

¹ Budburst timing within a functional trait framework

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²⁹ Running title: Budburst responses associated with traits

³¹ **Summary**

³² Species-level variation in phenology—the timing of recurring life history events—can vary seasonally
³³ with changes in climatic risk, light, and nutrients. This favours acquisitive growth strategies early in
³⁴ the spring season and conservative growth strategies under the more climatically benign, but compet-
³⁵ itive, environment later in the season. This framework infers suites of traits that may co-vary with
³⁶ phenologies, but high variability across environments makes this challenging to test. Here, we combine
³⁷ a new joint modeling approach to accommodate this variability with global data on plant traits and
³⁸ budburst responses in controlled environment experiments. We find that earlier species—which are
³⁹ generally most responsive to anthropogenic warming—are generally shorter with denser, lower nitro-
⁴⁰ gen leaves. These results suggest warming may reshape the trait structure of plant communities, and
⁴¹ could help improve predictions of how growth strategies and phenologies together shift with continued
⁴² climate change.

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⁴⁴ Key Words: Budburst, spring phenology, traits, trees, climate change, forest communities

⁴⁵ **Introduction**

⁴⁶ The timing of life history events—phenology—can shape both ecosystem services and community
⁴⁷ dynamics. Spring phenology, for example, defines the start and overall length of the growing season—
⁴⁸ shaping forest carbon storage and species interactions (Beard et al., 2019; Cleland et al., 2007; Gu
⁴⁹ et al., 2022). Shifts in phenology with climate change across systems (Menzel et al., 2006; Vitasse
⁵⁰ et al., 2021) have thus led to growing concerns over their possible impacts.

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⁵² Predicting these changes requires understanding the drivers of phenology both at a proximate scale—
⁵³ the environmental triggers of phenology each year, such as temperature and daylength—and at an
⁵⁴ ultimate scale, where long-term environmental pressures may select for different phenologies across
⁵⁵ species, (e.g., certain species are early or late relative to other species each year Ovaskainen et al.,
⁵⁶ 2013; Wolkovich and Donahue, 2021). At the proximate level, environmental conditions throughout
⁵⁷ the winter and spring cause species to start growth at different times. Similar environmental conditions
⁵⁸ appear to trigger spring phenological events across taxa, including the start of growth in woody plants
⁵⁹ each year (Flynn and Wolkovich, 2018; Laube et al., 2014), the timing of egg laying in birds (Crick
⁶⁰ et al., 1997; D’Alba et al., 2010), and the advance of spawning in amphibians (Kusano and Inoue,
⁶¹ 2008; Tryjanowski et al., 2003), but current work provides limited insights into the drivers of species
⁶² differences (Chuine et al., 2016; Flynn and Wolkovich, 2018; Laube et al., 2014).

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⁶⁴ At the ultimate level, species phenologies may vary due to changing pressures across the growing sea-
⁶⁵ son. Species that start growth early often risk high tissue loss—due to frost damage (Augspurger,
⁶⁶ 2009; Sakai and Larcher, 1987) or high herbivore appärenzy (Wainwright et al., 2012)—but benefit
⁶⁷ from higher resource availability (Hufkens et al., 2012; Rathcke and Lacey, 1985). In contrast, later
⁶⁸ species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008;
⁶⁹ Wolkovich and Ettinger, 2014). For plants, this variation in early to late season growth may mirror

70 the stressors from early to late successional communities, and may similarly shape phenology (Laube
71 et al., 2014).

72
73 Different pressures could shape a number of species attributes related to their growth strategies, in-
74 cluding phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced
75 if damaged (Reich et al., 1999), while species with later phenology may benefit from investing in tis-
76 sues that infer greater resource retention (Gorné et al., 2020). Differences in traits, and trade-offs in
77 allocation of resources to growth and tissue quality, can be related to a broader framework of species
78 growth strategies and functional traits (Wolkovich and Ettinger, 2014) (Fig 1), where species range
79 from acquisitive (fast) to more conservative (slow) growth (Chave et al., 2009; Wright et al., 2004).

80
81 Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation
82 of the leaf economic and the wood economic spectra (Chave et al., 2009; Díaz et al., 2016; Westoby,
83 1998; Westoby and Wright, 2006; Wright et al., 2004), but they can make limited predictions of trait
84 variability (Violle et al., 2012). As a result, highly variable traits like phenology are often excluded
85 from trait studies, leaving the relationships between broader trait syndromes and phenology largely un-
86 known. Understanding these relationships is critical to forecasting community dynamics and responses
87 to climate change. To date, studies have generally only examined the relationship between traits and
88 phenology within a single site (as (reviewed by Wolkovich and Cleland Wolkovich and Cleland, 2014)
89 and (Wolkovich and Donahue Wolkovich and Donahue, 2021)) where the problem of proximate drivers
90 causing phenological variation can be more easily ignored. Adding phenology to broader trait frame-
91 works becomes more complex when high levels of variation occurs across large spatial and temporal
92 ranges.

93
94 Consistently defining early to late phenology is possible using the underlying cues that predict gradi-
95 ents in phenology, (which do not generally vary strongly across space and time Chuine and Cour, 1999;
96 Flynn and Wolkovich, 2018; Harrington and Gould, 2015). For many plants, early species generally
97 have responses that are small in magnitude to all three major cues of spring leafout: warm spring
98 temperatures (forcing), cool winter temperatures (chilling) and daylength (photoperiod). In contrast,
99 later species have larger responses to chilling and/or photoperiod (Flynn and Wolkovich, 2018; Laube
100 et al., 2014), and likely larger forcing responses.

101
102 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-
103 nology into functional trait research. In addition to how well we understand the environmental cues
104 that trigger early versus late leafout, spring in many forests includes strong gradients in potential se-
105 lective environments (Fig 1). Based on trade-offs between early and late spring phenologies, we predict
106 acquisitive species to be shorter, with leaf traits favourable to higher light availability and tolerance
107 to late spring frost (high specific leaf area, SLA, and leaf nitrogen content, LNC; Fig 1). Such species
108 should exhibit early phenology, with small cue responses. Canopy species that budburst later via larger
109 cue responses, when competition for soil resources is greater, would then have traits associated with
110 conservative growth—taller with denser wood (Laughlin et al., 2010)—with leaf traits suited for more

variable light (low SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative continuum, as acquisitive species produce smaller seeds and conservative species produce larger—better provisioned—seeds (Fig 1).

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

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125 Methods

We merged three major databases for our analysis. We gathered phenological data from the OSPREE database (Ettinger et al., 2020), which contains budburst data for woody, species from experiments of forcing, chilling and photoperiod. We updated this database since its initial publication, the methods of which are discussed by (Morales-Castilla et al. Morales-Castilla et al., 2024). We gathered trait data from TRY and BIEN (v. 4.0) (Kattge et al., 2020; Maitner et al., 2018), both of which are large trait databases that include plant trait data across many individuals, species, and studies (Table S1). We obtained data from both databases on 5 December, 2018, with an updated version of the TRY data obtained 10 April, 2019. We focused our search for trait data on the subset of 234 OSPREE species used in (Morales-Castilla et al. Morales-Castilla et al., 2024). Using the BIEN R package (v. 1.2.5) (Maitner et al., 2018), we downloaded trait data for the 94 species available, for which there were 13 traits. The TRY database included data for 10 traits for 96 of our focal species (Kattge et al., 2020). Given our focus on the phenology of adult trees, we included trait data from adult individuals with a minimum height of 1.38 m. We further removed all data from experiments or from plants growing in non-natural habitats. We also grouped trait values where appropriate, for example categorizing trait values for “SLA”, “SLA with petioles”, and “SLA without petioles” as simply “SLA” in our analysis (see Table S1). Duplicated data in both the TRY and BIEN datasets were also removed ($n = 434905$). Based on our selection criteria, our final dataset included data for 11 traits from 91 of the species also represented in the OSPREE database, with each species differing in the number and types of traits measured.

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For our analysis, we only include species for which we had a complete trait profile (i.e., all traits measured for all species). We initially considered six commonly measured traits—SLA, leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species had at least one trait measurement for each trait. We then used a principle component analysis (PCA) to

understand trait correlations and adjusted which traits we included. A PCA of our six initial traits identified high correlations between SLA and LDMC, and between height and SSD. The first principal component explained 32% of variation while the second explained 24.2% of the variation (Fig. S1). By excluding one trait from each of these highly correlated trait pairs (specifically LDMC and SSD) we increased the number of species in our dataset from the 26 species with six traits, to 37 species for which we had complete datasets for four traits. The data for these 37 species were from 24 unique studies (samples sizes: height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n = 7656$). We subsampled height measurements to reduce the influence of the 13 most frequently measured tree species on our height model. Since these 13 species were measured 19 times more frequently than other species, for each species, we randomly sampled 3000 height measurements.

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161 Joint model of trait and phenology

To understand connections between phenology and species traits, we developed and then parameterized a joint model for each trait: height, SLA, LNC, and seed mass. Our model is a joint model insofar as it involves two types of data—trait observations and phenological observations—that arise from shared latent processes. In particular, we assume that species “true” trait values determine observed trait values across different studies (trait sub-model), and separately, that the same “true” trait values interact with phenological cues (forcing, chilling, and photoperiod) to determine observed phenology, specifically the day of year of budburst (phenology sub-model). Below we describe the two sub-models, noting which parameters are shared across sub-models and which are independent.

170 Trait sub-model

The trait sub-model describes the processes that determine trait observations for 1 to n species across each of the 1 to m studies in our trait dataset (TRY and BIEN data). We use hierarchical modeling to partition trait variation by measurement error, species identity, and study identity. In particular, we assume that a trait observation for species i from study j , $Y_{\text{trait}_{i,j}}$, has the following normal distribution:

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

with

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

where α_{trait_i} and α_{study_j} are elements of the normal random vectors:

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

The latent parameter $\alpha_{\text{grand trait}}$ represents a trait value that is independent of study and species, $\alpha_{\text{species},i}$ and $\alpha_{\text{study},j}$ are species and study-level offsets from that trait value, σ_m^2 is measurement error,

178 and σ_{trait}^2 and σ_{study}^2 represent species and study-level variances in trait values. Of these parameters,
 179 α_{trait} are shared by the phenology sub-model.

180 Phenology sub-model

181 The phenology sub-model describes the processes that determine phenological observations for 1 to
 182 n species, specifically the timing (day of year) of budburst from the updated OSPREE dataset. We
 183 assume that an observation of budburst day for species k under set g of chilling, forcing, and photoperiod
 184 treatments (c_g, f_g, p_g), $Y_{\text{pheno}_{k,g}}$ (which we z -scored to allow direct comparison of cues) has the
 185 following normal distribution:

$$Y_{\text{pheno}_{k,g}} \sim \mathcal{N}(\mu_{k,g}, \sigma_d^2) \quad (4)$$

with

$$\mu_{k,g} = \alpha_{\text{pheno},k} + \beta_{\text{chill}_k} \cdot c_g + \beta_{\text{force}_k} \cdot f_g + \beta_{\text{photo}_k} \cdot p_g \quad (5)$$

and

$$\begin{aligned} \beta_{\text{chill}_k} &= \alpha_{\text{chill},k} + \beta_{\text{trait.chill}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{force}_k} &= \alpha_{\text{force},k} + \beta_{\text{trait.force}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{photo}_k} &= \alpha_{\text{photo},k} + \beta_{\text{trait.photo}} \cdot \alpha_{\text{trait},k} \end{aligned} \quad (6)$$

186 where α_{pheno_k} , α_{chill_k} , α_{force_k} , and α_{photo_k} are elements of the normal random vectors:

$$\begin{aligned} \boldsymbol{\alpha}_{\text{pheno}} &= \{\alpha_{\text{pheno}_1}, \dots, \alpha_{\text{pheno}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \mathcal{N}(\mu_{\text{pheno}}, \sigma_{\text{pheno}}^2) \\ \boldsymbol{\alpha}_{\text{chill}} &= \{\alpha_{\text{chill}_1}, \dots, \alpha_{\text{chill}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chill}} \sim \mathcal{N}(\mu_{\text{chill}}, \sigma_{\text{chill}}^2) \\ \boldsymbol{\alpha}_{\text{force}} &= \{\alpha_{\text{force}_1}, \dots, \alpha_{\text{force}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{force}} \sim \mathcal{N}(\mu_{\text{force}}, \sigma_{\text{force}}^2) \\ \boldsymbol{\alpha}_{\text{photo}} &= \{\alpha_{\text{photo}_1}, \dots, \alpha_{\text{photo}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photo}} \sim \mathcal{N}(\mu_{\text{photo}}, \sigma_{\text{photo}}^2) \end{aligned} \quad (7)$$

187 Parameter $\alpha_{\text{pheno},k}$ represents the day of budburst for species k without the influence of chilling, forcing,
 188 or photoperiod treatments. Average day of budburst (independent of treatments) is μ_{pheno} , and
 189 σ_{pheno}^2 is the variance across species. The parameters $\alpha_{\text{chill},k}$, $\alpha_{\text{force},k}$, and $\alpha_{\text{photo},k}$ represent the trait-
 190 independent responses of species k to chilling, forcing, and photoperiod treatments respectively, each
 191 with an associated mean (μ_{chill} , μ_{force} , μ_{photo}) and variance (σ_{chill}^2 , σ_{force}^2 , σ_{photo}^2) across species. The
 192 effect of the species trait value, $\alpha_{\text{trait},k}$ (parameter shared with trait sub-model above), on its responses
 193 to chilling, forcing, and photoperiod are described by parameters $\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$. Fi-
 194 nally, σ_d^2 is the variance arising from measurement error.

195

196 We chose weakly informative priors, and validated them using a series of prior predictive checks.
 197 The model was coded in the Stan programming language, fit using the rstan package (v. 3.3.6)
 198 (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 S2). 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 (β_{chill_k}), forcing (β_{force_k}), and photoperiod (β_{photo_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 (β_{chill_k}) and photoperiod (β_{photo_k}), with taller species having larger responses to cues (-0.5 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). As illustrated for one characteristically acquisitive species, *Alnus incana*, and one characteristically conservative species, *Quercus rubra* (Fig S3), 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 S3).

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

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

²³⁷ **Discussion**

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

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²⁵³ **Effects of phenology-trait relationships on community assembly**

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

²⁶⁶

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

276 trait profiles, and further our understanding of how traits affect community dynamics under variable
277 environments.

278

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

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

285

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

293

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

301

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

312

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³¹⁵ used in this manuscript.

³¹⁶ **Author Contributions Statement**

³¹⁷ DL, FAMJ, GL, MG, DS, and EMW planned and designed the study. All authors conducted the
³¹⁸ literature review and cleaned the database. DL, FAMJ, GL, and EMW performed the data analysis
³¹⁹ and contributed code. DL, FAMJ, and GL created the figures. DL and EMW wrote the initial draft
³²⁰ and all authors reviewed and revised the manuscript.

³²¹ **Competing Interests Statement**

³²² The authors declare no competing interests.

³²³ **Data availability statement**

³²⁴ The phenological data used for this manuscript is a subset of the existing OSPREE dataset (doi:10.5063/F1CZ35KB)
³²⁵ and the trait data a subset of the TRY database (doi:10.1111/gcb.14904) and the BIEN database
³²⁶ (doi: 10.1111/2041-210X.1286).

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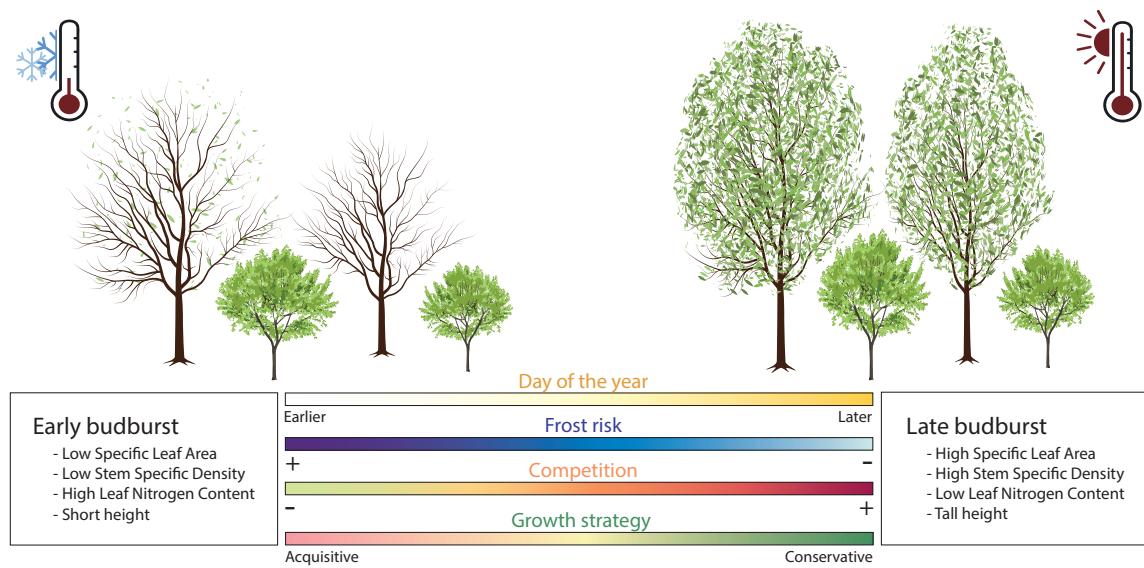


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost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

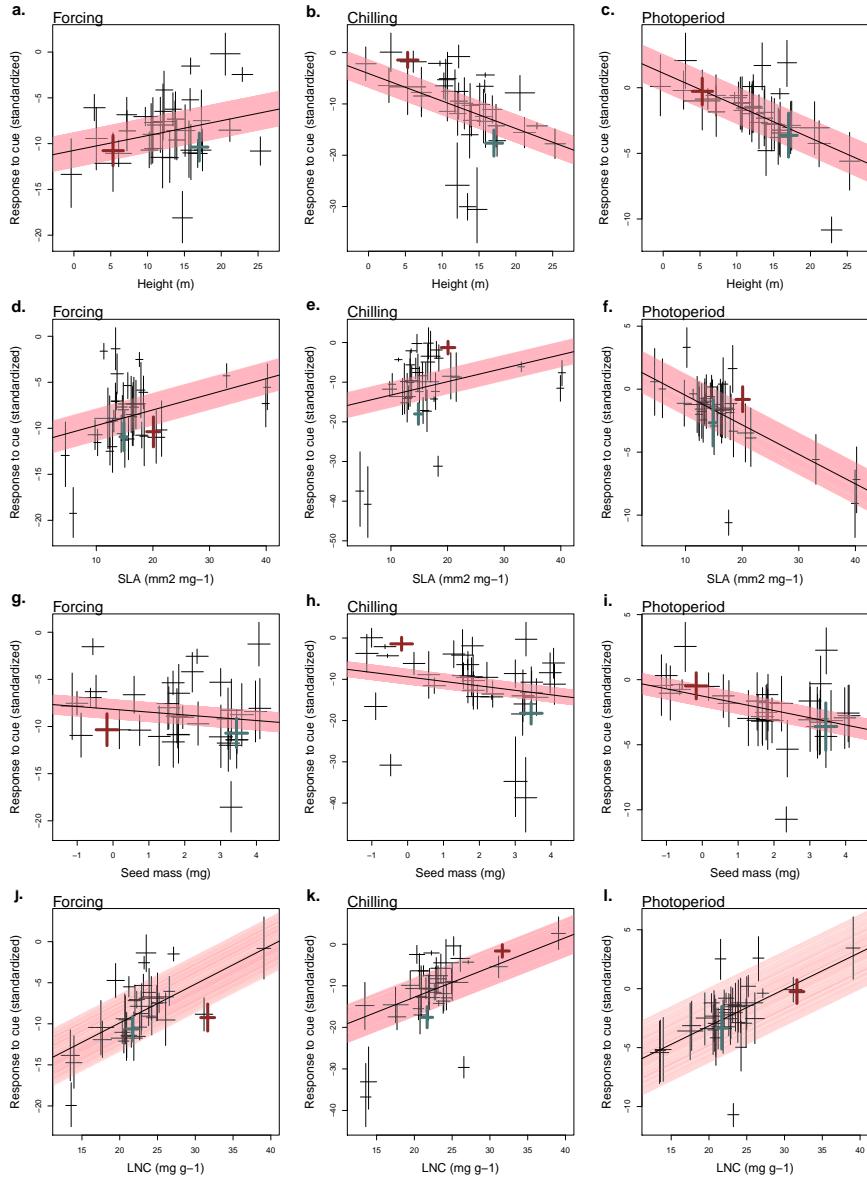


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third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

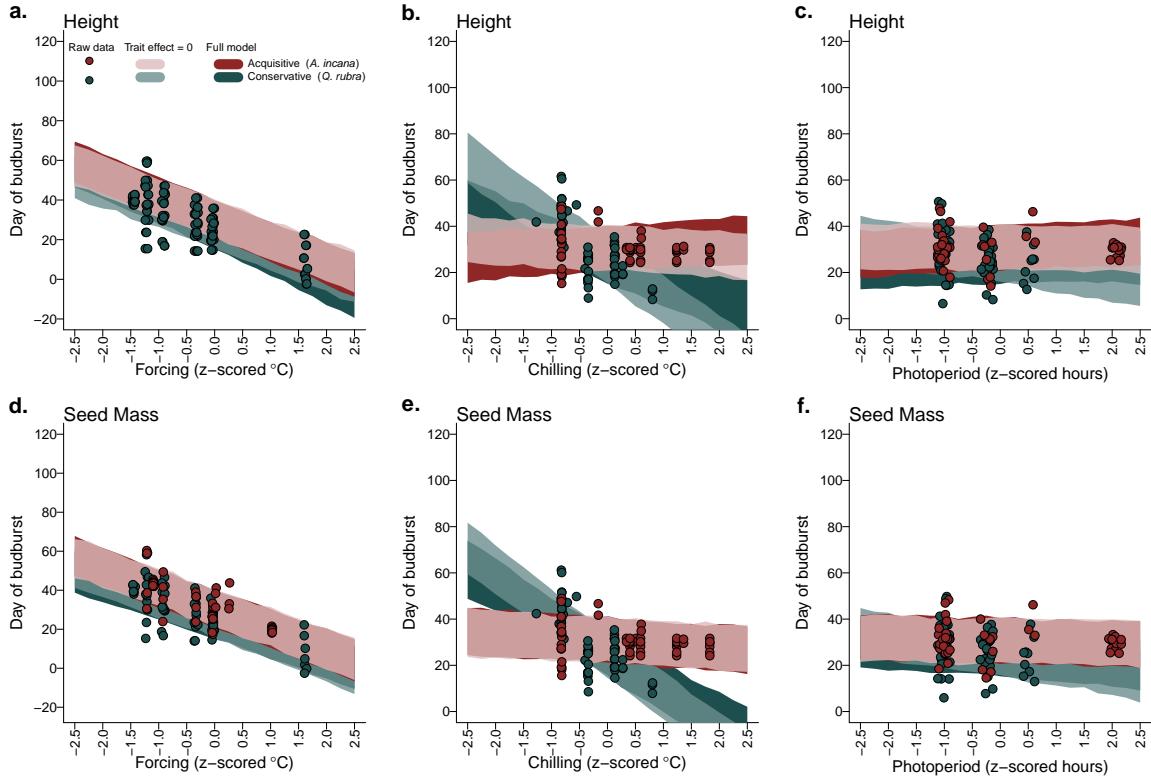


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with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

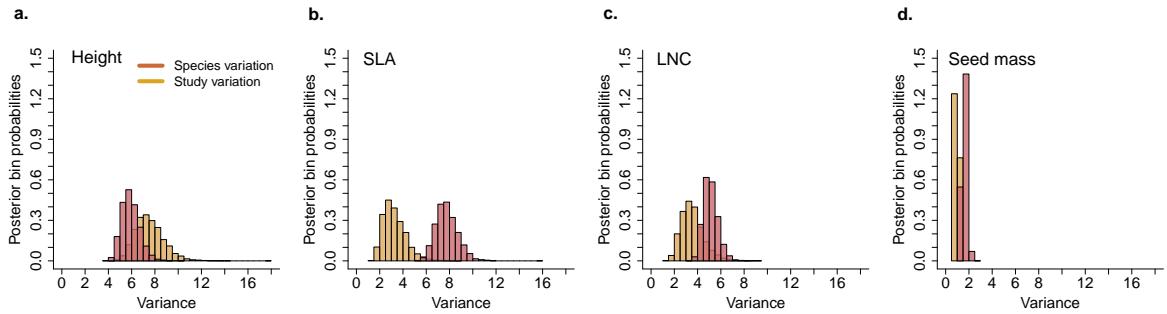


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation, with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf area, **c**, leaf nitrogen content, and **d**, seed mass models all estimated 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.