Changes and trends in budburst and leaf flush across Europe and North America

A meta-analysis of local adaptation in spring phenology studies

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Abstract

We conducted the first cross-continental meta-analysis of published studies from the peer-reviewed literature that reported spring event dates for a mix of angiosperm and gymnosperm tree species in the northern hemisphere, capturing data from 384 North American provenances and 101 European provenances with observations from 1962 to 2019.

1 Introduction

- Define spring event, fall event
- Background
- Importance: An accurate understanding of how species distribution might be influenced by environmental conditions at a continental scale is critical for future range shift prediction.
- Knowledge Gap: Anecdotally, the spring phenology of trees from European provenances appeared to exhibit stronger clines and less plasticity than in North American studies. Despite a growing interest in predicting local adaptation across locations, no study has comprehensively examined clines for spring and fall events and what factors may underlie differences observed across studies.
- Research question (links to results)

We ask: Across common garden studies, how strong are clines in spring and fall phenology?
To better understand these clines, we also aim to examine:

- If differences in clines exist across Europe and North America.
- If differences in clines exist across angiosperm and gymnosperm species.
- If climate overlap (see Figure 1) between the provenance and garden explains the similarities and differences in clines.

To our knowledge, this marks the first study to synthesize spring phenology data retrieved from studies across North America and Europe.

Ref notes

Good background information.

[Aitken and Bemmels, 2016]
"Geographic variation in trees has been investigated since the mid-18th century. Similar patterns of clinal variation have been observed along latitudinal and elevational gradients in common garden experiments for many temperate and boreal species."
"Scientists have studied relationships between tree populations and environmental characteristics of their provenances in common garden experiments for over 250 years."

[Alberto et al., 2013]
"Evolutionary responses are required for tree populations to be able to track climate change. Results of 250 years of common garden experiments show that most forest trees have evolved local adaptation, as evidenced by the adaptive differentiation of populations in quantitative traits, reflecting environmental conditions of population origins."
"Thus, responding to climate change will likely require that the quantitative traits of populations again match their environments. We examine what kind of information is needed for evaluating the potential

to respond, and what information is already available. We review the genetic models related to selection responses, and what is known currently about the genetic basis of the traits. We address special problems to be found at the range margins, and highlight the need for more modeling to understand specific issues at southern and northern margins. We need new common garden experiments for less known species. "
"Modeling work on the potential of populations and species to respond genetically to recent climate change is advancing (see Hoffmann & Sgrò, 2011; Franks & Hoffmann, 2012; Shaw & Etterson, 2012 for recent reviews). "

(see e.g., Valladares et al., 2007; Caffarra et al., 2011; Hänninen & Tanino, 2011) "The plastic response of different traits (e.g., phenology in trees) to variation in climate is, however, often much more complex than in heuristic models of adaptation."

[Loarie et al., 2009]
"It is also now understood that the rate of adaptation required by climate change varies among geographic regions."

need to read again

[Nicotra et al., 2010]
"The immediate responses via phenotypic plasticity have also been considered in the context of climate change."

need to read again

[Menzel and Fabian, 1999] **Growing season extended in Europe.**

good Europe background paper

[Menzel et al., 2006] **European phenological response to climate change matches the warming pattern.**

another good Europe background paper

[Parmesan, 2006]
"Trees exhibit a high degree of phenotypic plasticity with respect to climatic variation. Phenological shifts of bud flush in response to recent increases in temperatures have been widely documented ."

can cite more papers on this matter

[Gill et al., 2015] **Changes in autumn senescence in northern hemisphere deciduous trees: a meta-analysis of autumn phenology studies.**

GREAT paper for us to base our writing on: similar meta-analysis but focuses on fall events

"the effects of climate change on the phenology of vegetation have received increased attention over the past several decades as any factor that alters the timing of early growing season leaf-out and senescence has the potential to affect a variety of ecosystem properties. For example, the timing of leaf-out and senescence of deciduous plants has been shown to affect plant competition (Fridley, 2012), plant growth (Myneni et al., 1997) and ecosystem carbon uptake (Barichivich et al., 2012).

"While leaf-out has been shown to advance over the past century as a result of increasing air temperatures (Linderholm, 2006; Polgar and Primack, 2011), the relationship between temperature and leaf senescence remains less well understood (García-Plazaola et al., 2003; Richardson et al., 2013)."
"Thus, an extension of the growing season can contribute to reduced atmospheric CO_2 concentrations due to enhanced carbon sequestration in terrestrial plants (Penuelas et al., 2009; Richardson et al., 2013). However, the increase in carbon uptake may be partially offset by increased rates of ecosystem respiration (Piao et al., 2008)"
"The lack of consistent relationships between air temperature and timing of leaf senescence suggests that autumn senescence may be influenced by a variety of factors that obscure its relationship with temperature."

Cite some papers about the documented trends

tbc...

Alina says: I found AitkenBemmels2016's research question to be wonderfully phrased and think we can do something similar

[Aitken and Bemmels, 2016]
"To what extent are patterns of local adaptation along climatic gradients similar among species within a given geographic region? If clines in phenotypic traits are similar, can average patterns of sym-

patric variation guide AGF or identify critical climatic variables as a first approximation for untested species? We reanalysed data from the literature on provenance trials in temperate tree species from western North America to address these questions. This is an ideal region of focus because of the many provenance trials conducted on native tree species that are important for forestry, and because its high topographic complexity means that turnover in climate occurs rapidly and heterogeneously over short geographic spaces. Clines along climate gradients are thus espcially likely to reflect local adaptation to climate, rather than non-adaptive phenomena resulting from population demographic history."

"Defining budburst. Most studies defined budburst as initial 'green tips' (33 out of 49 papers). Select studies defined budburst as a specific increment of growth (for example, '0.5 cm of new growth') or as bud swell, leaf emergence, leaf unfolded, open bud scales or petiole emerged. The remaining papers (4 of 49) did not include a definition of budburst. Most papers using the above definitions (34 of 49) required only one bud to have met the defined criteria of budburst; however, the remaining studies implemented specific thresholds to be met (10–100% of all buds on an individual needed to have bursted bud). For studies that quantified multiple measurements of percentage budburst over time (days), we extracted one value of 'days to budburst' of these multiple measurements to make them comparable to other studies. To extract this summary value, we selected the days to budburst when percentage budburst was closest to 90%, including estimates as low as 49.5% budburst"

2 Methods

Our methods are divided into four main steps.

2.1 Literature Search

We searched the peer-reviewed literature for common garden experiments that documented the timing of spring events of woody plant species on 14 December 2022 using Web of Science (Thompson Reuters, New York, NY)with the following terms:

TOPIC = (common garden* OR provenance*) AND (leafout* OR leaf out* OR budburst OR spring phenolog*). The search returned 122 publications. We also contacted authors of previous review papers, including S.N. Aitken and R.D. Guy to help further search the literature.

We read the methods and results of all publications and limited our subsequent analysis to the ones that (a) focused on woody plants originating from either Europe or North America, (b) had provenance trails and common gardens on the same continent, (c) reported spring events in units of calendar days (day of year or DOY) instead of a quantitative scale on a particular day, and (d) reported latitude and longitude of provenances and gardens.

We had to exclude studies that reported spring events on a quantitative scale because (1) such studies usually only assessed where on the scale the spring event of a tree fell onto on the same days across different years (e.g. Robson et al., 2013; Vander et al., 2015; Santini et al., 2014; Schueler & Liesebach, 2004), and (2) scales are not always consistent across different studies (Chmura & Rozkowski 2002; Dhont et al., 2010; Wang et al., 2022). Such factors made it impossible to back convert the quantitative scale to DOY.

Some studies did not provide the exact latitude and longitude of the common garden (Bongarten, 1978) or the provenances (Hall et al., 2007; Soolanayakanahally et al., 2013), or they did not link the latitude and longitude of each provenance to the DOY of spring events (Deans & Harvey, 1996). We had to exclude these papers. We also left out studies in which woody plants from North American provenances were planted in common gardens in Europe because we wanted to test continental variations (Cannell et al., 1987; Lavadinovic et al., 2013). Finally, we excluded studies that focused on examining how provenance altitude influenced local adaptation in spring phenology since we are interested in testing latitudinal effects (Vitasse et al., 2009; Vitasse et al., 2010; Li et al., 1997; Alberto et al., 2011; Acevedo-Rodríguez et al., 2006).

2.2 Dataset Assembly

Out of the 122 common garden studies on spring phenology that we read, only 18 (?) ultimately supplied the data that we needed (DOY of spring events, latitude and longitude of provenances and common gardens). Studies were distributed throughout North America and Europe, with the majority of data concentrated in XXXXX (Figure X). The distribution was skewed toward North America (n = X), with only X located in Europe. We primarily focused our analysis on spring events, and made use of the fall event DOYs present in X of the studies we included rather than searching for publications entirely on fall events online.

display a table and a map here, and in the caption, clarify that some studies had more than one gardens and two studies shared the same garden

We assembled a data set that documents event DOY and geographic coordinates of provenances and gardens, during which we used ImageJ (version 1.53k; Rasband, 1997-2022) to extract values from figures whenever possible and necessary. We pooled the timing of budburst and leaf flush into a single category of 'spring events' and the timing of bud set, leaf senescence, growth cessation, and leaf abscission into 'fall events.' Such pooling is justified because of the shared pressures from natural selection that govern these events (Gill et al., 2015). Some studies documented event dates relative to a reference date that is not January 1 (e.g. Cannel et al., 1987; Rehfeldt, 1994). In this case, we converted such dates to DOY using the Lubridate Package in R for standardization purposes.

2.3 Climate Data Gathering & Analyses

2.3.1 placeholder

With information about provenance latitude, longitude, and elevation from original publications, we estimated the mean annual temperature (MAT) for each provenance using the Climate Information Tool by FAO (Food and Agriculture Organization of the United Nations, 2022) and ClimateWNA (Wang et al., 2012).

We hope that coarse metrics such as latitude and MAT ultimately represent how similar the climates are between the provenances and gardens in times that matter for the events. If climates are very similar, then we would expect similar timings [add more here]. To this end, we estimated climate overlap in relevant months: For spring events, we considered overlap across March to May. To assess climate overlap percentage (define this better), we extracted gridded daily temperature data for 2011 to 2020 for all European and North American provenances and gardens from E-OBS and the built-in Daymet package in R respectively (Cornes et al., 2018; Thornton et al., 2020). Using the Overlap package in R, we calculated the percentage overlap of the daily temperature of each provenance in spring months (March to May) from 2011 to 2020 in relation to the daily temperature of their corresponding gardens.

2.3.2 Calculate GDDs

Growing degree days (GDD) is a commonly used heat accumulation measure to forecast phenological development in plants (Miller et al., 2001). We calculated GDD based on the accumulation of mean daily temperatures (T_m)from 2011 to 2022 above a baseline of 0°C, from January 1 until budburst and leaf flush with the following formula: GDD = $\sum(T_m$ - 0°C for $T_m \geq$ 0°C; 0 for $T_m \leq$ 0°C) define this in caption, no need to have is as a section: Spherical distances hmmm need to better define this... On top of taking the difference between provenance latitude and garden latitude (maybe I could write this in subscript), we also use the dism() function in the Geosphere package in R to estimate the geospherical distance between locations (accounting for Earth curvature).

maybe there are different/better terms

2.3.3 Corrected for DOY (taking the difference)

will put results in supplement

(need to better define this as well)

2.4 Mixed effects modelling

Most tree species are only represented in one common garden study in our dataset. In such instances, it is difficult to statistically interpret if variations across gardens are due to the species or the garden's location and climate. To address this, we focused on estimating species effects as we expect a larger effect from species. Within publications, we considered unique gardens and species to represent independent data, and fitted each species & common gardens instead of just species.
We used hierarchical Bayesian models where we partially pooled by species. We estimated effects of continent and species type (angiosperm VS gymnosperm) from posterior estimates, in relation to single predictors (including provenance latitude, MAT) and two predictors (climate overlap percentage and standard deviation).

will elaborate later

3 Results

`Research questions recap`

Despite a growing interest in predicting local adaptation across locations, no study has comprehensively examined clines for spring and fall events and what factors may underlie differences observed across studies.
We ask: Across common garden studies, how strong are clines in spring and fall phenology?
To better understand these clines, we also aim to examine:

- If differences in clines exist across Europe and North America.
- If differences in clines exist across angiosperm and gymnosperm species.
- If climate overlap between the provenance and garden explains the similarities and differences in clines.

all subsection titles are placeholders

Our final dataset captures seven angiosperm and eight gymnosperm species from 19 common gardens, encompassing data from 384 North American provenances and 101 European provenances with observations from 1962 to 2019. Seven species had fall event information available.

add map here

add a table documenting studies attributes

3.1 Provenance latitude and MAT do not affect spring event timing

Overall, our models show that spring events are not related to provenance latitude or mean annual temperature in North America, and only weakly related in Europe (Fig. 1 & Supplement Table. 1).

Should I add climate overlap plots here too?

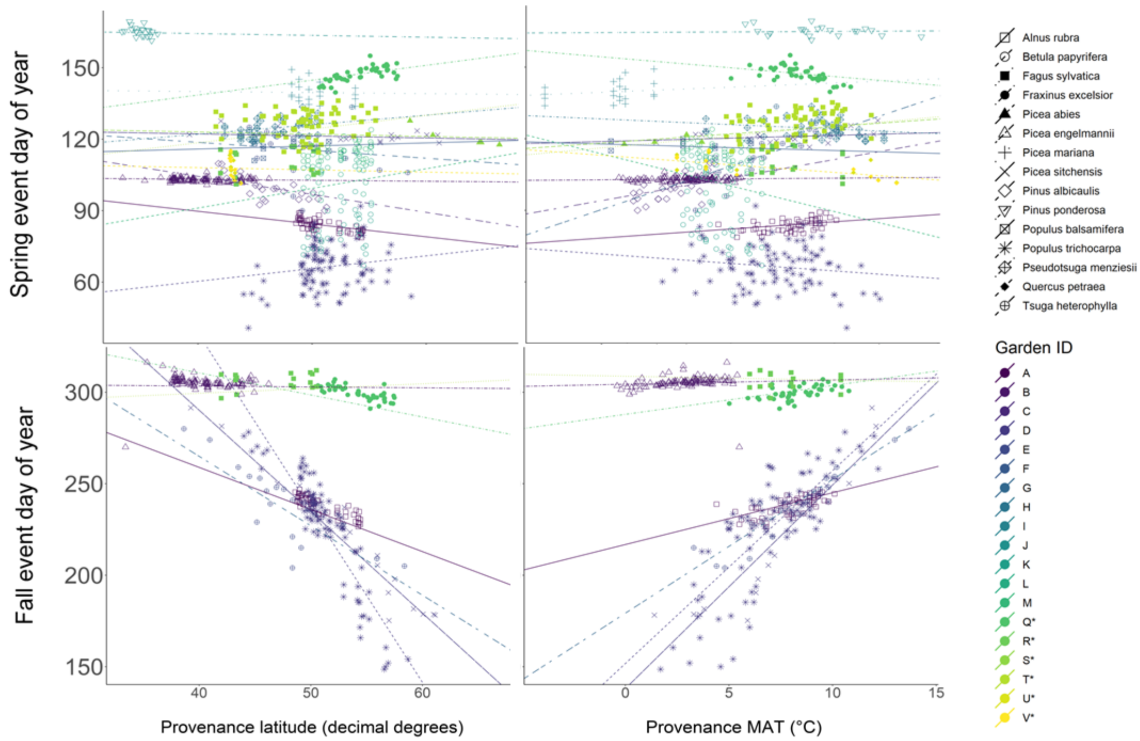

Figure 1: Spring event Day of Year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall event at the bottom.

3.1.1 Similar results across provenance latitude, latitude difference, and distance

need to find a name for each metric and stick to it.

Along with (a) provenance latitude, we also looked at how spring event timing is related to (b) the absolute difference between provenance latitude and garden latitude , as well as (c) the spherical distance between the garden and each provenance. All three metrics depict little to no relationship between spring event timing and the geographical location of the provenance (Supplement Fig.1).

3.1.2 Climate overlap does not predict event dates much better than provenance latitude or MAT

While comparing how similarity in climate relates to event dates, we observed very weak effects of climate overlap on spring events, nearly identical across angiosperms and gymnosperms. Fall events diverge as climate overlap declines for both angiosperms and gymnosperms, but slightly more strongly for gymnosperms (Fig.2).

3.2 Stronger clines in fall events observed in North America than Europe

We find that fall events (budset, leaf senescence, leaf abcission) advance strongly with provenance latitude and mean annual temperature, meaning fall events are earlier where provenance mean annual temperature is lower (higher, more northern latitudes). This relationship, however, is observed mostly in North America where fall events advance 4.2 days per degree we move north, or 6.4 days when the MAT decreases by 1 °C (Fig. 3). In Europe, such relationship is weak: advance 0.5 days per degree we move north, or 0.6 days when the MAT decreases by 1 °C(Fig. 3).

3.3 Effects of MAT on spring events diverge across angiosperms and gymnosperms

Effects of provenance latitude on both spring and fall events are similar across angiosperms and gymnosperms. However, effects of MAT on spring events weakly diverge: spring events get earlier as MAT increases in angiosperms and delay as MAT increases in gymnosperms, except for *Pseudotsuga menziesii*. Fall events delay in warmer locations for both species types, but slightly more so for gymnosperms (3.7 days VS. 6.2 days)(Fig. 4).

4 Discussion

The weak relationship between spring event dates and provenance latitude and MAT that we find in European studies might be explained by the higher extent of climate overlap in those studies. The more similar the climate is between provenances and gardens, the less difference between spring event dates.

The inconsistent and weak clines in spring events that we found suggest high plasticity in spring phenology across continents and species. Fall events, on the other hand, exhibit stronger clines which suggest more local adaptation, especially in North America. Overall, our results predict that warming springs will continue to be tracked more closely phenologically by trees than warming fall temperatures.

In contrast to spring events, we found strong latitudinal clines in fall events across both continents, with local adaptation appearing much stronger in North America than in Europe. Our results show that spring events are highly plastic, and thus may shift with warming, but data on more species and greater information on important factors, such as their geographic location in relation to their origins and elevation, are needed for forecasting.
Keir et al. [2011]

5 Figures

Rasband, W.S. (1997-2016). Image J.U.S. National Institute of Health, Bethesda, Maryland, USA. http://imagej.nih.gov/ij

References

Sally N. Aitken and Jordan B. Bemmels. Time to get moving: assisted gene flow of forest trees. *Evolutionary applications*, 9(1):271–290, 2016.

Florian J. Alberto, Sally N. Aitken, Ricardo Alía, Santiago C. González-Martínez, Heikki Hänninen, Antoine Kremer, François Lefèvre, Thomas Lenormand, Sam Yeaman, Ross Whetten, and Outi Savolainen. Potential for evolutionary responses to climate change - evidence from tree populations. *Global change biology*, 19(6):1645–1661, 2013.

Allison L. Gill, Amanda S. Gallinat, Rebecca Sanders-DeMott, Angela J. Rigden, Daniel J. Short Gianotti, Joshua A. Mantooth, and Pamela H. Templer. Changes in autumn senescence in northern hemisphere deciduous trees: a meta-analysis of autumn phenology studies. *Annals of botany*, 116 (6):875–888, 2015.

Karolyn R. Keir, Jordan B. Bemmels, and Sally N. Aitken. Low genetic diversity, moderate local adaptation, and phylogeographic insights in cornus nuttallii (cornaceae). *American Journal of Botany*, 98 (8):1327–1336, 2011. ISSN 00029122, 15372197. URL `http://www.jstor.org/stable/27975404`.

Scott R. Loarie, Philip B. Duffy, Healy Hamilton, Gregory P. Asner, Christopher B. Field, and David D. Ackerly. The velocity of climate change. *Nature (London)*, 462(7276):1052–1055, 2009.

Annette Menzel and Peter Fabian. Growing season extended in europe. *Nature (London)*, 397(6721): 659–659, 1999.

Annette Menzel, Tim H. Sparks, Nicole Estrella, Elisabeth Koch, Anto Aasa, Rein Ahas, Kerstin Alm-Kübler, Peter Bissolli, Ol'ga Braslavská, Agrita Briede, Frank M. Chmielewski, Zalika Crepinsek, Yannick Curnel, Åslög Dahl, Claudio Defila, Alison Donnelly, Yolanda Filella, Katarzyna Jatczak, Finn Måge, Antonio Mestre, Øyvind Nordli, Josep Peñuelas, Pentti Pirinen, Viera Remišová, Helfried Scheifinger, Martin Striz, andreja Susnik, Arnold J. H. Van Vliet, Frans-Emil Wielgolaski, Susanne Zach, and Ana Zust. European phenological response to climate change matches the warming pattern: European phenological response to climate change. *Global change biology*, 12(10):1969–1976, 2006.

A. B. Nicotra, O. K. Atkin, S. P. Bonser, A. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, M. D. Purugganan, C. L. Richards, F. Valladares, and M. van Kleunen. Plant phenotypic plasticity in a changing climate. *Trends in plant science*, 15(12):684–692, 2010.

Camille Parmesan. Ecological and evolutionary responses to recent climate change. *Annual review of ecology, evolution, and systematics*, 37(1):637–669, 2006.

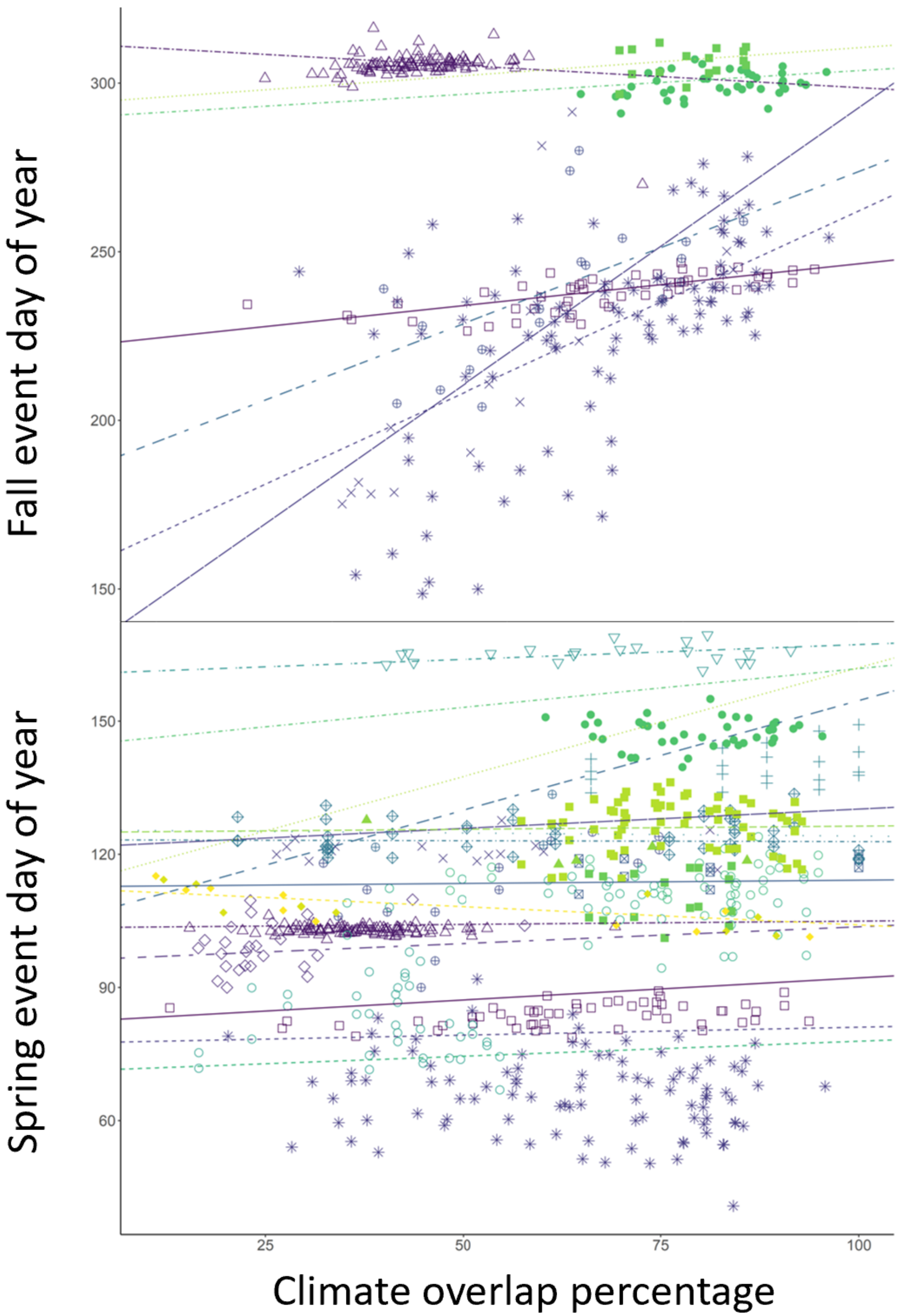

Figure 2: Caption placeholder

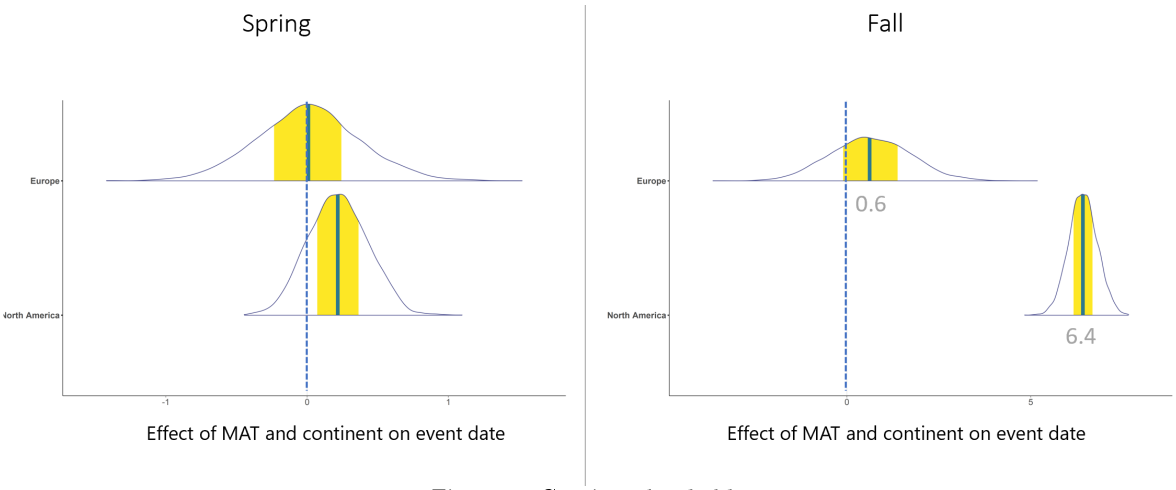

Figure 3: Caption placeholder

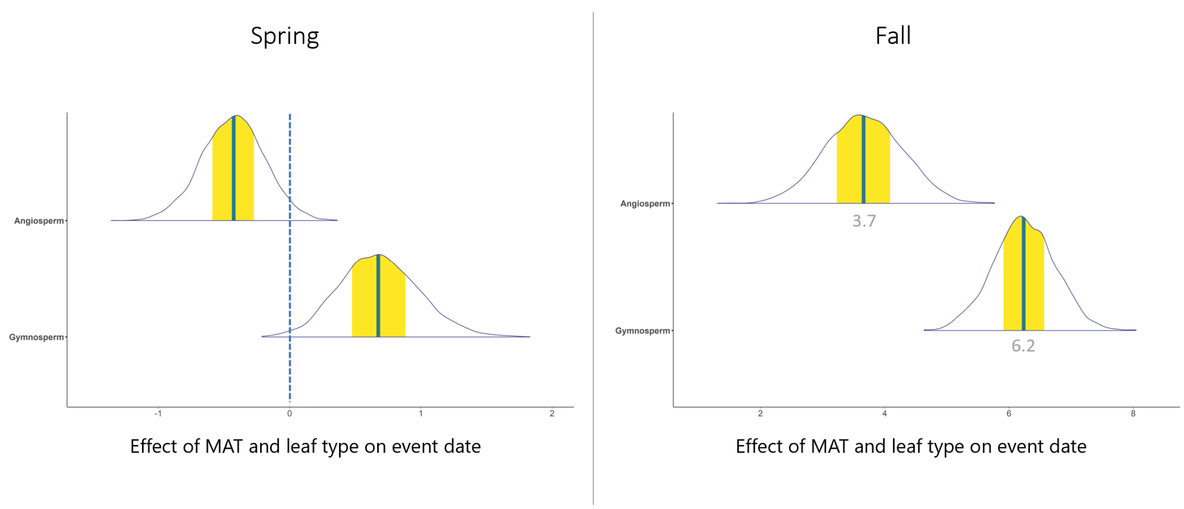

Figure 4: Caption placeholder