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

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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).

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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

x moisture even smaller (0.5 days), we found that these effects could have important implications. We found high variability in the response to shifted soil moisture across species; this combined with high variability in forecasts of drought and precipitation in many systems may increase the importance of soil moisture to phenology in the future in some locations. Forecasting shifts in soil moisture with warming, we find that soil moisture declines could 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 such as growth and carbon storage. Incorporating local context, including ecological knowledge of relevant species and downscaled climate change projections, will be critical for planning appropriate management and conservation in 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; Delpierre 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 as 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 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

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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

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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.

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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 (Fig. 1, Table S2). 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) days per SD of soil moisture (or -5.217 days per 10 percent increase in volumetric water content) and -7.89 (-10.51,-5.28) days 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] days per SD).

The magnitude of soil moisture effects varied across phenophases, with effects on budburst (-1.73 [-2.52,-0.95] days per SD increase in soil moisture) being stronger than those on leafout (-0.45 [-1.64,0.68] per SD increase in soil moisture) and flowering (-1.28 [-2.45,-0.11] per SD increase in moisture). Similar to budburst, temperature effects were stronger than soil moisture for leafout (for which the temperature effect was -10.35 [-12.18,-8.49] days per SD increase in temperature) and flowering (for which it was -7.94 [-9.68,-6.22] per SD increase in temperature), 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, Table S2). Species-level variance for the effect of 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 flowering. Species-level variance was even greater for temperature effects: 11.38 (9.45,13.45) for budburst, 10.26 (8.61,11.98) days for leafout, and 6.19 (4.76,7.69) for flowering. Analysis of posterior distributions suggests that species-level variability in responses to moisture is 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

Soil drying can delay phenology

Synthesizing results from climate change experiments, we quantify phenology responses to plot-level soil moisture across multiple 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,(e.g., Currier and Sala, 2022), which have found impacts of precipitation on phenology. 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. A larger literature from other systems has also 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). Our results highlight that, in mesic grasslands and forests, too, soil moisture can affect budburst, leafout, and flowering in plants. The delaying effect of dry soils that we quantify suggests

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

High variation in responses to soil moisture across species and phenophases

Despite the overall delaying effect of soil drying that we found for phenology, our results suggest that forecasts will need to contend with high variation in species responses, as well as differences across phenophases 1. This might suggest that predicting variable responses to moisture will be challenging, esepcially since our results indicate there may not be readily apparent differences in soil moisture responses by broad functional types, a finding that contrasts with some previous studies (e.g., Rollinson and Kaye, 2012; Castillioni et al., 2022). A growing body of evidence suggests that instead, species traits may be more predictive of plant responses to environmental change (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 leaf out later then diffuse-porous species Lechowicz (1984). Such interconnections between phenology and other traits have been described in other systems, too (e.g., Ocheltree et al., 2020), and suggest the potential for a framework to better predict the high variability of phenology responses across species (e.g., Morales-Castilla et al., 2024).

Our finding that sensitivity to soil moisture and interactions with temperature varies across phenophases aligns with recent studies, as well. 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 (2.72 compared to 3.83 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 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 negative 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 intersts with temperature shifts, among other factors.

Forecasting multiple drivers

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 important implications for 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.

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

Forecasting of phenological shifts with global change may be made more accurate, then, by incorporating the multiple drivers of phenology that have been identified in experimental studies. To do this forecasting, though, 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, whereas 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, which increasingly suggests an important role for soil moisture in phenology (e.g., Luo et al., 2021). 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

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 patternis. 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).

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 exagerated phenological shifts than would be expected based on temperature along- 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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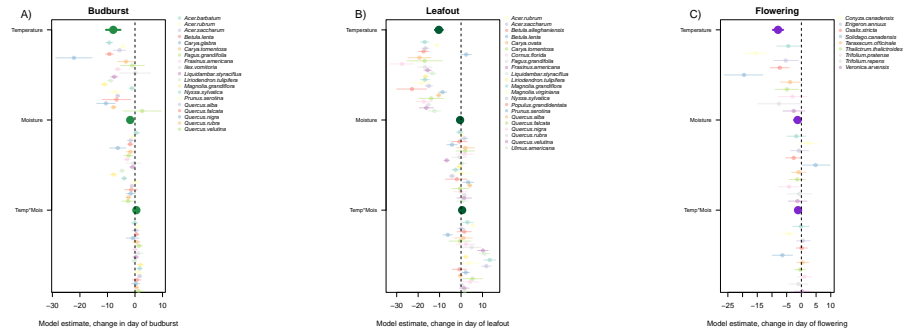
Figures

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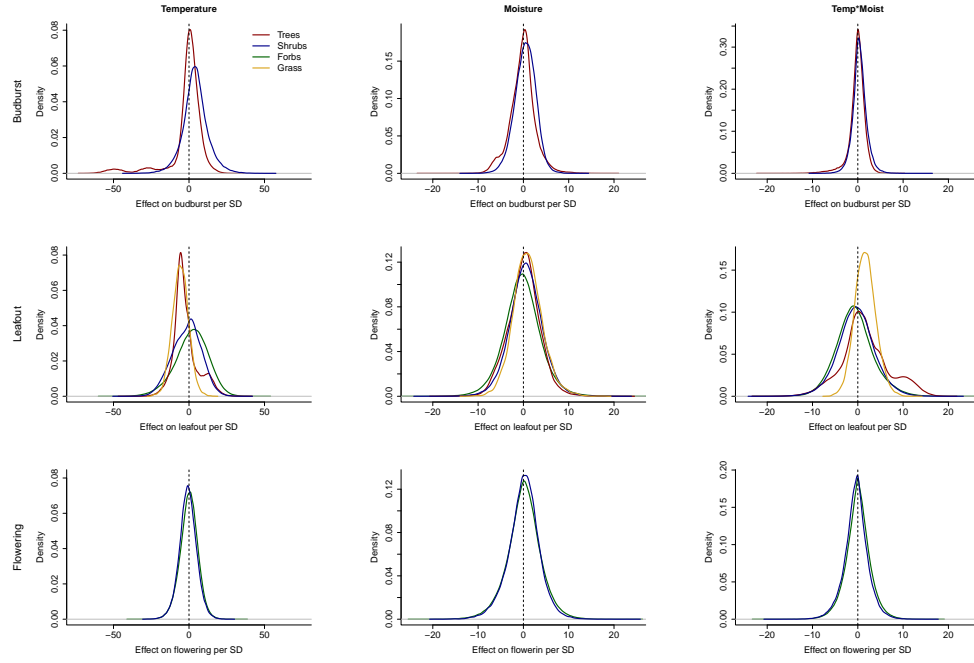
Figure 2: **Effects of temperature, soil moisture, and their interaction, summarized by life forms** reveal minimal differences in estimated responses to soil moisture (middle column). Curves show probability density functions for posterior samples of estimated effects for temperature, soil, and their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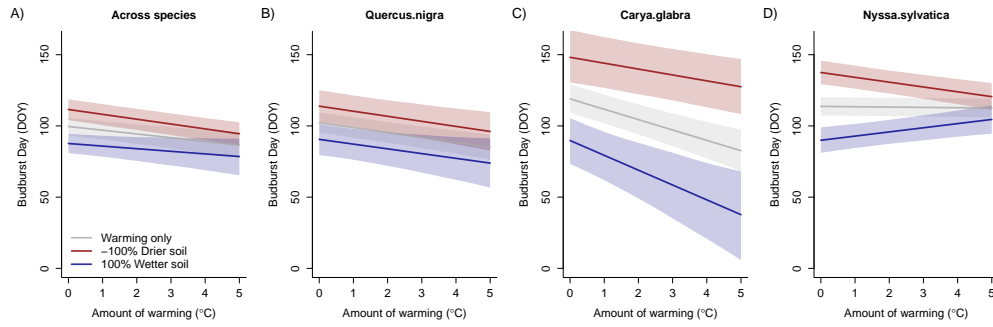
Figure 3: **Patterns of forecasted changes in budburst date with warming vary with soil moisture and across species**. Across all species, our model estimated negative effects (i.e., earlier) of both temperature and soil moisture on budburst and a weak interaction between the two effects (A, and example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