

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 for should be shaped by the unique environmental con-
⁴³ ditions across a species' geographic range.

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

48 the relationship between phenological cue-use and species' climatic range characteristics. We
49 then test these predictions using Bayesian models for a large suite of temperate woody species
50 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
55 the species phenological sensitivity to that cue. This hypothesis predicts that species with
56 a) high numbers growing degree days in their range should have stronger forcing cues, b)
57 higher amount of chilling should have stronger chilling cues and c) more annual photoperiod
58 variation should have stronger photoperiod cues.

59 0.2 Climate variability hypothesis

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

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

78 climate variability hypotheses is to first characterize relationships between spring temperature
79 variation at multiple spatio-temporal scales.

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

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

103 Methods

104 OSPREE database

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

¹⁰⁹ in Ettinger et al. (2020). Here we use a subset of data from an updated version of the
¹¹⁰ database containing all papers found in literature searches through June 2019, selecting
¹¹¹ species for which we could reliably estimate cue responses.

¹¹² Estimates of phenological cues (i.e., change in days of an event per change in level of chilling,
¹¹³ forcing or photoperiod) can vary strongly due to study location and methodological differ-
¹¹⁴ ences (CITES). For example, many studies often include only one—often extreme—level of a
¹¹⁵ cue, such as a photoperiod of 24 hours or very low chilling, and thus will provide estimated
¹¹⁶ responses to the manipulated cues (e.g., forcing) relevant only in those extremes. [Some
¹¹⁷ statistical methods can estimate responses across such data, but they will estimate cue re-
¹¹⁸ sponds as more similar across all species than they likely are (see Ettinger et al., 2020, for
¹¹⁹ example), making the type of inter-specific comparisons we were interested in here difficult.]
¹²⁰ As such, we included species that where: 1) included in two or more studies, 2) we had
¹²¹ data for at least two levels of each cue (chilling, forcing and photoperiod; but we excluded
¹²² species that only had field chilling), and 3) could obtain published range maps (see below).
¹²³ [While this approach limited our total species number, it provided more reliable estimates of
¹²⁴ phenological cues.]

¹²⁵ Species' range characteristics

¹²⁶ We extracted climate data from daily gridded meteorological datasets for both Europe and
¹²⁷ North America. For Europe, we extracted minimum and maximum daily temperatures
¹²⁸ 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
¹²⁹ 2016. Specifically, we used version 17 at a resolution of 0.5 latitudinal degrees. For North
¹³⁰ America, we extracted minimum and maximum daily temperatures from Justin Sheffield's
¹³¹ Princeton Global Forcing dataset (<http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/>)
¹³² for the same period. We used version v3 at a resolution of 0.25 latitudinal degrees.
¹³³

¹³⁴ For 22 European and 16 North American tree species, we obtained published distributional
¹³⁵ range maps in shapefile format. European species ranges were downloaded from <http://www.sciencedirect.com/science/article/pii/S2352340917301981?via%3Dihub#ec-research-data>
¹³⁶ (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-
¹³⁷ mate data corresponding to all grid cells contained within the range.
¹³⁸

¹³⁹ We used minimum and maximum daily temperatures within species ranges were then used to
¹⁴⁰

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

150 **Statistical analysis**

151 **Climate cue-use relationships**

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

158

159

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

160

where:

161

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

162 For each climate variable of interest, we fit a model with all species and then, to bet-
 163 ter evaluate the differences among North American and European taxa, additional mod-
 164 els for species from each continent separately. All versions of this model were fit in Stan
 165 (?) (www.mc-stan.org) using weakly informative priors. We ran each model on 4 chain with
 166 4000 iterations, with a 3000 iteration warm-up, for a total of 4000 sampling iterations per
 167 parameter.

168 **Intra vs. interspecific models**

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

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

178

$$y \sim normal(\alpha_0 + \alpha_{study[i]} + \alpha_{sp[pop[i]]} + \beta_{forcing_{sp[pop[i]]}} + \beta_{photoperiod_{sp[pop[i]]}} + \epsilon[i])$$

179

180

$$\epsilon_i \sim normal(0, \sigma_y)$$

181

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

182

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

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

188 **Results**

189 **Coherence of spatio-temporal spring climate variability**

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

197 **Climate intensity and cue use**

198 Overall, the mean forcing (GDDs) and chilling (Chill Portions) had weak effects on estimated
199 cue use. In our full species models mean GDDs and had a weakly negative or neutral associa-
200 tion with cue strength (GDD:Chill=X ,GDD:Force=Y, GDD:Photo=Z, (Fig. 2 a),b))). The
201 general sign of these relationships persisted in the continent subset models (Fig. 2 d),e),f))
202 with the exception of the relationship between mean GDDs and chilling for North American
203 species which became positive (mean= Z, (Fig. 2 c)). Generally, there was high uncertainty
204 around these estimates suggesting climate intensity is a poor predictor for cue use.

205 **Climate variation and cue use**

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

217 0.3 Cue use in North America and Europe

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

224 Local adaptation of phenological cues

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

228 Discussion

229 Hypotheses of bioclimatic cue use

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

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

245 Climate patterns in North America and Europe

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

253 When we consider our biological findings about cue-use differences among taxa in North
254 America vs. Europe in the context these climatic patterns, it is clear that this stark contrast
255 must be better accounted for in understanding the evolutionary histories and ecological tra-
256 jectories of the flora of these two continents. For any trait under selection, there must be
257 sufficient selection pressure to drive the evolution of a trait (). Our results suggest that the
258 recent magnitude of climate variation in Europe may be insufficient to drive the evolution
259 of phenological sensitivity to climate cues. Additionally the lack of correlations we found
260 between spatial and temporal climate variability in Europe could also suggest that the axes
261 of variability could be muting selection. **There is a known interaction of these forces**
262 **in a some papers that Lizzie sent to Faith, so maybe we can explain and cite**
263 **them here.** While previous work has suggested that climate variability drive cue use differ-
264 ences between North America and Europe (Zohner et al., 2017), the absence of a relationship
265 between climate variability and cue use we found in our European data subset, combined
266 with the the weaker sensitivity to secondary cues, suggests a slightly different formulation.
267 Our work suggest that climate variability may drive cue use only in North America where
268 variation is sufficiently high to drive selection and not in Europe where variation is more
269 limited.

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

276 Alternative hypotheses

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

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

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

307 In this study we found limited support for the assertion that the climate variables species
308 experiences across their geographic ranges shape the relative reliance of forcing, chilling and
309 photoperiod cues for spring phenology. Our results suggest that climate variability may drive

310 cue use pattern only when it is sufficiently high, like in contemporary North America. These
311 results suggests that future studies of phenological cue use would a holistic integration of these
312 bio-climatic hypotheses with phylogenetic, functional trait, and climatic legacy hypotheses to
313 fully understand the evolution of phenological cues in woody plants, and how cue use patterns
314 will impact species performance in the face of global change at across multiple spatial and
315 temporal scales.

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380 **Figures**

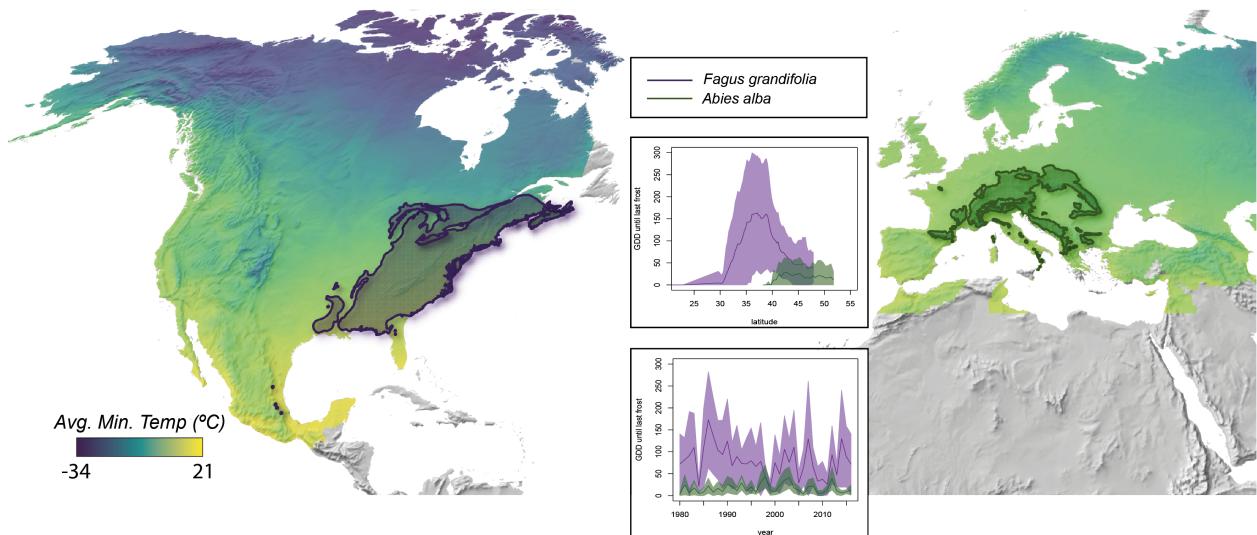


Figure 1: Nacho, do you want to try taking a stab at this caption? I am happy to work on it if you want to start by just jotting a few notes/ideas down

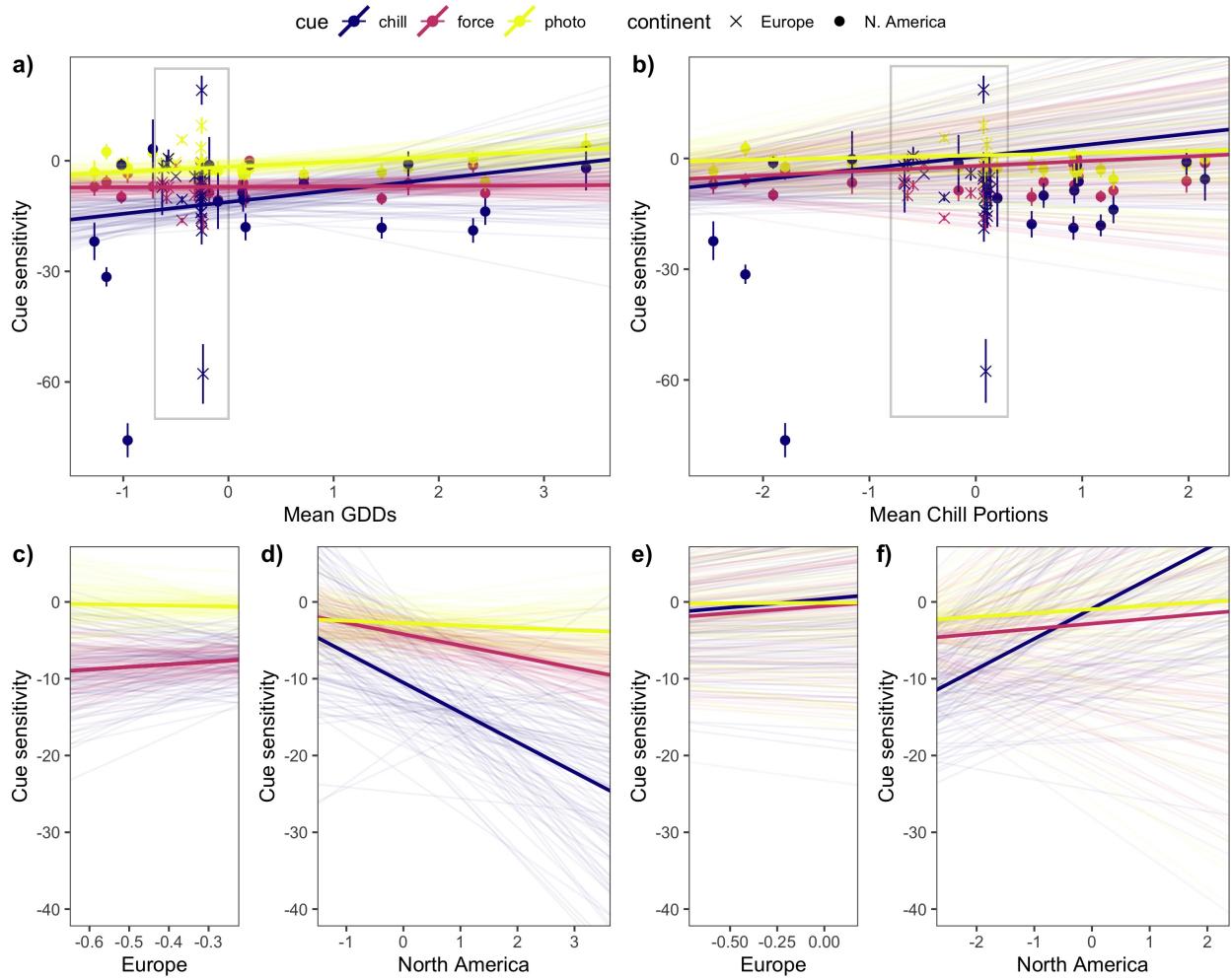


Figure 2: The effects of climate intensives on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of mean GDDs on cue sensitivity for all 40 species in the study and b) depicts effects of chilling on cue sensitivity. All values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

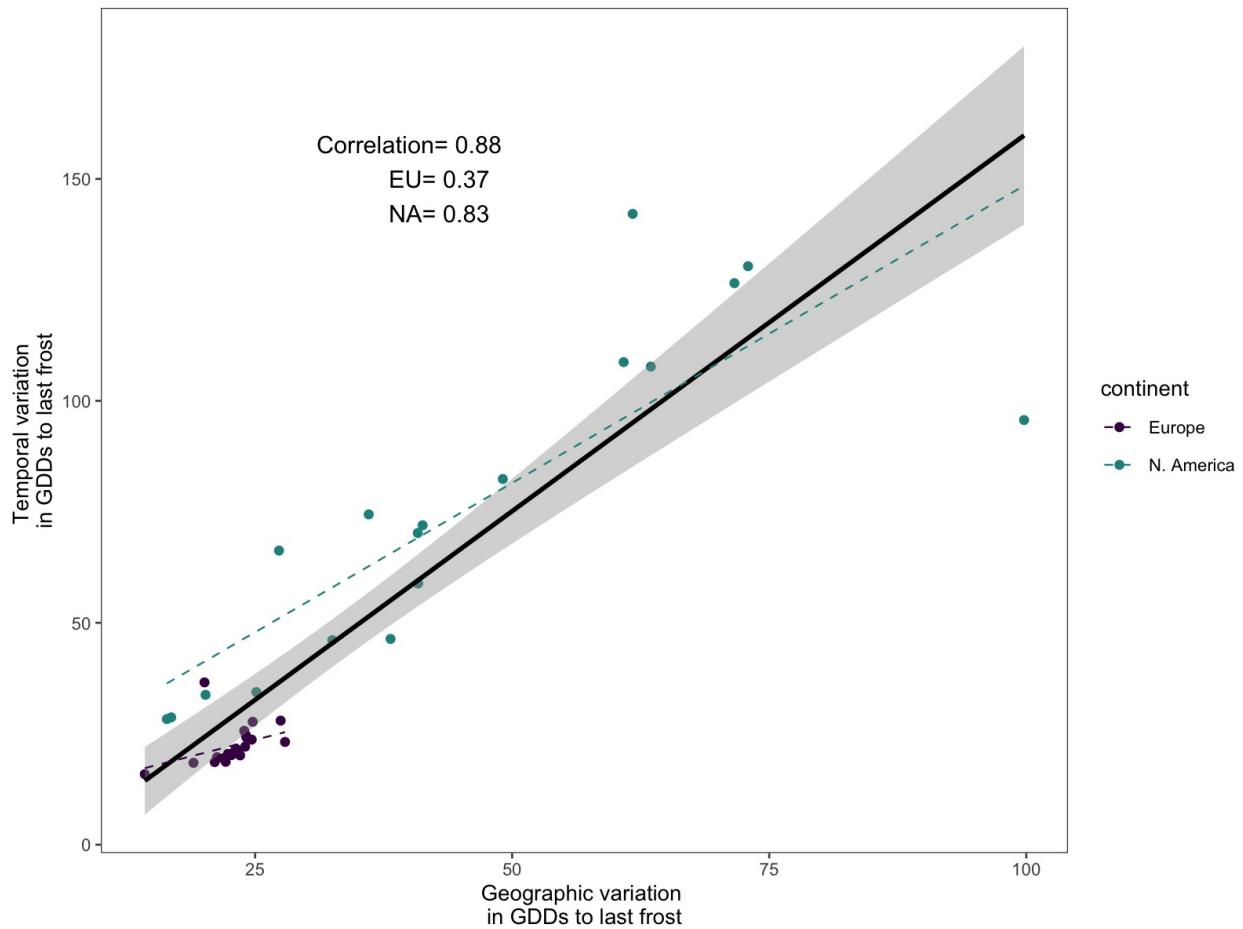


Figure 3: Could we combine this figure with the concept figure? Move it to suppliment. It doesnt' feel like it shoulld be a stand alone Correlations between spatio-temporal axes of climate variation and intensities in the full data set and across North American and European species ranges.

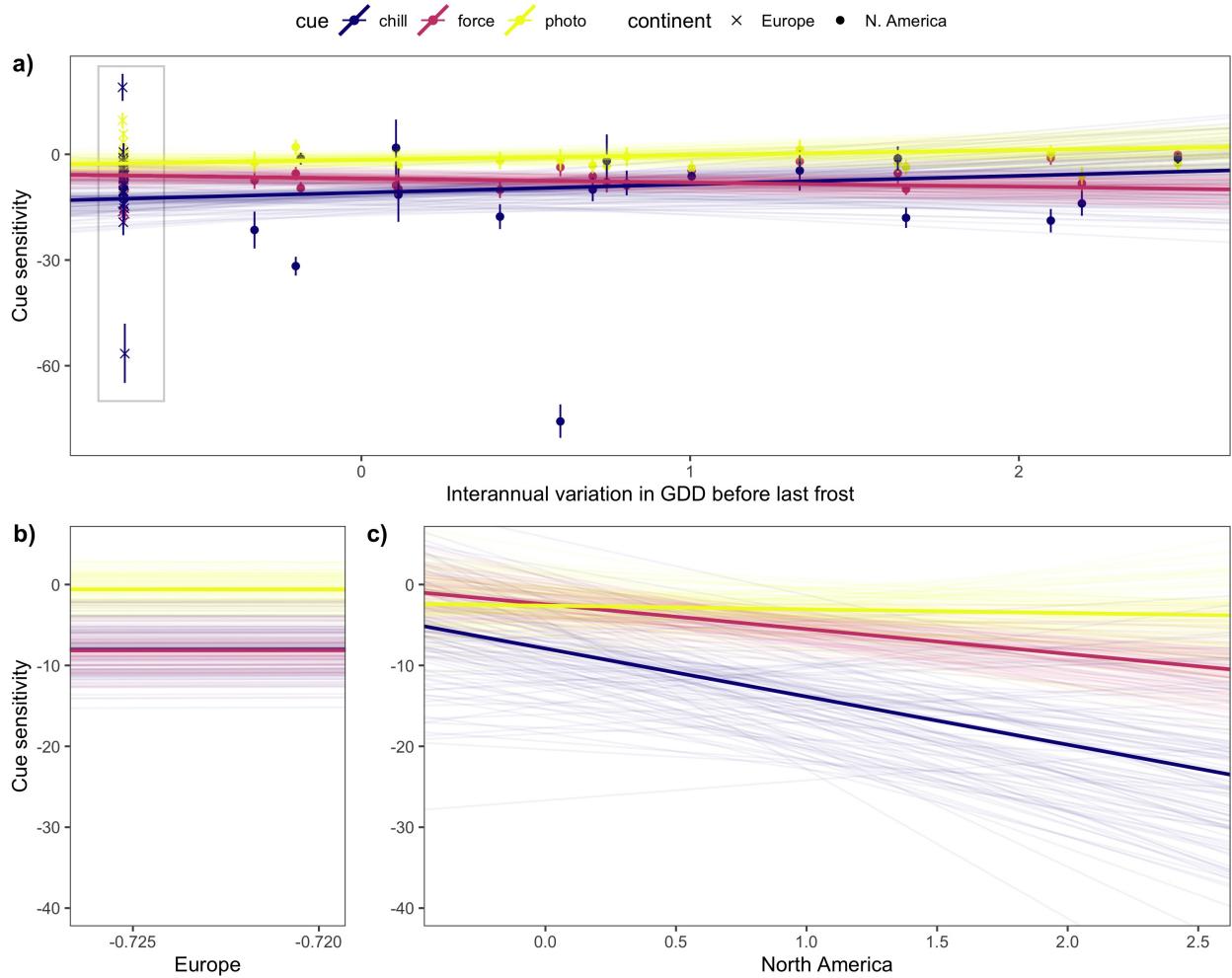


Figure 4: The effects of two measures of spring climate variability on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of variability in number of growing degree days to last frost on cue sensitivity for all 40 species in the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

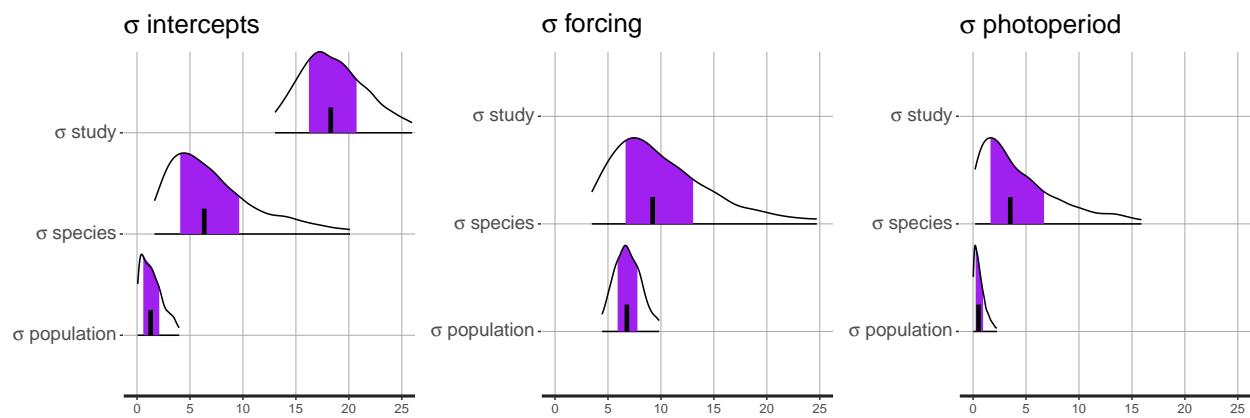


Figure 5: Interspecific variation exceeds intraspecific. Maybe Cat should write this?

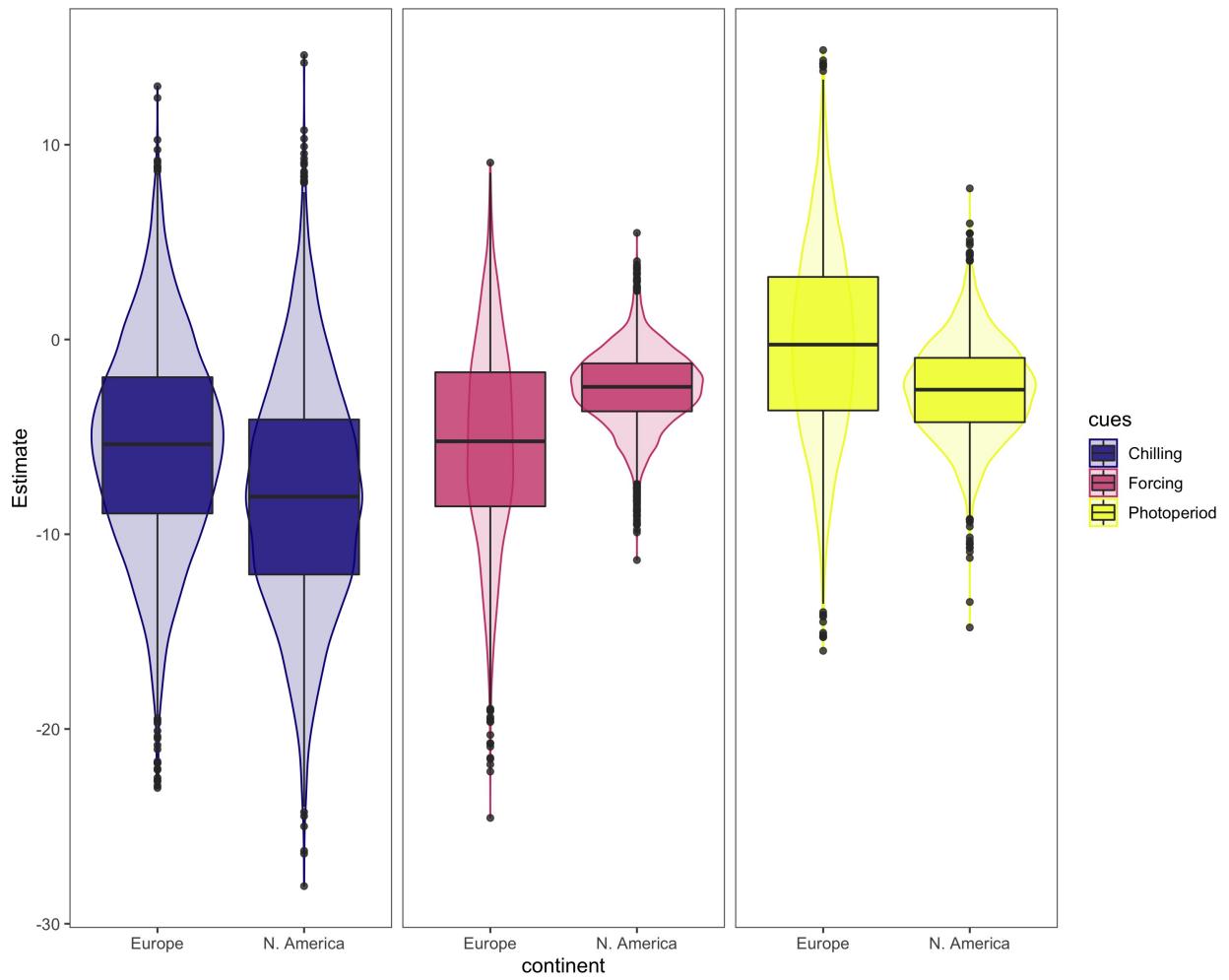


Figure 6: Estimates of phenological sensitivity to chilling, forcing, and photoperiod compared between North American and European taxa.