

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,b}, M.R. Johnston^{4,c}, C.R. Rollinson^{5,d}, and E.M. Wolkovich^{1,4,6,e}

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

²The Nature Conservancy, Seattle, Washington, USA

³Carnegie Institute

⁴University of Iowa

⁵The Morton Arboretum, Lisle, Illinois 60532, USA

⁶Forest & 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

February 5, 2025

Author contributions: All authors conceived of this manuscript, which began at a Radcliffe Exploratory Seminar in 2016, and all authors contributed to manuscript revisions. AKE and EMW conceived of the idea for the literature review, database compilation, and related Radcliffe Exploratory Seminar, and wrote the manuscript. AKE compiled the datasets; AKE analyzed the data and created the figures.

Data Accessibility The data reported in this paper are from the MC3E and the new ExPhen databases, which are both available at KNB (Ettinger and Wolkovich, 2018, 2022).

Running title Drier soils delay phenology

Key words (6-10) global warming, warming experiment, microclimate, phenology, bud-burst, leaf-out, flowering, fruiting, senescence

Paper type ‘Research Article’ for *Global Change Biology*

Number of words in abstract (300 or less): 221

Number of words in main text (8000 or less in Introduction, Materials and Methods, Results, Discussion, and Acknowledgements):

Submission Questions In lieu of a cover letter, authors must answer the following questions during submission (max 250 characters with spaces per answer):

1. What scientific question is addressed in this manuscript?
2. What is/are the key finding(s) that answer this question?
3. What are the novel results, ideas, or methods presented in your work?
4. Describe how your paper fits within the scope of GCB; What biological AND global change aspects does it address?
5. What are the three most recently published papers that are relevant to this manuscript (include DOIs)?

Abstract

Previous meta-analyses of phenology responses to climate change have focused largely on temperature as a driver of observed shifts. Yet climate change also affects soil moisture, which is limiting to many biological responses. Here we synthesize microclimate and phenology data from climate change experiments in temperate systems—both forests and grasslands—to quantify how soil moisture interacts with temperature to affect plant phenology. We find that phenology (budburst, leafout and flowering) delays in drier soils, with the largest delays seen in budburst. While effects of soil moisture were much smaller than for temperature (-1.73 versus -7.89 in standardized units), with interactive effects of temperature x moisture even smaller (0.5),

9 we found that these effects could have important implications. We found high variability in the response
10 to shifted soil moisture across species; this combined with high variability in forecasts of future drought
11 and precipitation in many systems may increase the importance of soil moisture to phenology in the future.
12 Forecasting shifts in soil moisture with warming, we find that soil moisture declines of just 10% would have
13 important effects on the phenology of some species, potentially muting advances due to warming alone. Our
14 results show that soil moisture plays an important role in the phenology of temperate systems, with varying
15 effects across species, and thus is likely to alter ecosystem functions tied to phenology such as growth and
16 carbon storage. Incorporating local context, including ecological knowledge for relevant species and down-
17 scaled climate change projections, will be critical for planning appropriate management and conservation in
18 response to phenological shifts and related ecosystem services.

INTRODUCTION

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

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

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

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

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

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

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

MATERIALS AND METHODS

Data— To investigate how soil moisture interacts with temperature to affect phenology, we used two databases that compiled data from climate change experiments. Microclimate data came from the MicroClimate from 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 and Wolkovich, 2022).

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

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

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

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

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

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

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

RESULTS

We found that both higher soil moisture and higher temperatures advance phenology, meaning two common effects of warming experiments—soil drying and warming—have contrasting effects on phenology. Soil drying delays phenology and warming temperatures advance phenology. For budburst, wetter soils and warmer temperatures alone advanced phenology by -1.73 (-2.52,-0.95) per SD of soil moisture (or -5.217 days per 10 percent increase in volumetric water content) and -7.89 (-10.51,-5.28) per SD of temperature (or -3.41 per degree Celsius). We did not find evidence of strong interactive effects of soil moisture and temperature on phenology: together, wetter and warmer conditions delayed budburst only a small amount (interaction effect of 0.5 [-0.16-1.11] per SD or 3.72 natural units).

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

These overall effects varied widely across species (Fig 1). Species-level variance for the effect of moisture was 2.72 (2.03,3.48) standardized units for budburst, 3.83 (2.6,5.32) for leafout, and 3.8 (2.45,5.16) for flowering. Species-level variance was even greater for temperature effects: 11.38 (9.45,13.45) for budburst, 10.26 (8.61,11.98) for leafout, and 6.19 (4.76,7.69) for flowering. Species-level variability in responses to moisture was not predictable by life form (trees, shrubs, herbs, grasses, Fig. 2, column 2) nor by ecosystem (grassland versus forests, Fig S2), across the three phenophases we studied. We did observe more negative effects of temperature on trees compared to shrubs for budburst, and on both trees and grasses compared to

shrubs and forbs for leafout (Fig. 2, column 1). Interactions between temperature and moisture effects on leafout also seemed to skew more positive for grasses compared to other life-forms (Fig. 2, column 3)

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

DISCUSSION

Synthesizing plot-level climate change experiments, we found that soil moisture affects plant phenology in temperate non-arid ecosystems, in addition to the arid ecosystems where effects of water availability on phenology have been more often reported (e.g., Reich and Borchert, 1984; van Schaik et al., 1993; Cleverly et al., 2016; Bertiller et al., 1991). These results are consistent with those from small-scale experiments, which have found impacts of precipitation on phenology (e.g., Currier and Sala, 2022). Our findings highlight that, in mesic grasslands and forests, too, plants need water to advance budburst, leafout, and flowering; the delaying effect of dry soils suggest that moisture can be a hidden, but potentially limiting, factor affecting phenology in temperate systems not typically thought to be water-stressed.

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

High variation in responses to soil moisture across species and phenophases

177 Despite the overall delaying effect of soil drying that we found for phenology, our results suggest that forecasts
178 will need to contend with high variation in species responses, as well as differences across phenophases ??.
179 There do not appear to be strong differences in soil moisture effects across broad functional types, though we
180 observed some differences across functional groups in temperature leafout responses, in which grass and tree
181 responses appear more negative than those of forbs and shrubs, Fig. 2). More positive interactive effects of
182 soil moisture and temperature are also apparent for grasses compared to other groups.

183 Our results that broad functional types do not systematically respond differently to soil moisture, temperature
184 and their interaction contrasts with some findings (e.g., Rollinson and Kaye, 2012; Castillioni et al., 2022),
185 but supports growing work suggesting that species traits may be far more predictive (e.g., Díaz et al., 2016).
186 Major traits related to root and leaf structure can impact species' drought tolerance. For trees, traits related
187 to drought tolerance may co-vary with frost-risk, as ring-porous species are generally more drought-tolerance
188 but risk greater damage from spring frosts compared to diffuse porous species (Bader et al., 2022; Wang
189 et al., 2022a); not surprisingly ring-porous species leafout later than diffuse-porous species Lechowicz (1984).
190 Such interconnections between phenology and other traits occur in other systems, too (e.g., Ocheltree et al.,
191 2020), and suggest the potential for a framework to better predict the high variability of responses across
192 species (e.g., Morales-Castilla et al., 2024).

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

204 **Forecasting multiple drivers**

The experimental data we synthesize here highlight that multiple drivers that are shifting with global change affect phenology and are important for accurate forecasts. Highly-cited phenology research in temperate grassland and forest systems has frequently ignored effects of soil moisture and other drivers, focusing instead on temperature. Our finding that soil drying has an overall delaying effect on phenology is consistent with Seyednasrollah et al. (2018), who found that moisture deficit generally delays phenology in forest ecosystems, and with recent experimental (Liu et al., 2022) and observational (Tao et al., 2020) studies in temperate grasslands. Our results align within a larger literature from other systems that have found moisture matters to phenology, including alpine systems dominated by snowpack (e.g., Dunne et al., 2004; Sherwood et al., 2017), and arid/semi-arid ecosystems where precipitation is known to be more limiting (Tao et al., 2019).

To do this forecasting, we need to improve how we relate experiments to the ‘real world’. This includes moving beyond treatments levels to analyze plot-level microclimate- closer to how plants may be experiencing treatments. Our study differs from some because we used field-measured soil moisture – most studies use precipitation (e.g., Tao et al., 2020) or gridded moisture products (e.g., Tao et al., 2019). The problems with these proxies are widely known, including challenges with validation at fine spatiotemporal resolutions, though a number of new products are available and seem promising (Peng et al., 2021; Brocca et al., 2024). Soil moisture has not been a focus of previous phenology meta-analyses (e.g., Wolkovich et al., 2013), nor of most multi-species phenology studies in temperate mesic grasslands and forest ecosystems (e.g., Vitasse et al., 2021), despite the reality that many experiments collect these data. Our findings offer robust, experimental evidence that builds on large-scale observational research that increasingly suggests an important role for soil moisture in phenology (e.g.,). Our use of measured soil moisture did create a data limitation, however, as we were able to use only a subset of all the climate change experiments included in the ExPhen and MC3E databases. Increased measurement, reporting, and sharing of environmental conditions– including soil moisture and temperature– could help to disentangle how temperature is affected by soil moisture, and how soil moisture is affected by temperature treatments.

The soil moisture-phenology relationships we quantify within species may scale up and interact with other factors to affect ecosystem-level functions such as biomass and carbon uptake or storage. Disentangling effects from climate versus soil can be challenging but has demonstrated the importance of species interactions and multiple limiting nutrients in vegetation responses to global change (Wilfahrt et al., 2021). In addition

to playing a role in budburst, leafout, and flowering phenology, for example, soil moisture affects plant resorption of nitrogen and phosphorus during leaf senescence (Estiarte et al., 2022). Shifts in soil moisture and cascading effects on phenology may ultimately lead to changes in growing season length and carbon uptake (cite grephon?), especially since soil moisture is a key control of nutrient cycling, including nitrogen and carbon (Liu et al., 2019).

Conclusions

Now underway for four decades, climate change experiments (e.g., Tamaki et al., 1981; Carlson and Bazzaz, 1982; Melillo et al., 2017) can provide a unique opportunity to disentangle multiple drivers and understand biological responses to climate change. Yet the full range of changes in environmental conditions imposed by these experiments is rarely presented. Using two databases that compile microclimate data and phenological responses from multiple warming experiments we show that soil moisture, in addition to temperature, affects plant phenology. We quantified phenological delays with soil drying across budburst, leafout, and flowering that suggest these effects should be more often included in modelling and forecasts of seasonal shifts with climate change. Given that the magnitude and direction of the response varied across species, and that projected shifts in soil moisture with climate change vary spatially, specific implications of our findings—e.g., whether incorporating shifts in moisture results in more muted or exaggerated phenological shifts than would be expected based on temperature alone—will depend on local context. Incorporating these findings with locally relevant biological and climate information can be used to assess biological impacts of climate change and manage natural resources for enhanced climate resilience.

Acknowledgements

We are grateful to those who shared their experimental climate data with us, allowing it to be included in the MC3E and ExPhenvdatabases. We thank the Radcliffe Institute for Advanced Study at Harvard University, which provided funding for an Exploratory Seminar at which the ideas in this paper were conceived. This research was also supported by the National Science Foundation (NSF DBI 14-01854 to A.K.E.). Any opinion,

findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

References

- Aronson, E. L., and S. G. McNulty. 2009. Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology* 149:1791–1799.
- Bader, M. K.-F., D. Scherrer, R. Zweifel, and C. Körner. 2022. Less pronounced drought responses in ring-porous than in diffuse-porous temperate tree species. *Agricultural and Forest Meteorology* 327:109184.
- Berg, A., J. Sheffield, and P. C. Milly. 2017. Divergent surface and total soil moisture projections under global warming. *Geophysical Research Letters* 44:236–244.
- Bertiller, M. B., A. M. Beeskow, and F. Coronato. 1991. Seasonal environmental variation and plant phenology in arid patagonia (argentina). *Journal of Arid Environments* 21:1–11.
- Brocca, L., J. Gaona, D. Bavera, G. Fioravanti, S. Puca, L. Ciabatta, P. Filippucci, H. Mosaffa, G. Esposito, N. Roberto, et al. 2024. Exploring the actual spatial resolution of 1 km satellite soil moisture products. *Science of the Total Environment* 945:174087.
- Buonaiuto, D., and E. Wolkovich. 2021. Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants. *Journal of Ecology* 109:2922–2933.
- Bürkner, P.-C. 2021. Bayesian item response modeling in r with brms and stan. *ournal of Statistical Software*, 100:1–54.
- Carlson, R. W., and F. A. Bazzaz. 1982. Photosynthetic and growth response to fumigation with SO₂ at elevated CO₂ for C₃ and C₄ plants. *Oecologia* 54:50–54.
- Carpenter, B., A. Gelman, M. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. A. Brubaker, J. Guo, P. Li, and R. Allen. 2017. Stan: A probabilistic programming language. *Journal of Statistical Software* 76:10.18637/jss.v076.i01.

- Castillioni, K., G. S. Newman, L. Souza, and A. M. Iler. 2022. Effects of drought on grassland phenology depend on functional types. *New Phytologist* 236:1558–1571.
- Chen, I.-C., J. K. Hill, R. Ohlemueller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* 22:357–365.
- Cleverly, J., D. Eamus, N. R. Coupe, C. Chen, W. Maes, L. Li, R. Faux, N. S. Santini, R. Rumman, Q. Yu, et al. 2016. Soil moisture controls on phenology and productivity in a semi-arid critical zone. *Science of the Total Environment* 568:1227–1237.
- Cook, B. I., E. M. Wolkovich, T. J. Davies, T. R. Ault, J. L. Betancourt, J. M. Allen, K. Bolmgren, E. E. Cleland, T. M. Crimmins, N. J. B. Kraft, L. T. Lancaster, S. J. Mazer, G. J. McCabe, B. J. McGill, C. Parmesan, S. Pau, J. Regetz, N. Salamin, M. D. Schwartz, and S. E. Travers. 2012. Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent databases. *Ecosystems* 15:1283–1294.
- Cui, T., L. Martz, and X. Guo. 2017. Grassland phenology response to drought in the canadian prairies. *Remote Sensing* 9:1258.
- Currier, C. M., and O. E. Sala. 2022. Precipitation versus temperature as phenology controls in drylands. *Ecology* 103:e3793.
- De Kauwe, M. G., B. E. Medlyn, A. P. Walker, S. Zaehle, S. Asao, B. Guenet, A. B. Harper, T. Hickler, A. K. Jain, Y. Luo, et al. 2017. Challenging terrestrial biosphere models with data from the long-term multifactor prairie heating and co₂ enrichment experiment. *Global Change Biology* 23:3623–3645.
- Delpierre, N., E. Dufrêne, K. Soudani, E. Ulrich, S. Cecchini, J. Boé, and C. François. 2009. Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in france. *Agricultural and Forest Meteorology* 149:938–948.
- Díaz, S., J. Kattge, J. H. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, et al. 2016. The global spectrum of plant form and function. *Nature* 529:167–171.

- Dunne, J. A., S. R. Saleska, M. L. Fischer, and J. Harte. 2004. Integrating experimental and gradient methods in ecological climate change research. *Ecology* 85:904–916.
- Essiamah, S., and W. Eschrich. 1986. Water uptake in deciduous trees during winter and the role of conducting tissues in spring reactivation. *IAWA Journal* 7:31–38.
- Estiarte, M., M. Campioli, M. Mayol, and J. Penuelas. 2022. Variability and limits in resorption of nitrogen and phosphorus during foliar senescence. *Plant Communications* page 100503.
- Ettinger, A., I. Chuine, B. Cook, J. Dukes, A. Ellison, M. Johnston, A. Panetta, C. Rollinson, Y. Vitasse, and E. Wolkovich. 2019. How do climate change experiments alter plot-scale climate? *Ecology Letters* 22:748–763.
- Ettinger, A., and E. Wolkovich. 2018. Microclimate from climate change experiments (MC3E). doi:10.5063/F1QV3JQR.
- . 2022. Phenology from warming experiments (EXPPHEN). doi TBA.
- Fujisawa, M., and K. Kobayashi. 2010. Apple (*malus pumila* var. *domestica*) phenology is advancing due to rising air temperature in northern japan. *Global Change Biology* 16:2651–2660.
- Gelman, A., and J. Hill. 2007. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York, NY, USA.
- Hamann, E., A. E. Weis, and S. J. Franks. 2018. Two decades of evolutionary changes in brassica rapa in response to fluctuations in precipitation and severe drought. *Evolution* 72:2682–2696.
- Howell, A., D. E. Winkler, M. L. Phillips, B. McNellis, and S. C. Reed. 2020. Experimental warming changes phenology and shortens growing season of the dominant invasive plant bromus tectorum (cheatgrass). *Frontiers in Plant Science* 11.
- Ibanez, I., R. B. Primack, A. J. Miller-Rushing, E. Ellwood, H. Higuchi, S. D. Lee, H. Kobori, and J. A. Silander. 2010. Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society B-Biological Sciences* 365.
- Kimball, B. 2005. Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology* 11:2041–2056.

- Kimball, B. A., M. M. Conley, S. Wang, X. Lin, C. Luo, J. Morgan, and D. Smith. 2008. Infrared heater arrays for warming ecosystem field plots. *Global Change Biology* 14:309–320.
- Lechowicz, M. J. 1984. Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *The American Naturalist* 124:821–842.
- Lian, X., S. Piao, L. Z. Li, Y. Li, C. Huntingford, P. Ciais, A. Cescatti, I. A. Janssens, J. Peñuelas, W. Buermann, et al. 2020. Summer soil drying exacerbated by earlier spring greening of northern vegetation. *Science advances* 6:eaax0255.
- Liu, L., M. Estiarte, and J. Peñuelas. 2019. Soil moisture as the key factor of atmospheric ch4 uptake in forest soils under environmental change. *Geoderma* 355:113920.
- Liu, Y., X. Liu, Z. Fu, D. Zhang, and L. Liu. 2024. Soil temperature dominates forest spring phenology in china. *Agricultural and Forest Meteorology* 355:110141.
- Liu, Z., Y. H. Fu, X. Shi, T. R. Lock, R. L. Kallenbach, and Z. Yuan. 2022. Soil moisture determines the effects of climate warming on spring phenology in grasslands. *Agricultural and Forest Meteorology* 323.
- Lu, C., J. Zhang, X. Min, J. Chen, Y. Huang, H. Zhao, T. Yan, X. Liu, H. Wang, and H. Liu. 2023. Contrasting responses of early-and late-season plant phenophases to altered precipitation. *Oikos* 2023:e09829.
- McDaniel, M., R. Wagner, C. Rollinson, B. Kimball, M. Kaye, and J. Kaye. 2014. Microclimate and ecological threshold responses in a warming and wetting experiment following whole tree harvest. *Theoretical and Applied Climatology* 116:287–299.
- Melillo, J., S. Frey, K. DeAngelis, W. Werner, M. Bernard, F. Bowles, G. Pold, M. Knorr, and A. Grandy. 2017. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science* 358:101–105.
- Morales-Castilla, I., T. Davies, G. Legault, D. Buonaiuto, C. J. Chamberlain, A. K. Ettinger, M. Garner, F. A. Jones, D. Loughnan, W. D. Pearce, et al. 2024. Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate Change* pages 1–7.

- Ocheltree, T., K. Mueller, K. Chesus, D. LeCain, J. Kray, and D. Blumenthal. 2020. Identification of suites of traits that explains drought resistance and phenological patterns of plants in a semi-arid grassland community. *Oecologia* 192:55–66.
- Olsson, C., and A. M. Jönsson. 2014. Process-based models not always better than empirical models for simulating budburst of norway spruce and birch in europe. *Global Change Biology* 20:3492–3507.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637–669.
- Peng, J., C. Albergel, A. Balenzano, L. Brocca, O. Cartus, M. H. Cosh, W. T. Crow, K. Dabrowska-Zielinska, S. Dadson, M. W. Davidson, et al. 2021. A roadmap for high-resolution satellite soil moisture applications—confronting product characteristics with user requirements. *Remote Sensing of Environment* 252:112162.
- Piao, S., Q. Liu, A. Chen, I. A. Janssens, Y. Fu, J. Dai, L. Liu, X. Lian, M. Shen, and X. Zhu. 2019. Plant phenology and global climate change: Current progresses and challenges. *Global change biology* 25:1922–1940.
- Polgar, C. A., R. B. Primack, J. S. Dukes, C. Schaaf, Z. Wang, and S. S. Hoeppepner. 2014. Tree leaf out response to temperature: comparing field observations, remote sensing, and a warming experiment. *International journal of biometeorology* 58:1251–1257.
- Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3:919.
- R Core Team. 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reich, P. B., and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of costa rica. *The Journal of Ecology* pages 61–74.
- Rollinson, C. R., and M. W. Kaye. 2012. Experimental warming alters spring phenology of certain plant functional groups in an early successional forest community. *Global Change Biology* 18:1108–1116.

382 Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints
383 of global warming on wild animals and plants. *Nature* 421:57–60. PT: J.

384 Seyednasrollah, B., J. J. Swenson, J.-C. Domec, and J. S. Clark. 2018. Leaf phenology paradox: Why warming
385 matters most where it is already warm. *Remote Sensing of Environment* 209:446–455.

386 Shen, M., S. Wang, N. Jiang, J. Sun, R. Cao, X. Ling, B. Fang, L. Zhang, L. Zhang, X. Xu, et al. 2022. Plant
387 phenology changes and drivers on the qinghai-tibetan plateau. *Nature Reviews Earth & Environment*
388 3:633–651.

389 Sherry, R. A., X. Zhou, S. Gu, J. A. A. 3rd, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo. 2007.
390 Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of*
391 *Sciences of the United States of America* 104:198–202.

392 Sherwood, J. A., D. M. Debinski, P. C. Caragea, and M. J. Germino. 2017. Effects of experimentally reduced
393 snowpack and passive warming on montane meadow plant phenology and floral resources. *Ecosphere* 8.

394 Tamaki, G., M. A. Weiss, and G. E. Long. 1981. Evaluation of plant density and temperature in predator-prey
395 interactions in field cages. *Environmental Entomology* 10:716–720.

396 Tao, Z., J. Dai, H. Wang, W. Huang, and Q. Ge. 2019. Spatiotemporal changes in the bud-burst date of
397 herbaceous plants in inner mongolia grassland. *Journal of Geographical Sciences* 29:2122–2138.

398 Tao, Z., W. Huang, and H. Wang. 2020. Soil moisture outweighs temperature for triggering the green-up
399 date in temperate grasslands. *Theoretical and Applied Climatology* 140:1093–1105.

400 Taylor, G., M. J. Tallis, C. P. Giardina, K. E. Percy, F. Miglietta, P. S. Gupta, B. Gioli, et al. 2008. Future
401 atmospheric CO₂ leads to delayed autumnal senescence. *Global Change Biology* 14:264–275.

402 van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive
403 significance and consequences for primary consumers. *Annual Review of ecology and Systematics* 24:353–
404 377.

405 Vitasse, Y., F. Baumgarten, C. M. Zohner, R. Kaewthongrach, Y. H. Fu, M. G. Walde, and B. Moser. 2021.
406 Impact of microclimatic conditions and resource availability on spring and autumn phenology of temperate
407 tree seedlings. *New Phytologist* 232:537–550.

- Wang, A.-Y., H.-X. Cui, X.-W. Gong, J.-J. Guo, N. Wu, and G.-Y. Hao. 2022*a*. Contrast in vulnerability to freezing-induced xylem embolism contributes to divergence in spring phenology between diffuse-and ring-porous temperate trees. *Forest Ecosystems* 9:100070.
- Wang, J., D. Liu, P. Ciais, and J. Penuelas. 2022*b*. Decreasing rainfall frequency contributes to earlier leaf onset in northern ecosystems. *Nature Climate Change* 12:386+.
- Wilfahrt, P. A., A. H. Schweiger, N. Abrantes, M. A. Arfin-Khan, M. Bahn, B. J. Berauer, M. Bierbaumer, I. Djukic, M. van Dusseldorp, P. Eibes, et al. 2021. Disentangling climate from soil nutrient effects on plant biomass production using a multispecies phytometer. *Ecosphere* 12:e03719.
- Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau, et al. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485:494–497.
- Wolkovich, E. M., T. J. Davies, H. Schaefer, E. E. Cleland, B. I. Cook, S. E. Travers, C. G. Willis, and C. C. Davis. 2013. Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany* 100:1407–1421.
- Zhou, H., X. Min, J. Chen, C. Lu, Y. Huang, Z. Zhang, and H. Liu. 2023. Climate warming interacts with other global change drivers to influence plant phenology: A meta-analysis of experimental studies. *Ecology Letters* 26:1370–1381.

Figures

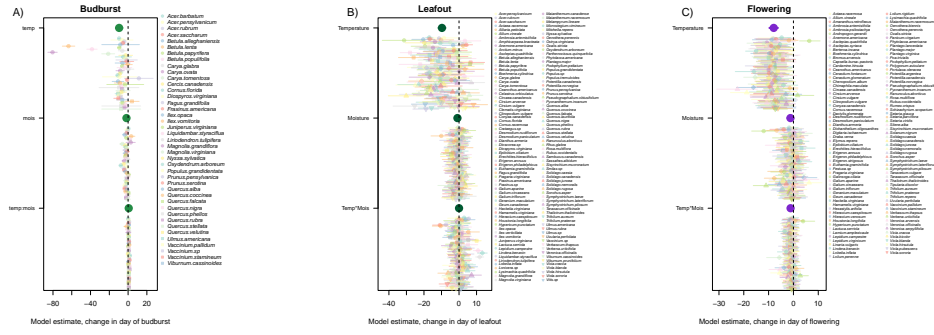


Figure 1: **Model coefficients from budburst, leafout, and flowering models (with centered predictors)** and including all species. We could show only the most common species here, to improve readability, and then show this version (with full species list) in the supplement. Thoughts?

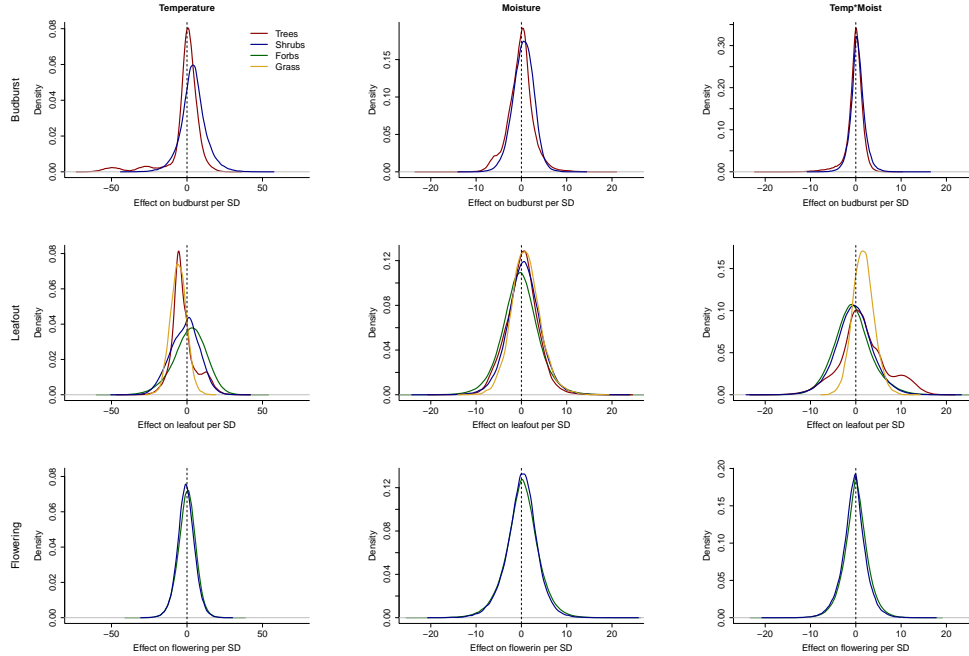


Figure 2: **Effects of temperature, soil moisture, and their interaction summarized life forms** reveal minimal differences in estimated responses to soil moisture (middle column). Curves show probability density functions for posterior samples of estimated effects for temperature, soil, and their interaction 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.

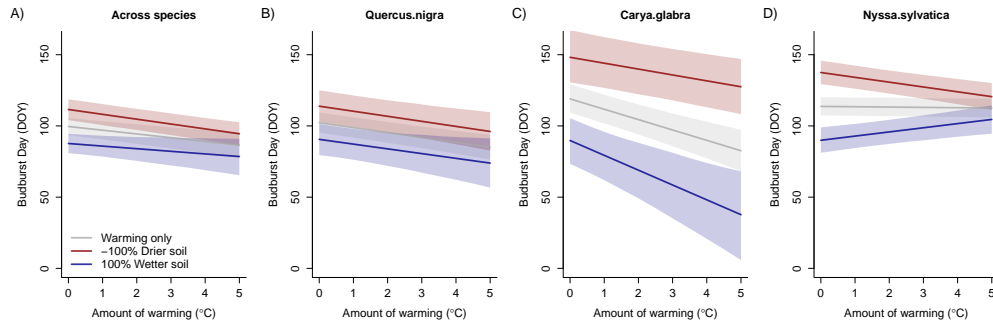


Figure 3: Patterns of forecasted changes in budburst date with warming and shifts in soil moisture vary across species. Across all species, our model estimated negative effects (i.e., earlier) of both temperature and soil moisture on budburst and a weak interaction between the two effects (A, and example 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.