Evolution constrains tree responses to environmental cues in experimental settings too - Outline

January 22, 2020

Authors:

The Wolkovich Lab in 2019 [1,2,3,4]

Author affiliations:

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

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

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

[4]Edificio 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?

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

1. How plants respond to environmental cues–i.e. temperature, daylight–may determine their resilience or vulnerability to ongoing climate change.

2. Phenology provides a good description of plant responses to to the environment.

3. Phenology has been regarded to as a rather plastic trait, thus with a lot of variation both intra- and inter-specifically.

4. Variation in phenology could have randomly accummulated 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).

5. Whether or not phenology is conserved has implications for the need to account for phylogenetic autocorrelation in cross-species analyses.

6. 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.

7. 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 abiltiy of phylogenetically informed models to improve predictive accuracy of phenology.

8. Results show non-random phylogenetic structuring of phenological responses, highly variable across cues.

9. 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 Nabity, 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 evoutionary 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

Methods

Phenological and Phylogenetic Data

1. Description of the OSPREE database (where it comes from, number of species, studies, etc.).

Help here would be much appreciated!

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.allsppmodel=T]
   (e) All angiosperm species in the latest version of OSPREE (including 215 species)[flags.for.allsppmodel=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.

Provenance-climate Data

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

I belive this can be done (roughly) through the NAm vs. Eur comparison?

Hierarchical models to estimate species-level cue sensitivity

1. Our approach used Bayesian hierarchical models to estimate the number of days until budburst as a function of forcing, chilling and photoperiod. We used different specifications of partial pooling to determine in which approach the sensitivies to the cues most accurately predict budburst. We used 5 model specifications:

(a) species as a grouping factor on the intercept (Eq. 1)

(b) species as grouping factor on the intercept and slopes too (Eq. 2)

(c) phylogeny as a grouping factor on the intercept and species as grouping factor on both intercept and slopes (Eq. 3)

(d) phylogeny as a grouping factor on the intercept and species as grouping factor on both intercept and slopes (Eq. 3)

2. In all specifications, the Bayesian hierarchical models were fit using the brms package (Bürkner, 2017), in R (R Development Core Team, 2017), version 3.5.1, and followed the notations:

$$Budbreak = \alpha_{species} + \beta_1 forcing + \beta_2 chilling + \beta_3 photo + \varepsilon \tag{1}$$

$$Budbreak = \alpha_{spp} + \beta_{1,spp} forcing + \beta_{2,spp} chilling + \beta_{3,spp} photo + \varepsilon \tag{2}$$

$$Budbreak = \alpha_{phylo,spp} + \beta_{1,spp} forcing + \beta_{2,spp} chilling + \beta_{3,spp} photo + \varepsilon \tag{3}$$

$$Budbreak = \alpha_{phylo,species} + \beta_1 forcing + \beta_2 chilling + \beta_3 photo + \varepsilon \tag{4}$$

3. We assessed model performance according to $\hat{R}$ values (that should be close to one to ensure convergence). As for metrics of model accuracy we computed R^2, and the expected log predictive density (ELPD) that results from *Leave-one-out* cross-validation, in addition to inspection of posterior predictive checks.

4. To test the ability of phylogeny to improve models/predictions of budburst we compared metrics of model accuracy between models that include phylogeny and models that do not.

The Bayesian phylogenetic model

1. To determine phylogenetic signal in the responses to each of the environmental cues–i.e. forcing, chilling, photoperiod–we run a second batch of models in brms, that use the slopes of the models specified above as a response variable, following the notation:

$$\beta_1 forcing = \alpha_{phylo} + \varepsilon_{phylo} + \varepsilon_{non-phylo} \tag{5}$$

$$\beta_2 chilling = \alpha_{phylo} + \varepsilon_{phylo} + \varepsilon_{non-phylo} \tag{6}$$

$$\beta_3 photo = \alpha_{phylo} + \varepsilon_{phylo} + \varepsilon_{non-phylo} \tag{7}$$

2. Once this set of models is computed, calculating phylogenetic signal (H^2) is straightforward:

$$H^2 = \frac{\varepsilon_{phylo}}{\varepsilon_{phylo} + \varepsilon_{non-phylo}} \tag{8}$$

3. H^2 is 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, for $\lambda = 0$ phylogenetically close species are not more similar than phylogenetically distant species and, for $\lambda = 1$, phylogenetically close species resemble each other according to a BM model, where phenotypic variance accummulates proportional to time.

4. In other words, the λ parameter can be defined as a scalar that multiplies the diagonal of the phylogenetic Variance-Covariance metric and that is estimated through *Maximum Likelihood* in traditional comparative approaches (Freckleton et al., 2002). Our approach, in contrast computes the ratio between amount of variance attributable to the phylogeny (ε_{phylo}) and the total amount of variance 8.

5. We compare the results from our H^2 metric against the results for λ computed through Phylogenetic Generalized Least Squares (Freckleton et al., 2002).

Results from our approach and PGLS differ in the 215spp dataset - to discuss

Phylogeny in forecasts of phenology

This sections needs to be fleshed out, but first we need to think and decide how to proceed:

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: model accuracy and correlations across cues

1. the model we used in the main model is the most accurate
2. Accuracy does not depend on whether partial pooling is on the phylogeny or on species
3. point towards the R2 and LOO tables
4. explain correlations across cues

Phylogenetic signal in phenological responses

1. Phenological responses to the three studied cues are overall phylogenetically conserved but estimates of phylogenetic signal differ across species subsets.
2. When all species (from main model) are considered, responses to forcing are more conserved ($H^2 = 0.73$) than responses to chilling ($H^2 = 0.47$) or to photoperiod ($H^2 = 0.55$) (see Figure 5).
3. When species belonging to the same genera (usually showing large polytomies in the phylogeny) are grouped into species complexes (for which data on cross-treatments are more complete), responses to forcing ($H^2 = 0.37$) and photoperiod ($H^2 = 0.68$) are conserved but responses to chilling ($H^2 = 0.18$) are not Figure 4).
4. The marked differences in the responses to each cue are buffered when only angiosperm species are considered, with all responses being mildly conserved: forcing ($H^2 = 0.33$), chilling ($H^2 = 0.37$) and photoperiod ($H^2 = 0.40$). This suggests gymnosperms, even few species can have a major effect in apparent differences across cues (Figure 6).
5. The correlations among responses to the cues are positive but only markedly high between photoperiod and chilling (Figure 1).

Budburst models, phylogenetic and non-phylogenetic

1. Insert table here summarizing changes in coefficients and Rsq with/without phylogeny

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 addings):

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 Bayesia 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

Table 1: R2 estimates for models fitted to two subsets of data.

Model	nsps	R2	Est.Error	Q2.5	Q97.5
mod.sps.intercept	52	0.369	0.012	0.346	0.392
mod.sps.phylo.intercept	52	0.370	0.012	0.345	0.393
mod.sps.interc.slope	52	0.478	0.011	0.456	0.498
mod.sps.interc.slope.phy.int	52	0.478	0.011	0.455	0.499
mod.sps.intercept	117	0.369	0.012	0.344	0.393
mod.sps.phylo.intercept	117	0.369	0.012	0.345	0.392
mod.sps.interc.slope	117	0.486	0.011	0.465	0.506
mod.sps.interc.slope.phy.int	117	0.487	0.011	0.465	0.507
mod.sps.intercept	215	0.582	0.007	0.566	0.596
mod.sps.phylo.intercept	215	0.582	0.007	0.567	0.596
mod.sps.interc.slope	215	0.659	0.006	0.646	0.670
mod.sps.interc.slope.phy.int	215	0.658	0.006	0.646	0.671

Table 2: Leave One Out analyses for models fitted to two subsets of data.

Model	nsps	elpd_diff	se_diff	elpd_loo	se_elpd_loo
mod.sps.interc.slope	52	0.000	0.000	-10944.890	75.627
mod.sps.interc.slope.phy.int	52	-0.090	0.366	-10944.980	75.572
mod.sps.phylo.intercept	52	-217.806	24.087	-11162.696	74.662
mod.sps.intercept	52	-218.150	24.041	-11163.040	74.719
mod.sps.interc.slope.phy.int	117	0.000	0.000	-10951.579	75.858
mod.sps.interc.slope	117	-0.543	0.591	-10952.122	75.803
mod.sps.phylo.intercept	117	-242.375	25.727	-11193.955	75.031
mod.sps.intercept	117	-242.582	25.691	-11194.161	75.097
mod.sps.interc.slope	215	0.000	0.000	-14195.898	89.929
mod.sps.interc.slope.phy.int	215	-1.945	2.411	-14197.843	90.075
mod.sps.phylo.intercept	215	-302.843	27.217	-14498.741	89.759
mod.sps.intercept	215	-305.035	27.306	-14500.933	89.765

Table 3: Comparison between phylogenetic signal from PGLS and BRMS.

subset	cue	λ	Lower95CI	Upper95CI	H^2	Lower95CI	Upper95CI
52-complex	forcing	0.171446841	NA	0.650638627	0.330834872	0.008358609	0.751811447
	chilling	1.00E-06	NA	0.396954468	0.194753034	0.000682814	0.610910681
	photo	0.655354248	0.186405507	0.897899618	0.662218791	0.208150902	0.920502832

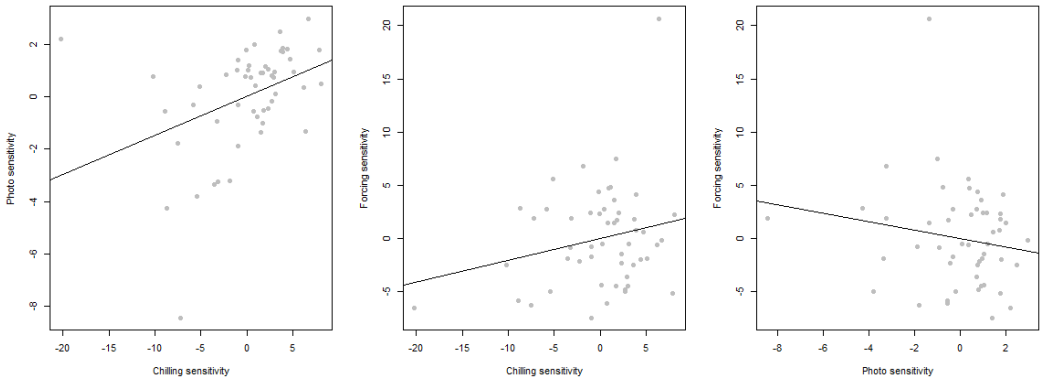

Figure 1: Scatterplots showing correlations between the sensitivities of the species complexes in OSPREE to chilling and photoperiod (A), chilling and forcing (B), and forcing and photoperiod (C). Sensitivities are positively correlated among chilling and photoperiod and chilling and forcing, but negatively correlated between forcing and photoperiod.

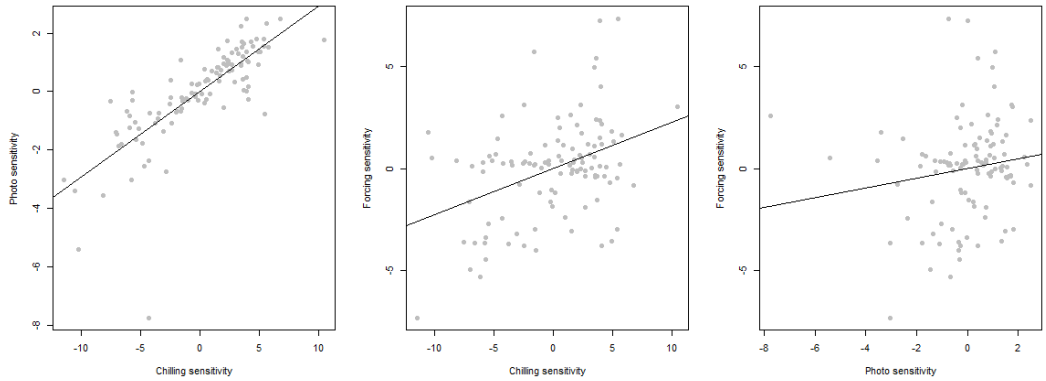

Figure 2: Scatterplots showing correlations between the sensitivities of the species in OSPREE to chilling and photoperiod (A), chilling and forcing (B), and forcing and photoperiod (C). Sensitivities are correlated overall, but more so between chilling and photoperiod.

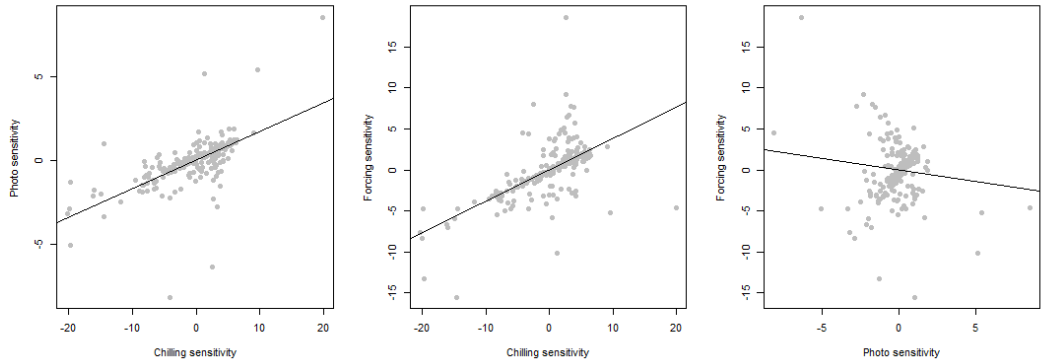

Figure 3: Scatterplots showing correlations between the sensitivities of the species in OSPREE (subset with all 231 species for which there is data) to chilling and photoperiod (A), chilling and forcing (B), and forcing and photoperiod (C). Sensitivities are positively correlated among chilling and photoperiod and chilling and forcing, but negatively correlated between forcing and photoperiod.

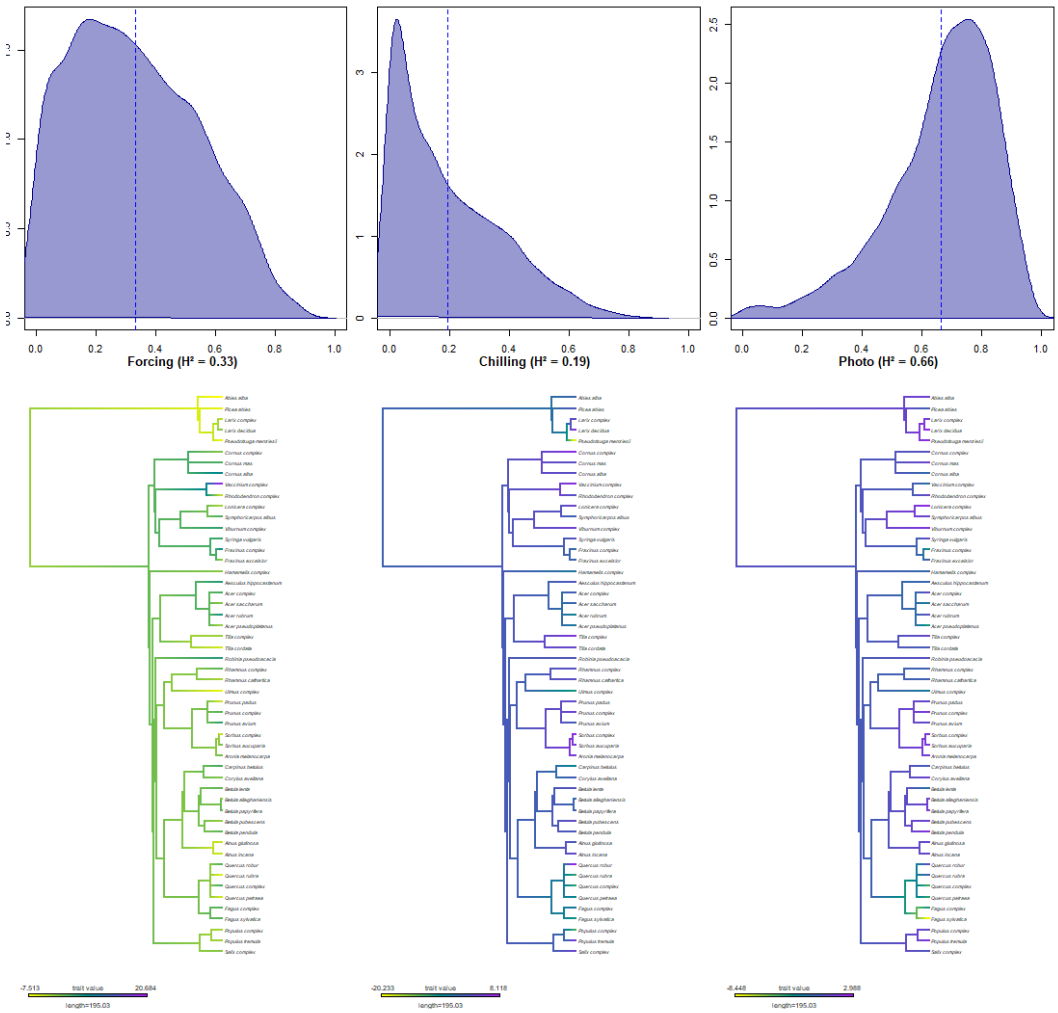

Figure 4: Phylogenetic signal results for the sensitivities of each species complex (species grouped by genera) to the forcing (A), chilling (B) and photoperiod (C) cues.

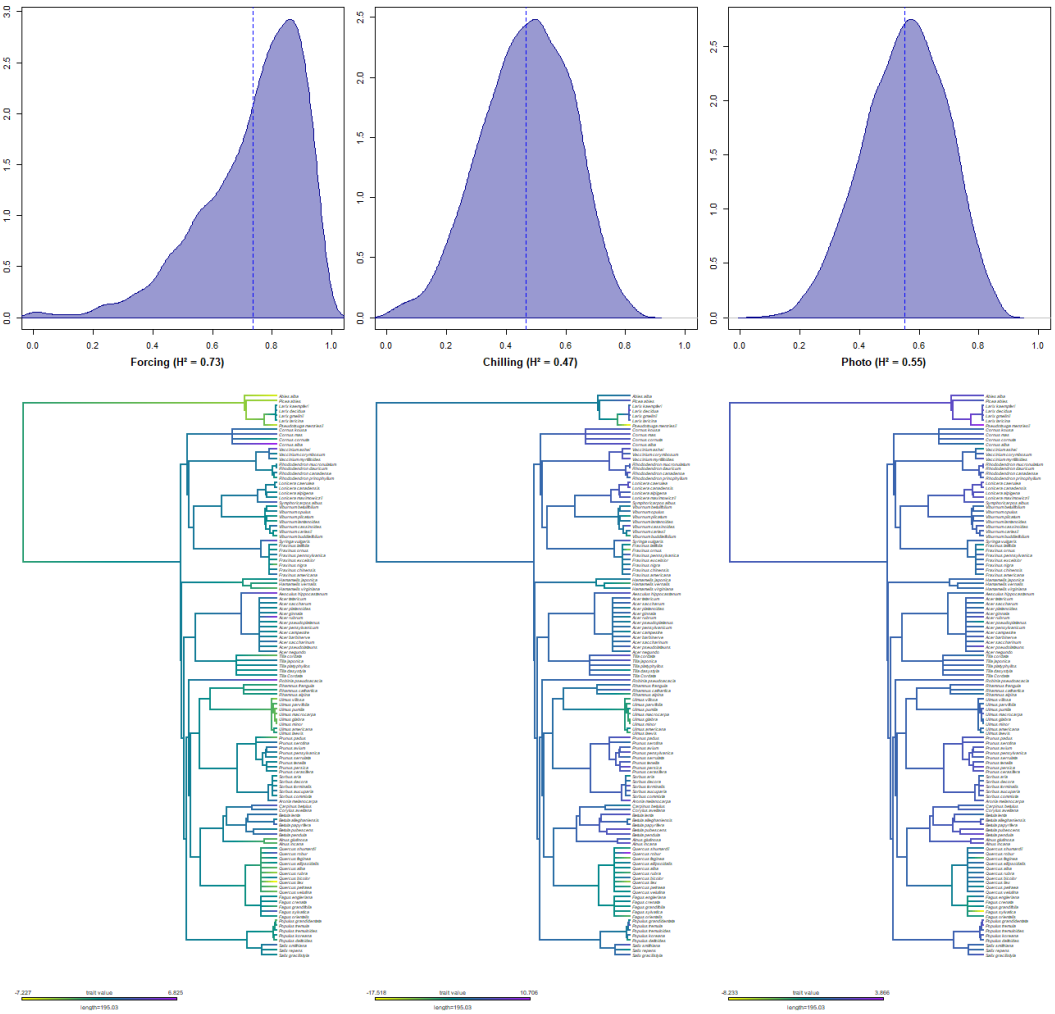

Figure 5: Phylogenetic signal results for the sensitivities of each species (ungrouped) to the forcing (A), chilling (B) and photoperiod (C) cues.

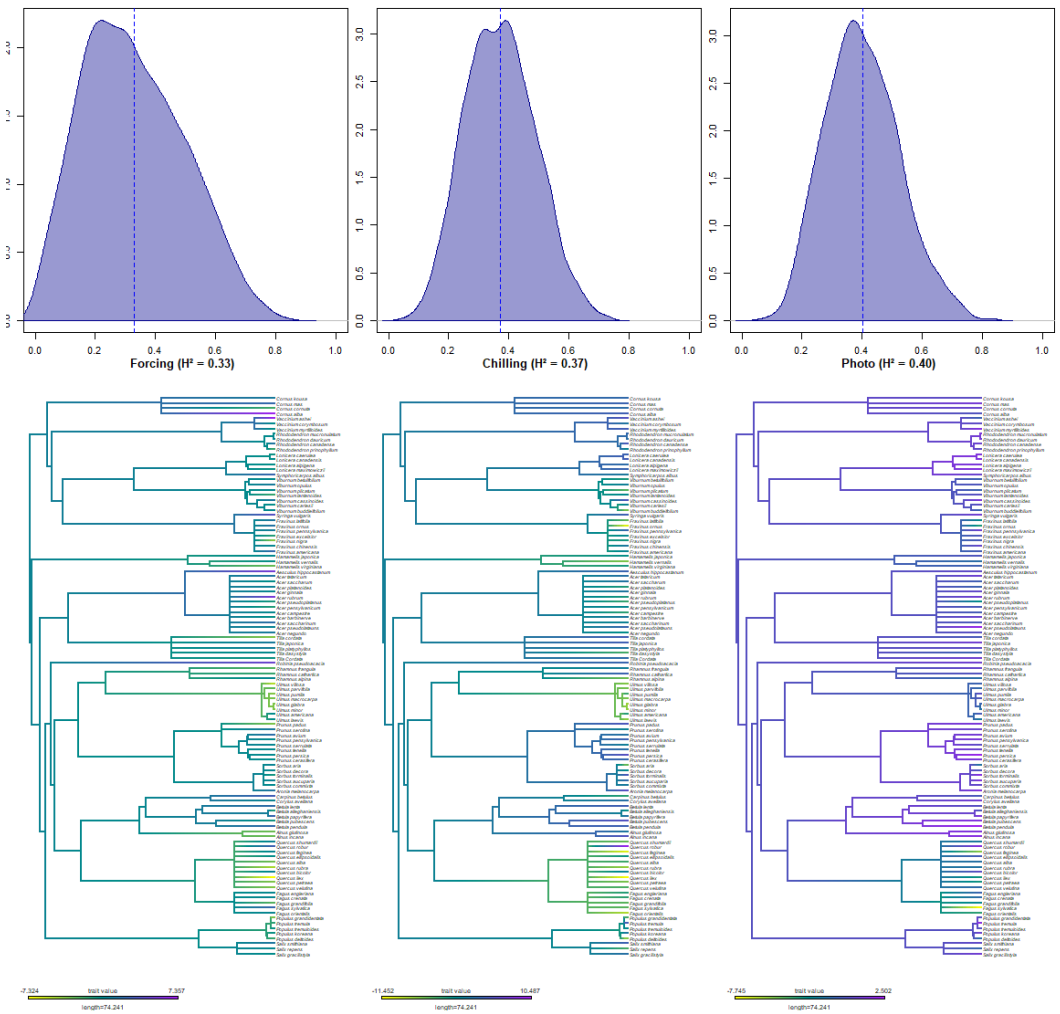

Figure 6: Phylogenetic signal results for the sensitivities of each species (excluding gymnosperms) to the forcing (A), chilling (B) and photoperiod (C) cues.

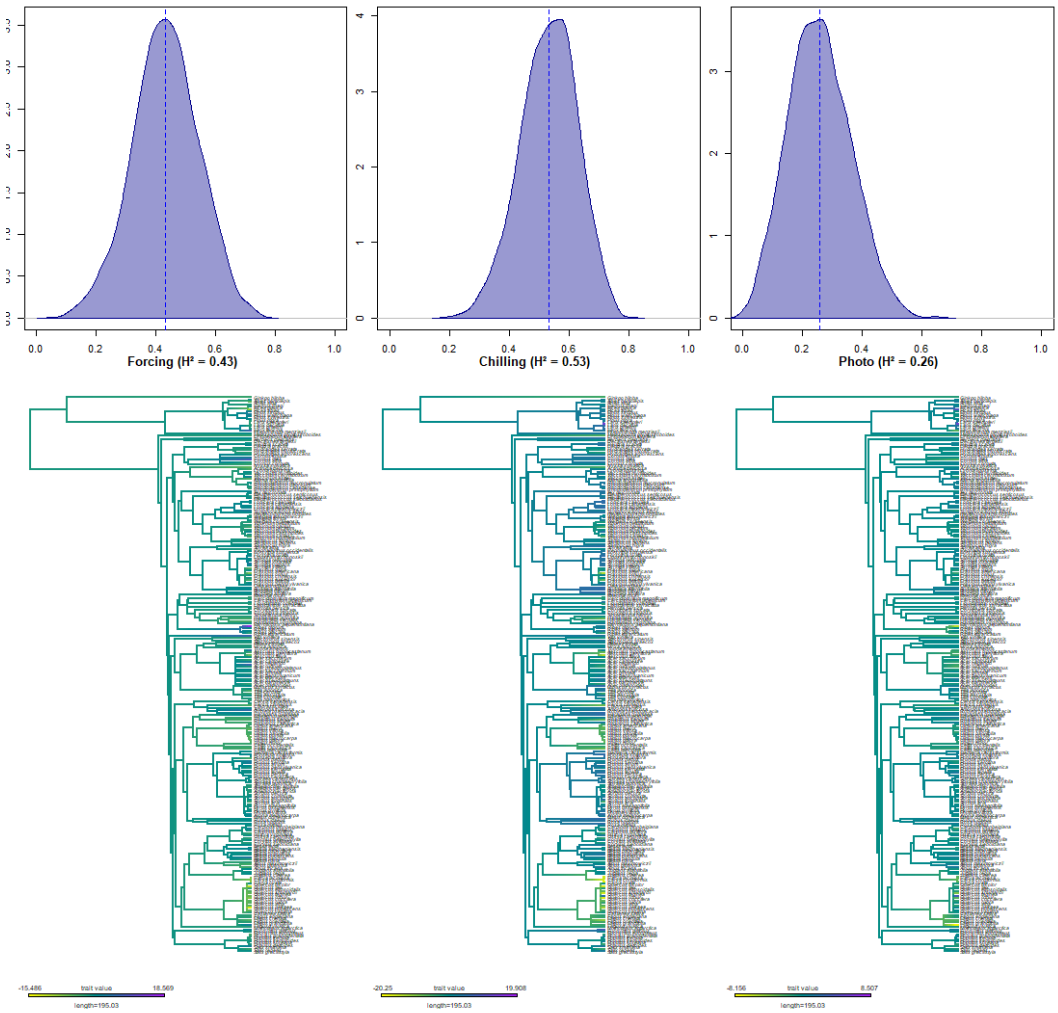

Figure 7: Phylogenetic signal results for the sensitivities of each species (231 species included) to the forcing (A), chilling (B) and photoperiod (C) cues.

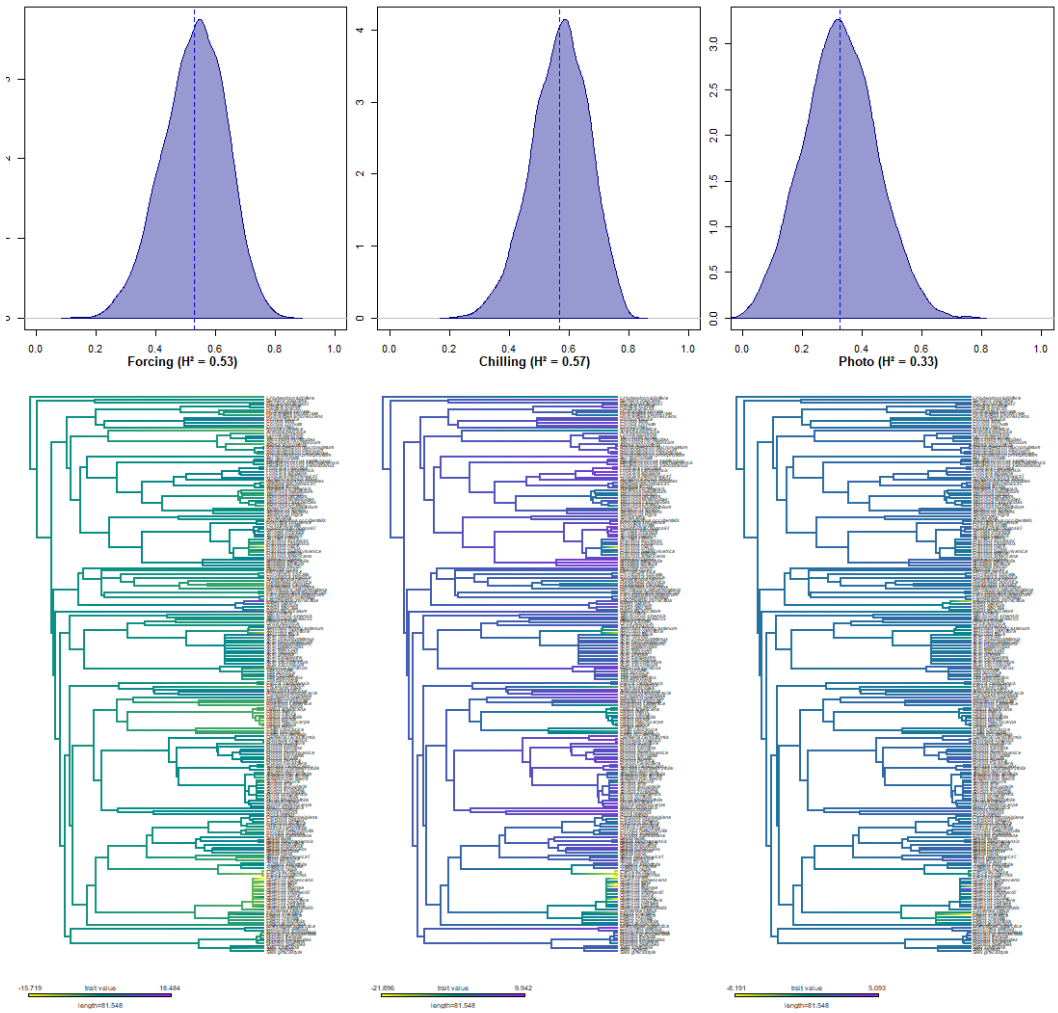

Figure 8: Phylogenetic signal results for the sensitivities of each species (215 angiosperm only species included) to the forcing (A), chilling (B) and photoperiod (C) cues.