

₁ Patterns of spring-freeze risk for temperate trees
₂ contributes to phenological cue differences, but leaves
₃ much unexplained

₄ Other

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₇ Abstract

₈ Introduction

₉ Phenology, the timing of annual life cycle events, allows for organisms to match critical
₁₀ life-cycle transitions with optimum environmental conditions. Through the phenology of
₁₁ spring budburst, temperate woody plants balance the resource and competition advantages
₁₂ of precocious leafout with the risk of damage from late season freezes (Savage and Cavender-
₁₃ Bares, 2013). To navigate this trade-off, woody plants have evolved complex physiological
₁₄ responses to sense environmental cues that signal the arrival of appropriate conditions for
₁₅ resuming growth (Polgar and Primack, 2011). Decades of research on phenology suggest that
₁₆ warming spring temperatures (forcing), cool winter temperatures (chilling) and day length
₁₇ (photoperiod) are the primary environmental cues for woody plant phenology in temperate
₁₈ regions (Ettinger et al., 2020; Forrest and Miller-Rushing, 2010). These studies also demon-
₁₉ strate the there are substantial cue-use differences among species, with some species relying
₂₀ more heavily on some cues over others (Laube et al., 2014; ?). Yet, our knowledge about
₂₁ why species differ in their cue responses is currently limited, and better understanding the
₂₂ ecological and evolutionary drivers that shape phenological cues is critical for our ability to
₂₃ predict the magnitude and impacts of phenological shifts with climate change.

24 The predictability of the arrival spring may strongly influence the evolution of phenological
25 cues (Zohner et al., 2017; ?; ?). In regions where the start of spring is unpredictable, species
26 should evolve stronger dependence on chilling and photoperiod cues to prevent premature
27 leafout and exposure to frost damage. In contrast, in regions where the seasonal warming
28 reliably indicates the start of spring, species should respond strongly to forcing and not
29 chilling or photoperiod. This spring predictability hypothesis (hereafter:SPH) is intuitive
30 and has found some recent support in the literature (Zohner et al., 2017). However, the SPH
31 hinges on the assumption that species phenological responses are at a stable equilibrium with
32 their environment, an assertion that is not well supported (??). It is also unclear the time scale
33 at which season predictability would shape cue responses. Spring predictability could drive
34 selective pressure to increase chilling and/or photoperiod sensitivity on an evolutionary time
35 scale, or define species ranges based on their inherited cue sensitivities on an ecological time
36 scale. Testing the predictions of SPH across multiple geographic scales can serve to evaluate
37 this hypothesis, and offer an improved understanding of the drivers of biogeographic patterns
38 of phenology cue sensitivity.

39 Spatial predictions of the SPH

40 Global circulation patterns generate substantially different spring climatic conditions on ei-
41 ther side of the North Atlantic (). In Eastern North America, the spring is marked by

42 instability, while in Europe, the arrival of spring is generally more consistent (Figure 1).

43 Given these contrasting climate regimes, the SPH predicts that North American species

44 should have stronger sensitivity to chilling and photoperiod and weaker to forcing (?). We

45 tested these predictions by comparing the cue sensitivities of North American and Europe

46 species estimated from Bayesian hierarchical models.

47 It is also possible that phenological responses to cues play a more important role in

48 determining species range limits (?). The distributions of species that rely primarily on forc-

49 ing, should be restricted geographic regions where spring predictability is high, while species

50 that rely more heavily on chilling and photoperiod can persist in regions where spring pre-

51 dictability is low. If this is the case, the SPH predicts that within each continent, species

52 with higher chilling and photoperiod cue responses should be associated with lower spring

53 predictability across their ranges. We tested this prediction by regressing the species-level

54 posterior estimates of forcing, chilling and photoperiod sensitivity from our previously de-

55 scribed model against the two metrics of spring predictability, with separate models for each

56 cue by continent.

57 Finally, it is possible local adaptation in phenological cue sensitivity overwhelms any relationship
58 between species-level cue use and range-wide climate conditions. However, if cues
59 are locally adapted, it follows that neither continental differences or range wide climate con-
60 ditions would be strongly associated with cue use. To assess this possibility in our data, we
61 designed a two-level, hierarchical model for studies in the OSPREE database that sampled
62 species from multiple provenance locations to partition variance between populations and
63 species.

64 Our study interrogated the SPH; one of the most fundamental biological assumptions relating
65 to the evolution of phenological cue presponses that is frequently asserted but rarely tested
66 (but see Zohner et al., 2017). In our analyses, we found only mixed support for the SPH, high-
67 lighting the need to more holistically integrate multiple other kinds of drivers (community,
68 phylogenetic) into the framework about the evolution of phenological cues.

69 Materials and Methods:

70 Species' range characteristics and climate data

71 We extracted climate data from daily gridded meteorological datasets for both Europe
72 and North America. For Europe, we extracted minimum and maximum daily tempera-
73 tures from the E-OBS dataset (<https://cds.climate.copernicus.eu/cdsapp#!/dataset/insitu-gridded-observations-europe?tab=overview>; last accessed on October 2021) cor-
74 responding to the period comprised between 1980 and 2016. Specifically, we used version
75 17 at a resolution of 0.5 latitudinal degrees. For North America, we extracted minimum
76 and maximum daily temperatures from Justin Sheffield's Princeton Global Forcing dataset
77 (<http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/>; last accessed on Oc-
78 tober 2021) for the same period. We used version v3 at a resolution of 0.25 latitudinal
79 degrees.

81 For 22 European and 16 North American tree species, we obtained published distributional
82 range maps in shapefile format. European species ranges were downloaded from (<http://www.sciencedirect.com/science/article/pii/S2352340917301981?via%3Dihub#ec-research-data>;
83 last accessed on XXX) (Caudullo et al., 2017) and North American ranges were obtained from
84 <https://www.fs.fed.us/nrs/atlas/littlefia/#> (Prasad, 2003). For each species' range,
85 we extracted climate data corresponding to all grid cells contained within the range.
86

87 We used minimum and maximum daily temperatures within species ranges were then used to
88 compute Growing Degree Days (GDD), Growing Degree Days until the last frost and Spring
89 Temperature Variability (STV). GDD was calculated as the summed temperatures above 10C
90 recorded from January 1st until May 31st. GDD to the last frost was calculated as GDD but
91 instead of summing temperatures above a threshold until a fixed date, the sum was performed
92 until the date at which the latest minimum temperature below -5C was recorded. We then
93 calculated the standard deviation (hereafter: Stdv in GDDs to last frost) to this date as
94 one proxy for spring predictability. We then calculated STV, the standard deviation of mean
95 minimum temperature from March 1st until May 31st (Zohner et al., 2017). Specifically, we
96 computed these metrics variability in the within each location across years (1980 to 2016)
97 and for each year across the grid cells comprised within each species' range.

98 Statistical analyses

99 To estimate species-level responses to forcing, chilling and photoperiod we analyzed pheno-
100 logical observations from the Observed Spring Phenology Responses in Experimental Envi-
101 ronments (OSPREE database (Wolkovich et al., 2019)) with a Bayesian Hierarchical model
102 developed by ?. This model estimates forcing, chilling and photoperiod sensitivities through
103 phylogenetically-structure partially pooling. The model was fit using Stan modeling language
104 (?) (www.mc-stan.org), and the data and code used to run this model are available at X.

105 To test whether European and North American taxa had systematically different cue sensi-
106 tivities, we extracted the species-levels posterior estimates of forcing, chilling and photoperiod
107 sensitivity and compared forcing, chilling and photoperiod cues using linear regression, with
108 native continent as a main effect predictor.

109 To assess the relationship between spring predictability—estimated across species' ranges—
110 and cue sensitivity, we regressed the posterior estimates of cue sensitivity against spring
111 predictability. We used separate models for European and North American taxa, and modeled
112 each cue sensitivity (forcing, chilling and photoperiod) separately. We also ran separate
113 models using STV and Stdv in GDDs to last frost as proxies for spring predictability, as
114 main effects. We ran these models using the r packages BRMS.

115 To assess variation within and across sites, we designed a two-level, hierarchical model using
116 data from the OSPREE database. We subsetted the studies to include only those that had
117 multiple provenance locations. Since chilling estimates were either from experimental chilling,
118 from field chilling or a combination of both, we removed 'chilling' as a predictor for this model

since it correlated so strongly with provenance latitude and would result in nonidentifiability in our results. We used a Bayesian mixed-effects hierarchical model approach to analyze our data to best estimate the day of budburst. We fit a Gaussian distribution model using study, species and population as intercepts, forcing and photoperiod as predictors (fixed effects) and species nested within population (i.e., site) as modeled groups (random effects). The Bayesian model was fit using Stan modeling language (?) (www.mc-stan.org), accessed via the *rstan* package (version 2.15.1), version 2.3.1, in R (?), version 3.3.1. We ran four chains, with 2,500 warm-up iterations followed by 3,000 sampling iterations, resulting in 12,000 posterior samples for each parameter.

For all models assessed good model performance through \hat{R} close to 1 and high n_{eff} as well as visual consideration of chain convergence and posteriors (?).

Results

Inter-continental Climatic Pattern

We found no substantial differences in cue sensitivity between continents (Figure: 2). Mean forcing sensitivity for European species was $-6.76 UI_{95}(-17.80, 2.08)$ and $-7.94 UI_{95}(-17.90, 1.93)$ for North American species. Mean photoperiod sensitivity was $8.44 UI_{95}(-22.60, 4.69)$ and $-8.76 UI_{95}(-26.90, 4.82)$ for North American species. Mean photoperiod sensitivity was $1.36 UI_{95}(-5.91, 2.89)$ and $-1.35 UI_{95}(-5.88, 2.98)$ for North American species.

Within continent ranges

We found mixed support for the continent level predictions of the SPH. With STV as the metric for spring predictability, we found that in Europe—spring predictability across a species' range had no clear relationship to forcing or photoperiod cues (mean forcing effect: -0.59, $UI_{95}[-4.44, 3.01]$, mean photoperiod effect: 1.34, $UI_{95}[-0.49, 3.24]$). Contrary to the predictor of the SPH, decreasing chilliness ($UI_{95}[6.37, 6.37]$, $UI_{95}[3.99, 7.97]$).

For North American species, spring predictability also had no clear relationship to forcing or photoperiod cue sensitivity (mean forcing effect: -0.05, $UI_{95}[-2.26, 2.06]$, mean photoperiod effect: 0.15 $UI_{95}[-0.93, 1.21]$). For chilling, decreasing spring predictability was associated with increased chilling ($UI_{95}[-3.45, -3.45]$, $UI_{95}[-7.50, 0.69]$), supporting the prediction of the SPH.

With standard deviation in growing degree days to last frost as the metric for spring pre-

dictability, we observed different relationships between spring predictability and species-level cue sensitivity than we found using STV. For European species, we found decreasing spring predictability was associated with both higher forcing sensitivity (mean forcing effect: -3.61, $UI_{95}[9.04, 1.64]$) and chilling sensitivity (mean chilling effect: -5.27, $UI_{95}[11.45, 1.36]$), while there was no clear relationship between spring predictability and chilling sensitivity (mean $-0.02UI_{95}[-0.34, 0.31]$). For photoperiod sensitivity, we observed a moderate association between decreasing photoperiod and increasing forcing sensitivity (mean $-0.04, UI_{95}[-0.11, 0.04]$).

For North American species, decreased predictability was associated with weaker forcing sensitivity though the strength of this association was relatively weak (mean forcing effect: 0.09 $UI_{95}[-0.04, 0.24]$). There was no clear relationship between spring predictability and chilling sensitivity (mean $-0.02UI_{95}[-0.34, 0.31]$). For photoperiod sensitivity, we observed a moderate association between decreasing photoperiod and increasing forcing sensitivity (mean $-0.04, UI_{95}[-0.11, 0.04]$).

133 Intra-and Interspecific cue variation

134 While we detected limited population level variation in forcing and photoperiod cue sensitivity, though this within species variation was less substantial than among species variation
135 (Fig. 6). Notably, we found the largest source of variation in phenological cue estimates was
136 the study effect Fig. 6). This result does not support the assertion that local adaptation is
137 masking relationships between cue sensitivity and range-level climatic patterns.

139 Discussion

140 In this study we compared estimates of cue sensitivity to climate conditions experienced by
141 species across their range at multiple scale to test the predictions that spring predictability
142 shape cue sensitivities. Across scales, we found support for the SPH to be weak, highlighting a
143 need to think more expansively about the factors that shape phenological cue response.

144 Contrary to expectations, we found no differences in cue sensitivities between North American
145 and European species. This is not particularly surprising given that recent studies have found there
146 to be strong phylogenetic conservatism in phenological cue responses, and that there are many
147 closely related congeners found in both North America and Europe. It is therefore likely that
148 patterns of cue use diverged among taxa well before the modern placement of continents,
149 under different climate conditions than North America and Europe experience today. (wow
150 say better). These results call into question the recent assertion that European plant species
151 successfully invade North American ecosystems because their higher reliance on forcing cues

allows them to leafout earlier and gain a growth advantage over their competitors (?). While these kinds phenological priority effects have been documented as contributing to the success of invaders (??) our findings indicate that other mechanisms are likely more important for explaining the success of European woody plants in North America. Instead, this finding may help us understand why many European timber species have been successfully established in Northern America (and visa versa), without becoming aggressive on the landscape. We should note that when we subset this analysis to include only the 29 for which we could find well developed range maps, we did in-fact observe European species to have a weaker chilling sensitivity (Figure S1, need to make it), which may further explain the pervasiveness of the idea that European invaders are successful in North America due to weaker secondary phenological cues.

0.1 Continetal scale

For Europe, we found spring predictability measured was associated with increased chilling sensitivity and forcing sensitivity, especially when we measured spring predictability with variation in growing degree days to last frost. These patterns qualitatively match the previous findings from Zohner et al. (2017), that report stronger reliance on secondary cues (i.e. chilling) in North American compared to Europe based on the substantial differences in STV between the continents.

North America has substantially weaker spring predictability (i.e., higher STV) than Europe, but despite this, we observed no clear relationship between

When considering the climate patterns experienced by species across their ranges, our analyses of the relationships between spring predictability and phenological sensitivity to forcing, chilling and photoperiod offer only marginal support for the SPH. For North American species, less spring predictability was associated with an increased reliance on chilling (i.e. chilling sensitivity) when we used STV as a metric of predictability and increased reliance on photoperiod when we used Stdv in GDDs to last frost as a metric of spring predictability. For European species spring predictability was associated with increased reliance on chilling (i.e. stronger chilling sensitivity) when we used Stdv in GDDs to last frost as a metric of predictability. However, in interpreting these relationships, it is important to recognize that the amount of variation in GDDs to last frost in Europe is very small (0.62 to 2.97), especially when compared to North America (13.68 to 56.01). This suggest that the arrival of spring in Europe is always relatively predictably from a growing degree day perspective, and

¹⁸⁴ we should exhibit caution in putting too much biological stock in the statistical association
¹⁸⁵ between European spring predictability and chilling cue sensitivity.

¹⁸⁶ There is currently a debate about the extent to which local adaptation shapes phenological
¹⁸⁷ cues (?), and it is likely the strength of local adaptation varies among species, and pheno-
¹⁸⁸ logical phases themselves (??).

¹⁸⁹ While these three facets of the predictability/cue relationship support the expectations of
¹⁹⁰ the SPH, all other aspects of the predictability/cue relationship either show no relationship
¹⁹¹ (i.e. forcing & photoperiod effects with STV in Europe & North America) or observed
¹⁹² relationships contrary to the expectations of the SPH (i.e., chilling in Europe with STV and
¹⁹³ forcing in North America with Stdv. GDDs). We argue that these mixed results should not
¹⁹⁴ serve to refute the claims of the SPH—it is clear that spring predictability has a role to play
¹⁹⁵ in shaping where and how species successfully leaf out. However, our study indicates a more
¹⁹⁶ complicated picture of the factors that shape species' level differences in phenological cues.

¹⁹⁷ Our study indicates that predictability of spring species' experience across their geographic
¹⁹⁸ ranges may play a role in shaping phenological cue sensitivities, there must be more to the
¹⁹⁹ story. When considering the fact that many species with divergent phenological cue sensi-
²⁰⁰ tives have highly overlapping ranges (Make Figure S2) and experience similar environmental
²⁰¹ conditions (i.e., spring predictability, late season frost risk, etc) across their ranges, it is
²⁰² worthwhile to consider phenological cues in a community context ()�.

²⁰³ I am hoping Deirdre and Lizzie have capacity to write a paragraph or two here
²⁰⁴ basically phenology should be considered like a functional trait in that they
²⁰⁵ not only relate to resource aquistion/growth/ survivial but also do niche stuff
²⁰⁶ and therefore end up under stabalizing selection though competition and species
²⁰⁷ interactions

²⁰⁸ 1 Conclusion:

²⁰⁹ In this study we found limited support for the assertion that the predictability of spring shap-
²¹⁰ ing their relative reliance on forcing, chilling and photoperiod cues for spring phenology. Our
²¹¹ results suggest that climate variability may drive cue use pattern only when it is sufficiently
²¹² high, like in contemporary North America. These results suggests that future studies of phe-
²¹³ nological cue-use would benefit from a holistic integration of these bio-climatic hypotheses
²¹⁴ with phylogenetic, functional trait, and climatic legacy hypotheses to fully understand the

215 evolution of phenological cues in woody plants, and how cue use patterns will impact species
216 performance in the face of global change at across multiple spatial and temporal scales.

217 References

- 218 Caudullo, G., E. Welk, and J. San-Miguel-Ayanz. 2017. Chorological maps for the main
219 European woody species. *Data in Brief* 12:662–666.
- 220 Ettinger, A. K., C. J. Chamberlain, I. Morales-Castilla, D. M. Buonaiuto, D. F. B. Flynn,
221 T. Savas, J. A. Samaha, and E. M. Wolkovich. 2020. Winter temperatures predominate in
222 spring phenological responses to warming. *Nature Climate Change* 10:1137–1142.
- 223 Forrest, J., and A. J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of
224 phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B:*
225 *Biological Sciences* 365:3101–3112.
- 226 Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling
227 outweighs photoperiod in preventing precocious spring development. *Global Change
228 Biology* 20:170–182.
- 229 Polgar, C., and R. Primack. 2011. Leaf-out phenology of temperate woody plants: From
230 trees to ecosystems. *New Phytologist* 191:926–41.
- 231 Prasad, A. 2003. Little's range and FIA importance value database for 135 eastern US tree
232 species. www.fs.fed.us/ne/delaware/4153/global/littlefia/index.html.
- 233 Savage, J. A., and J. Cavender-Bares. 2013. Phenological cues drive an apparent trade-off
234 between freezing tolerance and growth in the family salicaceae. *Ecology* 94:1708–1717.
- 235 Wolkovich, E. M., A. K. Ettinger, D. Flynn, T. Savas, C. Chamberlain, D. Buonaiuto, and
236 J. Samaha. 2019. Observed spring phenology responses in experimental environments
237 (OSPREE). doi:10.5063/F1CZ35KB.
- 238 Zohner, C. M., B. M. Benito, J. D. Fridley, J.-C. Svenning, and S. S. Renner. 2017. Spring
239 predictability explains different leaf-out strategies in the woody floras of north america,
240 europe and east asia. *Ecology Letters* 20:452–460.

²⁴¹ **Figures**

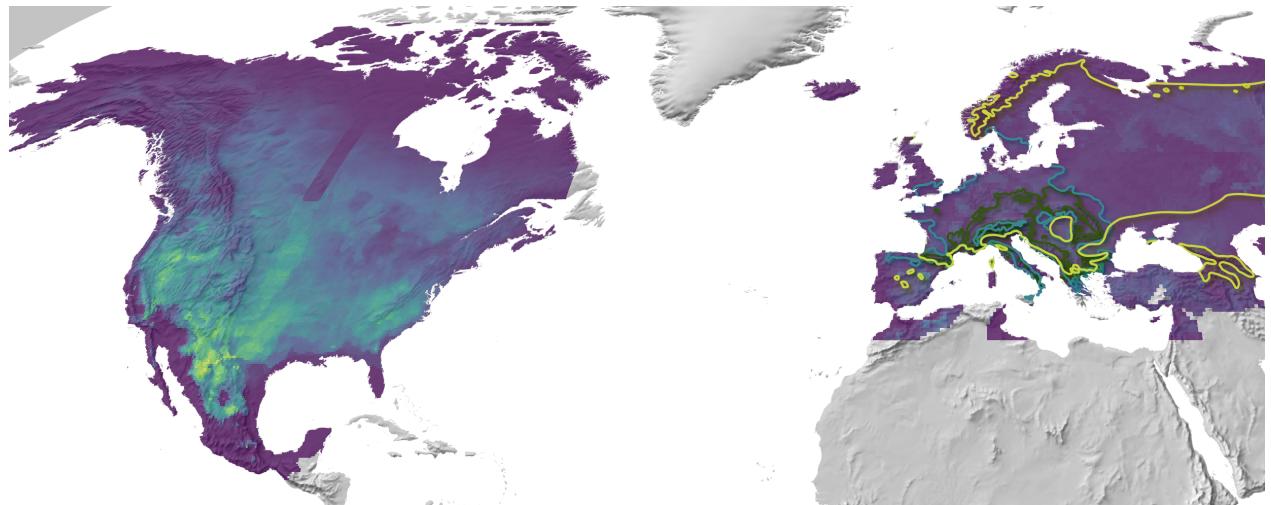


Figure 1: Contrasting patterns of spring predictability in North America and Europe.

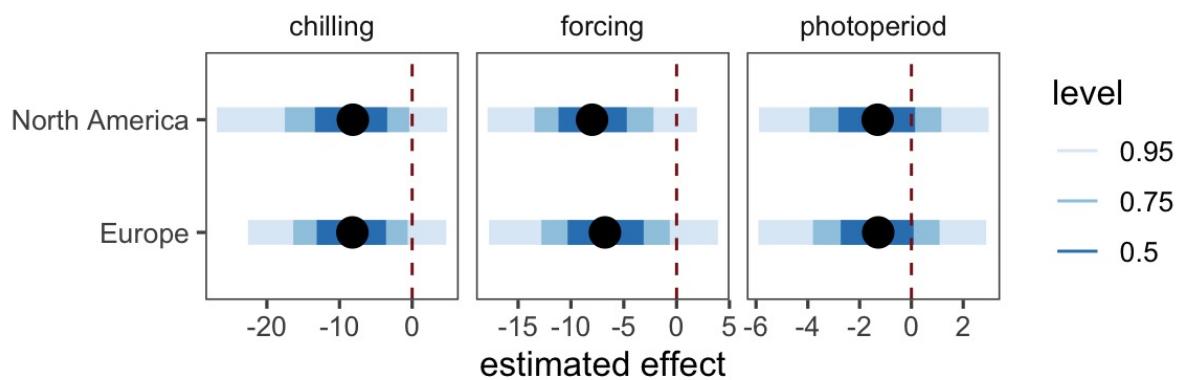


Figure 2: No difference between continents

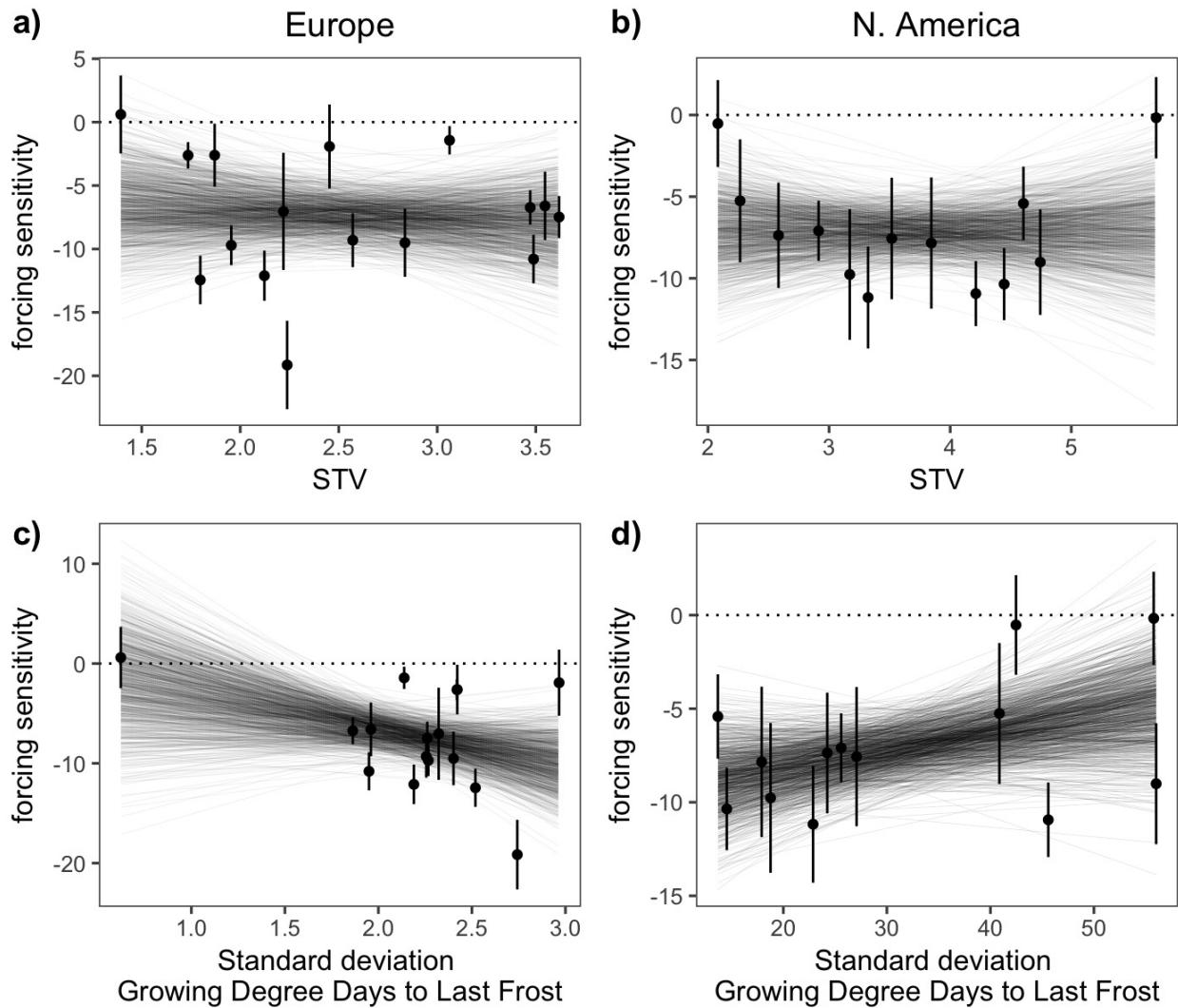


Figure 3: Forcing

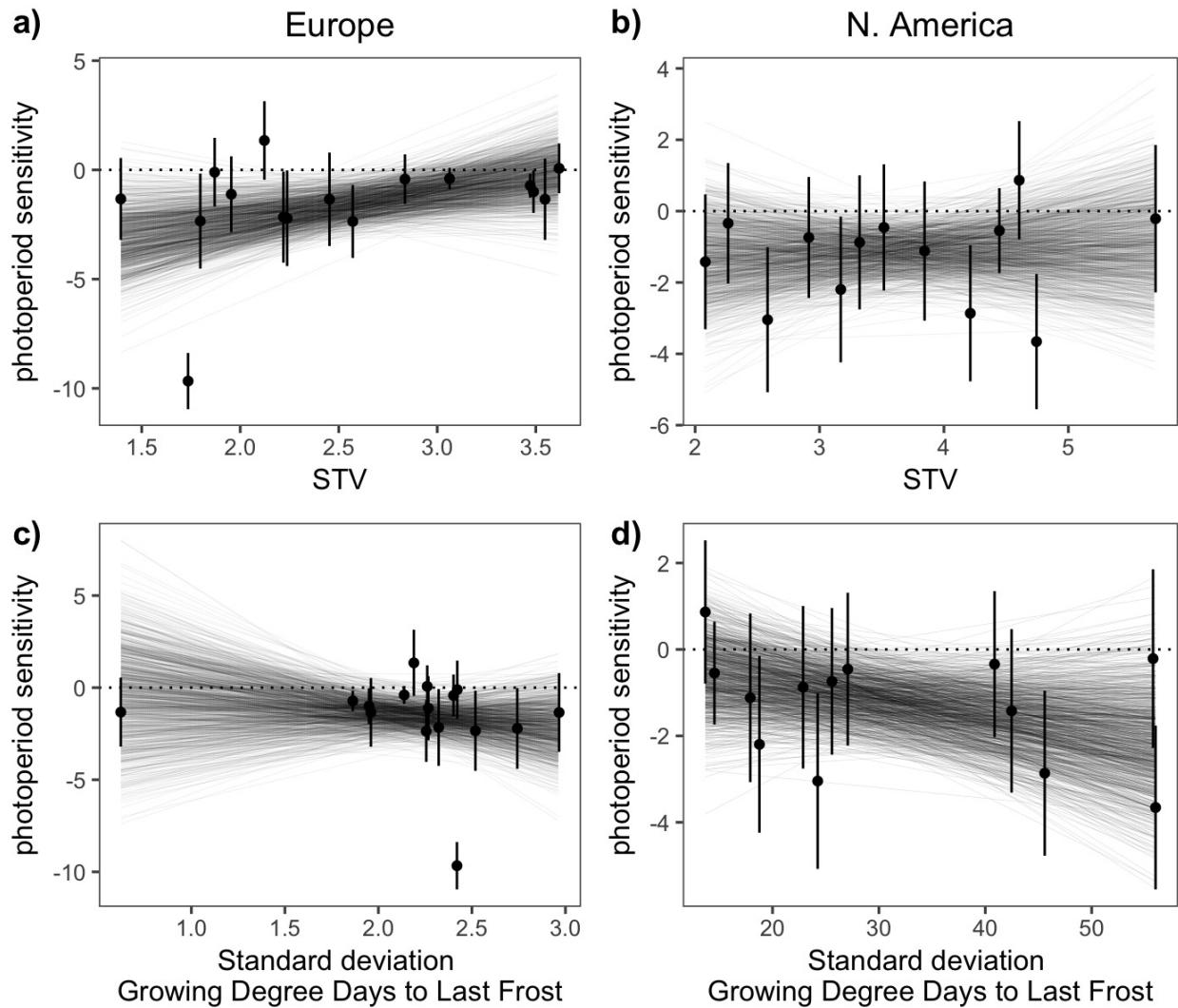


Figure 4: Photoperiod

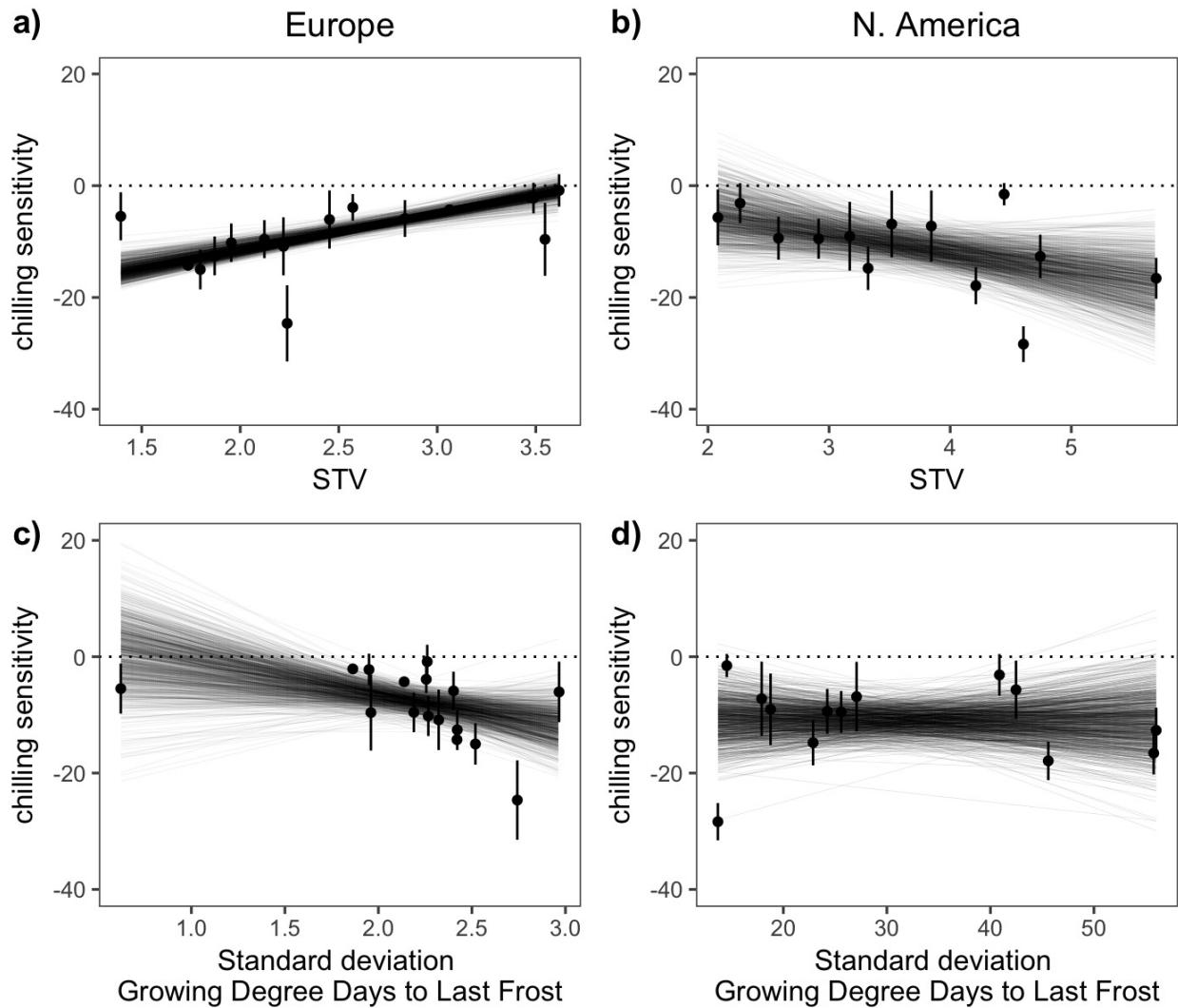


Figure 5: Chilling

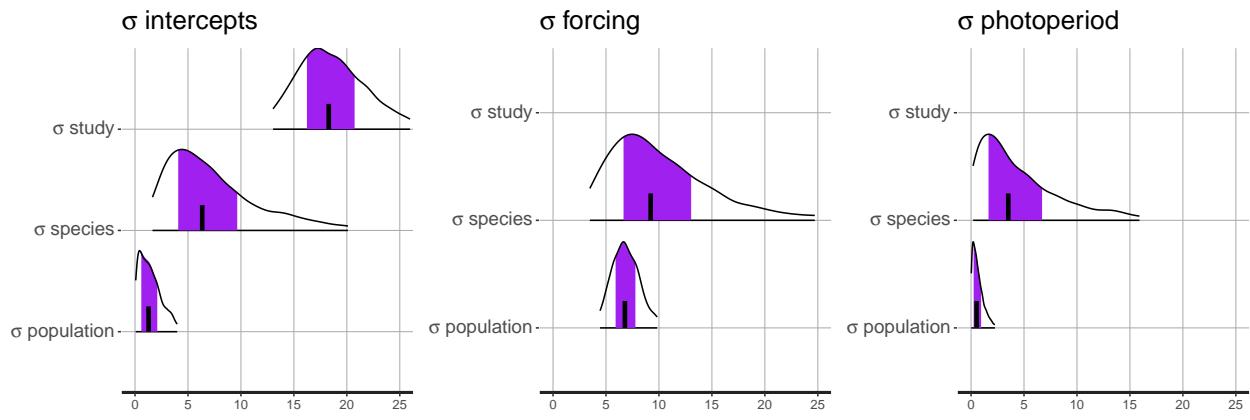


Figure 6: Local adaptation model estimates of variation partitioning in the intercept and forcing and photoperiod predictors using the OSPREE dataset. For both the forcing and photoperiod predictors, within species (intra-specific) variation is much smaller than across species (inter-specific) variation. Here we see that inter-specific variation exceeds intra-specific variation at the intercept-level as well but variation at the study level is largest, suggesting experimental design is driving the highest level of uncertainty.