

Phylogenetic estimates of species-level phenology improve ecological forecasting

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¹ Abstract

² Our ability to adapt to climate change requires accurate ecological forecasting ~~to predict of~~
³ shifts in key ecosystem services, such as carbon storage and biodiversity maintenance. Cur-
⁴ rent forecasts, however, have ~~generally~~ failed to capture ~~the~~ important variability in biologi-
⁵ cal responses, especially ~~observed~~ across species. ~~Here, using novel~~ Here, we present a novel
⁶ method using Bayesian hierarchical phylogenetic models ~~, we to~~ overcome this challenge ~~to and~~
⁷ estimate species-level responses. ~~We illustrate our method with an dataset on phenological~~
⁸ ~~responses to~~ Combining our new method with phenological experiments manipulating temper-
⁹ ature and daylength cues ~~, determined experimentally for 191 woody species. We find that~~
¹⁰ ~~variation is greater across species than across cues, of woody species, we find species differences~~
¹¹ dwarfed the mean differences between cues, especially for temperature, suggesting the current
¹² focus on ~~identifying which cue is the strongest may be less important than predicting how each~~
¹³ ~~species responds to a combination of cues comparing across cues misses most variation.~~ Fur-
¹⁴ ther, our model provides insights on how evolutionary history has shaped responses to cues,
¹⁵ suggesting stronger evolutionary dynamics in responses to temperature—especially cool winter
¹⁶ temperatures—than daylength. Our new approach provides a major advance in ecological fore-
¹⁷ casting, with implications for predicting the impacts of climate change and other anthropogenic
¹⁸ forces on ~~species interactions and ecosystem functioning~~ ecosystems.

¹⁹ **Introduction**

²⁰ The biological impacts of climate change will have major implications for ecosystem functioning
²¹ and stability. With rising global temperatures many species have shifted their geographic distri-
²² butions northward in space and recurring life-history events—their phenology—earlier in time
²³ (IPCC, 2014; Parmesan and Yohe, 2003), against a background of high variability. These shifts
²⁴ have cascading consequences on many ecosystem services including carbon storage, making both
²⁵ mitigation and human adaptation to future warming dependent on accurate ecological forecasts
²⁶ (Richardson et al., 2013).

²⁷ While ecological forecasting has improved over recent years (Dietze, 2017; Lewis et al., 2022),
²⁸ it remains a challenge to reproduce the high variability observed in biological responses such
²⁹ as phenology, physiology or demography to environmental cues (IPCC, 2014). Some of this
³⁰ variability results from the complexity of climate change itself, including regional and seasonal
³¹ variation in warming that underlies average trends alongside shifts in other climate axes (e.g.,
³² precipitation). Much of it, however, could be driven by species-specific variation, reflecting
³³ evolved differences in species sensitivities to underlying environmental cues and their interac-
³⁴ tions. Unfortunately, we can only estimate the sensitivities to cues for a few well-studied species
³⁵ (Chuine and Regniere, 2017; Ettinger et al., 2020). In the absence of detailed data on individual
³⁶ species, species groupings (e.g., functional groups) have improved ecosystem models (Moorcroft
³⁷ et al., 2001; Griffith et al., 2020), but still capture only a fraction of the important variability
³⁸ (Fuccillo Battle et al., 2022).

³⁹ Recent efforts that have attempted to model species-specific responses to the environment (Diez
⁴⁰ et al., 2012) are often restricted by data availability—especially the common problem that data
⁴¹ are often prevalent for some species and sparse across others. The rise of Bayesian hierarchical
⁴² models can allow inference across species in such cases. However, underlying most hierarchical
⁴³ models is an implicit assumption that species are exchangeable (all species represent samples
⁴⁴ drawn from the same underlying distribution, Gelman and Hill, 2006), and they thus partially
⁴⁵ pool ('shrink') towards estimates for species with the most data and least variable responses,
⁴⁶ making inference at the species-level unreliable (Ettinger et al., 2020). More reliable estimates
⁴⁷ of species-level responses would allow us to better incorporate species differences into models of
⁴⁸ ecosystem change.

⁴⁹ Including the evolutionary history of species relationships in models of species responses could
⁵⁰ provide more robust species-level estimates than current approaches and a better understanding
⁵¹ of the evolutionary constraints that might limit adaptation to change. For example, strong
⁵² phylogenetic niche conservatism (Wiens et al., 2010) could potentially inhibit adaptive responses
⁵³ by drawing species back to an evolutionary conserved optimum, which is sub-optimal under new
⁵⁴ conditions. While incorporating such evolutionary history is traditionally seen as necessary,
⁵⁵ either as a statistical correction or to better understand species evolutionary history, the use of
⁵⁶ such phylogenetic information should also improve model fitting and forecasts (Freckleton et al.,

57 2002).

58 Research using long-term observational data has highlighted the role that evolutionary history
59 may play in structuring plant phenological responses—which are critical to accurate forecasts
60 of carbon storage. Phylogenetic signal in plant phenology, including dates of budburst, leafout
61 and first flowering (Kochmer and Handel, 1986; Willis et al., 2008; Davies et al., 2013), suggests
62 that more closely related species share more similar phenologies, likely reflecting evolutionary
63 conservatism in responses to common cues. There are two broad explanations for why we
64 might expect phylogenetic conservatism in phenological traits. First, close relatives will tend to
65 share similar ecologies and physiologies, and thus be sensitive to similar environmental pressures.
66 Second, close relatives derive from common geographic centers of origin, and thus their ancestors
67 will have been exposed to—and have adapted to—similar environmental cues (Davies et al.,
68 2013). However, approaches using traditional phylogenetic comparative methods, have produced
69 conflicting results, with some studies reporting evidence of phylogenetic structure in phenology-
70 linked species declines (e.g., Willis et al., 2008) and in some phenophases, ~~such as first flowering,~~
71 but not others ~~, such as peak or last flowering~~ (e.g., CaraDonna and Inouye, 2014), and in
72 responses to some cues ~~, but not others~~ (e.g., Yang et al., 2021). In addition, evidence for
73 phylogenetic conservatism of phenological responses appears to depend on method and species,
74 even varying between sites with overlapping species sets (e.g., Rafferty and Nabity, 2017), which
75 violates the fundamental idea of shared evolutionary history (the common ancestor of two sets
76 of species cannot possess two separate evolutionary histories for the same trait). ~~A~~Thus, a first
77 challenge is ~~thus~~ how to better integrate evolutionary history into multi-species models of plant
78 phenological responses.

79 Generating robust ecological forecasts requires addressing a second major hurdle—underlying
80 environmental cues that are complex and interacting. Decades of research have informed our
81 understanding of how species use environmental cues to time their phenotypic responses with
82 the temporal distribution of key resources ~~and to avoid while avoiding~~ periods of high ~~abiotic or~~
83 ~~biotic~~ stress (Larcher, 1980; Bonamour et al., 2019). Commonly, however, responses to environ-
84 mental cues, and their evolution, are studied individually, linking a given phenotypic response
85 to a single cue, for example, time of leafout responding to summed heat during early spring
86 (Davies et al., 2013). These efforts fail to capture the more likely scenario for most pheno-
87 typic traits in which multiple cues interacting along evolutionary history have shaped species
88 responses (Ackerly, 2009). For many plant species, phenological events are determined by a com-
89 bination of temperature and light (Chuine and Regniere, 2017), with additional factors (e.g.,
90 other cues—like humidity, or species physiology—vasculature or leaf structure) likely further
91 mediating species responses. Although these mediating factors are not well understood (Chuine
92 and Regniere, 2017), they can be accounted for in models either as latent processes or by allowing
93 non-stationarity in responses across species (Davies et al., 2019).

94 Spring plant phenology may represent our best opportunity to improve forecasts of species
95 responses to interacting environmental cues. Beyond being the most studied biological impact

of climate change, the primary cue system is well established (Chuine and Regniere, 2017), especially for temperate woody species where phenology is generally thought to be determined by two components of temperature—chilling (cool temperatures during dormancy period over winter) and forcing (warm temperatures, generally in the spring)—and photoperiod (Ettinger et al., 2021). Plant phenology is also one of few phenotypic traits with extensive experimental data on responses to multiple environmental cues across species. Recent multi-species analyses considering forcing, chilling and photoperiod have shown that chilling and forcing together often determine complex non-linear responses to warming, but cannot forecast beyond several well-studied species (Ettinger et al., 2020).

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

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

Results & Discussion

Most species respond to all three primary cues—forcing, chilling, and photoperiod (Fig. 1, Supporting Table ??)—with responses to chilling approximately five-fold greater than to photoperiod (phenological advances of 6.9 days per standardized unit vs 1.2 days, for chilling and photoperiod, respectively; see Table ??). We estimated lower average responses to temperature compared to a model without phylogeny (model slopes for forcing and chilling decreased by 18% and 22%, respectively); responses to chilling and forcing were also more similar when including

133 phylogeny (though chilling was still greater: 6.9 vs. 6.1 per standard unit), which contrasts with
134 previous results suggesting chilling responses are much greater than forcing (Laube et al., 2014;
135 Ettinger et al., 2020).

136 These average estimates, however, fail to capture the large differences in species responses to both
137 chilling and forcing (Fig. 1, Supporting Table ??). By allowing species responses to vary, based
138 on a model including their shared evolutionary history, we found species differences dwarfed
139 the mean differences between cues, especially temperature cues (Fig. 1). The largest cue in
140 magnitude—chilling—varied 24-fold between species, while variation to forcing varied 7-fold.
141 This variation indicates large differences between chilling and forcing occur at the species-level
142 and not across species (as previously suggested, Laube et al., 2014; Ettinger et al., 2020). These
143 results highlight why robust phenological forecasts must account for both the complexity of
144 multiple cues and species-level variation in responses to them.

145 *Differences across clades & cues*

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

154 Some species responded strongly to both temperature cues, which could suggest the existence of
155 syndromes where the genetic basis for responses to one cue—e.g., forcing—has been selected for
156 alongside responses to another cue—e.g., chilling. This could occur if selection operates jointly
157 on responses to both cues; for example, if sensitivity to multiple cues provides greater insurance
158 against leafing out before the last frost (Bonamour et al., 2019; Wolkovich and Donahue, 2021).
159 Additionally, linkage or pleiotropism among loci associated with different cues (Nakagawa et al.,
160 2005) could induce across-cue correlations. However, the correlation in species responses across
161 cues was generally weak ($r = 0.31$; between forcing and chilling) and some genera, such as *Tilia*
162 and *Rhododendron* (Ericaceae), displayed strong responses to forcing but weak responses to
163 chilling, while others, such as *Acer* (Sapindaceae), show moderately strong responses to chilling
164 but weak responses to forcing (Fig. 1). Species sensitivity to one cue, thus, does not constrain
165 sensitivity to another cue, and it seems selection can operate independently on responses to
166 different cues (Bonamour et al., 2019).

167 In contrast to temperature cues (chilling and forcing), species-level responses to photoperiod were
168 almost uniform across species. This consistency provides novel insight on a large debate over
169 the prevalence of photoperiod cues in temperate trees, where previous experiments (Basler and
170 Körner, 2012; Zohner et al., 2016) and models (e.g., Hunter and Lechowicz, 1992; Schaber and

171 Badeck, 2003) suggested important variability across species that may constrain the responses
172 of certain species to warming (Way and Montgomery, 2015). Our results indicate variability is
173 limited to a handful of species in Fagaceae, which have been particularly well studied, especially
174 *Fagus sylvatica* (e.g., Basler and Körner, 2012; Zohner et al., 2016; Kramer et al., 2017). As
175 *Fagus sylvatica* is nearly five times more sensitive to photoperiod than most other measured tree
176 species, our results caution against using it to draw inferences of photoperiod responses more
177 widely. These same few species are also where most evidence of local adaptation in photoperiod
178 cues for spring phenology comes from (e.g., Kramer et al., 2017), in contrast with common
179 garden studies of other species, which find little evidence of local adaptation in spring (but not
180 fall) phenology (Aitken and Bemmels, 2016). The uniformity of response to photoperiod in our
181 results supports this latter view of generally low local adaptation in photoperiod cues for spring
182 phenology (i.e., if local adaptation were high in photoperiod cues, we would have expected more
183 variability *aeross species*).).

184 *Phylogenetic structure of phenological cues*

185 Variation—or lack thereof—in cues across species and clades provides possible insights into
186 the evolution of cues across the phylogeny. While responses to each cue were phylogenetically
187 structured, with closely related species exhibiting more similar sensitivities than distantly related
188 species, the strength of phylogenetic conservatism in response differed between cues (Fig. 2).
189 Responses to temperature (forcing and chilling) were moderately structured ($\lambda = 0.65$ and
190 $\lambda = 0.54$, for forcing and chilling, respectively). Phylogenetic structure in species responses to
191 photoperiod was comparatively weak ($\lambda = 0.4$; see Fig. 2, Table ??).

192 Differences among species in their temperature responses represent shifts in the slope of the
193 relationship between the observed phenology and the cue. The observed phylogenetic structure
194 in temperature responses (forcing and chilling) would be consistent with an interaction with a
195 latent trait that moderates responses, and which also covaries with phylogeny (Davies et al.,
196 2019). This fits fundamentally with the idea that early-season phenology plays a critical role in
197 shaping species temporal niches (Gotelli and Graves, 1996) and thus should covary with a suite
198 of life-history traits, including whether species are early-active with rapid return on investment
199 traits, or start later in the season and have traits associated with higher competitive abilities
200 (e.g., Grime, 1977; Wolkovich and Donahue, 2021).

201 Weak phylogenetic signal in photoperiod sensitivity (Fig. 2) might seem at odds with the unifor-
202 mity of species response—i.e., there is very little variation in the responses to photoperiod across
203 species. However, somewhat counterintuitively, both uniform and random responses can man-
204 ifest as low phylogenetic signal when indexed by Brownian motion expectations (Wiens et al.,
205 2010). While rapid local adaptation within species might erase the phylogenetic structure in
206 photoperiod responses, it does not agree with the uniformity we find in species responses. How-
207 ever, if responses to photoperiod evolved early in plants, as seems likely (Serrano-Bueno et al.,
208 2017), and subsequent selection on photoperiod sensitivity was constrained by stabilizing selec-

tion operating on other life-history attributes sensitive to photoperiod (e.g., Rinne et al., 1994; Wilczek et al., 2014; Azeez and Sane, 2015), we would predict both low interspecific variation and weak phylogenetic signal in responses, matching observations. This latter interpretation is also consistent with our estimates of lower σ for photoperiod responses (Fig. 2). Here, as in more traditional phylogenetic comparative methods, σ represents the rate of evolution, and thus our results suggest photoperiod responses are also evolving slower than temperature responses (see Fig. ??).

Phylogenetic conservatism (high λ) and slow evolutionary rates (low σ) in traits has sometimes been interpreted as indicative of evolutionary constraints to adaptive change (Wiens et al., 2010; Bennett et al., 2021). If this were the case, we might then conclude that species where responses are dominated by forcing cues might be more vulnerable to future warming because phylogenetic conservatism (λ) in forcing is higher compared to other cues and its evolutionary rate (σ) is lower than that estimated for chilling. This is misleading, however, as estimates of λ are independent from the rate of evolution, and macroevolutionary rates are estimated on phylogenetic trees that integrate across millions of years of evolutionary history, and thus do not necessarily inform us of maximum possible rates of evolution over much shorter timescales. ~~Indeed, there is accumulating evidence for rapid evolution to shifting climates (Bradshaw and Holzapfel, 2006; Franks et al., 2014).~~ Our estimates are thus more useful in providing unique insights into the evolutionary history of phenological cues, and emphasize the critical importance of incorporating species-level differences in ecological forecasts.

229 *Forecasting species-level responses*

Our results highlight that species-level variability can be extremely high—when properly estimated. Our approach, which partially pooled species responses based on their shared evolutionary history, estimated substantially higher variation across species compared with more widely used hierarchical models. This was especially noticeable in temperature responses (for chilling variance across species means, $var(\beta_{chill,j}$ from eqn. 2), was estimated as 23.55 in the phylogenetic model, versus 17.47 in the non-phylogenetic model; variance across means, $var(\beta_{force,j})$: 8.75 compared to 5.01) while photoperiod, which had low phylogenetic structure, was more similar across approaches (variance across means, $var(\beta_{photo,j})$: 0.83 compared to 0.64).

The consequences of including shared evolutionary history in forecasting are most apparent for poorly sampled species nested within more well-sampled clades. For example, forecasts for *Acer campestre*, which has only 6 observations, shift by up to 35% in the number of days until budburst after forcing starts, when comparing our phylogenetically informed model to one without phylogeny (see Fig. 4 for details). In contrast, forecasts for *Betula pendula*, which is one of the most sampled species, are nearly identical across models (Fig. 4). This occurs because cue estimates for *Acer campestre* in the phylogenetically informed model are strongly influenced by other *Acer* species, which diverge from other clades. In the non-phylogenetically informed model all species are equally exchangeable and thus *Acer campestre* is pulled strongly towards

247 well-sampled species, such as *Betula pendula* ($n = 311$), leading to forecasted shifts that are
248 more similar across all species (Fig. 4).

249 The increase in variability across species in our model with phylogenetic structure also decreased
250 the uncertainty in estimates for each individual species temperature responses (Fig. ??). Thus,
251 traditional (non-phylogenetically informed) approaches that partially pool across species (most
252 hierarchical models in ecology, e.g., Flynn and Wolkovich, 2018; Ettinger et al., 2020) may also
253 lead to less precise predictions and forecasts of phenology for individual species, although overall
254 model accuracy might still appear reasonable (see Fig. ??). Another advantage of our Bayesian
255 approach is that we are also better able to accommodate imprecision in the data that informs
256 our model, which might arise from multiple sources, including measurement or experimental
257 error, and the general stochasticity associated with limited sample sizes and unbalanced species
258 representation. Critically, by partially pooling across species and weighting by phylogeny, we
259 gain strength from species estimates that are informed by more data, such as within *Betula*
260 and *Fagaceae*, but avoid skewing estimates for phylogenetically distant clade that may have
261 been exposed to different selective regimes. ~~Robustness of species estimates was confirmed by~~
262 ~~cross-validation, showing~~ We found species estimates were robust through cross-validationL the
263 phylogenetic model better predicted observed values for held-out data, and yielded more stable
264 species coefficients compared to a hierarchical model (Figs. ??-??; see “Leave-One-Clade-Out
265 model cross validation”).

266 The contrasts between temperature and photoperiod responses—in both their variability across
267 species and phylogenetic structure—have important implications for generating multi-species
268 forecasts. Notably, responses to photoperiod appear weaker, more uniform across species, and
269 less phylogenetically constrained compared to temperature. For temperature responses, the
270 large variability among species makes predicting species-level responses challenging, but the
271 phylogenetic structure in responses lets us borrow information from close relatives to improve
272 our predictions. However, given that Brownian motion (our assumed model of evolution) is an
273 extremely noisy process, we recommend imputation only for missing taxa that are closely related
274 to other well sampled species or clades (Molina-Venegas et al., 2018, 2023).

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

284 **Methods & Materials**

285 **Phenological and Phylogenetic Data**

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

- 292 1. TOPIC = (budburst OR leaf-out) AND (photoperiod OR daylength) AND temperature*,
293 which yielded 623 publications
- 294 2. TOPIC = (budburst OR leaf-out) AND dorman*, which yielded 270 publications

295 We scraped data from all papers of woody species that tested for photoperiod and/or temper-
296 ature effects on budburst, leafout, or flowering, resulting in data from 155 experiments across
297 97 papers in the updated database. Ettinger et al. (2020), which used a portion (72 experi-
298 ments across 49 papers) of the earlier OSPREE databaseand provides extensive methods on
299 the-database creation and cleaning.

300 We focused on angiosperms (as gymnosperms are very poorly represented in spring phenology
301 experiments), and included all budburst experiments where we could quantify chilling, forc-
302 ing and photoperiod levels, resulting in 44 studies from 33 papers, resulting in and 2940 data
303 points. In our dataset most studies come from Europe ($n=37$) and a few from North America
304 ($n=7$). The same bias towards Europe is found across the full OSPREE dataset with less North
305 American ($n=19$) than European ($n=60$) studies and only 3 studies located in the Southern
306 Hemisphere. Given our need of daily gridded data for estimating chilling we only include stud-
307 ies from Europe and North America, with most of these sites in temperate areas and a few
308 in European Mediterranean areas (see Fig. ??). Our final dataset is both geographically and
309 taxonomically limited, mirroring the existing literature on phenological experiments. Enlarging
310 this body of literature will be critical to address important research questions, such as whether
311 variability in cue sensitivity across species is larger in temperate than in tropical latitudes. and
312 highlighting a critical need to expand this literature.

313 Across experiments chilling treatments were often fully or partially applied in the field, thus we
314 estimated chilling—both in the field and applied in controlled environments—using Utah units
315 with the **chillR** package. We estimated field chilling from 1 September to the date given for when
316 samples were taken from the field using daily temperature data (converted to hourly) from both
317 European (E-OBS, version 16, calculating the average of minimum and maximum daily temps,
318 Cornes et al., 2018) and North American (v3, Sheffield et al., 2006) gridded climate datasets.
319 We also converted experimental chilling into Utah chill units, based on reported treatments

320 (for studies with a mix of field and experimental treatments, we added field and experimentally
321 applied Utah units). To avoid numerical instability in our models (from having predictor values
322 on very different scales), we divided Utah units by 240 (roughly equivalent to 10 days of average
323 chilling).

324 We report the Utah model because a small number of studies reported chilling only in Utah
325 units, thus using this common metric allowed us to include the most data. The Utah model
326 relies on the assumption that temperatures between 1.4 and 15.9C affect endodormancy release
327 differently, though recent findings show possibly similar effects for a wide range of temperatures
328 (-2 to 10C, see Baumgarten et al., 2021). Because chilling is a latent process an accurate model
329 of it, especially for the 191 species in our dataset, is not currently possible (Ettinger et al.,
330 2020). We found consistent results, however, using another common model of chilling—chill
331 portions, suggesting our results are robust to the exact chilling metric used (see Tables ?? and
332 ?? in Supporting Information).

333 Forcing and photoperiod treatments occurred after chilling treatments; we report photoperiod as
334 the length of light and weighted these treatments by the reported photo- and thermo-periodicity
335 (Buonaiuto et al., 2023). Most studies reported two temperatures per day across the whole
336 experiment, one for day and night, but some had ramped temperatures and/or photoperiods (or
337 other complexities). In these cases we built an hourly model of the full treatment period until
338 budburst and took the mean value.

339 For a phylogenetic tree, we pruned the megatree for seed plants (Smith and Brown, 2018) to
340 extract the sub-tree containing only the species present in the OSPREE dataset, species not
341 included in the megatree were added to the congeneric basal node age (using the function
342 ‘congeneric.merge’ in Pearse et al., 2015), and assigned branch lengths to maintain tree ultra-
343 metricity. This addition of species to the tree can introduce polytomies (multifurcations) when
344 many species are added to the same ancestral node, as was the case for *Acer*, for which several
345 species where included in the OSPREE dataset but the megatree lacked species-level resolution
346 within the genus. In total, our pruned tree had 8 polytomies affecting 46 out of 191 species.
347 Our Bayesian hierarchical model, described below, is informed by the phylogenetic structure de-
348 scribing species evolutionary relationships. Errors in phylogenetic topology and branching times
349 could thus impact model estimates, although if errors were large the contribution of phylogeny
350 would simply be scaled to zero. To assess whether the inclusion of polytomies in our data biased
351 model estimates, we ran sensitivity analyses excluding these species from models (see Table ??
352 in Supporting Information). Our approach assumes a tree where branch lengths represent time,
353 but it could be possible to change this assumption. For example, if the genes underlying plant
354 responses to particular cues were known, branch lengths would directly represent mutational
355 changes along gene sequences. In the absence of such detailed gene specific data, evolutionary
356 time provides a useful proxy for species differences.

357

358 **Bayesian hierarchical phylogenetic model**

359 Commonly used phylogenetic regression methods today (e.g., phylogenetic generalized least
360 squares models, PGLS, Freckleton et al. (2002); phylogenetic mixed models, PMM, Hous-
361 worth et al. (2004)) were originally conceived as statistical corrections for phylogenetic non-
362 independence across observations—generally species—thus allowing multi-species studies to meet
363 the assumptions of linear regression (Freckleton et al., 2002). These corrections incorporated
364 phylogenetic structure by estimating the magnitude of a transformation of a variance-covariance
365 (VCV) matrix whose elements were derived from the amount of evolutionary history (branch
366 lengths) shared between species on a phylogeny. The most commonly used transformation was
367 Pagel’s λ —a multiplier of the off-diagonal elements—where estimates of $\lambda = 1$ essentially left the
368 VCV untransformed and suggested that the residuals of the regression had phylogenetic signal
369 consistent with Brownian motion; estimates of $\lambda = 0$ suggested no phylogenetic signal. Be-
370 cause the original aim of these methods was to correct for statistical bias introduced by shared
371 evolutionary history among species, the underlying assumption of phylogenetic regressions is
372 that phylogenetic relatedness would only affect either model residuals (in PGLS approaches,
373 Freckleton et al., 2002) or model intercepts (e.g., in many PMM approaches, Housworth et al.,
374 2004).

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

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

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

where

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

382 and σ_e^2 represents random error unrelated to the phylogeny.

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

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

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

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

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

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 σ_i^2 is the rate of evolution across a tree for a given trait or predictor (here assumed to be constant along all branches), λ_i scales branch lengths and therefore is a measure of the phylogenetic signal or extent of phylogenetic relatedness on each model parameter (i.e., α_j , $\beta_{force,j}$, $\beta_{photo,j}$), and ρ_{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_{α_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 ??-??).

To assess if the phylogenetic mixed model (PMM) presents any advantages with respect commonly used hierarchical mixed models (HMM; see e.g., Ettinger et al., 2020), beyond fitting evolutionary parameters to model predictors, we compare results of PMM and HMM. HMM is a simplified version of PMM where off-diagonal elements of the variance-covariance phylogenetic matrices are multiplied by zero ($\lambda = 0$). Both models account for differences in sample sizes and variances for each species, by partially pooling across all data while at the same time providing species-level estimates; however the PMM will pool more strongly to closely-related species

when λ is high. Additional grouping factors beyond species could be added to these models. For example, similar approaches can be used to estimate study or location effects; ~~however, many species occurred in only one study and location in our dataset, making it difficult to separate these effects, thus we do not include study as a separate parameter here (and thus average over it in our model estimates).~~

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554 **Data and code availability statement**

555 All data supporting the findings of this study are publicly available. Data analyses were per-
556 formed in R and Bayesian Hierarchical and Phylogenetic Mixed Models (HMM and PMM,
557 respectively) were performed within the Stan environment. All custom code will be made avail-
558 able through a GitHub repository for this project (see Supporting Information for details and
559 online links).

⁵⁶⁰ **Tables and Figures**

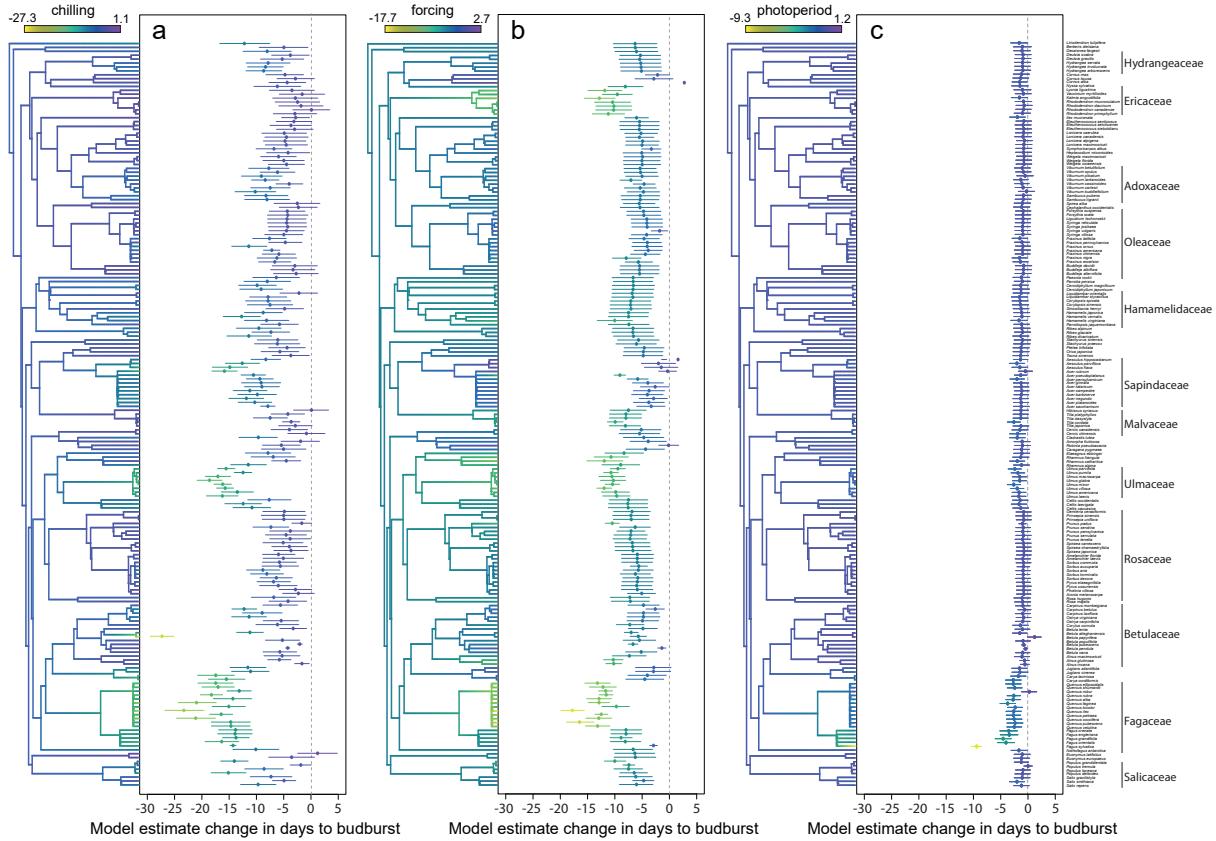


Figure 1: Phenological sensitivity to three environmental cues, chilling (a), forcing (b) and photoperiod (c) measured as change in days to budburst per standardized unit (z -transformation) of the cues across 191 woody species. The same phylogenetic tree is shown in each panel, colored according to 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.

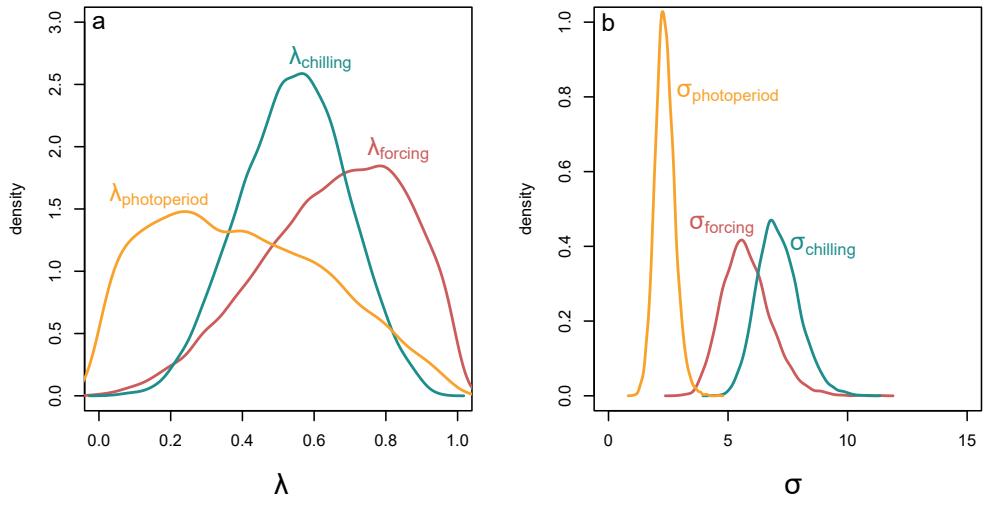


Figure 2: Density plots comparing the posterior distributions of phylogenetic parameters λ and σ estimated for each cue in the model: chilling (blue), forcing (red), and photoperiod (orange). Panels correspond to λ (a) and σ (b) from the phylogenetic model.

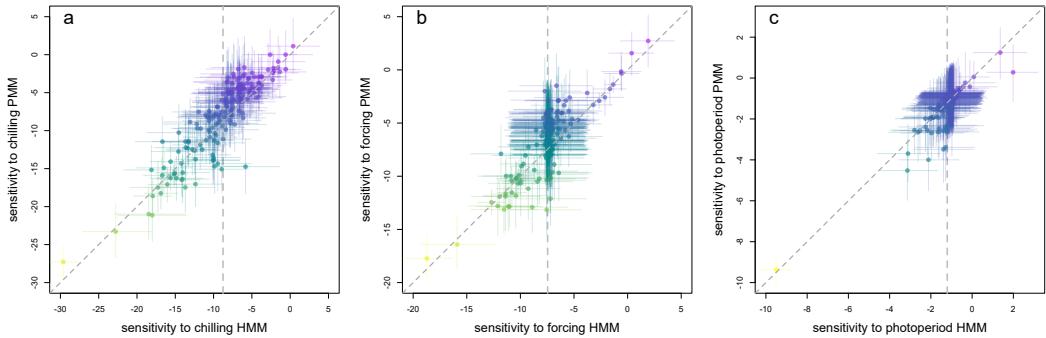


Figure 3: Correlations between model parameters as estimated by the model including phylogenetic structure on each phenological cue (phylogenetic mixed model, PMM; y -axis), and the more commonly used hierarchical mixed model (HMM) where species are exchangeable (where λ is constrained to be equal to 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.

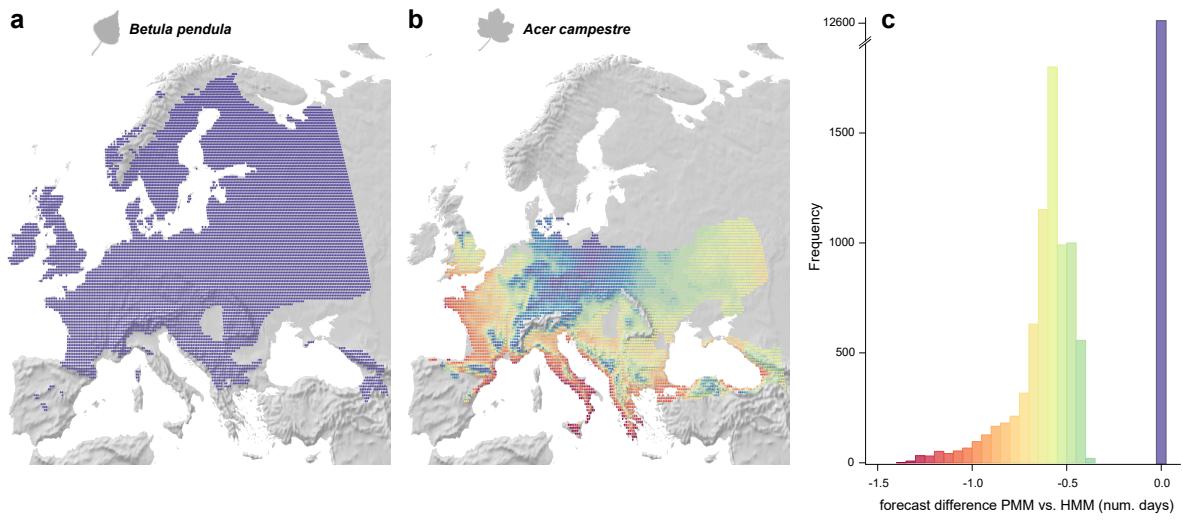


Figure 4: Comparison of forecasts of phenological shifts (i.e., computed as the difference between predictions under current climate vs. a 2°C warmer climate) resulting from a phylogenetic (PMM) and a non-phylogenetic but hierarchical (HMM) approach. Differences in forecasted shifts are negligible for 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.