

Evolution constrains tree responses to environmental cues in
experimental settings too - Outline
or
Revisiting the Phylogenetic Mixed Model

September 22, 2021

Authors:

The Wolkovich Lab in 2019 ^{1,2,3,4}

Author affiliations:

¹Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4;

²Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

³Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;

⁴Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

*Corresponding author: ignacio.moralesc@uah.es

Rationale & Significance

Previous work has looked at the phylogenetic conservatism of phenology across plant species, finding that, first flowering is significantly conserved (Davies et al., 2013) and, when using OU models so are shifts in first flowering and the slopes of the relationship between flowering and year (Rafferty and Nabity, 2017). Research in this area has focused on the phenotype (phenological event or its shifts) rather than on the cues—i.e. how shifts in the environment trigger species responses. Beyond whether or not phenology is phylogenetically conserved, determining evolutionary constraints in phenological responses to temperature and daylight, may have deeper implications for forecasting under ongoing change.

Nevertheless, previous work on the phylogenetic conservatism of phenology has still not addressed:

- Emphasis has been put on the phenotype rather than on the cues
- Are phenological responses in lab experiments conserved as well? In Joly et al. (2019) the authors check this with a focus on intraspecific variations
- How the sensitivities to different environmental cues are conserved?
- Are the responses to certain cues more strongly conserved than to others?
- How does accounting for phylogeny affects model estimations of cue sensitivity?

And beyond work on phylogenetic conservatisms, previous comparative research on phenological responses to cues (experimental or observational) has either:

- Ignored phylogenetic relationships (or the fact that species are not independent units)
- Accounted for phylogenetic relationships assuming that they are *stationary* across predictors-traits and can be modelled by including phylogenetic Variance-Covariance in model residuals. This is the rationale behind common-use PGLS approaches but it hides the partial phylogenetic constraints to model predictors.

An overlooked question so far is whether we could gain any additional information by accounting for independent phylogenetic structuring in each species responses to each predictor in a multi-linear response model setting. Typical methods are good to account for species non-independence but provide little insight relative to phylogenetic effects on each predictor.

The potential interest of findings in this direction stem from:

- better predictions of phenology (or need to account for it in models)
- better understanding of the mechanistic basis of plant responses to climate
- better design the next generation of experiments

Abstract

Plants have long evolved responses to environmental cues, able to inform the organisms about the temporal distribution of key resources—i.e. energy and light. The plasticity of these responses may ultimately determine species ability to withstand ongoing environmental change because non-plastic species may undergo developmental events under inadequate conditions—e.g. a species advancing flowering too much could see increased the risk of frost events. Phenology describes the responses to seasonal change in environmental cues and while it is often regarded to as a rather plastic trait, it is still unknown whether or not phenology is a phylogenetically conserved trait. Here we use Bayesian hierarchical models and the most complete dataset on tree species phenological responses measured in experimental conditions to: (a) test if tree species responses to cues are conserved phylogenetically, (b) compare the phylogenetic signal in the responses to different cues and, (c) test the ability of phylogenetically informed models to improve predictive accuracy of phenology. Results show non-random phylogenetic structuring of phenological responses, highly variable across cues. Taken together, our results suggest that phylogeny should be incorporated into studies modelling multi-species phenological responses, as such responses have been constrained through evolution and thus are not independent. How plants respond to environmental cues—i.e. temperature, daylight—may determine their resilience or vulnerability to ongoing climate change. Phenology provides a good description of plant responses to the environment. Phenology has been regarded to as a rather plastic trait, thus with a lot of variation both intra- and inter-specifically. Variation in phenology could have randomly accumulated across species (and then phenology would be an evolutionary labile trait), or be structured in the phylogeny so that closely related species resemble more each other in their phenological responses (conserved trait). Whether or not phenology is conserved has implications for the need to account for phylogenetic autocorrelation in cross-species analyses. More interestingly, given that phylogeny can act as a proxy for other (unaccounted) traits that may be linked to phenology, including it in models could lead to more accurate predictions. Here we use Bayesian hierarchical models and the most complete dataset on tree species phenological responses measured in experimental conditions to: (a) test if tree species responses to cues are conserved phylogenetically, (b) compare the phylogenetic signal in the responses to different cues and, (c) test the ability of phylogenetically informed models to improve predictive

accuracy of phenology. Results show non-random phylogenetic structuring of phenological responses, highly variable across cues. Taken together, our results suggest that phylogeny should be incorporated into studies modelling multi-species phenological responses, as such responses have been constrained through evolution and thus are not independent.

Introduction

1. Phenology is a critical trait to studying biological responses to climate change.
2. Forecasts of phenological responses to environmental change are very important (e.g. agriculture, pest management, etc.) but they are not successful, partly due to data limitations: many species lack data and even those with data may have incomplete time series for all relevant phenophases. Could we impute missing data using phylogeny as a proxy? Even if we have the data, should multi-species forecasts be concerned with phylogenetic constraints?
3. Phenology has been shown to be phylogenetically conserved, but studies to date are limited by:
 - (a) focused on flowering (and leafout some) times and shifts in them (but see Joly et al. (2019), and add REFs!! on other phenological stages: budburst, ripening)
 - (b) studied trait correlation (Bolmgren and D. Cowan, 2008) (not a limitation, but a different focus)
 - (c) studied different evolutionary models best fitting the data (Rafferty and Nabity, 2017)
 - (d) measured shifts based on field observation data for both climate and phenology (when slopes are available, they represent shifts with time, not shifts with the environment).
 - (e) most efforts are on the phenotype rather than on the magnitude of species phenological responsiveness to different environmental cues.
4. Few examples in the literature have tested for phylogenetic signal of phenological responses using growth chamber data (e.g. Joly et al. (2019), and yet such a source of data could have advantages such as:
 - (a) it makes possible to examine responses to more than one cue and thus not restrict analyses to responses to forcing.
 - (b) it is possible to compare responses to cues (are some more conserved than others?)
 - (c) they may allow testing whether phylogeny can improve models of phenology as a response to a cue
5. Shifting the focus to phylogenetic conservatism of the responses to cues may provide additional insights:

- (a) by allowing comparison across cues, which cues are more conserved? which selective processes have been stronger?
 - (b) Do we need to care about phylogenetic constraints when we forecast phenology?
 - (c) Understand what dimensions of the environment may be more limiting or may be less subject to further adaptation.
 - (d) Is the phylogenetic conservatism of phenology affected by geography and/or taxonomy? (e.g. North America vs. Europe; Gymnosperms vs. Angiosperms)
6. Here we use the largest dataset on experimental phenology to model species responses to three major environmental cues—i.e. forcing, chilling, photoperiod—and test their. We expect non-random phylogenetic conservatism of the cues based on previous research (Davies et al., 2013; Rafferty and Nability, 2017; Joly et al., 2019) and expect that temperature-related cues display higher phylogenetic signal than photoperiod because the latter has remained more constant through evolutionary time.

The intro topics need punch and relevant antecedents (I'm still getting acquainted with the literature), help with bibliographic review of the topic would be awesome

Methods

Phenological and Phylogenetic Data

1. Description of the OSPREE database (where it comes from, number of species, studies, etc.).
2. We analyze 5 different subsets of species in the OSPREE database to explore differences across taxa (effect of gymnosperms?) and to test to what extent data resolution affects the results:
 - (a) Species grouped in generic complexes, to ensure enough cross-treatment data, as in Ettinger et al. (under review) (including 52 complexes)[flags.for.mainmodel=T]
 - (b) All species in the main model (including 117 species resulting from) [flags.for.mainmodel=T]
 - (c) All angiosperm species in the main model (including 110 species)[flags.for.mainmodel=T]
 - (d) All species in the latest version of OSPREE (including 231 species resulting from) [flags.for.allspmodel=T]
 - (e) All angiosperm species in the latest version of OSPREE (including 215 species)[flags.for.allspmodel=T]
3. Two phylogenetic hypotheses have been considered to build a tree containing the species in OSPREE. First the vascular plant megatree by Zanne et al. (2014);Nature and, second the megatree by Smith & Brown (2019);AJB.
4. The backbone phylogenies were pruned to contain only the studied species in each subset.
5. Species not in the backbone phylogeny were added as polytomies at the generic level (using the function *congeneric.merge*; (Pearse et al., 2015)).
6. To build a phylogeny for species complexes, the terminal branches of species belonging to the same complexes were collapsed.

Help here
would be
much appre-
ciated!

Provenance-climate Data

1. Should we test/analyze provenance or climate-effects?

The Bayesian hierarchical phylogenetic model

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

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

I believe this
can be done
(roughly)
through the
NAM vs.
Eur compar-
ison?

where

$$\mu_j = \alpha_j + \beta_{1,j}X_1 + \beta_{2,j}X_2 + \beta_{3,j}X_3 \quad (2)$$

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 traits. These traits, including the species-specific intercept α_j , are elements of the following normal random vectors:

$$\begin{aligned} \boldsymbol{\alpha} &= \{\alpha_1, \dots, \alpha_n\}^T \text{ such that } \boldsymbol{\alpha} \sim \mathcal{N}(\mu_{\boldsymbol{\alpha}}, \boldsymbol{\Sigma}_{\boldsymbol{\alpha}}) \\ \boldsymbol{\beta}_1 &= \{\beta_{1,1}, \dots, \beta_{1,n}\}^T \text{ such that } \boldsymbol{\beta}_1 \sim \mathcal{N}(\mu_{\beta_1}, \boldsymbol{\Sigma}_{\beta_1}) \\ \boldsymbol{\beta}_2 &= \{\beta_{2,1}, \dots, \beta_{2,n}\}^T \text{ such that } \boldsymbol{\beta}_2 \sim \mathcal{N}(\mu_{\beta_2}, \boldsymbol{\Sigma}_{\beta_2}) \\ \boldsymbol{\beta}_3 &= \{\beta_{3,1}, \dots, \beta_{3,n}\}^T \text{ such that } \boldsymbol{\beta}_3 \sim \mathcal{N}(\mu_{\beta_3}, \boldsymbol{\Sigma}_{\beta_3}) \end{aligned} \quad (3)$$

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

$$\begin{bmatrix} \sigma_i^2 & \lambda_i \times \sigma_i \times \rho_{12} & \dots & \lambda_i \times \sigma_i \times \rho_{1n} \\ \lambda_i \times \sigma_i \times \rho_{21} & \sigma_i^2 & \dots & \lambda_i \times \sigma_i \times \rho_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \lambda_i \times \sigma_i \times \rho_{n1} & \lambda_i \times \sigma_i \times \rho_{n2} & \dots & \sigma_i^2 \end{bmatrix} \quad (4)$$

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” within a species trait, 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 exactly equivalent to writing equation ?? in terms of root trait values and residuals, such that:

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

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 ??.

Interpretation of λ_i

In contrast to classic approaches to controlling for phylogenetic non-independence of analysis units (i.e. species), see (Freckleton et al., 2002), where Pagel's Pagel (1999) λ is assumed constant across multiple predictors if those enter a PGLS model, our approach retrieves

The λ in our models is analogous to, but not fully equivalent 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). This is because in our approach, a λ is estimated for each predictor in the model whilst in PGLS and similar approaches, λ is computed simultaneously across the predictor matrix.

Phylogeny in forecasts of phenology

This sections needs to be fleshed out, but first we need to think and decide how to proceed (or if we want to proceed at all):

1. How we define the two scenarios (regular scenario; climate change scenario; see below)?
2. For which subset of species do we test it?
3. Are we predicting with and without phylogeny? I'm still not sure about how to do this.

Results

Cue sensitivities: are there major shifts when phylogeny is accounted for?

Perhaps we can compare the new results against those in Ailene's paper more closely ??, and ??.

A first glance comparing results here with those in the NCC paper suggest that after taking phylogeny into account, the associations with photoperiod may decrease and the variance around estimations of sensitivity to chilling gets larger.

Phylogenetic signal in phenological responses

1. Phenological responses to the three studied cues are overall phylogenetically conserved but estimates of phylogenetic signal differ strongly across species subsets (angio vs. gymno).

Should we compare Results from our approach and those from PGLS? - to discuss

2. When angiosperm species (from main model) are considered, responses to forcing are more conserved ($\lambda = 0.64$) than responses to chilling ($\lambda = 0.66$) or to photoperiod ($\lambda = 0.35$) (see Figure ??).
3. When gymnosperm species are considered, all responses to cues are similarly low (yet different from zero): forcing ($\lambda = 0.36$), chilling ($\lambda = 0.32$) and photoperiod ($\lambda = 0.37$) and show almost overlapping posterior distributions, which may be driven by a low number of species (19) ??).

Budburst models, phylogenetic and non-phylogenetic

1. Do we still want to do this comparison?

Discussion

To be fleshed out.

Next steps and directions (based on Lizzie's suggestions)

1. Compute phylogenetic signal on the outcome of the cues – that is, we could calculate budburst day given our model (maybe a model without phylogeny?) under perhaps two scenarios:
 - (a) High chill, long-ish photoperiod, and moderate forcing (regular scenario)
 - (b) Low chill, shorter photoperiod, higher forcing (climate change scenario)
 - (c) The trick will be first, which model to use to calculate these values and how to keep the paper then logically consistent.

Questions to be addressed

Some questions we need to answer (suggestions by Lizzie and Nacho's additions):

1. How do we approach wanting to use species-level output from the models and wanting to fit phylogenetically-informed models? I think our current approach of using phylo-corrected and uncorrected models is fine, but we should discuss.
2. Do we want to compare North America and Europe somehow? sounds cool!

3. Do we want to add any traits or range stuff? - I don't think I'd go there unless there is a really pressing question or idea to address
4. Can people add refs? Especially recent refs and refs about leafout and budburst? We also should have some refs on WITHIN-species variation. This is a task that would be great if people could contribute.
5. Would it make sense to look at other response variables in OSPREE (other than budburst)?

And a very important question:

6. How do we want to pitch this paper? About phenology? About moving beyond phenotypes? About using experimental (lab) data? About climate change forecasts being affected by phylogenetic structuring?
7. If the latter, can we think of ways to show how accounting for phylogenetic structuring would affect (or best case scenario, improve) forecasts of phenology? Perhaps by focusing on well studied species (usual PEP75 suspects?)...
8. Probably still early for this, but any ideas for target journals? JoE seems a natural outlet given where previous work has been published, but if the pitch is more into forecasts, could we aim higher?

References

- Bolmgren, K., and P. D. Cowan. 2008. Time-size tradeoffs: A phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. *Oikos* 117:424–429.
- Bürkner, P.-C. 2017. brms: An R Package for Bayesian Multilevel Models. *Journal of Statistical Software* 80:1–28.
- Davies, T., E. Wolkovich, N. Kraft, N. Salamin, and S. E. Travers. 2013. Phylogenetic conservatism in plant phenology. *Journal of Ecology* 101:1520–1530.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* 160:712–726.
- Housworth, E. A., E. P. Martins, and M. Lynch. 2004. The phylogenetic mixed model. *The American Naturalist* 163:84–96.
- Joly, S., D. F. Flynn, and E. M. Wolkovich. 2019. On the importance of accounting for intraspecific genomic relatedness in multi-species studies. *Methods in Ecology and Evolution* .

- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Pearse, W. D., M. W. Cadotte, J. Cavender-Bares, A. R. Ives, C. M. Tucker, S. C. Walker, and M. R. Helmus. 2015. *Pez*: Phylogenetics for the environmental sciences. *Bioinformatics* 31:2888–2890.
- R Development Core Team. 2017. *R*: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria .
- Rafferty, N. E., and P. D. Nabity. 2017. A global test for phylogenetic signal in shifts in flowering time under climate change. *Journal of Ecology* 105:627–633.

Tables and Figures

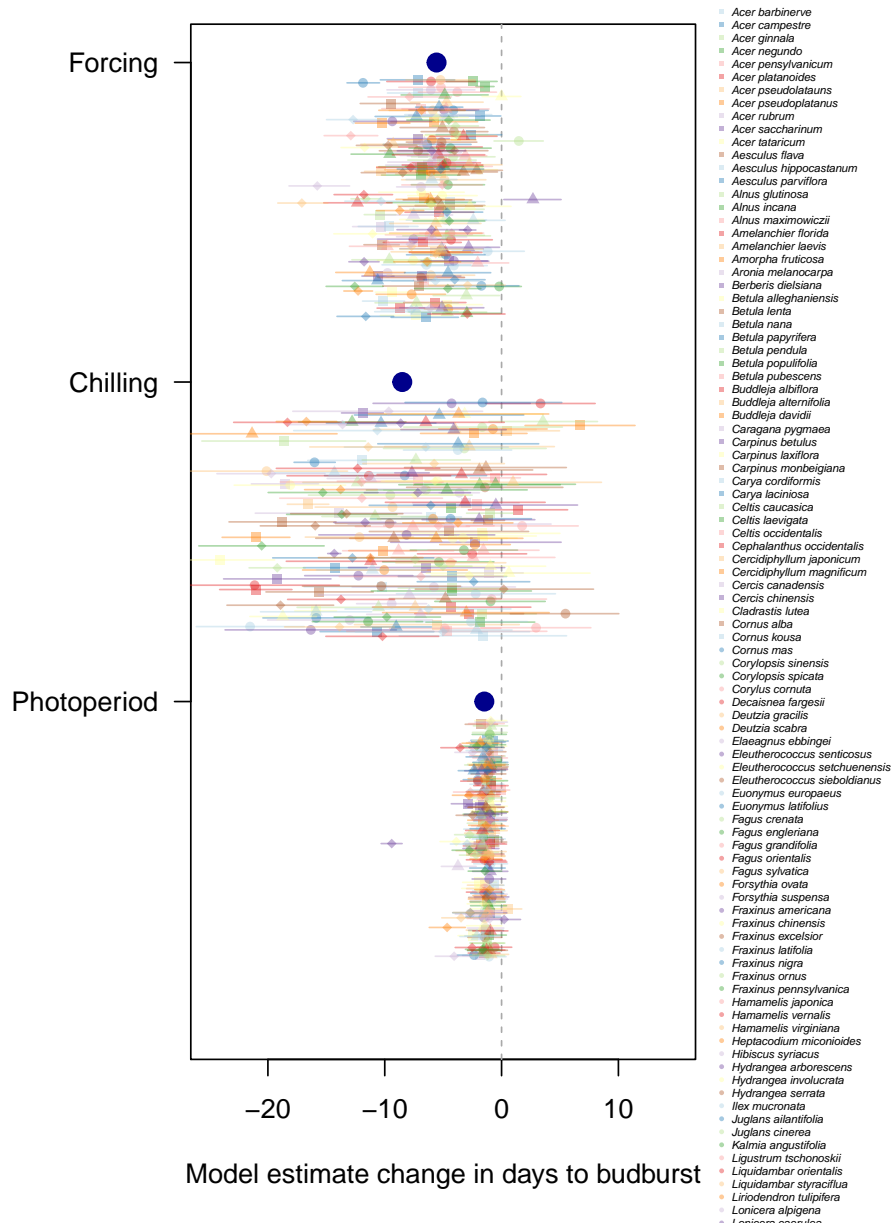


Figure 1: Cue sensitivity estimation by hierarchical phylogenetic model showing slopes for forcing, chilling and photoperiod for 194 angiosperm species.

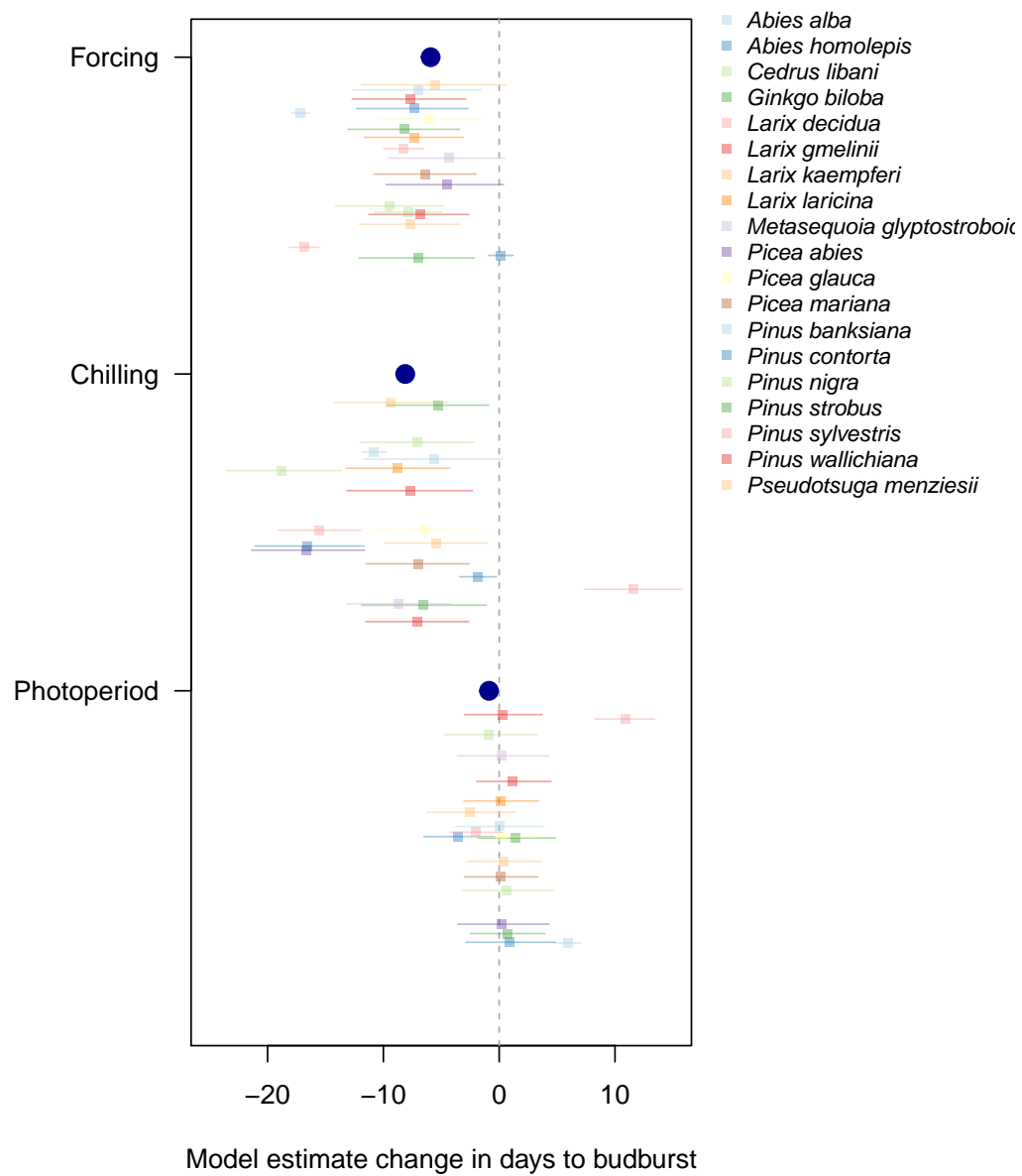


Figure 2: Cue sensitivity estimation by hierarchical phylogenetic model showing slopes for forcing, chilling and photoperiod for 19 gymnosperm species.

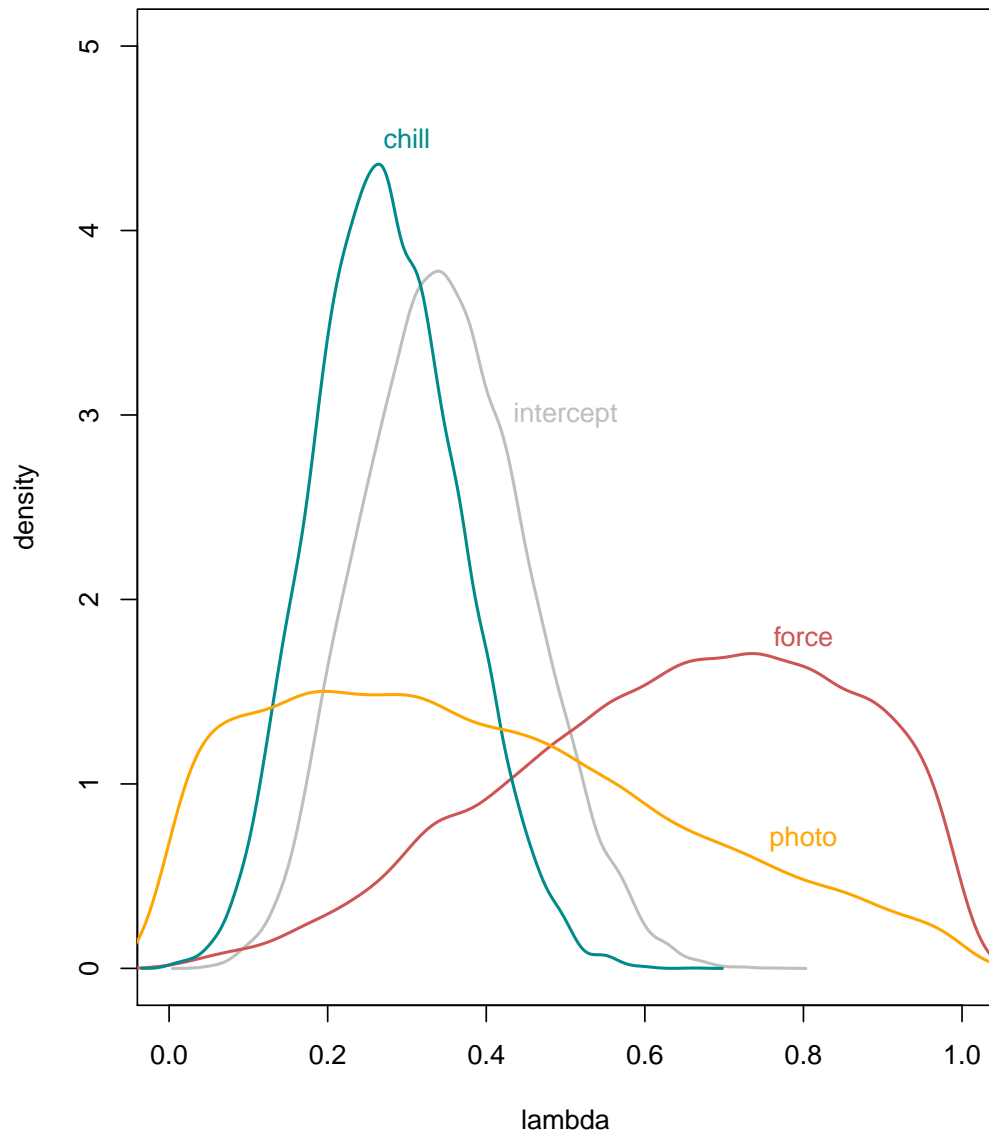


Figure 3: Posterior distribution of phylogenetic signal measured by lambda for each cue included as a predictor in the model for angiosperms: forcing (red), chilling (blue), photoperiod (orange) and for the model intercept (grey).

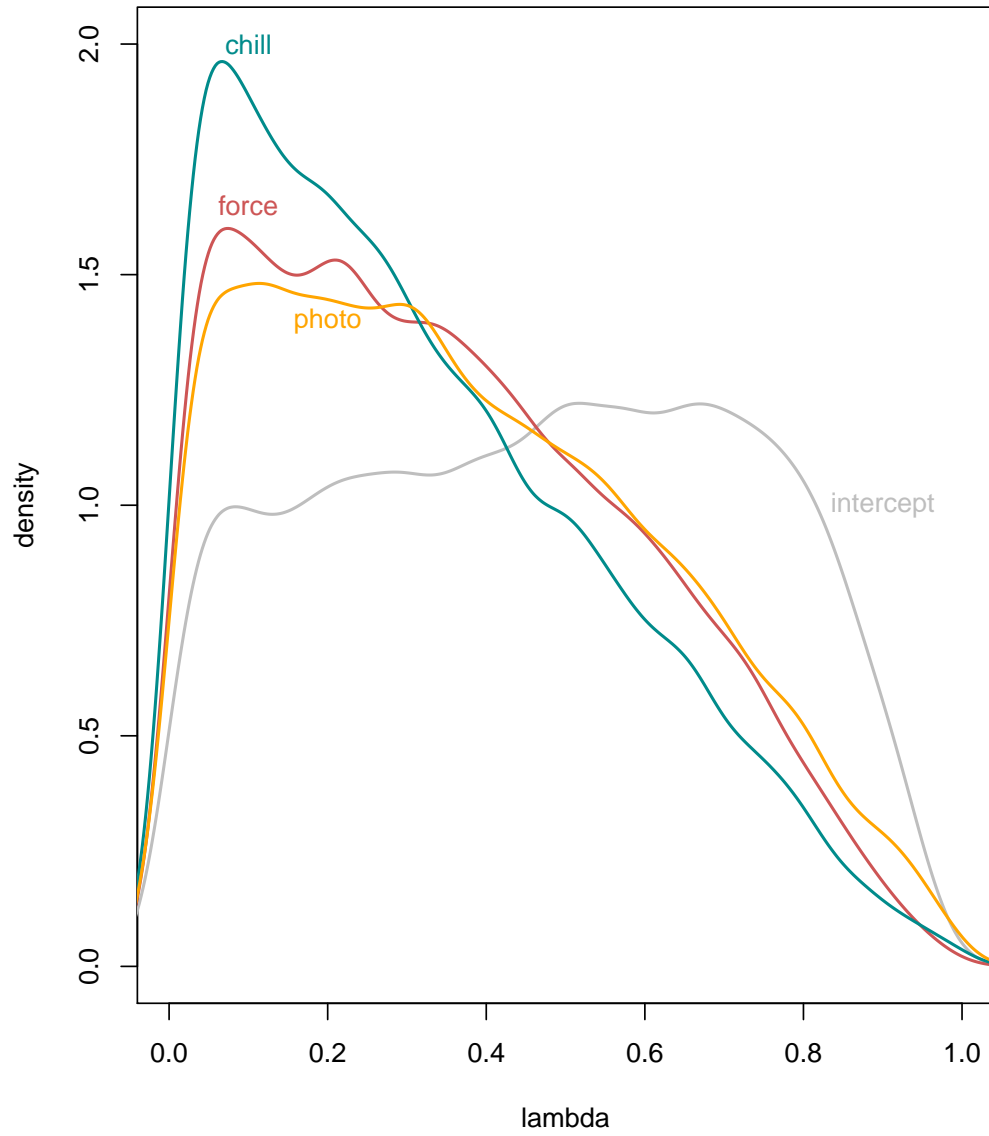


Figure 4: Posterior distribution of phylogenetic signal measured by lambda for each cue included as a predictor in the model for angiosperms: forcing (red), chilling (blue), photoperiod (orange) and for the model intercept (grey).