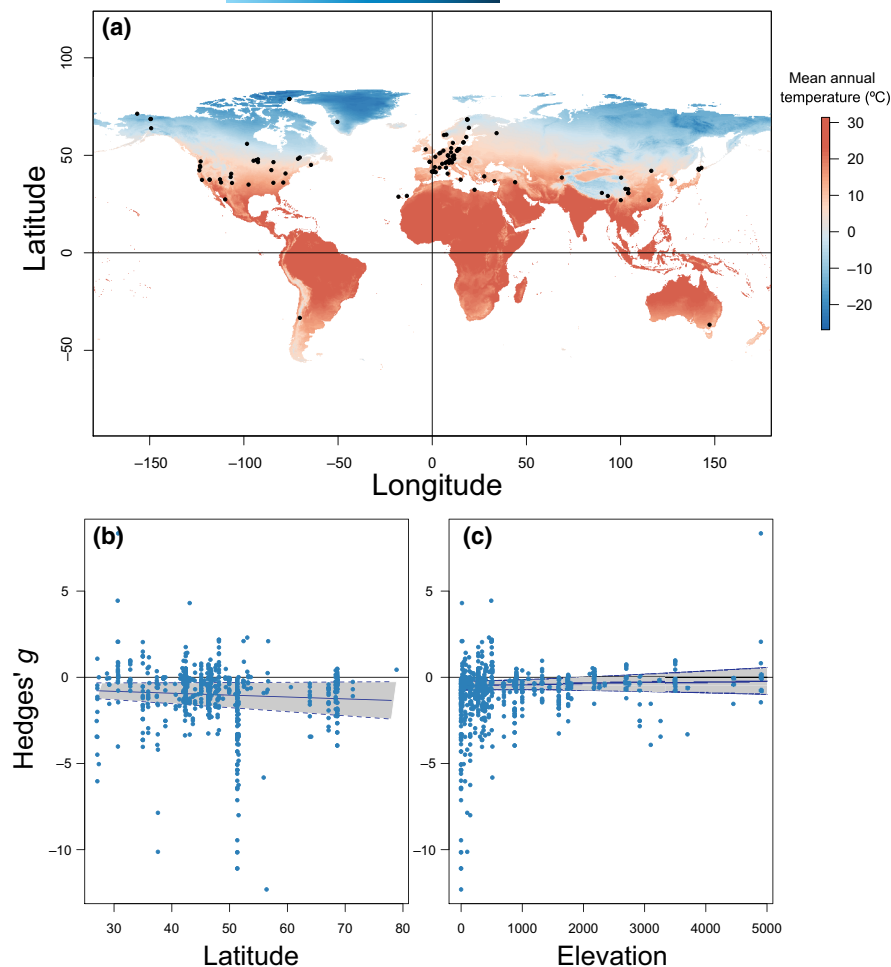


FIGURE 2 The majority of experimental warming studies that measured plant phenology were located in North America and Europe (a). We did not detect a change in the magnitude of effect of warming across latitude (b) or elevation (c). Points represent the mean effect size (Hedges' *g*) of experimental warming relative to ambient temperatures on early-season plant phenology and negative values indicate that plant phenology advanced in warmed relative to ambient temperature treatments. Regression line and 95% confidence intervals represent the predicted mean effect as a function of absolute latitude (b) or elevation (c) and were derived from mixed-effect models accounting for plant phylogenetic relatedness and the average temperature difference between warmed and ambient treatments [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Plant characteristics

More than three-quarters of the observations in our data set consisted of reproductive adult plants ($n = 457$, 78.3%), and 90% of the observations were of plants with perennial life cycles ($n = 646$). There was slightly more even representation of plants across various functional forms. Herbaceous forbs made up 43% ($n = 303$) and trees made up 29% ($n = 203$) of the observations, whereas grasses ($n = 96$) and shrubs ($n = 97$) each comprised approximately 15% of the remaining observations. Plants that were native to the study ecosystem comprised 85% of observations ($n = 596$).

The effect of warming on the phenology of plants with annual life cycles was two times greater than the effect of warming on plants with perennial life cycles ($Q_M = 6.99$, $df = 1$, $p = 0.008$; Figure 3a; Tables S4h and S5d). Likewise, the effect of warming was nearly two times greater for species of nonnative origin relative to species of native origin ($Q_M = 3.57$, $df = 1$, $p = 0.06$; Figure 3b; Tables S4i and S5e). However, the proportion of observations of annual nonnative plants (32%, or 33 of 70 nonnative observations) was significantly larger than the proportion of observations of annual native plants (3%, or 20 of 576 observations) in our early-season data set ($\chi^2 = 99.06$, $df = 1$, $p < 0.0001$). Because of this overrepresentation of annual nonnatives relative to annual natives in our data set, we created a four-factor variable combining species' origin and duration

(annual native, annual nonnative, perennial native, perennial nonnative) to test how warming influenced these factors in combination. Again, we found that the effect of warming on plant phenology varied by species' origin and life cycle ($Q_M = 8.55$, $df = 3$, $p = 0.04$; Figure 3c; Table S4j) and Holm-corrected pairwise comparisons showed that the effect of warming on phenological advancement was significantly greater for nonnative annuals relative to native perennials ($z = -2.82$, $p = 0.03$; Figure 3; Table S5f).

The effect of warming on juvenile plants was over two times greater than the effect of warming on adult plants ($Q_M = 3.95$, $df = 2$, $p = 0.14$) although our Holm-corrected pairwise comparison showed no significant difference ($z = -0.45$, $p = 1.0$; Tables S4k and S5g). We found no difference in the effect of warming across plant growth forms ($Q_M = 0.89$, $df = 3$, $p = 0.83$; Tables S4l and S5h).

3.3 | Experimental characteristics

The magnitude of phenological shifts in response to warming were relatively consistent across a range of experimental contexts. The strongest effects of experimental warming were reported in common garden experiments (Figure 4a), where plants were grown outdoors, typically in pots and in a common location, usually on the grounds of a research facility, with passive or active warming

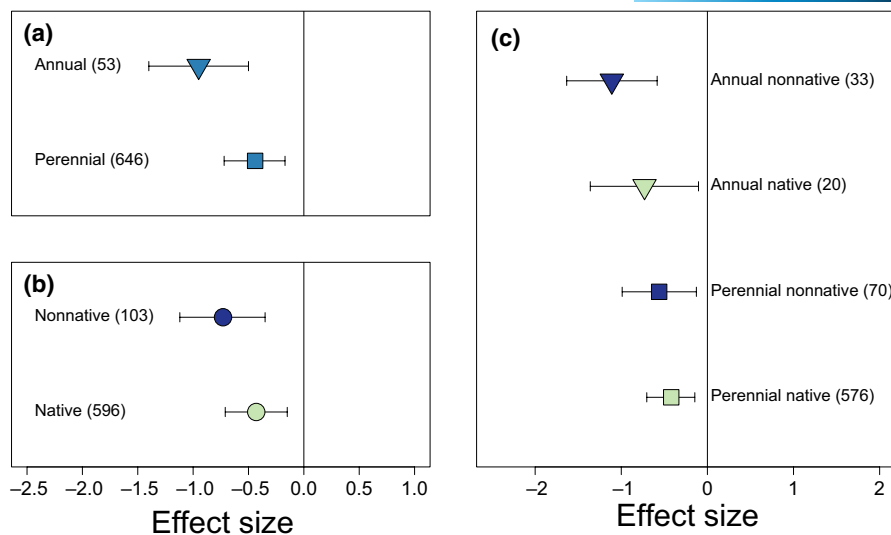


FIGURE 3 The effect of warming on the phenology of plants varied based on origin (a) and life cycle (b). Taken together, the effect of warming on phenological advancement was significantly greater for nonnative annuals relative to native perennials, but did not vary for other pairwise combinations of plant origin and life cycle (c). Values are mean effect sizes (Hedges' g) estimated from mixed-effect meta-analysis models accounting for plant phylogenetic relatedness and the average temperature difference between warmed and ambient treatments. Negative values indicate that the timing of a phenophase was earlier in warmed treatments relative to ambient temperature treatments. Error bars represent 95% confidence intervals calculated from Wald-type tests and numbers in parentheses represent the number of observations for each phenophase [Colour figure can be viewed at wileyonlinelibrary.com]

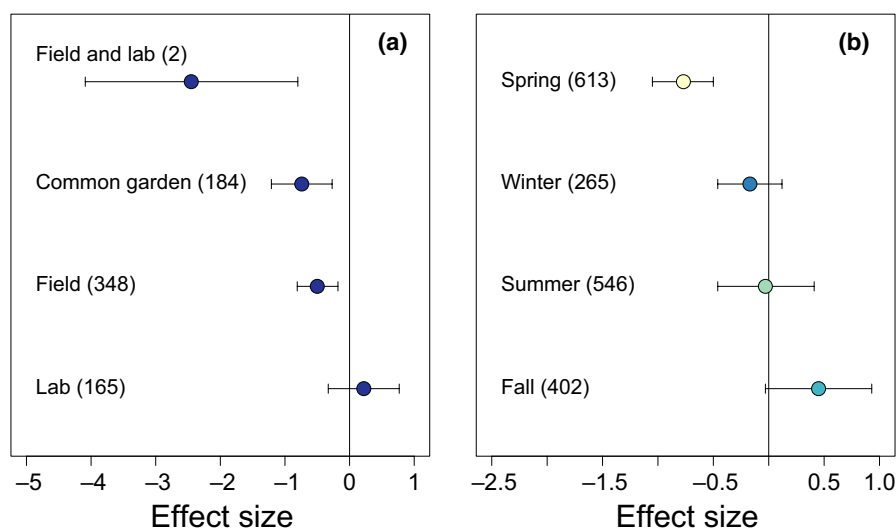


FIGURE 4 The effects of experimental warming varied depending on the location of the experiment (a) and on the seasons warmed (b). Early-season plant phenology advanced to a greater degree when experiments were conducted in a common garden relative to a lab (growth chamber or greenhouse) but did not differ significantly from field experiments. Early-season phenophases advanced to a greater degree when warming occurred in the spring relative to other seasons. Values are mean effect sizes (Hedges' g) estimated from mixed-effect meta-analysis models accounting for plant phylogenetic relatedness and the average temperature difference between warmed and ambient treatments. Negative values indicate that the timing of a phenophase was earlier in warmed treatments relative to ambient temperature treatments. Error bars represent 95% confidence intervals calculated from Wald-type tests and numbers in parentheses represent the number of observations for each phenophase [Colour figure can be viewed at wileyonlinelibrary.com]

chambers or infrared heaters ($Q_M = 14.46$, $df = 3$, $p = 0.002$; Tables S4m and S5i). The effects of warming were nearly two-thirds larger in common gardens relative to field warming experiments, which also significantly advanced early-season plant phenology. We did not find a consistent effect of warming in lab (growth chamber or

greenhouse) experiments on phenological shifts. We did not find differences in the magnitude of phenological shifts across different methods of experimental warming ($Q_M = 10.81$, $df = 11$, $p = 0.46$; Tables S4n and S5j). Strength of phenological shift was not contingent on whether warming was achieved actively or passively

($Q_M = 0.09$, $df = 1$, $p = 0.76$; Tables S4o and S5k) nor duration of experimental warming ($Q_M = 0.44$, $df = 1$, $p = 0.51$; Table S4p). We tested whether the effects of experimental warming were consistent for studies that reported multiple years of data (24 studies and 511 observations). We found that for each additional year of warming reported, the effect of warming significantly increased plant phenological response ($Q_M = 17.01$, $df = 1$, $p < 0.001$). However, only three studies (Dunne et al., 2003; Hoffmann et al., 2010; Xia & Wan, 2012) reported more than 3 years of warming. When we excluded the later year observations from these three studies ($n = 51$ observations), the relationship between number of years of a study and the magnitude of the effect of warming was no longer significant ($Q_M = 0.86$, $df = 1$, $p = 0.35$).

Although there was no difference in experiments that used pulse or continuous warming throughout the experimental duration ($Q_M = 0.05$, $df = 1$, $p = 0.82$; Tables S4q and S4l), there was an effect of what season(s) were warmed within an experiment ($Q_M = 37.43$, $df = 4$, $p < 0.0001$; Table S4r). Specifically, only spring and winter warming treatments significantly advanced plant phenology for early-season phenophases (Figure 4b). Warming during the spring had a larger effect on phenological advancement than did warming during the summer ($z = 2.58$, $p = 0.05$), fall ($z = 4.23$, $p = 0.0001$), or winter ($z = 2.38$, $p = 0.07$) while there were no pairwise differences in the effect of warming for the other seasons ($p > 0.05$; Table S5m).

4 | DISCUSSION

We find that, cumulatively, experimental temperature manipulations offer compelling evidence that warming broadly shifts plant phenology, generally advancing early-season phenophases. However, limited late-season data made it impossible to detect a significant delay in late-season phenophases. The strength of phenological shifts across phenophases (e.g., leaf out, flowering, etc.) in response to warming is consistent. However, we find that the magnitude of these shifts is variable across a number of important axes related to organismal characteristics including species origin, and annual or perennial life history. But there are numerous gaps in these data sets that limit our ability to fully summarize the effects of warming on plant phenology. Encouragingly for researchers, outcomes were generally robust across experimental methods, with the exception of season of warming. We highlight many areas where future experimental warming studies are uniquely poised to expand our understanding of plant phenological responses to climate warming.

Although it is well established that, on average, plant phenology is changing as the climate warms, little is known about the sensitivity of sequential phenophases within a season, such as flowering and fruiting, to warming (CaraDonna et al., 2014; Zani et al., 2020; Zohner & Renner, 2019). While the timing and length of earlier phenophases tend to be predictive of the timing of later phenophases (Ettinger et al., 2018), the relative sensitivities of different phenophases to warming likely differs between woody and herbaceous life

forms (CaraDonna et al., 2014; Zohner & Renner, 2019) and across growth forms (Zohner & Renner, 2019). Experimental warming studies, with their strong controls of the magnitude of warming across an entire growing season, can offer unique insights into phenological shifts across multiple phenophases, without the complication of variation in temperatures across seasons (i.e., warm spring but cool summer) often experienced in observational studies. We found that, on average across all species and ecosystems, experimental warming consistently advanced all early-season phenophases to the same extent. The directionality of early-season phenological shifts was in line with those observed for flowering and leafing in a previous synthesis of experimental warming (Wolkovich et al., 2012). However, averaging across species and ecosystems likely masks important differences in how warming shifts phenophases within individual species. For example, CaraDonna et al. (2014) found that the first flowering dates of perennial native forbs were more sensitive to warming compared with last flowering dates. However, there was also a huge amount of interspecific variability in the magnitude of shifts across phenophases, resulting in unequal shifts in flowering season, for example. Such uneven shifts across both phenophases and species have the potential to alter biotic interactions as well as the structure and function of ecosystems. Unfortunately, such nuances in phenological responses to warming within and among plant species are understudied (CaraDonna et al., 2014). Likewise, Zohner and Renner (2019) found woody plant bud set and leaf senescence phenologies responded to warming to differing extents, and that each phenophase responded differently to variation in the season(s) of experimental warming. Individual studies in our analysis only recorded ~2 phenophases on average. Future experimental studies could contribute to our understanding of the relationships between warming and the responses of sequential phenophases by exploring the effects of warming on multiple phenophases within the same species.

Late-season phenophases were dramatically under-represented in our data set relative to early-season phenophases, suggesting more intensive experimental study of late-season phenology is a critical area for future research (Gallinat et al., 2015; Gill et al., 2015). We found over 10-fold more observations of early-season phenological responses to experimental warming relative to late-season phenological responses. As a result, our discussion is limited to trends in early-season phenology. Although more than half of our observations ($n = 402$) were gleaned from experiments that continued warming treatments throughout the fall, less than 15% of the observations were of late-season phenophases ($n = 108$). As such, increasing the availability of data on late-season phenophases would often not entail extending experimental warming treatments, only extending monitoring throughout the growing season.

We did not find an overall significant effect of warming on late-season phenology, although the effect was consistently positive suggesting that late-season phenophases are, on average, delayed with warming. Our inability to detect significant effects of warming on late-season phenophases is likely, at least in part, a function of the low number of observations decreasing our ability to detect significant

differences. However, there is also the possibility that later-season phenophases are, in fact, more variable in their response to warming than early-season phenophases (Zani et al., 2020; Zohner & Renner, 2019), which could also have contributed to our insignificant effects. Variability in phenological shifts in late-season phenophases could occur because of a few non-mutually exclusive mechanisms. First, if warming is inconsistent (i.e., a warm spring but cool summer) within a single season, the downstream effects on later phenophases may be more variable depending on the environmental conditions and responsiveness of the plant species to that variation. Second, later season phenology may be less sensitive to temperature and more sensitive to other environmental cues (e.g., precipitation or photoperiod) than are early-season phenologies (Gallinat et al., 2015; Reeb et al., 2020), increasing the variation in their response. Finally, there is some evidence that plants that leaf out earlier in the spring in response to warming will also senesce earlier in the fall, potentially owing to limited supplies of nutrients or photosynthates, or other physiological constraints on the annual leaf or plant life span (Zani et al., 2020; Zohner & Renner, 2019). Because of these multiple mechanisms that may enhance late-season plant phenological variation in response to warming, we may find that we need more studies of late-season plant phenology relative to early-season phenophases to adequately predict plant phenological responses to warming.

Sensitivity of plant phenology to experimental warming did not vary along latitudinal or elevational gradients. Long-term observational data provide much of the prior evidence for variable phenological shifts along latitudinal and elevational gradients, but these data sets yield mixed results. Such long-term data have found greater sensitivity of organisms at higher latitudes (Parmesan, 2007; Prev  y et al., 2017) and lower latitudes (Ge et al., 2015; Shen et al., 2015) as well as higher elevations (Cufar et al., 2012; Ge et al., 2015; Li et al., 2019; Vitasse et al., 2018; Ziello et al., 2009) and lower elevations (Crimmins et al., 2010; Rafferty et al., 2020). Cumulatively, these seemingly contradictory results likely point to strong contingencies in geographic patterns of phenological shifts. Multiple mechanisms may explain this variable sensitivity to warming across latitudinal or elevational gradients when explored over long time periods. One mechanism may be that species' thermal tolerances or reliance on non-temperature cues (such as photoperiod or precipitation) may vary across these broad environmental gradients (Chmura et al., 2019; Suonan et al., 2019). Additionally, observed phenological shifts along these geographic gradients may be confounded by variability in other abiotic characteristics along these same gradients, such as precipitation and CO₂ (Chmura et al., 2019; Ge et al., 2015; Suonan et al., 2019), generating high variability across spatial scales (Chmura et al., 2019). Our synthesis of phenological shifts driven by warming experiments (rather than long-term climate warming) across latitude and elevation allows us to explore the geographic fingerprint in warming-mediated phenological shifts, unencumbered by co-occurring changes in other factors such as precipitation that may co-vary across these gradients. We find that there is not strong evidence for systematic shifts in phenological sensitivity to warming, alone, across broad latitudinal or elevational gradients.

Similarly, we did not find the effect of warming on plant phenology to vary with MAT or MAP, which also may vary along latitudinal or elevational gradients. This is in agreement with another synthesis which also failed to detect a signal of MAT on phenological sensitivity using both experimental and observational data (Wolkovich et al., 2012). Here, isolating the impacts of temperature through experimental manipulations along these larger environmental gradients provides an opportunity to test questions about the relative sensitivity of species' phenology to warming. Although we might have expected to see early-season phenophases respond more strongly to warming at sites with lower MAT, we find no evidence for such a trend when synthesizing this global data set. Intentionally manipulating multiple environmental cues within the same experiment will refine our understanding of how variation in multiple global change drivers may alter plant phenology (Suonan et al., 2019). The field would also benefit from more systematic temperature manipulations across environmental gradients.

The magnitude of phenological shifts in response to warming across biomes and habitat types was consistent; however, there were obvious geographic biases in experimental warming studies. The vast majority of observations came from temperate forest and grassland ecosystems in the Northern Hemisphere. In temperate systems, plant phenology may be more sensitive to temperature cues while plants in arid or tropical ecosystems may be more sensitive to precipitation (Chmura et al., 2019; Cleland et al., 2007; Liu et al., 2015; Yang et al., 2015), but limited data collection in tropical regions to date make it difficult to confirm these generalizations. Our findings of consistent responses across habitats and biomes are similar to previous findings from studies of predominantly temperate mesic ecosystems (Wolkovich et al., 2012; Wu & Liu, 2013) but differ from studies that include larger numbers of observations in arid habitats (Liu et al., 2015; Yang et al., 2015). Clearly, experimental studies in underrepresented biomes and habitats—such as desert, Mediterranean, subtropical, and tropical ecosystems—would broaden our understanding of plant phenological sensitivity to climate warming.

The advancement of phenology in response to warming was relatively equal across plant growth forms. This is in line with other studies that synthesize results across many species and have found weak (if any) differences in phenological shifts among plant growth forms when averaging the phenological response of plants to changing temperatures across large numbers of species and diverse ecosystems and geographic regions (Calinger et al., 2013; Ge et al., 2015). However, studies that account for other environmental variables, including precipitation and soil moisture, tend to find variation in phenological responses across plant growth forms (K  nig et al., 2017; Liancourt et al., 2012; Suonan et al., 2019). Likewise, studies that monitor multiple plant species within the same study site have demonstrated variability in the sensitivity of plant growth forms to warming at smaller spatial scales (Bock et al., 2014; Heberling et al., 2019). Interestingly, there were significant differences in proportion of plant growth forms represented in our early- and late-season data sets (Chi-square test: $\chi^2 = 50.8$, $df = 3$, $p < 0.001$). Herbaceous forbs

and grasses represented 59% of the observations in our early-season data set, whereas woody shrubs and trees represented 72% of the observations in our late-season data set. This bias in what types of plants we study when limits our ability to synthesize plant phenological responses to warming. Although many studies in our analysis reported the phenological responses of multiple species within their experiment (mean and median number of species studied was 4 and 2, respectively), 70% of the studies only surveyed plants representing a single growth form ($n = 49$).

We observed juveniles to be over three times more sensitive to warming than were adult plants, although this difference was not significant in post-hoc tests. To date, there has been very little exploration of phenological sensitivities to warming across life stages. A global meta-analysis on spring phenology in woody plants found little evidence for differences in phenological responses to warming across ontogenies (Ettinger et al., 2020). However, we do know that juveniles and adults can differ in the timing of life history events, such as bud break (Augspurger & Bartlett, 2003) and leaf unfolding (Vitasse, 2013), and there is some evidence that leaf phenology may be more plastic in juveniles than adults (Mediavilla & Escudero, 2009). Although phenological sensitivities to warming are rarely explored across ontogenies, these contingencies almost certainly have important implications for how organisms respond to warming and for ecosystem functioning (Levy et al., 2016; Yang & Rudolf, 2010).

The effect of warming on the phenology of nonnative plants with annual life cycles was two times larger than the effects of warming on phenology of native plants with perennial life cycles. This aligns with previous research that has found non-native species tend to have greater sensitivity to warming than native species (Calinger et al., 2013; Giejsztowt et al., 2020; Willis et al., 2010; Wolkovich et al., 2013; Zettlemoyer et al., 2019). This phenological sensitivity in nonnative plants is unsurprising given the relatively high phenotypic plasticity generally expressed by nonnative species (Davidson et al., 2011; Lamarque et al., 2015); and, in fact, these differences in phenological sensitivity may play a role in the success of some nonnative invaders (Willis et al., 2010; Zettlemoyer et al., 2019). Likewise, several long-term observational studies have also shown the phenology of annuals to be more sensitive to warming than that of perennials (Fitter & Fitter, 2002; Munson & Long, 2017). Furthermore, the disparity in the phenological sensitivities of native and non-native species may have important ecological consequences. Giejsztowt et al. (2020) showed that increased overlap in flowering time between native and nonnative plants as a result of uneven phenological shifts resulted in increased competition and decreased fitness in native plants.

Similarly, annual plants may have greater responses to warming temperatures as a result of their fast growth rates relative to perennials (Garnier, 1992), allowing them to capitalize on reproduction during favorable conditions. Shorter generation times also allow annuals to adapt more quickly to consistently warming climates (Franks et al., 2007). It is notable that a majority of observations of nonnative

species in our review came from North American grassland ecosystems. Expanding warming studies to include a wider diversity of nonnative functional groups, such as nonnative woody perennials in forested ecosystems or perennial grasses in tropical and subtropical grasslands will further expand our understanding of how plant communities comprised of species of mixed origin or functional groups respond to warming.

Encouragingly, we found plant responses to experimental warming to be relatively robust across experimental warming methods. One exception was common gardens, in which the per degree impacts of warming were greater than in studies conducted in the field. The impacts of warming did not vary across active and passive modes of warming (similar to Wolkovich et al., 2012). We did not detect a signal of experimental duration on the magnitude of phenological shift, although this has been suggested by others to drive of experimental outcomes (Hoffmann et al., 2010; Wang et al., 2019). As might be expected, early-season phenophases were most responsive to warming applied during the spring and winter, indicating that warming immediately prior to the phenological event is an important driver of phenology. This is in keeping with empirical studies showing that temperatures in the months immediately preceding the phenological event are most responsible for driving temporal shifts in the phenophase (Fitter & Fitter, 2002; Gordo & Sanz, 2010; Menzel, Sparks, Estrella, Koch, et al., 2006; Miller-Rushing & Primack, 2008). Although, for some systems, there is clear evidence for winter temperatures driving impacts, as is the case in some species with strong winter chilling requirements (e.g. Yu et al., 2010). Finally, we found some evidence suggesting that within a study, the effect of warming on phenology increases with each year of study, suggesting that long-duration warming experiments may elicit stronger phenological shifts; although it is important to note these results were driven by three particularly long studies (>3 years in duration Dunne et al., 2003; Hoffmann et al., 2010; Xia & Wan, 2012).

Although experimental climate manipulations can offer insights into the likely implications of future climate change, they do not come without their fair share of caveats. One key criticism leveled against experimental warming manipulations is that they may not accurately reflect shifts that have been observed in long-term empirical studies (Wolkovich et al., 2012). Nonetheless, these studies generate useful information by allowing isolation of warming as a mechanism of phenological shift and will be important for understanding the mechanisms driving phenological mismatches in plant communities. If anything, we might expect the results of this analysis to be conservative, as experimental warming may underrepresent the impacts of climate change on phenological shifts (Ettinger et al., 2019; Wolkovich et al., 2012).

5 | CONCLUSIONS

Shifting phenologies associated with global climate change have been an important driver of changes in species abundances and distributions, as well as the composition of communities (Chuine,

2010; Rudolph, 2019). Species that fail to track the changing climate may be at a disadvantage and ultimately decline in abundance (Willis et al., 2008). Likewise, mismatches in the rate of change between co-occurring plants could lead to exclusion of plants with lower sensitivity to warming temperatures (Heberling et al., 2019). Understanding how phenological responses to experimental warming vary across study systems, species, and experimental designs may help us to contextualize and understand the multiple mechanisms leading to differential phenological response across plants in response to future climate warming. Here, in one of the most comprehensive syntheses of experimental warming to date, we find broad patterns of variability in phenological sensitivity across species of different origins and life history strategies. However, numerous gaps remain, hindering our ability to fully understand the impacts of warming on phenology across species globally. Future experimental warming studies should consider measuring multiple plant phenophases (particularly late-season phenophases) as well as measuring the responses of species that vary in their origin, growth form, and life cycles. Likewise, replicating warming studies in under-represented biomes and habitats—including desert, Mediterranean, subtropical, and tropical ecosystems—would reduce the severe biogeographic bias in current experimental studies. Filling these gaps will help us identify broad patterns of phenological sensitivities to warming in plants across geography and taxonomy; improving our understanding of how ecosystems will change in the face of future climate warming.

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AUTHOR CONTRIBUTION

Katharine L. Stuble and Sara E. Kuebbing designed the study and Leland D. Bennion led the data analysis with help from Sara E. Kuebbing. All authors contributed to the data collection and the writing of the manuscript.

DATA AVAILABILITY STATEMENT

The data are publicly available in the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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