

₁ Continental divides: Spring climate variability shapes
₂ the phenological cue strength of woody species in
₃ temperate North America, not Europe

₄ or

₅ Spring climate stability shapes phenological cue
₆ sensitivities of temperate forest in North America but
₇ not Europe

₈ or

₉ Limited support for range-wide climate patterns shaping
₁₀ phenological cue differences among woody plants of
₁₁ temperate North America and Europe

₁₂ or

₁₃ Other

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¹⁶ **Abstract**

¹⁷ **Introduction**

¹⁸ For woody plants of the temperate zone the phenology, or annual timing, of spring budburst
¹⁹ influences a myriad of ecological processes including patterns of resource allocation (Seiwa
²⁰ and Kikuzawa, 1991), trophic interactions (Memmott et al., 2007) and biogeochemical cycling
²¹ (Piao et al., 2007). Through budburst timing, woody plants balance the advantages of
²² precocious growth resumption for resource gains with the risk of damage from late season frost
²³ (Savage and Cavender-Bares, 2013). To navigate this trade-off, woody plants have evolved
²⁴ complicated networks of sensory organs, hormone signaling, and physiological responses to
²⁵ sense environmental cues; changes in their physical environment, that signal the arrival of
²⁶ appropriate conditions for resuming growth (Visser et al., 2010; ?).

²⁷ Decades of research suggest that warming spring temperatures (forcing), cool winter temper-
²⁸ atures (chilling) and day length (photoperiod) are primary environmental cues utilized by
²⁹ woody plants to determine the timing of spring phenological events Ettinger et al. (2020);
³⁰ Forrest and Miller-Rushing (2010). These studies also demonstrate the there are substantial
³¹ cue-use differences among species, with some species relying more heavily on some cues over
³² others (Laube et al., 2014; ?). As anthropogenic climate change has already driven shifts in
³³ spring phenology (Menzel et al., 2006), identifying these inter-specific differences in cue use
³⁴ has emerged as a major goal of phenological research (Chuine et al., 2002). These differences
³⁵ have strong implications for both predicting the rate of phenological shifts as the climate
³⁶ continues to warm (?), and anticipating the ecological consequences of these shifts (Cleland
³⁷ et al., 2012).

³⁸ Climate is the major selective force on both species' geographic ranges (Morin and Lechow-
³⁹ icz, 2011) and their phenology (Savage and Cavender-Bares, 2013), and therefore, it is widely
⁴⁰ assumed that phenological cue-use differences among species reflect the climate of their re-
⁴¹ spective ranges (Zohner et al., 2017; Silvestro et al., 2019). That is, a species' relative reliance
⁴² on forcing, chilling and photoperiod should be shaped by the unique environmental conditions
⁴³ across a species' geographic range.

⁴⁴ Despite this intuitive link between climate and cues, direct tests of this assumption are
⁴⁵ rare (but see (Zohner et al., 2017)). With the recent quantification of cue-use differences
⁴⁶ of many species (Ettinger et al., 2020) and the accessibility of high resolution climate data
⁴⁷ it is now possible to rigorously test this theory with data. Below, we briefly outline two

⁴⁸ hypotheses about the relationship between phenological cue-use and species' climatic range
⁴⁹ characteristics. We then test these predictions using Bayesian models for a large suite of
⁵⁰ temperate woody species from North America and Europe.

⁵¹ 0.1 Climate intensity hypothesis

⁵² One hypothesis for the evolution of cue-use differences across species is that species utilize
⁵³ the climate cues to which they have the most exposure. Simply stated, there should be a
⁵⁴ positive correlation between the amount or intensity of a cue across a species' range and the
⁵⁵ species phenological sensitivity to that cue. This hypothesis predicts that species with a)
⁵⁶ high numbers growing degree days in their range should have stronger forcing cues and b)
⁵⁷ higher amount of chilling should have stronger chilling cues.

⁵⁸ 0.2 Climate variability hypothesis

⁵⁹ Current understanding of the evolution of phenological cues assume that forcing is the pre-
⁶⁰ dominant cue. In this framework, a secondary reliance on photoperiod and/or chilling cues
⁶¹ evolve when forcing alone is not a reliable cue of safe growing condition (Körner and Basler,
⁶² 2010). Forcing is an unreliable cue when temperatures unstable in the spring time. The
⁶³ climate variability hypothesis predicts species with high variation in spring temperature in
⁶⁴ there range should evolve a stronger response to all three cues, especially chilling and or
⁶⁵ photoperiod (Wang et al., 2014; Muffler et al., 2016).

⁶⁶ **I want to move the following paragraph to de-emphasize this point. I am thinking**
⁶⁷ **maybe somewhere in the methods.** However, a major hurdle to robustly testing this
⁶⁸ hypothesis is that, when considered in the context of a species' geographic range, spring
⁶⁹ temperature variation occurs on multiple temporal and spatial scale. Phenology may be
⁷⁰ shaped by intra-annual temperature variation (e.g. frequency of late season frost, diurnal
⁷¹ temperature functions), inter-annual variation (e.g. annual mean temperatures) and the
⁷² interaction between them (e.g. inter-annual variation in last season frost episodes). Further,
⁷³ each of the level of variation be quite different across a species range, suggesting geographic
⁷⁴ variation with the range must also be accounted for. Any of these level of variation could
⁷⁵ itself drive selection for secondary cue usage (photoperiod/chilling), and it is unclear how
⁷⁶ they interact or which is most important (Zagmajster et al., 2014). Key to testing the
⁷⁷ climate variability hypotheses is to first characterize relationships between spring temperature

78 variation at multiple spatio-temporal scales.

79 An implicit assumption of the previously stated hypotheses is that among species cue-use
80 variation is higher than within species (IE cue use is “conserved” at the species level). If
81 rather, cue use patterns are locally adapted, while climate intensity and climate variability
82 may still drive cue-use patterns at the population level, it would be difficult to detect con-
83 sistent patterns across a species full geographic range. There is not yet a strong consensus
84 about to what degree cue-use is locally adapted and it likely varies between phenophases and
85 organisms (Vitasse et al., 2013; ?; ?). As such, any analysis considering species ranges and
86 cue use must account for intra-specific differences as well.

87 We leveraged over 50 years worth of phenology experiments in the OSPREE database
88 (Wolkovich et al., 2019) and climate data collected across the ranges of temperate woody
89 species in North America and Europe to test these major climate-cue use hypotheses. We
90 used a Bayesian hierarchical approach to jointly fit models estimating of forcing, chilling
91 and photoperiod sensitivity for each species and the effects of several dimensions of climate
92 intensity and variability in the species ranges on these estimates. Then for a subset of well
93 represented species in our dataset, we modeled the among and within species variation in
94 cue use to quantify the relative strength of local adaptation of pattern of phenological cue
95 use. With this approach we 1) clarify the relationships between climatic variability across
96 multiple scales of spatio-temporality, 2) identify the climate drivers that are more and less
97 likely to drive selection on phenological cues and 3) compare variation in cue-use among
98 and within species and between temperate Europe and North America. Our interrogation of
99 these relationships between climate and cue use not only elucidates the evolutionary drivers
100 of phenological cues, but offers new insights regarding implications of climate change as both
101 species’ ranges and phenology continue to shift with warming.

102 Methods

103 OSPREE database

104 To estimate phenological responses to chilling, forcing and photoperiod we used data from the
105 Observed Spring Phenology Responses in Experimental Environments (OSPREE) database
106 (Wolkovich et al., 2019). This database aims to include data from all published studies of
107 experiments on woody plant responses to chilling, forcing and photoperiod cues, as described
108 in Ettinger et al. (2020). Here we use a subset of data from an updated version of the

¹⁰⁹ database containing all papers found in literature searches through June 2019, selecting
¹¹⁰ species for which we could reliably estimate cue responses.

¹¹¹ Estimates of phenological cues (i.e., change in days of an event per change in level of chilling,
¹¹² forcing or photoperiod) can vary strongly due to study location and methodological differ-
¹¹³ ences (CITES). For example, many studies often include only one—often extreme—level of a
¹¹⁴ cue, such as a photoperiod of 24 hours or very low chilling, and thus will provide estimated
¹¹⁵ responses to the manipulated cues (e.g., forcing) relevant only in those extremes. [Some
¹¹⁶ statistical methods can estimate responses across such data, but they will estimate cue re-
¹¹⁷ sponds as more similar across all species than they likely are (see Ettinger et al., 2020, for
¹¹⁸ example), making the type of inter-specific comparisons we were interested in here difficult.]
¹¹⁹ As such, we included species that where: 1) included in two or more studies, 2) we had
¹²⁰ data for at least two levels of each cue (chilling, forcing and photoperiod; but we excluded
¹²¹ species that only had field chilling), and 3) could obtain published range maps (see below).
¹²² [While this approach limited our total species number, it provided more reliable estimates of
¹²³ phenological cues.]

¹²⁴ Species' range characteristics

¹²⁵ We extracted climate data from daily gridded meteorological datasets for both Europe and
¹²⁶ North America. For Europe, we extracted minimum and maximum daily temperatures
¹²⁷ 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
¹²⁸ 2016. Specifically, we used version 17 at a resolution of 0.5 latitudinal degrees. For North
¹²⁹ America, we extracted minimum and maximum daily temperatures from Justin Sheffield's
¹³⁰ Princeton Global Forcing dataset (<http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/>)
¹³¹ for the same period. We used version v3 at a resolution of 0.25 latitudinal degrees.

¹³² For 22 European and 16 North American tree species, we obtained published distributional
¹³³ range maps in shapefile format. European species ranges were downloaded from <http://www.sciedirect.com/science/article/pii/S2352340917301981?via%3Dihub#ec-research-data>
¹³⁴ (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 cli-
¹³⁵ mate data corresponding to all grid cells contained within the range.

¹³⁶ We used minimum and maximum daily temperatures within species ranges were then used to
¹³⁷ compute Growing Degree Days (GDD), Growing Degree Days until the last frost (GDDlf) and

141 Spring Temperature Variability (STV). GDD was calculated as the summed temperatures
 142 above 10C recorded from January 1st until May 31st. GDDlf was calculated as GDD but
 143 instead of summing temperatures above a threshold until a fixed date, the sum was performed
 144 until the date at which the latest minimum temperature below -5C was recorded. STV was
 145 calculated as the standard deviation of mean minimum temperature **10th Oct - 28Feb**
 146 (**should be march to may**). (Zohner et al., 2017). **Some notes: can we add a sentence**
 147 **about temporal vs. spatial variation here? Also, we calculated Chill portions so**
 148 **we should include that here as well.**

149 Statistical analysis

150 Climate cue-use relationships

151 To assess the relationships between range-wide climate variables and phenological sensitiv-
 152 ity to forcing, chilling and photoperiod we fit Bayesian hierarchical phenology using a joint
 153 modeling framework in which parameter estimates for each cue response are influenced by a
 154 range-wide climate variable sub-model (eek! that's hard to describe. **Does someone else**
 155 **want to take a stab at describing what a joint model is?**. A first attempt of at the
 156 model formulation is written below:

157

$$\hat{y}_{pheno,i} = \alpha_{pheno,sp[i]} + \beta_{forcing_{sp[i]}} * F_i + \beta_{chilling_{sp[i]}} * C_i + \beta_{photoperiod_{sp[i]}} * P_i$$

where:

158

$$\begin{aligned}
 \beta_{forcing_{sp}} &= \alpha_{forcing_{sp}} + \beta_{traitxpheno} * Variable_{climate} \\
 \beta_{chilling_{sp}} &= \alpha_{chilling_{sp}} + \beta_{traitxpheno} * Variable_{climate} \\
 \beta_{photoperiod_{sp}} &= \alpha_{photoperiod_{sp}} + \beta_{traitxpheno} * Variable_{climate} \\
 \alpha_{pheno,sp} &\sim N(\mu_{\alpha,pheno}, \sigma_{\alpha,pheno}) \\
 \alpha_{forcing_{sp}} &\sim N(\mu_{\alpha,forcing}, \sigma_{\alpha,forcing}) \\
 \alpha_{chilling_{sp}} &\sim N(\mu_{\alpha,chilling}, \sigma_{\alpha,chilling}) \\
 \alpha_{photoperiod_{sp}} &\sim N(\mu_{\alpha,photoperiod}, \sigma_{\alpha,photoperiod}) \\
 y_{pheno} &\sim N(\hat{y}_{pheno}, \sigma^2_{y,pheno})
 \end{aligned}$$

159 For each climate variable of interest, we fit a model with all species and then, to bet-
160 ter evaluate the differences among North American and European taxa, additional mod-
161 els for species from each continent separately. All versions of this model were fit in Stan
162 (?)www.mc-stan.org) using weakly informative priors. We ran each model on 4 chain with
163 4000 iterations, with a 3000 iteration warm-up, for a total of 4000 sampling iterations per
164 parameter.

165 **Intra vs. interspecific models**

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

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

175

$$\begin{aligned} y &\sim \text{normal}(\alpha_0 + \alpha_{study[i]} + \alpha_{sp[pop[i]]} + \beta_{forcing_{sp[pop[i]]}} + \beta_{photoperiod_{sp[pop[i]]}} + \epsilon[i]) \\ \epsilon_i &\sim \text{normal}(0, \sigma_y) \end{aligned}$$

176

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

177

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

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

183 Results

184 Coherence of spatio-temporal spring climate variability

185 I'd like to remove this as a full on "result" and either put in in the methods
 186 sections to explain why we use one version of variation or elaborate on it in the
 187 suppliment but I am not so sure The spatio-temporal coherence of spring climate vari-
 188 ability and intensity varied across continent and scales. Generally climate intensity (mean
 189 GDDs in range mean Chill Portions in range and Mean GDDs to last frost) were well cor-
 190 related with climate variability (Fig. 3) though strong differences can be observed between
 191 North American and Europe.

192 Climate intensity and cue use

193 Overall, the mean forcing (GDDs) and chilling (Chill Portions) had weak effects on estimated
 194 cue-use. In our full species models mean GDDs and had a weakly negative or neutral associa-
 195 tion with cue strength (GDD:Chill=X ,GDD:Force=Y, GDD:Photo=Z, (Fig. 2 a),b))). The

196 general sign of these relationships persisted in the continent subset models (Fig. 2 d),e,f))
197 with the exception of the relationship between mean GDDs and chilling for North American
198 species which became positive (mean= Z, (Fig. 2 c)). Generally, there was high uncertainty
199 around these estimates.

200 Climate variation and cue use

201 In our full models, variation in growing degree days before the last frost of the season was
202 weakly positively associated with forcing and photoperiod sensitivity and negatively asso-
203 ciated with chilling sensitivity (Fig. 4a))). However, our continent subset models shows
204 different effects. The effect of variation in GDDs to last frost (GDDlf) is poorly estimated
205 in the European data subset, and has almost no effect on cue use over the narrow range of
206 spring climate variation present in Europe (Fig. 4b). In the North America subset, vari-
207 ation in GDDlf increases sensitivity in all three cues (Chilling:X Forcing:Y Photoperiod:Z,
208 (Fig. 4c))) suggesting there may be support for the climate variation hypotheses in North
209 America where spring climate variation can be extreme. We found qualitatively similar con-
210 tinental patterns in the relationships between cue-use and climate variability using STV as
211 an alternative metric inter-annual variation (see Supp).

212 Cue use in North America and Europe

213 We found that the strength of secondary cue use (chilling and photoperiod) was higher in
214 North America than in Europe (Chilling: NA-X, EU-Y, Photoperiod NA-X, EU-Y, Fig.6),
215 while forcing sensitivity was higher in Europe than North America (NA-X, EU-Y). This
216 result is consistent with the observation that the spring climate of North America is much
217 less stable than Europe and our finding that the climate-cue use hypotheses appear to be
218 better supported in North America.

219 Local adaptation of phenological cues

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

²²⁴ **Discussion**

²²⁵ **Hypotheses of bioclimatic cue use**

²²⁶ Similar to previous studies, we found stronger support for the climate variability hypothesis
²²⁷ than the climate intensity hypothesis (Zohner et al., 2017). While, as predicted by the
²²⁸ climate intensity hypothesis, mean growing degree days in the range were positively associated
²²⁹ with forcing sensitivity in North America, chilling sensitivity has no clear relationship with
²³⁰ mean chilling in the range for species on either continent (Fig 2e,f). Further, there is high
²³¹ uncertainty surrounding the estimates in our climate intensity models, suggesting climate
²³² intensity is a poor predictor of phenological cue-use.

²³³ By contrast, climate variability was associated with increased forcing, chilling and photope-
²³⁴ riod sensitivities in North American species (Fig 4,c) as predicted by the climate variability
²³⁵ hypothesis. Interestingly, there was virtually no relationship between climate variability and
²³⁶ cue-use in European species (Fig 4,b). We recovered these contrasting patterns among con-
²³⁷ tinents using multiple metrics of climate variability (see Fig. S??, and “STV”). We also
²³⁸ found secondary cue use (photoperiod and chilling) sensitivity was higher in North American
²³⁹ taxa than in European ones (Fig. 6). These contrasting biological patterns appear to reflect
²⁴⁰ the strong climatic differences we observed between the continents.

²⁴¹ **Climate patterns in North America and Europe**

²⁴² Our study highlights that patterns of temperature variation and intensity are much stronger
²⁴³ in temperate North America in Europe (Fig. 1). This is a well meteorological phenomenon
²⁴⁴ drive by large local climate pattern like the jet steam and enso and stuff (**say better.**
²⁴⁵ **maybe, Ben can write this paragraph**). Additionally, we found that in North America,
²⁴⁶ there was a strong correlation between temporal and spatial climatic variability across the
²⁴⁷ geographic ranges of the species we studied, while in Europe this correlation was weakly
²⁴⁸ negative.

²⁴⁹ When we consider our biological findings about cue-use differences among taxa in North
²⁵⁰ America vs. Europe in the context these climatic patterns, it is clear that this stark contrast
²⁵¹ must be better accounted for in understanding the evolutionary histories and ecological tra-
²⁵² jectories of the flora of these two continents. For any trait under selection, there must be
²⁵³ sufficient selection pressure to drive the evolution of a trait (). Our results suggest that the

254 recent magnitude of climate variation in Europe may be insufficient to drive the evolution
255 of phenological sensitivity to climate cues. Additionally the lack of correlations we found
256 between spatial and temporal climate variability in Europe could also suggest that the axes
257 of variability could be muting selection. **There is a known interaction of these forces**
258 **in a some papers that Lizzie sent to Faith, so maybe we can explain and cite**
259 **them here.** While previous work has suggested that climate variability drive cue use differ-
260 ences between North America and Europe (Zohner et al., 2017), the absence of a relationship
261 between climate variability and cue use we found in our European data subset, combined
262 with the the weaker sensitivity to secondary cues, suggests a slightly different formulation.
263 Our work suggest that climate variability may drive cue use only in North America where
264 variation is sufficiently high to drive selection and not in Europe where variation is more
265 limited.

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

272 Alternative hypotheses

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

284 Additionally, while we found that species level variation in cue-use was higher than population
285 level variation in our data, this finding was based on a limited subset of data because studies

286 across many populations are rare. Further, we were unable to evaluate the level of local
287 adaptation in chilling responses due to the way chilling treatments are most commonly applied
288 ().**Maybe add a sentence explain why weinberger method doesn't allow for this.**
289 There is a live debate surrounding the degree to which woody plant phenology is driven
290 by local adaptation (), and phenological studies that contracts the responses of multiple
291 populations are needed to understand these within species patterns. Importantly, when
292 while comparing the variation in population and species level phenological responses, we
293 found that study effect to be significantly greater than either of these two axes of biological
294 variation. (Maybe briefly elude to Zohner results here? but could cut if the new STV results
295 are great.)

296 Increasing the geographic and taxonomic breadth of phenological cue experiments is critical
297 to understanding the evolution of phenological cues, and predicting how these inter-specific
298 differences in cues will impact forest ecology with global change. In Both North America
299 and Europe, the ranges of the species in our study we highly overlapping (**To do: make**
300 **a mappy figure for supplement**). It is possible that the influence of climate in range
301 of species on differences in phenological cue use would be more pronounced for species with
302 more discrete ranges (IE west vs. east coast of North America), but there is not currently
303 enough taxonomic breadth in our phenological data to assess this.

304 In this study we found limited support for the assertion that the climate variables that species
305 encounter across their geographic ranges shape the relative reliance on forcing, chilling and
306 photoperiod cues for spring phenology. Our results suggest that climate variability may drive
307 cue use pattern only when it is sufficiently high, like in contemporary North America. These
308 results suggests that future studies of phenological cue-use would benefit from a holistic
309 integration of these bio-climatic hypotheses with phylogenetic, functional trait, and climatic
310 legacy hypotheses to fully understand the evolution of phenological cues in woody plants,
311 and how cue use patterns will impact species performance in the face of global change at
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377 **Figures**

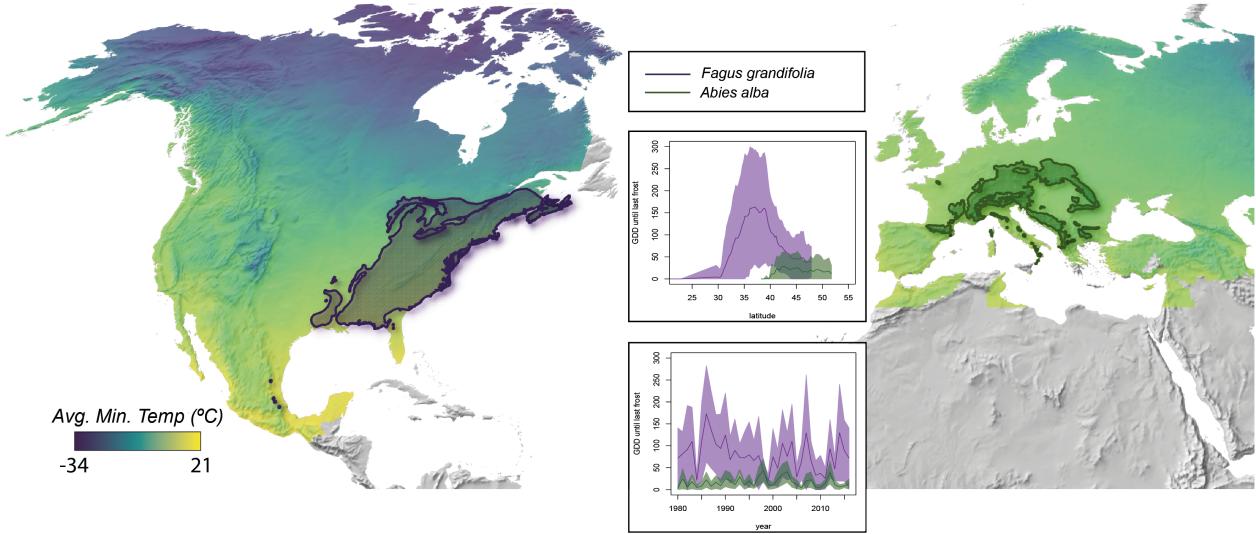


Figure 1: Nacho, do you want to try taking a stab at this caption? I am happy to work on it if you want to start by just jotting a few notes/ideas down

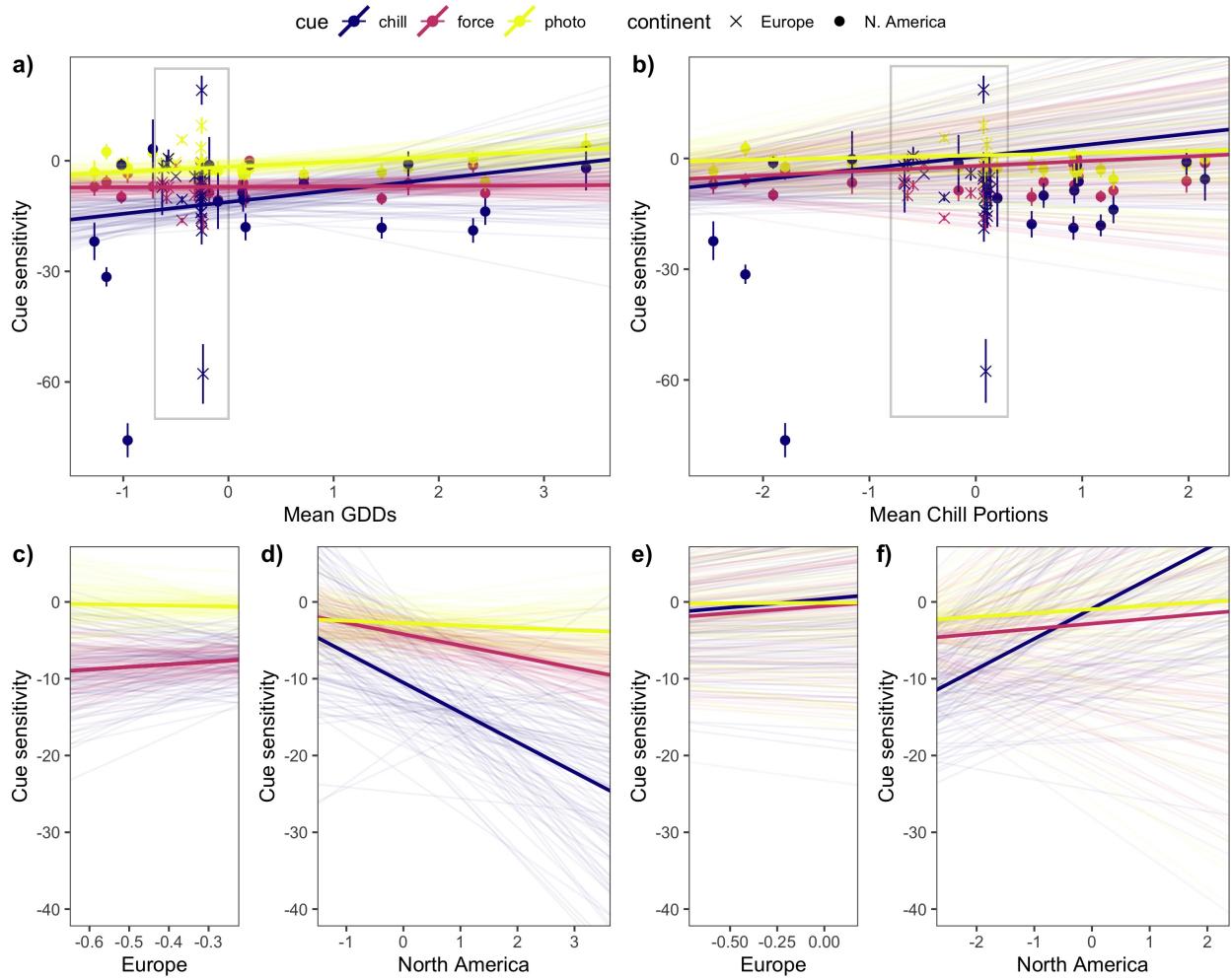


Figure 2: The effects of climate intensives on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of mean GDDs on cue sensitivity for all 40 species in the study and b) depicts effects of chilling on cue sensitivity. All values on the x axis are standardized with zscoring for comparision 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.

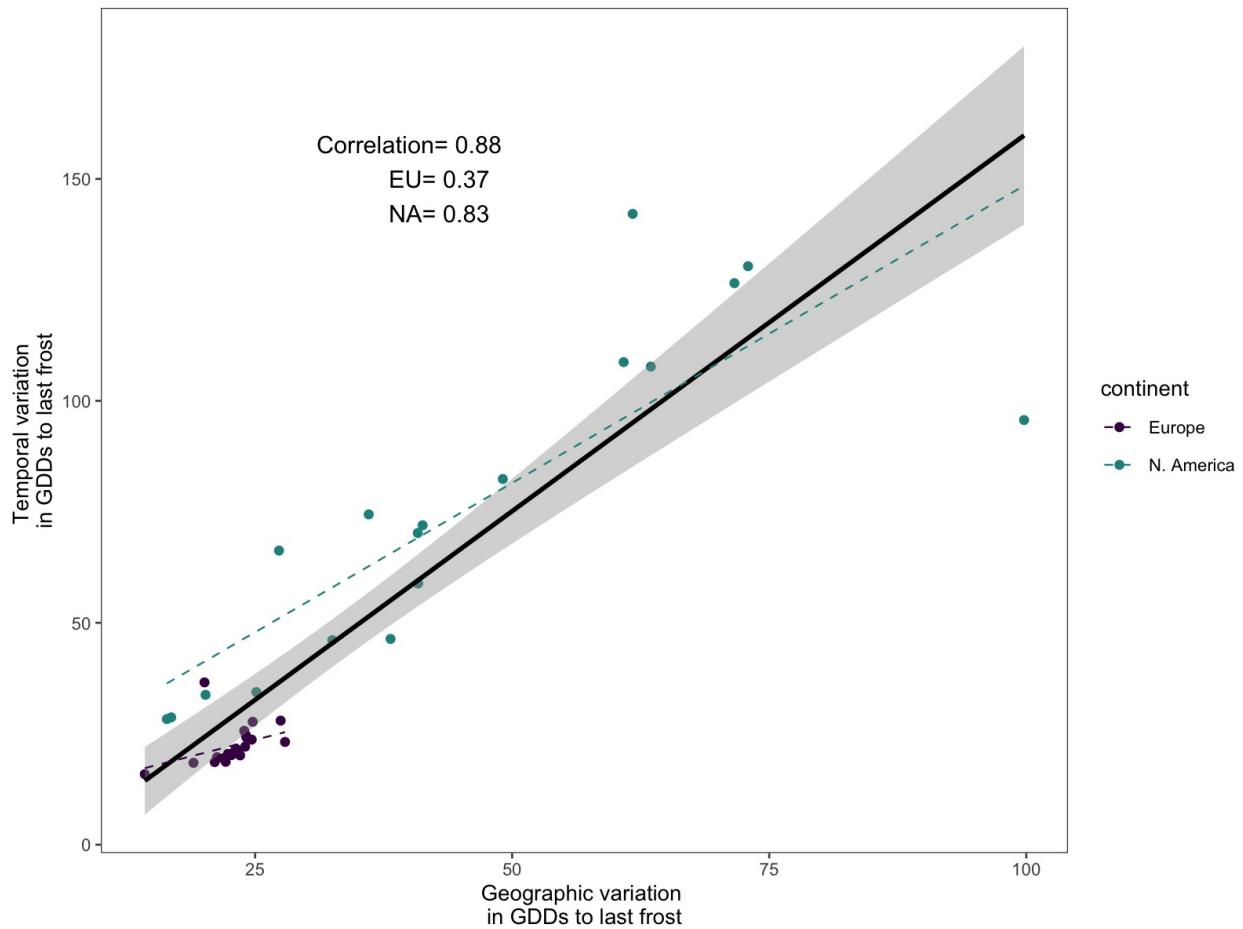


Figure 3: Could we combine this figure with the concept figure? Move it to suppliment. It doesnt' feel like it shoulld be a stand alone Correlations between spatio-temporal axes of climate variation and intensities in the full data set and across North American and European species ranges.

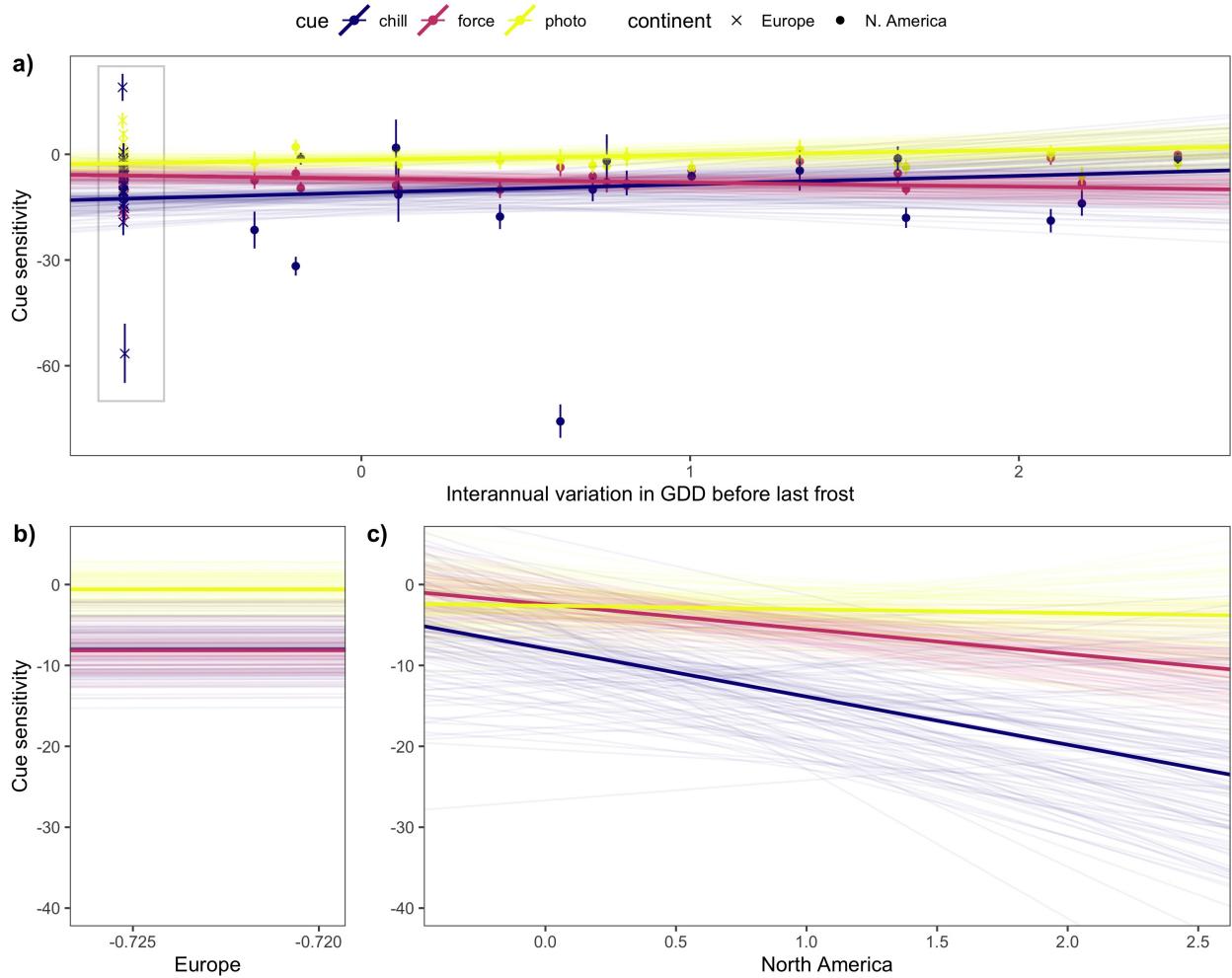


Figure 4: The effects of two measures of spring climate variability on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of variability in number of growing degree days to last frost on cue sensitivity for all 40 species in the 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 comparision 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 distrubrion 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 respectivey.

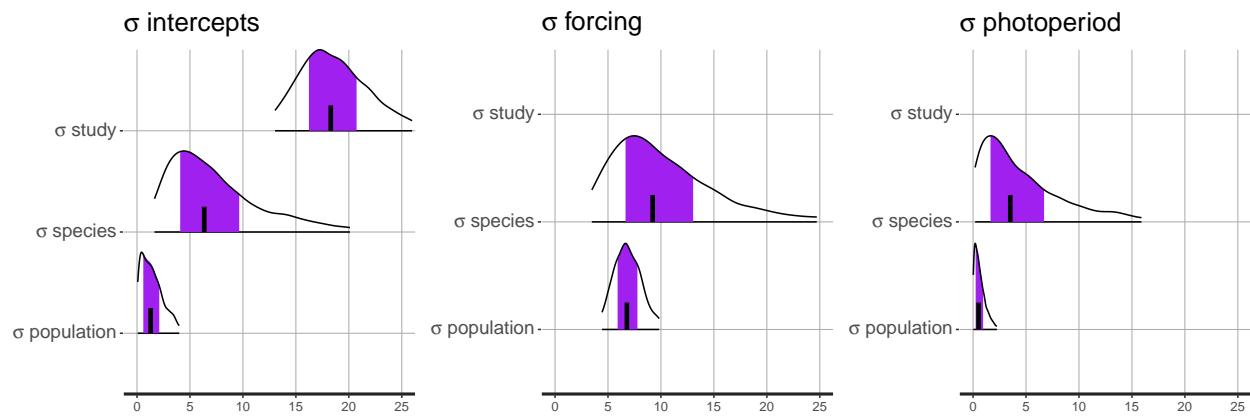


Figure 5: Interspecific variation exceeds intraspecific. Maybe Cat should write this?

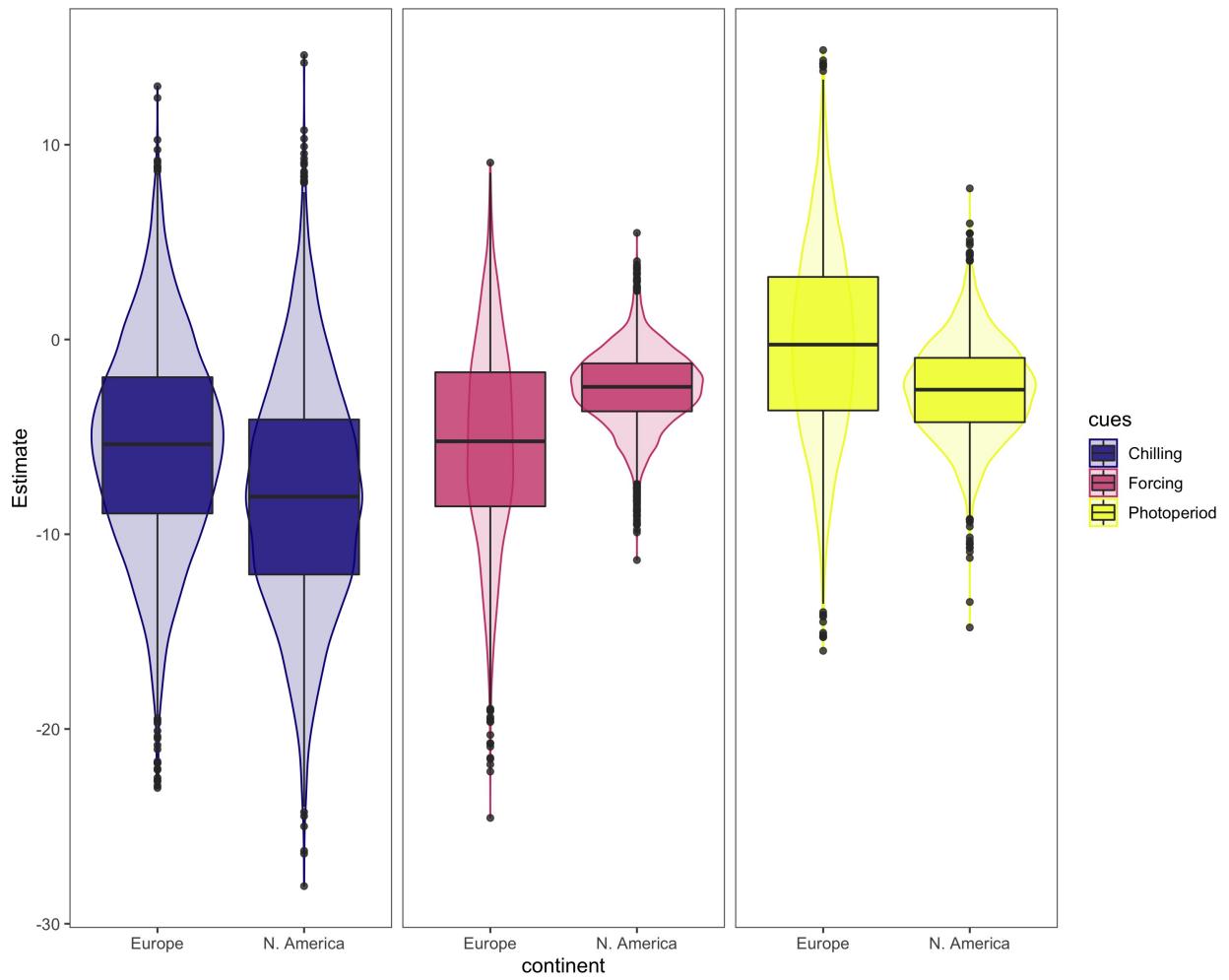


Figure 6: Estimates of phenological sensitivity to chilling, forcing, and photoperiod compared between North American and European taxa.