Evolution constrains tree phenology in experimental settings - Outline

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Rationale & Significance

Previous work has looked at the phylogenetic conservatism of phylogenies 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?

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 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 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 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?

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 provenace or climate-effects? If so, we would need to

Data Analysis

1. We used a Bayesian hierarchical model approach to estimate the number of days until budburst is reached as a function of forcing, chilling and photoperiod.

2. The Bayesian hierarchical model was fit using the brms package (Bürkner, 2017), in R (R Development Core Team, 2017), version 3.5.1, and followed the notation:

3. Copy model specifications below (TBD).

4. Specify model evaluation and metrics of accuracy (Rhat, Rsq, more?)

5. To test the ability of phylogeny to improve models/predictions of budburst we: (describe procedure)

The Bayesian Phylogenetic hierarchical model

6. Explain how the model is fit, and how the H^2 metric is analogous to lambda in PGLS.

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.

References

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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.
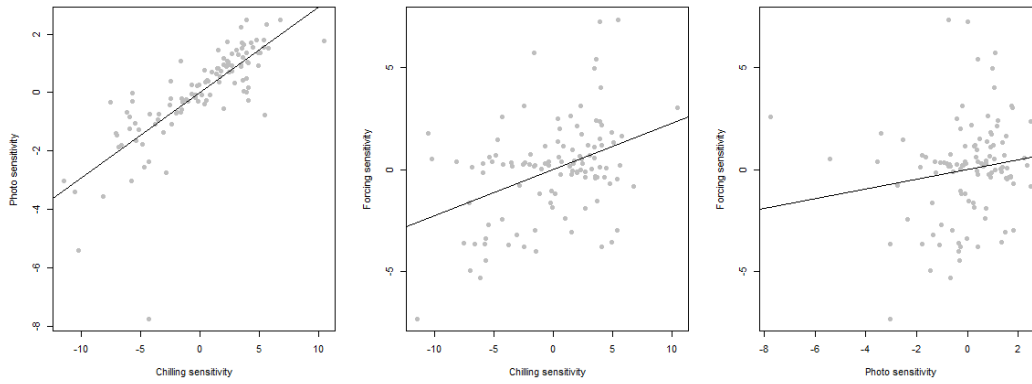
Tables and Figures

Figure 1: 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.
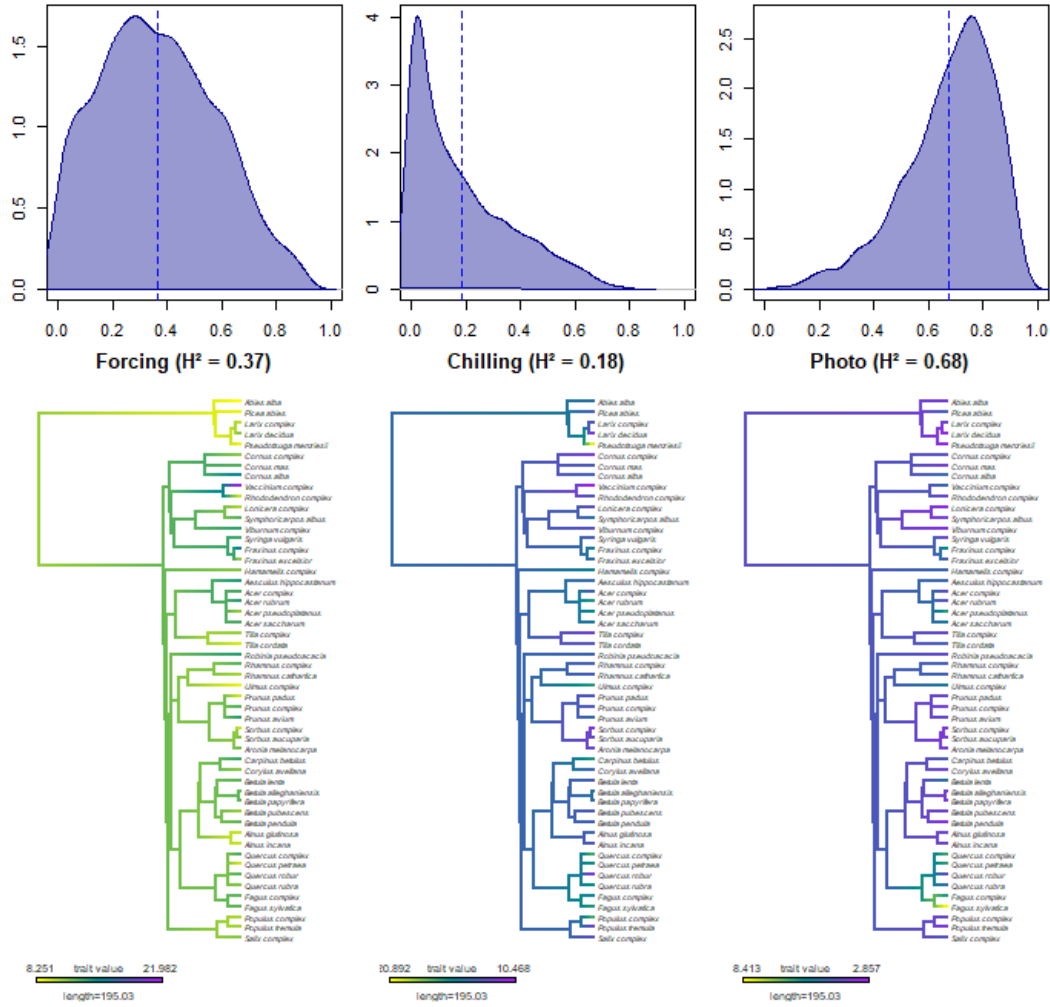
Figure 2: Phylogenetic signal results for the sensitivities of each species complex (species grouped by genera) to the forcing (A), chilling (B) and photoperiod (C) cues.
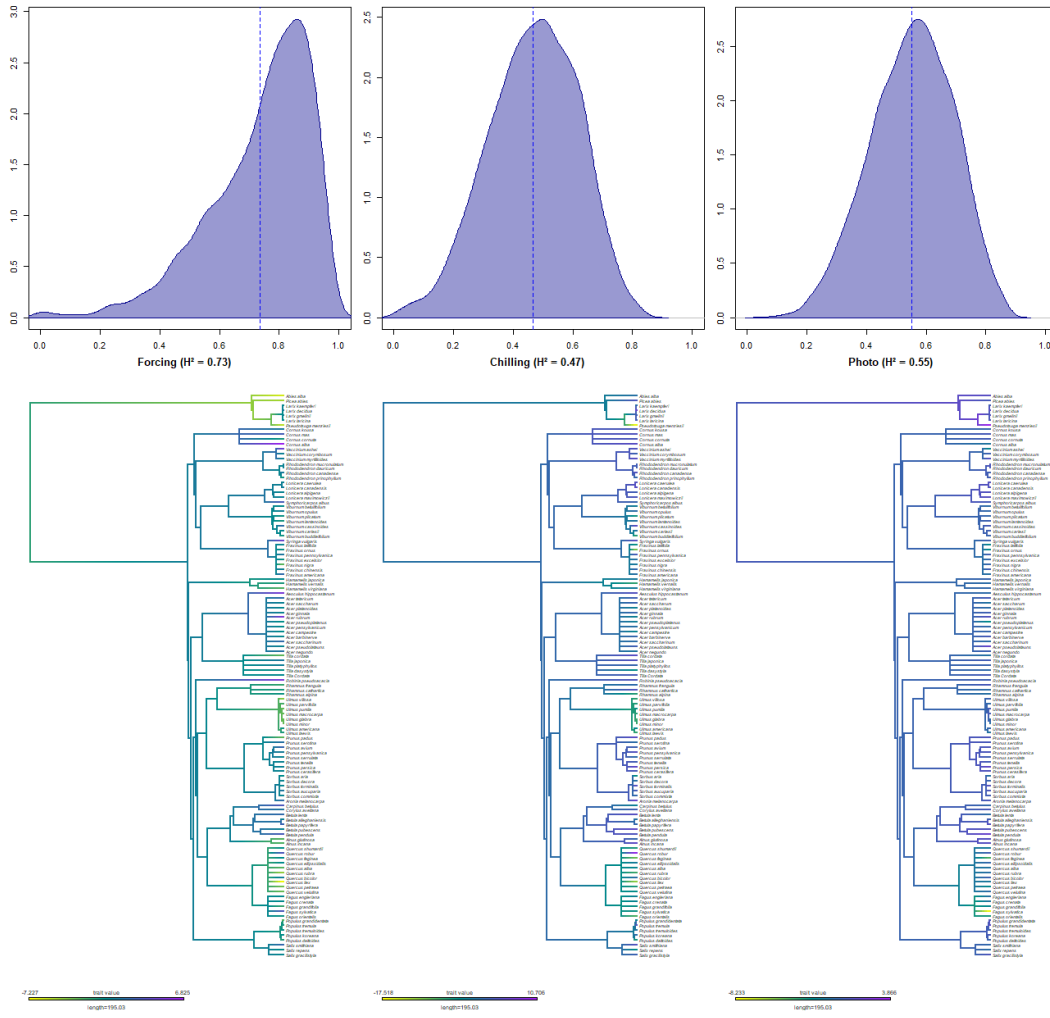
Figure 3: Phylogenetic signal results for the sensitivities of each species (ungrouped) to the forcing (A), chilling (B) and photoperiod (C) cues.
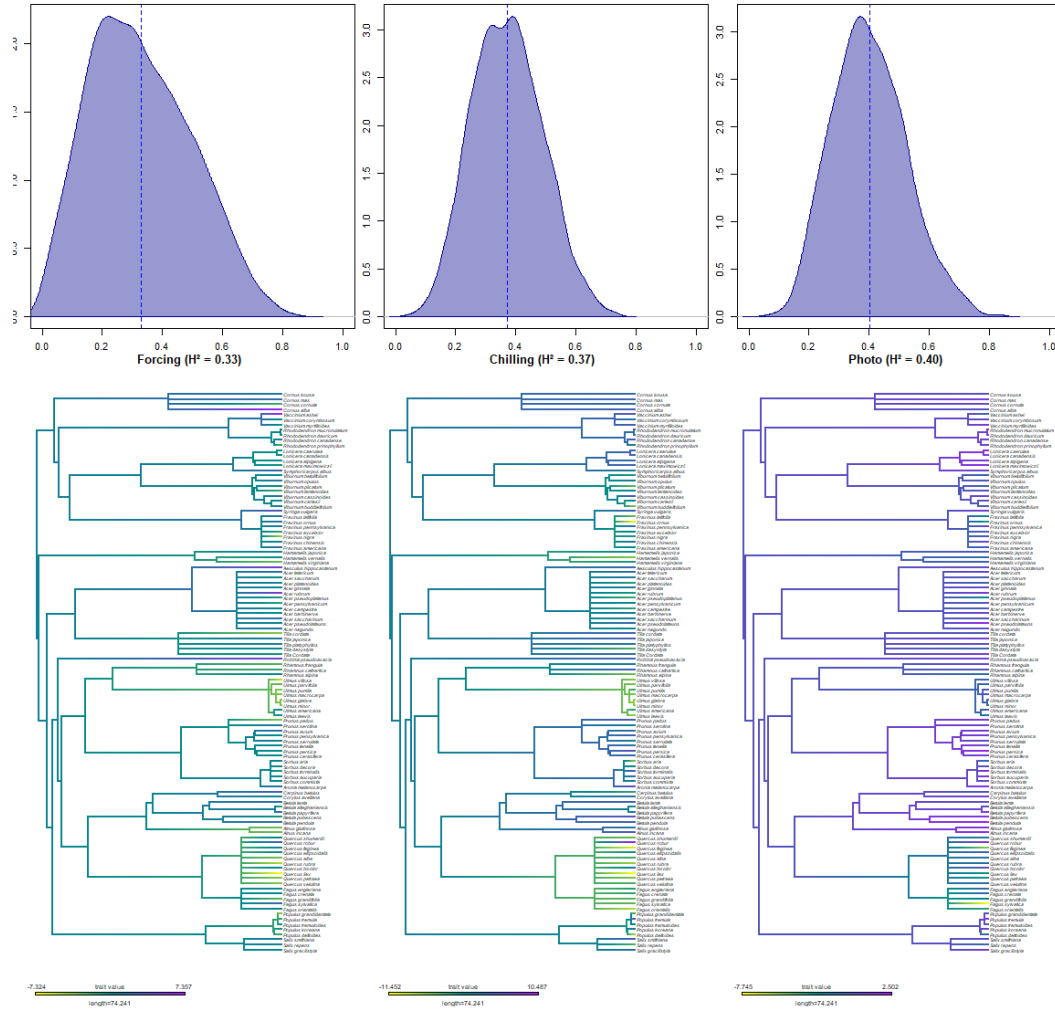
Figure 4: Phylogenetic signal results for the sensitivities of each species (excluding gymnosperms) to the forcing (A), chilling (B) and photoperiod (C) cues.