

¹ Budburst timing within a functional trait framework

²

³ Running title: Budburst responses associated with traits

⁴ **Summary**

⁵ 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.

¹⁵ 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).

¹⁸ 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.

²¹ 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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²⁵ Key Words: Budburst, spring phenology, traits, trees, climate change, forest communities

²⁶ **Introduction**

²⁷ The timing of life history events—phenology—can shape both ecosystem services and community
²⁸ dynamics. Spring phenology, for example, defines the start and overall length of the growing season—
²⁹ shaping forest carbon storage and species interactions (Beard et al., 2019; Cleland et al., 2007; Gu
³⁰ et al., 2022). Shifts in phenology with climate change across systems (Menzel et al., 2006; Vitasse
³¹ et al., 2021) have thus led to growing concerns over their possible impacts.

³²

³³ Predicting these changes requires understanding the drivers of phenology both at a proximate scale—
³⁴ the environmental triggers of phenology each year, such as temperature and daylength—and at an
³⁵ ultimate scale, where long-term environmental pressures may select for different phenologies across
³⁶ species, (e.g., certain species are early or late relative to other species each year Ovaskainen et al.,
³⁷ 2013; Wolkovich and Donahue, 2021). At the proximate level, environmental conditions throughout
³⁸ the winter and spring cause species to start growth at different times. Similar environmental conditions
³⁹ appear to trigger spring phenological events across taxa, including the start of growth in woody plants
⁴⁰ each year (Flynn and Wolkovich, 2018; Laube et al., 2014), the timing of egg laying in birds (Crick
⁴¹ et al., 1997; D’Alba et al., 2010), and the advance of spawning in amphibians (Kusano and Inoue,
⁴² 2008; Tryjanowski et al., 2003), but current work provides limited insights into the drivers of species
⁴³ differences (Chuine et al., 2016; Flynn and Wolkovich, 2018; Laube et al., 2014).

⁴⁴

⁴⁵ At the ultimate level, species phenologies may vary due to changing pressures across the growing sea-
⁴⁶ son. Species that start growth early often risk high tissue loss—due to frost damage (Augspurger,
⁴⁷ 2009; Sakai and Larcher, 1987) or high herbivore apperency (Wainwright et al., 2012)—but benefit
⁴⁸ from higher resource availability (Hufkens et al., 2012; Rathcke and Lacey, 1985). In contrast, later
⁴⁹ species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008;
⁵⁰ Wolkovich and Ettlinger, 2014). For plants, this variation in early to late season growth may mirror
⁵¹ the stressors from early to late successional communities, and may similarly shape phenology (Laube
⁵² et al., 2014).

⁵³

⁵⁴ Different pressures could shape a number of species attributes related to their growth strategies, in-
⁵⁵ cluding phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced
⁵⁶ if damaged (Reich et al., 1999), while species with later phenology may benefit from investing in tis-
⁵⁷ sues that infer greater resource retention (Gorné et al., 2020). Differences in traits, and trade-offs in
⁵⁸ allocation of resources to growth and tissue quality, can be related to a broader framework of species
⁵⁹ growth strategies and functional traits (Wolkovich and Ettlinger, 2014) (Fig 1), where species range

60 from acquisitive (fast) to more conservative (slow) growth (Chave et al., 2009; Wright et al., 2004).

61

62 Globally, gradients from acquisitive to conservative strategies appear common, and form the foun-
63 dation of the leaf economic and the wood economic spectra (Chave et al., 2009; Díaz et al., 2016;
64 Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004), but they can make limited predictions
65 of trait variability (Violle et al., 2012). As a result, highly variable traits like phenology are often
66 excluded from trait studies, leaving the relationships between broader trait syndromes and phenology
67 largely unknown. Understanding these relationships is critical to forecasting community dynamics and
68 responses to climate change. To date, studies have generally only examined the relationship between
69 traits and phenology within a single site (as reviewed by Wolkovich and Cleland (2014) and Wolkovich
70 and Donahue (2021)) where the problem of proximate drivers causing phenological variation can be
71 more easily ignored. Adding phenology to broader trait frameworks becomes more complex when high
72 levels of variation occurs across large spatial and temporal ranges.

73

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

81

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

94

95 To test our predicted relationships between budburst responses to environmental cues and common
96 functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases—
97 BIEN (Maitner et al., 2018) and TRY (Kattge et al., 2020)—with budburst data from the OSPREE
98 database of controlled environment studies (Ettinger et al., 2020). We developed a hierarchical Bayesian
99 joint model that predicts phenological responses to forcing, chilling and photoperiod treatments based
100 on species-level trait values, while allowing additional variation due to species. This approach takes
101 a step towards predicting variation via species traits instead of species identity (when traits explain
102 a significant portion of the variation, species identity will explain only a small amount), which could
103 help forecast species phenological responses based on trait values alone.

104

105 Methods

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

111

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

114

115 We then scraped the data from all articles of woody species that experimentally manipulated both
116 photoperiod and/or temperature cues of budburst, leafout, or flowering phenology, and for which there
117 was a quantifiable response to each cue. We updated this database in July 2019 reviewing all new
118 articles found using the previous search terms. Additional details on the methods used to assemble,
119 clean, and update this database are discussed by Ettinger et al. (2020) and Morales-Castilla et al.
120 (2024). For the purpose of this study, we used a subset of the OSPREE database, using data only for
121 budburst phenology and for the subset of 234 species used in Morales-Castilla et al. (2024).

122

123 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge et al., 2020; Maitner et al.,
124 2018), both of which are large trait databases that include plant trait data across many individuals,
125 species, and studies (Table S1). We obtained data from both databases on 5 December, 2018, and
126 requested an updated version of the TRY data on 10 April, 2019. We again focused our search for trait
127 data on the subset of 234 OSPREE species used in Morales-Castilla et al. (2024). Using the BIEN

128 R package (v. 1.2.5) (Maitner et al., 2018), we downloaded all available trait data for the 94 species
129 available, for which there were 13 unique traits. From the TRY database we received data for 10
130 unique traits for 96 of our focal species (Kattge et al., 2020). Given our focus on the phenology of
131 adult trees, we subset the available data to only include traits measured from adult individuals with
132 a minimum height of 1.38 m. We further removed all data from manipulative experiments or from
133 plants growing in non-natural habitats. We also grouped trait values where appropriate, for example
134 pooling trait values for specific leaf area (SLA) with those denoted as “SLA with petioles”, and “SLA
135 without petioles” in our analysis (see Table S1). We also removed data that was duplicated in both
136 the TRY and BIEN datasets ($n = 434905$).

137

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

152

153 Joint model of trait and phenology

154 To understand connections between phenology and species traits, we developed and then parameterized
155 a joint model for each trait: height, SLA, LNC, and seed mass. Our model is a joint model insofar as
156 it involves two sub-models—one that models trait observations and a second that uses shared latent
157 processes to model phenological observations. In particular, we assume that trait values are the result
158 of multiple sources of variation, include species and study-level variation, combining into one trait
159 value that we observe (trait sub-model). This trait value (α_{trait}) has a separate interaction with the
160 environmental cues (forcing, chilling, and photoperiod) that determine phenology—specifically the

¹⁶¹ day of year of budburst (phenology sub-model). Below we describe the two sub-models, noting which
¹⁶² parameters are shared across sub-models and which are independent.

¹⁶³ Trait sub-model

¹⁶⁴ Our trait sub-model describes the processes that determine trait observations for 1 to n species across
¹⁶⁵ each of the 1 to m studies in our trait dataset. We use hierarchical modeling to partition trait values
¹⁶⁶ by measurement error (σ_m^2), species identity $\alpha_{\text{species}_i}$, and study α_{study_j} . In particular, we assume that
¹⁶⁷ 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

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

¹⁶⁸ where $\alpha_{\text{species}_i}$ and α_{study_j} are elements of the normal random vectors:

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

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

¹⁶⁹ The latent parameter or overall mean trait value, $\alpha_{\text{grand trait}}$ represents a trait value that is independent
¹⁷⁰ of the species ($\alpha_{\text{species},i}$) and study-level ($\alpha_{\text{study},j}$) offsets from that trait value. The σ_m^2 parameter
¹⁷¹ is the measurement error, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and study-level variances in trait
¹⁷² values. Of these parameters, the $\boldsymbol{\alpha}_{\text{trait}}$ are shared by the phenology sub-model.

¹⁷³ Phenology sub-model

¹⁷⁴ Our phenology sub-model describes the processes that determine the relationships between traits and
¹⁷⁵ environment cues and their effects on phenological observations for 1 to n species, specifically the
¹⁷⁶ timing (day of year) of budburst from the updated OSPREE dataset. We assume that an observation
¹⁷⁷ of budburst for species k under g treatments levels of chilling, forcing, and photoperiod (c_g, f_g, p_g),
¹⁷⁸ parameter $Y_{\text{pheno}_{k,g}}$ representing the observed day of budburst (which we z -scored to allow direct
¹⁷⁹ 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

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

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

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

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

190
 191 We chose weakly informative priors, and validated them using a series of prior predictive checks.
 192 The model was coded in the Stan programming language, fit using the rstan package (v. 3.3.6)
 193 (Stan Development Team, 2018), with 1,000 iterations per chain across 4 chains (4,000 total sampling
 194 iterations), and all models met basic diagnostic checks, including no divergences, high effective sample
 195 size (n_{eff}), and \hat{R} close to 1, fitting the data well (Fig S2). Here we present our model estimates as
 196 the means and 90% posterior uncertainty intervals.

197 **Results**

198 Across traits, height, SLA, and LNC strongly related to chilling ($\beta_{\text{chilling}_k}$), forcing (β_{forcing_k}), and
199 photoperiod ($\beta_{\text{photoperiod}_k}$) treatments, Fig 2 a-f & j-l), but the direction of these relationships only
200 showed consistent trends for LNC (Fig. 2 j-l). As we predicted, height was negatively related to
201 chilling ($\beta_{\text{chilling}_k}$) and photoperiod ($\beta_{\text{photoperiod}_k}$), with taller species having larger responses to cues
202 (-0.5 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized
203 photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). As illustrated for one characteristically acquisitive
204 species, *Alnus incana*, and one characteristically conservative species, *Quercus rubra* (Fig S3), the cue
205 relationships with height led to generally later budburst relative to estimates without trait effects ($\mu_{k,g}$;
206 Fig. 3). In contrast, seed mass had the smallest responses, with no relationship between seed mass
207 and any cue (Fig. 2 g-i, Fig 3 d-f, & Table S3).

208

209 Of our leaf traits, we found that species SLA related to photoperiod ($\beta_{\text{photoperiod}_k}$, -0.2 mm²/mg per
210 standardized photoperiod; 90% UI: -0.4, 0.0, Fig. 2 f, Table S4), but did not strongly predict responses
211 to chilling ($\beta_{\text{chilling}_k}$) or forcing treatments (β_{forcing_k} , Fig. 2 d and e). Thus, species with more acquisi-
212 tive growth strategies (thin leaves and a lower investment in leaf mass that leads to large SLA values),
213 had larger responses to photoperiod, contrary to our predictions (Fig. 2 f). For LNC, we found that
214 species that produce leaves with high nitrogen content, which relates generally to high photosynthetic
215 rates and acquisitive growth, show smaller responses to cues (Fig. 2 j-l). These findings are in line
216 with our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g
217 per standardized chilling; 90% UI: 0.3, 1.2, Table S5), but we also found high LNC species to be less
218 responsive to photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6) and to forcing
219 (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig 2 j-l & Fig S3 d-f).

220

221 We found species-level variation across traits (σ_{trait}^2) were comparable to or greater than variation
222 across studies (σ_{study}^2 , Fig 4). The magnitude of study-level variation (σ_{study}^2) that we found, however,
223 suggests that models using large trait databases that fail to separate out study from species-level vari-
224 ation (σ_{trait}^2) may poorly estimate species traits. Variation across studies was greatest for height (with
225 σ_{study}^2 of 7.5 m compared to 5.9 m for σ_{trait}^2 , Fig 4a). For seed mass and LNC, study-level variation
226 was less than that of the species-level variation, with estimates of 1 mg for study-level variation versus
227 1.6 mg for species-level variation in seed mass and estimates of 3.6 mg g⁻¹ for study-level variation
228 and 5.1 mg g⁻¹ for the species-level variation in LNC (Fig 4c and d). At the lowest end, study-level
229 variation in SLA was approximately half the value of the species-level variation (3.3 mm² mg⁻¹ versus
230 7.8 mm² mg⁻¹ for σ_{study}^2 and σ_{trait}^2 , respectively, Fig 4b).

232 Discussion

233 We found species traits influenced the timing of budburst in response to the three primary cues of
 234 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or
 235 later phenology following well-established gradients in growth strategies predicted by functional trait
 236 frameworks (Chave et al., 2009; Díaz et al., 2016; Westoby, 1998; Westoby and Wright, 2006; Wright
 237 et al., 2004): early species tended to have traits associated with fast and acquisitive strategies while
 238 later species had traits associated with conservative, slower strategies. We found the largest bud-
 239 burst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and
 240 height all showing large responses across our three cues. In contrast, our one reproductive trait—seed
 241 mass—showed a smaller response. Our results provide a major step forward in integrating phenology
 242 into broader trait syndromes that shape species growth strategies, and support previous findings from
 243 more local scales that found strong relationships between height and species phenology (Segrestin et al.,
 244 2020; Sporbert et al., 2022; Sun and Frelich, 2011). Our more global analysis is also in agreement with
 245 previous studies of plant phenological events, in which no relation is found between phenology and
 246 seed mass in woody plants (Bolmgren and Cowan, 2008; Ettinger et al., 2018).

248 Effects of phenology-trait relationships on community assembly

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

262 The traits with cue responses that deviated from our expectations also offer novel insights into the
263 tradeoffs between traits and environmental cues. All of our traits are associated with multiple aspects
264 of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our
265 predictions, we found large responses to forcing for short trees, which could prevent frost damage or
266 xylem cavitation under a late spring frost (Clements et al., 1972; Marquis et al., 2020) and influence
267 annual cambial meristem growth (Lenz et al., 2016). Similarly, the lack of a response to chilling or
268 forcing by high SLA individuals could be driven by other trait attributes and environmental cues—
269 selecting for species relative growth rates or leaf longevity—and not photosynthetic potential (Reich,
270 2014; Westoby, 1998). These findings highlight the complexity of determining the drivers of species
271 trait profiles, and further our understanding of how traits affect community dynamics under variable
272 environments.

273

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

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

280

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

288

289 Our analytical approach and results may be especially useful to help forecast changes in forest dy-
290 namics. Identifying the varying trait syndromes of forest communities over a spring season can aid
291 predictions of how climate change will alter species growth and productivity. For example, our results
292 suggest that, by favoring more phenologically responsive species (i.e., with small chilling and pho-
293 toperiod responses), warming may also favor species with acquisitive growth strategies. In contrast,
294 conservative species, which appear less phenologically responsive to changes in temperature (due to

295 larger chilling and photoperiod responses) could face greater abiotic and biotic stress (Guy, 2014).

296

297 Our results could further help identify which species are most likely to be negatively impacted under
298 future climates, and develop better strategies for climate change mitigation and conservation. Species
299 that fail to advance phenologically with warming might experience more competition (Alexander and
300 Levine, 2019; Carter et al., 2018), as species that begin growth increasingly earlier with warming have
301 more time to deplete resources. In addition to altering the timing and interactions between species
302 within a season, species trait syndromes have the potential to further redefine the environmental condi-
303 tions under which growth occurs, and as a result, shape community assembly and productivity within
304 ecological communities. By identifying the species most vulnerable to climate change impacts, we can
305 develop more effective management practices that prevent the loss of critical ecosystem services and
306 preserve community diversity under future conditions.

307

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311 Author Contributions Statement

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

316 Competing Interests Statement

317 The authors declare no competing interests.

318 Data availability statement

319 The phenological data used for this manuscript is a subset of the existing OSPREE dataset (doi:10.5063/F1CZ35KB)
320 and the trait data a subset of the TRY database (doi:10.1111/gcb.14904) and the BIEN database
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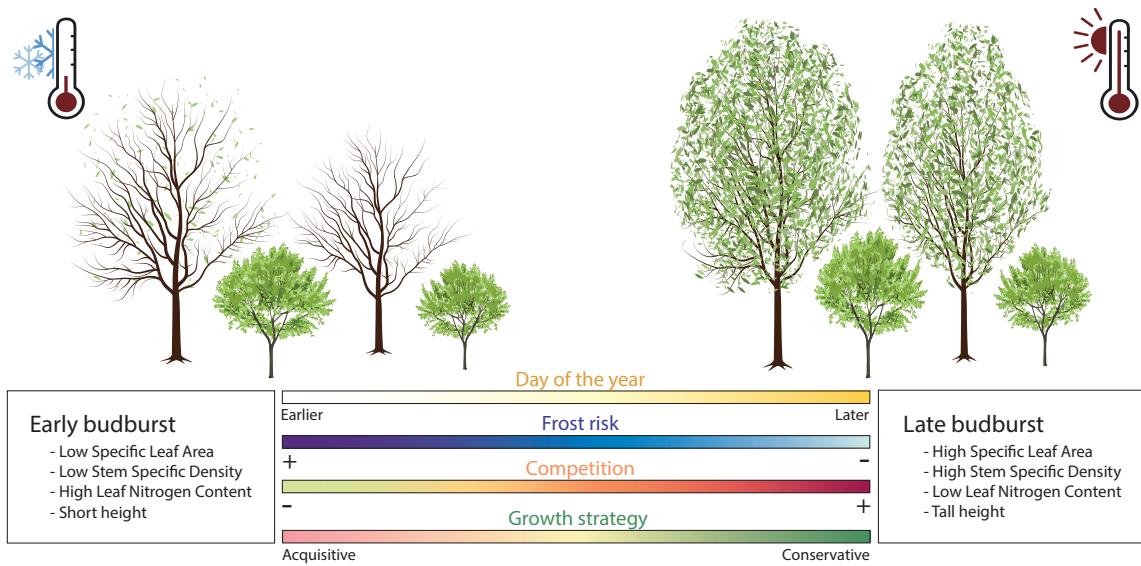


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost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

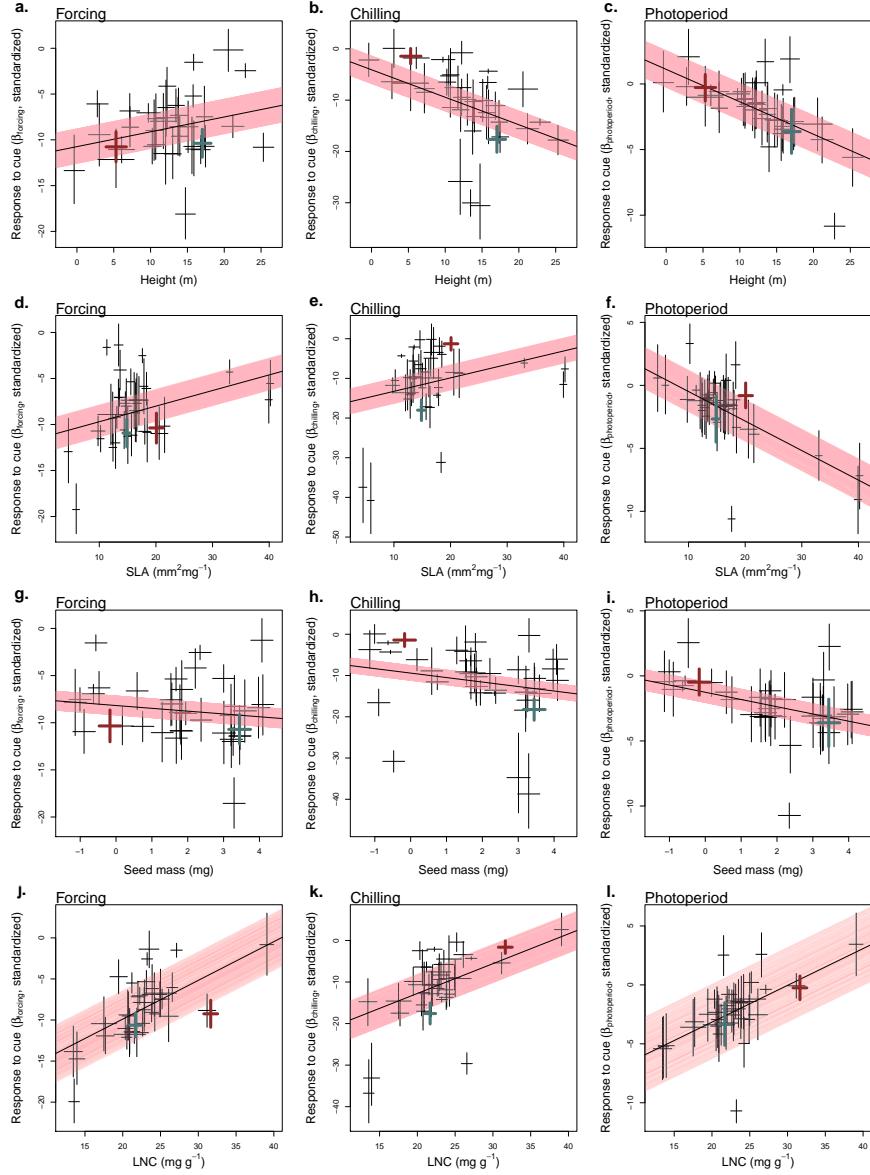


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third 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.

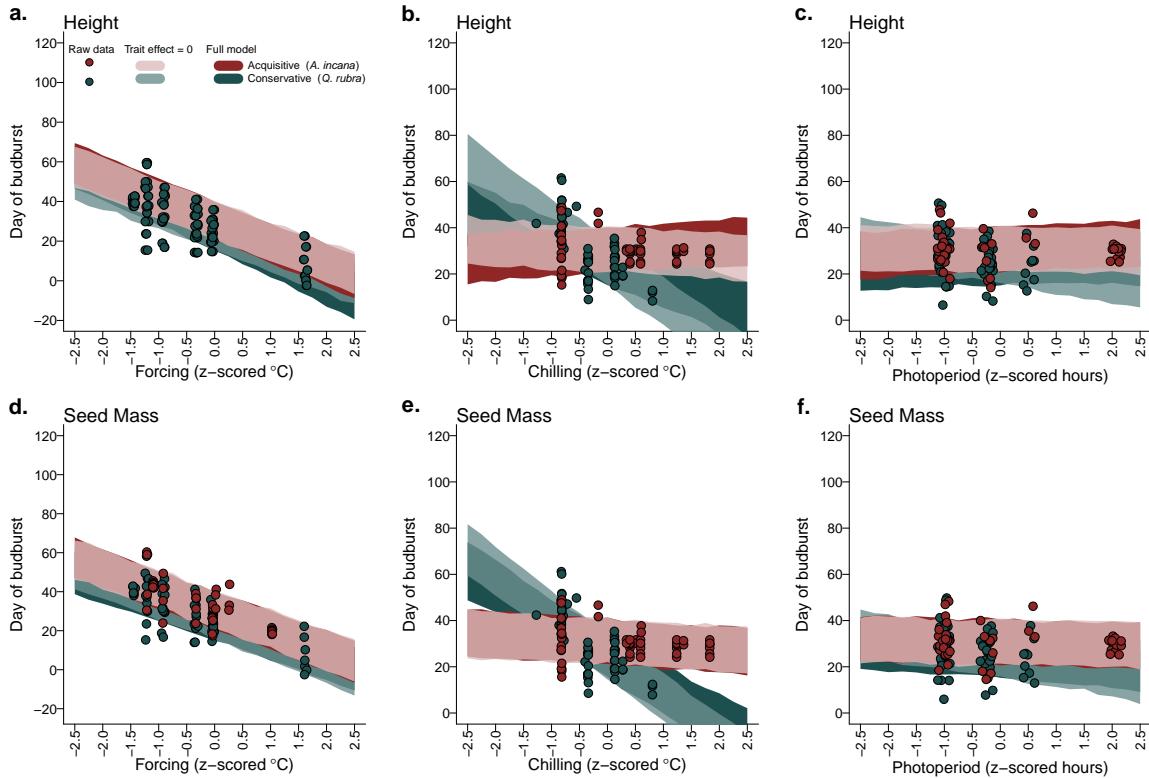


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with 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.

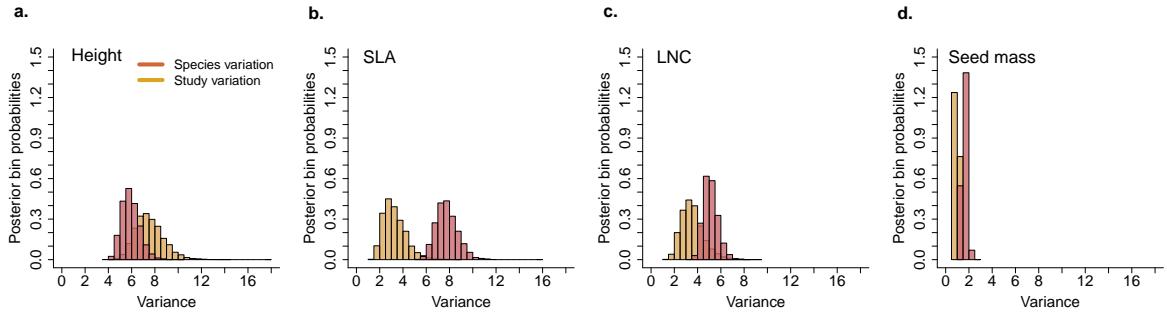


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf area, **c**, leaf 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.