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]

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

[2] The Nature Conservancy, Seattle, Washington, USA

[3] Carnegie Institute

[4] University of Iowa

[5] The Morton Arboretum, Lisle, Illinois 60532, USA

[6] Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada

[a] Corresponding 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 tem-
5 perate systems—both forests and grasslands—to quantify how soil moisture interacts with temperature to
6 affect plant phenology. We find that phenology (budburst, leafout and flowering) delays in drier soils, with
7 the largest delays seen in budburst (-52.2 days per percent reduction in soil VWC). Effects of soil moisture
8 were much smaller than for temperature (-1.7 versus -7.9 in standardized units), with interactive effects of

temperature x moisture even smaller (0.5). However, there was high variability in the response across species. Forecasting shifts in soil moisture with warming, we find that soil moisture declines of 10% would have important effects on the phenology of some species, potentially muting advances due to warming alone. Our results show that soil moisture plays an important role in the phenology of temperate systems, with varying effects across species, and thus is likely to alter ecosystem functions tied to phenology at fine spatial scales. Incorporating local context, including relevant species and downscaled climate change projections, will be critical for planning appropriate management and conservation.

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; Delpierre et al., 2009).

Phenological shifts are typically attributed to warming temperature, a known and well-studied driver of plant phenology. 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 may be due to increases in chilling and/or forcing with global warming (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 documented in some cases. Many climate change experiments have focused on the effects of altered precipitation regimes, with meta-analyses highlighting the diversity of findings (Lu et al., 2023), and the importance of interactive effects of precipitation shifts with global change drivers (Zhou et al., 2023). In particular, recent work suggests warming combined with drought treatments may slow advances in phenology (Zhou et al., 2023). Budburst can be slowed by water stress through inhibiting cell elongation (Essiamah and Eschrich, 1986), and growing season start may be delayed by drought in grasslands Cui et al. (2017). Conversely, flowering phenology can be advanced by drought conditions (Hamann et al., 2018). Effects of soil moisture on phenology have been most well- quantified in arid and grassland ecosystems (e.g., Essiamah and Eschrich, 1986; Reich and Borchert, 1984; van Schaik et al., 1993; Tao et al., 2019); the role of soil moisture on phenology in other ecosystem types, especially more mesic ones, is less explored.

Recent studies have suggested that moisture may play an important—but complicated—role in the phenology of temperate ecosystems as climate change progresses (e.g., Seyednasrollah et al., 2018; Wang et al., 2022*b*). For example, Wang et al. (2022*b*) 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 suggested 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. Perhaps unsurprisingly then, many studies have attempted to manipulate moisture via experimental precipitation or drought treatments (e.g., Morin et al., 2010; Hoeppner and Dukes, 2012; Rollinson et al., 2012; Clark et al., 2014), though few experiments have directly reported on moisture effects of phenology in temperate, non-arid and non-crop systems. Effects in more arid systems are diverse, often with no overall shift in phenology (e.g., Sherry et al., 2007; De Kauwe et al., 2017; Howell et al., 2020), suggesting that identifying clear trends from single experiments may be difficult.

Field-based climate change experiments that warm plots to different levels and apply precipitation or drought treatments are valuable tools to study effects of temperature and moisture on plant phenology, and can be leveraged for additional insights 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. Further, these treatments allow for studying effects of "no-analog" climate scenarios forecasted for the future, particularly when they employ active-warming methods, such as forced air heaters, soil warming cables, or infrared heaters (Shaver et al., 2000; Williams et al., 2007; Aronson and McNulty, 2009). Climate change experiments can monitor daily soil moisture and air temperature at the plot-level, allowing detailed quantification of how microclimate affects 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), 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). Because we wished to 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

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125 a common technique in regression analysis; here we z-scored predictor variables (subtracting the mean and
126 dividing by the standard deviation) and report coefficients from standardized predictor models as per SD
127 (standard deviation), alongside estimates of coefficients in their natural units.

RESULTS

129 We found that both higher soil moisture and higher temperatures advance phenology, meaning two common
130 effects of warming experiments—soil drying and warming—have contrasting effects on phenology. We found
131 that soil drying delays phenology and warming temperatures advance phenology. For budburst, wetter soils
132 and warmer temperatures alone advanced phenology by -1.7 per SD of soil moisture (or -5.22 days per 10
133 percent increase in volumetric water content) and -7.9 per SD of temperature (-3.4 per degree Celsius),
134 respectively. We did not find evidence of strong interactive effects of soil moisture and temperature on
135 phenology: together, wetter and warmer conditions delayed budburst only a small amount (interaction effect
136 of 0.5 per SD [95% uncertainty intervals: -0.6 to 1.4] or 3.7 natural units).

137 The magnitude of soil moisture effects varied across phenophases, with effects on budburst being stronger than
138 those on leafout (-0.4 per SD of soil moisture) and flowering (-1.3 per SD). Similar to budburst, temperature
139 effects were stronger than soil moisture for leafout (for which the temperature effect was -10.3 per SD) and
140 flowering (for which it was -7.9 per SD), across all species (Fig 1). Estimates of interactions between soil
141 moisture and temperature on phenology also varied by phenophase, with weak positive interactive effects
142 estimated for leafout (0.5) and budburst (0.5) and a stronger but negative the interaction for flowering (-1.1).
143 This negative interaction implies that there may be synergistic effects of soil moisture and temperature (both
144 of which also have negative estimated effects on flowering), resulting in flowering that advances even more
145 strongly than would be expected by simply adding together the estimated effects of temperature and moisture
146 each acting alone.

147 These overall effects varied widely across species (Fig 1). Species-level variance for the effect of moisture
148 was 2.7 standardized units for budburst, 3.8 for leafout, and 3.8 for flowering. Species-level variance was
149 even greater for temperature effects: 11.4 for budburst, 10.3 for leafout, and 6.2 for flowering. Species-level
150 variability in responses to moisture was not predictable by life form (trees, shrubs, herbs, grasses, Fig. 2,

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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 above 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

We have synthesized climate change experiments to find 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). This offers new insights because there has been little synthetic research across experimental sites to understand impacts of soil moisture on phenology, despite the reality that many experiments collect these data. 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), Our work helps develop robust, experimental evidence that builds on large-scale observational research that increasingly suggests an important role for soil moisture in phenology (e.g.,). It also builds on 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.

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

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

Our findings that sensitivity to soil moisture and interactions with temperature vary across phenophases align with other recent studies. (Buonaiuto and Wolkovich, 2021), for example, also found varying sensitivity of flower and leaf phenology to environmental cues, even within species. In our study, variability across species in the soil moisture response was lowest for budburst (2.7 compared to 3.8 for leafout and 3.8 for flowering), perhaps suggesting that, across species, soil moisture is a key control on timing of budburst (e.g., by affecting

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cell elongation (Essiamah and Eschrich, 1986)). The direction of interactive effects of soil moisture and temperature also varied in sign across phenophases, with weak positive estimates for budburst and leafout, and stronger positive interactive effects for flowering (Fig. 1). Thus, the implications of climate change driven shifts in soil moisture for phenology are likely to depend on when during the growing season shifts are greatest and, especially for flowering, how it intersections with temperature shifts, among other factors. Such shifts are likely to affect fitness, as well, with some species more strongly affected than othersm thus scaling up to impact community structure and function, as (Buonaiuto and Wolkovich, 2021) also suggest.

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).

Forecasting phenological shifts with global change also, then, depends on integrating multiple drivers. Soil moisture, temperature, and their interactions were our focus here but other global change factors intersect to affect phenology. CO2, for example, and soil moisture may actually mediate plant phenology responses to warming and nitrogen addition (Liu et al., 2022).

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). However, our use of measured soil moisture also created a data limitation, 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 phenologyical 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 along- 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.

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443 # 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?
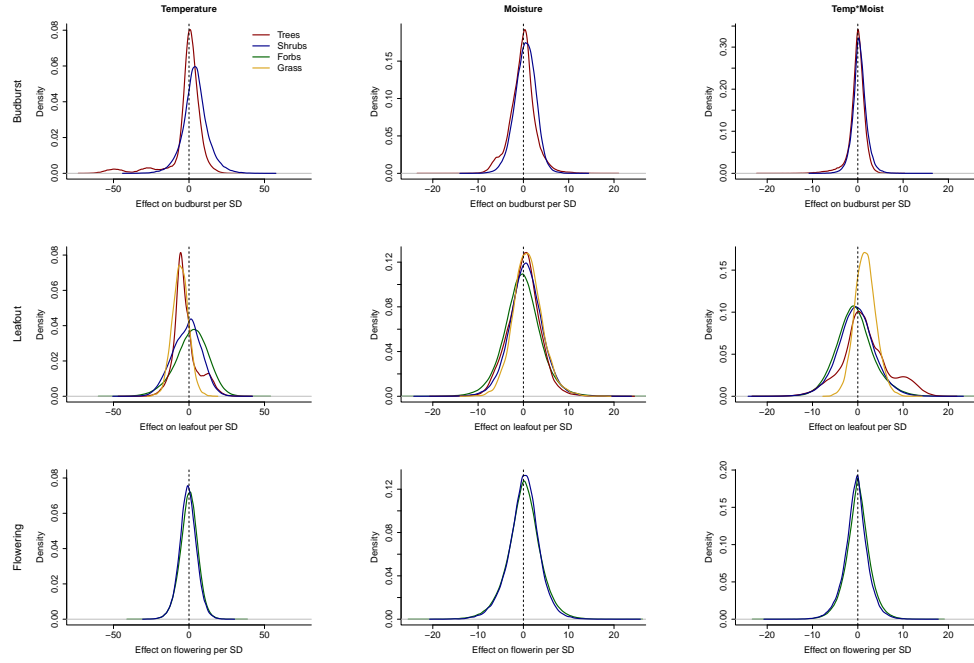
Figure 2: **Effects of temperature, soil moisture, and their interaction summarized life forms** reveal minimal differences in estimated responses to soil moisture (middle column). Curves show probability density functions for posterior samples of estimated effects for temperature, soil, and their interaction 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.
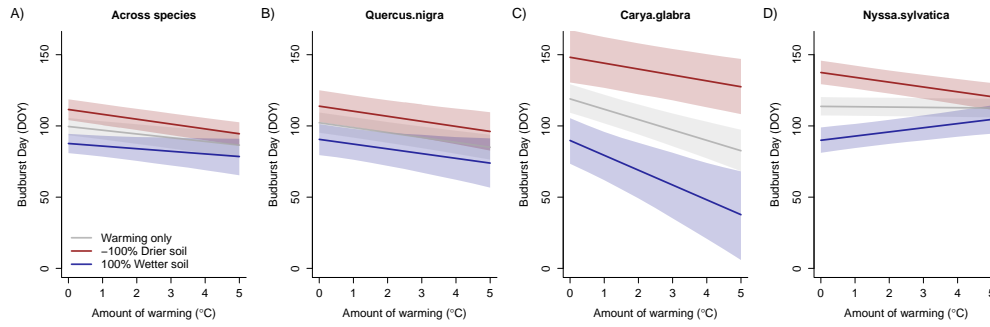
Figure 3: **Patterns of forecasted changes in budburst date with warming and shifts in soil moisture vary across species**. Across all species, our model estimated negative effects (i.e., earlier) of both temperature and soil moisture on budburst and a weak interaction between the two effects (A, and 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.