

Unravelling the phenology-phylogeny tangle.

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Results & Discussion

Most species are sensitive to all three primary cues—forcing, chilling, and photoperiod (Figs. 1, Supporting Table ??)(see also Laube et al., 2014; Ettinger et al., 2020)—with sensitivity to chilling approximately five-fold greater than sensitivity to photoperiod, on average (phenological advances of 7.2 days per standardized unit vs 1.4 days, for chilling and photoperiod, respectively; see Table ??). However, these average sensitivities estimated across species, fail to capture the large differences in species’ responses to chilling and forcing (Figs. 1, Supporting Table ??).

By allowing species responses to vary, based on a model including their shared evolutionary history, we found species differences dwarfed differences between cues, especially temperature cues (Fig. 1). The largest in magnitude cue—chilling—varied 25-fold between species, while variation to forcing varied 6-fold. These results suggest the strong focus on comparing cues may miss the largest variation. Robust phenological forecasts must then account for both the complexity of multiple cues and species-level variation in responses to them.

Differences across clades & cues

The large differences across species generally occurred coherently within clades, producing striking differences between clades. Oaks and beeches (Fagaceae), elms (Ulmaceae) and buckthorns (Rhamnaceae) are highly sensitive to chilling while rhododendrons (Ericaceae), butterfly bushes (Scrophulariaceae) or spindles (Celastraceae) show little to no response to chilling (Fig. 1 a). Similar clade-level variation was observed for forcing, where some of these clades—e.g., Ericaceae, Rhamnaceae, Ulmaceae, or Fagaceae—were particularly sensitive (advancing their budburst more than 10 days per standardized unit of forcing) and others such as the Sapindaceae, Cornaceae or Juglandaceae families show little response (Fig. 1 b).

Some species responded strongly to both temperature cues (chilling and forcing), which could suggest the existence of syndromes where the genetic basis for responses to one cue (e.g., forcing) has been selected for alongside responses to another cue (e.g. chilling). We might expect, for example, early-season species to be sensitive to multiple cues as mistiming phenology could result in exposure to harsh conditions, leading to tissue loss or death (Sakai and Larcher, 1987), and sensitivity to multiple cues likely provides greater insurance against mistiming (Wolkovich and Donahue, 2021). Alternatively or additionally, linkage or pleiotropism among loci associated with sensitivity to different cues (Nakagawa et al., 2005) could induce correlated cues. However, the correlation in species sensitivities across cues was weak ($r = 0.31$; between forcing and chilling) and some genera, such as *Tilia* and Ericaceae[genus?], displayed strong responses to forcing but weak responses to chilling, while others, such as XXXXExamplesXXXX, show strong responses to chilling but weak responses to forcing (Fig. 1). Species sensitivity to one cue, thus, does not constrain sensitivity

to another cue, and selection might operate independently on responses to different cues (Bonamour et al., 2019).

In contrast to both chilling and forcing, species-level responses to photoperiod were almost uniform—present across nearly all species. This provides novel insight on a large debate over the prevalence of photoperiod cues in temperate trees, where previous experiments (Basler and Körner, 2012; Zohner et al., 2016) and modeling exercises (e.g., Hunter and Lechowicz, 1992; Schaber and Badeck, 2003) suggested important variability across species that may constrain the responses of certain species to warming (Way and Montgomery, 2015). Our results suggest variability is constrained to a very limited set of species in Fagaceae, which have been heavily studied, including *Fagus sylvatica* (e.g., Basler and Körner, 2012; Zohner et al., 2016; Kramer et al., 2017). These same few species are also where most evidence of local adaptation in photoperiod cues for spring phenology comes from (e.g., Kramer et al., 2017), in contrast with common garden studies of other species, which found little evidence of local adaptation in spring (but not fall) phenology (Aitken and Bemmels, 2016). The uniformity of response to photoperiod that we found supports this latter view of generally low local adaptation in photoperiod cues for spring phenology: given that studies spanned a range of latitudes (with many species studied in only a narrow latitudinal range), if local adaptation was high in photoperiod cues we would expect more variability across species.

Our results suggest that while chilling and forcing are the dominant cues in terms of the magnitude of their effect sizes, most species are also sensitive to photoperiod, highlighting the potential importance of this cue to both climate change responses in the future, and through evolutionary history. In plants, photoperiod regulates a number of fundamental processes including growth, flowering, stress tolerance, and circadian rhythm (Serrano-Bueno et al., 2017; Singh et al., 2017), with photoperiodic sensing and adaptation to shifting daylength likely occurred early in the evolution of plants, with origins in the green algae (Serrano-Bueno et al., 2017). It is possible, therefore, that phenological responses to photoperiod reflect ancestral sensitivities with origins in deep time. Large plasticity in responses to additional environmental cues (e.g., temperature) for a given photoperiod cue (e.g., Kramer, 1995) may allow species to track interannual variation in climate with little directional selection on photoperiod sensitivities. Alternatively, photoperiod might thus provide a reliable calibration of the underlying biological clock (Jackson, 2009) upon which seasonal variation in climate modifies the tempo.

Phylogenetic structure of phenological cues

Variation—or lack thereof—in cues across species and clades, alongside related estimates from our modeling approach, provides possible insights into the evolution of cues across the phylogeny. While responses to each cue were phylogenetically structured, the strength of phylogenetic conservatism in response differs between cues (Fig. 3). Responses to temperature (forcing and chilling) were moderately structured ($\lambda = 0.65$

and $\lambda = 0.54$, for forcing and chilling, respectively), with closely related species exhibiting more similar sensitivities than distantly related species. Phylogenetic structure in species responses to photoperiod was comparatively weaker ($\lambda = 0.39$) (see Fig. ??, Table ??), emphasizing again that photoperiod diverges from other climate cues. In addition to be weaker and more uniform across species, sensitivity to photoperiod appears to also be less evolutionarily constrained than sensitivities to temperature cues. While our approach is unique in focusing on species cues, our results support previous work showing phylogenetic signal in plant phenological timing observed from floras or long-term data Kochmer and Handel (1986); Davies et al. (2013)

What might drive phylogenetic structure in species temperature responses? Differences between species in their responses represent shifts in the slope of the relationship between the observed phenology and the cue. Thus, the observed phylogenetic structure in temperature responses (forcing and chilling) would be consistent with an interaction with a non-measured trait that moderates responses, and which also covaries with phylogeny (Davies et al., 2019). This fits fundamentally with the idea that early-season phenology plays a critical role in shaping species temporal niches (Gotelli and Graves, 1996) and thus should covary with a suite of life-history traits, including whether species are early-active with other rapid return on investment trait, or start later in the season but have higher competitive abilities (e.g., Wolkovich and Cleland, 2014). Geography may drive structured phylogenetic variation, especially in regions where clades have radiated such that close relatives have experienced the same suite of environmental cues and thus been subject to similar selection regimes. Conversely, if species are not generally geographically constrained, as may be more likely the case, especially across deep time (Fitzpatrick and Turelli, 2006), then we might expect phylogenetic structure in phenology to also weaken, especially when aggregating across locations with different cues (Davies et al., 2013).

Weak phylogenetic signal in photoperiod sensitivity (Fig. 3) might seem at odds with observations that distantly related species respond more similarly (and less variably) to photoperiod than they do to forcing or chilling. However, somewhat counterintuitively, both uniform and random responses can manifest as low phylogenetic signal when estimated by Brownian motion expectations (see Wiens et al.). Rapid local adaptation within species might thus erase the phylogenetic structure in photoperiod responses, but seems at odds with the uniformity we find in species' responses. Alternatively, if responses to photoperiod evolved early in plants, as we suggest above, and subsequent selection on photoperiod sensitivity was constrained by stabilizing selection operating on other life-history attributes sensitive to photoperiod (e.g., Rinne et al., 1994; Wilczek et al., 2014; Azeez and Sane, 2015), we would predict both low interspecific variation and weak phylogenetic signal in responses, matching observations. This latter interpretation is also consistent with our estimates of lower σ for photoperiod responses (CITE FIGURE). Here, as in more traditional phylogenetic comparative methods, σ represents the rate of evolution, and thus our results suggest photoperiod responses are also evolving slower than temperature responses. However, we also show (see Appendix XXX) that an

early burst model of evolution, in which trait variation accumulates rapidly early in the history of a clade and then slows through time, consistent with our interpretation of photoperiod evolution.

Phylogenetic conservatism (high λ) and slow evolutionary rates (low σ) in traits has sometimes been interpreted as indicative of evolutionary constraints to adaptive change (cite Wiens et al. and others cites XXX). If this were the case, we might then suggest that species with strong forcing response might be more vulnerable to future warming because phylogenetic conservatism (λ) in responses to forcing is higher compared to other cues, and its evolutionary rate (σ) is lower. This is misleading, however, as estimates of λ are independent from the rate of evolution, and macroevolutionary rates estimated on phylogenetic trees that integrate across millions of years of evolutionary history, and thus do not necessarily inform us of maximum possible rates of evolution over much shorter timescales. Indeed, there is accumulating evidence for rapid evolution to shifting climates Bradshaw and Holzapfel (2006); Franks et al. (2014). Our estimates of phylogenetic structure are thus more useful in improving our understanding of the evolutionary history of species phenological cues, and highlighting the importance of robustly estimating species differences in ecological forecasts.

Forecasting species-level responses

Our results highlight that species-level variability can be extremely high—when properly estimated. Our approach, which partially pooled species responses based on their shared evolutionary history, did not have major effect on the overall average across species (model slopes for forcing and chilling shifted by 7.2% and 3.7%, respectively; Fig. 4), but estimated substantially higher variation across species compared with widely used hierarchical models. This was especially noticeable in temperature responses (for chilling variance across species was $\beta_{phylo} = 23.45$ compared to $\beta_{non-phylo} = 17.47$, for forcing it was $\beta_{phylo} = 8.74$ compared to $\beta_{non-phylo} = 5.01$) while photoperiod, which had low phylogenetic structure was more similar across approaches (variance of $\beta_{phylo} = 0.82$ compared to $\beta_{non-phylo} = 0.93$). Counterintuitively, induced reductions in cross-species variance, far from increasing estimation accuracy could lead to increased type-II error by failing to detect actual relationships among cue and responses that would only emerge when phylogeny is correctly accounted for (see Supporting Information XX).

The increase in variability across species in our model with phylogenetic structure decreased the uncertainty in estimates for each individual species temperature responses. Thus, traditional approaches that partially pool across species may also lead to less precise predictions and forecasts of phenology for individual species although overall model accuracy might still appear reasonable (see Appendix XX in Supporting Information).

Our results could help inform which clades will be more sensitive to different axes of climate change—e.g., changes temperatures over winter (associated with chilling) versus spring (associated with forcing). For example, using a hierarchical model would not have identified oaks (genus *Quercus*) as being among the most sensitive taxa to forcing and chilling (see e.g., (Ettinger et al., 2020)), but we show that species within this

genus advance phenology by 2 days per standard unit of forcing and 4 days per standard unit of chilling. These results highlight the need to move beyond current very general classifications currently used in models (e.g., functional groups ... Cat/Dan, can you offer better ref? Moorcroft, 2003) or groupings at coarse taxonomic levels (e.g., Ettinger et al., 2020) to make improved ecological forecasts for individual species.

The contrasts between temperature sensitivities and photoperiod sensitivities—in both their variability across species and phylogenetic structure—allow for improved multi-species forecasts. For temperature responses, the large variability among species makes predicting species individual responses challenging, but the phylogenetic structure in responses lets us borrow information from close relatives to improve our predictions. While this must be done with care (Molina-Venegas et al., 2018), especially given our very limited sampling of species, our results could provide reasonable predictions for many temperate woody plant species from clades for which we have multiple species and experimental observations at varying treatment levels. For photoperiod, the weak phylogenetic structure in responses indicates that phylogeny retains little information, but because species responses are generally more uniform, we can be more confident in assuming the mean species response across species, comforted in the knowledge that small errors will likely not have large impact given the relatively weak overall contribution of this cue, except for *Fagus sylvatica*. As *Fagus sylvatica* is nearly five times more sensitive to photoperiod than most other measured tree species, our results caution against using it to draw inferences of photoperiod responses more widely.

While we focused on spring phenology here, our modeling approach suggests a path towards more robust forecasting via useful species-level estimates of climate change responses. Our results show how including the phylogenetic relationship of species can overcome major limitations of most current hierarchical models (producing biased model estimates, underestimating the full variability across species, and increasing uncertainty around individual species’ estimates) while at once providing insight into the evolutionary history of biological responses. [And, bam, something a little more here ...]

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Tables and Figures

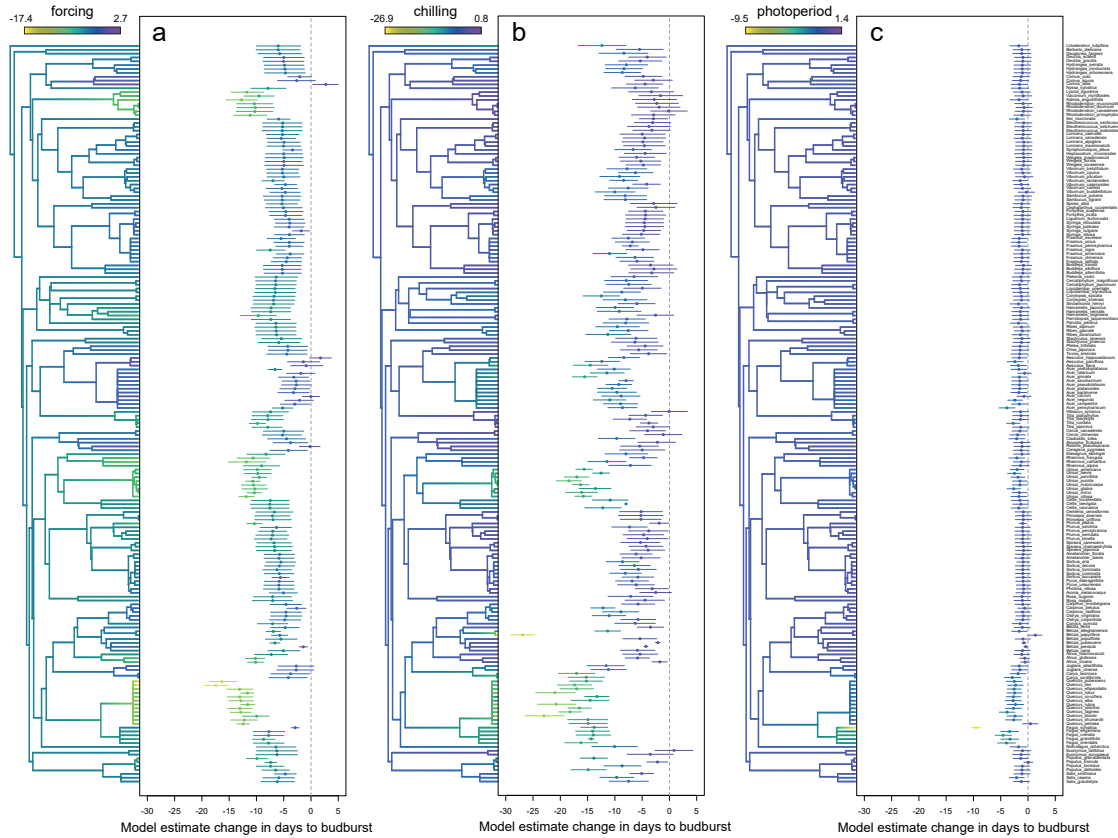


Figure 1: Phenological sensitivity to three environmental cues, forcing (a), chilling (b) and photoperiod (c) measured in change in days to budburst per standardized unit (z-transformation) of the cues across 192 angiosperm species. The same phylogenetic tree is shown in each panel, colored according to an estimation of ancestral character states, being the states at the tips the model slopes of our hierarchical phylogenetic model. Note that the color scale varies in each panel. Total tree depth is 81. My.

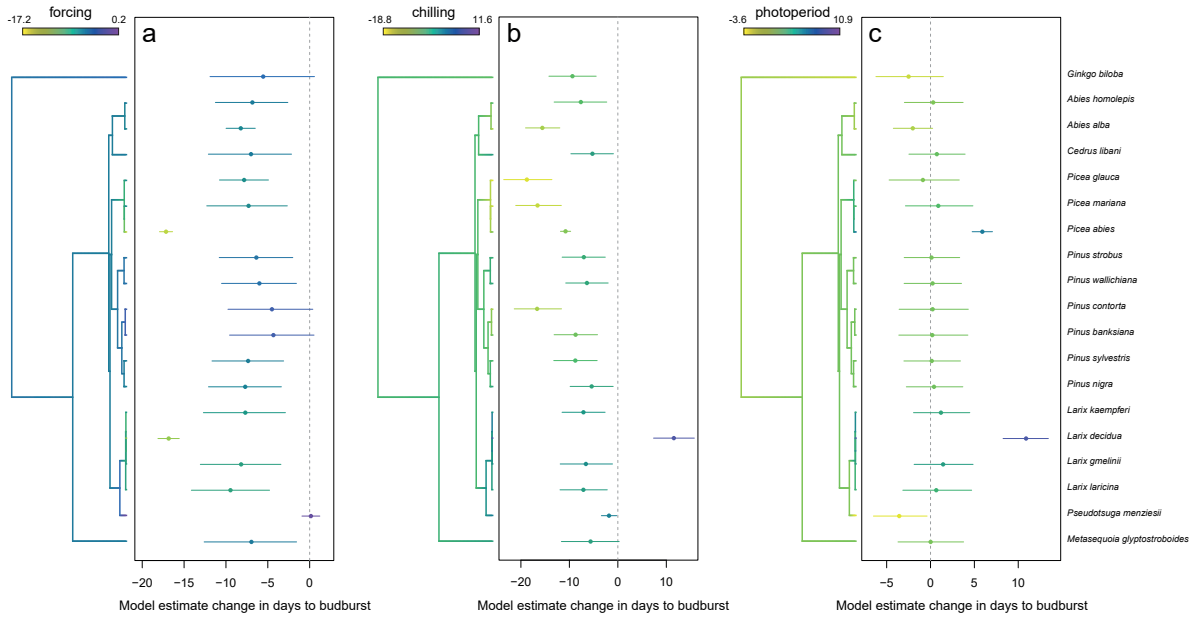


Figure 2: Phenological sensitivity to thee environmental cues, forcing (a), chilling (b) and photoperiod (c) measured in change in days to budburst per standardized unit (z-transformation) of the cues across 19 gymnosperm species. The same phylogenetic tree is shown in each panel, colored according to an estimation of ancestral character states, being the states at the tips the model slopes of our hierarchical phylogenetic model. Note that the color scale varies in each panel. Total tree depth is 81. My.

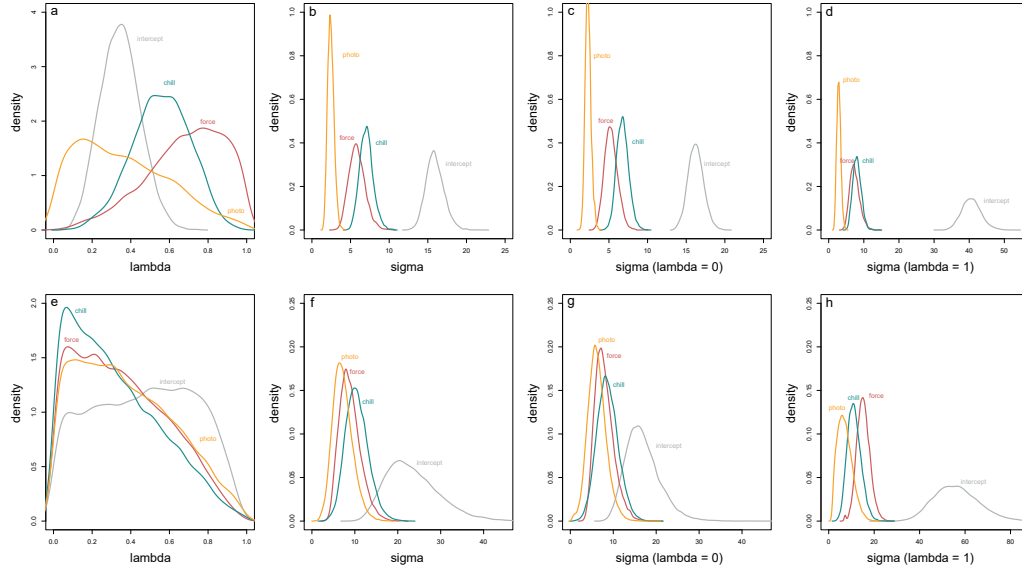


Figure 3: Density plots for the posterior distribution of phylogenetic signal measured by λ for each cue included as a predictor in the model for angiosperms: forcing (red), chilling (blue), photoperiod (orange) and for the model intercept (grey). Panels correspond to angiosperms (a-d) and gymnosperms (e-h). Note that λ estimations corresponding to panels c-d and g-h as they are constrained to be either equal zero or equal 1.

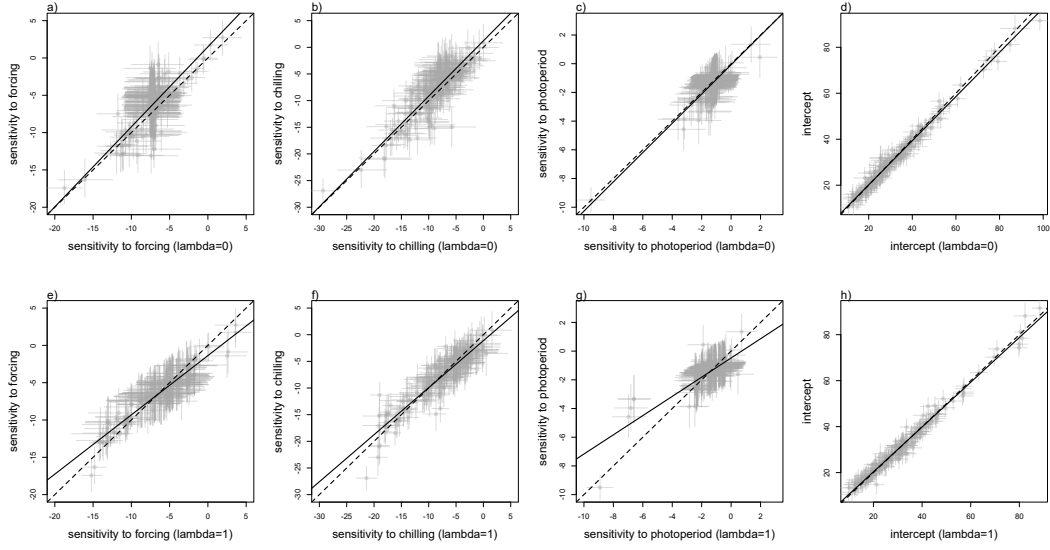


Figure 4: Correlations between model parameters as estimated by the full model and the models where λ is constrained to be equal zero (upper row) or one (bottom row), for angiosperms. Panels correspond to sensitivity to forcing (a,e), to chilling (b,f), to photoperiod (c,g) and to model intercepts (d,h).

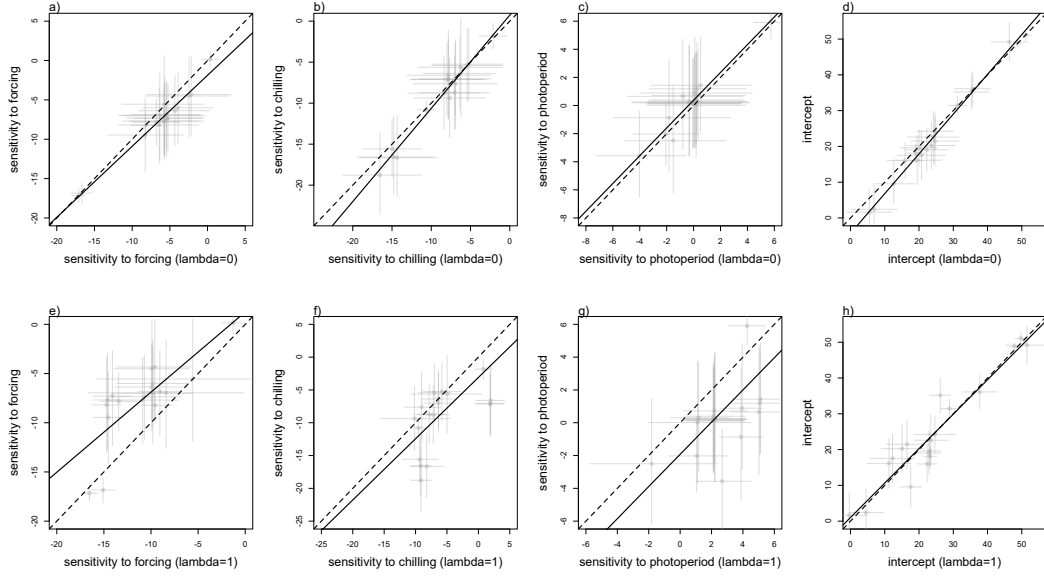


Figure 5: Correlations between model parameters as estimated by the full model and the models where λ is constrained to be equal zero (upper row) or one (bottom row), for gymnosperms. Panels correspond to sensitivity to forcing (a,e), to chilling (b,f), to photoperiod (c,g) and to model intercepts (d,h).

Table 1: Full model parameters estimated for 192 angiosperm species.

| parameter | mean | sd | 2.50% | 50% | 97.50% | n_eff |
|--------------------------------|-------|------|--------|-------|--------|---------|
| μ_α | 30.57 | 3.41 | 23.68 | 30.59 | 37.14 | 5031.19 |
| $\mu_{\beta forcing}$ | -5.84 | 2.01 | -9.72 | -5.89 | -1.79 | 2374.73 |
| $\mu_{\beta chilling}$ | -7.19 | 2.03 | -11.15 | -7.18 | -3.18 | 3694.93 |
| $\mu_{\beta photoperiod}$ | -1.37 | 0.76 | -2.92 | -1.35 | 0.14 | 1565.41 |
| λ_α | 0.35 | 0.10 | 0.16 | 0.34 | 0.56 | 3416.51 |
| $\lambda_{\beta forcing}$ | 0.68 | 0.20 | 0.23 | 0.71 | 0.98 | 185.35 |
| $\lambda_{\beta chilling}$ | 0.56 | 0.15 | 0.25 | 0.56 | 0.83 | 738.57 |
| $\lambda_{\beta photoperiod}$ | 0.36 | 0.24 | 0.02 | 0.33 | 0.88 | 296.51 |
| σ_α^2 | 15.93 | 1.17 | 13.84 | 15.85 | 18.41 | 2988.37 |
| $\sigma_{\beta forcing}^2$ | 5.84 | 1.04 | 4.03 | 5.78 | 8.15 | 502.74 |
| $\sigma_{\beta chilling}^2$ | 7.05 | 0.87 | 5.48 | 7.02 | 8.92 | 1026.77 |
| $\sigma_{\beta photoperiod}^2$ | 2.45 | 0.41 | 1.74 | 2.42 | 3.32 | 469.46 |
| σ_y^2 | 12.81 | 0.18 | 12.47 | 12.80 | 13.17 | 4017.16 |

Table 2: Full model parameters estimated for 19 gymnosperm species.

| parameter | mean | sd | 2.50% | 50% | 97.50% | n_eff |
|--------------------------------|-------|------|--------|-------|--------|----------|
| μ_α | 25.75 | 4.50 | 16.88 | 25.73 | 34.73 | 33151.86 |
| $\mu_{\beta forcing}$ | -5.92 | 3.80 | -12.97 | -6.05 | 1.90 | 16443.03 |
| $\mu_{\beta chilling}$ | -8.11 | 3.63 | -15.31 | -8.09 | -0.94 | 21379.81 |
| $\mu_{\beta photoperiod}$ | -0.88 | 3.33 | -8.01 | -0.67 | 5.19 | 16301.93 |
| λ_α | 0.47 | 0.26 | 0.02 | 0.48 | 0.90 | 15934.03 |
| $\lambda_{\beta forcing}$ | 0.36 | 0.23 | 0.02 | 0.33 | 0.84 | 14336.60 |
| $\lambda_{\beta chilling}$ | 0.32 | 0.23 | 0.01 | 0.28 | 0.82 | 13230.88 |
| $\lambda_{\beta photoperiod}$ | 0.37 | 0.24 | 0.02 | 0.34 | 0.88 | 11199.49 |
| σ_α^2 | 23.47 | 6.20 | 13.87 | 22.59 | 37.81 | 18272.58 |
| $\sigma_{\beta forcing}^2$ | 8.89 | 2.45 | 4.96 | 8.60 | 14.51 | 8126.51 |
| $\sigma_{\beta chilling}^2$ | 10.47 | 2.66 | 5.78 | 10.30 | 16.17 | 8539.38 |
| $\sigma_{\beta photoperiod}^2$ | 7.18 | 2.29 | 3.29 | 6.96 | 12.25 | 5625.69 |
| σ_y^2 | 15.81 | 0.41 | 15.04 | 15.81 | 16.63 | 28640.16 |