

Continental divides: Spring climate variability shapes
the phenological cue strength of woody species in
temperate North America, not Europe

or

Spring climate stability shapes phenological cue
sensitivities of temperate forest in North America but
not Europe

or

Limited support for range-wide climate patterns shaping
phenological cue differences among woody plants of
temperate North America and Europe

or

Other

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Abstract

Introduction

For woody plants of the temperate zone the phenology, or annual timing, of spring budburst influences a myriad of ecological processes including patterns of resource allocation (Seiwa and Kikuzawa, 1991), trophic interactions (Memmott et al., 2007) and biogeochemical cycling (Piao et al., 2007). Through budburst timing, woody plants balance the advantages of precocious growth resumption for resource gains with the risk of damage from late season frost (Savage and Cavender-Bares, 2013). To navigate this tradeoff, woody plants have evolved complicated networks of sensory organs, hormone signaling, and physiological responses to sense environmental cues; changes in their physical environment, that signal the arrival of appropriate conditions for resuming growth.

Decades of research suggest that warming spring temperatures (forcing), cool winter temperatures (chilling) and day length (photoperiod) are primary environmental cues utilized by woody plants that determine the timing of spring phenological events Ettinger et al. (2020); Forrest and Miller-Rushing (2010). These studies also demonstrate there are substantial cue-use differences among species, with some species relying more heavily on some cues over others (Laube et al., 2014). As anthropogenic climate change has already driven shifts in spring phenology (Menzel et al., 2006), identifying these inter-specific differences in cue use has emerged as a major goal of phenological research (). These differences have strong implications for both predicting the rate of phenological shifts as the climate continues to warm (), and anticipating the ecological consequences of these shifts ().

Climate is the major selective force on both species' geographic ranges (Morin and Lechowicz, 2011) and their phenology (Savage and Cavender-Bares, 2013), and therefore, it is widely assumed that phenological cue-use differences among species reflect the climate of their respective ranges (Zohner et al., 2017; Silvestro et al., 2019). That is, a species' relative reliance on forcing, chilling and photoperiod for should be shaped by the unique environmental conditions across a species' geographic range.

Despite this intuitive link between climate and cues, direct tests of this assumption are rare (but see (Zohner et al., 2017)). With the recent quantification for cue use of many species (Ettinger et al., 2020) and the accessibility of high resolution climate data it is now possible to rigorously test this theory with data. Below, we briefly outline two hypotheses about the relationship between phenological cue-use and species' climatic range characteristics. We

then test these predictions using Bayesian models for a large suite of temperate woody species from North America and Europe.

0.1 Climate intensity hypothesis

One hypothesis for the evolution of cue use differences across species is that species utilize the climate cues to which they have the most exposure. Simply stated, there should be a positive correlation between the amount or intensity of a cue across a species' range and the species phenological sensitivity to that cue. This hypothesis predicts that species with a) high numbers growing degree days in their range should have stronger forcing cues, b) higher amount of chilling should have stronger chilling cues and c) more annual photoperiod variation should have stronger photoperiod cues. This hypothesis has been applied to explain large, macro-ecological patterns in phenology like why the tropical phenology cues primary to forcing and temperate and arctic phenology is more dependent on photoperiod and/or chilling () but has not been widely tested within biomes for species with overlapping ranges.

0.2 Climate variability hypothesis

Current understanding of the evolution of phenological cues assume that forcing is the predominant cue. In this framework, a secondary reliance on photoperiod and/or chill cues evolve when forcing alone is not a reliable cue of safe growing condition (Körner and Basler, 2010). Forcing is an unreliable cue when temperatures unstable in the spring time. The climate variability hypothesis predicts species with high variation in spring temperature in their range should evolve a stronger response to all three cues, especially chilling and or photoperiod, (Wang et al., 2014; Muffler et al., 2016). This hypothesis potentially explains the stronger cue sensitivity of temperate North American species to those in Europe where there is less climate variability in the spring (?).

However, a major hurdle to robustly testing this hypothesis is that, when considered in the context of a species' geographic range, spring temperature variation occurs on multiple temporal and spatial scale. Phenology may be shaped by intra-annual temperature variation (e.g. frequency of late season frost, diurnal temperature functions), inter-annual variation (e.g. annual mean temperatures) and the interaction between them (e.g. inter-annual variation in last season frost episodes). Further, each of the level of variation be quite different across a species range, suggesting geographic variation with the range must also be accounted for.

Any of these level of variation could itself drive selection for secondary cue usage (photoperiod/chilling), and it is unclear how they interact or which is most important (Zagmajster et al., 2014). Key to testing the climate variability hypotheses is to first characterize relationships between spring temperature variation at multiple spatio-temporal scales.

An implicit assumption of the previously stated hypotheses is that among species cue-use variation is higher than within species (ie cue use is “conserved” at the species level). If rather, cue use patterns are locally adapted, while climate intensity and climate variability may still drive cue-use patterns at the population level, it would be difficult to detect consistent patterns across a species full geographic range. There is not yet a strong consensus about to what degree cue use is locally adapted and it likely varies between phenophases (), and organisms (). As such, any analysis considering species ranges and cue use must account for intra-specific differences as well.

We leveraged over 50 years worth of phenology experiments in the OSPREE database () and climate data collected across the ranges of temperate woody species in North America and Europe to test the three major climate-cue use hypotheses. We used a Bayesian hierarchical approach to jointly fit models estimating of forcing, chilling and photoperiod sensitivity for each species and the effects of several dimensions of climate intensity and variability in the species ranges on these estimates. Then for a subset of well represented species in our dataset, we modeled the among and within species variation in cue use to quantify the relative strength of local adaptation of pattern of phenological cue use. With this approach we 1) clarify the relationships between climatic variability across multiple scales of spatio-temporality, 2) identify the climate drivers that are more and less likely to drive selection on phenological cues and 3) compare variation in cue-use among and within species and between temperate Europe and North America. Our interrogation of these relationships between climate and cue use not only elucidates the evolutionary drivers of phenological cues, but offers new insights regarding implications of climate change as both species’ ranges and phenology continue to shift with warming.

Methods

Phenological data and cue-use estimates

Dan and/or Lizzie write:

- Introduce OSPREE
- Species selection
- Model description

OSPREE database

To estimate phenological responses to chilling, forcing and photoperiod we used data from the Observed Spring Phenology Responses in Experimental Environments (OSPREE) database (?). This database aims to include data from all published studies of experiments on woody plant responses to chilling, forcing and photoperiod cues, as described in ?. Here we use a subset of data from an updated version of the database containing all papers found in literature searches through June 2019, selecting species for which we could reliably estimate cue responses.

Estimates of phenological cues (i.e., change in days of an event per change in level of chilling, forcing or photoperiod) can vary strongly due to study location and methodological differences (CITES). For example, many studies often include only one—often extreme—level of a cue, such as a photoperiod of 24 hours or very low chilling, and thus will provide estimated responses to the manipulated cues (e.g., forcing) relevant only in those extremes. [Some statistical methods can estimate responses across such data, but they will estimate cue responses as more similar across all species than they likely are (see ?, for example), making the type of inter-specific comparisons we were interested in here difficult.] As such, we included species that where: 1) included in two or more studies, 2) we had data for at least two levels of each cue (chilling, forcing and photoperiod; but we excluded species that only had field chilling), and 3) could obtain published range maps (see below). [While this approach limited our total species number, it provided more reliable estimates of phenological cues.]

Species' range characteristics

Cat and/or Nacho write?

- Climate data Climate data was extracted from daily gridded meteorological datasets for both Europe and North America. For Europe, we extracted minimum and maximum

daily temperatures from the E-OBS dataset (<https://cds.climate.copernicus.eu/cdsapp!/dataset/insitu-gridded-observations-europe?tab=overview>) corresponding to the period comprised between 1980 and 2016. Specifically, we used version 17 at a resolution of 0.5 latitudinal degrees. For North America, we extracted minimum and maximum daily temperatures from Justin Sheffield's Princeton Global Forcing dataset (<http://hydrology.princeton.edu/data/pgf/v3>) for the same period. We used version v3 at a resolution of 0.25 latitudinal degrees.

(Figure of range maps with one climate variable, other could go to supplement)

- Species distributional data For 22 European and 16 North American tree species, we obtained published distributional range maps in shapefile format. European species ranges were downloaded from <http://www.sciencedirect.com/science/article/pii/S2352340917301981?via%3Dihub#ec-research-data> (Caudullo et al., 2017) and North American ranges were obtained from <https://www.fs.fed.us/nrs/atlas/littlefia/> # (Prasad, 2003). For each species' range, we extracted climate data corresponding to all grid cells contained within the range.
- Climate variables Minimum and maximum daily temperatures within species ranges were then used to compute Growing Degree Days (GDD), Growing Degree Days until the last frost (GDDlf) and Spring Temperature Variability (STV). GDD was calculated as the summed temperatures above 10C recorded from January 1st until May 31st. GDDlf was calculated as GDD but instead of summing temperatures above a threshold until a fixed date, the sum was performed until the date at which the latest minimum temperature below -5C was recorded. STV was calculated as the standard deviation of...

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- Temporal vs. geographic variation in climate variables

Statistical analysis

Coherence of climate variability

climate cue-use relationships

Dan write description of joint model

Intra vs. interspecific models

To assess variation within and across sites, we designed a two-level, hierarchical model using data from the OSPREE database. We subsetting the studies to include only those that had multiple provenance locations.

We used a Bayesian mixed-effects hierarchical model approach to analyze our data to best estimate the day of budburst. We fit a gaussian distribution model using study, species and population as intercepts, forcing and photoperiod as predictors (fixed effects) and species nested within population (i.e., site) as modeled groups (random effects). The Bayesian model was fit using Stan modeling language (www.mc-stan.org), accessed via the *rstan* package (version 2.15.1), version 2.3.1, in R (www.r-project.org/), version 3.3.1, and was written as follows:

)

$$\epsilon_i \sim \text{normal}(0, \sigma_y)$$

The α and each of the 5 β coefficients were modeled at the study, species, population, or species and population level, as follows:

$$\begin{aligned}\alpha_{study} &\sim \text{normal}(\mu_{study}, \sigma_{study}) \\ \alpha_{sp[pop]} &\sim \text{normal}(\mu_{sp}, \sigma_{sp}) \\ \mu_{sp} &\sim \text{normal}(\mu_{pop}, \sigma_{pop}) \\ \beta_{forcing_{sp[pop]}} &\sim \text{normal}(\mu_{forcing[sp]}, \sigma_{forcing[sp]}) \\ \beta_{forcing_{sp}} &\sim \text{normal}(\mu_{forcing[pop]}, \sigma_{forcing[pop]}) \\ \beta_{photoperiod_{sp[pop]}} &\sim \text{normal}(\mu_{photoperiod[sp]}, \sigma_{photoperiod[sp]}) \\ \beta_{photoperiod_{sp}} &\sim \text{normal}(\mu_{photoperiod[pop]}, \sigma_{photoperiod[pop]})\end{aligned}$$

We ran four chains, with 2,500 warm-up iterations followed by 3,000 sampling iterations, resulting in 12,000 posterior samples for each parameter. We assessed good model performance through \hat{R} close to 1 and high n_{eff} as well as visual consideration of chain convergence and posteriors (?). Using the *Gabry2017* package (?), we then plotted the partition of variance across the intercepts and predictors to determine intra- vs. interspecific variation.

Results

Climate intensity and cue use

Overall, the mean forcing (GDDs) and chilling (Chill Portions) had weak effects on estimated cue use. In our full species models mean GDDs and had a weakly negative or neutral association with cue strength (GDD:Chill=X, GDD:Force=Y, GDD:Photo=Z, (Fig. ??)). The general sign of these relationships persisted in the continent subset models (Fig. ?? d),e),f)) with the exception of the relationship between mean GDDs and chilling for North American species which became positive (mean= Z, (Fig. ?? c)). Generally, there was high uncertainty around these estimates suggesting climate intensity is a poor predictor for cue use.

Coherence of spatio-temporal spring climate variability

The spatio-temporal coherence of spring climate variability and intensity varied across continent and scales. Generally climate intensity (mean GDDs in range mean Chill Portions in range and Mean GDDs to last frost) were well correlated with climate variability (Fig. 3a),b),c),d),h)) though strong differences can be observed between North American and Europe. Intra-annual, inter-annual and spatial variability in spring climate were also well correlated (Fig. 3e),f),g)), though the variability of spring climate in Europe was very low, suggesting that these correlation are likely more relevant in North America.

Climate variation and cue use

In our full models, variation in growing degree days before the last frost of the season was weakly positively associated with forcing and photoperiod sensitivity and negatively associated with chilling sensitivity (Fig. 4a)). However, our continent subset models shows

different effect. The effect of Variation in GDDs to last frost is poorly estimated in the European data subset, and has almost no effect on cue use over the narrow range of spring climate variation present in Europe (Fig. 4b). In the North America subset, variation in GDD to last frost increases sensitivity in all three cues (Chilling:X Forcing:Y Photoperiod:Z, (Fig. 4c))) suggesting there may be support for the climate variation hypotheses in North America where spring climate variation can be extreme. We found qualitatively similar continental patterns in the relationships between cue-use and climate variability using STV as an alternative metric inter-annual variation (SUPP).

Local adaptation of phenological cues

We detected limited population level variation in forcing and photoperiod cue sensitivity, though this within species variation was less substantial than among species variation (Fig. 5). Notably, we found the largest source of variation in phenological was

0.3 Cue use in North America and Europe

We found that the strength of secondary cue use (chilling and photoperiod) was higher in North America than in Europe (Chilling: NA-X, EU-Y, Photoperiod NA-X, EU-Y, Fig. ??), while forcing sensitivity was higher in Europe than North America (NA-X, EU-Y). This result is consistent with the observation that the spring climate of North America is much less stable than Europe and our finding that the climate-cue use hypotheses appear to be better supported in North America.

Discussion

Hypotheses of bioclimatic cue use

Similar to previous studies, we found stronger support for the climate variability hypothesis than the climate intensity hypothesis (). While, as predicted by the climate intensity hypothesis, mean growing degree days in the range were positively associated with forcing sensitivity in North America, chilling sensitivity has no clear relationship with mean chilling in the range for species on either continent (Fig. ??e,f). Further, there is high uncertainty

surrounding the estimates in our climate intensity models, suggesting climate intensity is a poor predictor of phenological cue use.

By contrast, climate variability was associated with increased forcing, chilling and photoperiod sensitivities in North American species (Fig ??,c) as predicted by the climate variability hypothesis. Interestingly, there was virtually no relationship between climate variability and cue use in European species (Fig ??,b). We recovered these contrasting patterns among continents using multiple metrics of climate variability (see ??, and “STV”). We also found secondary cue use (photoperiod and chilling) sensitivity was higher in North American taxa than in European ones (Fig. 6). These contrasting biological patterns appear to reflect the strong climatic differences we observed between the continents.

Climate patterns in North America and Europe

Our study highlights that patterns of temperature variation and intensity are much stronger in temperate North America than in Europe (Fig. 1). This is a well meteorological phenomenon driven by large local climate patterns like the jet stream and ENSO and stuff (say better maybe, Ben can write this paragraph). Additionally, we found that in North America, there was a strong correlation between temporal and spatial climatic variability across the geographic ranges of the species we studied, while in Europe this correlation was weakly negative.

When we consider our biological findings about cue-use differences among taxa in North America vs. Europe in the context of these climatic patterns, it is clear that this stark contrast must be better accounted for in understanding the evolutionary histories and ecological trajectories of the flora of these two continents. For any trait under selection, there must be sufficient selection pressure to drive the evolution of a trait (). Our results suggest that the recent magnitude of climate variation in Europe may be insufficient to drive the evolution of phenological sensitivity to climate cues. Additionally, the lack of correlations we found between spatial and temporal climate variability in Europe could also suggest that the axes of variability may be muting selection. There is a known interaction of these forces in some papers that Lizzie sent to Faith, so maybe we can cite them here. While previous work has suggested that climate variability drives cue use differences between North America and Europe, the absence of a relationship between climate variability and cue use we found in our European data subset, combined with the weaker sensitivity to secondary cues, suggests a slightly different formulation. Our work suggests that climate variability may drive cue use only in North America where variation is sufficiently high to drive selection and not

in Europe where variation is more limited.

While phenological data collected across Europe and North America are often utilized in tandem to test basic evolutionary and ecological theories, our finding supports the assertion of a growing number of researchers that given the differences in land use and geological history and contemporary and predicted climate change, that treating the flora of these two regions as discrete units may facilitate more nuanced understanding and precise predictions for temperate forest ecology (I actually don't know if this is true).

Alternative hypotheses

A major implication of our findings is the field of phenology must continue to expand the range of hypotheses we test and consider regarding the evolution of phenological cues. Phenology should continue to draw from studies of paleoclimate, biogeography, evolutionary ecology and community ecology. There is a rich literature predicting that phenological cue differences among species may be the product of historic climate legacies (), strong phylogenetic constraints () or driven by community processes of phenological assembly like competition, niche theory (). It is likely all of these factors along with the bioclimatic drivers we tested above drive selection on phenology and the the selection strength differs across time and space. Therefore, as we continue to gather more data on phenological cue use patterns for a more species, these hypotheses must be rigorously tested alongside the bioclimatic ones we address here.

Additionally, while we found that species level variation in cue use was higher than population level variation in our data, this finding was based on a limited subset of data because studies across many populations are rare. Further we were unable to evaluate the level of local adaptation in chilling responses due to the way chilling treatments are most commonly applied. Weinberger co varies. There is a live debate surrounding the degree to which woody plant phenology is driven by local adaptation (), and phenological studies that contracts the responses of multiple populations are needed to understand these within species patterns. Importantly, when while comparing the variation in population and species level phenological responses, we found that study effect to be significantly greater than either of these two axes of biological variation. Maybe briefly elude to Zohner results here? but could cut if the new stv results are great.

Increasing the geographic and taxonomic breadth of phenological cue experiments is critical to understanding the evolution of phenological cues, and predicting how these interspecific

differences in cues will impact forest ecology with global change. In Both North America and Europe, the ranges of the species in our study we highly overlapping (make a mappy figure). It is possible that the influence of climate in range of species on differences in phenological cue use would be more pronounced for species with more discrete ranges (ie west vs. east coast of North America), but there is not currently enough taxonomic breadth in phenology to assess this. Further

In this study we found limited support for the assertion that the climate variables species experiences across their geographic ranges shape the relative reliance of forcing, chilling and photoperiod cues for spring phenology. Our results suggest that climate variability may drive cue use pattern only when it is sufficiently high, like in contemporary North America. These results suggests that future studies of phenological cue use would a holistic integration of these bioclimatic hypotheses with phylogenetic, functional trait, and climatic legacy hypotheses to fully understand the evolution of phenological cues in woody plants, and how cue use patterns will impact species performance in the face of global change at across multiple spatial and temporal scales.

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Figures

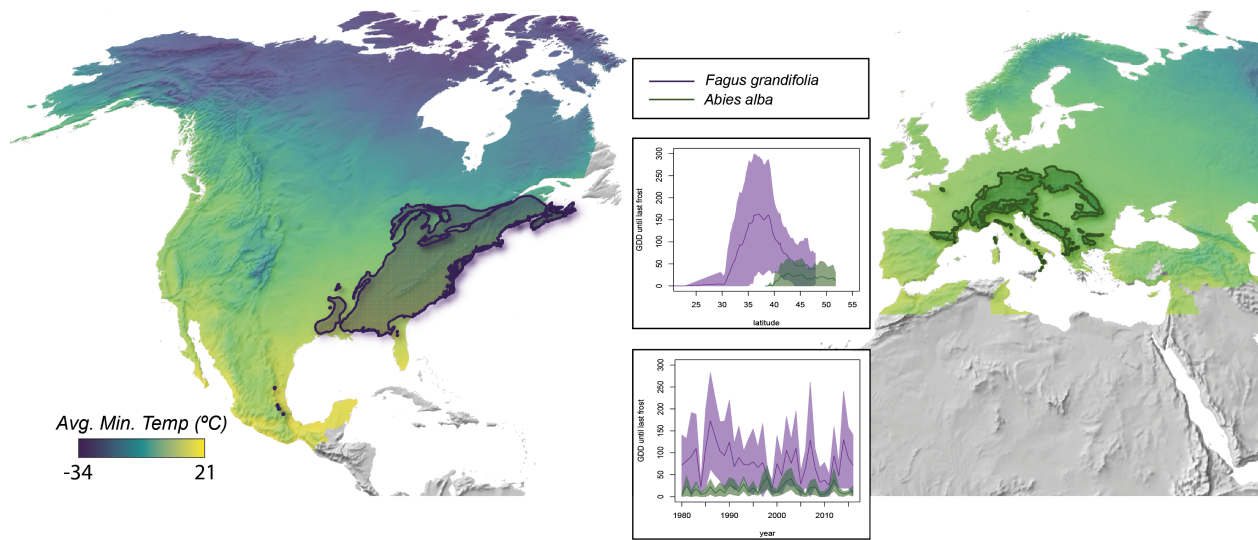


Figure 1: .

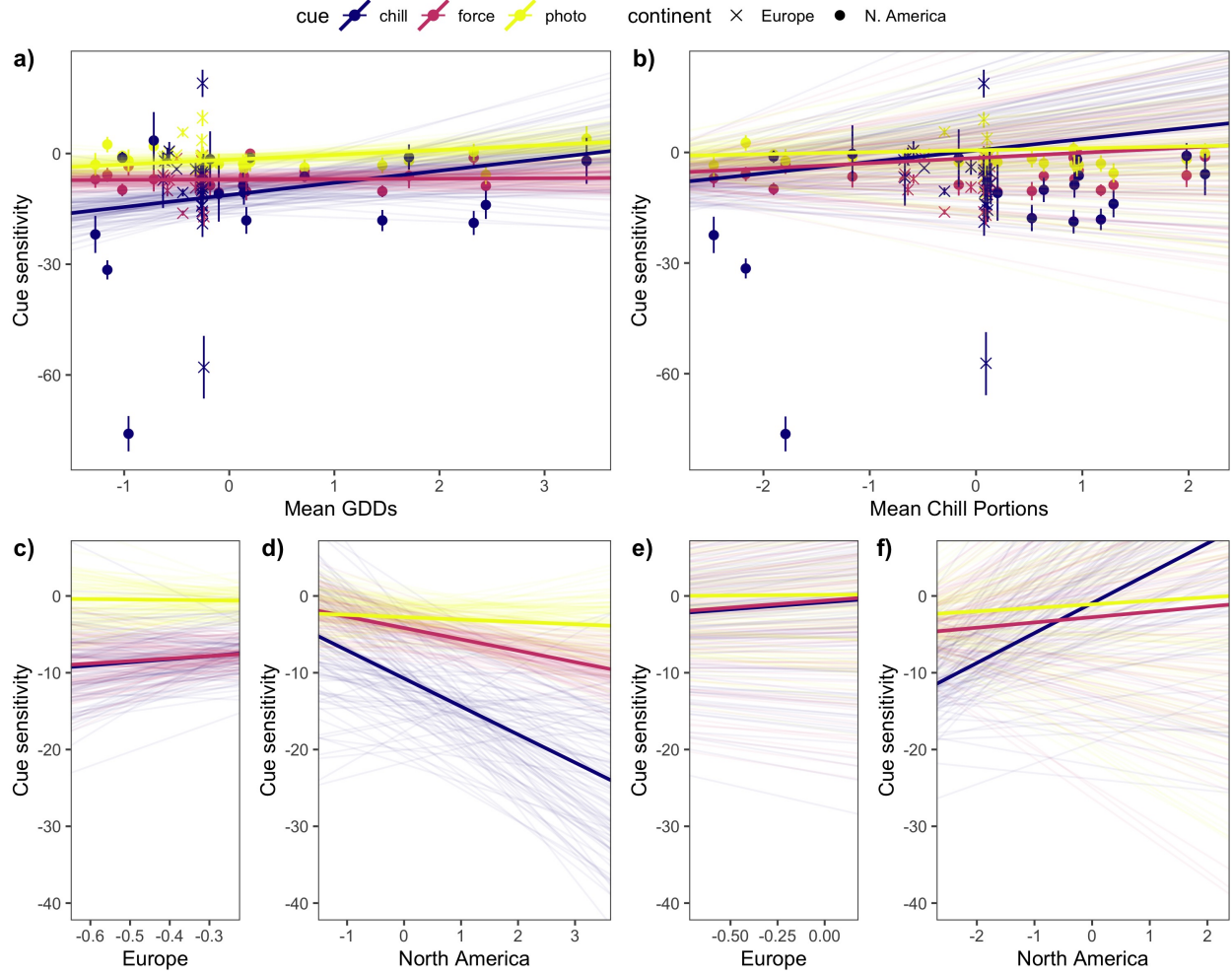


Figure 2: The effects of climate intensives on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of mean GDDs on cue sensitivity for all 40 species in the study and b) depicts effects of chilling on cue sensitivity. All values on the x axis are standardized with zscoring for comparison across plots. The thick, bolded lines indicated the mean estimates of the effect of the climate variables on cue sensitivity estimates and the thinner lines represent 100 random draws from the posterior distribution of these estimates to characterize uncertainty. c) and d) depict the relationships between mean GDD and cue sensitivity and e) and f) the relationships between mean chilling and cue sensitivity for models run on only North American species or European species respectively.

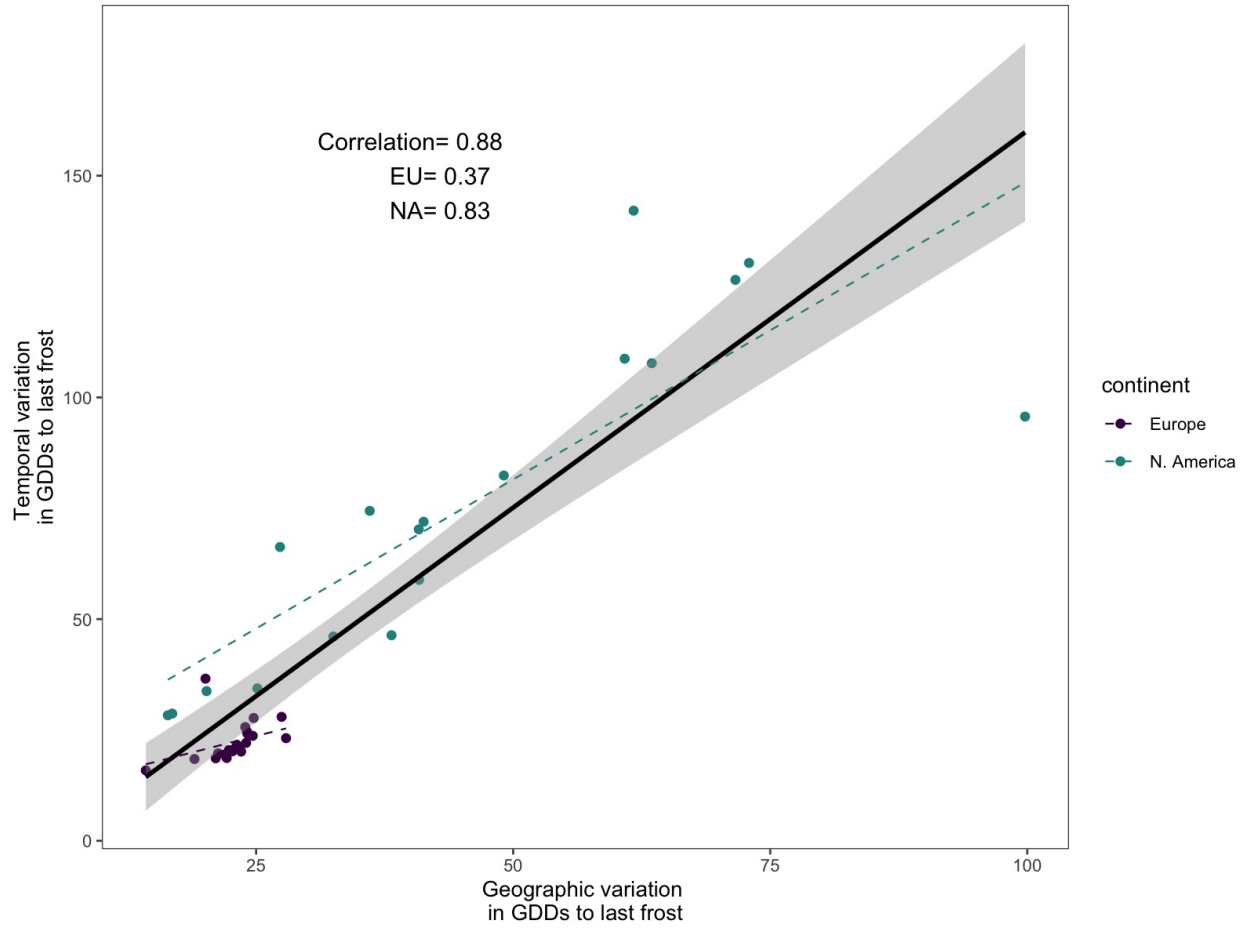


Figure 3: Corelations between spatio-temporal axes of climate variation and intesities in the full data set and across North American and European species ranges. a) and b) depicts correlation between inter-annual variation in growing degrees to last frost and mean growing degree days and mean levels of chilling in range respectively. c) and d) depicts correlation between interannual variation in mean spring temperature (STV) and mean growing degree days and mean levels of chilling in range respectively. e) demonstrate correlations between temporal and spatial inter-annual variation in growing degrees to last frost. f) and g) show the correlations between temporal and spatial variation in GDDs to last frost and STV respectively and h) the correlations between variation in GDDs to last frost and mean number of GDDs to last frost.

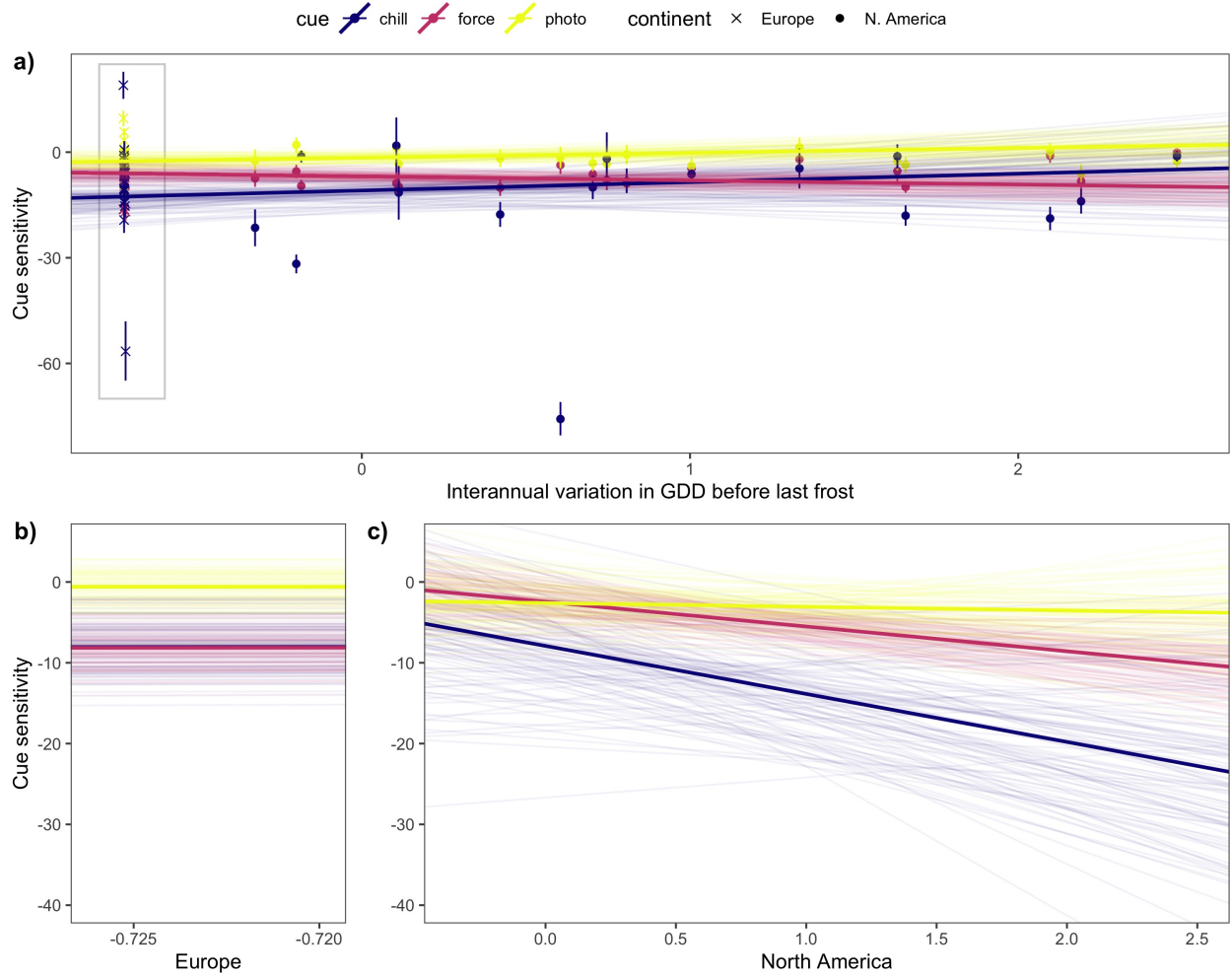


Figure 4: The effects of two measures of spring climate variability on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of variability in number of growing degree days to last frost on cue sensitivity for all 40 species in the study and b) depicts effects of interannual mean spring temperature variation (STV) on cue sensitivity. All values on the x axis are standardized with zscoring for comparison across plots. The thick, bolded lines indicated the mean estimates of the effect of the climate variables on cue sensitivity estimates and the thinner lines represent 100 random draws from the posterior distribution of these estimates to characterize uncertainty. c) and d) depict the relationships between variation in GDDs to last frost and cue sensitivity and e) and f) the relationships between STV and cue sensitivity for models run on only North American species or European species respectively.

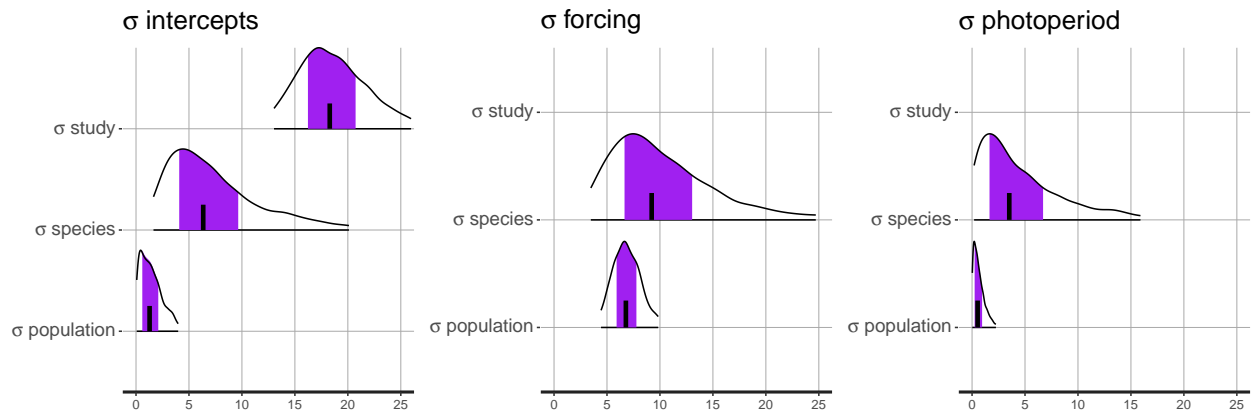


Figure 5: Interspecific variation exceeds intraspecific. Maybe Cat should write this?

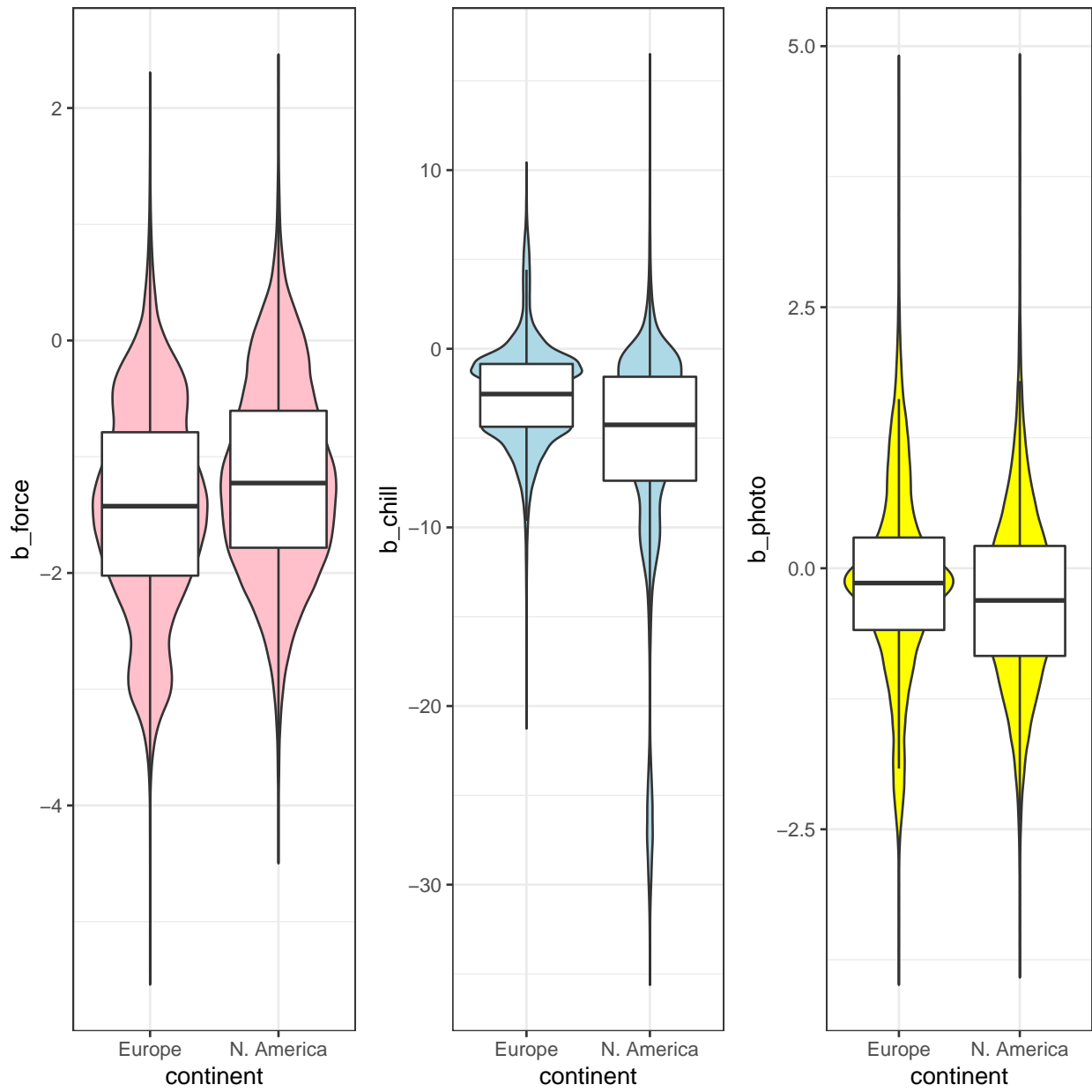


Figure 6: Secondary cues are stronger in North America. Need to check this using new models.