

Unravelling the phenology-phylogeny tangle.

November 30, 2022

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Results & Discussion

Most species were sensitive to all three primary cues—forcing, chilling, and photoperiod (Figs. 1, Supporting Table ??)(see also ?)(FlynnWolkovich)—but 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 ??). These average sensitivities across species, however, 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. Our results showed that interspecific variation in responses to chilling and forcing is of a greater magnitude than the average species differences in responses between cues (need some stats). Robust phenological forecasts must, therefore, account for both the complexity of multiple cues and species-level variation in responses to them.

Clade-wise differences in phenological cues

Clade-wide differences in the strength of species responses to different cues are striking. For example, 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 is observed for forcing, where some of these clades—e.g., Ericaceae, Rhamnaceae, Ulmaceae, or Fagaceae—are 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 respond strongly to both chilling and forcing, which could suggest the existence of syndromes where the genetic basis for responses to one cue (e.g., forcing) could have been selected for along with 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 of plants (cite?), and sensitivity to multiple cues likely provides greater insurance against mistiming (cite? Pau et al.). It is also possible that there may be linkage or pleiotropism among loci associated with sensitivity to different cues (cite: <https://link.springer.com/article/10.1007/s00122-004-1905-4>). However, the correlation in species sensitivities across cues is only weak ($r = 0.31$; between forcing and chilling) and some genera, such as *Tilia* and Ericaceae[genus?], display 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, do not constrain their sensitivities to another cue, and selection might operate independently on responses to different cues (cite?).

In contrast to both chilling and forcing, species-level responses to photoperiod were almost uniform. These results contrast with model-fitting exercises in earlier analyses (e.g. Hunter & Lechowicz (1992); Schaber & Badeck (2003)). Evidence for advances in timing of budburst and flowering with recent warming indicate that photoperiod does not strongly constrain spring phenology (cite: <https://onlinelibrary.wiley.com/doi/full/10.1111/pce.12431>); nonetheless, our results suggest that while chilling and forcing are the dominant cues by the magnitude of their effect sizes, most species are also sensitive to photoperiod (see also: <https://onlinelibrary.wiley.com/doi/full/10.1111/pce.12431>). In plants, photoperiod regulates a number of fundamental processes including growth, flowering, stress tolerance, and circadian rhythm (cite: Serrano-Beuno 2017: <https://doi.org/10.1016/j.pbi.2017.03.007>), and photoperiodic sensing and adaptation to shifting daylength likely occurred early in the evolution of plants, with origins in the green algae (cite: Serrano-Beuno 2017: <https://doi.org/10.1016/j.pbi.2017.03.007>). 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 for a given photoperiod cue (e.g. Kramer 1995, Phenotypic plasticity of the phenology of seven European tree species, in relation to climatic warming) may allow species to track interannual variation in climate with little directional selection on photoperiod sensitivities.

Phylogenetic structure of phenological cues

Our modelling approach provides information on the evolution of phenological cues across the phylogeny. Consistent with previous work showing phylogenetic signal in plant phenology (Davies et al.; Rafferty; etc.), we find responses to all three cues are phylogenetically structured, but the strength of phylogenetic conservatism in response differs between cues (Fig. 3). Responses to forcing and chilling are strongly to 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. We observe weaker phylogenetic structure in species responses to photoperiod ($\lambda = 0.39$) (see Fig. ??, Table ??), emphasising once more that photoperiod (or how we measure it) diverges from other climate cues. Sensitivity to photoperiod is weaker, more uniform across species, and appears to be less evolutionarily constrained than sensitivities to temperature cues.

What might drive phylogenetic structure in species temperature responses? Within our statistical modelling framework, differences in species responses represent shifts in the slope of the relationship between the observed phenology and the cue. Phylogenetic structure in the change in slope across the phylogeny would be

consistent with an interaction with a non-measured trait that moderates species sensitivities, and which also covaries with phylogeny (cite PWR). Our results indicate the presence of important modifiers for responses to chilling and forcing. Plant life history traits (citeXXX) provide a source of likely modifiers; early season species with fast life histories ... late season species Geography may be an additional source of structured variation, especially in regions where clades have radiated such that close relatives will have been exposed to the same suite of environmental cues and thus subject to similar selection regimes. Conversely, if species are not generally geographically constrained, as may be more likely the case, especially across deep time (<https://doi.org/10.1111/j.0014-3820.2006.tb01140.x>), then we might expect phylogenetic structure in phenology to also weaken, especially when aggregating across locations with different cues (citeXXX Davies phylo sig paper?).

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 indexed by Brownian motion expectations (see Wiens et al.). Rapid local adaptation within species might thus erase the phylogenetic structure in photoperiod responses, but would seem at odds with the uniformity 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 stabilising selection operating on other life-history attributes sensitive to photoperiod (XXCITE), 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 model suggests photoperiod responses are also evolving slower than temperature responses. However, we also reveal (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 (cites 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 spring temperatures because phylogenetic signal in response to forcing is strong, while species may be able to better adapt to changes in chilling as λ is lower, and σ is higher. However, this is misleading as estimates of λ are independent from the rate of evolution, and macroevolutionary rates estimated on phylogenetic trees are integrated across millions of years of evolutionary history, and thus do not

necessarily inform us of maximum possible rates of evolution over shorter timescales. Indeed, there is accumulating evidence for rapid evolution to warming climate ... (cites XXXX). We highlight these parameter here to improve our understanding of the evolutionary history of species phenological cues, and to underscore the importance of correctly modelling species differences in ecological forecasts.

Forecasting species-level responses

Not accounting for phylogeny had an effect on model coefficients (model slopes for forcing and chilling shifted by 7.2% and 3.7%, respectively; Fig. 4) and shifted cross-species variance in their responses to forcing ($\text{Var } \beta_{\text{phylo}} = 8.74$; $\text{Var } \beta_{\text{non-phylo}} = 5.01$), chilling ($\text{Var } \beta_{\text{phylo}} = 23.45$; $\text{Var } \beta_{\text{non-phylo}} = 17.47$), and photoperiod responses ($\text{Var } \beta_{\text{phylo}} = 0.82$; $\text{Var } \beta_{\text{non-phylo}} = 0.93$). 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). Either ignoring ($\lambda = 0$) or overestimating phylogenetic structuring of predictors ($\lambda = 1$) can bias model coefficients (predictors with high λ are biased in non-phylogenetic models and those with low λ are biased if Brownian Motion is imposed). Importantly, not accounting for phylogeny increased the uncertainty around each individual species estimation of their responses to forcing and chilling (see Fig. SXX in Supporting Information), which could 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).

Phylogenetic hierarchical models such as those used here, have the potential to inform on which clades will be more sensitive to different axes of climate change—e.g., changes in cold temperatures over winter or in warm temperatures in spring and summer. For example, in standard non-phylogenetic models, we 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. Ignoring phylogeny and species-level variation may (i) introduce bias into estimated model coefficients, (ii) underestimate true variability in species biological responses and, (iii) increase uncertainty around species-level estimates. Our integrative phylogenetic approach allows us to move beyond crude classifications based upon functional groups (e.g., !REFS) and species complexes (e.g. Ettinger et al. (2020)), to make improved ecological forecasts for individual species. Our model, highlighting strong phylogenetic structure in species responses, also highlights the potential for predicting phenological sensitivities in unmeasured species. While phylogenetic imputation must be done with extreme care (Molina-Venegas et al., 2018), we can make predictions with reasonable accuracy for close relatives of well studied species when there is strong phylogenetic structure in species responses. Notably this is likely to

be the case for many temperate woody plant clades, for which we have multiple experimental observations at varying treatment levels for well-known drivers of phenology.

Accurate forecasts of phenology remain elusive; recent records have suggested an apparent decline in species phenological sensitivity to increasing temperatures (Fu et al., 2015; Piao et al., 2017), but such observations may simply reflect non-linear responses to warming trends (Wolkovich et al., 2021), perhaps reflecting the complex interactions, trade-offs and synergies among multiple cues. While all species appear sensitive to all cues, forcing and chilling dominating over photoperiod, and species-level variation in responses is large, of a magnitude similar to, or greater than, the difference in average effect sizes between cues. Phylogenetic conservatism in species phenology has been well documented (Davies et al., 2013; Rafferty and Nability, 2017; Joly et al., 2019), and may thus help explain species differences. Here, using a novel hierarchical Bayesian model, we allow for phylogenetic non-stationarity in species sensitivities (allowing slopes to vary across species; see (Davies et al., 2019)) to generate species-specific estimates of responses to shifting cues. Uniquely, our model additionally provides information on the evolutionary of species sensitivities, and how they may have been configured along evolutionary time. Our results are consistent with an early origin of photoperiod sensitivity, followed by a history of stabilising selection. Forcing and chilling have evolved more rapidly. However, we caution that macroevolutionary rates provide a poor guide to future adaptive potential over short timescales, and accurate ecological forecasting requires well-designed experiments analysed appropriately.

Chunks that need to fit into the forecasting section

Helpfully, the contrasts between temperature sensitivities and photoperiod sensitivities in both their variability across species and phylogenetic structuring allow for improved multi-species forecasts: (1) the large variability among species in temperature responses makes predicting species individual responses challenging, but the phylogenetic structure in responses lets us borrow information from close relatives to improve our predictions; (2) the weak phylogenetic structure in photoperiod 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.

The genus *Fagus* is recognised as being particularly sensitive to photoperiod (Fu et al., 2019). Specifically, *Fagus sylvatica* is nearly five times more sensitive to photoperiod than most other measured tree species. The question arises as to whether species with outlying responses should be chosen as the model from which to extrapolate knowledge as done with *Fagus sylvatica* in the phenology literature (REFs for PEP75?!).

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Tables and Figures

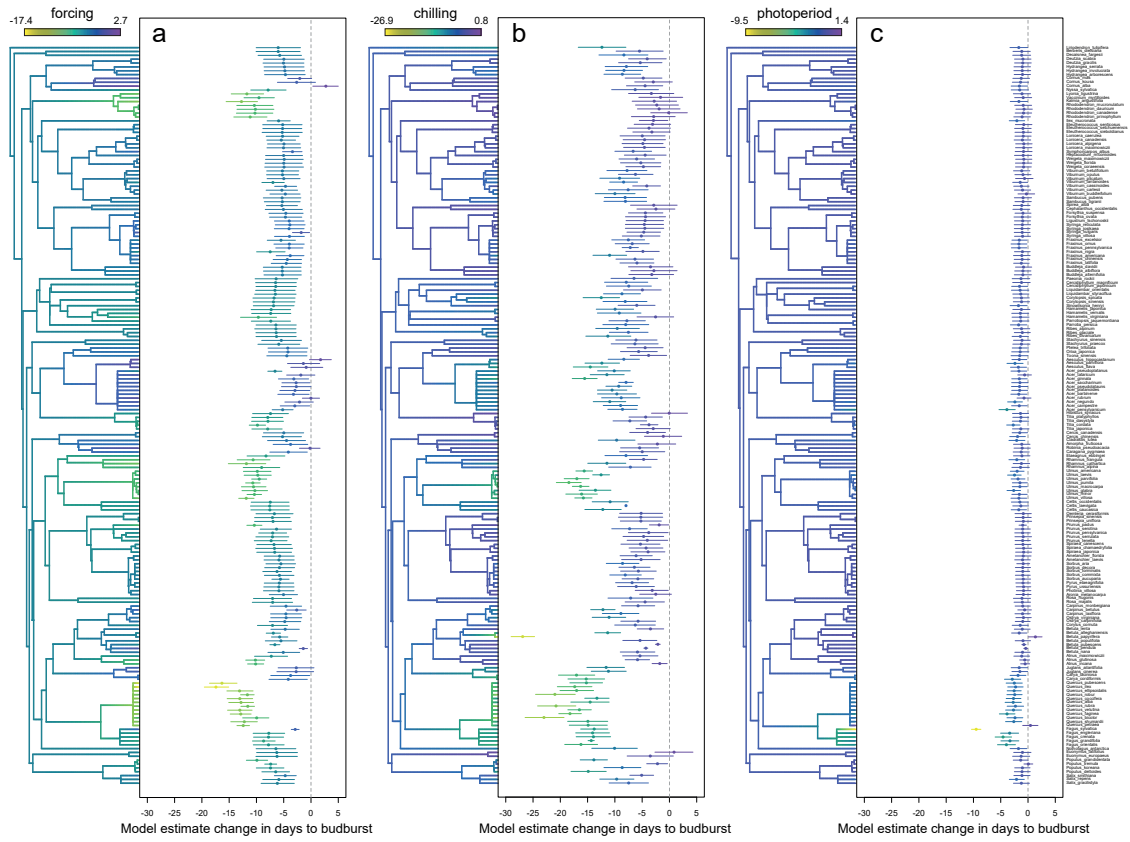


Figure 1: Phenological sensitivity to three environmental cues, forcing (a), chilling (b) and photoperiod (c) measured in change in days to budburst per standardized unit (z-transformation) of the cues across 192 angiosperm species. The same phylogenetic tree is shown in each panel, colored according 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.

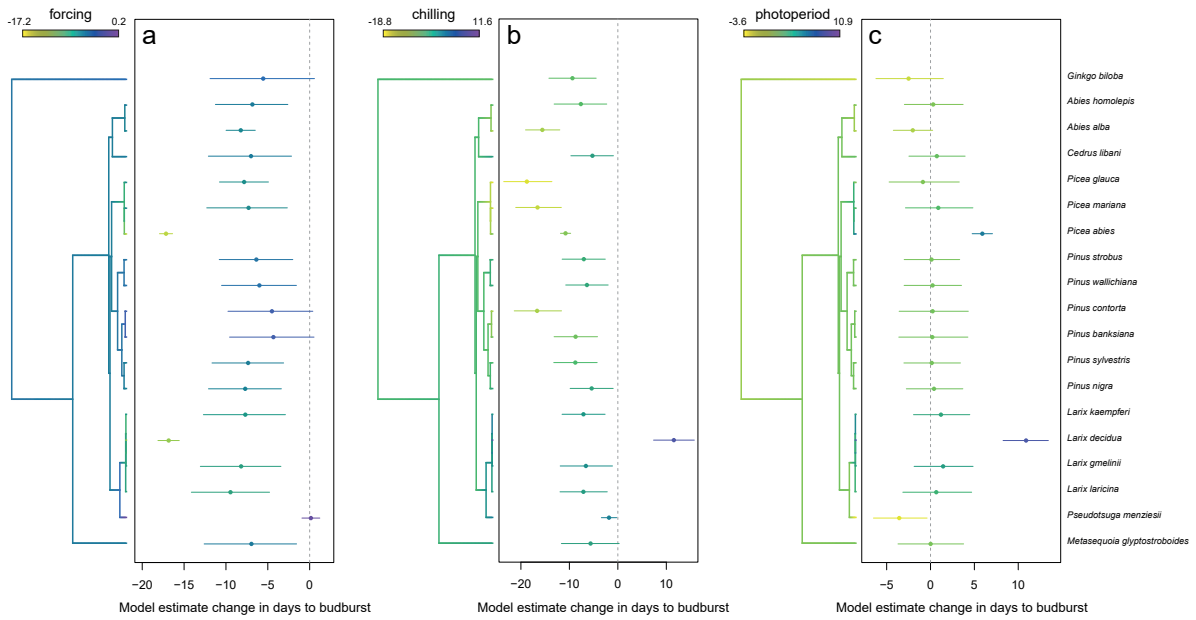


Figure 2: Phenological sensitivity to three environmental cues, forcing (a), chilling (b) and photoperiod (c) measured in change in days to budburst per standardized unit (z-transformation) of the cues across 19 gymnosperm species. The same phylogenetic tree is shown in each panel, colored according 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.

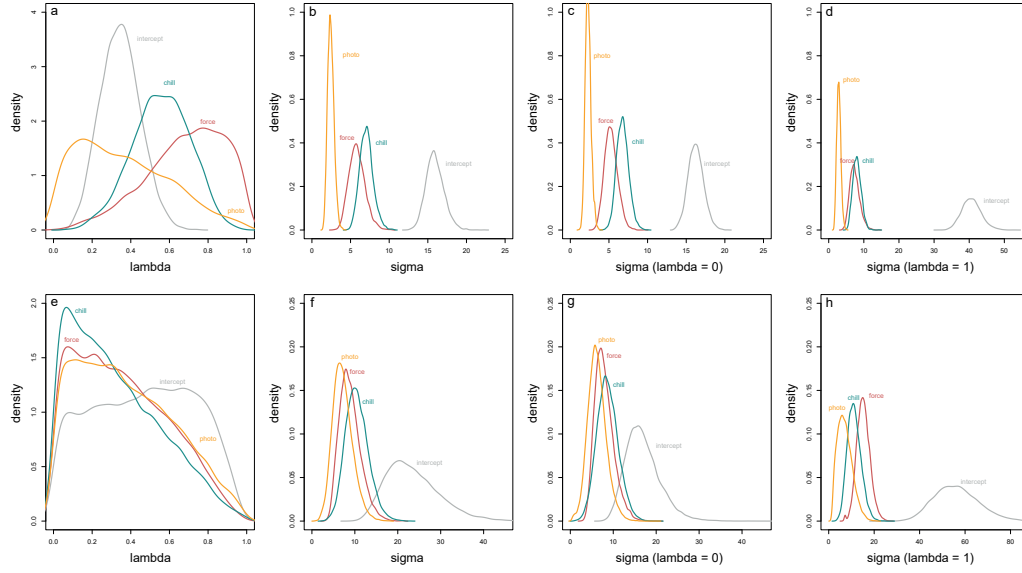


Figure 3: Density plots for the posterior distribution of phylogenetic signal measured by λ for each cue included as a predictor in the model for angiosperms: forcing (red), chilling (blue), photoperiod (orange) and for the model intercept (grey). Panels correspond to angiosperms (a-d) and gymnosperms (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.

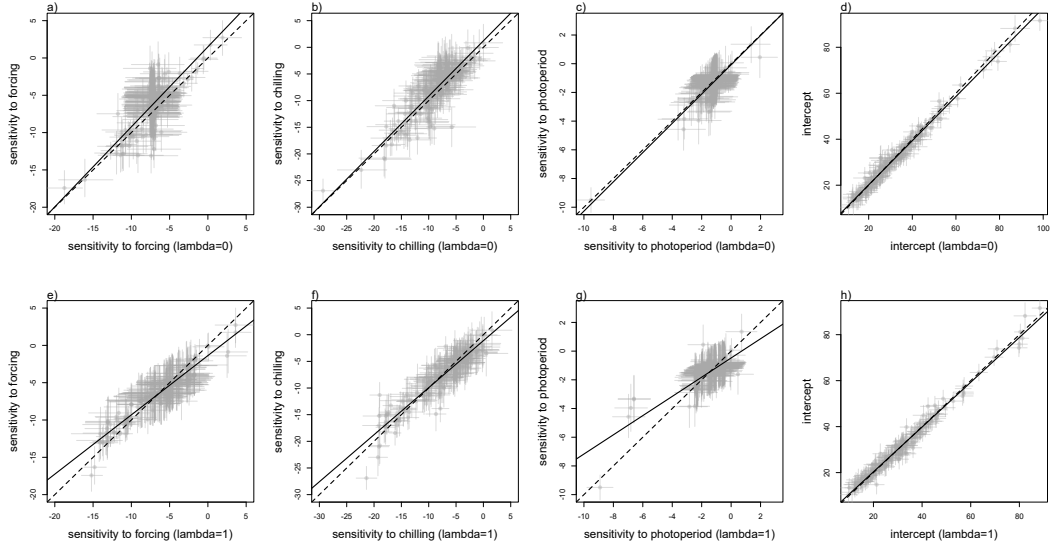


Figure 4: Correlations between model parameters as estimated by the full model and the models where λ is constrained to be equal zero (upper row) or one (bottom row), for angiosperms. Panels correspond to sensitivity to forcing (a,e), to chilling (b,f), to photoperiod (c,g) and to model intercepts (d,h).

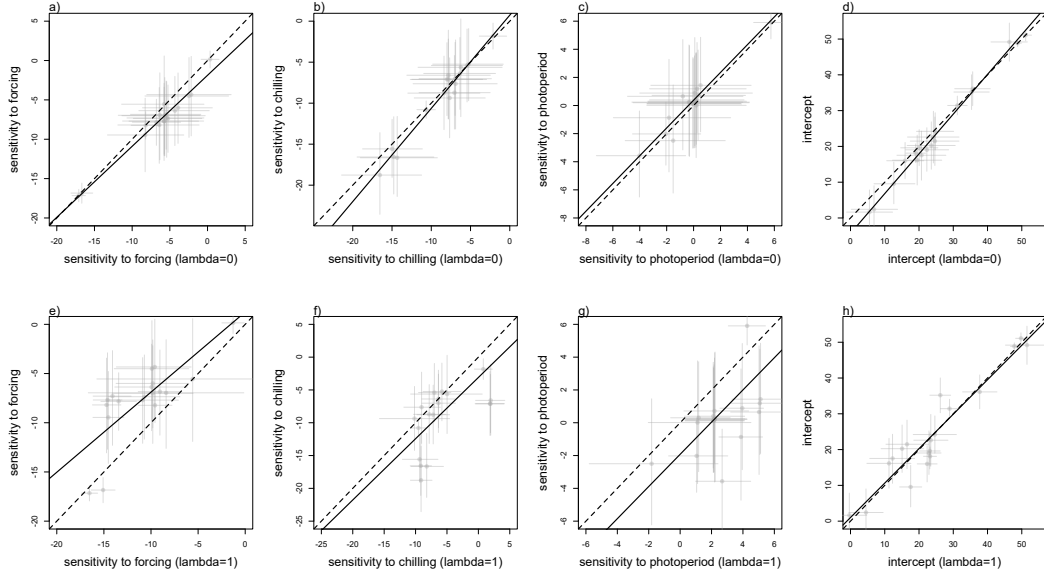


Figure 5: Correlations between model parameters as estimated by the full model and the models where λ is constrained to be equal zero (upper row) or one (bottom row), for gymnosperms. Panels correspond to sensitivity to forcing (a,e), to chilling (b,f), to photoperiod (c,g) and to model intercepts (d,h).

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