Unravelling the phenology-phylogeny tangle.

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Abstract

Not updated yet ... Plants have evolved responses to environmental cues able to inform them about the temporal distribution of key resources—i.e. energy and light. The responses to individual cues such as forcing (or spring warming) have shown to be subjected to some degree of evolutionary conservatism. Yet, plants do not respond to isolated cues but to a combination of interacting cues, which difficults accurate predictions of phenology in the face of environmental change. Whether and how evolution has constrained phenological responses to combinations of interacting cues is not yet understood even when this knowledge could enhance model predictions and inform how different plant lineages have adapted to environmental change along their evolutionary histories. Here we use Bayesian hierarchical models and the most complete dataset on tree species phenological responses measured in experimental conditions to: (a) test if phenological responses to three major interacting cues are conserved phylogenetically when considered jointly, (b) compare the phylogenetic signal in the responses to different cues and, (c) test whether coefficient estimates differ between models assuming phylogenetic independence among species and models that explicitly incorporate phylogeny. Results show non-random phylogenetic structuring of phenological responses, highly variable across species and cues. More interestingly, regression coefficients shift when models control for phylogenetic effects, particularly so for forcing, which becomes the most important cue. Taken together, our results suggest that phylogeny should be incorporated into studies modelling multi-species phenological responses, as such responses have been jointly constrained through evolution and thus are not independent.

Introduction

Predicting the biological impacts of climate change has major implications for the future sustainability of ecosystems. With rising global temperatures species have shifted northward in space and earlier in time on average (IPCC, 2014). These shifts can have cascading consequences on many ecosystem services including carbon storage, which determines future climate change itself, making both mitigation and human adaptation to future warming dependent on accurate ecological forecasts.

While ecological forecasting has improved over recent years (CITES), it remains a challenge to reproduce the high variability observed in responses to date (IPCC, 2014). Some of this variability results from the complexity of climate change itself, including regional and seasonal variation in warming that underlies average trends alongside shifts in other climate axes (e.g. precipitation). Much of it, however, is driven by species-specific variation, reflecting evolved differences in species' sensitivities to underlying environmental cues and their interactions, which we know well for only a few well-studied species. In the absence of detailed data on individual species, species groupings (e.g., functional groups) have been included in ecosystem models, and show promise, but these still fail to capture important variability. Improving forecasts, thus, will require models that accurately predict species-level differences in responses to complex environmental change.

Recent efforts that have attempted to model species responses to the environment (CITES) are often confounded by data availability—especially the common problem of data highly biased to some species and sparse across others. The rise of Bayesian hierarchical models can allow inference across species in such cases. However, underlying most hierarchical models is an implicity assumption that all species are exchangeable, and they thus partially pool ('shrink') towards estimates for species with the most data (and least variable responses) (CITES), making inference at the species-level unreliable (Ettinger et al., 2020). Including the evolutionary history of species relationships in models of species responses could at once provide more robust species-level estimates than current approaches and a better understanding of the evolutionary constraints that might limit future adaptation to change. For example, strong phylogenetic niche conservatism (Wiens et al. 2010: https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2010.01515.x) could potentially inhibit adaptive responses by drawing species back to an evolutionary conserved theorectical optimum which is no onger optimal under new conditions. Evidence that species' climatic niches show strong evolutionary conservatism (Wiens Graham 2005: https://www.jstor.org/stable/30033815), thus, has major implications for projecting species range shifts, a key response to environmental change (Urban et al. 2016: DOI: 10.1126/science.aad8466). More recent work has demonstrated the strength of evolutionary conservatims in species temporal responses, and multiple studies have found dates of budburst, leafout and first flowering are more similar among closely related species (Kochmer and Handel, 1986; Willis et al., 2008; Davies et al., 2013).

Research using long-term observational data has especially highlighted the role that evolutionary history may play in structuring plant phenological responses—which are critical to accurate forecasts of carbon storage. Phylogenetic signal in plant phenology (Davies et al., 2013; Rafferty and Nabity, 2017)) suggests species responses to cues have diverged over macro-evolutionary timescales, helping explain species present day differences. Almost all these studies, however, have focused on the phenotype (e.g., day of year of a phenological event), which is strongly determined by the local environment (e.g., the climate where phenology was measured). More direct measures of species intrinsic responses to the environment may derive from studies examining species long-term change over time (e.g., Willis et al., 2008)—likely capturing a composite of multiple cues—or change per C (Yang et al., 2021)—argued to be a proxy for forcing—and similar metrics, instead of day of year (e.g., CaraDonna and Inouye, 2014). However, approaches using traditional phylogenetic comparative methods (e.g., **?**Yang et al., 2021), have produced conflicting results. Evidence for phylogenetic conservatism appears to depend on method and species, even varying from one site to the next for the same clade (e.g., Rafferty and Nabity, 2017), which violates the fundamental idea of shared evolutionary history—the common ancestor of two sets of species cannot possess two separate evolutionary histories for the same trait.

If closely related species have similar phenological responses to environmental cues it could facilitate forecasting to unmeasured species, and yield insights into how evolutionary history may constrain future response, but testing for this will require addressing a second major hurdle in ecological forecasting—underlying environmental cues that are complex and interacting. Decades of research have informed our understanding of how species use environmental cues to time their phenotypic responses with the temporal distribution of key resources and to avoid periods of high abiotic or biotic stress (Larcher, 1980; Bonamour et al., 2019). Commonly, however, responses to environmental cues, and their evolution, are studied individually, for example, linking a given phenotypic response to a single cue, such as time of leafout and summed heat during early spring (e.g., Davies et al., 2013). Such efforts ignore a more likely scenario for most phenotypic traits where multiple cues interacting along evolutionary history have shaped responses (Ackerly, 2009). For many plant species, phenolological events are determined by a combination of temperature and light (Chuine and Regniere, 2017), and it is likely that additional cues (such as soil moisture) and species' physiology, further mediate species responses, but are often less well understood (Chuine and Regniere, 2017).

Spring plant phenology may represent our best opportunity to improve forecasts of species' responses to interacting environmental cues. Beyond being the most studied biological impact of climate change, the primary interacting cue system is well established (Chuine and Regniere, 2017), especially for temperate woody species where phenology is generally thought to be determined by two components of temperature—chilling (cool temperatures during dormancy period over winter) and forcing (warm temperatures, generally in the spring)—and photoperiod (**?**). Plant phenology is also one of few phenotypic traits with extensive

experimental data on responses to multiple environmental cues across species. Recent multi-species analyses considering forcing, chilling and photoperiod have shown that chilling and forcing together often determine complex non-linear responses to warming, but cannot forecast beyond several well-studied species (Ettinger et al., 2020).

Useful species-level forecasts of phenological responses will require new approaches that better model the evolution of species responses. Our understanding of the underlying cues that drive spring phenology suggest we need to model phenology as a composite outcome of the underlying cues—chilling, forcing and photoperiod—allowing evolution in the responses to each. By allowing non-stationarity in species responses across phylogeny (Davies et al., 2019), such an approach would depart from most previous work and assumptions of traditional phylogenetic comparative methods (e.g. Freckleton et al., 2002; Ives and Helmus, 2011; Hadfield, 2010), and move towards integrating evolutionary history in models of phenological responses to environmental change.

Here we present a novel Bayesian framework that extends upon phylogenetic mixed models (Housworth et al., 2004) to examine how chilling, forcing (metrics of temperature) and photoperiod together determine plant phenology. We illustrate our method with an unprecedented dataset on phenological responses to environmental cues determined experimentally for 192 deciduous woody species (by far the most studied group of species in phenology experiments, see Ettinger et al., 2020). Our method allows us to ask: which cue has the largest effect on budburst, how do cues vary across species, and how evolutionary history has shaped species responses to individual cues? Our results allow us to identify historical regime shifts (Uyeda et al., 2017) in phenological responses across the plant phylogeny, and have relevance for forecasting under ongoing change.

Methods

Chunks to maybe work in...

- Common phylogenetic regression accounts for phylogenetic relationships as a grouping factor either explicitly (PMM) or implicitly (PGLS). Here we present one possible approach that accounts for more complex interactions going on among predictors, which would be reflected in the species-level slopes being allowed to vary as a function of the phylogeny, rather than keeping slopes constant and only allowing the intercepts (or residuals) to vary.
- In a first attempt at establishing whether or not it is important, we compare results from a common hierarchical model with partial pooling on the slopes that does not allow for phylogenetic constraints to affect slope estimates against results from a phylogenetic hierarchical model allowing phylogeny to constrain partially pooled slopes.

Phenological and Phylogenetic Data

Phenological data: To estimate phenological responses to chilling, forcing and photoperiod we used data from phenological experiments of temperate woody species conducted in controlled environments, brought together in the Observed Spring Phenology Responses in Experimental Environments (OSPREE) database. In July 2019, we updated an earlier version of this database (Wolkovich et al., 2019) by reviewing all papers found through searching ISI Web of Science and Google Scholar with the following terms:

1. TOPIC = (budburst OR leaf-out) AND (photoperiod OR daylength) AND temperature*, which yielded 623 publications
2. TOPIC = (budburst OR leaf-out) AND dorman*, which yielded 270 publications

We scraped data from all papers of woody species that tested for photoperiod and/or temperature effects on budburst, leafout, or flowering, resulting in 56 papers. **?** used a portion (72 experiments across 49 papers) of the earlier OSPREE database and provides extensive methods on the database creation and cleaning. For our analysis here, we included all budburst experiments where we could quantify chilling, forcing and photoperiod levels, resulting in 44 studies from 33 papers. Across experiments chilling treatments were often fully or partially applied in the field, thus we estimated field chilling ourselves using daily temperature data from ... [Cat and Nacho – add here: Be sure to include updated info on our datasets and which chilling metric we used]. **?** provides additional details on these calculations (however, to have climate data through all our study years, we used a different climate dataset here for North America).

We analyze 2 different subsets of species in the OSPREE database to explore differences across two major groups of taxa, angiosperms and gymnosperms, for which there are markedly different number of species (194 angiosperms vs. 19 gymnosperms), and whose deep evolutionary divergence advises for separate analyses ().

We used the phylogenetic megatree for seed plant from Smith and Brown (2018) to extract a subset phylogenetic tree containing only the species in the OSPREE dataset (Wolkovich et al., 2019). We pruned the megatree to generate to sub-trees containing only the species in each subset of data. The species that were not present in the megatree were added as polytomies at the generic level (using the function *congeneric.merge*; (Pearse et al., 2015)) with a branch length of zero. Polytomies represent 26.8% of the full angiosperm dataset. To test for the ability of polytomies to bias our results we run sensitivity analyses excluding these species from models (which lead to 142 angiosperms; see Supporting Information).

Bayesian hierarchical phylogenetic model

Commonly used phylogenetic regression methods today (e.g., PGLS and PMM) were originally conceived as statistical corrections for phylogenetic non-independence across observations—generally species—thus allowing multi-species studies to meet the assumptions linear regression (Freckleton et al., 2002). These corrections incorporated phylogenetic structure in the regression by modifying the residual variance-covariance matrix to substitute off-diagonal elements of zero (the value given the assumption of independence across observations) for shared phylogenetic branch lengths representing pairwise covariances (under phylogenetic non-independece among observations). Off-diagonals were also allowed to include a multiplying parameter—generally referred to as lambda—which is a transformation indicating the amount of phylogenetic relatedness among species (see below). Because the original aim of these methods was to correct for statistical nuance, the underlying assumption of phylogenetic regressions is that phylogenetic relatedness would only affect either model residuals (in PGLS approaches, Freckleton et al., 2002), or the model intercepts (e.g., in many PMM approaches, Housworth et al., 2004).

Because our aim is to understand how evolution may have imprinted biological responses to multiple interactive cues, our approach expands the above methods by explicitly incorporating phylogenetic structure accross model intercepts and slopes. Doing so allows explicitly estimating the amount of phylogenetic relatedness in species' sensitivities to each cue, when these sensitivities are modelled in a multi-predictor regression setting.

For each j species, we assumed that data were generated from the following sampling distribution:

$$y_j \sim \mathcal{N}(\mu_j, \sigma_e^2) \tag{1}$$

where

$$\mu_j = \alpha_j + \beta_{1,j} X_2 + \beta_{2,j} X_2 + \beta_{3,j} X_3 \tag{2}$$

Predictors X_1, X_2, X_3 are standardized forcing, chilling, and photoperiod, and their effects on the phenology of species j are determined by parameters $\beta_{1,j}$, $\beta_{2,j}$, $\beta_{3,j}$, representing species' responses (or sensitivities) to each of the cues. These responses, including the species-specific intercept α_j, are elements of the following normal random vectors:

$$\begin{aligned}
\boldsymbol{\alpha} &= \{\alpha_1, \ldots, \alpha_n\}^T \text{ such that } \boldsymbol{\alpha} \sim \mathcal{N}(\mu_\alpha, \boldsymbol{\Sigma_\alpha}) \\
\boldsymbol{\beta_1} &= \{\beta_{1,1}, \ldots, \beta_{1,n}\}^T \text{ such that } \boldsymbol{\beta_1} \sim \mathcal{N}(\mu_{\beta_1}, \boldsymbol{\Sigma_{\beta_1}}) \\
\boldsymbol{\beta_2} &= \{\beta_{2,1}, \ldots, \beta_{2,n}\}^T \text{ such that } \boldsymbol{\beta_2} \sim \mathcal{N}(\mu_{\beta_2}, \boldsymbol{\Sigma_{\beta_2}}) \\
\boldsymbol{\beta_3} &= \{\beta_{3,1}, \ldots, \beta_{3,n}\}^T \text{ such that } \boldsymbol{\beta_3} \sim \mathcal{N}(\mu_{\beta_3}, \boldsymbol{\Sigma_{\beta_3}})
\end{aligned} \tag{3}$$

where the means of the multivariate normal distributions are root trait values (i.e., values of cue responses prior to evolving across a phylogenetic tree) and $\boldsymbol{\Sigma_i}$ are $n \times n$ phylogenetic variance-covariance matrices of the form:

$$\begin{bmatrix}
\sigma_i^2 & \lambda_i \times \sigma_i \times \rho_{12} & \ldots & \lambda_i \times \sigma_i \times \rho_{1n} \\
\lambda_i \times \sigma_i \times \rho_{21} & \sigma_i^2 & \ldots & \lambda_i \times \sigma_i \times \rho_{2n} \\
\vdots & \vdots & \ddots & \vdots \\
\lambda_i \times \sigma_i \times \rho_{n1} & \lambda_i \times \sigma_i \times \rho_{n2} & \ldots & \sigma_i^2
\end{bmatrix} \tag{4}$$

where σ_i^2 is the rate of evolution across a tree for trait i (here assumed to be constant along all branches), λ_i scales branch lengths and therefore is a measure of the "phylogenetic signal" or extent of phylogenetic relatedness on each model parameter (i.e., α_j, $\beta_{1,j}$, $\beta_{2,j}$, $\beta_{3,j}$), and ρ_{xy} is the phylogenetic correlation between species x and y, or the fraction of the tree shared by the two species.

The above specification is equivalent to writing equation 2 in terms of root trait values and residuals, such that:

$$\mu_j = \mu_\alpha + \mu_{\beta_1} X_1 + \mu_{\beta_2} X_2 + \mu_{\beta_3} X_3 + e_{\alpha_j} + e_{\beta_{1,j}} + e_{\beta_{2,j}} + e_{\beta_{3,j}} \tag{5}$$

where the residual error terms (e.g., e_{α_j}) are elements of normal random vectors from multivariate normal distributions centered on 0 with the same phylogenetic variance-covariance matrices as in equation 4.

Interpretation of λ_j and σ_j^2 on slopes and intercepts

Most current phylogenetic regression approaches aimed at controlling for phylogenetic non-independence of analysis units (i.e. species, see Revell, 2010) assume the λ scaling parameter is constant across the full set of predictors in the model. Thus, λ is estimated as a single parameter based on one single residual term VCV matrix. While useful for correcting for phylogenetic non-independence this approach does not allow the phylogeny to differntially affect different predictors (i.e. environmental cues in our example, which refer to simply as cues hereafter). In models with multiple cues, species responses to all cues are estimated as similarly phylogenetically structured, but this may not be the case. For example, in a PGLS model with three cues, it would be possible to have a high (i.e. close to 1) value of λ, due to either a strong phylogenetic signal in the response, but no phylogenetic structuring in the cues, or one or more predictors being strongly phylogenetically structured. In the latter case, phylogenetic structuring of responses to cues could be correlated (i.e., responses to cues evolving in a correlated fashion) or uncorrelated (i.e., independent evolution of responses to cues). Discerning these different situations is not trivial as they would inform whether responses to predictors configure in a structured fashion along the evolutionary process. However, most current approaches act as a black box regarding this information; they simply inform whether or not model residuals are phylogenetically structured (i.e. in PGLS) or the amount of model variance attributable to the phylogeny and independent from other sources of variation (i.e., in PMM, see Housworth et al. (2004)).

Because we are specifically interested in estimating the phylogenetic structure of each cues, our approach explicitly partitions variance into specific components relative to the model intercept and predictor (cue) slopes (see equation 5). The multivariate normal distributions of the intercept and slope terms include each a variance term (see equation 3), modelled with a λ scaling parameter. The interpretation of λs in our models are analogous to Pagel's Pagel (1999) λ parameter (Housworth et al., 2004), constrained to range from 0 to 1, with values of 0 indicating absence of phylogenetic relatedness, and values of 1 indicating *Brownian Motion* evolution (BM). Estimated λs are not fully equivalent to computing phylogenetic signal of the slopes of each cue separately (i.e., fitting a multilevel regression model with species as a grouping factor on intercepts, and subsequently estimating phylogenetic signal for model slopes). Instead, they are a relative metric of phylogenetic relatedness allowing us to compare among responses known to interact with each other and estimated simultaneously. This approach has the further benefit of adjusting our partial pooling ('random effect' of species) based on evolutionary distance, more strongly pooling closely related species, and only

weakly pooling distantly related species (see Gaussian process models in Gelman et al., 2014).

A traditional interpretation of σ^2s under Brownian Motion evolution, is an 'evolutionary rate' or phenotypic accummulation over time (Revell et al., 2008). In PGLS, σ^2_ϵ is estimated for the model error term, which is distributed as a multivariate normal with VCV matrix given by $\sigma^2_\epsilon \mathbf{\Sigma_i}$. Here, similar to our approach to λ, we estimate four σ^2 values, corresponding to each model parameter. In our particular case (i.e., modelling a phenological response to three environmental cues), σ^2_α for the intercept could be interpreted as the phenological variation across species accummulated along evolution independently from the cues. The $\sigma_{\beta 1}^2$, $\sigma_{\beta 2}^2$, and $\sigma_{\beta 3}^2$, corresponding to model slopes, would represent the phylogenetic variance linked to species responses to each of the modelled cues (i.e., forcing, chilling, and photoperiod, respectively). This is, the variability in how species shift their phenology responding to temperature and light, accummulated along the evolutionary process and considered in concert.

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Tables and Figures

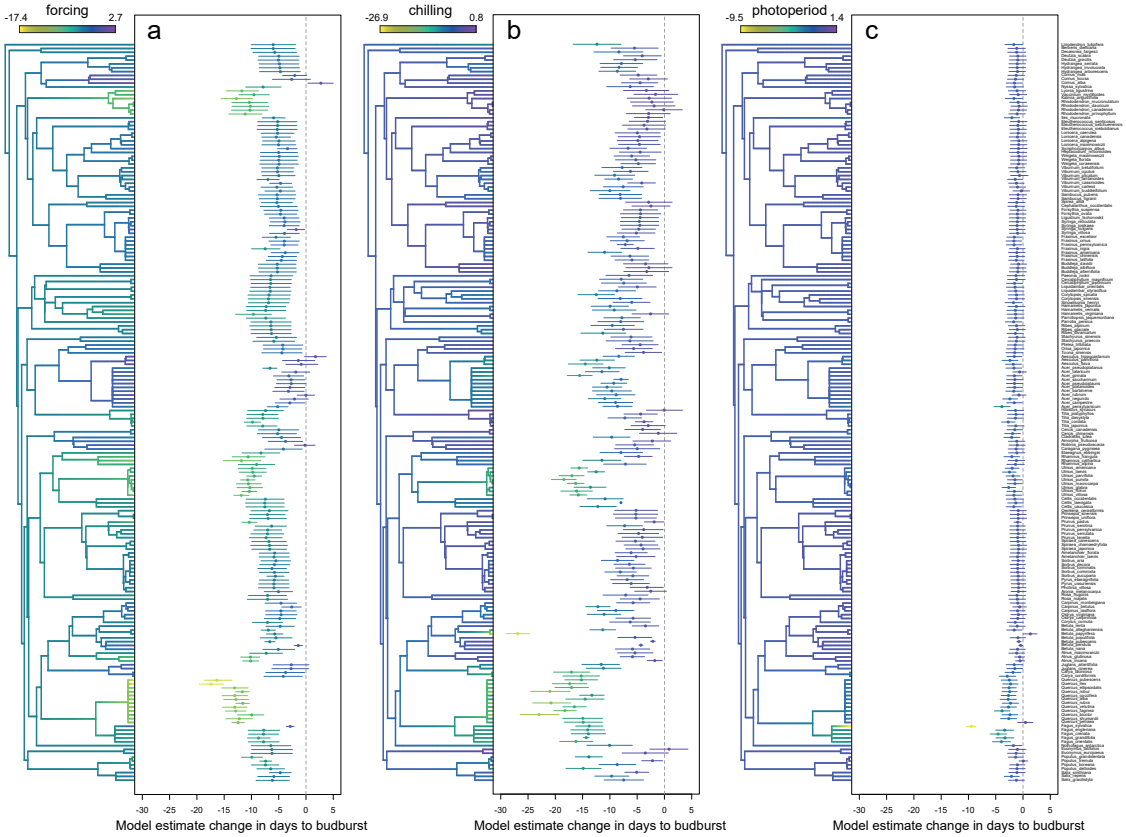

Figure 1: Phenological sensitivity to thee environmental cues, forcing (a), chilling (b) and photoperiod (c) measured in change in days to budburst per standardized unit (z-transformation) of the cues across 192 angiosperm species. The same phylogenetic tree is shown in each panel, colored acording to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

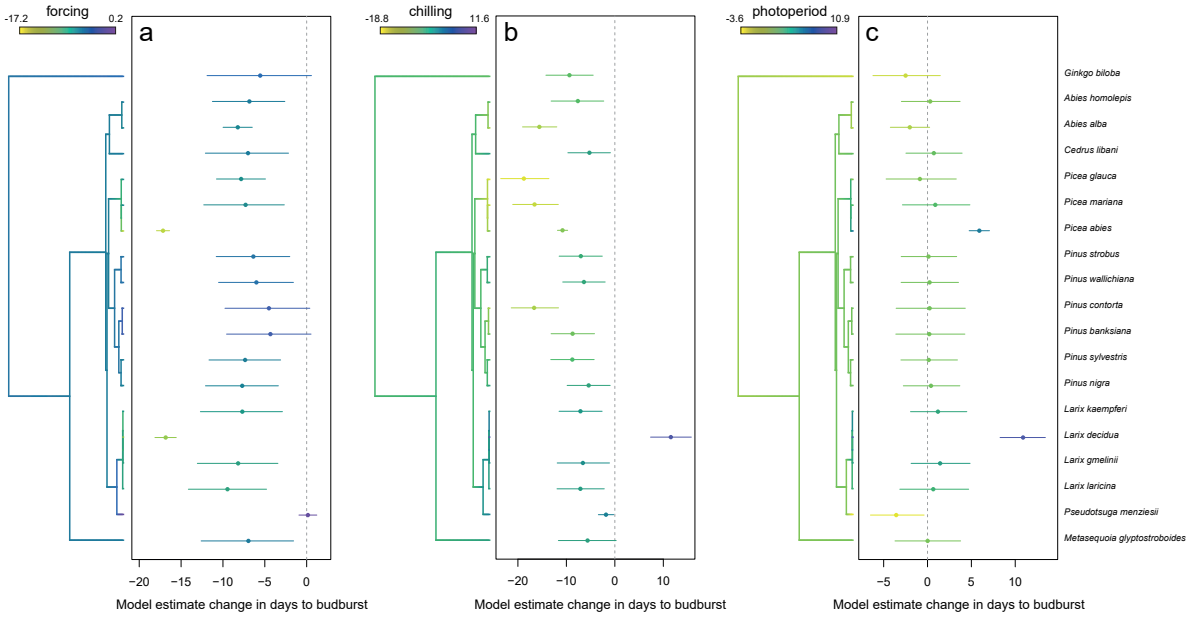

Figure 2: Phenological sensitivity to thee environmental cues, forcing (a), chilling (b) and photoperiod (c) measured in change in days to budburst per standardized unit (z-transformation) of the cues across 19 gymnosperm species. The same phylogenetic tree is shown in each panel, colored acording to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

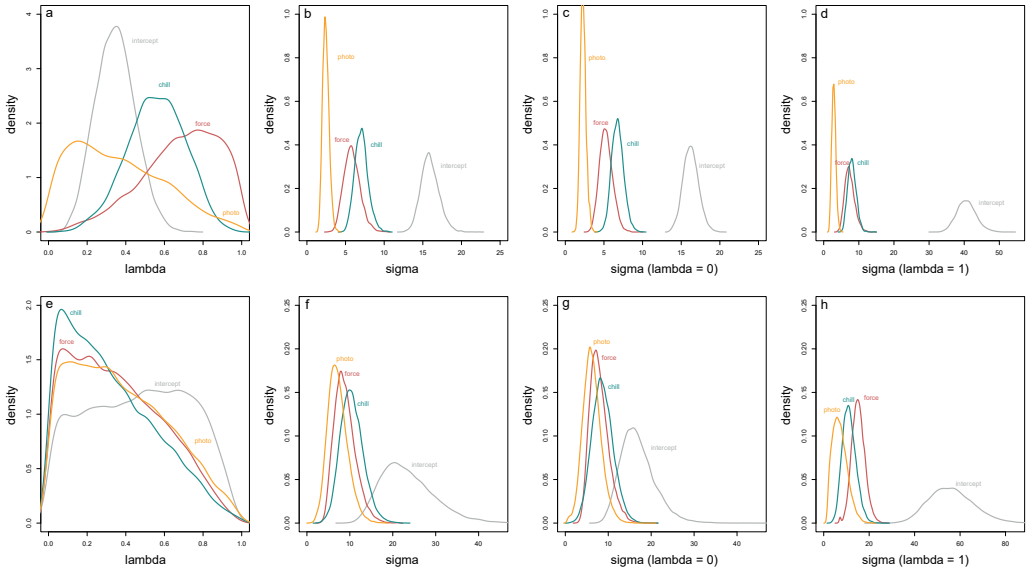

Figure 3: Density plots for the posterior distribution of phylogenetic signal measured by lambda for each cue included as a predictor in the model for angiosperms: forcing (red), chilling (blue), photoperiod (orange) and for the model intercept (grey). Panels correspond to angiosperms (a-d) and gymnosperms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

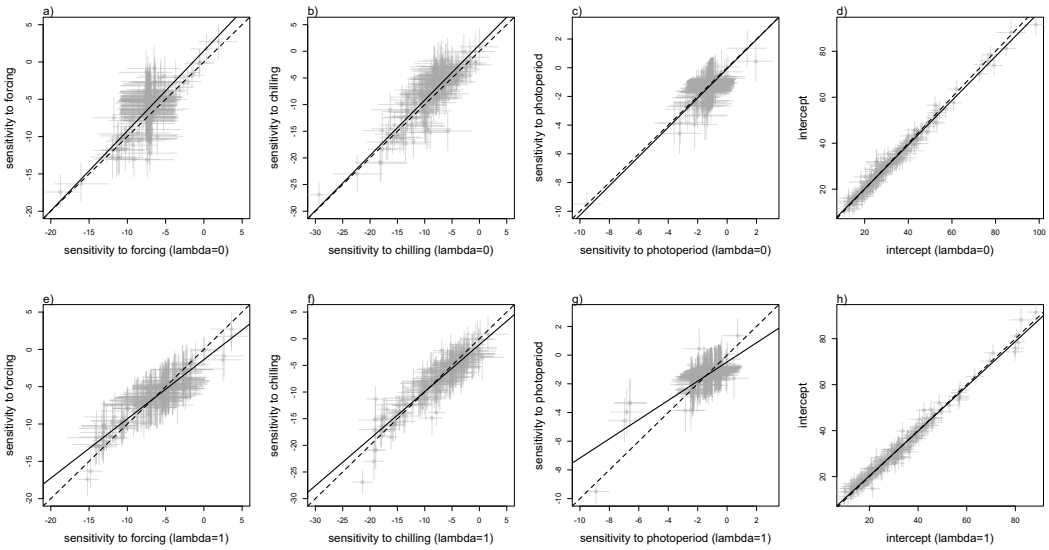

Figure 4: Correlations between model parameters as estimated by the full model and the models where lambda is constrained to be equal zero (upper row) or one (bottom row), for angiosperms. Panels correspond to sensitivity to forcing (a,e), to chilling (b,f), to photoperiod (c,g) and to model intercepts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

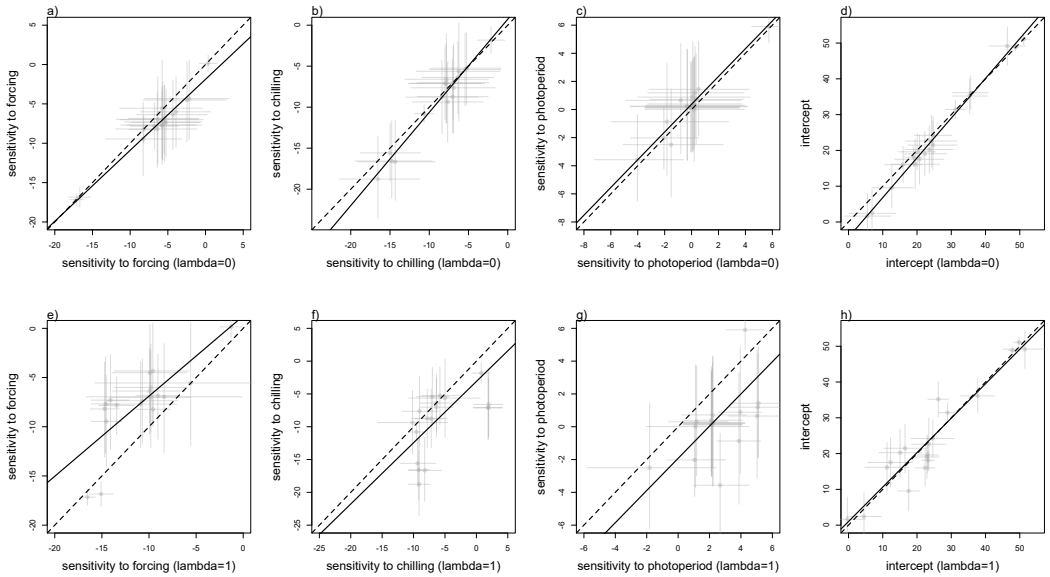

Figure 5: Correlations between model parameters as estimated by the full model and the models where lambda is constrained to be equal zero (upper row) or one (bottom row), for gymnosperms. Panels correspond to sensitivity to forcing (a,e), to chilling (b,f), to photoperiod (c,g) and to model intercepts (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^2_α	15.93	1.17	13.84	15.85	18.41	2988.37
$\sigma^2_{\beta forcing}$	5.84	1.04	4.03	5.78	8.15	502.74
$\sigma^2_{\beta chilling}$	7.05	0.87	5.48	7.02	8.92	1026.77
$\sigma^2_{\beta photoperiod}$	2.45	0.41	1.74	2.42	3.32	469.46
σ^2_y	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^2_α	23.47	6.20	13.87	22.59	37.81	18272.58
$\sigma^2_{\beta forcing}$	8.89	2.45	4.96	8.60	14.51	8126.51
$\sigma^2_{\beta chilling}$	10.47	2.66	5.78	10.30	16.17	8539.38
$\sigma^2_{\beta photoperiod}$	7.18	2.29	3.29	6.96	12.25	5625.69
σ^2_y	15.81	0.41	15.04	15.81	16.63	28640.16