

Unravelling the phenology-phylogeny tangle.

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Results & Discussion

Most analyzed species were sensitive to all three environmental cues—i.e., forcing, chilling, and photoperiod (Figs. 1, Supporting Table ??). Cue sensitivity led to phenological advances of 7.2 days per unit of standardized chilling, 5.8 days per unit of forcing, and 1.4 days/standard unit of photoperiod (see Table ??), on average. These average sensitivities to cues vary widely across species with larger variation found in responses to chilling, then to forcing and very little variation in how species respond to photoperiod (Figs. 1, Supporting Table ??). Overall, these findings coincide in their ranking of cue importance with previous ones (?).

Our results reveal how responses to cues greatly differ among clades. For example, oaks and beeches (Fagaceae), elms (Ulmaceae) and buckthorns (Rhamnaceae) are highly sensitive to chilling while rhododendrons (Ericaceae), butterfly bushes (Scrophulariaceae) or spindles (Celastraceae) show little to no response to chilling (Fig. 1 a). A similar clade-level variation is found for forcing, where some of these clades—e.g., Ericaceae, Rhamnaceae, Ulmaceae, or Fagaceae—are particularly sensitive (advancing their budburst more than 10 days per standardized unit of forcing) and others such as the Sapindaceae, Cornaceae or Juglandaceae families show little response (Fig. 1 b).

Considering more than one cue, some clades are highly sensitive to two cues at the same time, which would suggest the existence of syndromes where the genetic basis for responses to one cue (e.g., forcing) could have been selected for along responses to another cue (e.g. chilling). However, clade-level responses to multiple cues are significantly but weakly correlated ($r = 0.31$; between forcing and chilling) as responses to chilling are more variable and, the relationship among responses is non-linear (see Supporting Information XX). Weak correlations likely reflect how other clades such as *Tilia* and Ericaceae display strong responses to forcing but weak responses to chilling, or how genera such as *Betula* and *Populus* show strong intra-clade differences in their responses to chilling (Fig. 1). Interestingly, whichever the type, phenological responses to cues show structuring at the clade level that could have an evolutionary imprint in the phylogeny.

Our modelling approach allows to explicitly test whether there is phylogenetic structuring in how species respond to environmental cues. Phylogenetic signal as measured by our ‘phylogenetic shrinkage parameter’ (λ) differs markedly across cues (Fig. 3). Tree phenological responses to environmental cues were strongly phylogenetically clustered for forcing ($\lambda = 0.65$), moderately so for chilling ($\lambda = 0.54$) and weakly for photoperiod ($\lambda = 0.39$) (see Fig. ??, Table ??). Sensitivity to photoperiod treatments did not vary across clades

while responses to forcing are more variable across species and tend to be similar among closely related species (Fig. 1). Results showing that phylogenetically close species tend to show similar responses to some cues but not others, support the need to account for phylogeny in multi-species, multi-predictor modelling of phenological responses to cues.

Along evolution, tree species would have been constrained in their ability to develop responses to forcing that differ much from those of their close relatives, and somewhat less constrained in their responses to chilling. In contrast, responses to photoperiod seem evolutionarily labile, with little variation across most species (0.86 days per standard unit of photoperiod) and a few exceptions from the genus *Fagus*, known as particularly sensitive to photoperiod (?). Specifically, *Fagus sylvatica* is nearly five times more sensitive to photoperiod than most tree species. The question arises as to whether species with outlying responses should be chosen as the model from which to extrapolate knowledge as done with *Fagus sylvatica* in the phenology literature (REFs for PEP75?!).

Why would distantly related species respond more similarly and less variably to photoperiod than they do to forcing or chilling? Clearly, daylength is a more 'reliable' cue in temperate latitudes, as it varies (and has varied) less than forcing or chilling both across years and along evolutionary time. As such, it would have enabled species scheduling their phenological events to match most suitable environmental conditions (?). The adaptation to shifting daylength may have occurred very early in the evolution of photoperiodic sensing—i.e., as early as in cyanobacteria (??). If responses to photoperiod had evolved early in plants and kept more or less constant afterwards in absence of novel selective advantages—i.e., consistent with an Early Burst model of evolution—that would be consistent with our pattern of little variation in the responses to photoperiod across species and clades. Such degree of variation would be measured by our cue-level σ parameter, and is significantly smaller for photoperiod than for other cues. We run simulation tests that show how our results for photoperiodic responses would be consistent with the outcome of an Early Burst model of evolution (see Appendix XXX).

From a statistical perspective, accounting for the effects of phylogenetic structuring on the effects of jointly modelled cues had an effect on model coefficients (Fig. 4). Not accounting for phylogeny (or assuming $\lambda = 0$) biased model coefficients, particularly so for forcing and somewhat less for chilling (Fig. 4). Specifically, species sensitivities to forcing and chilling were underestimated on average (model slopes shifted by 7.2% and 3.7%, respectively). Sensitivities to photoperiod, which showed weak phylogenetic signal were not biased in non-phylogenetic models (Fig. 4), likely associated to their low estimated λ values. Model intercepts were

not affected either (Fig. 4).

Not accounting for phylogeny also had an effect in decreasing cross-species variance in their responses to forcing ($\text{Var } \beta_{\text{phylo}} = 8.74$; $\text{Var } \beta_{\text{non-phylo}} = 5.01$), chilling ($\text{Var } \beta_{\text{phylo}} = 23.45$; $\text{Var } \beta_{\text{non-phylo}} = 17.47$), and a smaller effect in increasing variance to photoperiod responses ($\text{Var } \beta_{\text{phylo}} = 0.82$; $\text{Var } \beta_{\text{non-phylo}} = 0.93$). Counterintuitively, induced reductions in cross-species variance, far from increasing estimation accuracy could lead to increased type-II error by failing to detect actual relationships among cue responses that would only emerge clearly when phylogeny is accounted for (see Supporting Information XX). For example, the correlation between species responses to forcing and chilling decreased by 50% when model lambda was equal zero (e.g. $r_{\text{force-chill}} = \text{XX}$). Importantly, not accounting for phylogeny increased the uncertainty around each individual species estimation of their responses to forcing and chilling (see Fig. SXX in Supporting Information), which could lead to less precise predictions and forecasts of phenology.

Assuming phylogenetic structuring to follow a Brownian Model of evolution ($\lambda = 1$) biased model coefficients too (Fig. 4) although in the opposite direction. Doing so overestimated sensitivities to forcing and chilling (model slopes shifted by 20.5% and 11.8%, respectively) and even more to photoperiod (model slopes shifts of 33.1%; Fig. 4). Bias in model coefficients due to either ignoring or overestimating phylogenetic structuring of predictors seems to correlate with the estimated value of λ so that, if their actual value is high, coefficients may suffer stronger bias if phylogeny is disregarded. In contrast, if predictor's λ is actually low, bias would arise by imposing a Brownian Motion on the evolution of those predictors. Beyond leading to coefficient shifts, overestimation of phylogenetic structuring of predictors decreased model accuracy—i.e., $\text{Bayes}R^2$ decreased by 1%. Ignoring phylogeny did not affect accuracy with respect to our approach (see Appendix XX in Supporting Information).

Accurate forecasts of phenology remain elusive, partly due to recent records of declines in species phenological sensitivity to increasing temperatures (??)—although such declines could derive from statistical artifacts (?). Whatever the case, tests of declines in phenological sensitivity to warming will rely in accurate estimation of responses to cues, and we show here that such estimations are improved by accounting for phylogenetic relationships. The need to incorporate phylogenetic information into the phenology research programme has been suggested before (Davies et al., 2013; Joly et al., 2019), mostly grounded on findings of non-random phylogenetic signal in both phenological traits (Davies et al., 2013; Rafferty and Nabity, 2017) and phenological responses to cues (Davies et al., 2013; Joly et al., 2019). Yet, our approach differs from previous research in that it estimates simultaneously phylogenetic signal for each environmental cue driving phenological sen-

sitivity to such cues. Doing so provides insights on how responses to cues have configured along evolutionary time—e.g., if such responses have evolved independently or in concert with each other, and/or if they tend to be shared within certain clades.

Identifying strong patterns in clade-level responses to cues may open (at least for clades with the strongest signal) a venue for imputation of phenological sensitivities in unmeasured species. Imputation must be done with extreme care (?), but would allow expanding the short list of plant species for which forecasting phenology is feasible. In any case, the above results have implications for future analyses of phenological responses to cues as they support use of species complexes as done in ?, given the strong structuring of closely related species.

Ultimately, this knowledge would inform which clades will be more sensitive to specific climate shifts—e.g., changes in cold temperatures over winter or in warm temperatures in spring and summer—or, which clades emerge as particularly sensitive to cues only after phylogeny is accounted for. For example, oaks (genus *Quercus*) would not be amongst the most sensitive ones to forcing and chilling in non-phylogenetic models (see e.g., (?)), but its species gain sensitivity (2 days per standard unit of forcing and 4 days per standard unit of chilling, on average) through the phylogenetic Bayesian models used here.

In sum, non-phylogenetic models can (i) induce significant bias in estimated model coefficients, (ii) decrease variability in cross-species biological responses and, (iii) increase uncertainty around estimates of individual species sensitivity to cues. Further, non-phylogenetic models hide information on whether the evolution of species responses—i.e., phenological shift in our case—to their determining environmental cues has occurred in a correlated fashion, and if so, identifying which clades are more likely to respond in concert to a set of cues (see Fig. 1). Together, our results indicate that either ignoring the phylogeny or imposing stronger phylogenetic relationships than actual ones would compromise model ability to generate accurate inference and prediction, which are increasingly needed in a warming world.

References

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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 according 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.

../../../../analyses/phylogeny/figures/Fig1b_phylo_muplots_gymno.pdf

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.

../../../../analyses/phylogeny/figures/Fig2_lambdas_sigmas.pdf

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.

../../../../analyses/phylogeny/figures/Est_correls_vs_lamb01_angio.pdf

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).

../../../../analyses/phylogeny/figures/Est_correls_vs_lamb01_gymno.pdf

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_α^2	15.93	1.17	13.84	15.85	18.41	2988.37
$\sigma_{\beta forcing}^2$	5.84	1.04	4.03	5.78	8.15	502.74
$\sigma_{\beta chilling}^2$	7.05	0.87	5.48	7.02	8.92	1026.77
$\sigma_{\beta photoperiod}^2$	2.45	0.41	1.74	2.42	3.32	469.46
σ_y^2	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_α^2	23.47	6.20	13.87	22.59	37.81	18272.58
$\sigma_{\beta forcing}^2$	8.89	2.45	4.96	8.60	14.51	8126.51
$\sigma_{\beta chilling}^2$	10.47	2.66	5.78	10.30	16.17	8539.38
$\sigma_{\beta photoperiod}^2$	7.18	2.29	3.29	6.96	12.25	5625.69
σ_y^2	15.81	0.41	15.04	15.81	16.63	28640.16