

# Phylogenetic estimates of species-level phenology improve ecological forecasting

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## Abstract

Adaptation to ongoing climate change hinges on accurate ecological forecasting to predict shifts in key ecosystem services, such as carbon storage and biodiversity maintenance. Current forecasts, however, have generally failed to capture the important variability in biological responses, especially observed across species. Here, using novel Bayesian hierarchical phylogenetic models, we overcome this challenge to estimate species-level responses to two major environmental cues of spring phenology: temperature and daylength. We find that variation is greater across species than across cues, suggesting the current focus on identifying which cue is the strongest may be less important than predicting how each species responds to a combination of cues. Further, our model provides insights on how evolutionary history has shaped responses to cues, suggesting stronger evolutionary dynamics in responses to temperature—especially cool winter temperatures—than daylength. Our approach provides a major advance in ecological forecasting, with implications for predicting the impacts of climate change and other anthropogenic forces on species interactions and ecosystem functioning.

## <sup>1</sup> Introduction

<sup>2</sup> The biological impacts of climate change will have major implications for ecosystem functioning  
<sup>3</sup> and stability. With rising global temperatures many species have shifted their geographic distri-  
<sup>4</sup> butions northward in space and recurring life-history events—their phenology—earlier in time  
<sup>5</sup> (IPCC, 2014; Parmesan and Yohe, 2003), against a background of high variability. These shifts  
<sup>6</sup> have cascading consequences on many ecosystem services including carbon storage, making both  
<sup>7</sup> mitigation and human adaptation to future warming dependent on accurate ecological forecasts  
<sup>8</sup> (?).

<sup>9</sup> While ecological forecasting has improved over recent years (Dietze, 2017; Lewis et al., 2022), it  
<sup>10</sup> remains a challenge to reproduce the high variability observed in responses (IPCC, 2014). Some  
<sup>11</sup> of this variability results from the complexity of climate change itself, including regional and  
<sup>12</sup> seasonal variation in warming that underlies average trends alongside shifts in other climate axes  
<sup>13</sup> (e.g. precipitation). Much of it, however, is driven by species-specific variation, reflecting evolved  
<sup>14</sup> differences in species' sensitivities to underlying environmental cues and their interactions, which  
<sup>15</sup> we know for only a few well-studied species (Chuine and Regniere, 2017; Ettinger et al., 2020).  
<sup>16</sup> In the absence of detailed data on individual species, species groupings (e.g., functional groups)  
<sup>17</sup> have improved ecosystem models (Moorcroft et al., 2001; Griffith et al., 2020), but still capture  
<sup>18</sup> only a fraction of the important variability (?). Improving forecasts, will require models that  
<sup>19</sup> accurately predict species-level differences in responses to complex environmental change.

<sup>20</sup> Recent efforts that have attempted to model species-specific responses to the environment (Diez  
<sup>21</sup> et al., 2012) are often confounded by data availability—especially the common problem that data  
<sup>22</sup> are often prevalent for some species and sparse across others. The rise of Bayesian hierarchical  
<sup>23</sup> models can allow inference across species in such cases. However, underlying most hierarchical  
<sup>24</sup> models is an implicit assumption that species are exchangeable (Gelman and Hill, 2006), and they  
<sup>25</sup> thus partially pool ('shrink') towards estimates for species with the most data and least variable  
<sup>26</sup> responses, making inference at the species-level unreliable (Ettinger et al., 2020). More reliable  
<sup>27</sup> estimates of species-level responses would allow us to better incorporate species differences into  
<sup>28</sup> models of ecosystem change.

<sup>29</sup> Including the evolutionary history of species relationships in models of species responses could  
<sup>30</sup> at once provide more robust species-level estimates than current approaches and a better under-  
<sup>31</sup> standing of the evolutionary constraints that might limit adaptation to change. For example,  
<sup>32</sup> strong phylogenetic niche conservatism (Wiens et al., 2010) could potentially inhibit adaptive  
<sup>33</sup> responses by drawing species back to an evolutionary conserved optimum, which is sub-optimal  
<sup>34</sup> under new conditions. Whereas, traditionally, incorporating such evolutionary history is seen  
<sup>35</sup> as necessary either as a statistical correction or to better understand species' evolutionary his-  
<sup>36</sup> tory, the use of such phylogenetic information should also improve model fitting and forecasts  
<sup>37</sup> (Freckleton et al., 2002).

38 Research using long-term observational data has especially highlighted the role that evolutionary  
39 history may play in structuring plant phenological responses—which are critical to accurate  
40 forecasts of carbon storage. Phylogenetic signal in plant phenology (Kochmer and Handel, 1986;  
41 Willis et al., 2008; Davies et al., 2013) suggests species responses to cues have diverged over  
42 macro-evolutionary timescales, helping explain species present day differences. However, ap-  
43 proaches using traditional phylogenetic comparative methods, have produced conflicting results  
44 (e.g., Willis et al., 2008; CaraDonna and Inouye, 2014; Yang et al., 2021). In addition, evi-  
45 dence for phylogenetic conservatism of phenological responses appears to depend on method  
46 and species, even varying between sites with overlapping species sets (e.g., Rafferty and Nabity,  
47 2017), which violates the fundamental idea of shared evolutionary history (the common ancestor  
48 of two sets of species cannot possess two separate evolutionary histories for the same trait). A  
49 first challenge is thus how to better integrate evolutionary history into multi-species models of  
50 plant phenological responses.

51 Generating robust ecological forecasts requires addressing a second major hurdle—underlying  
52 environmental cues that are complex and interacting. Decades of research have informed our  
53 understanding of how species use environmental cues to time their phenotypic responses with  
54 the temporal distribution of key resources and to avoid periods of high abiotic or biotic stress  
55 (Larcher, 1980; Bonamour et al., 2019). Commonly, however, responses to environmental cues,  
56 and their evolution, are studied individually, linking a given phenotypic response to a single cue,  
57 for example, time of leafout responding to summed heat during early spring (Davies et al., 2013).  
58 These efforts fail to capture the more likely scenario for most phenotypic traits in which multiple  
59 cues interacting along evolutionary history have shaped species' responses (Ackerly, 2009). For  
60 many plant species, phenological events are determined by a combination of temperature and  
61 light (Chuine and Regnieri, 2017), with additional factors (e.g., other cues—like humidity, or  
62 species physiology—vasculature or SLA) likely further mediating species responses. Although  
63 these mediating factors are often less well understood (Chuine and Regnieri, 2017), they can be  
64 accounted for in models either as latent processes or by allowing non-stationarity in responses  
65 across species (Davies et al., 2019).

66 Spring plant phenology may represent our best opportunity to improve forecasts of species'  
67 responses to interacting environmental cues. Beyond being the most studied biological impact  
68 of climate change, the primary cue system is well established (Chuine and Regnieri, 2017),  
69 especially for temperate woody species where phenology is generally thought to be determined  
70 by two components of temperature—chilling (cool temperatures during dormancy period over  
71 winter) and forcing (warm temperatures, generally in the spring)—and photoperiod (Ettinger  
72 et al., 2021). Plant phenology is also one of few phenotypic traits with extensive experimental  
73 data on responses to multiple environmental cues across species. Recent multi-species analyses  
74 considering forcing, chilling and photoperiod have shown that chilling and forcing together often  
75 determine complex non-linear responses to warming, but cannot forecast beyond several well-  
76 studied species (Ettinger et al., 2020).

<sup>77</sup> Here we present a novel Bayesian framework that extends upon phylogenetic mixed models  
<sup>78</sup> (Housworth et al., 2004) to examine how chilling, forcing (both metrics of temperature) and  
<sup>79</sup> photoperiod together determine spring plant phenology. By allowing non-stationarity in species  
<sup>80</sup> responses across the phylogeny (Davies et al., 2019), our model departs from most previous work  
<sup>81</sup> and assumptions of traditional phylogenetic comparative methods (e.g. Freckleton et al., 2002;  
<sup>82</sup> Ives and Helmus, 2011; Hadfield, 2010), and moves towards integrating evolutionary history  
<sup>83</sup> in models of phenological responses to environmental change. To understand how evolution  
<sup>84</sup> has shaped the cues underlying shifting phenology with climate change (Uyeda et al., 2017), we  
<sup>85</sup> explicitly incorporate phylogenetic structure across model intercepts and slopes (that is, allowing  
<sup>86</sup> a separate model of evolutionary history for chilling, forcing and photoperiod, see Methods &  
<sup>87</sup> Materials for a complete description).

<sup>88</sup> We illustrate our method with an unprecedented dataset on phenological responses to environ-  
<sup>89</sup> mental cues (chilling, forcing and photoperiod) determined experimentally for 191 deciduous  
<sup>90</sup> woody species (by far the most studied group of species in phenology experiments, see Ettinger  
<sup>91</sup> et al., 2020), in an updated version of the Observed Spring Phenology Responses in Experi-  
<sup>92</sup> mental Environments (OSPREE) database (Wolkovich et al., 2019). These data combined with  
<sup>93</sup> the Smith and Brown (2018) megatree adjusted to our species and modeling approach allows  
<sup>94</sup> us to address the common question of which cue has the largest effect on budburst and, at the  
<sup>95</sup> same time, provide robust estimates of how cues vary across species. Using spring phenology,  
<sup>96</sup> we identify historical regime shifts (Uyeda et al., 2017) in phenological responses, and highlight  
<sup>97</sup> how our approach could advance forecasting of other critical responses to ongoing global change.

## <sup>98</sup> Results & Discussion

<sup>99</sup> Most species respond to all three primary cues—forcing, chilling, and photoperiod (Fig. 1,  
<sup>100</sup> Supporting Table ??)—with responses to chilling approximately five-fold greater than to pho-  
<sup>101</sup> toperiod (phenological advances of 6.9 days per standardized unit vs 1.2 days, for chilling and  
<sup>102</sup> photoperiod, respectively; see Table ??). We estimated lower average responses to temperature  
<sup>103</sup> compared to a model without phylogeny (model slopes for forcing and chilling decreased by 19%  
<sup>104</sup> and 21%, respectively); responses to chilling and forcing were also more similar when including  
<sup>105</sup> phylogeny (though chilling was still greater: 6.9 vs. 6 per standard unit), which contrasts with  
<sup>106</sup> previous results suggesting chilling responses are much greater than forcing (Laube et al., 2014;  
<sup>107</sup> Ettinger et al., 2020).

<sup>108</sup> These average estimates, however, fail to capture the large differences in species' responses  
<sup>109</sup> to both chilling and forcing (Fig. 1, Supporting Table ??). By allowing species responses to  
<sup>110</sup> vary, based on a model including their shared evolutionary history, we found species differences  
<sup>111</sup> dwarfed the mean differences between cues, especially temperature cues (Fig. 1). The largest cue  
<sup>112</sup> in magnitude—chilling—varied 25-fold between species, while variation to forcing varied 6-fold.  
<sup>113</sup> This variation indicates large differences between chilling and forcing occur at the species-level

and not across species (as previously suggested Laube et al., 2014; Ettinger et al., 2020). These results highlight why robust phenological forecasts must account for both the complexity of multiple cues and species-level variation in responses to them.

#### 117 *Differences across clades & cues*

The large differences across species produced striking differences between clades. For example, several groups—oaks and beeches (Fagaceae), elms (Ulmaceae) and buckthorns (Rhamnaceae)—are highly sensitive to chilling while others—rhododendrons (Ericaceae), butterfly bushes (Scrophulariaceae) and spindles (Celastraceae)—show little to no response to chilling (Fig. 1a). Similar clade-level variation was observed for forcing, where some of these clades—e.g., Ericaceae, Rhamnaceae, Ulmaceae, or Fagaceae—were particularly sensitive (advancing their budburst more than 10 days per standardized unit of forcing) and others, such as the Sapindaceae, Cornaceae or Juglandaceae, show little response (Fig. 1b).

Some species responded strongly to both temperature cues, which could suggest the existence of syndromes where the genetic basis for responses to one cue—e.g. forcing—has been selected for alongside responses to another cue—e.g. chilling. This could occur if selection operates jointly on responses to both cues; for example, if sensitivity to multiple cues provides greater insurance against leafing out before the last frost (Bonamour et al., 2019; Wolkovich and Donahue, 2021). Additionally, linkage or pleiotropism among loci associated with different cues (Nakagawa et al., 2005) could induce across-cue correlations. However, the correlation in species responses across cues was generally weak ( $r = 0.31$ ; between forcing and chilling) and some genera, such as *Tilia* and *Rhododendron* (Ericaceae), displayed strong responses to forcing but weak responses to chilling, while others, such as *Acer* (Sapindaceae), show moderately strong responses to chilling but weak responses to forcing (Fig. 1). Species sensitivity to one cue, thus, does not constrain sensitivity to another cue, and it seems selection can operate independently on responses to different cues (Bonamour et al., 2019).

In contrast to temperature cues (chilling and forcing), species-level responses to photoperiod were almost uniform across species. This consistency provides novel insight on a large debate over the prevalence of photoperiod cues in temperate trees, where previous experiments (Basler and Körner, 2012; Zohner et al., 2016) and models (e.g., Hunter and Lechowicz, 1992; Schaber and Badeck, 2003) suggested important variability across species that may constrain the responses of certain species to warming (Way and Montgomery, 2015). Our results indicate variability is limited to a handful of species in Fagaceae, which have been particularly well studied, especially *Fagus sylvatica* (e.g., Basler and Körner, 2012; Zohner et al., 2016; Kramer et al., 2017). As *Fagus sylvatica* is nearly five times more sensitive to photoperiod than most other measured tree species, our results caution against using it to draw inferences of photoperiod responses more widely. These same few species are also where most evidence of local adaptation in photoperiod cues for spring phenology comes from (e.g., Kramer et al., 2017), in contrast with common garden studies of other species, which find little evidence of local adaptation in spring (but not

fall) phenology (Aitken and Bemmels, 2016). The uniformity of response to photoperiod in our results supports this latter view of generally low local adaptation in photoperiod cues for spring phenology (i.e., if local adaptation were high in photoperiod cues we would have expected more variability across species).

#### 156 *Phylogenetic structure of phenological cues*

157 Variation—or lack thereof—in cues across species and clades provides possible insights into  
158 the evolution of cues across the phylogeny. While responses to each cue were phylogenetically  
159 structured, with closely related species exhibiting more similar sensitivities than distantly related  
160 species, the strength of phylogenetic conservatism in response differed between cues (Fig. 2).  
161 Responses to temperature (forcing and chilling) were moderately structured ( $\lambda = 0.65$  and  
162  $\lambda = 0.54$ , for forcing and chilling, respectively). Phylogenetic structure in species responses to  
163 photoperiod was comparatively weak ( $\lambda = 0.4$ ) (see Fig. 2, Table ??).

164 Differences among species in their temperature responses represent shifts in the slope of the  
165 relationship between the observed phenology and the cue. The observed phylogenetic structure  
166 in temperature responses (forcing and chilling) would be consistent with an interaction with a  
167 latent trait that moderates responses, and which also covaries with phylogeny (Davies et al.,  
168 2019). This fits fundamentally with the idea that early-season phenology plays a critical role in  
169 shaping species temporal niches (Gotelli and Graves, 1996) and thus should covary with a suite  
170 of life-history traits, including whether species are early-active with rapid return on investment  
171 traits, or start later in the season and have traits associated with higher competitive abilities  
172 (e.g., Grime, 1977; Wolkovich and Donahue, 2021).

173 Weak phylogenetic signal in photoperiod sensitivity (Fig. 2) might seem at odds with the uniformity  
174 of species response—i.e., there is very little variation in the responses to photoperiod across  
175 species. However, somewhat counterintuitively, both uniform and random responses can manifest  
176 as low phylogenetic signal when indexed by Brownian motion expectations (Wiens et al.,  
177 2010). While rapid local adaptation within species might erase the phylogenetic structure in  
178 photoperiod responses, it does not agree with the uniformity we find in species' responses. How-  
179 ever, if responses to photoperiod evolved early in plants, as seems likely (Serrano-Bueno et al.,  
180 2017), and subsequent selection on photoperiod sensitivity was constrained by stabilizing selec-  
181 tion operating on other life-history attributes sensitive to photoperiod (e.g., Rinne et al., 1994;  
182 Wilczek et al., 2014; Azeez and Sane, 2015), we would predict both low interspecific variation  
183 and weak phylogenetic signal in responses, matching observations. This latter interpretation is  
184 also consistent with our estimates of lower  $\sigma$  for photoperiod responses (Fig. 2). Here, as in  
185 more traditional phylogenetic comparative methods,  $\sigma$  represents the rate of evolution, and thus  
186 our results suggest photoperiod responses are also evolving slower than temperature responses  
187 (see Fig. ??).

188 Phylogenetic conservatism (high  $\lambda$ ) and slow evolutionary rates (low  $\sigma$ ) in traits has sometimes  
189 been interpreted as indicative of evolutionary constraints to adaptive change (Wiens et al., 2010;

190 Bennett et al., 2021). If this were the case, we might then conclude that species where responses  
191 are dominated by forcing cues might be more vulnerable to future warming because phylogenetic  
192 conservatism ( $\lambda$ ) in forcing is higher compared to other cues and its evolutionary rate ( $\sigma$ ) is lower  
193 than that estimated for chilling. This is misleading, however, as estimates of  $\lambda$  are independent  
194 from the rate of evolution, and macroevolutionary rates are estimated on phylogenetic trees that  
195 integrate across millions of years of evolutionary history, and thus do not necessarily inform us of  
196 maximum possible rates of evolution over much shorter timescales. Indeed, there is accumulating  
197 evidence for rapid evolution to shifting climates (Bradshaw and Holzapfel, 2006; Franks et al.,  
198 2014). Our estimates are thus more useful in providing unique insights into the evolutionary  
199 history of phenological cues, and emphasize the critical importance of incorporating species-level  
200 differences in ecological forecasts

201 *Forecasting species-level responses*

202 Our results highlight that species-level variability can be extremely high—when properly esti-  
203 mated. Our approach, which partially pooled species responses based on their shared evolution-  
204 ary history, estimated substantially higher variation across species compared with more widely  
205 used hierarchical models. This was especially noticeable in temperature responses (for chilling  
206 variance across species means,  $var(\beta_{chill,j}$  from eqn. 2), was estimated as 23.86 in the phyloge-  
207 netic model, versus 17.41 in the non-phylogenetic model; variance across means,  $var(\beta_{force,j})$ :  
208 8.88 compared to 5.05) while photoperiod, which had low phylogenetic structure, was more  
209 similar across approaches (variance across means,  $var(\beta_{photo,j})$ : 0.82 compared to 0.62).

210 The consequences of including shared evolutionary history in forecasting are most apparent for  
211 poorly sampled species nested within more well-sampled clades. For example, forecasts for *Acer*  
212 *campestre*, which has only 6 observations, shift by up to 35% in our phylogenetically informed  
213 model compared to one without phylogeny (Fig. 4). In contrast, forecasts for *Betula pendula*,  
214 which is one of the most sampled species, are nearly identical across models (Fig. 4). This occurs  
215 because cue estimates for *Acer campestre* in the phylogenetically informed model are strongly  
216 influenced by other *Acer* species, which diverge from other clades. In the non-phylogenetically  
217 informed model all species are equally exchangeable and thus *Acer campestre* is pulled strongly  
218 towards well-sampled species, such as *Betula pendula* ( $n = 311$ ), leading to forecasted shifts that  
219 are more similar across all species (Fig. 4).

220 The increase in variability across species in our model with phylogenetic structure also decreased  
221 the uncertainty in estimates for each individual species temperature responses (Fig. ??). Thus,  
222 traditional (non-phylogenetically informed) approaches that partially pool across species (most  
223 hierarchical models in ecology, e.g., Ettinger et al., 2020) may also lead to less precise predictions  
224 and forecasts of phenology for individual species, although overall model accuracy might still  
225 appear reasonable (see Fig. ??).

226 The contrasts between temperature and photoperiod responses—in both their variability across  
227 species and phylogenetic structure—have important implications for generating multi-species

forecasts. Notably, responses to photoperiod appear weaker, more uniform across species, and less phylogenetically constrained compared to temperature. For temperature responses, the large variability among species makes predicting species-level responses challenging, but the phylogenetic structure in responses lets us borrow information from close relatives to improve our predictions. However, given that Brownian motion (our assumed model of evolution) is an extremely noisy process, we recommend imputation only for missing taxa that are closely related to other well sampled species or clades (Molina-Venegas et al., 2018; ?).

While we focused on spring phenology here, our approach suggests a path forward for more general forecasting of species-level climate change responses. Our results show how including the phylogenetic relationship of species in a mechanistic model of underlying cues can overcome major limitations of most current hierarchical models—correcting biased model estimates, estimating the full variability across species and reducing uncertainty around individual species estimates—while at once providing insight into the evolutionary history of biological responses. Using this approach improved forecasts of phenological responses to climate change and could help anticipate impacts on critical ecosystem services from species-level shifts and thus aid mitigation and human adaption to warming.

244 **Methods & Materials**

245 **Phenological and Phylogenetic Data**

246 *Phenological data:* To estimate phenological responses to chilling, forcing and photoperiod we  
247 used data from phenological experiments in controlled environments of temperate woody species,  
248 brought together in the Observed Spring Phenology Responses in Experimental Environments  
249 (OSPREE) database. In July 2019, we updated an earlier version of this database (Wolkovich  
250 et al., 2019) by reviewing all papers found through searching ISI Web of Science and Google  
251 Scholar with the following terms:

- 252 1. TOPIC = (budburst OR leaf-out) AND (photoperiod OR daylength) AND temperature\*,  
253 which yielded 623 publications
- 254 2. TOPIC = (budburst OR leaf-out) AND dorman\*, which yielded 270 publications

255 We scraped data from all papers of woody species that tested for photoperiod and/or tempera-  
256 ture effects on budburst, leafout, or flowering, resulting in data from 155 experiments across 97  
257 papers in the updated database. Ettinger et al. (2020) used a portion (72 experiments across  
258 49 papers) of the earlier OSPREE database and provides extensive methods on the database  
259 creation and cleaning. For our analysis here, we focused on angiosperms (as gymnosperms are  
260 very poorly represented in spring phenology experiments), and included all budburst experi-  
261 ments where we could quantify chilling, forcing and photoperiod levels, resulting in 44 studies  
262 from 33 papers.

263 Across experiments chilling treatments were often fully or partially applied in the field, thus we  
264 estimated field chilling ourselves in Utah units with the `chillR` package combined with daily  
265 temperature data (converted to hourly) from both European (E-OBS, version 16, calculating  
266 the average of minimum and maximum daily temps, Cornes et al., 2018) and North American  
267 (v3, Sheffield et al., 2006) gridded climate datasets. Ettinger et al. (2020) provides additional  
268 details on these calculations (however, to have climate data through all study years given the  
269 updated OSPREE database, we used a different climate dataset here for North America).

270 For a phylogenetic tree, we pruned the phylogenetic megatree for seed plants (Smith and Brown,  
271 2018) to extract a subset of the phylogenetic tree containing only the angiosperm species in the  
272 OSPREE dataset, then added species that were not present in the megatree as polytomies at  
273 the generic level (using the function ‘congeneric.merge’ in Pearse et al., 2015), with a branch  
274 length of zero. Our pruned tree had 8 Polytomies affecting 46 out of 191 species. To test for the  
275 ability of polytomies to bias our results we ran sensitivity analyses excluding these species from  
276 models (see Supporting Information).

277

278 Bayesian hierarchical phylogenetic model

279 Commonly used phylogenetic regression methods today (e.g., phylogenetic generalized least  
280 squares models, PGLS, Freckleton et al. (2002); phylogenetic mixed models, PMM, Hous-  
281 worth et al. (2004)) were originally conceived as statistical corrections for phylogenetic non-  
282 independence across observations—generally species—thus allowing multi-species studies to meet  
283 the assumptions of linear regression (Freckleton et al., 2002). These corrections incorporated  
284 phylogenetic structure by estimating the magnitude of a transformation of a variance-covariance  
285 (VCV) matrix whose elements were derived from the amount of evolutionary history (branch  
286 lengths) shared between species on a phylogeny. The most commonly used transformation was  
287 Pagel’s  $\lambda$ —a multiplier of the off-diagonal elements—where estimates of  $\lambda = 1$  essentially left the  
288 VCV untransformed and suggested that the residuals of the regression had phylogenetic signal  
289 consistent with Brownian motion; estimates of  $\lambda = 0$  suggested no phylogenetic signal. Be-  
290 cause the original aim of these methods was to correct for statistical bias introduced by shared  
291 evolutionary history among species, the underlying assumption of phylogenetic regressions is  
292 that phylogenetic relatedness would only affect either model residuals (in PGLS approaches,  
293 Freckleton et al., 2002) or model intercepts (e.g., in many PMM approaches, Housworth et al.,  
294 2004).

295 Because our aim is to understand how evolution may have imprinted biological responses to  
296 multiple interactive cues, our approach expands the above methods by explicitly incorporating  
297 phylogenetic structure across model intercepts and slopes. Doing so allows explicitly estimating  
298 the amount of phylogenetic relatedness in species’ sensitivities to each cue, when these sensitiv-  
299 ities are modelled in a multi-predictor regression setting.

300 For each observation  $i$  of species  $j$ , we assumed that the timing of phenological events were  
301 generated from the following sampling distribution:

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

where

$$\mu_j = \alpha_j + \beta_{chill,j} X_{chill} + \beta_{force,j} X_{force} + \beta_{photo,j} X_{photo} \quad (2)$$

302 and  $\sigma_e^2$  represents random error unrelated to the phylogeny.

303 Predictors  $X_{chill}$ ,  $X_{force}$ ,  $X_{photo}$  are standardized chilling, forcing, and photoperiod, and their  
304 effects on the phenology of species  $j$  are determined by parameters  $\beta_{chill,j}$ ,  $\beta_{force,j}$ ,  $\beta_{photo,j}$ ,  
305 representing species’ responses (or sensitivities) to each of the cues. These responses, including  
306 the species-specific intercept  $\alpha_j$ , are elements of the following normal random vectors:

$$\boldsymbol{\alpha} = [\alpha_1, \dots, \alpha_n]^T \text{ such that } \boldsymbol{\alpha} \sim \mathcal{N}(\mu_{\boldsymbol{\alpha}}, \boldsymbol{\Sigma}_{\boldsymbol{\alpha}}) \quad (3)$$

$$\boldsymbol{\beta}_{chill} = [\beta_{chill,1}, \dots, \beta_{chill,n}]^T \text{ such that } \boldsymbol{\beta}_{chill} \sim \mathcal{N}(\mu_{\boldsymbol{\beta}_{chill}}, \boldsymbol{\Sigma}_{\boldsymbol{\beta}_{chill}})$$

$$\boldsymbol{\beta}_{force} = [\beta_{force,1}, \dots, \beta_{force,n}]^T \text{ such that } \boldsymbol{\beta}_{force} \sim \mathcal{N}(\mu_{\boldsymbol{\beta}_{force}}, \boldsymbol{\Sigma}_{\boldsymbol{\beta}_{force}})$$

$$\boldsymbol{\beta}_{photo} = [\beta_{photo,1}, \dots, \beta_{photo,n}]^T \text{ such that } \boldsymbol{\beta}_{photo} \sim \mathcal{N}(\mu_{\boldsymbol{\beta}_{photo}}, \boldsymbol{\Sigma}_{\boldsymbol{\beta}_{photo}})$$

where the means of the multivariate normal distributions are root trait values (i.e., values of cue responses 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  $\sigma_i^2$  is the rate of evolution across a tree for trait  $i$  (here assumed to be constant along all branches),  $\lambda_i$  scales branch lengths and therefore is a measure of the phylogenetic signal or extent of phylogenetic relatedness on each model parameter (i.e.,  $\alpha_j$ ,  $\beta_{force,j}$ ,  $\beta_{chill,j}$ ,  $\beta_{photo,j}$ ), and  $\rho_{xy}$  is the phylogenetic correlation between species  $x$  and  $y$ , or the fraction of the tree shared by the two species.

The above specification is equivalent to writing equation 2 in terms of root trait values and residuals, such that:

$$\mu_j = \mu_{\alpha} + \mu_{\beta_{chill}} X_{chill} + \mu_{\beta_{force}} X_{force} + \mu_{\beta_{photo}} X_{photo} + e_{\alpha_j} + e_{\beta_{force,j}} + e_{\beta_{chill,j}} + e_{\beta_{photo,j}} \quad (5)$$

where the residual phylogenetic error terms (e.g.,  $e_{\alpha_j}$ ) are elements of normal random vectors from multivariate normal distributions centered on 0 with the same phylogenetic variance-covariance matrices as in equation 4. Model code, including priors used here, are given in the supplement. We fit all models to our data using RStan using 4 chains of 4,000 iterations with a warmup of 2,000 each (resulting 8,000 posterior samples), and assessed fit via  $\hat{R}$  near 1 and adequate effective sample sizes (see Tables ??-??).

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<sup>452</sup> **Tables and Figures**

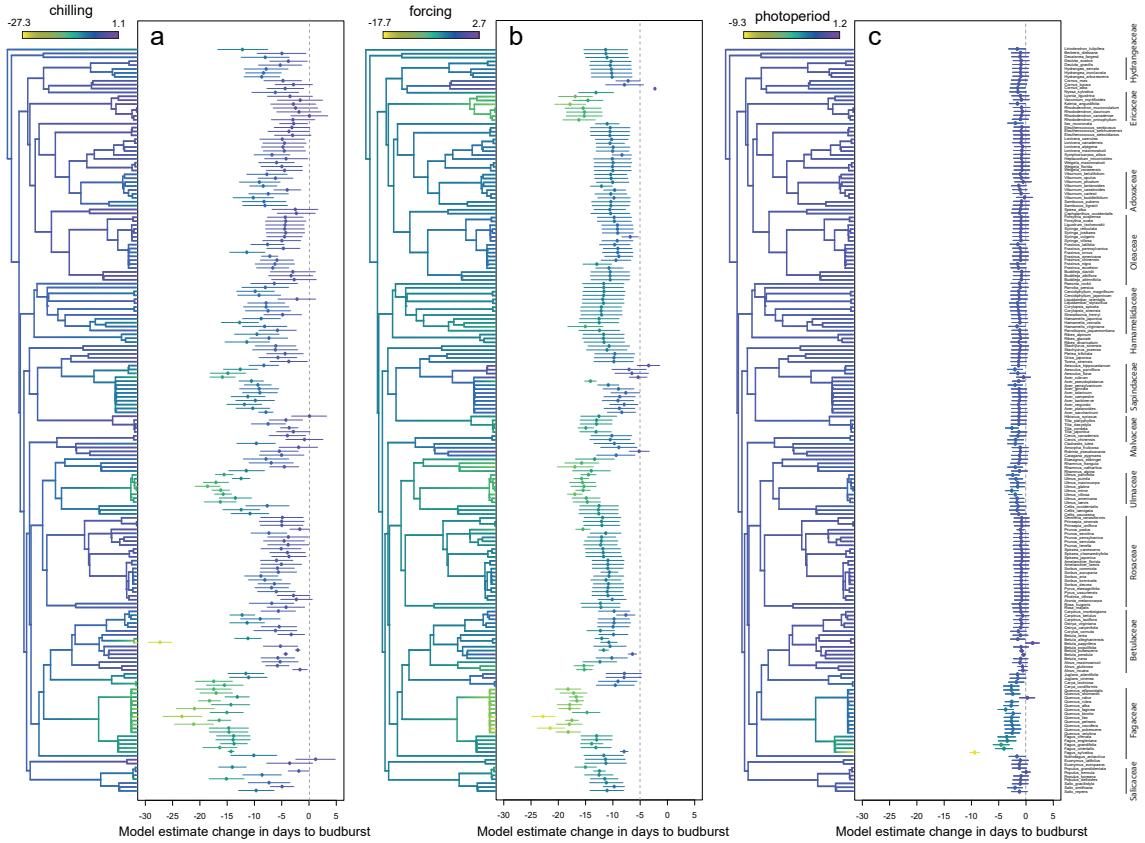


Figure 1: Phenological sensitivity to three environmental cues, chilling (a), forcing (b) and photoperiod (c) measured as change in days to budburst per standardized unit ( $z$ -transformation) of the cues across 191 tree species. The same phylogenetic tree is shown in each panel, colored according to an estimation of ancestral character states, being the states at the tips the species' sensitivities to a cue, as estimated by our hierarchical phylogenetic model. Species sensitivities are shown along with 50% uncertainty intervals in the diagrams. Note that the color scale varies in each panel. Total tree depth is 81 My.

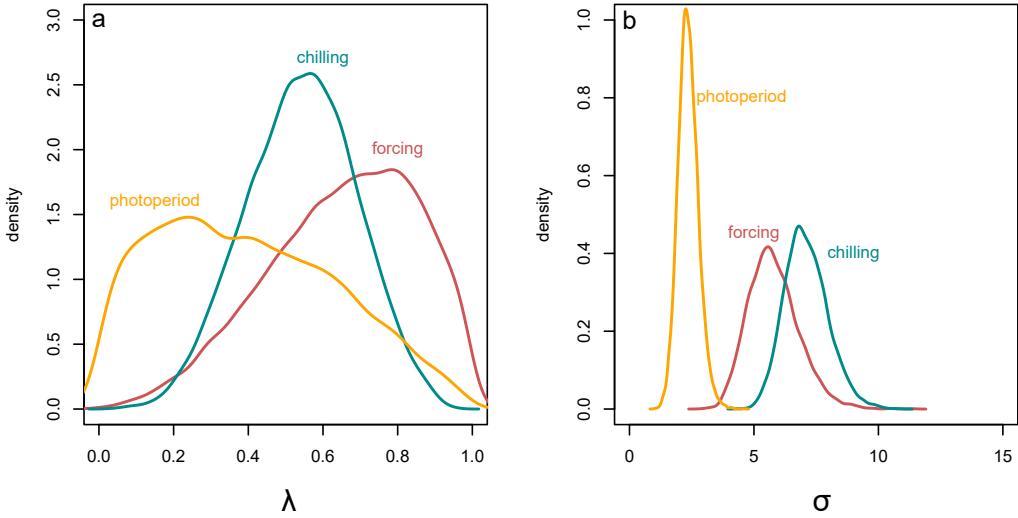


Figure 2: Density plots comparing the posterior distributions of phylogenetic parameters  $\lambda$  and  $\sigma$  estimated for each cue in the model: chilling (blue), forcing (red), and photoperiod (orange). Panels correspond to  $\lambda$  (a) and  $\sigma$  (b) from the phylogenetic model.

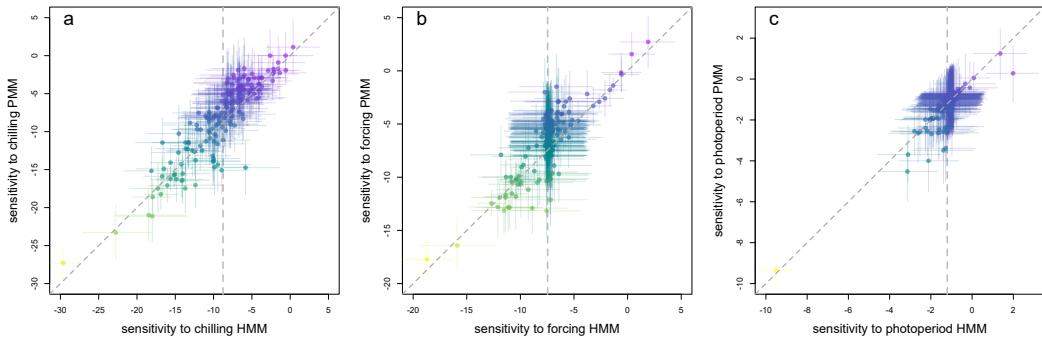


Figure 3: Correlations between model parameters as estimated by the model including phylogenetic structure on each phenological cue ( $y$ -axis), and the more commonly used hierarchical model (HMM) where species are exchangeable (where  $\lambda$  is constrained to be equal to zero,  $x$ -axis). While species with large amounts of data may be estimated similarly by both models, in the more commonly used hierarchical model ( $x$ -axis) many species are pulled towards the overall average (shown by dashed grey vertical lines). The strength and prevalence of pulling across species is particularly obvious for forcing (b). Panels correspond to sensitivity to chilling (a), forcing (b), and photoperiod (c). Dashed grey 1:1 lines also shown. Estimate colors are in the same scale as in 2, and error lines correspond to 50% uncertainty intervals.

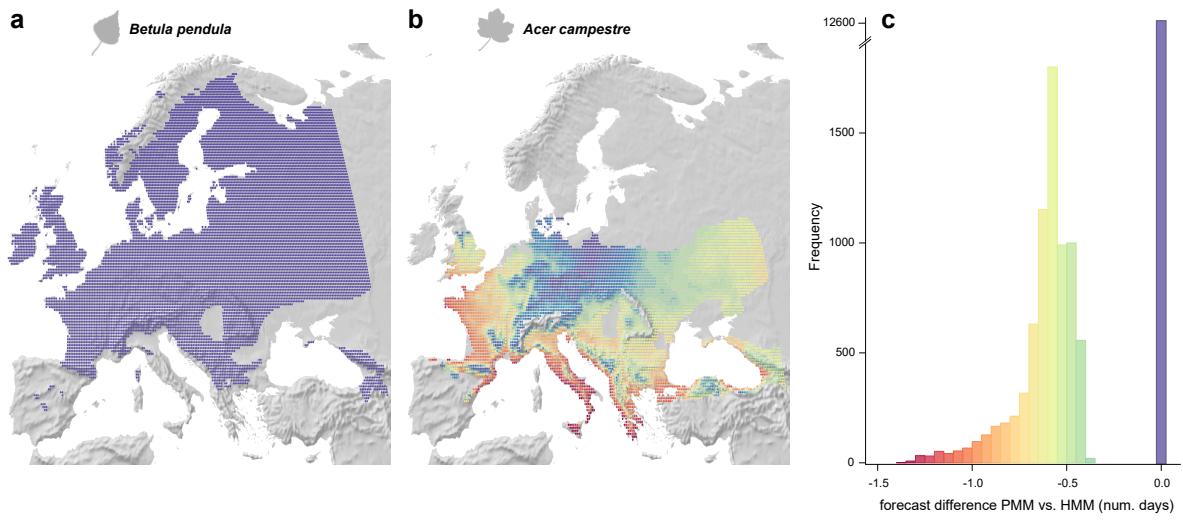


Figure 4: Comparison of forecasts of phenological shifts (i.e., computed as the difference between predictions under current climate vs. a  $2^{\circ}\text{C}$  warmer climate) resulting from a phylogenetic (PMM) and a non-phylogenetic (HMM) approach. Differences in forecasted shifts are negligible for well sampled species (*Betula pendula*,  $n = 311$ , a), but can be substantially different for poorly sampled species in well-sampled clades (*Acer campestre*,  $n = 6$ , b). The maps show the difference in number of days between the shifts predicted by PMM and HMM, with values colored according to histograms in panel c (days here are relative to start of forcing conditions, not calendar days). See Supplementary Material for details on forecast calculation.