

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 **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 **tree** traits to test the relationships between traits and cues for tree budburst (forcing, chilling, and photoperiod).

¹⁸ 3. We found that **earlier budbursting species are shorter with denser, lower nitrogen leaves, while later-active species were taller with high 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.

²² 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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²⁶ Key Words: Leafout, spring phenology, traits, trees, climate change, forest communities

²⁷ **Introduction**

²⁸ The timing of life history events—phenology—can shape both ecosystem services and community
²⁹ dynamics. Spring phenology, for example, defines the start and overall length of the growing season—
³⁰ shaping forest carbon storage and species interactions (Beard *et al.*, 2019; Cleland *et al.*, 2007; Gu
³¹ *et al.*, 2022). Shifts in phenology with climate change across systems (Menzel *et al.*, 2006; Vitasse
³² *et al.*, 2021) have thus led to growing concerns over their possible impacts.

³³

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

⁴³

⁴⁴ At the ultimate level, plant phenologies may vary due to changing pressures across the growing sea-
⁴⁵ son. Species that start growth early often risk high tissue loss—due to frost damage (Augspurger,
⁴⁶ 2009; Sakai & Larcher, 1987) or high herbivore apprenency (Wainwright *et al.*, 2012)—but benefit from
⁴⁷ higher resource availability (Hufkens *et al.*, 2012; Rathcke & Lacey, 1985). In contrast, **later active**
⁴⁸ **species** face greater biotic pressures, especially from high competition for resources (Lopez *et al.*, 2008;
⁴⁹ Wolkovich & Ettinger, 2014). This variation in early to late season growth may mirror the stressors
⁵⁰ from early to late successional communities, and may similarly shape phenology (Laube *et al.*, 2014).

⁵¹

⁵² Different pressures could shape a number of species attributes related to their growth strategies, in-
⁵³ cluding phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced
⁵⁴ if damaged (Reich *et al.*, 1999), while species with later phenology may benefit from investing in tis-
⁵⁵ sues that infer greater resource retention (Gorné *et al.*, 2020). Differences in traits, and trade-offs in
⁵⁶ allocation of resources to growth and tissue quality, can be related to a broader framework of species
⁵⁷ growth strategies and functional traits (Wolkovich & Ettinger, 2014) (Fig 1), where species range from
⁵⁸ acquisitive (fast) to more conservative (slow) growth (Chave *et al.*, 2009; Wright *et al.*, 2004).

⁵⁹

⁶⁰ Globally, gradients from acquisitive to conservative strategies appear common, and form the foun-

dation of the leaf economic and the wood economic spectra (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004), but they can make limited predictions of trait variability (Violle *et al.*, 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving the relationships between broader trait syndromes and phenology largely unknown. Understanding these relationships is critical to forecasting community dynamics and responses to climate change. To the best of our knowledge, studies have generally only examined the relationship between traits and phenology for a single or limited number of sites (as reviewed by Wolkovich & Cleland (2014) and Wolkovich & Donahue (2021), but see Sporbert *et al.* (2022) and ?) where the problem of proximate drivers causing phenological variation can be more easily ignored. Adding phenology to broader trait frameworks becomes more complex when high levels of variation occurs across large spatial and temporal ranges.

72

73 Consistently defining early to late phenology is possible using the underlying cues that predict gradients
74 in phenology, (Chuine & Cour, 1999; Flynn & Wolkovich, 2018; Harrington & Gould, 2015). For many
75 plants, early species generally have responses that are small in magnitude to all three major cues of
76 spring leafout: warm spring temperatures (forcing), cool winter temperatures (chilling) and daylength
77 (photoperiod). In contrast, later species have larger responses to chilling and/or photoperiod (Flynn
78 & Wolkovich, 2018; Laube *et al.*, 2014), and likely larger forcing responses.

79

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

92

93 To test our predicted relationships between budburst responses to environmental cues and common
94 functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases—
95 BIEN (Maitner *et al.*, 2018) and TRY (Kattge *et al.*, 2020)—with budburst data from the OSPREE

96 database of controlled environment studies (Ettinger *et al.*, 2020). We developed a hierarchical
97 Bayesian joint model that predicts phenological responses to forcing, chilling and photoperiod treat-
98 ments based on species-level trait values, while allowing additional variation due to species. This
99 approach takes a step towards predicting variation via species traits instead of species identity (when
100 traits explain a significant portion of the variation, species identity will explain only a small amount),
101 which could help forecast species phenological responses based on trait values alone.

102

103 Methods

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

109

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

112

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

120

121 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020; Maitner
122 *et al.*, 2018), both of which are large trait databases that include plant trait data across many individ-
123 uals, species, and studies (Table S1Bibliographic information for trait data sources from both BIEN
124 and Try trait databases. Datasets without references or incomplete references are denoted below as
125 ‘unreferenced’.table.caption.5). We obtained data from both databases on 5 December, 2018, and re-
126 quested 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 S1Bibliographic information for trait data sources from
136 both BIEN and Try trait databases. Datasets without references or incomplete references are denoted
137 below as 'unreferenced'.table.caption.5). We also removed data that was duplicated in both the TRY
138 and BIEN datasets ($n = 434905$).

139

140 For our analysis, we only include species for which we had a complete trait profile (i.e., all traits mea-
141 sured for all species). We initially considered six commonly measured traits—SLA, leaf dry matter
142 content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species had
143 at least one trait measurement for each trait. We then used a principle component analysis (PCA) to
144 understand trait correlations and adjusted which traits we included. The PCA of the six initial traits
145 identified high correlations between SLA and LDMC, and between height and SSD. The first principal
146 component explained 32% of variation while the second explained 24.2% of the variation (Fig. S1A
147 projection of tree traits across the first and second principle component axis. Arrows represent the
148 direction of vectors for six functional traits. Points represent the 26 species for which complete trait
149 data was availablefigure.caption.2). By excluding one trait from each of these highly correlated trait
150 pairs (specifically LDMC and SSD) we increased the number of species in our dataset from the 26
151 species with six traits, to 37 species for which we had complete datasets for four traits. The data for
152 these 37 species were from 24 unique studies (samples sizes: height $n = 47781$, seed mass $n = 281$,
153 LNC $n = 3853$, SLA $n = 7656$). We subsampled height measurements to reduce the influence of the
154 13 most frequently measured tree species on our height model. Since these 13 species were measured
155 19 times more frequently than other species, we randomly sampled 3000 height measurements for each
156 species.

157

158 Joint model of trait and phenology

159 To understand connections between phenology and species traits, we developed a joint model for
160 each trait: height, SLA, LNC, and seed mass. Our model is a joint model insofar as it involves two
161 sub-models—one that models trait observations and a second that uses shared latent processes to

¹⁶² model phenological observations. In particular, we assume that trait values are the result of multiple
¹⁶³ sources of variation, including species and study-level variation, that combine into one observed trait
¹⁶⁴ value (trait sub-model). This trait value (α_{trait}) has a separate interaction with the environmental
¹⁶⁵ cues (forcing, chilling, and photoperiod) that determines phenology—specifically the day of year of
¹⁶⁶ budburst (phenology sub-model). Below we describe the two sub-models, noting which parameters are
¹⁶⁷ shared across sub-models and which are independent.

¹⁶⁸ Trait sub-model

¹⁶⁹ Our trait sub-model describes the processes that determine trait observations for 1 to n species across
¹⁷⁰ each of the 1 to m studies in our trait dataset. We use hierarchical modeling to partition trait values
¹⁷¹ by measurement error (σ_m^2), species identity ($\alpha_{\text{species}_i}$), and study (α_{study_j}). In particular, we assume
¹⁷² that a trait observation for species i from study j , $Y_{\text{trait}_{i,j}}$, has the following normal distribution:

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

¹⁷³ with

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

¹⁷⁴ where $\alpha_{\text{species}_i}$ and α_{study_j} are elements of the normal random vectors:

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

$$(4)$$

¹⁷⁵ The latent parameter or overall mean trait value, $\alpha_{\text{grand trait}}$ represents a trait value that is independent
¹⁷⁶ of the species ($\alpha_{\text{species},i}$) and study-level ($\alpha_{\text{study},j}$) offsets from that trait value. The σ_m^2 parameter
¹⁷⁷ is the measurement error, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and study-level variances in trait
¹⁷⁸ values. Of these parameters, the α_{trait} are shared by the phenology sub-model.

¹⁷⁹ Phenology sub-model

¹⁸⁰ Our phenology sub-model describes the processes that determine the relationships between traits and
¹⁸¹ environment cues and their effects on phenological observations for 1 to n species, specifically the
¹⁸² timing (day of year) of budburst from the updated OSPREE dataset. We assume that an observation

183 of budburst for species k under g treatments levels of chilling, forcing, and photoperiod (c_g, f_g, p_g) ,
 184 parameter $Y_{\text{pheno}_{k,g}}$ representing the observed day of budburst (which we z -scored to allow direct
 185 comparison of cues) has the following normal distribution:

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

186 with

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

187 and

$$\beta_{\text{chilling}_k} = \alpha_{\text{chilling},k} + \beta_{\text{trait.chilling}} \cdot \alpha_{\text{trait},k} \quad (7)$$

$$\beta_{\text{forcing}_k} = \alpha_{\text{forcing},k} + \beta_{\text{trait.forcing}} \cdot \alpha_{\text{trait},k}$$

$$\beta_{\text{photoperiod}_k} = \alpha_{\text{photoperiod},k} + \beta_{\text{trait.photoperiod}} \cdot \alpha_{\text{trait},k}$$

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

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

$$\boldsymbol{\alpha}_{\text{chilling}} = \{\alpha_{\text{chilling}_1}, \dots, \alpha_{\text{chilling}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chilling}} \sim \mathcal{N}(\mu_{\text{chilling}}, \sigma_{\text{chilling}}^2)$$

$$\boldsymbol{\alpha}_{\text{forcing}} = \{\alpha_{\text{forcing}_1}, \dots, \alpha_{\text{forcing}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{forcing}} \sim \mathcal{N}(\mu_{\text{forcing}}, \sigma_{\text{forcing}}^2)$$

$$\boldsymbol{\alpha}_{\text{photoperiod}} = \{\alpha_{\text{photoperiod}_1}, \dots, \alpha_{\text{photoperiod}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photoperiod}} \sim \mathcal{N}(\mu_{\text{photoperiod}}, \sigma_{\text{photoperiod}}^2)$$

189 The model partitions day of budburst for species (k) as combination of their overall mean day of
 190 budburst without the influence of chilling, forcing, or photoperiod treatments ($\alpha_{\text{pheno},k}$, normally
 191 distributed with a mean of μ_{pheno} and variance σ_{pheno}^2) combined with the effects of treatments both
 192 dependent and independent of trait values.

193 The parameters $\alpha_{\text{chilling},k}$, $\alpha_{\text{forcing},k}$, and $\alpha_{\text{photoperiod},k}$ represent the trait-independent responses of
 194 species k to chilling, forcing, and photoperiod treatments respectively, each with an associated mean
 195 (μ_{chilling} , μ_{forcing} , $\mu_{\text{photoperiod}}$) and variance ($\sigma_{\text{chilling}}^2$, $\sigma_{\text{forcing}}^2$, $\sigma_{\text{photoperiod}}^2$) across species. The shared
 196 parameter between the trait and phenology sub-model, $\alpha_{\text{trait},k}$, represents the effect of the species trait
 197 value on its responses to chilling ($\beta_{\text{trait.chilling}}$), forcing ($\beta_{\text{trait.forcing}}$), and photoperiod ($\beta_{\text{trait.photoperiod}}$).
 198 Finally, σ_d^2 is the variance arising from measurement error.

199

200 We chose weakly informative priors, and validated them using a series of prior predictive checks.
 201 The model was coded in the Stan programming language, fit using the rstan package (v. 3.3.6)

(Stan Development Team, 2018), with 1,000 iterations per chain across 4 chains (4,000 total sampling iterations), and all models met basic diagnostic checks, including no divergences, high effective sample size (n_{eff}), and \hat{R} close to 1, fitting the data well (Fig S2Comparisons of estimated model fits and raw data from joint models of trait effects on budburst phenological cues for 37 species of woody deciduous plants. Four functional traits – a. height, b. SLA, c. seed mass, and d. LNC – were modeled individually, with the calculated trait value being used to jointly model species responses to standardized chilling, forcing, and photoperiod cues. Model posteriors are shown in black, with the thicker line depicting the 66% interval and the thinner black line the 97% interval. Overall species level model posterior distributions were well aligned with the raw data, shown in red, and the species level means from the raw data, denoted as a purple stars.figure.caption.3). Here we present our model estimates as the means and 90% posterior uncertainty intervals.

Results

Across traits, height, SLA, and LNC strongly related to chilling ($\beta_{chilling_k}$), forcing ($\beta_{forcing_k}$), and photoperiod ($\beta_{photoperiod_k}$) treatments, Fig 2 a-f & j-l), but the direction of these relationships only showed consistent trends for LNC (Fig. 2 j-l). As we predicted, height was negatively related to chilling ($\beta_{chilling_k}$) and photoperiod ($\beta_{photoperiod_k}$), with taller species having larger responses to cues (-1 m per standardized chilling; 90% uncertainty interval (UI): -0.2, -0.2 and -0.2 m per standardized photoperiod; 90% UI: 0, 0.0, Fig 2 a-c, Table S2Summary of model estimates using measurements of tree height for our 37 focal species ($n = 42781$)table.caption.6). As illustrated for one characteristically acquisitive species, *Alnus incana*, and one characteristically conservative species, *Quercus rubra* (Fig S3We expected species with traits associated with acquisitive (e.g., low specific leaf area, SLA, and leaf nitrogen content, LNC) versus conservative (e.g., high SLA and LNC) growth strategies would have different budburst responses to phenological cues. Our joint model allows traits of species to influence their responses to cues. We show an example here with an acquisitive species, *Alnus incana* shown in red, and a conservative species, *Quercus rubra* shown in blue, for SLA (**a-c**) and LNC (**d-f**). Our joint model estimated later budburst due to trait effects for both SLA and LNC in response to forcing (**a, d,**) and chilling (**b, e**) and for LNC in response to photoperiod (**f**). Only in response to photoperiod did we estimate the effect of SLA to lead to slightly earlier budburst with longer photoperiods (**c**). The coloured bands represent the 50% uncertainty intervals of the model estimates and points individual trait measurements.figure.caption.4), the cue relationships with height led to generally later budburst relative to estimates without trait effects ($\mu_{k,g}$; Fig. 3). In contrast, seed mass had the smallest responses, with no relationship between seed mass and any cue (Fig. 2 g-i, Fig 3 d-f, & Table S3Summary of model estimates using measurements of seed mass data for our 37 focal species ($n =$

281).table.caption.7).

236

237 Of our leaf traits, we found that species SLA related to photoperiod ($\beta_{\text{photoperiod}_k}$, -0.2 mm²/mg per
238 standardized photoperiod; 90% UI: 0, 0.0, Fig. 2 f, Table S4Summary of model estimates using mea-
239 surements of specific leaf area for our 37 focal species ($n = 7656$).table.caption.8), but did not strongly
240 predict responses to chilling ($\beta_{\text{chilling}_k}$) or forcing treatments (β_{forcing_k} , Fig. 2 d and e). Thus, species
241 with more acquisitive growth strategies (thin leaves and a lower investment in leaf mass that leads to
242 large SLA values), had larger responses to photoperiod, contrary to our predictions (Fig. 2 f). For
243 LNC, we found that species that produce leaves with high nitrogen content, which relates generally to
244 high photosynthetic rates and acquisitive growth, show smaller responses to cues (Fig. 2 j-l). These
245 findings are in line with our predictions that high LNC species (acquisitive) would be less responsive
246 to chilling (0.7 mg/g per standardized chilling; 90% UI: 1.1, 1.1, Table S5Summary of model esti-
247 mates using measurements of leaf nitrogen content for our 37 focal species ($n = 3853$).table.caption.9),
248 but we also found high LNC species to be less responsive to photoperiod (0.3 mg/g per standardized
249 photoperiod; 90% UI: 0.6, 0.6) and to forcing (0.5 mg/g per standardized forcing; 90% UI: 0.8, 0.8,
250 Fig 2 j-l & Fig S3We expected species with traits associated with acquisitive (e.g., low specific leaf
251 area, SLA, and leaf nitrogen content, LNC) versus conservative (e.g., high SLA and LNC) growth
252 strategies would have different budburst responses to phenological cues. Our joint model allows traits
253 of species to influence their responses to cues. We show an example here with an acquisitive species,
254 *Alnus incana* shown in red, and a conservative species, *Quercus rubra* shown in blue, for SLA (**a-c**)
255 and LNC (**d-f**). Our joint model estimated later budburst due to trait effects for both SLA and LNC
256 in response to forcing (**a, d**) and chilling (**b, e**) and for LNC in response to photoperiod (**f**). Only
257 in response to photoperiod did we estimate the effect of SLA to lead to slightly earlier budburst with
258 longer photoperiods (**c**). The coloured bands represent the 50% uncertainty intervals of the model
259 estimates and points individual trait measurements.figure.caption.4 d-f).

260

261 We found species-level variation across traits (σ_{trait}^2) were comparable to or greater than variation
262 across studies (σ_{study}^2 , Fig 4). The magnitude of study-level variation (σ_{study}^2) that we found, however,
263 suggests that models using large trait databases that fail to separate out study from species-level vari-
264 ation (σ_{trait}^2) may poorly estimate species traits. Variation across studies was greatest for height (with
265 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
266 was less than that of the species-level variation, with estimates of 1 mg for study-level variation versus
267 1.6 mg for species-level variation in seed mass and estimates of 3.6 mg g⁻¹ for study-level variation
268 and 5.1 mg g⁻¹ for the species-level variation in LNC (Fig 4c and d). At the lowest end, study-level
269 variation in SLA was approximately half the value of the species-level variation (3.3 mm² mg⁻¹ versus

270 7.8 mm² mg⁻¹ for σ_{study}^2 and σ_{trait}^2 , respectively, Fig 4b).

271

272 Discussion

273 We found species traits influenced the timing of budburst in response to the three primary cues of
274 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or
275 later phenology following well-established gradients in growth strategies predicted by functional trait
276 frameworks (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby & Wright, 2006; Wright
277 *et al.*, 2004): early species tended to have traits associated with fast and acquisitive strategies while
278 later species had traits associated with conservative, slower strategies. We found the largest bud-
279 burst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and
280 height all showing large responses across our three cues. In contrast, our one reproductive trait—seed
281 mass—showed a smaller response. Our results provide a major step forward in integrating phenol-
282 ogy into broader trait syndromes that shape species growth strategies, and support previous findings
283 from more local scales that found strong relationships between height and species phenology (Segrestin
284 *et al.*, 2020; Sporbert *et al.*, 2022; Sun & Frelich, 2011). Our more global analysis is also in agreement
285 with previous studies of plant phenological events, in which no relation is found between phenology
286 and seed mass in woody plants (??).

287

288 Effects of phenology-trait relationships on community assembly

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

301

302 The traits with cue responses that deviated from our expectations also offer novel insights into the
303 tradeoffs between traits and environmental cues. All of our traits are associated with multiple aspects
304 of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our
305 predictions, we found large responses to forcing for short trees, which could prevent frost damage or
306 xylem cavitation under a late spring frost (Clements *et al.*, 1972; Marquis *et al.*, 2020) and influence
307 annual cambial meristem growth (Lenz *et al.*, 2016). Similarly, the lack of a response to chilling or
308 forcing by high SLA individuals could be driven by other trait attributes and environmental cues—
309 selecting for species relative growth rates or leaf longevity—and not photosynthetic potential (Reich,
310 2014; Westoby, 1998). These findings highlight the complexity of determining the drivers of species
311 trait profiles, and further our understanding of how traits affect community dynamics under variable
312 environments.

313

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

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

320

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

328

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

³³⁵ larger chilling and photoperiod responses) could face greater abiotic and biotic stress (Guy, 2014).

³³⁶

³³⁷ Our results could further help identify which species are most likely to be negatively impacted under
³³⁸ future climates, and develop better strategies for climate change mitigation and conservation. Species
³³⁹ that fail to advance phenologically with warming might experience more competition (Alexander &
³⁴⁰ Levine, 2019; Carter *et al.*, 2018), as species that begin growth increasingly earlier with warming have
³⁴¹ more time to deplete resources. In addition to altering the timing and interactions between species
³⁴² within a season, species trait syndromes have the potential to further redefine the environmental condi-
³⁴³ tions under which growth occurs, and as a result, shape community assembly and productivity within
³⁴⁴ ecological communities. By identifying the species most vulnerable to climate change impacts, we can
³⁴⁵ develop more effective management practices that prevent the loss of critical ecosystem services and
³⁴⁶ preserve community diversity under future conditions.

³⁴⁷

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³⁵¹ Author Contributions Statement

³⁵² DL, FAMJ, GL, MG, DS, and EMW planned and designed the study. All authors conducted the
³⁵³ literature review and cleaned the database. DL, FAMJ, GL, and EMW performed the data analysis
³⁵⁴ and contributed code. DL, FAMJ, and GL created the figures. DL and EMW wrote the initial draft
³⁵⁵ and all authors reviewed and revised the manuscript.

³⁵⁶ Competing Interests Statement

³⁵⁷ The authors declare no competing interests.

³⁵⁸ Data availability statement

³⁵⁹ The phenological data used for this manuscript is a subset of the existing OSPREE dataset (doi:10.5063/F1CZ35KB)
³⁶⁰ and the trait data a subset of the TRY database (doi:10.1111/gcb.14904) and the BIEN database
³⁶¹ (doi: 10.1111/2041-210X.1286).

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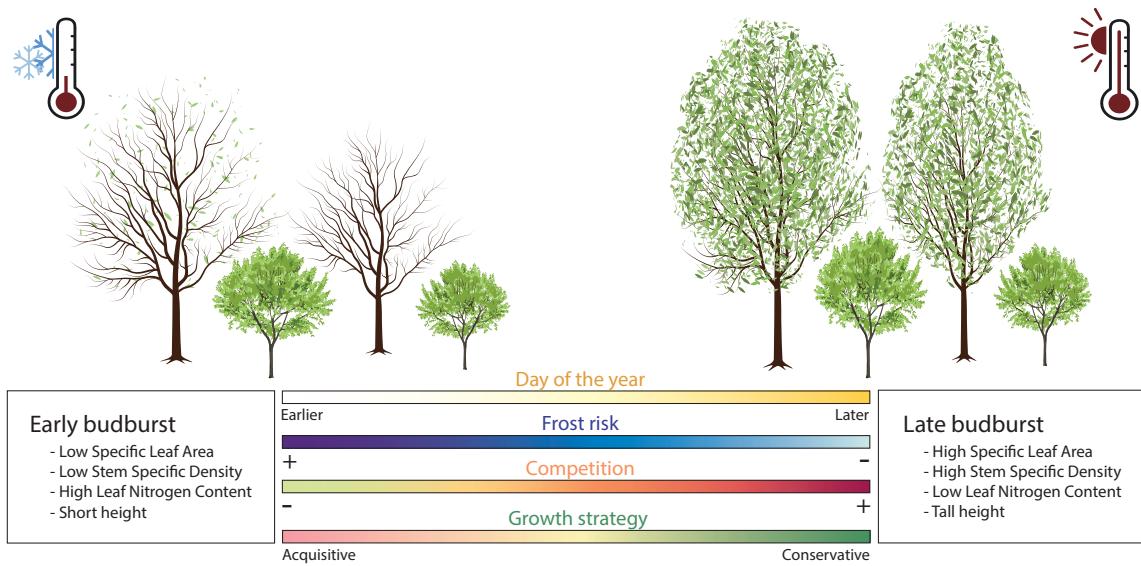


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost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

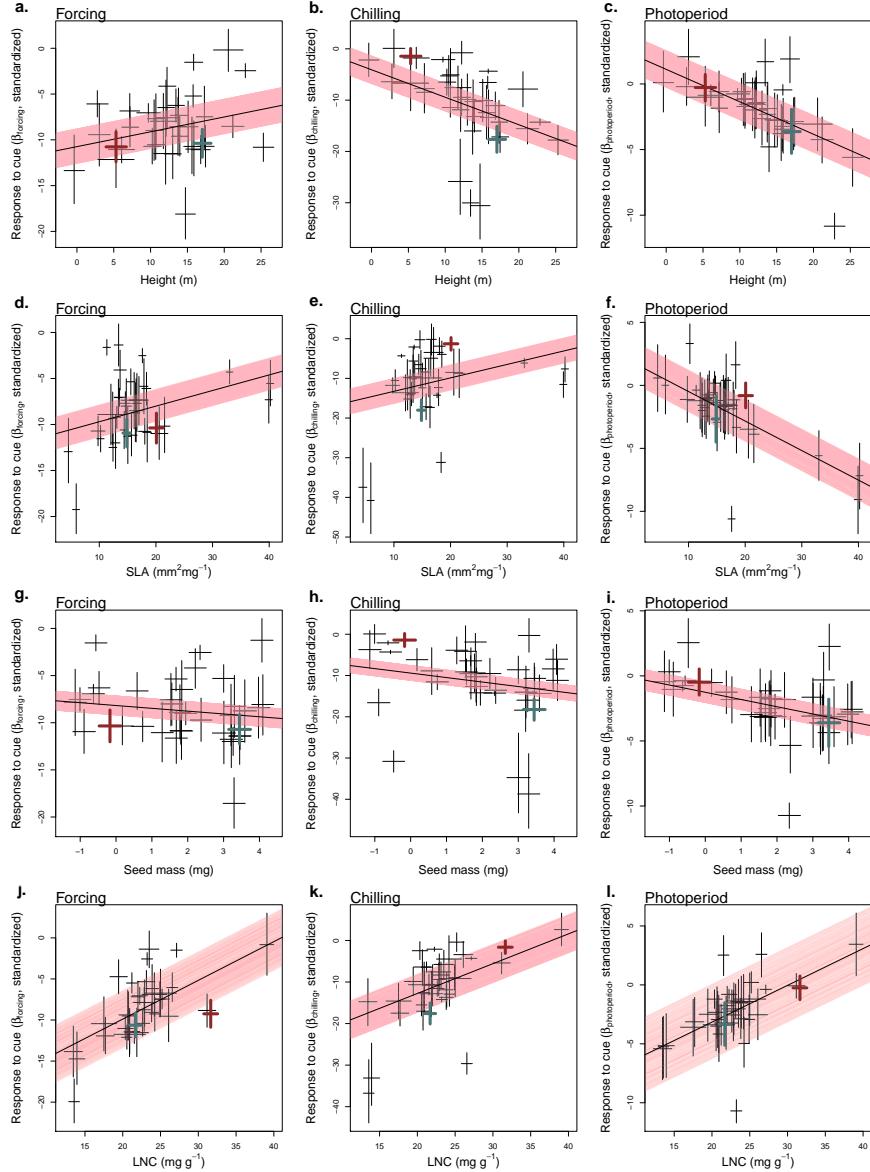


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third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

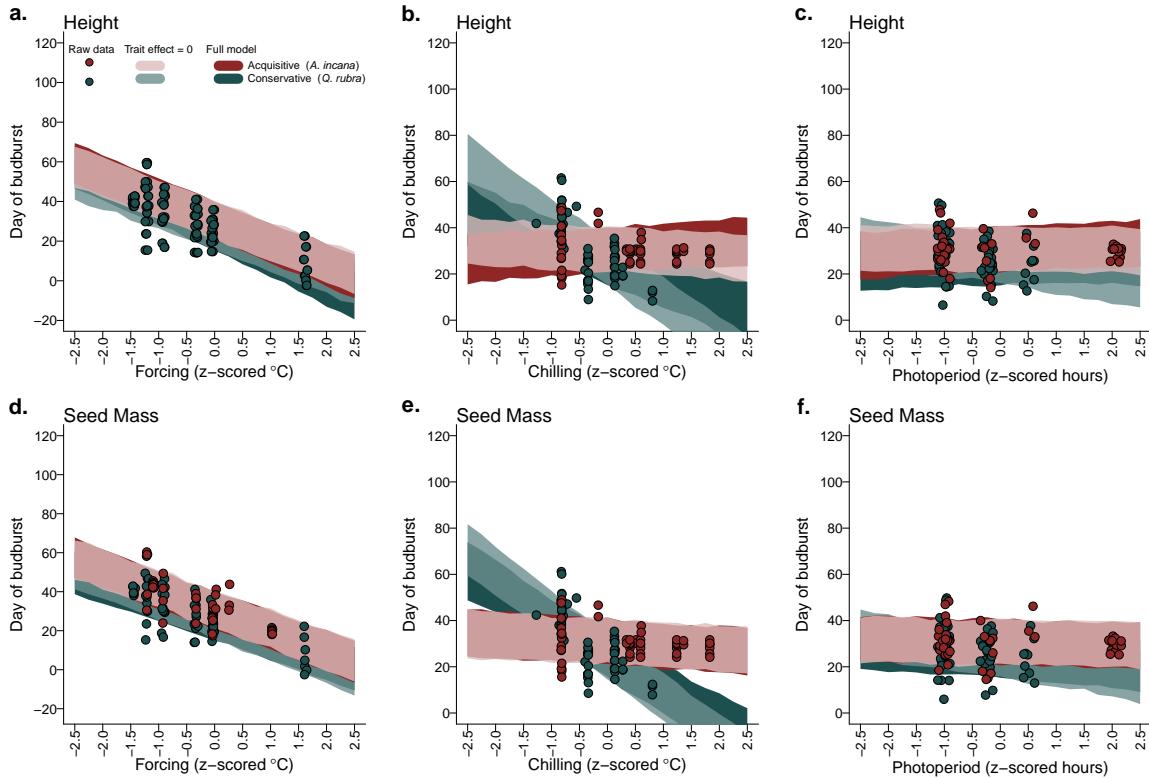


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with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

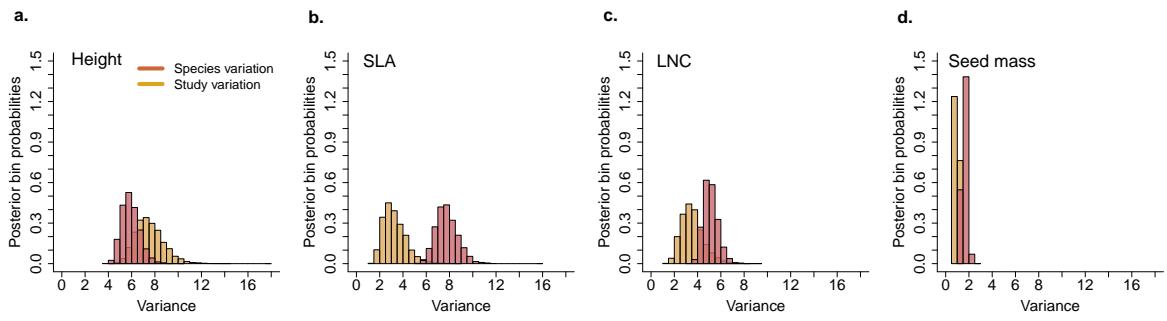


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf area, **c**, leaf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