

¹ Budburst timing within a functional trait framework

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²⁹ Running title: Budburst responses associated with traits

³⁰ **Summary**

- ³¹ 1. Phenologies—the timing of recurring life history events—can vary substantially in different environments and for different species. While climate change has shifted phenology by altering its proximate drivers—such as temperature—changes in the ultimate drivers that select for species-level variation remain poorly explained. Theory suggests that species-level variation in phenology can result from shifting environmental pressures that favour different strategies across the early (spring) growing season: from the early season, where higher abiotic risks and greater availability of nutrients and light favour acquisitive growth strategies, to later when a more benign environment and greater competition favour conservative growth strategies. From this we can infer suites of traits that may co-vary with species phenologies, but the high variability in traits—and especially phenology—across environments, have made testing the role of phenology within a trait framework challenging.
- ⁴¹ 2. Using a modelling framework that accommodates this variability we performed a meta-analysis using phenological data from controlled environment experiments and plant traits to test the relationships between traits and cues for tree budburst (forcing, chilling, and photoperiod).
- ⁴⁴ 3. We found that earlier species are shorter with denser, lower nitrogen leaves, while later-active species were taller with low nitrogen leaves. How budburst timing related to leaf density, however, was less in line with our predictions, as species with denser leaves had large responses to only some cues.
- ⁴⁷ 4. Synthesis: Our findings show how spring leafout phenology fits within a functional trait framework of acquisitive to conservative growth strategies, and better predicts how communities may shift in their growth strategies alongside changing phenology with climate change.

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⁵¹ Key Words: Budburst, spring phenology, traits, trees, climate change, forest communities

⁵² **Introduction**

⁵³ The timing of life history events—phenology—can shape both ecosystem services and community dynamics. Spring phenology, for example, defines the start and overall length of the growing season—shaping forest carbon storage and species interactions (Beard et al., 2019; Cleland et al., 2007; Gu et al., 2022). Shifts in phenology with climate change across systems (Menzel et al., 2006; Vitasse et al., 2021) have thus led to growing concerns over their possible impacts.

58

59 Predicting these changes requires understanding the drivers of phenology both at a proximate scale—
60 the environmental triggers of phenology each year, such as temperature and daylength—and at an
61 ultimate scale, where long-term environmental pressures may select for different phenologies across
62 species, (e.g., certain species are early or late relative to other species each year Ovaskainen et al.,
63 2013; Wolkovich and Donahue, 2021). At the proximate level, environmental conditions throughout
64 the winter and spring cause species to start growth at different times. Similar environmental conditions
65 appear to trigger spring phenological events across taxa, including the start of growth in woody plants
66 each year (Flynn and Wolkovich, 2018; Laube et al., 2014), the timing of egg laying in birds (Crick
67 et al., 1997; D’Alba et al., 2010), and the advance of spawning in amphibians (Kusano and Inoue,
68 2008; Tryjanowski et al., 2003), but current work provides limited insights into the drivers of species
69 differences (Chuine et al., 2016; Flynn and Wolkovich, 2018; Laube et al., 2014).

70

71 At the ultimate level, species phenologies may vary due to changing pressures across the growing sea-
72 son. Species that start growth early often risk high tissue loss—due to frost damage (Augspurger,
73 2009; Sakai and Larcher, 1987) or high herbivore apparencty (Wainwright et al., 2012)—but benefit
74 from higher resource availability (Hufkens et al., 2012; Rathcke and Lacey, 1985). In contrast, later
75 species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008;
76 Wolkovich and Ettinger, 2014). For plants, this variation in early to late season growth may mirror
77 the stressors from early to late successional communities, and may similarly shape phenology (Laube
78 et al., 2014).

79

80 Different pressures could shape a number of species attributes related to their growth strategies, in-
81 cluding phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced
82 if damaged (Reich et al., 1999), while species with later phenology may benefit from investing in tis-
83 sues that infer greater resource retention (Gorné et al., 2020). Differences in traits, and trade-offs in
84 allocation of resources to growth and tissue quality, can be related to a broader framework of species
85 growth strategies and functional traits (Wolkovich and Ettinger, 2014) (Fig 1), where species range
86 from acquisitive (fast) to more conservative (slow) growth (Chave et al., 2009; Wright et al., 2004).

87

88 Globally, gradients from acquisitive to conservative strategies appear common, and form the foun-
89 dation of the leaf economic and the wood economic spectra (Chave et al., 2009; Díaz et al., 2016;
90 Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004), but they can make limited predictions
91 of trait variability (Violle et al., 2012). As a result, highly variable traits like phenology are often
92 excluded from trait studies, leaving the relationships between broader trait syndromes and phenology

93 largely unknown. Understanding these relationships is critical to forecasting community dynamics and
94 responses to climate change. To date, studies have generally only examined the relationship between
95 traits and phenology within a single site (as reviewed by Wolkovich and Cleland (2014) and Wolkovich
96 and Donahue (2021)) where the problem of proximate drivers causing phenological variation can be
97 more easily ignored. Adding phenology to broader trait frameworks becomes more complex when high
98 levels of variation occurs across large spatial and temporal ranges.

99

100 Consistently defining early to late phenology is possible using the underlying cues that predict gradi-
101 ents in phenology, (which do not generally vary strongly across space and time Chuine and Cour, 1999;
102 Flynn and Wolkovich, 2018; Harrington and Gould, 2015). For many plants, early species generally
103 have responses that are small in magnitude to all three major cues of spring leafout: warm spring
104 temperatures (forcing), cool winter temperatures (chilling) and daylength (photoperiod). In contrast,
105 later species have larger responses to chilling and/or photoperiod (Flynn and Wolkovich, 2018; Laube
106 et al., 2014), and likely larger forcing responses.

107

108 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-
109 nology into functional trait research. In addition to how well we understand the environmental cues
110 that trigger early versus late leafout, spring in many forests includes strong gradients in potential se-
111 lective environments (Fig 1). Based on trade-offs between early and late spring phenologies, we predict
112 acquisitive species to be shorter, with leaf traits favourable to higher light availability and tolerance
113 to late spring frost (high specific leaf area, SLA, and leaf nitrogen content, LNC; Fig 1). Such species
114 should exhibit early phenology, with small cue responses. Canopy species that budburst later via larger
115 cue responses, when competition for soil resources is greater, would then have traits associated with
116 conservative growth—taller with denser wood (Laughlin et al., 2010)—with leaf traits suited for more
117 variable light (low SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to
118 conservative continuum, as acquisitive species produce smaller seeds and conservative species produce
119 larger—better provisioned—seeds (Fig 1).

120

121 To test our predicted relationships between budburst responses to environmental cues and common
122 functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases—
123 BIEN (Maitner et al., 2018) and TRY (Kattge et al., 2020)—with budburst data from the OSPREE
124 database of controlled environment studies (Ettinger et al., 2020). We developed a hierarchical Bayesian
125 joint model that predicts phenological responses to forcing, chilling and photoperiod treatments based
126 on species-level trait values, while allowing additional variation due to species. This approach takes
127 a step towards predicting variation via species traits instead of species identity (when traits explain

¹²⁸ a significant portion of the variation, species identity will explain only a small amount), which could
¹²⁹ help forecast species phenological responses based on trait values alone.

¹³⁰

¹³¹ Methods

¹³² We merged three major databases for our analysis. We gathered phenological data from the OSPREE
¹³³ database (Ettinger et al., 2020), which contains budburst data for woody, species from experiments of
¹³⁴ forcing, chilling and photoperiod. We constructed the OSPREE database by performing a systematic
¹³⁵ review of the literature, and searched both ISI Web of Science and Google Scholar using the following
¹³⁶ two search terms:

¹³⁷

- ¹³⁸ 1. TOPIC = (budburst OR leafout) AND (photoperiod or daylength) AND temperature*
- ¹³⁹ 2. TOPIC = (budburst OR leafout) AND dorman*

¹⁴⁰

¹⁴¹ We then scraped the data from all articles of woody species that experimentally manipulated both
¹⁴² photoperiod and/or temperature cues of budburst, leafout, or flowering phenology, and for which there
¹⁴³ was a quantifiable response to each cue. We updated this database in July 2019 reviewing all new
¹⁴⁴ articles found using the previous search terms. Additional details on the methods used to assemble,
¹⁴⁵ clean, and update this database are discussed by Ettinger et al. (2020) and Morales-Castilla et al.
¹⁴⁶ (2024). For the purpose of this study, we used a subset of the OSPREE database, using data only for
¹⁴⁷ budburst phenology and for the subset of 234 species used in Morales-Castilla et al. (2024).

¹⁴⁸

¹⁴⁹ We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge et al., 2020; Maitner et al.,
¹⁵⁰ 2018), both of which are large trait databases that include plant trait data across many individuals,
¹⁵¹ species, and studies (Table S1). We obtained data from both databases on 5 December, 2018, and
¹⁵² requested an updated version of the TRY data on 10 April, 2019. We again focused our search for trait
¹⁵³ data on the subset of 234 OSPREE species used in Morales-Castilla et al. (2024). Using the BIEN
¹⁵⁴ R package (v. 1.2.5) (Maitner et al., 2018), we downloaded all available trait data for the 94 species
¹⁵⁵ available, for which there were 13 unique traits. From the TRY database we received data for 10
¹⁵⁶ unique traits for 96 of our focal species (Kattge et al., 2020). Given our focus on the phenology of
¹⁵⁷ adult trees, we subset the available data to only include traits measured from adult individuals with
¹⁵⁸ a minimum height of 1.38 m. We further removed all data from manipulative experiments or from
¹⁵⁹ plants growing in non-natural habitats. We also grouped trait values where appropriate, for example
¹⁶⁰ pooling trait values for specific leaf area (SLA) with those denoted as “SLA with petioles”, and “SLA

161 without petioles” in our analysis (see Table S1). We also removed data that was duplicated in both
162 the TRY and BIEN datasets ($n = 434905$).

163

164 For our analysis, we only include species for which we had a complete trait profile (i.e., all traits mea-
165 sured for all species). We initially considered six commonly measured traits—SLA, leaf dry matter
166 content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species had
167 at least one trait measurement for each trait. We then used a principle component analysis (PCA) to
168 understand trait correlations and adjusted which traits we included. The PCA of our six initial traits
169 identified high correlations between SLA and LDMC, and between height and SSD. The first principal
170 component explained 32% of variation while the second explained 24.2% of the variation (Fig. S1).
171 By excluding one trait from each of these highly correlated trait pairs (specifically LDMC and SSD)
172 we increased the number of species in our dataset from the 26 species with six traits, to 37 species for
173 which we had complete datasets for four traits. The data for these 37 species were from 24 unique
174 studies (samples sizes: height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n = 7656$). We
175 also subsampled height measurements to reduce the influence of the 13 most frequently measured tree
176 species on our height model. Since these 13 species were measured 19 times more frequently than other
177 species, we randomly sampled 3000 height measurements for each species.

178

179 Joint model of trait and phenology

180 To understand connections between phenology and species traits, we developed and then parameterized
181 a joint model for each trait: height, SLA, LNC, and seed mass. Our model is a joint model insofar as
182 it involves two sub-models—one that models trait observations and a second that uses shared latent
183 processes to model phenological observations. In particular, we assume that trait values are the result
184 of multiple sources of variation, include species and study-level variation, combining into one trait
185 value that we observe (trait sub-model). This trait value (α_{species}) has a separate interaction with
186 the environmental cues (forcing, chilling, and photoperiod) that determine phenology—specifically the
187 day of year of budburst (phenology sub-model). Below we describe the two sub-models, noting which
188 parameters are shared across sub-models and which are independent.

189 Trait sub-model

190 Our trait sub-model describes the processes that determine trait observations for 1 to n species across
191 each of the 1 to m studies in our trait dataset. We use hierarchical modeling to partition trait values
192 by measurement error (σ_m^2), species identity $\alpha_{\text{species}_i}$, and study α_{study_j} . In particular, we assume that

¹⁹³ a trait observation for species i from study j , $Y_{\text{trait}_{i,j}}$, has the following normal distribution:

$$Y_{\text{trait}_{i,j}} \sim \mathcal{N}(\mu_{i,j}, \sigma_m^2) \quad (1)$$

with

$$\mu_{i,j} = \alpha_{\text{grand trait}} + \alpha_{\text{species}_i} + \alpha_{\text{study}_j} \quad (2)$$

¹⁹⁴ where $\alpha_{\text{species}_i}$ and α_{study_j} are elements of the normal random vectors:

$$\begin{aligned} \boldsymbol{\alpha}_{\text{trait}} &= \alpha_{\text{grand trait}} + \alpha_{\text{species}_i} \\ \boldsymbol{\alpha}_{\text{species}} &= \{\alpha_{\text{species}_1}, \dots, \alpha_{\text{species}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{species}} \sim \mathcal{N}(0, \sigma_{\text{species}}^2) \end{aligned} \quad (3)$$

$$\begin{aligned} \boldsymbol{\alpha}_{\text{study}} &= \{\alpha_{\text{study}_1}, \dots, \alpha_{\text{study}_m}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \mathcal{N}(0, \sigma_{\text{study}}^2) \end{aligned} \quad (4)$$

¹⁹⁵ The latent parameter or overall mean trait value, $\alpha_{\text{grand trait}}$ represents a trait value that is independent
¹⁹⁶ of the species ($\alpha_{\text{species},i}$) and study-level ($\alpha_{\text{study},j}$) offsets from that trait value. The σ_m^2 parameter
¹⁹⁷ is the measurement error, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and study-level variances in trait
¹⁹⁸ values. Of these parameters, the $\boldsymbol{\alpha}_{\text{trait}}$ are shared by the phenology sub-model.

¹⁹⁹ Phenology sub-model

²⁰⁰ Our phenology sub-model describes the processes that determine the relationships between traits and
²⁰¹ environment cues and their effects on phenological observations for 1 to n species, specifically the
²⁰² timing (day of year) of budburst from the updated OSPREE dataset. We assume that an observation
²⁰³ of budburst for species k under g treatments levels of chilling, forcing, and photoperiod (c_g, f_g, p_g),
²⁰⁴ parameter $Y_{\text{pheno}_{k,g}}$ representing the observed day of budburst (which we z -scored to allow direct
²⁰⁵ comparison of cues) has the following normal distribution:

$$Y_{\text{pheno}_{k,g}} \sim \mathcal{N}(\mu_{k,g}, \sigma_d^2) \quad (5)$$

with

$$\mu_{k,g} = \alpha_{\text{pheno},k} + \beta_{\text{chilling}_k} \cdot c_g + \beta_{\text{forcing}_k} \cdot f_g + \beta_{\text{photoperiod}_k} \cdot p_g \quad (6)$$

and

$$\begin{aligned}\beta_{\text{chilling}_k} &= \alpha_{\text{chilling},k} + \beta_{\text{trait.chilling}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{forcing}_k} &= \alpha_{\text{forcing},k} + \beta_{\text{trait.forcing}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{photoperiod}_k} &= \alpha_{\text{photoperiod},k} + \beta_{\text{trait.photoperiod}} \cdot \alpha_{\text{trait},k}\end{aligned}\quad (7)$$

206 where α_{pheno_k} , $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$ are elements of the normal random vectors:

$$\begin{aligned}\boldsymbol{\alpha}_{\text{pheno}} &= \{\alpha_{\text{pheno}_1}, \dots, \alpha_{\text{pheno}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \mathcal{N}(\mu_{\text{pheno}}, \sigma_{\text{pheno}}^2) \\ \boldsymbol{\alpha}_{\text{chilling}} &= \{\alpha_{\text{chilling}_1}, \dots, \alpha_{\text{chilling}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chilling}} \sim \mathcal{N}(\mu_{\text{chilling}}, \sigma_{\text{chilling}}^2) \\ \boldsymbol{\alpha}_{\text{forcing}} &= \{\alpha_{\text{forcing}_1}, \dots, \alpha_{\text{forcing}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{forcing}} \sim \mathcal{N}(\mu_{\text{forcing}}, \sigma_{\text{forcing}}^2) \\ \boldsymbol{\alpha}_{\text{photoperiod}} &= \{\alpha_{\text{photoperiod}_1}, \dots, \alpha_{\text{photoperiod}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photoperiod}} \sim \mathcal{N}(\mu_{\text{photoperiod}}, \sigma_{\text{photoperiod}}^2)\end{aligned}\quad (8)$$

207 Parameter $\alpha_{\text{pheno},k}$ represents the overall mean day of budburst for species k without the influence
208 of chilling, forcing, or photoperiod treatments. The species average day of budburst (independent of
209 treatments) is μ_{pheno} , and σ_{pheno}^2 is the variance across species. The parameters $\alpha_{\text{chilling},k}$, $\alpha_{\text{forcing},k}$,
210 and $\alpha_{\text{photoperiod},k}$ represent the trait-independent responses of species k to chilling, forcing, and photo-
211 peroid treatments respectively, each with an associated mean (μ_{chilling} , μ_{forcing} , $\mu_{\text{photoperiod}}$) and
212 variance ($\sigma_{\text{chilling}}^2$, $\sigma_{\text{forcing}}^2$, $\sigma_{\text{photoperiod}}^2$) across species. The effect of the species trait value, $\alpha_{\text{trait},k}$ —
213 the parameter shared with trait sub-model above—on its responses to chilling, forcing, and photoperiod
214 are described by parameters $\beta_{\text{trait.chilling}}$, $\beta_{\text{trait.forcing}}$, $\beta_{\text{trait.photoperiod}}$. Finally, σ_d^2 is the variance arising
215 from measurement error.

216

217 We chose weakly informative priors, and validated them using a series of prior predictive checks.
218 The model was coded in the Stan programming language, fit using the rstan package (v. 3.3.6)
219 (Stan Development Team, 2018), with 1,000 iterations per chain across 4 chains (4,000 total sampling
220 iterations), and all models met basic diagnostic checks, including no divergences, high effective sample
221 size (n_{eff}), and \hat{R} close to 1, fitting the data well (Fig S2). Here we present our model estimates as
222 the means and 90% posterior uncertainty intervals.

223 Results

224 Across traits, height, SLA, and LNC strongly related to chilling ($\beta_{\text{chilling}_k}$), forcing (β_{forcing_k}), and
225 photoperiod ($\beta_{\text{photoperiod}_k}$) treatments, Fig 2 a-f & j-l), but the direction of these relationships only
226 showed consistent trends for LNC (Fig. 2 j-l). As we predicted, height was negatively related to

227 chilling ($\beta_{\text{chilling}_k}$) and photoperiod ($\beta_{\text{photoperiod}_k}$), with taller species having larger responses to cues
228 (-0.5 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized
229 photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). As illustrated for one characteristically acquisitive
230 species, *Alnus incana*, and one characteristically conservative species, *Quercus rubra* (Fig S3), the cue
231 relationships with height led to generally later budburst relative to estimates without trait effects ($\mu_{k,g}$;
232 Fig. 3). In contrast, seed mass had the smallest responses, with no relationship between seed mass
233 and any cue (Fig. 2 g-i, Fig 3 d-f, & Table S3).

234

235 Of our leaf traits, we found that species SLA related to photoperiod ($\beta_{\text{photoperiod}_k}$, -0.2 mm²/mg per
236 standardized photoperiod; 90% UI: -0.4, 0.0, Fig. 2 f, Table S4), but did not strongly predict responses
237 to chilling ($\beta_{\text{chilling}_k}$) or forcing treatments (β_{forcing_k} , Fig. 2 d and e). Thus, species with more acquisi-
238 tive growth strategies (thin leaves and a lower investment in leaf mass that leads to large SLA values),
239 had larger responses to photoperiod, contrary to our predictions (Fig. 2 f). For LNC, we found that
240 species that produce leaves with high nitrogen content, which relates generally to high photosynthetic
241 rates and acquisitive growth, show smaller responses to cues (Fig. 2 j-l). These findings are in line
242 with our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g
243 per standardized chilling; 90% UI: 0.3, 1.2, Table S5), but we also found high LNC species to be less
244 responsive to photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6) and to forcing
245 (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig 2 j-l & Fig S3 d-f).

246

247 We found species-level variation across traits (σ^2_{trait}) were comparable to or greater than variation
248 across studies (σ^2_{study} , Fig 4). The magnitude of study-level variation (σ^2_{study}) that we found, however,
249 suggests that models using large trait databases that fail to separate out study from species-level vari-
250 ation (σ^2_{trait}) may poorly estimate species traits. Variation across studies was greatest for height (with
251 σ^2_{study} of 7.5 m compared to 5.9 m for σ^2_{trait} , Fig 4a). For seed mass and LNC, study-level variation
252 was less than that of the species-level variation, with estimates of 1 mg for study-level variation versus
253 1.6 mg for species-level variation in seed mass and estimates of 3.6 mg g⁻¹ for study-level variation
254 and 5.1 mg g⁻¹ for the species-level variation in LNC (Fig 4c and d). At the lowest end, study-level
255 variation in SLA was approximately half the value of the species-level variation (3.3 mm² mg⁻¹ versus
256 7.8 mm² mg⁻¹ for σ^2_{study} and σ^2_{trait} , respectively, Fig 4b).

257

258 **Discussion**

259 We found species traits influenced the timing of budburst in response to the three primary cues of
260 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or
261 later phenology following well-established gradients in growth strategies predicted by functional trait
262 frameworks (Chave et al., 2009; Díaz et al., 2016; Westoby, 1998; Westoby and Wright, 2006; Wright
263 et al., 2004): early species tended to have traits associated with fast and acquisitive strategies while
264 later species had traits associated with conservative, slower strategies. We found the largest bud-
265 burst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and
266 height all showing large responses across our three cues. In contrast, our one reproductive trait—seed
267 mass—showed a smaller response. Our results provide a major step forward in integrating phenology
268 into broader trait syndromes that shape species growth strategies, and support previous findings from
269 more local scales that found strong relationships between height and species phenology (Segrestin et al.,
270 2020; Sporbert et al., 2022; Sun and Frelich, 2011). Our more global analysis is also in agreement with
271 previous studies of plant phenological events, in which no relation is found between phenology and
272 seed mass in woody plants (Bolmgren and Cowan, 2008; Ettinger et al., 2018).

273

274 **Effects of phenology-trait relationships on community assembly**

275 Our findings suggest the changing pressures across the early growing season may affect the temporal
276 assembly of communities. Strong abiotic pressures alongside weak competition early in the season were
277 associated with early-budbursting species with acquisitive traits (shorter heights and low LNC) that
278 allow faster return on resource investments (Chave et al., 2009; Grime, 1977; Westoby, 1998). These
279 traits should allow early species to more easily replace tissue if lost to frost or other abiotic distur-
280 bances, and benefit from greater light availability in the open canopy of many temperate forests in
281 the early spring. In contrast, later-budbursting species had traits associated with greater competitive
282 abilities and slower growth (Chave et al., 2009; Grime, 1977; Westoby, 1998) (Fig 2), which may help
283 them compete for soil and light resources when most other species are already growing. These traits
284 can be linked to other ecological processes and species characteristics, such as species successional po-
285 sition, as illustrated by the differences between early and late successional species (e.g., *Alnus incana*
286 and *Quercus rubra*; Fig 2).

287

288 The traits with cue responses that deviated from our expectations also offer novel insights into the
289 tradeoffs between traits and environmental cues. All of our traits are associated with multiple aspects
290 of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our

291 predictions, we found large responses to forcing for short trees, which could prevent frost damage or
292 xylem cavitation under a late spring frost (Clements et al., 1972; Marquis et al., 2020) and influence
293 annual cambial meristem growth (Lenz et al., 2016). Similarly, the lack of a response to chilling or
294 forcing by high SLA individuals could be driven by other trait attributes and environmental cues—
295 selecting for species relative growth rates or leaf longevity—and not photosynthetic potential (Reich,
296 2014; Westoby, 1998). These findings highlight the complexity of determining the drivers of species
297 trait profiles, and further our understanding of how traits affect community dynamics under variable
298 environments.

299

300 **Phenology-trait relationships under future climates**

301 Incorporating phenology within broader trait syndromes could aid forecasting of species and commu-
302 nity responses to climate change. While decades of research have documented phenological shifts with
303 anthropogenic climate change, increasing research suggests a potential connection between phenolog-
304 ical responses to warming and performance with warming, where species that shift their phenology
305 more also perform better (Cleland et al., 2012; Macgregor et al., 2019).

306

307 Our results suggest this phenology-performance relationship could be driven in part by a suite of traits
308 that covary with phenological cues to determine how responsive species are to warming. Species with
309 smaller responses to all cues, especially chilling and photoperiod, would tend to advance more with
310 warming, which our results suggest would allow these species to also grow more quickly. These results
311 could further aid in predicting the potential for invasion, as communities with similar phenologies
312 and suites of traits, appear more susceptible to fast growing, phenologically more responsive invasive
313 species (Alexander and Levine, 2019; Schuster et al., 2021; Wolkovich and Cleland, 2011).

314

315 Our analytical approach and results may be especially useful to help forecast changes in forest dy-
316 namics. Identifying the varying trait syndromes of forest communities over a spring season can aid
317 predictions of how climate change will alter species growth and productivity. For example, our results
318 suggest that, by favoring more phenologically responsive species (i.e., with small chilling and pho-
319 toperiod responses), warming may also favor species with acquisitive growth strategies. In contrast,
320 conservative species, which appear less phenologically responsive to changes in temperature (due to
321 larger chilling and photoperiod responses) could face greater abiotic and biotic stress (Guy, 2014).

322

323 Our results could further help identify which species are most likely to be negatively impacted under

324 future climates, and develop better strategies for climate change mitigation and conservation. Species
325 that fail to advance phenologically with warming might experience more competition (Alexander and
326 Levine, 2019; Carter et al., 2018), as species that begin growth increasingly earlier with warming have
327 more time to deplete resources. In addition to altering the timing and interactions between species
328 within a season, species trait syndromes have the potential to further redefine the environmental condi-
329 tions under which growth occurs, and as a result, shape community assembly and productivity within
330 ecological communities. By identifying the species most vulnerable to climate change impacts, we can
331 develop more effective management practices that prevent the loss of critical ecosystem services and
332 preserve community diversity under future conditions.

333

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337 **Author Contributions Statement**

338 DL, FAMJ, GL, MG, DS, and EMW planned and designed the study. All authors conducted the
339 literature review and cleaned the database. DL, FAMJ, GL, and EMW performed the data analysis
340 and contributed code. DL, FAMJ, and GL created the figures. DL and EMW wrote the initial draft
341 and all authors reviewed and revised the manuscript.

342 **Competing Interests Statement**

343 The authors declare no competing interests.

344 **Data availability statement**

345 The phenological data used for this manuscript is a subset of the existing OSPREE dataset (doi:10.5063/F1CZ35KB)
346 and the trait data a subset of the TRY database (doi:10.1111/gcb.14904) and the BIEN database
347 (doi: 10.1111/2041-210X.1286).

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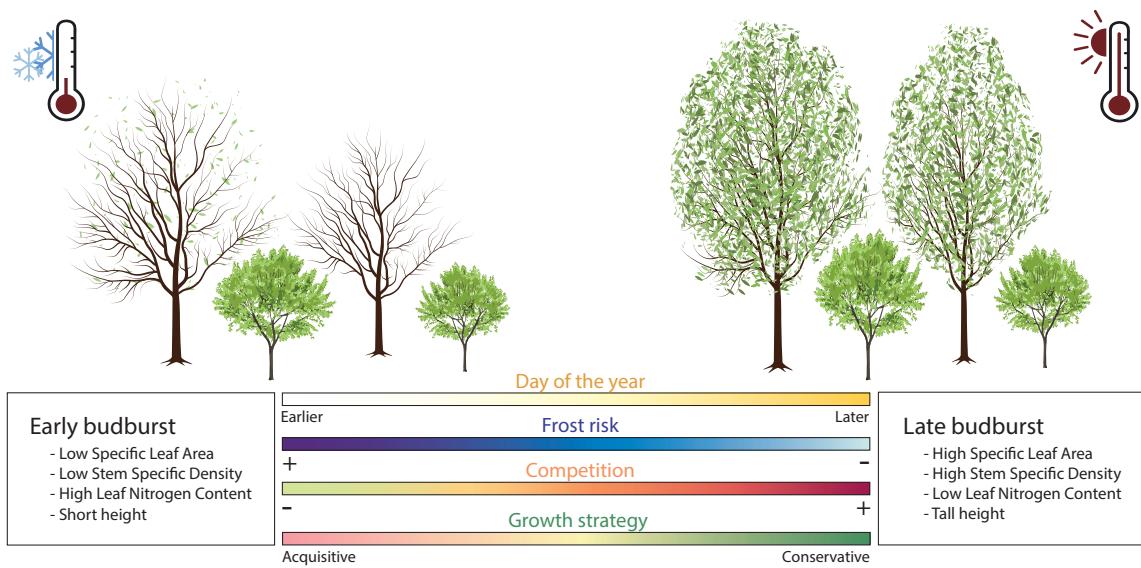


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost but reduced competition. In contrast, we expected later-budbursting species would have traits associated with conservative growth, as they experience greater competition but a more climatically benign environment.

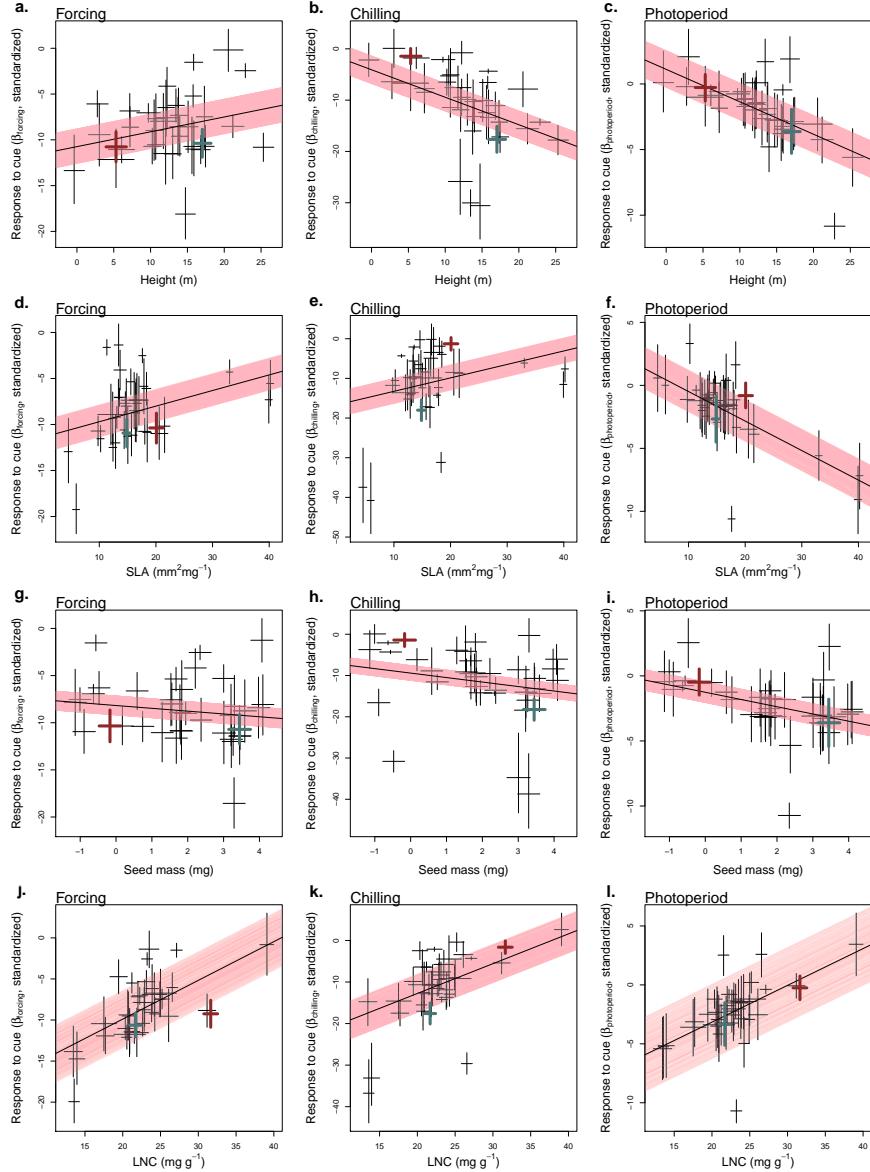


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the black line depicting the mean linear relationship between estimated trait effects and the slope of the cue response (either β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$ for each respective cues) and the pink band the 50% uncertainty interval. Each set of crossed lines represents one species (with each line spanning the 50% uncertainty interval), with the species depicted in Fig 3 colored in each panel, with the acquisitive species (*Alnus incana*) shown in red, and the conservative species (*Quercus rubra*) shown in blue.

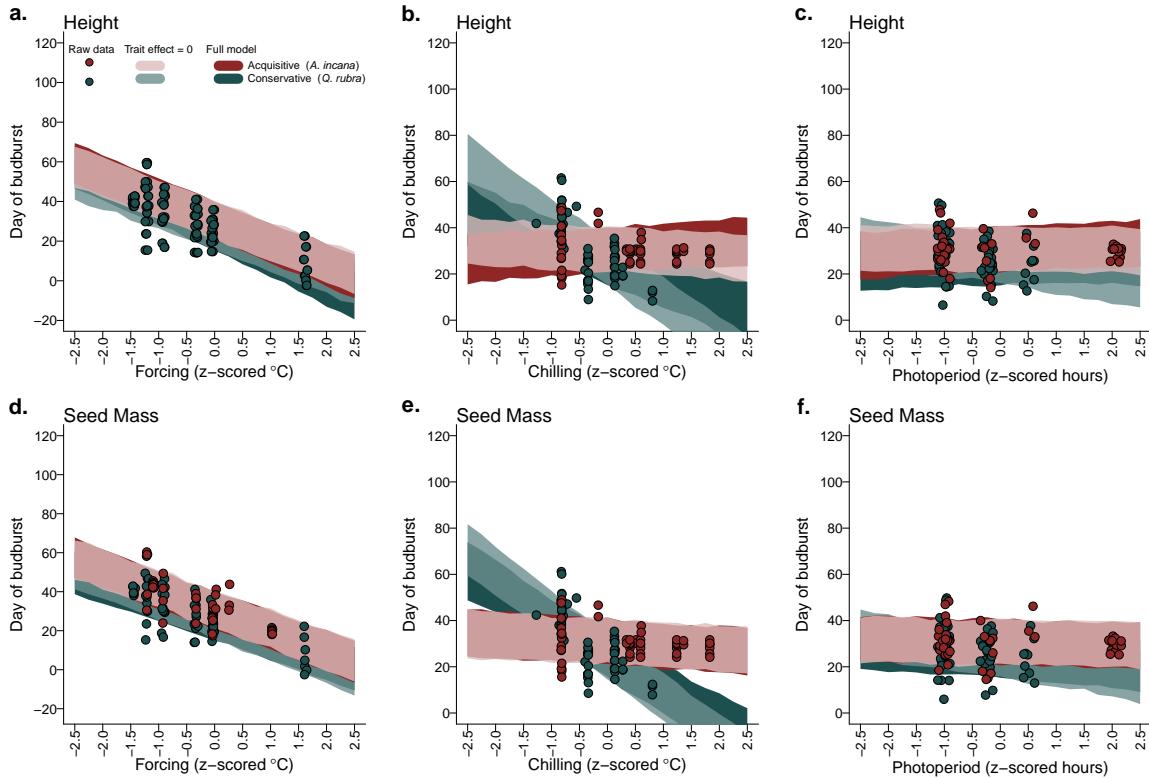


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with height (a-c) and seed mass (d-f) for an acquisitive species, *Alnus incana* shown in red, and a conservative species, *Quercus rubra*, shown in blue. **a**, The effect of height on budburst timing was smaller in response to forcing cues, but larger in response to both **b**, chilling and **c**, photoperiod. In contrast, seed mass had a negligible effect on **d**, forcing and **f**, photoperiod responses, **e**, but a greater response to chilling. Points represent the raw data and the coloured bands the 50% uncertainty intervals of the model estimates and points individual trait measurements.

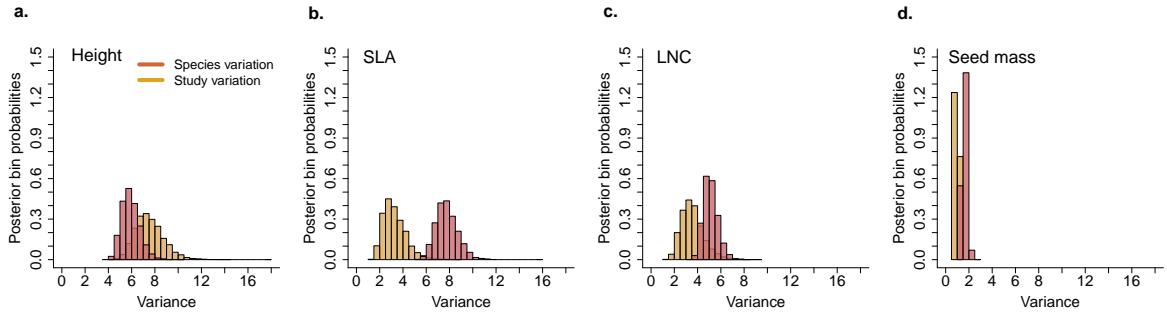


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf area, **c**, leaf nitrogen content, and **d**, seed mass models all estimated higher species-level variation. Shown here are the posterior densities for the species-level variation, shown in red, and study-level variation, shown in yellow. For comparison, we show all x-axes spanning the minimum to maximum variances across all four traits. The histograms depict the full distribution of the study and species-level variance, where each bin is normalized by the total count of the posterior estimate.