

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

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

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

<sup>44</sup> Despite this intuitive link between climate and cues, direct tests of this assumption are rare  
<sup>45</sup> (but see (Zohner et al., 2017)). With the recent quantification for cue use of many species  
<sup>46</sup> (Ettinger et al., 2020) and the accessibility of high resolution climate data it is now possible  
<sup>47</sup> 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. This hypothesis has been applied to explain  
59 large, macro-ecological patterns in phenology like why the tropical phenology cues primary  
60 to forcing and temperate and arctic phenology is more dependent on photoperiod and/or  
61 chilling () but has not been widely tested within biomes for species with overlapping ranges.

## 62 0.2 Climate variability hypothesis

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

70 **I want to move the following paragraph to de-emphasize this point. I am thinking**  
71 **maybe somewhere in the methods.** However, a major hurdle to robustly testing this  
72 hypothesis is that, when considered in the context of a species' geographic range, spring  
73 temperature variation occurs on multiple temporal and spatial scale. Phenology may be  
74 shaped by intra-annual temperature variation (e.g. frequency of late season frost, diurnal  
75 temperature functions), inter-annual variation (e.g. annual mean temperatures) and the  
76 interaction between them (e.g. inter-annual variation in last season frost episodes). Further,  
77 each of the level of variation be quite different across a species range, suggesting geographic

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

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

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

<sup>106</sup> **Methods**

<sup>107</sup> **OSPREE database**

<sup>108</sup> To estimate phenological responses to chilling, forcing and photoperiod we used data from the  
<sup>109</sup> Observed Spring Phenology Responses in Experimental Environments (OSPREE) database  
<sup>110</sup> (Wolkovich et al., 2019). This database aims to include data from all published studies of  
<sup>111</sup> experiments on woody plant responses to chilling, forcing and photoperiod cues, as described  
<sup>112</sup> in Ettinger et al. (2020). Here we use a subset of data from an updated version of the  
<sup>113</sup> database containing all papers found in literature searches through June 2019, selecting  
<sup>114</sup> species for which we could reliably estimate cue responses.

<sup>115</sup> Estimates of phenological cues (i.e., change in days of an event per change in level of chilling,  
<sup>116</sup> forcing or photoperiod) can vary strongly due to study location and methodological differ-  
<sup>117</sup> ences (CITES). For example, many studies often include only one—often extreme—level of a  
<sup>118</sup> cue, such as a photoperiod of 24 hours or very low chilling, and thus will provide estimated  
<sup>119</sup> responses to the manipulated cues (e.g., forcing) relevant only in those extremes. [Some  
<sup>120</sup> statistical methods can estimate responses across such data, but they will estimate cue re-  
<sup>121</sup> sponds as more similar across all species than they likely are (see Ettinger et al., 2020, for  
<sup>122</sup> example), making the type of inter-specific comparisons we were interested in here difficult.]  
<sup>123</sup> As such, we included species that where: 1) included in two or more studies, 2) we had  
<sup>124</sup> data for at least two levels of each cue (chilling, forcing and photoperiod; but we excluded  
<sup>125</sup> species that only had field chilling), and 3) could obtain published range maps (see below).  
<sup>126</sup> [While this approach limited our total species number, it provided more reliable estimates of  
<sup>127</sup> phenological cues.]

<sup>128</sup> **Species' range characteristics**

<sup>129</sup> We extracted climate data from daily gridded meteorological datasets for both Europe and  
<sup>130</sup> North America. For Europe, we extracted minimum and maximum daily temperatures  
<sup>131</sup> 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  
<sup>132</sup> 2016. Specifically, we used version 17 at a resolution of 0.5 latitudinal degrees. For North  
<sup>133</sup> America, we extracted minimum and maximum daily temperatures from Justin Sheffield's  
<sup>134</sup> Princeton Global Forcing dataset (<http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/>)  
<sup>135</sup> for the same period. We used version v3 at a resolution of 0.25 latitudinal degrees.  
<sup>136</sup>

<sup>137</sup> For 22 European and 16 North American tree species, we obtained published distributional  
<sup>138</sup> range maps in shapefile format. European species ranges were downloaded from <http://www.sciedirect.com/science/article/pii/S2352340917301981?via%3Dihub#ec-research-data>  
<sup>139</sup> (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-  
<sup>140</sup> mate data corresponding to all grid cells contained within the range.  
<sup>141</sup>

<sup>142</sup> We used ,minimum and maximum daily temperatures within species ranges were then used to  
<sup>143</sup> compute Growing Degree Days (GDD), Growing Degree Days until the last frost (GDDlf) and  
<sup>144</sup> Spring Temperature Variability (STV). GDD was calculated as the summed temperatures  
<sup>145</sup> above 10C recorded from January 1st until May 31st. GDDlf was calculated as GDD but  
<sup>146</sup> instead of summing temperatures above a threshold until a fixed date, the sum was performed  
<sup>147</sup> until the date at which the latest minimum temperature below -5C was recorded. STV was  
<sup>148</sup> calculated as the standard deviation of mean minimum temperature **10th Oct - 28Feb**  
<sup>149</sup> (**should be march to may**). (Zohner et al., 2017). [Some notes: can we add a sentence  
<sup>150</sup> about temporal vs. spatial variation here? Also, we calculated Chill portions so we should  
<sup>151</sup> include that here as well.]  
<sup>152</sup>

## <sup>153</sup> Statistical analysis

### <sup>154</sup> climate cue-use relationships

<sup>155</sup> To assess the relationships between range-wide climate variables and phenological sensitiv-  
<sup>156</sup> ity to forcing, chilling and photoperiod we fit Bayesian hierarchical phenology using a joint  
<sup>157</sup> modeling framework in which parameter estimates for each cue response are influenced by a  
<sup>158</sup> range-wide climate variable sub-model (eek! that's hard to describe. **Does someone else**  
<sup>159</sup> **want to take a stab at describing what a joint model is?**. A first attempt of at the  
<sup>160</sup> model formulation is written below:

<sup>161</sup>

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

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](http://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](http://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

)

179

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

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

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

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

## 185 Results

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

187 I'd like to remove this as a full on "result" and either put in in the methods  
188 sections to explain why we use one version of variation or elaborate on it in the  
189 suppliment but I am not so fusre The spatio-temporal coherence of spring climate vari-  
190 ability and intensity varied across continent and scales. Generally climate intensity (mean

<sup>191</sup> GDDs in range mean Chill Portions in range and Mean GDDs to last frost) were well corre-  
<sup>192</sup> lated with climate variability (Fig. 3a),b),c),d),h)) though strong differences can be observed  
<sup>193</sup> between North American and Europe.

## <sup>194</sup> Climate intensity and cue use

<sup>195</sup> Overall, the mean forcing (GDDs) and chilling (Chill Portions) had weak effects on estimated  
<sup>196</sup> cue use. In our full species models mean GDDs and had a weakly negative or neutral associa-  
<sup>197</sup> tion with cue strength (GDD:Chill=X ,GDD:Force=Y, GDD:Photo=Z, (Fig. 2 a),b))). The  
<sup>198</sup> general sign of these relationships persisted in the continent subset models (Fig. 2 d),e),f))  
<sup>199</sup> with the exception of the relationship between mean GDDs and chilling for North American  
<sup>200</sup> species which became positive (mean= Z, (Fig. 2 c)). Generally, there was high uncertainty  
<sup>201</sup> around these estimates suggesting climate intensity is a poor predictor for cue use.

## <sup>202</sup> Climate variation and cue use

<sup>203</sup> In our full models, variation in growing degree days before the last frost of the season was  
<sup>204</sup> weakly positively associated with forcing and photoperiod sensitivity and negatively asso-  
<sup>205</sup> ciated with chilling sensitivity (Fig. 4a))). However, our continent subset models shows  
<sup>206</sup> different effect. The effect of Variation in GDDs to last frost is poorly estimated in the  
<sup>207</sup> European data subset, and has almost no effect on cue use over the narrow range of spring  
<sup>208</sup> climate variation present in Europe (Fig. 4b). In the North America subset, variation in  
<sup>209</sup> GDD to last frost increases sensitivity in all three cues (Chilling:X Forcing:Y Photoperiod:Z,  
<sup>210</sup> (Fig. 4c))) suggesting there may be support for the climate variation hypotheses in North  
<sup>211</sup> America where spring climate variation can be extreme. We found qualitatively similar con-  
<sup>212</sup> tinental patterns in the relationships between cue-use and climate variability using STV as  
<sup>213</sup> an alternative metric inter-annual variation (SUPP).

### <sup>214</sup> 0.3 Cue use in North America and Europe

<sup>215</sup> We found that the strength of secondary cue use (chilling and photoperiod) was higher in  
<sup>216</sup> North America than in Europe (Chilling: NA-X, EU-Y, Photoperiod NA-X, EU-Y, Fig.6),  
<sup>217</sup> while forcing sensitivity was higher in Europe than North America (NA-X, EU-Y). This  
<sup>218</sup> result is consistent with the observation that the spring climate of North America is much

<sup>219</sup> less stable than Europe and our finding that the climate-cue use hypotheses appear to be  
<sup>220</sup> better supported in North America.

## <sup>221</sup> Local adaptation of phenological cues

<sup>222</sup> We detected limited population level variation in forcing and photoperiod cue sensitivity,  
<sup>223</sup> though this within species variation was less substantial than among species variation(Fig.  
<sup>224</sup> 5). Notably, we found the largest source of variation in phenological was

## <sup>225</sup> Discussion

### <sup>226</sup> Hypotheses of bioclimatic cue use

<sup>227</sup> Similar to previous studies, we found stronger support for the climate variability hypothesis  
<sup>228</sup> than the climate intensity hypothesis (Zohner et al., 2017). While, as predicted by the  
<sup>229</sup> climate intensity hypothesis, mean growing degree days in the range were positively associated  
<sup>230</sup> with forcing sensitivity in North America, chilling sensitivity has no clear relationship with  
<sup>231</sup> mean chilling in the range for species on either continent (Fig 2e,f). Further, there is high  
<sup>232</sup> uncertainty surrounding the estimates in our climate intensity models, suggesting climate  
<sup>233</sup> intensity is a poor predictor of phenological cue use.

<sup>234</sup> By contrast, climate variability was associated with increased forcing, chilling and photope-  
<sup>235</sup> riod sensitivities in North American species (Fig 4,c) as predicted by the climate variability  
<sup>236</sup> hypothesis. Interestingly, there was virtually no relationship between climate variability and  
<sup>237</sup> cue use in European species (Fig 4,b). We recovered these contrasting patterns among con-  
<sup>238</sup> tinents using multiple metrics of of climate variability (see ??, and “STV”). We also found  
<sup>239</sup> secondary cue use (photoperiod and chilling) sensitivity was higher in North American taxa  
<sup>240</sup> than in European ones (Fig. 6). These contrasting biological patterns appear to reflect the  
<sup>241</sup> strong climatic differences we observed between the continents.

### <sup>242</sup> Climate patterns in North America and Europe

<sup>243</sup> Our study highlights that patterns of temperature variation and intensity are much stronger  
<sup>244</sup> in temperate North America in Europe (Fig. 1). This is a well meteorological phenomenon

245 drive by large local climate pattern like the jet steam and enso and stuff (**say better.**  
246 **maybe, Ben can write this paragraph**). Additionally, we found that in North America,  
247 there was a strong correlation between temporal and spatial climatic variability across the  
248 geographic ranges of the species we studied, while in Europe this correlation was weakly  
249 negative.

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

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

## 273 Alternative hypotheses

274 A major implication of our findings is the field of phenology must continue to expand the range  
275 of hypotheses we test and consider regarding the evolution of phenological cues. Phenology  
276 should continue to draw from studies of paleoclimate, biogeography, evolutionary ecology

and community ecology. There is a rich literature predicting that phenological cue differences among species may be the product of historic climate legacies (), strong phylogenetic constraints () or driven by community processes of phenological assembly like competition, niche theory (). It is likely all of these factors along with the bio-climatic drivers we tested above drive selection on phenology and the the selection strength differs across time and space. Therefore, as we continue to gather more data on phenological cue use patterns for a more species, these hypotheses must be rigorously tested alongside the bio-climatic ones we address here.

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

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

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

<sup>311</sup> will impact species performance in the face of global change at across multiple spatial and  
<sup>312</sup> temporal scales.

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377 **Figures**

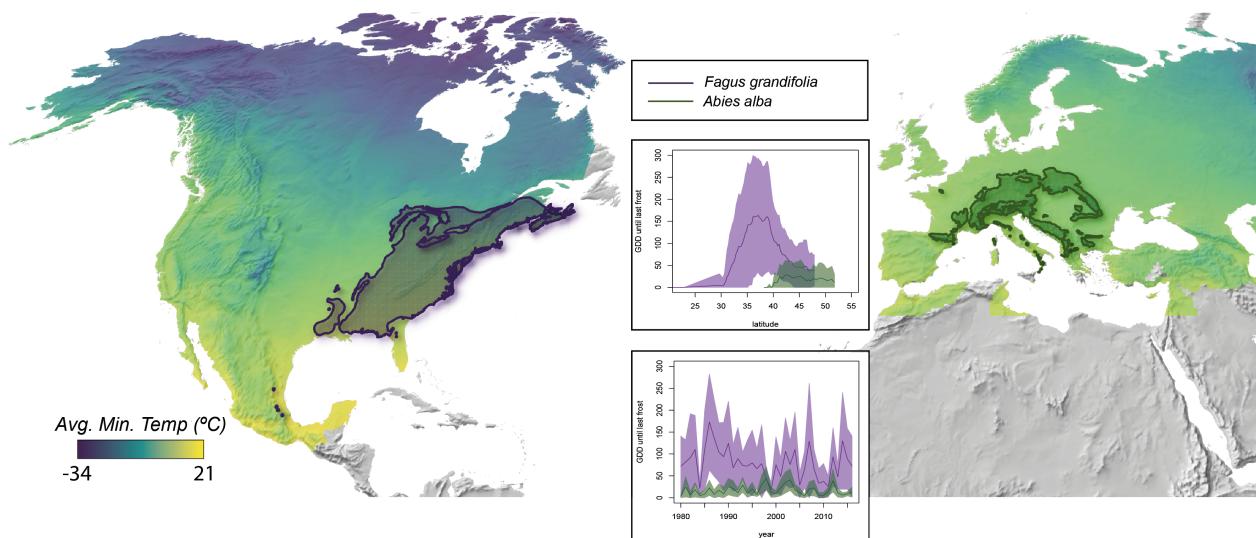


Figure 1: .

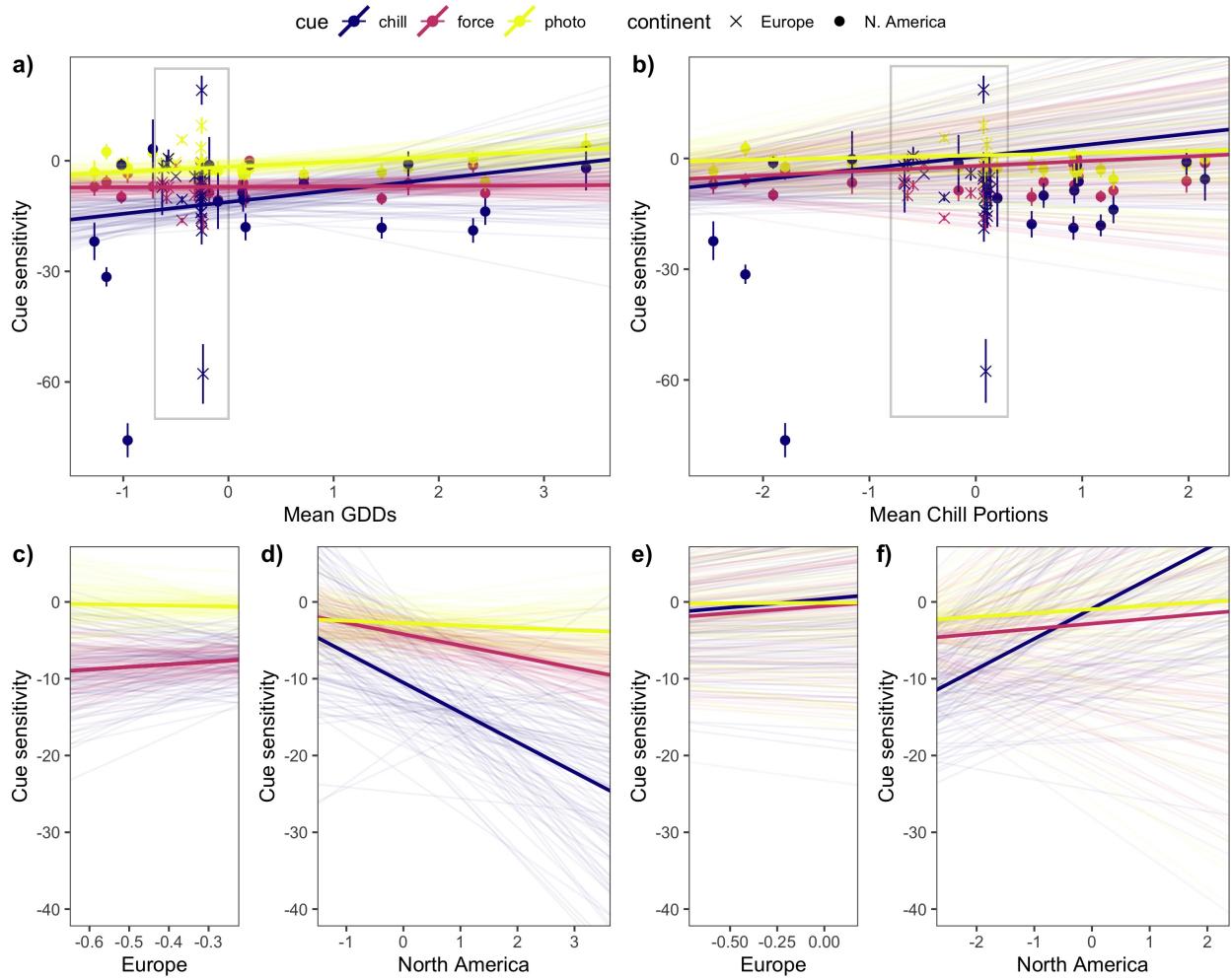


Figure 2: The effects of climate intensives on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of mean GDDs on cue sensitivity for all 40 species in the study and b) depicts effects of chilling on cue sensitivity. All values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

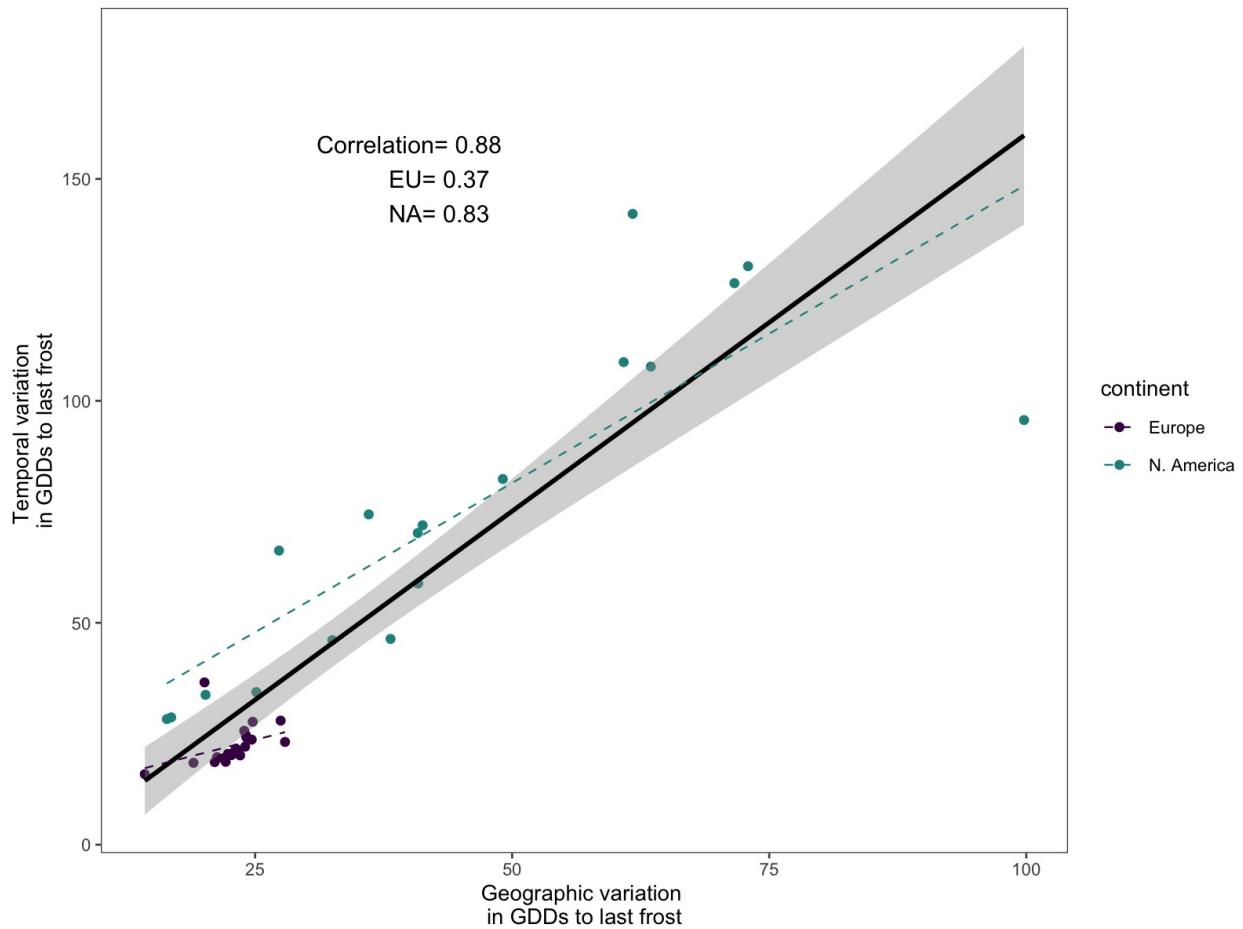


Figure 3: Could we combine this figure with the concept figure? Move it to suppliment. It doesnt' feel like it shoulld be a stand alone Correlations between spatio-temporal axes of climate varation and intesities in the full data set and across North American and European species ranges.

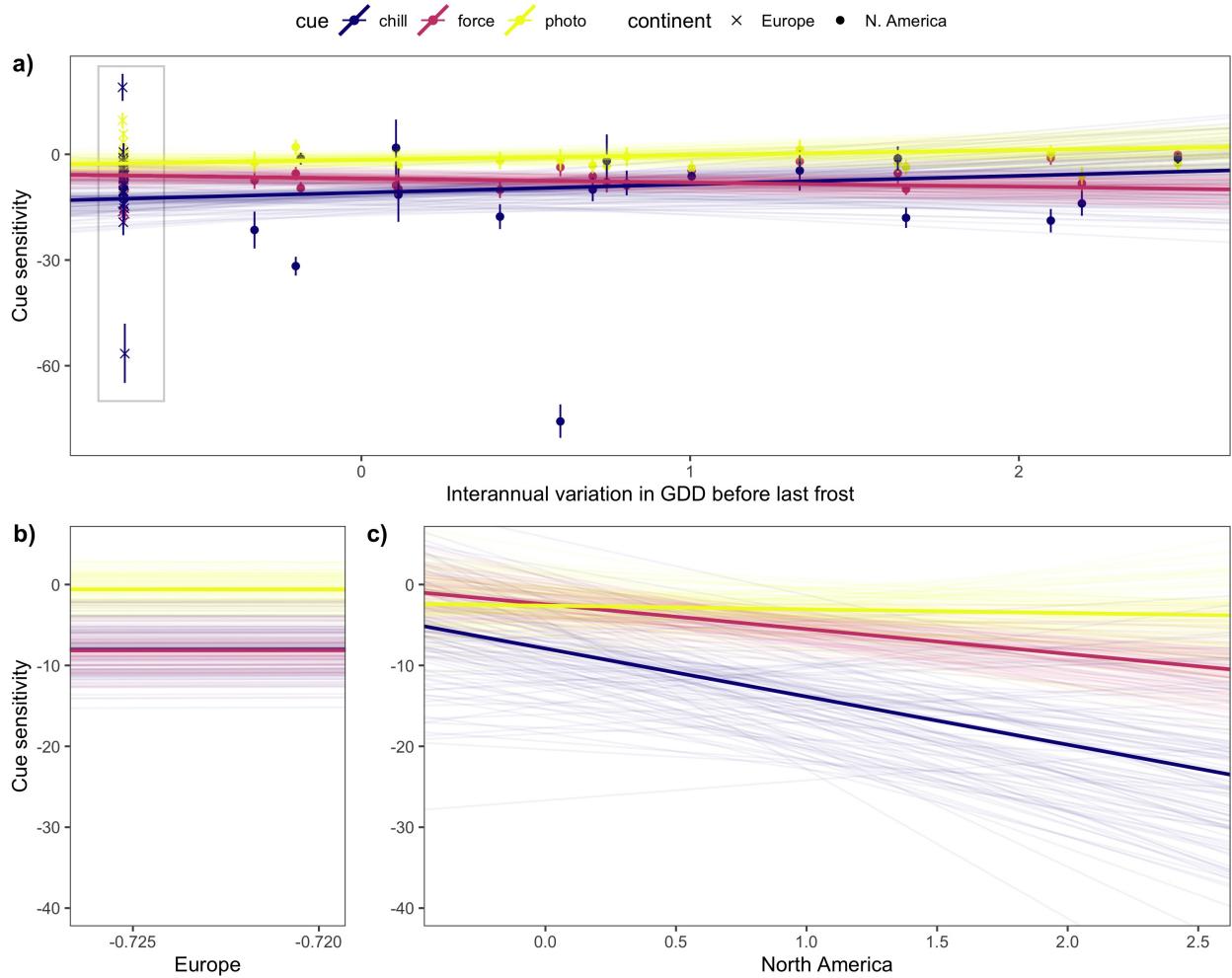


Figure 4: The effects of two measures of spring climate variability on the phenological sensitivity to chilling, forcing and photoperiod of temperate woody species. Figure a) depicts the effects of variability in number of growing degree days to last frost on cue sensitivity for all 40 species in the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

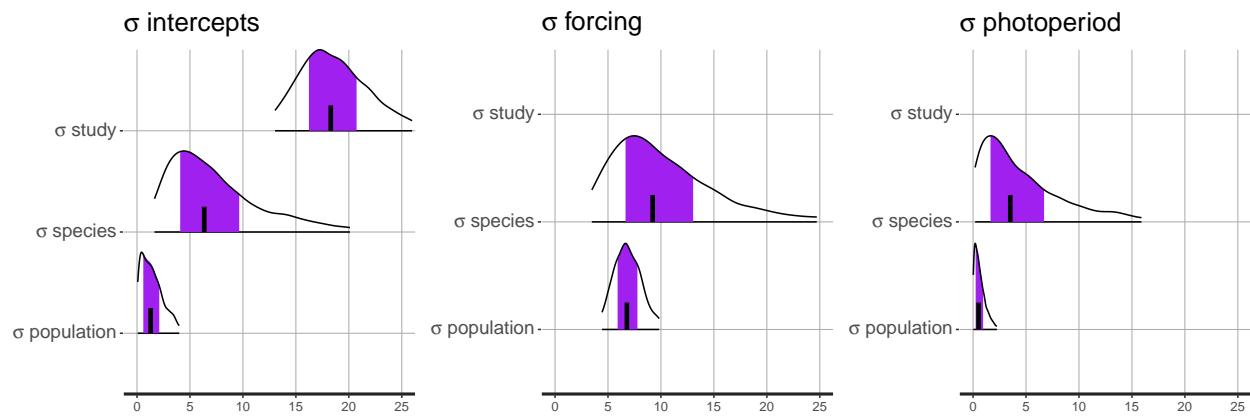


Figure 5: Interspecific variation exceeds intraspecific. Maybe Cat should write this?

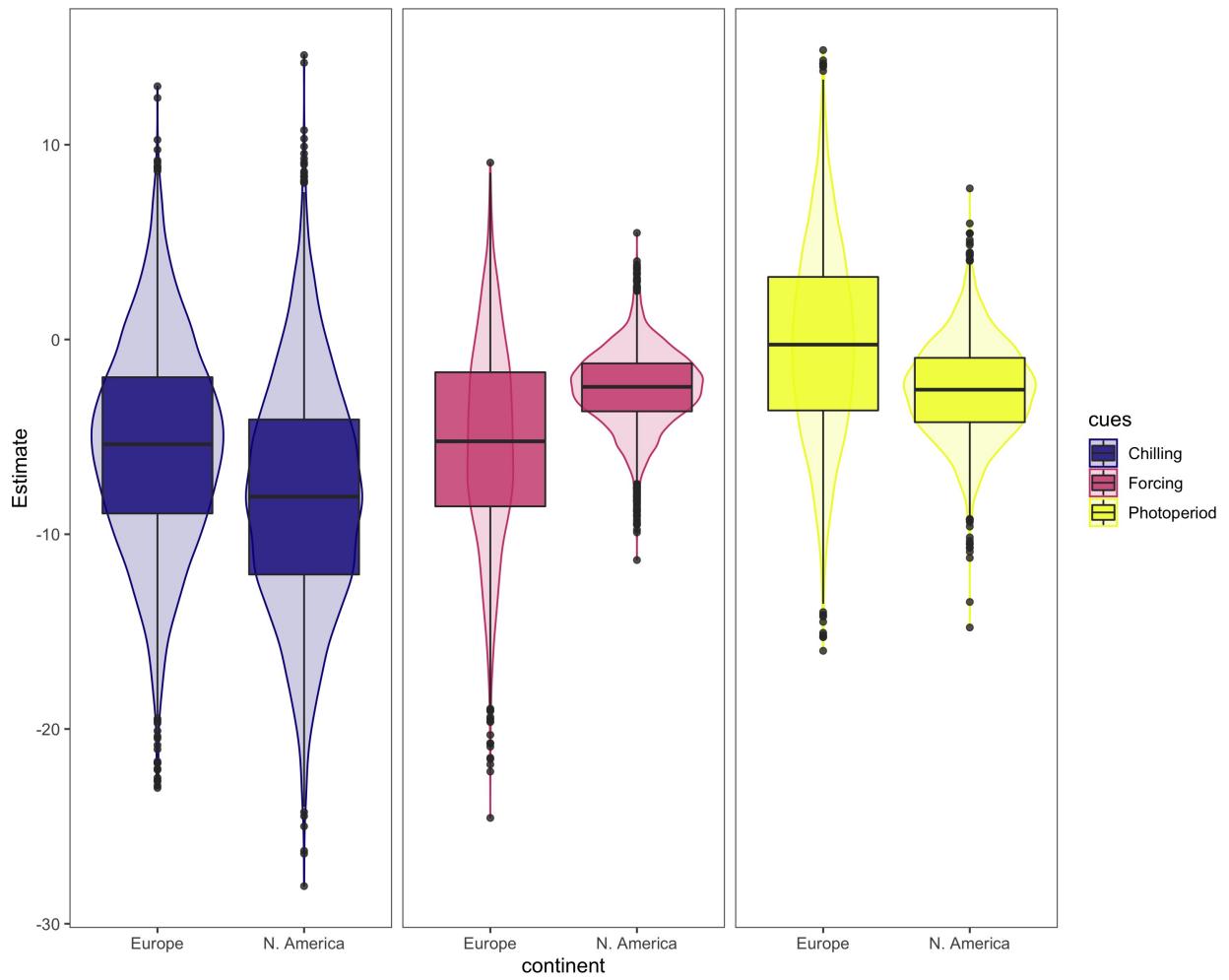


Figure 6: Estimates of phenological sensitivity to chilling, forcing, and photoperiod compared between North American and European taxa.