

Soil moisture interacts with temperature to affect plant phenology

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Data Accessibility The data reported in this paper are from the MC3E and ExPhen databases, which are

available at KNB (Ettinger and Wolkovich, 2018, 2021)

Running title Soil moisture affects phenology

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Abstract

Previous meta-analyses of phenology responses to climate change have focused largely on temperature as a driver of observed shifts. However, soil moisture is also affected by climate change and likely to alter biological responses. Here we synthesize microclimate and phenology data from climate change experiments to quantify how soil moisture interacts with temperature to affect plant phenology. We find that soil drying generally delays plant phenology, especially for budburst for which this delay occurs at a rate of 0.42 days per percent reduction in soil VWC, on average. The magnitude of effects we quantify suggest that, on average, climate change-induced shifts in soil moisture will play a small role in altering future phenology, compared to shifts in temperature, both because of the strong sensitivity of plant phenology to temperature and because of the large magnitude of projected shifts in temperature, compared to shifts in soil moisture. Nonetheless, although effects of soil moisture are comparably small on average, sensitivity to soil moisture varied dramatically by species, and soil moisture levels differed by site and among years. Thus, soil moisture is likely to play a role in phenological shifts with climate change for some species, particularly in some locations and years. Quantifying phenological sensitivity to changes in soil moisture will therefore improve forecasts of shifts in phenology with future climate change.

INTRODUCTION

Climate change is affecting organisms by altering temperature and soil moisture around the world (Parmesan, 2006; Chen et al., 2011). One of most widespread biological responses to climate change is a shift in phenology, the timing of recurring biological events, which has 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, leaf-out, 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). Recent trends of advancing phenology may be due to increases in both/either chilling and/or forcing with global warming (Fujisawa and Kobayashi, 2010; Ibanez et al., 2010; Cook et al., 2012). In places where delays in spring phenology have occurred, reductions in winter chilling are often the attributed cause (Yu et al., 2010).

Effects of altered precipitation and soil moisture on phenology have received less attention, but are likely to be important drivers of plant phenology. For example, budburst, flowering, and leaf drop are affected by tree water status in dry ecosystems (e.g., Essiamah and Eschrich, 1986; Reich and Borchert, 1984; van Schaik et al., 1993). 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). Flowering phenology, on the other hand, can be advanced by drought conditions (Hamann et al., 2018). When effects of soil moisture on phenology have been quantified, this has occurred largely in arid and grassland or meadow ecosystems (e.g., Cleverly 2016, Tao et al 2019, Ganjurjac et al 2020); its role in other ecosystem types is less explored.

could add a paragraph on challenges of observational studies of soil moisture vs temperature as drivers because they are often correlated/affect one another?

Here we conduct a meta-analysis of climate change experiments to test whether and how soil moisture interacts with temperature to affect plant phenology. Field-based climate change experiments that warm

plots to different levels offer valuable tools to study climate change impacts on plant phenology. Experiments can combine temperature and precipitation treatments to create the “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 often monitor daily soil moisture, as well as daily air temperature, at the plot-level, allowing detailed quantification of how microclimate affects plant phenology.

Previous meta-analyses of phenology in climate change experiments have focused primarily on effects of temperature (e.g., Wolkovich et al., 2013). We expected that soil moisture may also affect phenology, with drier soils delaying budburst and leafout phenology and advancing flowering and fruiting phenology (add refs?). We use measured microclimate and phenology data from two databases of climate change experiments: MicroClimate from Climate Change Experiments (MC3E, Ettinger and Wolkovich, 2018)) and Experimental Phenology (ExPhen) to quantify effects of soil moisture and above-ground temperature on plant phenology (bud-burst, leaf-out, flowering, fruiting, senescence; see Materials and Methods). We also use forecasted changes in temperature and soil moisture to investigate how including soil moisture alters expected future shifts in 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). Phenology data came from a ExPhen, a new database of phenology from climate change experiments (Ettinger and Wolkovich, 2021).

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., 2013). We carried out a full literature review to identify potential active-warming field experiments, following the methods and search terms of Wolkovich et al. (2013) 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 both/either 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, which is available at KNB (Ettinger and Wolkovich, 2018). The phenology data from the same 15 experiments comprise the ExPhen database of experimental phenology, which is also available at KNB (Ettinger and Wolkovich, 2021).

Analysis— To understand how soil moisture interacts with temperature to affect phenology, we fit models with measured soil moisture, measured temperature, and their interaction to phenology response data (budburst, leafout, flowering, fruiting, senescence). Microclimate data came from the MC3E database, and phenology data came from the ExPhen database. 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 air temperature, soil moisture, and their interaction. Random effects for all phenology models were species (with random slopes and intercepts), site (random intercept), and year nested within site (random intercept). Equations for these models can be found in the Supplemental Methods.

Keep or cut the below, or move to supp?

To better understand the interactive effects of measured temperature and soil moisture, experimental treatment effects, and feedbacks between temperature and soil moisture conditions, we conducted follow-up analyses in which we fit the same phenology models to subsets of the data (controls only, low temperature treatments only, and high temperature treatments only). We also fit a model with soil temperature in place of air temperature, for the subset of sites these data were available.

To quantify how climate manipulations affect temperature and soil moisture, we used microclimate data from

the 4 sites in the MC3E database that manipulated both precipitation and temperature, and measured both above-ground temperature and soil moisture (exp01,exp05,exp07,exp12). We then fit two groups of hierarchical models to microclimate data from these sites: one group with temperature response variables (including mean annual, and mean seasonal temperatures), and the other group with soil moisture as response variables (including mean annual, and mean seasonal soil moisture). For both groups of models, explanatory variables were temperature treatment, precipitation treatment, and their interaction. The models included a random effect of site, with a random slope and intercept structure, to allow effects of experimental treatments to vary across sites. Models also included random effects of day-of-year, nested within year, on the intercept only, to account for non-independence of measurements taken on the same day within the same year. Equations for these models can be found in the Supplemental Methods.

RESULTS

We found that soil drying delays phenology and warming temperatures advance phenology, for most phenophases. The magnitude of these effects varies across phenophases, species, and sites. Add summary sentence about life forms (trees, shrubs, herbs, grasses, Fig 4)? And ecosystems, if we add grassland vs forest comparison.

Effects of soil moisture were strongest for budburst and leafout, and affected all phenophases except fruiting (Figures 1, 1S). Soil drying delays spring budburst at a rate of 0.42 days per percent reduction in soil VWC. Thus, if soil moisture is reduced by 10% of its current state (mean across all sites for which budburst was monitored= XX), as is expected over the next 50 years in the northeastern US (Berg et al., 2017) budburst would be delayed by approximately XX days on average, due to changes in soil moisture alone.

Increasing air temperature advanced phenology for all phenophases except senescence (Figure 1S). Our models estimate that warming advances budburst phenology at a rate of 3.42 days per °C, advances leafout at a rate of XX, advances flowering a rate of XX, and advances fruiting at a rate of XX. These estimates are consistent with estimates from previous meta-analyses (Wolkovich et al., 2013).

Add a paragraph about variation in interactions between soil moisture and temperature?

Keep or cut the below, or move to supp?

- **Soil moisture effect size is bigger in full dataset than in controls only, for BB.** Mean and range of SM is similar (though max is a bit higher in full dataset; min is similar).
- **Effects of climate manipulations on temperature and soil moisture**

Mean annual soil moisture is negatively affected by target temperature treatment, and positively affected by precipitation treatment. (Figure ??). These effects varied by site; for example, at exp07 soil moisture was positively affected by temperature treatment. Air temperature is positively affected by target temperature treatment, and negatively affected by precipitation treatment. (Figure S??).

DISCUSSION

Across the life forms included in the ExPhen database (Table ??), soil moisture affects phenology. Soil moisture had previously been investigated primarily in arid ecosystems (e.g. XXX), and has not been a focus of experiments and meta-analyses (e.g. Wolkovich). We quantify effects of soil moisture across forest and grassland ecosystems.

Effects of temperature and soil moisture, and their interaction, on phenology vary across phenophases and species . - Discussion of functional groups- trees, shrubs, grasses, forbs.

Global change factors interact to affect phenology. -temperature and soil moisture here -also interactions with CO₂ -limiting resources: Variable responses to moisture (and precip) may be caused by temporal and spatial variation in the most limiting resource (e.g., temperature vs moisture). As global warming reduces temperature limitation, importance of moisture limitation in plant phenology may increase.

Relating experiments to "real world": -Moving beyond treatments levels to analyze plot-level microclimate- closer to how plants may be experiencing treatments -how temperature is affected by soil moisture, and how soil moisture is affected by temperature treatments

Conclusions

Questions for Lizzie at this stage

- 1) Do you think adding 2 more sites (Jasper Ridge and Cedar Creek, both grasslands) would add a lot to the paper? Would take some effort, but not a TON of effort?
- 2) What figures or main points do you think would strengthen/support the paper?
- 3) Target Journal: Some ideas are AJB, New Phytologist, Ecology. What do you think?

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.
- 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.
- 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.
- 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.
- 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.

- 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.
- Ettinger, A., and E. Wolkovich. 2018. Microclimate from climate change experiments (MC3E). doi:10.5063/F1QV3JQR.
- . 2021. 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.
- 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.
- 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.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637–669.
- Polgar, C. A., R. B. Primack, J. S. Dukes, C. Schaaf, Z. Wang, and S. S. Hoepfner. 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.
- 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.

- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60. PT: J.
- Shaver, G. R., J. Canadell, F. S. Chapin, J. Gurevitch, J. Harte, G. Henry, P. Ineson, S. Jonasson, J. Melillo, L. Pitelka, et al. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis ecosystem responses to global warming will be complex and varied. Ecosystem warming experiments hold great potential for providing insights on ways terrestrial ecosystems will respond to upcoming decades of climate change. Documentation of initial conditions provides the context for understanding and predicting ecosystem responses. *BioScience* 50:871–882.
- Taylor, G., M. J. Tallis, C. P. Giardina, K. E. Percy, F. Miglietta, P. S. Gupta, B. Gioli, et al. 2008. Future atmospheric CO₂ leads to delayed autumnal senescence. *Global Change Biology* 14:264–275.
- van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of ecology and Systematics* 24:353–377.
- Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America* 104:5738–5742.
- 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.
- Yu, H., E. Luedeling, and J. Xu. 2010. Winter and spring warming result in delayed spring phenology on the tibetan plateau. *Proceedings of the National Academy of Sciences* 107:22151–22156.

Figures

Additional Figures to make:

- Plots of (mean?) soil moisture and temperature by site, year, and phenophase

- 216 • Histograms by form and/or ecosystem
- 217 • Map of studies with symbols varying by ecosystem? (for Supp)
- 218 • Tables of models (for Supp)

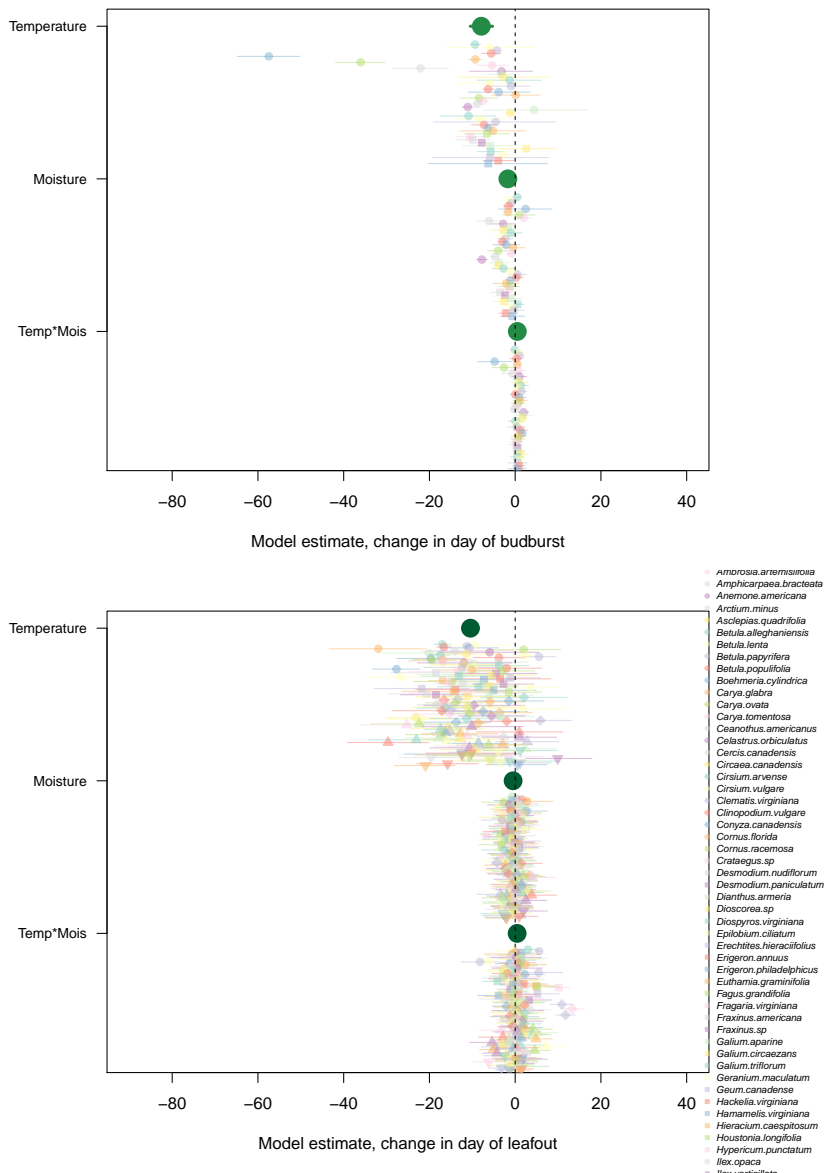


Figure 1: Model coefficients from budburst and leafout models (with centered predictors).

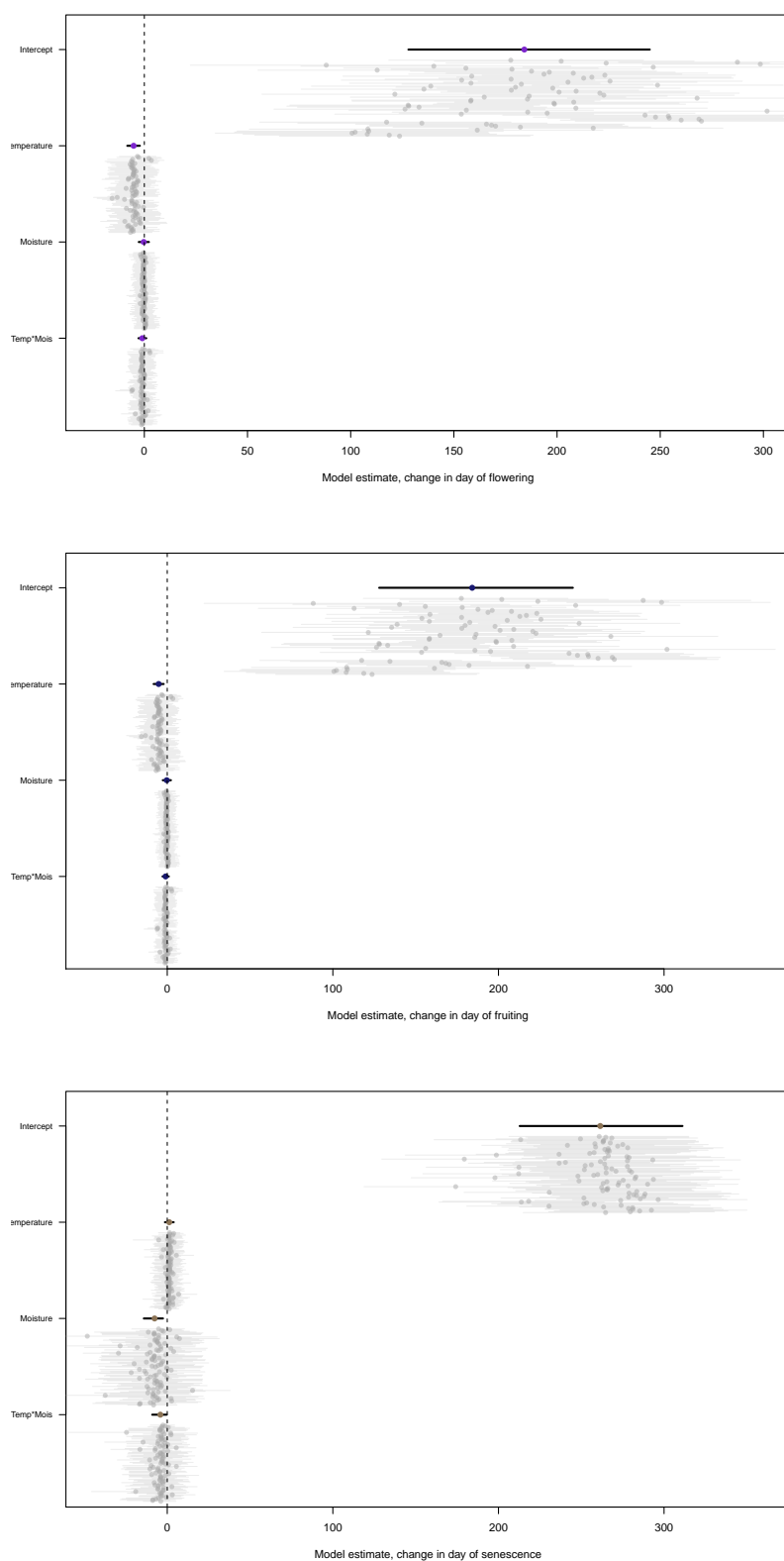


Figure 2: Model coefficients from flowering, fruiting, and senescence models (with centered predictors). Move to Supp! Also, remove intercept.

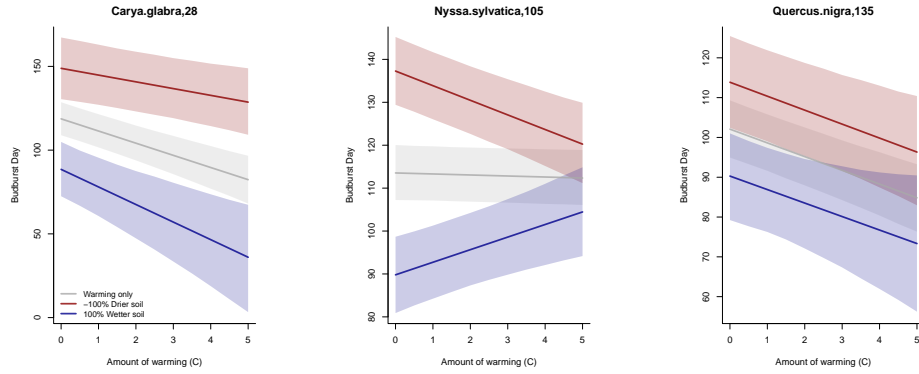


Figure 3: **Patterns of forecasted changes in budburst date with warming and shifts in soil moisture vary across species.** For nearly all species, our model estimated negative effects (i.e., earlier) of both temperature and soil moisture on budburst; however, the magnitude of these effects, as well as the sign and magnitude of the estimated interaction between soil moisture and temperature, differed across species, potentially resulting in divergent patterns with forecasting changes in climate change. Budburst may occur much earlier in wetter vs drier soils with warming for species such as *Carya glabra* (left panel), with a strong estimated negative interaction between soil moisture and temperature. Other species, such as *Nyssa sylvatica* (middle panel), may experience delayed budburst in wet soils but advances in dry soils, with a strong positive interaction between moisture and temp. Still other species' budburst, such as *Quercus nigra* (right panel), exhibits weak interactive effects of temperature and soil moisture and are therefore likely to advance with warming regardless of changes in soil moisture.

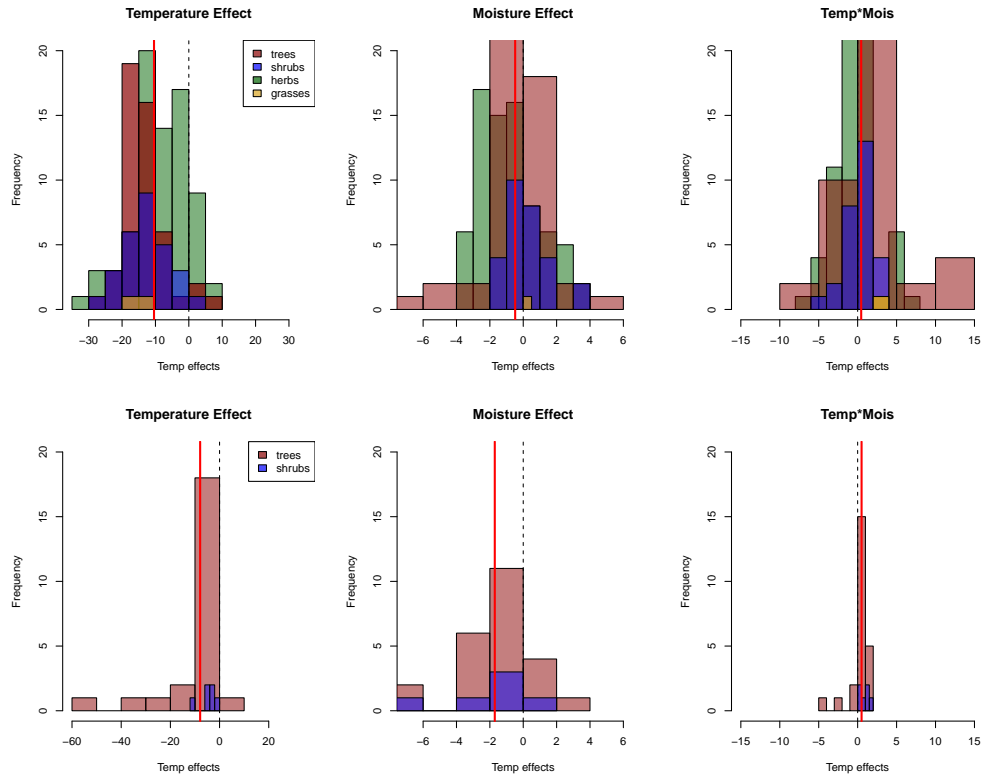


Figure 4: Effects of temperature, soil moisture, and their interaction do not differ strongly across life forms.