

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

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Rationale & Significance

Previous work has looked at the phylogenetic conservatism of phenologies 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 (Rafferty and Nabity, 2017).

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

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

The potential interest of findings in this direction stem from:

- better predictions of phenology (or need to account for it in models)
- better understand 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 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 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).
5. Whether or not phenology is conserved has implications for the need to account for phylogenetic auto-correlation 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 ability 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?
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))
 - (b) studied trait correlation (Bolmgren and D. Cowan, 2008)
 - (c) studied 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 the response to one cue only: forcing)
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

Methods

Phenological and Phylogenetic Data

1. Description of the OSPREE database (where it comes from, number of species, studies, etc.) and how we prune it to retain the final list of 62 species.
2. 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.

Provenance-climate Data

1. Should we test/analyze provenance or climate-effects? If so, we would need to

Hierarchical models to estimate 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 from the simplest models with species as a grouping factor on the intercept (Eq. 1), to more sophisticated models with species as grouping factor on the slopes too (Eq. 2) and adding phylogeny as a grouping factor on the intercept (Eq. 3).
2. 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:

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

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

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

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

3. These models were run for three subsets of species:
 - All species in the latest version of OSPREE (including 231 species)
 - All angiosperm species in the latest version of OSPREE (including XX species)
 - Species grouped in generic complexes, to ensure enough cross-treatment data, as in Ettinger et al. (under review) (including XX complexes)
4. 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 *Leave One Out* (LOO) metrics, in addition to inspection of posterior predictive checks.
5. 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

6. 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:

$$\beta_1 forcing = \alpha_{phylo} + \varepsilon_{phylo} + \varepsilon_{non-phylo} \quad (5)$$

$$\beta_2 chilling = \alpha_{phylo} + \varepsilon_{phylo} + \varepsilon_{non-phylo} \quad (6)$$

$$\beta_3 photo = \alpha_{phylo} + \varepsilon_{phylo} + \varepsilon_{non-phylo} \quad (7)$$

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

$$H^2 = \frac{\varepsilon_{phylo}}{\varepsilon_{phylo} + \varepsilon_{non-phylo}} \quad (8)$$

8. 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.

9. 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). Mathematically, this is equivalent to the ratio between amount of variance attributable to the phylogeny (ε_{phylo}) and the total amount of variance.
10. The interpretation of λ is as a metric that informs how much phylogenetically closely related species resemble each other.

Results

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 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 3).
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 2).
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 4).
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

1. 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?)...

References

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Tables and Figures

Table 1: Leave One Out analyses for models fitted to two subsets of data.

Model	nsps	elpd_diff	se_diff	elpd_loo	se_elpd_loo
phylo.FULL.c	117	0	0	-10951.57927	75.85827637
NOfylo.FULL.b	117	-0.543111109	0.591327747	-10952.12239	75.80314884
phylo.int.slope	117	-0.729725786	2.427434551	-10952.309	75.723124
phylo.int.only	117	-242.3752625	25.72665616	-11193.95454	75.0307041
NOfylo.FULL	117	-242.5815496	25.69052496	-11194.16082	75.09682333
NOfylo.FULL.b.sps	215	0	0	-14195.89791	89.9292618
phylo.FULL.c.sps	215	-1.945200656	2.410917044	-14197.84311	90.07455729
phylo.int.only.sps	215	-302.8426832	27.21650046	-14498.74059	89.75867558
NOfylo.FULL.sps	215	-305.0350316	27.30609914	-14500.93294	89.76455198

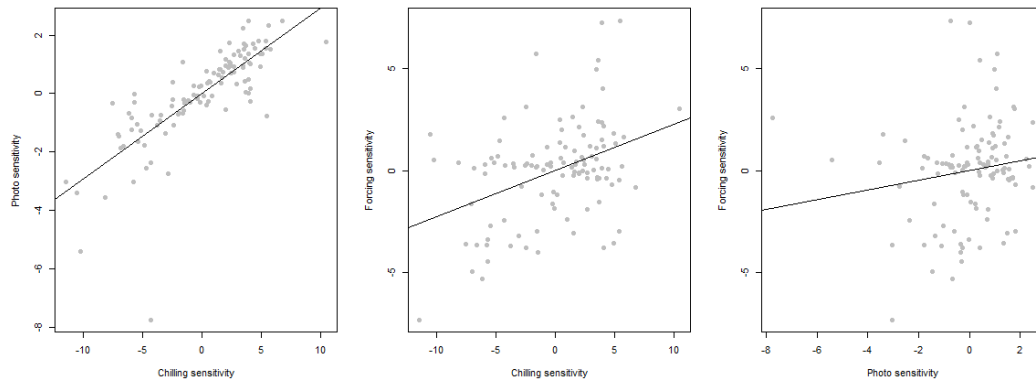


Figure 1: Scatterplots showing correlations between the sensitivities of the species in OSPREE to chilling and photoperiod (A), chilling and forcing (B), and forcing and photoperiod (C). Sensitivities are correlated overall, but more so between chilling and photoperiod.

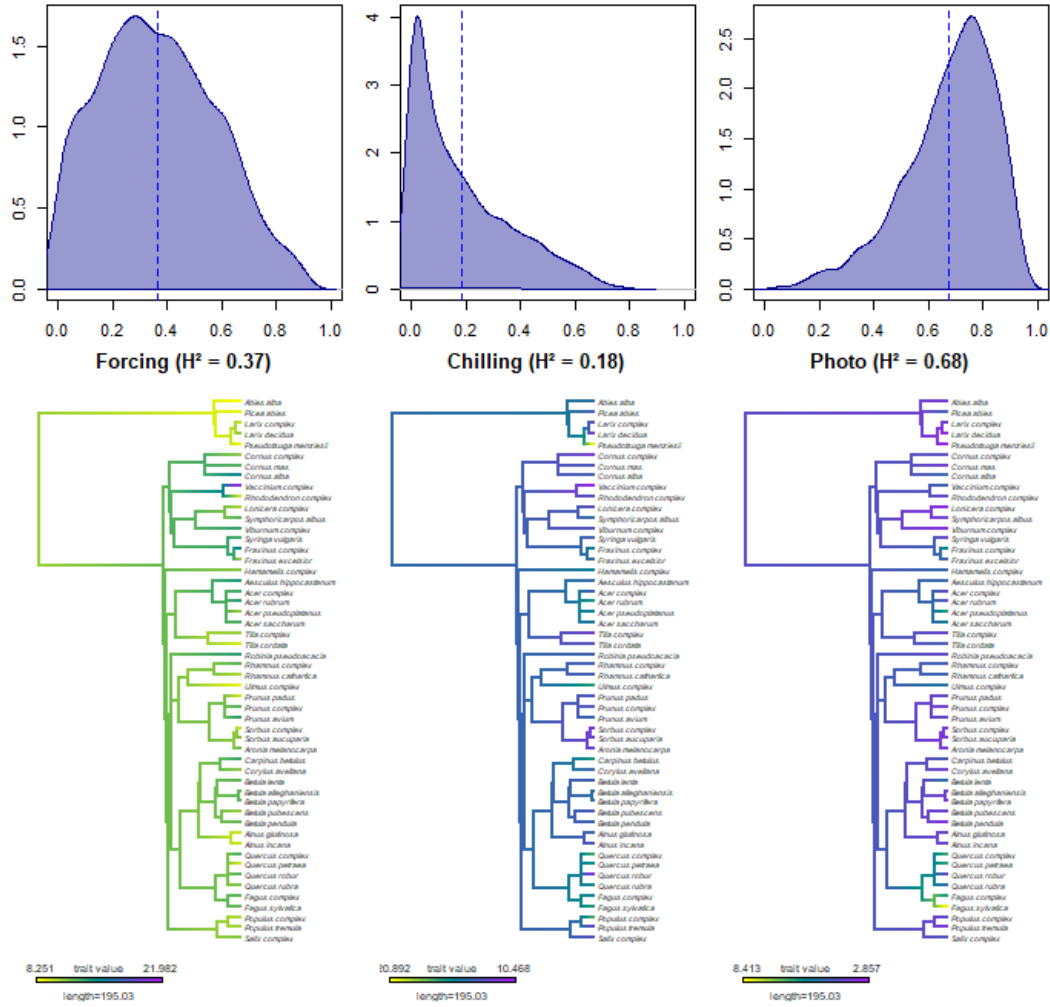


Figure 2: Phylogenetic signal results for the sensitivities of each species complex (species grouped by genera) to the forcing (A), chilling (B) and photoperiod (C) cues.

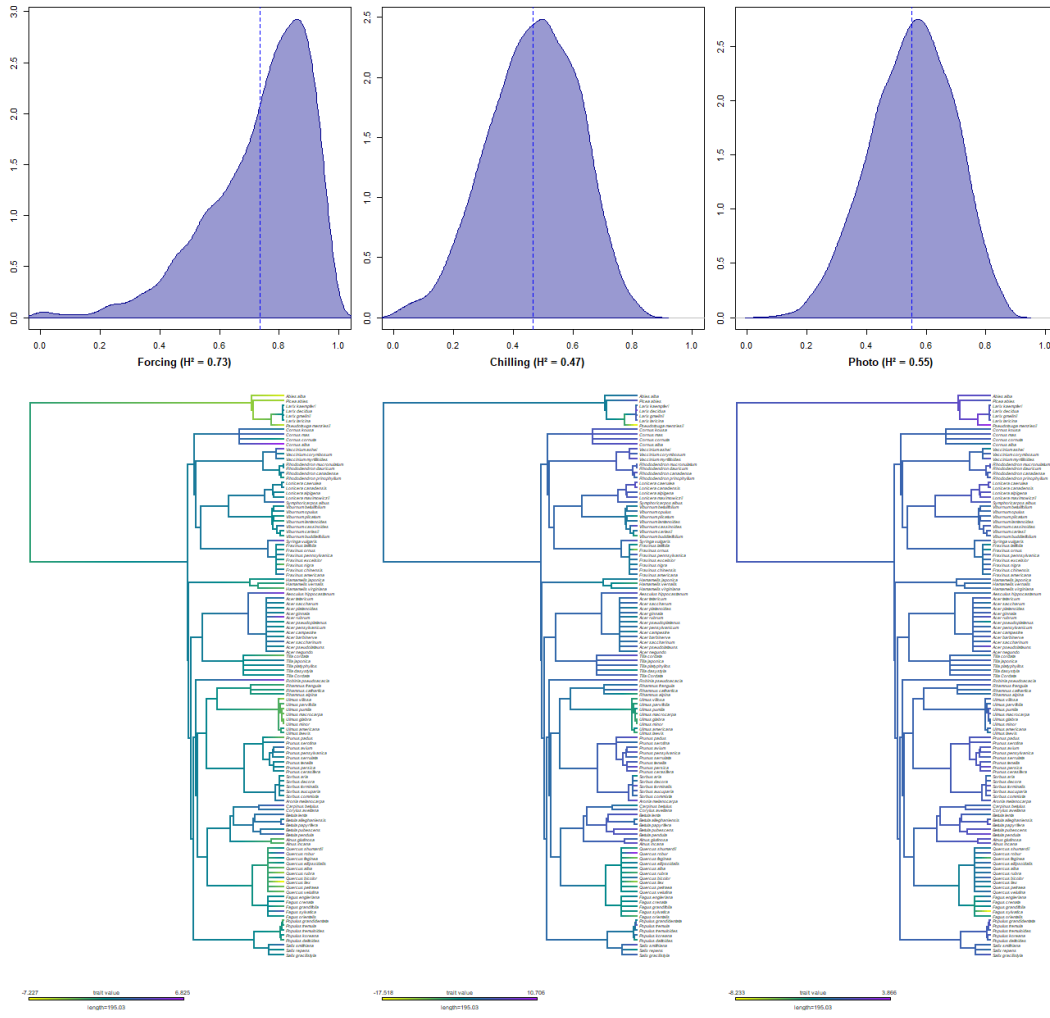


Figure 3: Phylogenetic signal results for the sensitivities of each species (ungrouped) to the forcing (A), chilling (B) and photoperiod (C) cues.

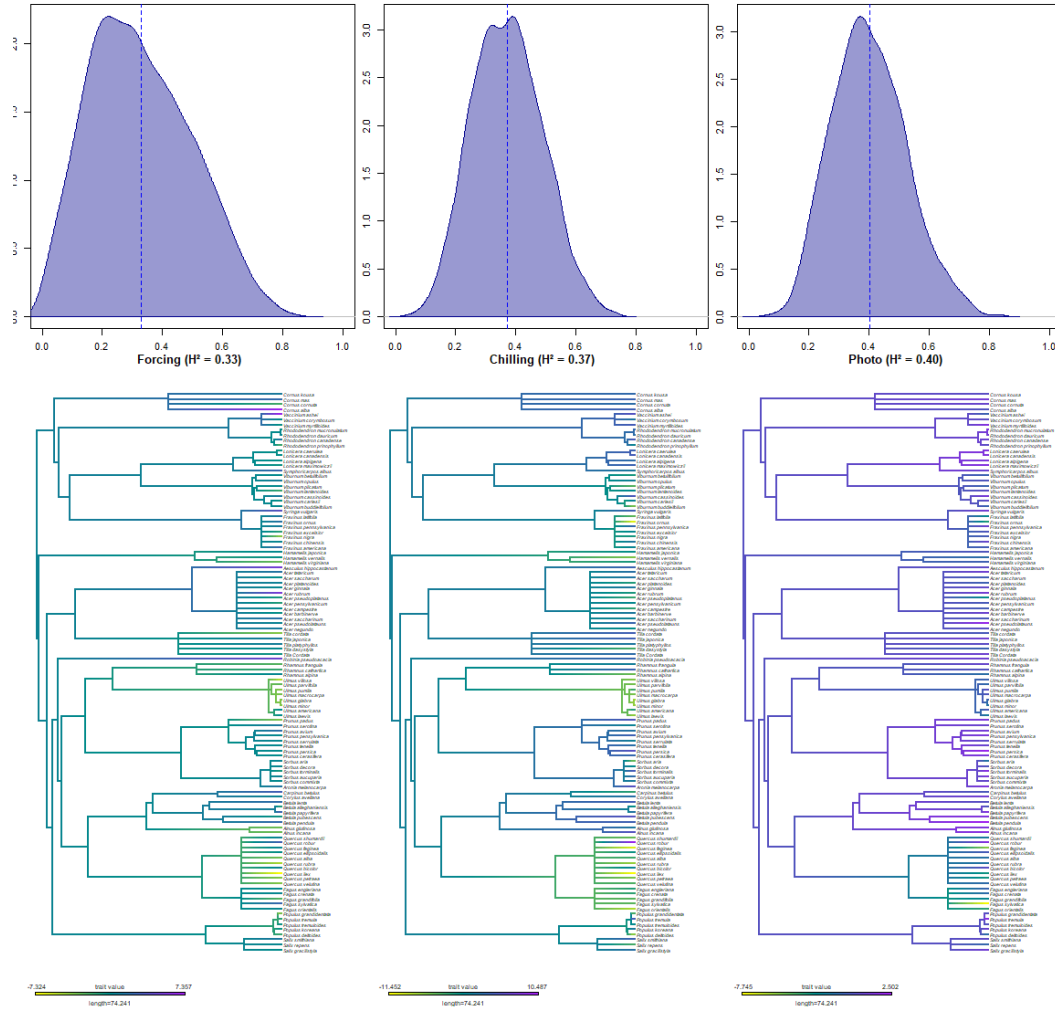


Figure 4: Phylogenetic signal results for the sensitivities of each species (excluding gymnosperms) to the forcing (A), chilling (B) and photoperiod (C) cues.

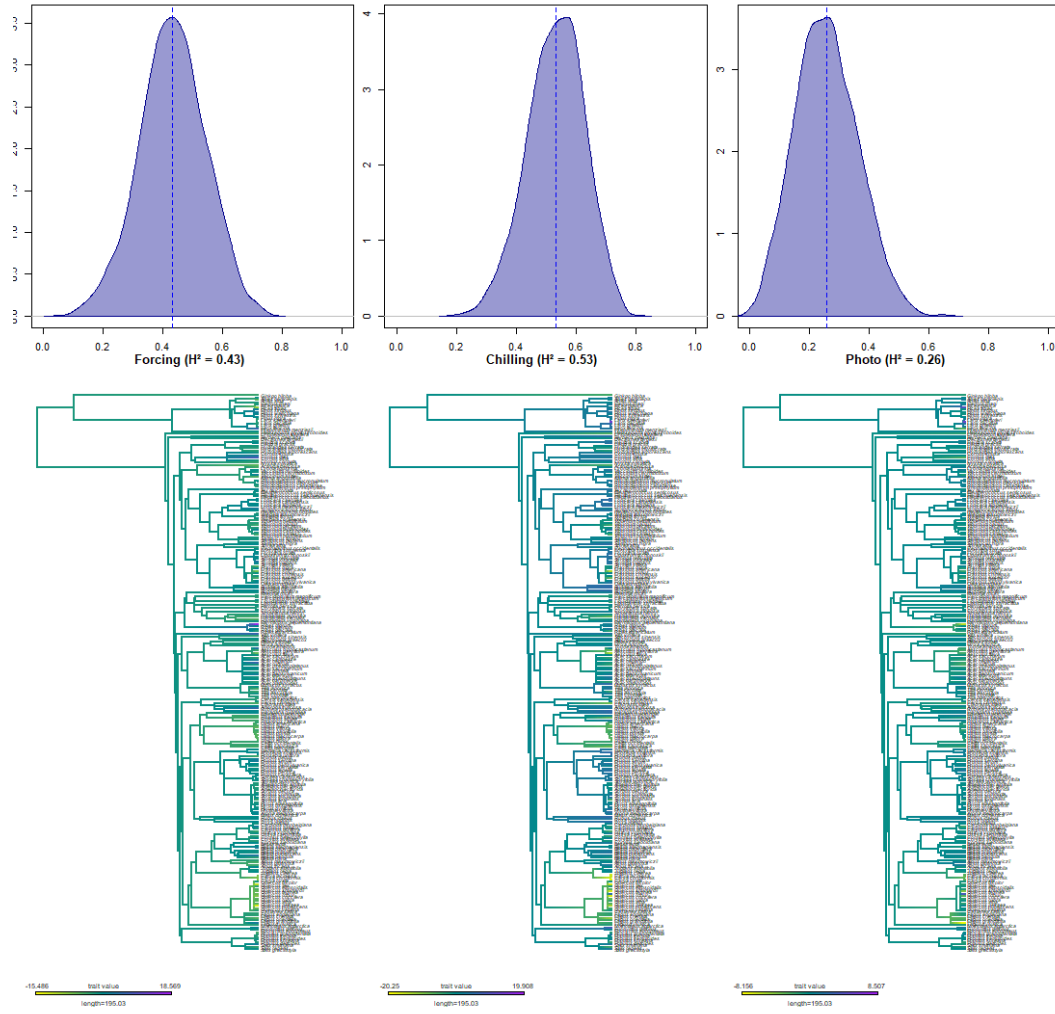


Figure 5: Phylogenetic signal results for the sensitivities of each species (231 species included) to the forcing (A), chilling (B) and photoperiod (C) cues.

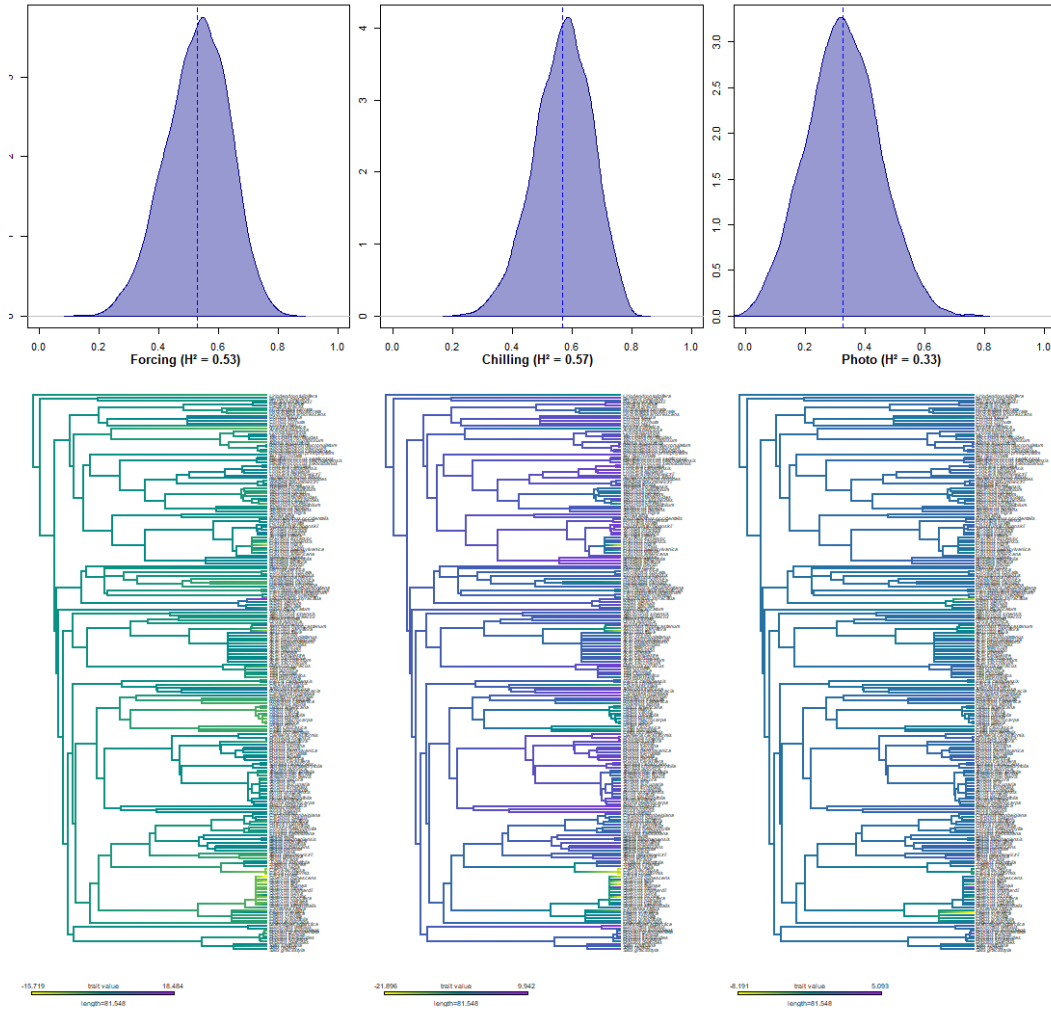


Figure 6: Phylogenetic signal results for the sensitivities of each species (215 angiosperm only species included) to the forcing (A), chilling (B) and photoperiod (C) cues.