

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

<sub>4</sub> or

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

<sub>8</sub> or

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

<sub>12</sub> or

<sub>13</sub> Other

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<sub>15</sub> January 25, 2022

<sup>16</sup> **Abstract**

<sup>17</sup> **Introduction**

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

<sup>26</sup> Decades of research suggest that warming spring temperatures (forcing), cool winter temper-  
<sup>27</sup> atures (chilling) and day length (photoperiod) are primary environmental cues utilized by  
<sup>28</sup> woody plants that determine the timing of spring phenological events ???. These studies also  
<sup>29</sup> demonstrate the there are substantial cue-use differences among species, with some species  
<sup>30</sup> relying more heavily on some cues over others (??). As anthropogenic climate change has  
<sup>31</sup> already driven shifts in spring phenology (?), identifying these inter-specific differences in cue  
<sup>32</sup> use has emerged as a major goal of phenological research (?). These differences have strong  
<sup>33</sup> implications for both predicting the rate of phenological shifts as the climate continues to  
<sup>34</sup> warm (), and anticipating the ecological consequences of these shifts (?).

<sup>35</sup> Climate is the major selective force on both species' geographic ranges (?) and their phe-  
<sup>36</sup> nology (?), and therefore, it is widely assumed that phenological cue-use differences among  
<sup>37</sup> species reflect the climate of their respective ranges (??). That is, a species' relative re-  
<sup>38</sup>liance on forcing, chilling and photoperiod for should be shaped by the unique environmental  
<sup>39</sup> conditions across a species' geographic range.

<sup>40</sup> Despite this intuitive link between climate and cues, direct tests of this assumption are rare  
<sup>41</sup> (but see (?)). With the recent quantification for cue use of many species (?) and the ac-  
<sup>42</sup>cessibility of high resolution climate data it is now possible to rigorously test this theory  
<sup>43</sup> with data. Below, we briefly outline two hypotheses about the relationship between phe-  
<sup>44</sup>nological cue-use and species' climatic range characteristics. We then test these predictions  
<sup>45</sup> using Bayesian models for a large suite of temperate woody species from North America and  
<sup>46</sup> Europe.

<sup>47</sup> **0.1 Climate intensity hypothesis**

<sup>48</sup> One hypothesis for the evolution of cue use differences across species is that species utilize  
<sup>49</sup> the climate cues to which they have the most exposure. Simply stated, there should be a  
<sup>50</sup> positive correlation between the amount or intensity of a cue across a species' range and  
<sup>51</sup> the species phenological sensitivity to that cue. This hypothesis predicts that species with  
<sup>52</sup> a) high numbers growing degree days in their range should have stronger forcing cues, b)  
<sup>53</sup> higher amount of chilling should have stronger chilling cues and c) more annual photoperiod  
<sup>54</sup> variation should have stronger photoperiod cues. This hypothesis has been applied to explain  
<sup>55</sup> large, macro-ecological patterns in phenology like why the tropical phenology cues primary  
<sup>56</sup> to forcing and temperate and arctic phenology is more dependent on photoperiod and/or  
<sup>57</sup> chilling () but has not been widely tested within biomes for species with overlapping ranges.

<sup>58</sup> **0.2 Climate variability hypothesis**

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

<sup>65</sup> **I want to move the following paragraph to de-emphasize this point. I am thinking  
66 maybe somewhere in the methods.** However, a major hurdle to robustly testing this  
<sup>67</sup> hypothesis is that, when considered in the context of a species' geographic range, spring  
<sup>68</sup> temperature variation occurs on multiple temporal and spatial scale. Phenology may be  
<sup>69</sup> shaped by intra-annual temperature variation (e.g. frequency of late season frost, diurnal  
<sup>70</sup> temperature functions), inter-annual variation (e.g. annual mean temperatures) and the  
<sup>71</sup> interaction between them (e.g. inter-annual variation in last season frost episodes). Further,  
<sup>72</sup> each of the level of variation be quite different across a species range, suggesting geographic  
<sup>73</sup> variation with the range must also be accounted for. Any of these level of variation could  
<sup>74</sup> itself drive selection for secondary cue usage (photoperiod/chilling), and it is unclear how they  
<sup>75</sup> interact or which is most important (?). Key to testing the climate variability hypotheses  
<sup>76</sup> is to first characterize relationships between spring temperature variation at multiple spatio-  
<sup>77</sup> temporal scales.

<sup>78</sup> An implicit assumption of the previously stated hypotheses is that among species cue-use

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

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

## 101 Methods

### 102 OSPREE database

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

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

## 122 Species' range characteristics

123 We extracted climate data from daily gridded meteorological datasets for both Europe and  
124 North America. For Europe, we extracted minimum and maximum daily temperatures  
125 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  
126 2016. Specifically, we used version 17 at a resolution of 0.5 latitudinal degrees. For North  
127 America, we extracted minimum and maximum daily temperatures from Justin Sheffield's  
128 Princeton Global Forcing dataset (<http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/>)  
129 for the same period. We used version v3 at a resolution of 0.25 latitudinal degrees.  
130  
131 For 22 European and 16 North American tree species, we obtained published distributional  
132 range maps in shapefile format. European species ranges were downloaded from <http://www.sciedirect.com/science/article/pii/S2352340917301981?via%3Dihub#ec-research-data>  
133 (?) and North American ranges were obtained from <https://www.fs.fed.us/nrs/atlas/littlefia/#> (?). For each species' range, we extracted climate data corresponding to all  
134 grid cells contained within the range.  
135  
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  
138 Spring Temperature Variability (STV). GDD was calculated as the summed temperatures  
139 above 10C recorded from January 1st until May 31st. GDDlf was calculated as GDD but  
140 instead of summing temperatures above a threshold until a fixed date, the sum was performed  
141

142 until the date at which the latest minimum temperature below -5C was recorded. STV was  
 143 calculated as the standard deviation of mean minimum temperature **10th Oct - 28Feb**  
 144 (**should be march to may**). (?). [Some notes: can we add a sentence about temporal vs.  
 145 spatial variation here? Also, we calculated Chill portions so we should include that here as  
 146 well.]

## 147 Statistical analysis

### 148 climate cue-use relationships

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

155

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

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

162 **Intra vs. interspecific models**

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

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

172

)

173

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

The  $\alpha$  and each of the 5  $\beta$  coefficients were modeled at the study, species, population, or species and population level, as follows:

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

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

## 179 Results

### 180 Coherence of spatio-temporal spring climate variability

181 I'd like to remove this as a full on "result" and either put in in the methods  
182 sections to explain why we use one version of variation or elaborate on it in the  
183 suppliment but I am not so sure The spatio-temporal coherence of spring climate variabil-  
184 ity and intensity varied across continent and scales. Generally climate intensity (mean GDDs  
185 in range mean Chill Portions in range and Mean GDDs to last frost) were well correlated with  
186 climate variability (Fig. ??a),b),c),d),h)) though strong differences can be observed between  
187 North American and Europe.

### 188 Climate intensity and cue use

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

### 197 Climate variation and cue use

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

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

### 209 0.3 Cue use in North America and Europe

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

### 216 Local adaptation of phenological cues

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

## 220 Discussion

### 221 Hypotheses of bioclimatic cue use

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

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

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

## 237 Climate patterns in North America and Europe

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

245 When we consider our biological findings about cue-use differences among taxa in North  
246 America vs. Europe in the context these climatic patterns, it is clear that this stark contrast  
247 must be better accounted for in understanding the evolutionary histories and ecological tra-  
248 jectories of the flora of these two continents. For any trait under selection, there must be  
249 sufficient selection pressure to drive the evolution of a trait (). Our results suggest that the  
250 recent magnitude of climate variation in Europe may be insufficient to drive the evolution  
251 of phenological sensitivity to climate cues. Additionally the lack of correlations we found  
252 between spatial and temporal climate variability in Europe could also suggest that the axes  
253 of variability could be muting selection. **There is a known interaction of these forces**  
254 **in a some papers that Lizzie sent to Faith, so maybe we can explain and cite**  
255 **them here.** While previous work has suggested that climate variability drive cue use differ-  
256 ences between North America and Europe (?), the absence of a relationship between climate  
257 variability and cue use we found in our European data subset, combined with the the weaker  
258 sensitivity to secondary cues, suggests a slightly different formulation. Our work suggest that

259 climate variability may drive cue use only in North America where variation is sufficiently  
260 high to drive selection and not in Europe where variation is more limited.

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

## 267 Alternative hypotheses

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

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

290 Increasing the geographic and taxonomic breadth of phenological cue experiments is critical

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

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

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371 **Figures**

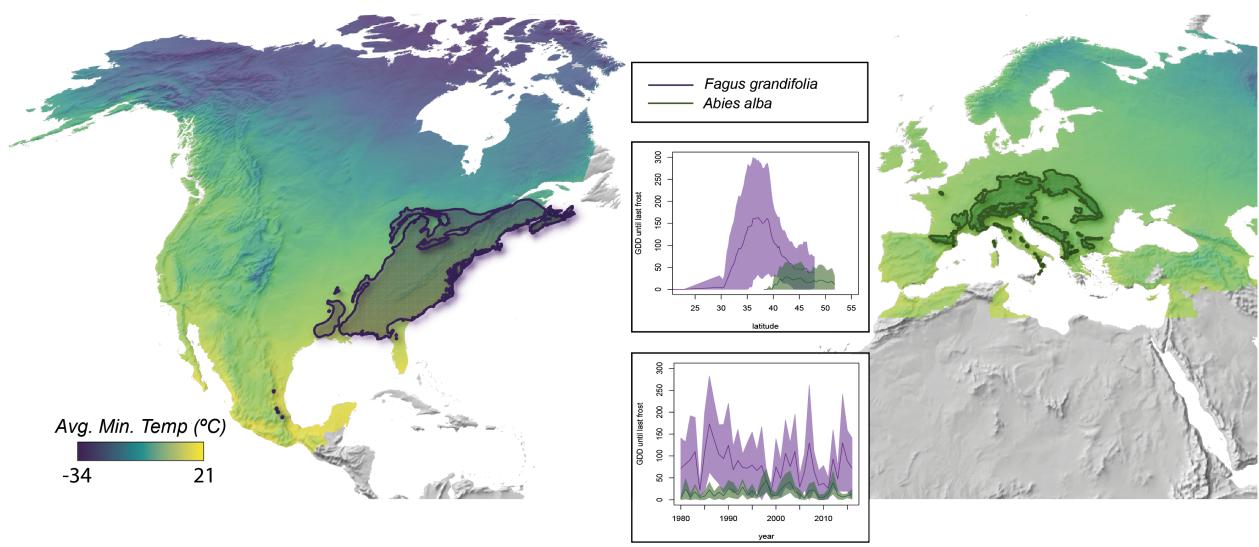


Figure 1: .

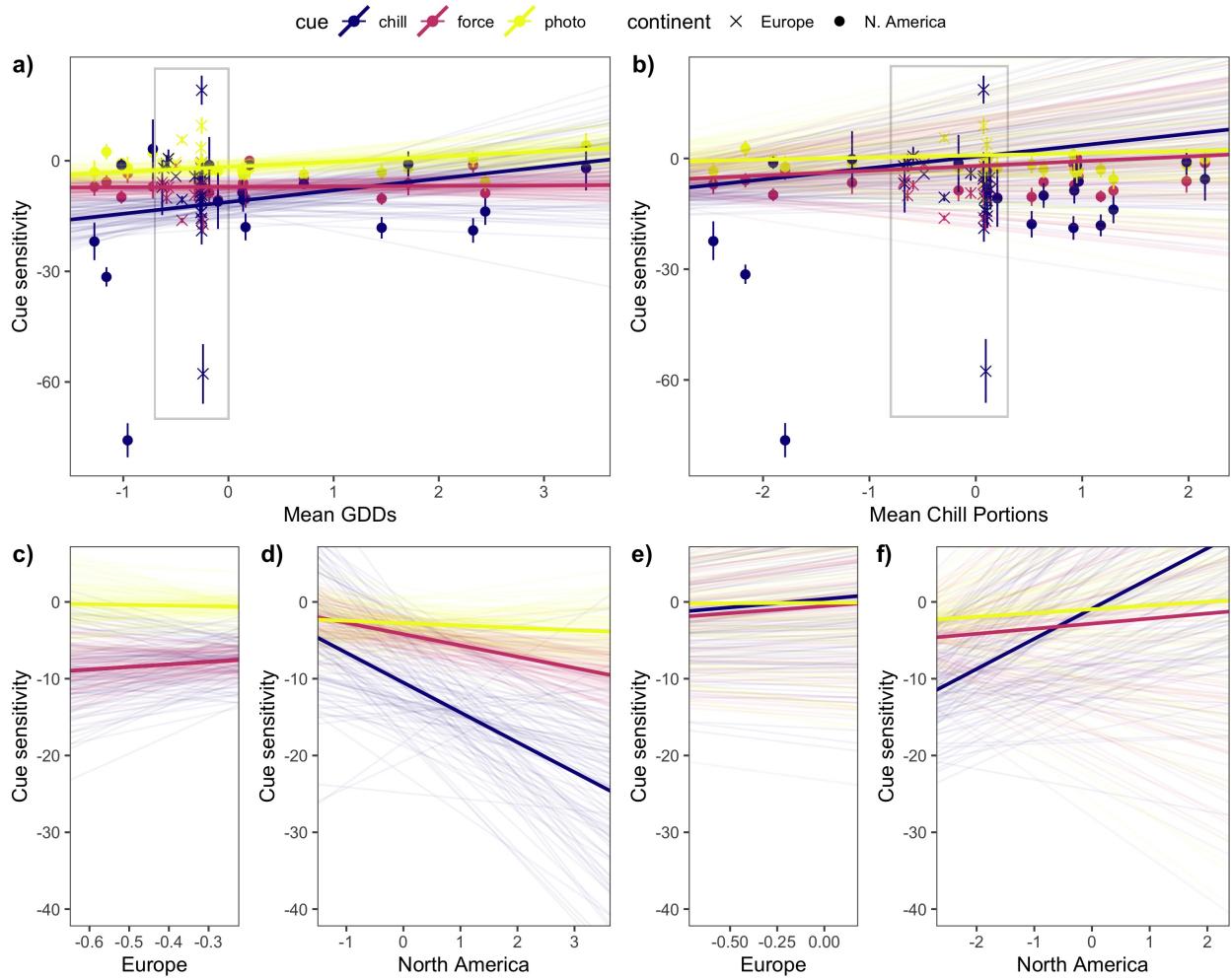


Figure 2: The effects of climate intensives on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of mean GDDs on cue sensitivity for all 40 species in the study and b) depicts effects of chilling on cue sensitivity. All values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

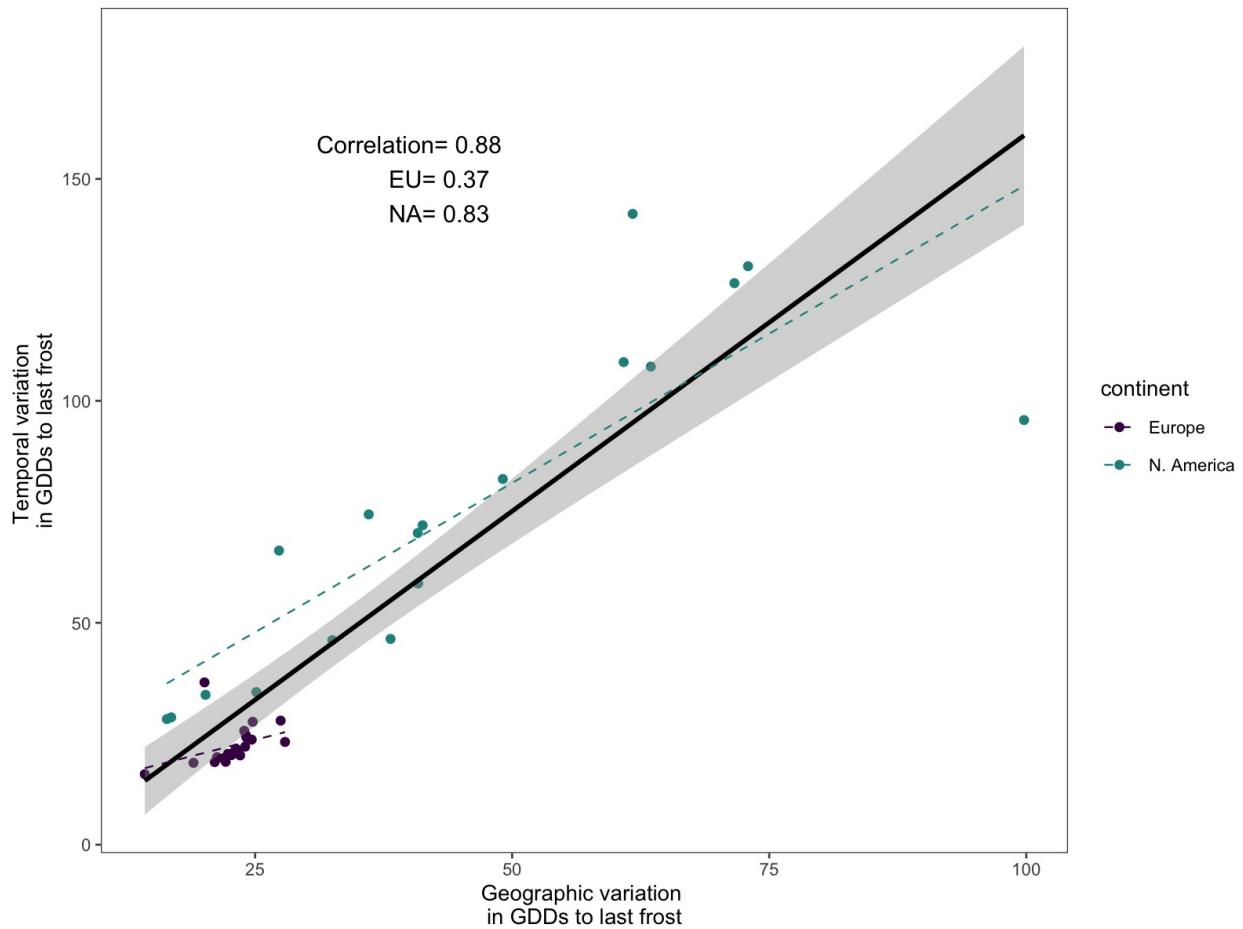


Figure 3: Could we combine this figure with the concept figure? Move it to suppliment. It doesnt' feel like it shoulld be a stand alone Correlations between spatio-temporal axes of climate variation and intensities in the full data set and across North American and European species ranges.

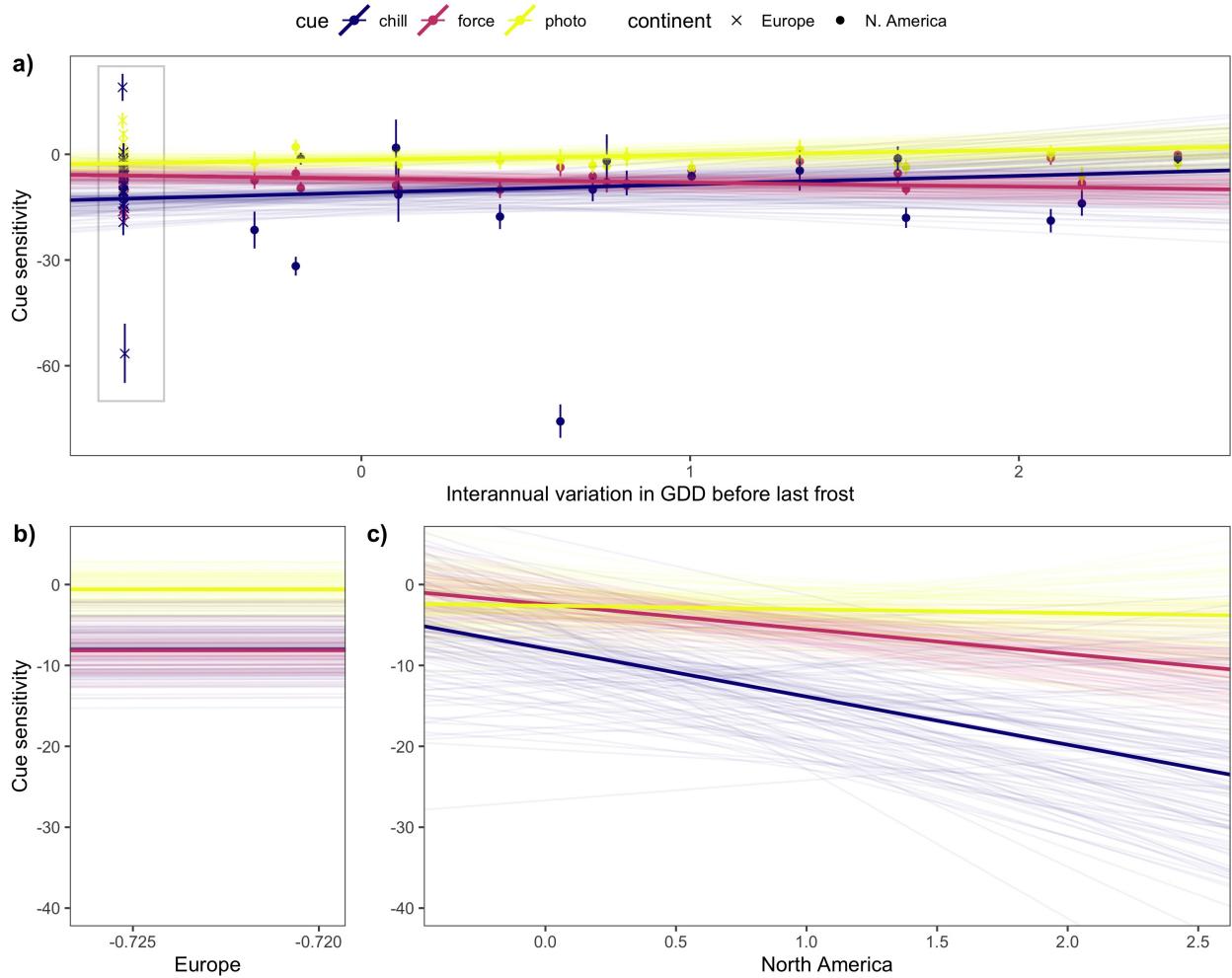


Figure 4: The effects of two measures of spring climate variability on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of variability in number of growing degree days to last frost on cue sensitivity for all 40 species in the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

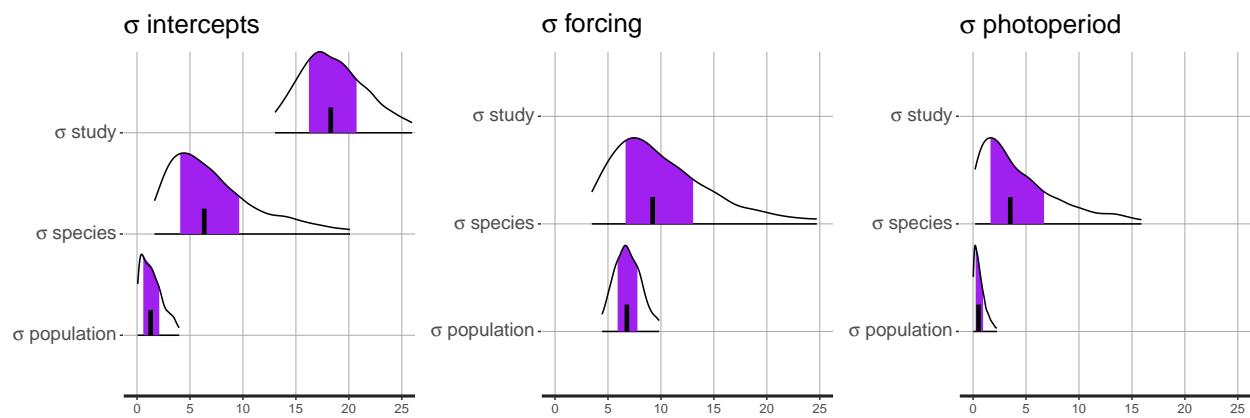


Figure 5: Interspecific variation exceeds intraspecific. Maybe Cat should write this?

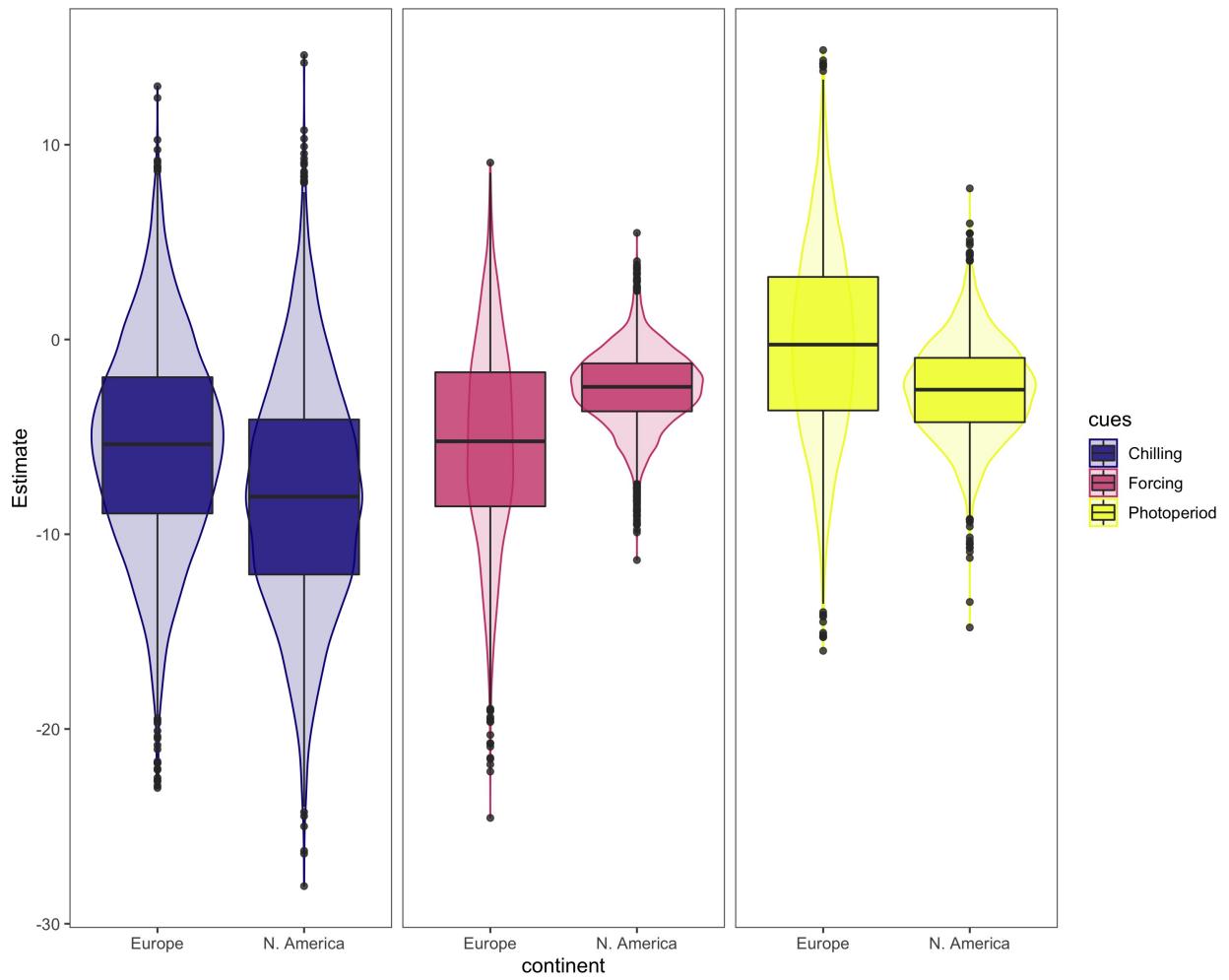


Figure 6: Estimates of phenological sensitivity to chilling, forcing, and photoperiod compared between North American and European taxa.