

Drier soils delay plant phenology across climate change experiments in temperate forest and grassland systems

A.K. Ettinger^{1,2,a}, J.S. Dukes^{3,4,b}, M.R. Johnston^{5,c}, C.R. Rollinson^{6,d}, and E.M. Wolkovich^{1,7,e}

¹Arnold Arboretum of Harvard University, Boston, Massachusetts 02131, USA

²The Nature Conservancy, Seattle, Washington, USA

³Carnegie Institute

⁴Cary Institute of Ecosystem Studies

⁵University of Maryland Center for Environmental Science

⁶The Morton Arboretum, Lisle, Illinois 60532, USA

⁷Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia,
Vancouver, BC, Canada

^aCorresponding author; email: ailene.ettinger@tnc.org; phone: 781-296-4821; mailing
address: 74 Wall Street. Seattle, WA 98121, USA

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1. What scientific question is addressed in this manuscript?
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¹ Abstract

² Previous meta-analyses of phenology responses to climate change have focused largely on temperature as a
³ driver of observed shifts. Yet climate change also affects soil moisture, which is limiting to many biological
⁴ responses. Here we synthesize microclimate and phenology data from climate change experiments in temper-
⁵ ate systems—both forests and grasslands—to quantify how soil moisture interacts with temperature to affect
⁶ plant phenology. We find that phenology (budburst, leafout and flowering) delays in drier soils, with the
⁷ largest delays seen in budburst. While effect sizes of soil moisture were much smaller than for temperature

8 (-1.73 days versus -7.89 days in models with standardized predictors), with interactive effects of temperature
9 x moisture even smaller (0.5 days), we found that these effects could have important implications. We found
10 high variability in the response to shifted soil moisture across species; this combined with high variability
11 in forecasts of drought and precipitation in many systems may increase the importance of soil moisture to
12 phenology in the future in some locations. Forecasting shifts in soil moisture with warming, we find that
13 soil moisture declines could have important effects on the phenology of some species, potentially muting
14 advances due to warming alone. Our results show that soil moisture plays an important role in the phenology
15 of temperate systems, with varying effects across species, and thus is likely to alter ecosystem functions tied
16 to phenology such as growth and carbon storage. Incorporating local context, including ecological knowl-
17 edge of relevant species and downscaled climate change projections, will be critical for planning appropriate
18 management and conservation in response to phenological shifts and related ecosystem services.

¹⁹ INTRODUCTION

²⁰ Climate change is affecting organisms by altering conditions such as temperature and soil moisture around
²¹ the world (Parmesan, 2006; Chen et al., 2011). Some of the most widespread biological responses to climate
²² change are shifts in phenology, the timing of recurring biological events, which have occurred at rates of 2.3-
²³ 5.1 days per decade (Parmesan, 2006; Poloczanska et al., 2013; Root et al., 2003). Shifts in plant phenology
²⁴ are the most widely documented, with spring phenology (budburst, leafout, and flowering) occurring earlier
²⁵ in recent years (Wolkovich et al., 2013), and senescence occurring later (Taylor et al., 2008; Delpierre et al.,
²⁶ 2009).

²⁷ Phenological shifts are typically attributed to warming temperature, a known and well-studied driver of
²⁸ plant phenology (e.g., Cleland et al., 2007; Piao et al., 2019). The timing of spring budburst, for example,
²⁹ depends on temperature through both chilling (the prolonged exposure to cold temperatures after growth
³⁰ cessation in the fall) and forcing (exposure to warm temperatures). Forcing effects are typically considered
³¹ more dominant, so much so that many models use only forcing to predict phenology. These include common
³² models of ‘growing degree days’ (GDD) in which phenological events are triggered after a certain thermal
³³ sum is reached (e.g., Olsson and Jönsson, 2014). Recent trends of advancing spring phenology have generally
³⁴ attributed this advance to warming springs—and potentially winters—with myriad studies focused on the
³⁵ complexity of how chilling and forcing together may determine spring phenology (Fujisawa and Kobayashi,
³⁶ 2010; Ibanez et al., 2010; Cook et al., 2012)

³⁷ Effects of changing patterns of precipitation and soil moisture on plant phenology have received less attention,
³⁸ but fundamental plant biology suggests they should play an important role. Budburst can be slowed when
³⁹ water stress is high enough to inhibit cell elongation (Essiamah and Eschrich, 1986), suggesting woody plant
⁴⁰ spring phenology is fundamentally limited by water even as this is rarely observed. Similarly, in grasslands,
⁴¹ growing season start can be delayed by drought Cui et al. (2017). For plants already growing, however,
⁴² drought conditions can advance flowering (Hamann et al., 2018), as plants try to complete fruiting before
⁴³ water is too limiting.

⁴⁴ Though many climate change experiments have focused on effects of altered precipitation regimes, the role
⁴⁵ of soil moisture on phenology has been most reported in arid and grassland ecosystems (e.g., Essiamah and

⁴⁶ Eschrich, 1986; Reich and Borchert, 1984; van Schaik et al., 1993; Tao et al., 2019). Effects in arid systems
⁴⁷ are diverse, often with no overall shift or trend in phenology for most single experiments (e.g., Sherry et al.,
⁴⁸ 2007; De Kauwe et al., 2017; Howell et al., 2020), as well as meta-analyses (Lu et al., 2023). Results in
⁴⁹ mesic regions have been equally diverse: Wang et al. (2022b) found that decreasing precipitation frequency
⁵⁰ correlates with earlier leafout in many regions, while others have found variation in moisture sensitivity across
⁵¹ ecoregions (Seyednasrollah et al., 2018). Increasing research using large-scale observational phenology data
⁵² (e.g., remote sensing products such as NDVI) has documented an important role for soil moisture from forests
⁵³ to grasslands (Lian et al., 2020; Shen et al., 2022; Liu et al., 2024), and suggest temperature may play a role
⁵⁴ through moderating soil moisture (Liu et al., 2024). Teasing out the role of soil moisture from temperature
⁵⁵ is challenging through long-term climate trends alone, however.

⁵⁶ Field-based climate change experiments that warm plots to different levels and apply precipitation or drought
⁵⁷ treatments could help tease apart the effects of temperature and moisture on plant phenology, especially if
⁵⁸ leveraged through synthesis across studies. Experiments can combine temperature and precipitation treat-
⁵⁹ ments to decouple them compared to what may be observed in nature, allowing their effects to be more
⁶⁰ robustly quantified. Additionally, experiments that monitor daily soil moisture and air temperature at the
⁶¹ plot-level can help translate how these treatments alter microclimates to affect plant phenology (Ettinger
⁶² et al., 2019). While previous meta-analyses of phenology in climate change experiments have focused pri-
⁶³ marily on effects of temperature (e.g., Wolkovich et al., 2012), or compared treatment effects (Zhou et al.,
⁶⁴ 2023), there has been little synthetic work on moisture effects across experiments.

⁶⁵ Here we use measured microclimate and phenology data across experiments (Fig. S1) to test how soil
⁶⁶ moisture and above-ground temperature together affect plant phenology (budburst, leafout, flowering). Our
⁶⁷ aims were to: (1) quantify effects of soil moisture versus temperature alone and synergistically across species;
⁶⁸ (2) evaluate how consistent effects were across species, functional groups and biomes (forest versus grassland),
⁶⁹ and (3) forecast effects to understand future implications of moisture shifts with warming for phenology.

70 MATERIALS AND METHODS

71 **Data**— To investigate how soil moisture interacts with temperature to affect phenology, we used two databases
72 that compiled data from climate change experiments. Microclimate data came from the MicroClimate from
73 Climate Change Experiments (MC3E) database (Ettinger and Wolkovich, 2018; Ettinger et al., 2019). Phenology data came from a ExPhen, a new database of phenology from climate change experiments (Ettinger
74 and Wolkovich, 2022).

75 Both databases were created by first identifying published, active-warming field experiments, many of which
76 included precipitation manipulations. We focused on *in situ* active-warming manipulations because recent
77 analyses indicate that active-warming methods are the most controlled and consistent methods available
78 for experimental warming (Kimball, 2005; Kimball et al., 2008; Aronson and McNulty, 2009; Wolkovich
79 et al., 2012). We carried out a full literature review to identify potential active-warming field experiments,
80 following the methods and search terms of Wolkovich et al. (2012) for their Synthesis of Timings Observed in
81 iNcrease Experiments (STONE) database (Wolkovich et al., 2013), but restricting our focus to active-warming
82 experiments. Further, because our goal was to tease out variation in microclimate (including temperature and
83 soil moisture), we focused on warming studies that included multiple levels of warming and/or precipitation
84 treatments. These additional restrictions constrained the list to 11 new studies published after the STONE
85 database, as well as six of the 37 studies in the STONE database. We contacted authors to obtain daily
86 microclimate and phenological data for these 17 studies and received data (or obtained publicly available
87 data) for 10 of them, as well as datasets from five additional sites offered or suggested to us over the course
88 of our literature review and data analysis. The daily temperature and soil moisture data from these 15
89 experiments comprise the MC3E database (Ettinger and Wolkovich, 2018; Ettinger et al., 2019). Of these,
90 we were able to obtain plot-level phenology data from 14 experiments, which comprise the ExPhen database
91 of experimental phenology, available at KNB (Ettinger and Wolkovich, 2022).

92 Here, we analyze phenology data from the eight experiments in ExPhen that contain both regularly monitored
93 plot-level soil moisture and above-ground temperature data (Table S1). To help examine variation among
94 species and across sites, we focus on the most common phenophases monitored, which were measured in three
95 or more different experiments: budburst, leafout, and flowering. Two of the eight experiments were located

97 in grassland ecosystems; the remaining six were in forests (Table S1). The database is species-rich, including
98 41 species monitored for budburst across five sites, 137 for leafout (across five sites), and 124 for flowering
99 (across all eight sites), for a total of 190 species. These species span grasses (16 species), forbs (109 species),
100 shrubs (29 species), and trees (36 species).

101 **Analysis**— To understand how soil moisture interacts with temperature to affect phenology, we fit models
102 with microclimate predictor variables of measured soil moisture, measured above-ground temperature, and
103 their interaction to phenology response data (budburst, leafout, flowering day of year). We excluded conifers
104 from the analysis, because their phenology has distinct differences from angiosperm phenology Polgar et al.
105 (2014) and conifer data existed from only one site in the database. For all phenophases, the response variable
106 was day of year of the phenological event.

107 Predictors for our primary models were measured plot-level above-ground temperature, soil moisture, and
108 their interaction. We chose to use measured microclimate as explanatory variables, rather than categori-
109 cal treatment levels or target warming level, in our meta-analysis because experimental treatment effects
110 from warming and drought can interact to alter microclimate conditions, in part due to feedbacks between
111 temperature and soil moisture conditions (Ettinger et al., 2019; McDaniel et al., 2014).

112 We used hierarchical Bayesian models to test for effects for each species, as well as an overall effect, while
113 accounting for site, year and plot-level effects. Grouping factors (often called ‘random effects’) for all phe-
114 nology models were species (with random slopes and intercepts), site (random intercept), and year nested
115 within site (random intercept). We fit models using the programming language **Stan** (Carpenter et al., 2017)
116 (www.mc-stan.org), accessed via the **brms** (Bürkner, 2021) package in **R** (R Core Team, 2022), version 4.1.3.
117 For each model fit, we ran four chains simultaneously, each with 4 000 iterations (2 000 of which were used
118 for warm-up). Equations for these models can be found in the Supplemental Methods.

119 Given our aim to directly compare moisture and temperature effects, we used standardized predictors, which
120 have an added benefit of improving model stability (Gelman and Hill, 2007). Standardizing predictors is
121 a common technique in regression analysis; here we z-scored predictor variables (subtracting the mean and
122 dividing by the standard deviation) and report coefficients from standardized predictor models as per SD
123 (standard deviation), alongside estimates of coefficients in their natural units. We report 80% uncertainty
124 intervals throughout the manuscript, unless otherwise stated.

₁₂₅ **RESULTS**

₁₂₆ We found that both higher soil moisture and higher temperatures advance phenology, meaning two common
₁₂₇ effects of warming experiments—soil drying and warming—have contrasting effects on phenology (Fig. 1,
₁₂₈ Table S2). Soil drying delays phenology and warming temperatures advance phenology. For budburst, wetter
₁₂₉ soils and warmer temperatures alone advanced phenology by -1.73 (-2.52,-0.95) days per SD of soil moisture
₁₃₀ (or -5.217 days per 10 percent increase in volumetric water content) and -7.89 (-10.51,-5.28) days per SD
₁₃₁ of temperature (or -3.41 per degree Celsius). We did not find evidence of strong interactive effects of soil
₁₃₂ moisture and temperature on phenology: together, wetter and warmer conditions delayed budburst only a
₁₃₃ small amount (interaction effect of 0.5 [-0.16-1.11] days per SD).

₁₃₄ The magnitude of soil moisture effects varied across phenophases, with effects on budburst (-1.73 [-2.52,-
₁₃₅ 0.95] days per SD increase in soil moisture) being stronger than those on leafout (-0.45 [-1.64,0.68] per SD
₁₃₆ increase in soil moisture) and flowering (-1.28 [-2.45,-0.11] per SD increase in moisture). Similar to budburst,
₁₃₇ temperature effects were stronger than soil moisture for leafout (for which the temperature effect was -10.35
₁₃₈ [-12.18,-8.49] days per SD increase in temperature) and flowering (for which it was -7.94 [-9.68,-6.22] per SD
₁₃₉ increase in temperature), across all species (Fig. 1). Estimates of interactions between soil moisture and
₁₄₀ temperature on phenology also varied by phenophase, with weakly positive or no interactive effects estimated
₁₄₁ for leafout (0.51) [-0.37,1.37] and budburst (0.5 [-0.16,1.11]) and a stronger but negative interaction for
₁₄₂ flowering (-1.13 [-2.07,-0.2]). This negative interaction implies that there may be synergistic effects of soil
₁₄₃ moisture and temperature (both of which also have negative estimated effects on flowering), resulting in
₁₄₄ flowering that advances even more strongly than would be expected by simply adding together the estimated
₁₄₅ effects of temperature and moisture each acting alone.

₁₄₆ These overall effects varied widely across species (Fig. 1, Table S2). Species-level variance for the effect of
₁₄₇ moisture was 2.72 (2.03,3.48) days for budburst, 3.83 (2.6,5.32) for leafout, and 3.8 (2.45,5.16) for flower-
₁₄₈ ing. Species-level variance was even greater for temperature effects: 11.38 (9.45,13.45) for budburst, 10.26
₁₄₉ (8.61,11.98) days for leafout, and 6.19 (4.76,7.69) for flowering. Analysis of posterior distributions suggests
₁₅₀ that species-level variability in responses to moisture is not predictable by life form (trees, shrubs, herbs,
₁₅₁ grasses, Fig. 2, column 2) nor by ecosystem (grassland versus forests, Fig. S2), across the three phenophases

152 we studied. We did observe more negative effects of temperature on trees compared to shrubs for budburst,
153 and on both trees and grasses compared to shrubs and forbs for leafout (Fig. 2, column 1). Interactions
154 between temperature and moisture effects on leafout also seemed to skew more positive for grasses compared
155 to other life-forms (Fig. 2, column 3)

156 We applied the budburst model to forecast possible effects of climate change on phenology. Based on the
157 estimated effects, wetter soils advanced spring budburst at a rate of 5 days per 10% increase in soil volumetric
158 water content (VWC). Thus, if soil moisture is reduced by 10% of its current state, as is expected over the
159 next 50 years in areas where many of the experiments were conducted (the northeastern United States) (Berg
160 et al., 2017) (moving from, e.g., 21.5% VWC – the mean value for January–March across all sites for which
161 budburst was monitored – to 19.4% VWC), budburst would be delayed by approximately 1 day on average,
162 due to changes in soil moisture alone (Fig 3).

163 DISCUSSION

164 Soil drying can delay phenology

165 Synthesizing results from climate change experiments, we quantify phenology responses to plot-level soil
166 moisture across multiple experiments. We found that soil moisture affects plant phenology in temperate
167 non-arid ecosystems, in addition to the arid ecosystems where effects of water availability on phenology have
168 been more often reported (e.g., Reich and Borchert, 1984; van Schaik et al., 1993; Cleverly et al., 2016;
169 Bertiller et al., 1991). These results are consistent with those from small-scale experiments,(e.g., Currier and
170 Sala, 2022), which have found impacts of precipitation on phenology. Our finding that soil drying has an
171 overall delaying effect on phenology is consistent with Seyednasrollah et al. (2018), who found that moisture
172 deficit generally delays phenology in forest ecosystems, and with recent experimental (Liu et al., 2022) and
173 observational (Tao et al., 2020) studies in temperate grasslands. A larger literature from other systems has
174 also found moisture matters to phenology, including alpine systems dominated by snowpack (e.g., Dunne
175 et al., 2004; Sherwood et al., 2017), and arid/semi-arid ecosystems where precipitation is known to be more
176 limiting (Tao et al., 2019). Our results highlight that, in mesic grasslands and forests, too, soil moisture can
177 affect budburst, leafout, and flowering in plants. The delaying effect of dry soils that we quantify suggests

¹⁷⁸ that moisture can be a hidden, but potentially limiting, factor affecting phenology in temperate systems not
¹⁷⁹ typically thought to be water-stressed ((Ettinger et al., 2019)).

¹⁸⁰ **High variation in responses to soil moisture across species and phenophases**

¹⁸¹ Despite the overall delaying effect of soil drying that we found for phenology, our results suggest that forecasts
¹⁸² will need to contend with high variation in species responses, as well as differences across phenophases 1. This
¹⁸³ might suggest that predicting variable responses to moisture will be challenging, especially since our results
¹⁸⁴ indicate there may not be readily apparent differences in soil moisture responses by broad functional types,
¹⁸⁵ a finding that contrasts with some previous studies (e.g., Rollinson and Kaye, 2012; Castillioni et al., 2022).
¹⁸⁶ A growing body of evidence suggests that instead, species traits may be more predictive of plant responses
¹⁸⁷ to environmental change (e.g., Díaz et al., 2016). Major traits related to root and leaf structure can impact
¹⁸⁸ species' drought tolerance. For trees, traits related to drought tolerance may co-vary with frost-risk, as ring-
¹⁸⁹ porous species are generally more drought-tolerance but risk greater damage from spring frosts compared
¹⁹⁰ to diffuse porous species (Bader et al., 2022; Wang et al., 2022a); not surprisingly ring-porous species leaf
¹⁹¹ out later than diffuse-porous species Lechowicz (1984). Such interconnections between phenology and other
¹⁹² traits have been described in other systems, too (e.g., Ocheltree et al., 2020), and suggest the potential for a
¹⁹³ framework to better predict the high variability of phenology responses across species (e.g., Morales-Castilla
¹⁹⁴ et al., 2024).

¹⁹⁵ Our finding that sensitivity to soil moisture and interactions with temperature varies across phenophases
¹⁹⁶ aligns with recent studies, as well. Buonaiuto and Wolkovich (2021), for example, also found varying sen-
¹⁹⁷ sitivity of flower and leaf phenology to environmental cues, even within species. In our study, variability
¹⁹⁸ across species in the soil moisture response was lowest for budburst (2.72 compared to 3.83 for leafout and
¹⁹⁹ 3.8 for flowering), perhaps suggesting that, across species, soil moisture is a key control on timing of budburst
²⁰⁰ (e.g., by affecting cell elongation (Essiamah and Eschrich, 1986)). The direction of interactive effects of soil
²⁰¹ moisture and temperature also varied in sign across phenophases, with weak positive estimates for budburst
²⁰² and leafout, and stronger negative interactive effects for flowering (Fig. 1). Thus, the implications of climate
²⁰³ change driven shifts in soil moisture for phenology are likely to depend on when during the growing season
²⁰⁴ shifts are greatest and, especially for flowering, how it interacts with temperature shifts, among other factors.

²⁰⁵ **Forecasting multiple drivers**

206 Soil moisture is and will continue to shift with climate change (Berg et al., 2017), so while we found soil
207 moisture had a smaller effect size than temperature, it could have important implications for phenology.
208 Some areas, such as the northeastern United States (where many of the experiments were conducted) are
209 getting wetter, and other places are expected to get drier (Berg et al., 2017). Overall, our forecasting suggests
210 that temperature will continue to be a dominant controller of phenology, but that soil moisture also matters,
211 especially for certain species.

212 The experimental data we synthesize here highlight that multiple drivers that are shifting with global change
213 affect phenology. Highly-cited phenology research in temperate grassland and forest systems has frequently
214 ignored effects of soil moisture and other drivers, focusing instead on temperature. But warming can interact
215 with other global change drivers; indeed, both synergistic and antagonistic interactions between warming
216 and other global changes, including precipitation, were found to influence plant phenology in a recent meta-
217 analysis of experimental studies (Zhou et al., 2023),

218 Forecasting of phenological shifts with global change may be made more accurate, then, by incorporating the
219 multiple drivers of phenology that have been identified in experimental studies. To do this forecasting, though,
220 we need to improve how we relate experiments to the ‘real world’. This includes moving beyond treatments
221 levels to analyze plot-level microclimate—closer to how plants may be experiencing treatments. Our study
222 differs from some because we used field-measured soil moisture, whereas most studies use precipitation (e.g.,
223 Tao et al., 2020) or gridded moisture products (e.g., Tao et al., 2019). The problems with these proxies are
224 widely known, including challenges with validation at fine spatiotemporal resolutions, though a number of
225 new products are available and seem promising (Peng et al., 2021; Brocca et al., 2024). Soil moisture has not
226 been a focus of previous phenology meta-analyses (e.g., Wolkovich et al., 2013), nor of most multi-species
227 phenology studies in temperate mesic grasslands and forest ecosystems (e.g., Vitasse et al., 2021), despite
228 the reality that many experiments collect these data.

229 Our findings offer robust, experimental evidence that builds on large-scale observational research, which
230 increasingly suggests an important role for soil moisture in phenology (e.g., Luo et al., 2021). Our use of
231 measured soil moisture did create a data limitation, however, as we were able to use only a subset of all the
232 climate change experiments included in the ExPhen and MC3E databases. Increased measurement, reporting,
233 and sharing of environmental conditions—including soil moisture and temperature—could help to disentangle

²³⁴ how temperature is affected by soil moisture, and how soil moisture is affected by temperature treatments.

²³⁵ The soil moisture-phenology relationships we quantify across species may scale up to result in community-

²³⁶ level shifts in phenology patterns. And further, may interact with other factors to affect ecosystem-level

²³⁷ functions such as biomass and carbon uptake or storage. Disentangling effects from climate versus soil can be

²³⁸ challenging, but has demonstrated the importance of species interactions and multiple limiting nutrients in

²³⁹ vegetation responses to global change (Wilfahrt et al., 2021). In addition to playing a role in budburst, leafout,

²⁴⁰ and flowering phenology, for example, soil moisture affects plant resorption of nitrogen and phosphorus during

²⁴¹ leaf senescence (Estiarte et al., 2022). Shifts in soil moisture and cascading effects on phenology may ultimately

²⁴² lead to changes in growing season length and carbon uptake (Wolkovich et al., 2025), especially since soil

²⁴³ moisture is a key control of nutrient cycling, including nitrogen and carbon (Liu et al., 2019).

²⁴⁴ Conclusions

²⁴⁵ Now underway for four decades, climate change experiments (e.g., Tamaki et al., 1981; Carlson and Bazzaz,

²⁴⁶ 1982; Melillo et al., 2017) can provide a unique opportunity to disentangle multiple drivers, understand

²⁴⁷ biological responses to climate change, and inform global climate forecasting models. Yet the full range of

²⁴⁸ changes in environmental conditions imposed by these experiments is rarely presented. Using two databases

²⁴⁹ that compile microclimate data and phenological responses from multiple warming experiments we show that

²⁵⁰ soil moisture, in addition to temperature, affects plant phenology. We quantified phenological delays with

²⁵¹ soil drying across budburst, leafout, and flowering that suggest these effects should be more often included

²⁵² in modelling and forecasts of seasonal shifts with climate change. Given that the magnitude and direction

²⁵³ of the response varied across species, and that projected shifts in soil moisture with climate change vary

²⁵⁴ spatially, specific implications of our findings—e.g., whether incorporating shifts in moisture results in more

²⁵⁵ muted or exaggerated phenological shifts than would be expected based on temperature alone—will depend

²⁵⁶ on local context. Incorporating these findings with locally relevant biological and climate information can be

²⁵⁷ used to assess impacts of climate change and manage natural resources for enhanced climate resilience.

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435 Figures

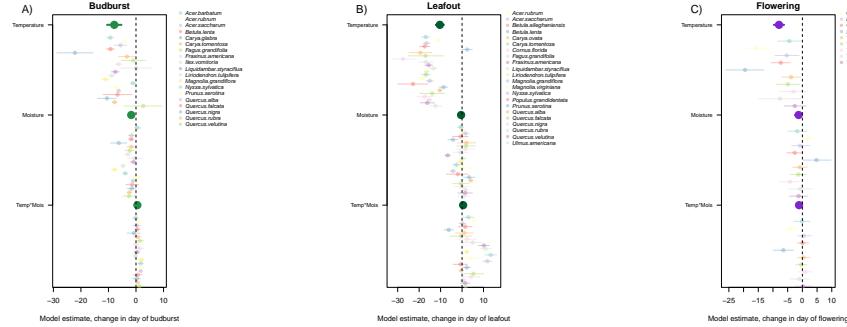


Figure 1: Model coefficients from budburst, leafout, and flowering models (with centered predictors) for the most common species (i.e., those at more than one study site). Plot of species effects across all species available in Supplemental Materials, Fig. S3.

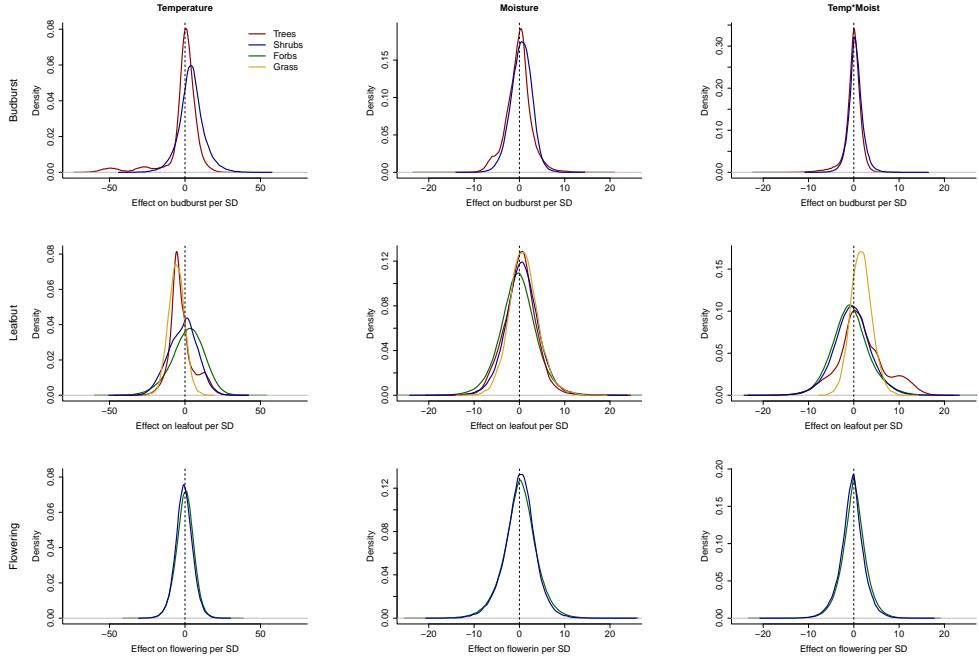


Figure 2: Effects of temperature, soil moisture, and their interaction, summarized by life forms reveal minimal differences in estimated responses to soil moisture (middle column). Curves show probability density functions for posterior samples of estimated effects for temperature, soil, and their interaction summarized by species and grouped into four life forms (trees, shrubs, forbs, and grasses). Patterns do appear to vary by life form for temperature (first column) and interactions (third column). For budburst, temperature effects were more negative for trees compared to shrubs, and more negative for both trees and grasses compared to shrubs and forbs for leafout. Interactions between temperature and moisture effects on leafout, on the other hand, seemed to skew more positive for grasses compared to other life-forms.

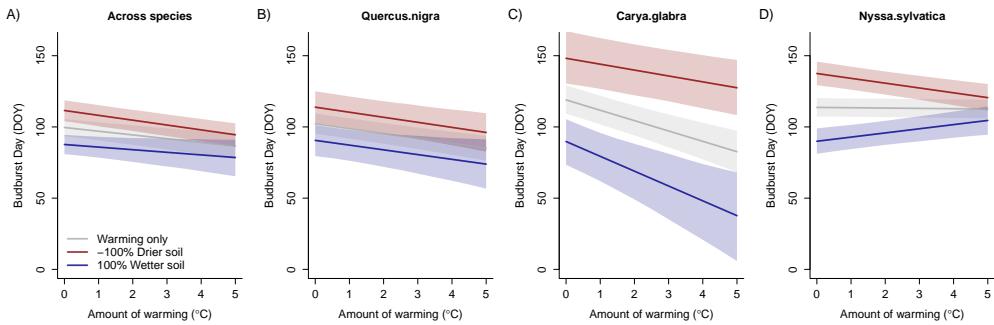


Figure 3: Patterns of forecasted changes in budburst date with warming vary with soil moisture and across species. Across all species, our model estimated negative effects (i.e., earlier) of both temperature and soil moisture on budburst and a weak interaction between the two effects (A, and example species *Quercus nigra* in B); however, the magnitude of these effects, as well as the sign and magnitude of the estimated interaction between soil moisture and temperature, differed across species, resulting in divergent patterns with forecasted conditions under climate change. Budburst may occur much earlier in wetter vs drier soils with warming for species that have a synergistic interaction between soil moisture and temperature, such as *Carya glabra* (C). Whereas, other species with an antagonistic interaction, such as *Nyssa sylvatica* (D), may experience delayed budburst in wet soils but advance in dry soils.