

Patterns of spring-freeze risk across the geographic ranges of temperate trees contributes to their phenological cue differences, but leaves much unexplained Other

Dan, Cat, Nacho, Ben Cook, Faith, Deidre, Mira Geoff and Lizzie

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Abstract

Introduction

Phenology, the timing of annual life cycle events, allows for organisms to match critical life-cycle transitions with optimum environmental conditions. Through the phenology of spring budburst, temperate woody plants balance the advantages of precocious growth resumption for resource gains with the risk of damage from late season freezes (Savage and Cavender-Bares, 2013). To navigate this trade-off, woody plants have evolved complex physiological responses to sense environmental cues that signal the arrival of appropriate conditions for resuming growth. Decades of research on phenology have elucidated these environmental cues, suggesting that warming spring temperatures (forcing), cool winter temperatures (chilling) and day length (photoperiod) are primary environmental cues utilized by woody plants to determine the timing of spring phenological events (Ettinger et al., 2020; Forrest and Miller-Rushing, 2010). Yet These studies also demonstrate that there are substantial cue-use differences among species, with some species relying more heavily on some cues over others (Laube et al., 2014). However, our knowledge about why species differ in their cue responses

is currently limited, and better understanding the ecological and evolutionary drivers that shape phenological cues is critical for our ability to the magnitude and impacts of phenological shifts with climate change.

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

Continental Climatic Pattern

Global circulation patterns generate substantially different spring climatic conditions on either side of the North Atlantic (). In Eastern North America, the spring is marked by instability, while in Europe, the arrival of spring is generally more consistent (Figure 1). Given these contrasting climate regimes, the SPH predicts that North American species should have stronger sensitivity to chilling and photoperiod and weaker to forcing (?). We tested these predictions using phenological observations from the OSPREE database () with Bayesian Hierarchical models developed by ? to estimate species level cues and account for phylogeny. We compared the cue sensitivities of North American and Europe species by extracted all species level posterior estimates for forcing, chilling and photoperiod sensitivity and grouping them by continent to which species' were native (See Supporting Information: Methods for details).

There were no substantial differences in clue sensitivity between continents (Fig 2). Mean forcing sensitivity for European species was $-6.76 \text{ UI}_{95}(-17.80, 2.08)$ and $-7.94 \text{ UI}_{95}(-17.90, 1.93)$ for North A

8.44 $UI_{95}(-22.60, 4.69)$ and $-8.76UI_{95}(-26.90, 4.82)$ for North American species. Mean photoperiod sensitivity is 1.36 $UI_{95}(-5.91, 2.89)$ and $-1.35UI_{95}(-5.88, 2.98)$ for North American species.

This finding does not support to the SPH, though it is not particularly surprising given that recent studies have found there to be strong phylogenetic conservatism in phenological cue responses, and that there are many closely related congeners found in both North America and Europe. It is therefore likely that patterns of cue use diverged among taxa well before the modern placement of continents, under different climate conditions than North America and Europe experience today. (wow say better).

This finding calls into question the recent assertion that European plant species successfully invade North American ecosystem because their higher reliance on forcing cues allows them to leafout earlier and gain a growth advantage over their competitors (?). While these kinds of 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 (Sup Fig), which may further explain the pervasiveness of the idea that European invaders are successful in North America due to weaker secondary phenological cues.

Range Patterns

Instead of continental-scale patterns of biogeography driving divergent evolutionary trajectories of cue use, it is also possible that phenological responses to cues play a more important role in determining species range limits (Chaine). The distributions of species that rely primarily on forcing, should be restricted geographic regions where spring predictability is high, while species that rely more heavily on chilling and photoperiod can persist in regions where spring predictability is low. If this is the case, the SPH predicts that within each continent, species with higher chilling and photoperiod cue responses should be associated with lower spring predictability across their ranges.

We tested this prediction by regressing the species-level posterior estimates of forcing, chilling and photoperiod sensitivity from our previously described model against the two metrics of

spring predictability: Spring Temperature Variability (STV), defined as the standard deviation of mean minimum temperature from March-May (Zohner et al., 2017, See Supporting Information Methods), and the standard deviation in growing degree days to last frost. We analyzed this relationship between spring predictability and cue responses using a Bayesian hierarchical framework, with separate models for each cue by continent (see Supporting Information: Methods for details).

When we used STV as our 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* 6.37 , $UI_{95}[3.99, 7.97]$). *For North American species, spring predictability also had no clear relationship to forcing* -0.05 , $UI_{95}[-2.26, 2.06]$, *mean photoperiod effect* : 0.15 , $UI_{95}[-0.93, 1.21]$). *For chilling, decreasing spring* -3.45 , $UI_{95}[-7.50, 0.69]$), *supporting the prediction of the SPH.*

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. While STV may be a reasonable proxy for spring predictability in many cases, it does not capture the within-season variability in frost risk that is what actually drives environmental filtering on phenological cues. A measure of variability in the number of growing degree days before the last frost is a more biologically realistic proxy for spring predictability

When we used standard deviation in growing degree days to last frost as our metric for spring predictability we observed different relationships between spring predictability and species-level cue sensitivity that 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* -0.80 , $UI_{95}[-3.62, 2.09]$). *In interpreting these relationships, it is important to recognize that the amount of va*

For North American species, decreased predictability was weakly associated with weaker forcing sensitive 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* (-0.02 , $UI_{95}[-0.34, 0.31]$). *For photoperiod sensitivity, we observed a moderate association between decreasing* -0.04 , $UI_{95}[-0.11, 0.04]$).

This observed relationship between spring predictability and photoperiod match the expectations of the SPH. Photoperiod is generally the weakest cue influencing spring phenology (Ettinger et al., 2020), and there is comparatively little interspecific variation in cue strength compared to forcing and chilling (?).

In sum, our analyses of the relationships between spring predictability across species' ranges and those species' estimates phenological sensitivity to forcing, chilling and photoperiod offer only marginal support at best 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 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, though as we caution above, we feel that given the low levels of variability in in GDDs to last frost observed in Europe, it is hard to imagine this climatic element exerting strong filtering pressure on species' ranges. While these three facets of the predictability/cue relationship support the expectations of the SPH, all other aspects of the predictability/cue relationship either show no relationship (i.e. forcing & photoperiod effects with STV in Europe & North America) or observed relationships contrary to the expectations of the SPH (i.e., chilling in Europe with STV and forcing in North America with Stdv. GDDs). We argue that these mix results should not serve to refute the claims of the SPH; it is clear that spring predictability has a role to play in shaping where, and how species successfully leaf out. However, our study indicates a more complicated picture of the factors that shape species' level differences in phenological cues. We discuss these aspects in the sections below.

Does local adaptation swamp the SPH

One possible reason for the weak support for the SPH we found in our analyses is that local adaptation in phenological cue sensitivity overwhelms any relationship between species-level cue use and range-wide climate conditions. There is currently a debate about the extent to which local adaptation shapes phenological cues (), and it is likely the strength of local adation varies among species, and phenological phases themselves (). However, if cues are locally adapted, it follows that neither continental differences or range wide climate conditions would be strongly associated with cue use.

To assess this possibility in our data, we designed a two-level, hierarchical model for studies in the OSPREE database that sampled species from multiple provenance locations. We model study, species and population as intercepts, forcing and photoperiod as predictors (fixed effects) with species nested within population (i.e., site) as modeled groups (random effects). While we detected limited population level variation in forcing and photoperiod cue sensi-

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

Phenological cue differences: More than climate drivers

Our results do not support the simple predictions of the Spring Predictability Hypothesis. This lack of support does not inherently challenge the theoretical importance of spring predictability in driving selection of cue sensitivity, but calls into question the wisdom of related differences in phenological sensitivity to the contemporary environmental conditions that species experience in their present ranges. As mentioned above, several studies have identified a strong phylogenetic signal in cue sensitivity (Nacho and Others), suggesting that if spring predictability shaped modern-day cue responses in woody plants, we would need to look to the paleo-environment to see such an association. The lack of support for the SPH further supports evidence that species phenological responses are not in equilibrium with their environment—we know that species ranges are still rebounding from the most recent glacial period (). In North America, where the predictability of spring varies substantially across the continent, high chilling sensitivity may have allowed some species to expand their ranges into regions where spring predictability is low but this pattern was not apparent in Europe, where spring predictability is consistently high across the continent.

While the combination of strong phylogenetic conservation and climate disequilibrium is alone a good enough explanation for why this relationship is weak, there are other selective factors that may be drivers of cue differences among species. Recently studies have connected phenological cues to functional traits (Deirdre) community assembly, and niche partitioning (). The role of community interactions in shaping cue sensitivity patterns within a community could be explored more (Maybe Lizzie has more to say on this based on her coexistence review).

1 Conclusion:

In this study we found limited support for the assertion that the predictability of spring that species encounter across their geographic ranges shape their relative reliance on 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 benefit from 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 will impact species performance in the face of global change at across multiple spatial and temporal scales.

References

- Ettinger, A. K., C. J. Chamberlain, I. Morales-Castilla, D. M. Buonaiuto, D. F. B. Flynn, T. Savas, J. A. Samaha, and E. M. Wolkovich. 2020. Winter temperatures predominate in spring phenological responses to warming. *Nature Climate Change* 10:1137–1142.
- Forrest, J., and A. J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3101–3112.
- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- Savage, J. A., and J. Cavender-Bares. 2013. Phenological cues drive an apparent trade-off between freezing tolerance and growth in the family salicaceae. *Ecology* 94:1708–1717.
- Zohner, C. M., B. M. Benito, J. D. Fridley, J.-C. Svenning, and S. S. Renner. 2017. Spring predictability explains different leaf-out strategies in the woody floras of north america, europe and east asia. *Ecology Letters* 20:452–460.

Figures

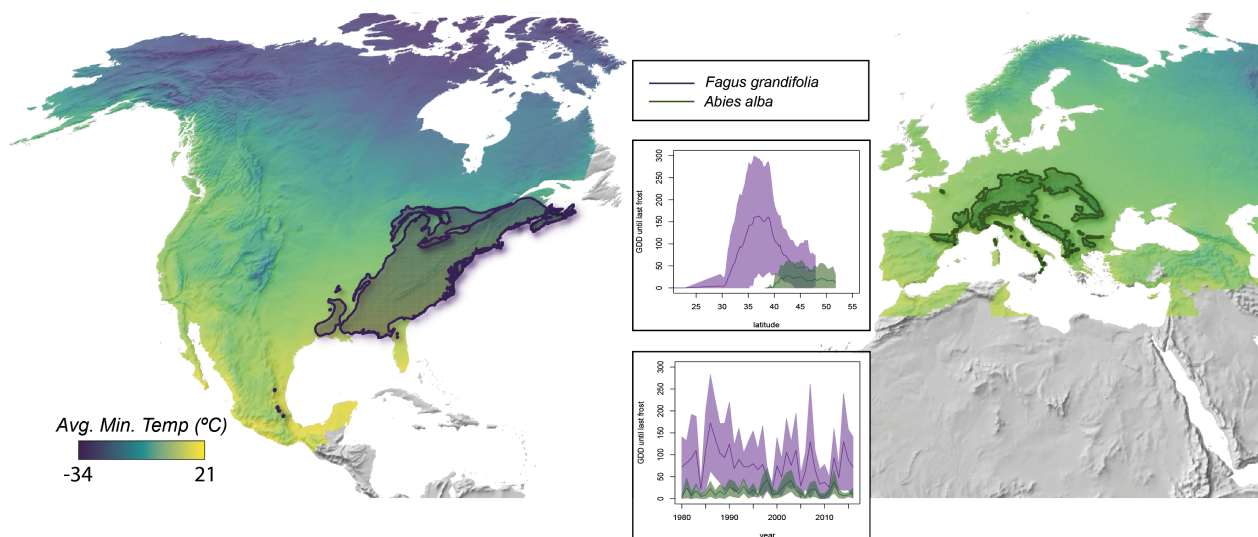


Figure 1: I am now thinking we should just have a figure comparing Spring variability on North America vs. Europe

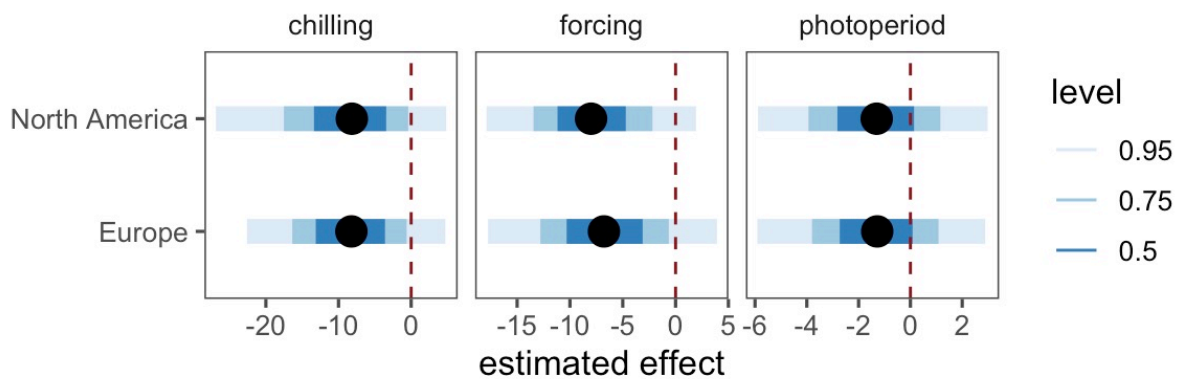


Figure 2: No difference between continents

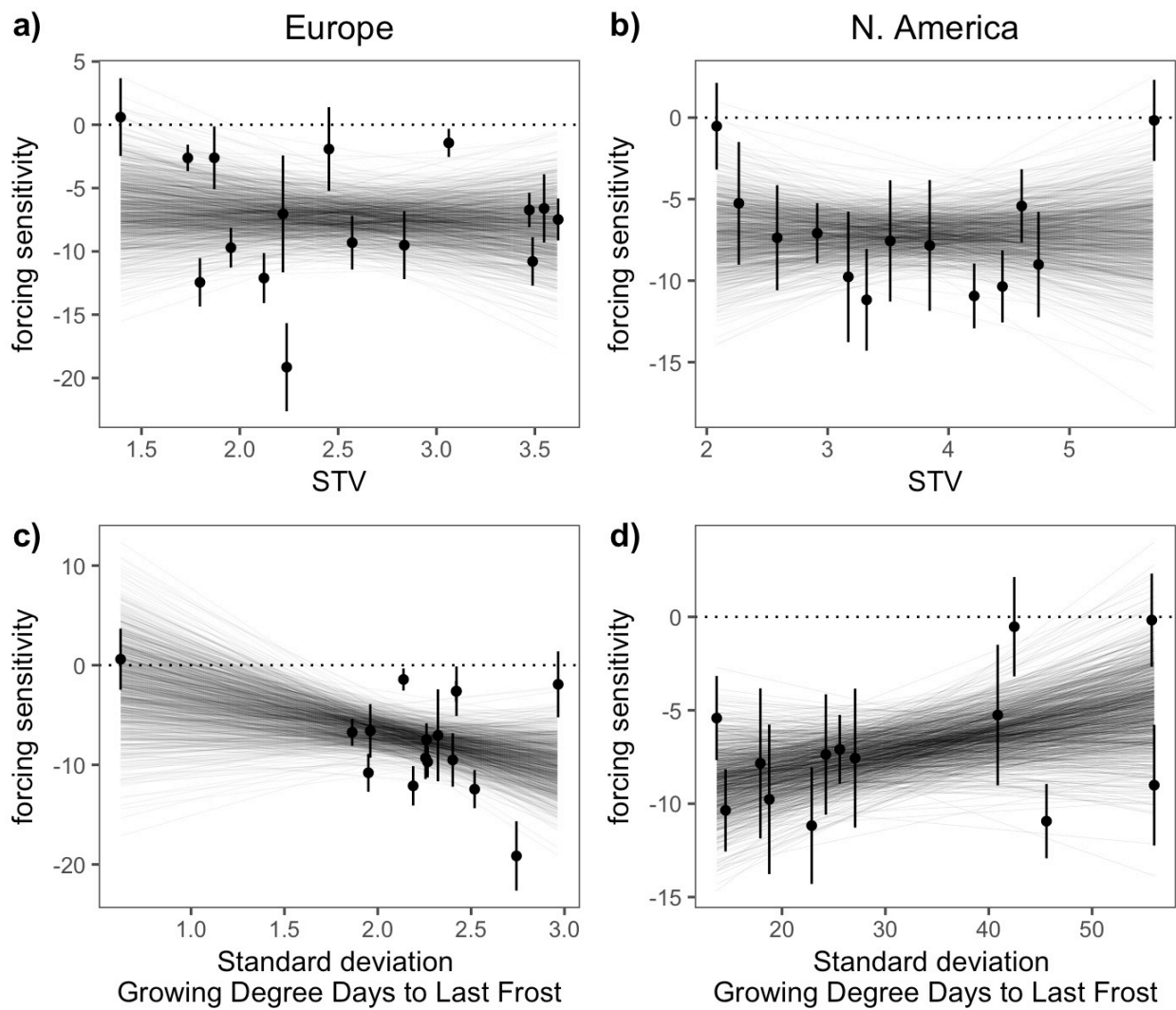


Figure 3: Forcing

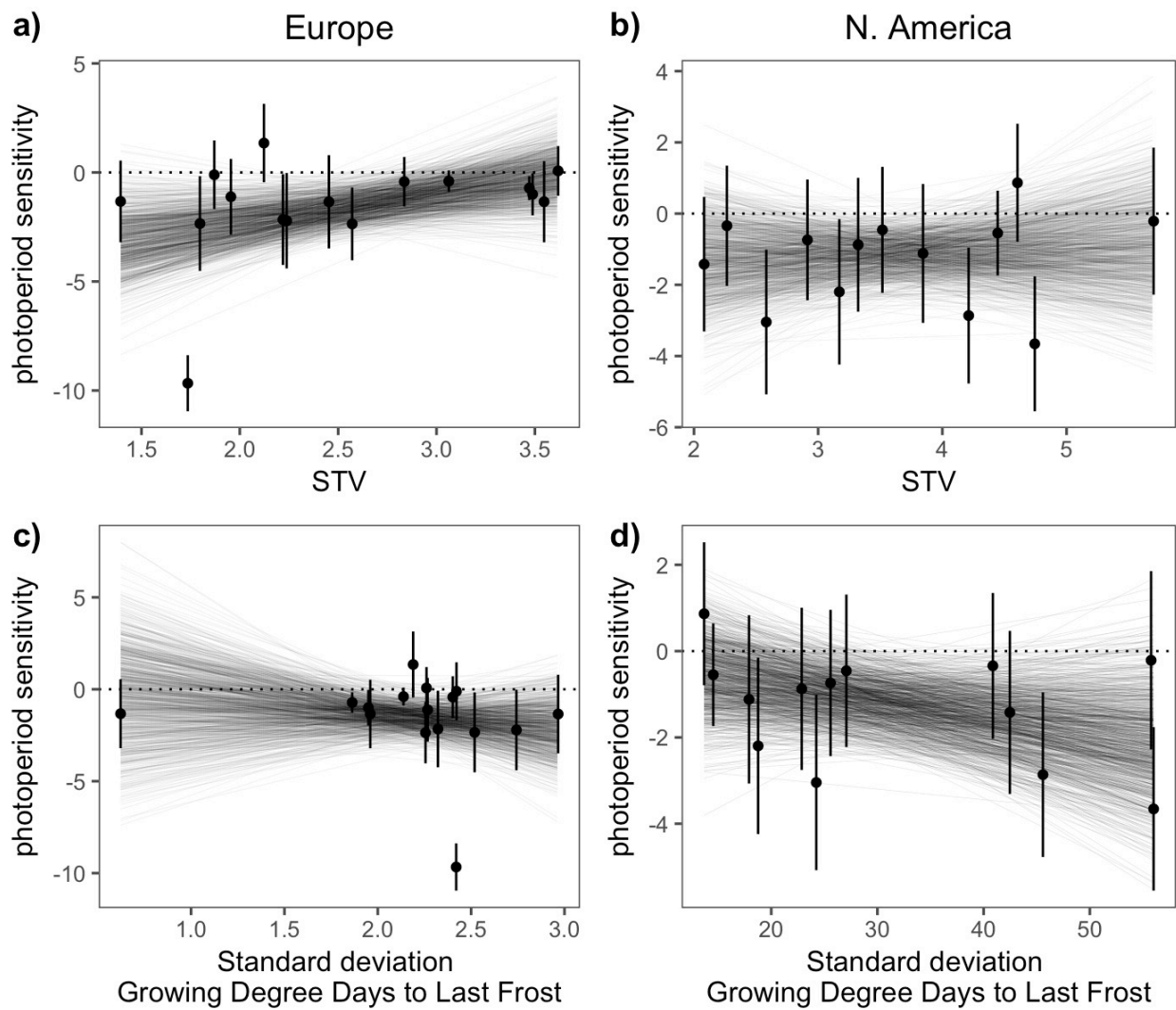


Figure 4: Photoperiod

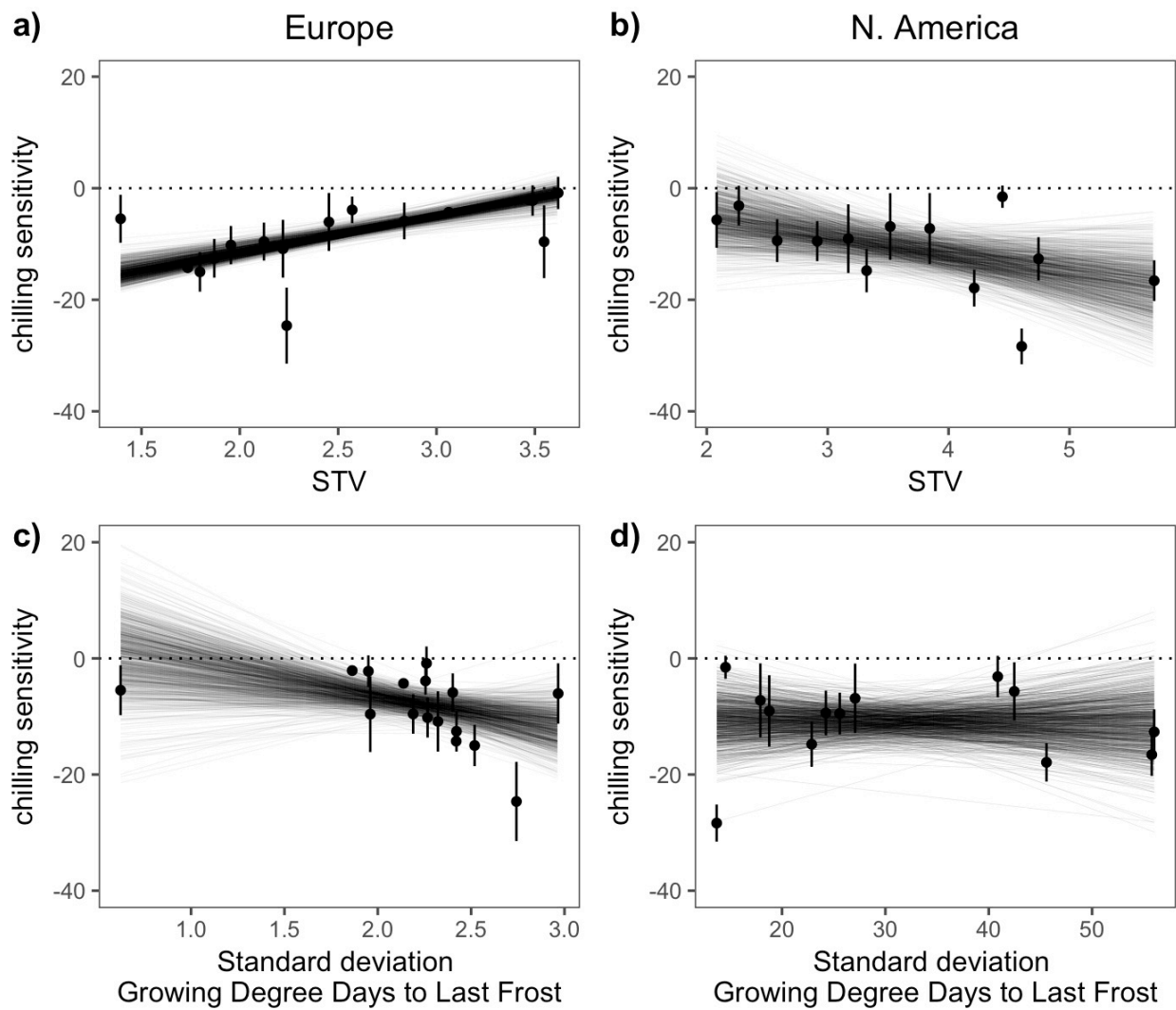


Figure 5: Chilling

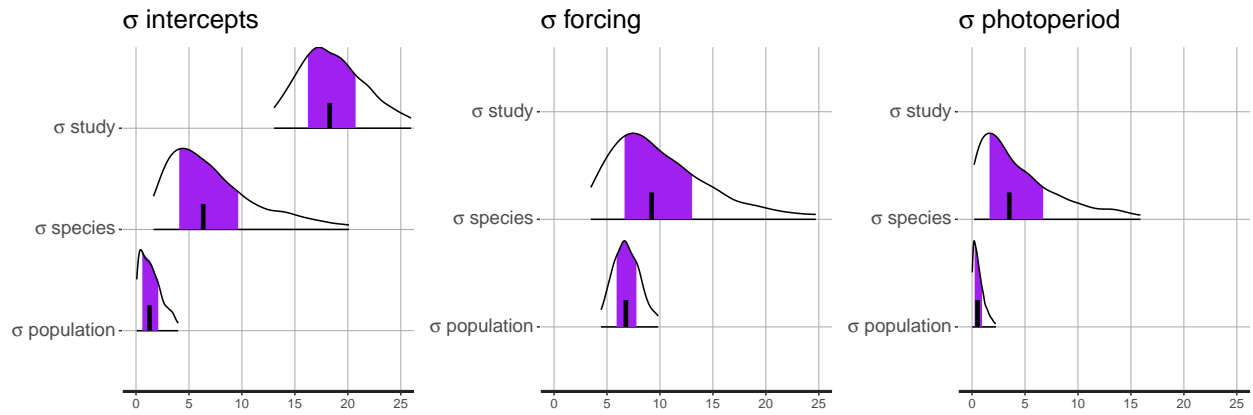


Figure 6: **Local adaptation model estimates of variation partitioning in the intercept and forcing and photoperiod predictors using the OSPREE dataset.** For both the forcing and photoperiod predictors, within species (intraspecific) variation is much smaller than across species (interspecific) variation. Here we see that interspecific variation exceeds intraspecific 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.