

¹ Budburst timing within a functional trait framework

²

³ Running title: Budburst responses associated with traits

⁴ **Summary**

- ⁵ 1. Phenology, **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 environmental triggers, **such as temperature**, changes in the 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 cheaper leaves and acquisitive growth strategies, to later when a more benign environment and lower levels of light and nutrients favour conservative growth strategies. This framework predicts a suite of traits that may co-vary with species phenologies, but the high variability in **phenology** across environments has made testing its role within a trait framework challenging.
- ¹⁵ 2. Using a modelling framework that accommodates this variability, with phenological data from a database of controlled environment experiments and tree trait data from two major databases we tested for relationships between traits and spring phenology in trees. Specifically, we examined the cues that drive early to late budburst: spring temperatures (forcing), winter temperatures (chilling), and daylength (photoperiod).
- ²⁰ 3. We found mixed support for our predictions for how traits relate to budburst timing and phenology. Species with cues that lead to earlier budburst (**small responses to experimental chilling and photoperiod**) were shorter with **higher leaf nitrogen content**, both traits related to acquisitive strategies and thus in line with our predictions. However our one reproductive trait of seed mass showed no relationship with phenology, and other traits (e.g., specific leaf area) showed relationships in the opposite direction to our predictions.
- ²⁶ 4. Synthesis: Our findings show how spring budburst phenology partially fits within a functional trait framework of acquisitive to conservative growth strategies. Leveraging these relationships could improve predictions of how communities shift in their growth strategies alongside changing phenology

29 with future warming.

30

31 Key words: Leafout, spring phenology, traits, trees, climate change, forest communities

32

Introduction

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

38

39 Predicting these changes requires understanding the environmental triggers of phenology, including
40 temperature or photoperiod, throughout the winter and spring that cause species to start growth at
41 different times. Groups of species may have more similar responses to these environmental triggers
42 because they are from similar functional groups, successional stages (Laube *et al.*, 2014) or growth
43 forms (Flynn & Wolkovich, 2018) that cause them to have similar growth strategies. But current work
44 provides limited insights into the drivers of these differences across species and how they can be used to
45 predict future changes in community dynamics (Chuine *et al.*, 2016; Flynn & Wolkovich, 2018; Laube
46 *et al.*, 2014).

47

48 Understanding these species-level differences requires considering how long-term environmental and
49 biotic pressures may select for certain species to be early or late relative to other species each year
50 (Ovaskainen *et al.*, 2013; Wolkovich & Donahue, 2021). Species that start growth early often risk high
51 tissue loss due to frost damage (Augspurger, 2009; Sakai & Larcher, 1987) or high herbivore apparenacy
52 (Wainwright *et al.*, 2012), but benefit from higher resource availability (Hufkens *et al.*, 2012; Rathcke
53 & Lacey, 1985). In contrast, later active species face greater biotic pressures, especially from high
54 competition for resources (Lopez *et al.*, 2008; Wolkovich & Ettinger, 2014). Such differences could
55 shape physical and phenological traits related to species growth strategies and fitness (Violle *et al.*,
56 2007). Species leaf and wood traits can reflect trade-offs between the construction costs and longevity
57 of tissue (Reich *et al.*, 1997; Wright *et al.*, 2004), with cheaper-to-construct tissue being associated
58 with faster growth rates (Westoby & Wright, 2006; Wright *et al.*, 2004). Previous studies have high-
59 lighted associations between trade-offs in phenology with structural and leaf traits in both woody
60 (Wang *et al.*, 2021; Wolkovich & Ettinger, 2014) and herbaceous species (Sporbert *et al.*, 2022), and
61 hypothesized that phenology may fit within the acquisitive (fast) to more conservative (slow) growth

62 strategies associated with existing trait frameworks (Chave *et al.*, 2009; Wright *et al.*, 2004, Fig 1).

63

64 Globally, gradients from acquisitive to conservative strategies appear common and form the foundation
65 of the leaf and wood economic spectra (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby &
66 Wright, 2006; Wright *et al.*, 2004), but they make limited predictions of trait variability (Violle *et al.*,
67 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving
68 the relationships between broader trait syndromes and phenology largely unknown. Understanding
69 these relationships, however, can improve forecasts of community dynamics and responses to climate
70 change. Most studies have examined the relationship between traits and phenology for a single or
71 limited number of sites (as reviewed by Wolkovich & Cleland, 2014; Wolkovich & Donahue, 2021),
72 though recent studies have explored these relationships across sites for herbaceous species (Rauschkolb
73 *et al.*, 2024; Sporbert *et al.*, 2022). At more local spatial scales the problem of disentangling the local
74 environmental triggers that shape traits (and vary across sites) and cause variation within or across
75 species, can be more easily ignored in some systems (but see Albert *et al.*, 2011; Siefert *et al.*, 2015;
76 Zuleta *et al.*, 2022, for discussion of systems with high variation within one species, site, or year).
77 Adding phenology to broader trait frameworks therefore becomes more complex as high levels of vari-
78 ation occur across larger spatial and temporal scales.

79

80 Recent climate change has highlighted how variable plant phenology is when observed over time and
81 space across different species (Rudolf, 2019; Vitasse, 2013; Yu *et al.*, 2010), with many studies docu-
82 menting how quickly phenology can shift with warming (Fitter & Fitter, 2002; Menzel *et al.*, 2006).
83 But experiments conducted under controlled environments have shown that it is possible to consis-
84 tently define early to late phenology from the known underlying cues (Chuine & Cour, 1999; Flynn &
85 Wolkovich, 2018; Harrington & Gould, 2015). This work has found early species have small responses
86 to the three major cues that determine woody plant budburst: forcing (accumulated warm tempera-
87 tures usually in the spring), chilling (cool temperatures usually accumulated in the fall and winter),
88 and photoperiod, while later species generally have larger responses to these cues (Flynn & Wolkovich,
89 2018; Laube *et al.*, 2014). These responses suggest early species require lower amounts of forcing, chill-
90 ing and shorter photoperiods to budburst, while species that budburst later require higher amounts of
91 forcing, chilling and longer photoperiods (see Flynn & Wolkovich, 2018, for further details). The con-
92 sistency of these relationships, alongside increasing evidence that intra-specific variation in tree spring
93 phenology is low given the same climate (Aitken & Bemmels, 2016; Zeng & Wolkovich, 2024), allows
94 us to estimate early to later active species across plant communities and diverse species assemblages.

95

96 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phenol-

97 ogy into functional trait research. In addition to how well we understand the environmental cues that
98 lead to early versus late budburst, in many forests strong gradients in frost risk or nutrient availability
99 from the start to the end of the spring growing season likely shape other traits (Fig 1). These gradients
100 should drive differences in growth strategies of early versus late species, and thus be related to differ-
101 ences in traits (Horbach *et al.*, 2023; Wang *et al.*, 2021), such as the differences in traits that facilitate
102 frost tolerance versus avoidance (Lenz *et al.*, 2013; Sakai & Larcher, 1987) or in herbivory (Coley *et al.*,
103 1985). Broadly we predict acquisitive species to be shorter, with leaf traits favorable to the low light
104 conditions of the understory later in the growing season—that is, they should produce leaves with high
105 specific leaf area (SLA) and leaf nitrogen content (LNC) (Díaz *et al.*, 2016; Reich *et al.*, 1997; Wright
106 *et al.*, 2004). We would predict such species to exhibit early budburst phenology. Canopy species that
107 budburst later when competition for soil resources is greater, would then have traits associated with
108 conservative growth—taller with denser wood (Chave *et al.*, 2009; Laughlin *et al.*, 2010) and leaf traits
109 suited for the higher light conditions of the canopy (low SLA and low LNC, Fig 1). Seed size may
110 similarly be predicted from this acquisitive to conservative continuum, as acquisitive species produce
111 smaller seeds and taller and more conservative species produce larger, better provisioned seeds (Díaz
112 *et al.*, 2016).

113
114 To test these predictions between budburst responses to environmental cues and common functional
115 traits (height, SLA, seed mass, and LNC), we merged available data from global databases of plant
116 traits—BIEN (Maitner *et al.*, 2018) and TRY (Kattge *et al.*, 2020a)—with global budburst data from
117 the OSPREE database of controlled environment studies (Ettinger *et al.*, 2020). We developed a hier-
118 archical Bayesian joint model that predicts phenological responses to forcing, chilling and photoperiod
119 treatments based on species-level trait values, while allowing additional variation due to study. This
120 approach takes a step towards predicting variation via species traits instead of species identity. When
121 traits explain a significant portion of the variation, species identity will explain only a small amount
122 and thereby help forecast species phenological responses based on trait values alone.

123

124 Methods

125 We merged three major databases for our analysis. We gathered phenological data from the OSPREE
126 database (Ettinger *et al.*, 2020), which contains data from experiments of dormant plant tissue from
127 woody plants growing either in the field or in controlled environments. From OSPREE, we used the
128 available budburst data for temperate tree species from studies that each manipulated forcing, chilling
129 and photoperiod. We originally constructed the OSPREE database by performing a systematic review

130 of the literature, and searched both ISI Web of Science and Google Scholar using the following two
131 search terms:

132

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

135

136 We then scraped the data from all articles reporting experiments that manipulated both photoperiod
137 and/or temperature cues of woody species budburst, leafout, or flowering phenology, and for which
138 there was a quantifiable response to each cue. We updated this database in July 2019 reviewing all
139 new articles found using the previous search terms. Additional details on the methods used to as-
140 semble, clean, and update this database are discussed by Ettinger *et al.* (2020) and Morales-Castilla
141 *et al.* (2024). For the purpose of this study, we obtained a subset of the budburst data from OSPREE
142 database and initially aimed to use data for 234 species used in Morales-Castilla *et al.* (2024).

143

144 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020a; Maitner
145 *et al.*, 2018), both of which are large trait databases that include plant trait observations across many
146 individuals, species, and studies (Table S1) and are available through slightly different mechanisms.
147 BIEN is accessible via the BIEN R package (here we used v. 1.2.5, Maitner *et al.*, 2018), and TRY
148 is requested. **We obtained data from the BIEN databases on 5 December 2018 and the TRY data**
149 **on 10 April 2019.** We initially searched for trait data on the subset of 234 OSPREE species used
150 in Morales-Castilla *et al.* (2024). From BIEN, this resulted in 94 of the 234 species available in the
151 database, for which there were 13 unique traits. From the TRY database we received data for 10
152 unique traits for 96 of the 234 requested species (Kattge *et al.*, 2020a). As we were interested in the
153 trait-phenology relationships of adult trees we subsetted the available data to **remove any observations**
154 **denoted as being from juvenile individuals or with heights less than 2 m (following Natural Resources**
155 **Canada, 2020, we assume this removes most individuals that were saplings when measured; analyses**
156 **using an alternative cut-off of 1.37 m showed similar results).** We further removed all data from ma-
157 nipulative experiments or from plants growing in non-natural habitats. We then grouped trait values
158 where appropriate, for example pooling trait values for specific leaf area (SLA) with those denoted as
159 ‘SLA with petioles’, and ‘SLA without petioles’ in our analysis (see Table S1). We also removed data
160 that was duplicated in both the TRY and BIEN datasets ($n = 434,905$). For a full depiction of our
161 data cleaning process and decisions see Fig. S1.

162

163 For our analysis, we only included species for which we had a complete trait profile (i.e., all traits
164 measured for all species). For this profile, **we initially considered six commonly measured traits: SLA,**

leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC. There were 26 species that had at least one trait measurement for each of these traits. We then used a principle component analysis (PCA) to identify which (if any) of our six traits were strongly correlated. The first principal component explained 32% of variation while the second explained 24.2% of the variation, with high correlations between SLA and LDMC, and between height and SSD (Fig. S2). By excluding the trait from each of these highly correlated trait pairs with the least amount of data (specifically LDMC and SSD) we were able to increase the number of species in our dataset from the 26 species with complete data for six traits, to 37 species with complete data for four traits. The data for these 37 species were from 24 unique studies (Fig S3, sample sizes: height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n = 7656$). Our dataset of tree height included 13 species that were measured over 19 times more frequently than most other species. We therefore subsampled the height measurements of these 13 most frequently measured trees to reduce their influence on our height model, randomly sampling 3000 height measurements for each individual species while including all height data for the remaining, less frequently measured, 24 species. This subsampling was not required for any of the other traits included in our study.

Joint model of trait and phenology

To understand connections between phenology and species traits, we developed a Bayesian joint model that allowed us to relate each trait (height, SLA, LNC, and seed mass) to species budburst cues. We consider this a ‘joint’ model because it involves two sub-models, one that models trait observations and a second that uses shared latent processes to model how a given trait relates to the cues that shape the phenological observations. In particular, we assume that trait values are the result of multiple sources of variation, including species (α_{species}) and study-level variation (α_{study}), that combine into one observed trait value (trait sub-model). Species-specific trait values (α_{trait} , described below) have a separate interaction with the three cues (β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$) that determine phenology and 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.

Trait sub-model

Our trait sub-model describes the processes that shape a given trait observations for 1 to n species across each of the 1 to m studies in our trait dataset. We use hierarchical modeling to partition trait values by the error across all observations not otherwise explained by the model (σ_m^2 , often considered measurement error), species identity ($\alpha_{\text{species}_i}$), and study (α_{study_j}). In particular, we assume that a trait observation for species i from study j ($Y_{\text{trait}_{i,j}}$) has the following normal distribution:

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

197 with

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

$$\alpha_{\text{trait}} = \alpha_{\text{grand trait}} + \alpha_{\text{species}_i} \quad (3)$$

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

$$\boldsymbol{\alpha}_{\text{species}} = \begin{bmatrix} \alpha_{\text{species}_1} \\ \alpha_{\text{species}_2} \\ \vdots \\ \alpha_{\text{species}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{species}} \sim \text{Normal}(0, \sigma_{\text{species}}^2) \quad (4)$$

$$\boldsymbol{\alpha}_{\text{study}} = \begin{bmatrix} \alpha_{\text{study}_1} \\ \alpha_{\text{study}_2} \\ \vdots \\ \alpha_{\text{study}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \text{Normal}(0, \sigma_{\text{study}}^2) \quad (5)$$

199 Mathematically, the latent parameter or overall mean trait value ($\alpha_{\text{grand trait}}$) represents a trait value
200 that is independent of the other parameters in the model, namely the parameter for species ($\alpha_{\text{species},i}$)
201 and study-level ($\alpha_{\text{study},j}$) offsets from that overall mean trait value. The σ_m^2 parameter is the mea-
202 surement error for the observed trait values, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and study-level
203 variances in trait values. Of these parameters, we combine the mean trait value ($\alpha_{\text{grand trait}}$) with
204 species-specific offsets from the mean trait value ($\alpha_{\text{species},i}$) to form $\boldsymbol{\alpha}_{\text{trait}}$, which is shared by the
205 phenology sub-model (equation 3).

206 Phenology sub-model

207 Our phenology sub-model describes the processes that determine the relationships between traits and
208 environmental cues and their effects on phenological observations for 1 to n species, specifically the
209 timing (day of year) of budburst from the updated OSPREE dataset. The observations of budburst
210 for species k under g treatment levels of each cue (c_g, f_g, p_g , for chilling, forcing and photoperiod
211 treatments respectively, which we z -scored to allow direct comparison between cues) is represented by
212 parameter $Y_{\text{pheno}_{k,g}}$, and assumed to follow a normal distribution:

$$Y_{\text{pheno}_{k,g}} \sim \text{Normal}(\mu_{k,g}, \sigma_d^2) \quad (6)$$

²¹³ with

$$\mu_{k,g} = \alpha_{\text{pheno}_k} + \beta_{\text{chilling}_k} \cdot c_g + \beta_{\text{forcing}_k} \cdot f_g + \beta_{\text{photoperiod}_k} \cdot p_g \quad (7)$$

²¹⁴ and

$$\beta_{\text{chilling}_k} = \alpha_{\text{chilling}_k} + \beta_{\text{trait.chilling}} \cdot \alpha_{\text{trait}_k} \quad (8)$$

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

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

²¹⁵ where α_{pheno_k} , $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$ are elements of the normal random vectors:

$$\boldsymbol{\alpha}_{\text{pheno}} = \begin{bmatrix} \alpha_{\text{pheno}_1} \\ \alpha_{\text{pheno}_2} \\ \vdots \\ \alpha_{\text{pheno}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \text{Normal}(0, \sigma_{\text{pheno}}^2) \quad (9)$$

$$\boldsymbol{\alpha}_{\text{chilling}} = \begin{bmatrix} \alpha_{\text{chilling}_1} \\ \alpha_{\text{chilling}_2} \\ \vdots \\ \alpha_{\text{chilling}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{chilling}} \sim \text{Normal}(0, \sigma_{\text{chilling}}^2) \quad (10)$$

$$\boldsymbol{\alpha}_{\text{forcing}} = \begin{bmatrix} \alpha_{\text{forcing}_1} \\ \alpha_{\text{forcing}_2} \\ \vdots \\ \alpha_{\text{forcing}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{forcing}} \sim \text{Normal}(0, \sigma_{\text{forcing}}^2) \quad (11)$$

$$\boldsymbol{\alpha}_{\text{photoperiod}} = \begin{bmatrix} \alpha_{\text{photoperiod}_1} \\ \alpha_{\text{photoperiod}_2} \\ \vdots \\ \alpha_{\text{photoperiod}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{photoperiod}} \sim \text{Normal}(0, \sigma_{\text{photoperiod}}^2) \quad (12)$$

(13)

²¹⁶ The model partitions day of budburst for species (k) as a combination of the overall mean day of
²¹⁷ budburst without the influence of chilling, forcing, or photoperiod treatments ($\alpha_{\text{pheno},k}$, normally dis-
²¹⁸ tributed with a mean of μ_{pheno} and variance σ_{pheno}^2) combined with the effects of treatments both
²¹⁹ dependent and independent of trait values. The parameters $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$
²²⁰ represent the trait-independent responses of species k to chilling, forcing, and photoperiod treat-
²²¹ ments respectively, each with an associated mean (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 parameter between the trait and phenology sub-model, α_{trait_k} , represents the effect of the species trait value on its responses to chilling ($\beta_{\text{trait.chilling}}$), forcing ($\beta_{\text{trait.forcing}}$), and photoperiod ($\beta_{\text{trait.photoperiod}}$). Finally, our model provides an estimate of σ_d^2 , which is the variance arising from measurement error for the observed day of budburst.

226

The model was coded in the Stan (Stan Development Team, 2024), which is a probabilistic programming language for building Bayesian models. We used the rstan package (Stan Development Team, 2018) to interface with and run the Stan code in R version 3.3.6 (R Development Core Team, 2017). For our model, we chose weakly informative priors, and validated them using a series of prior predictive checks. The model was fit 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 S4). In our discussion of the results we present our model estimates as the means and 90% posterior uncertainty intervals (UI), with the 50% UI depicted in the figures and both the 90% and 50% UI included in the supplementary tables to allow assessing and comparing the strength of relationships. We consider parameters with a 90% UI that overlap to be similar to each other and those that cross zero in the 90% UI to have no effect.

238

Results

239 Across traits, height, SLA, and LNC were related to one or more environmental cue ($\beta_{\text{chilling}_k}$, β_{forcing_k} ,
240 or $\beta_{\text{photoperiod}_k}$, Fig 2 a-f & j-l), with only LNC showing a relationship with all three cues (Fig. 2 j-l). As we predicted, height was negatively related to chilling ($\beta_{\text{chilling}_k}$) and photoperiod ($\beta_{\text{photoperiod}_k}$),
242 with taller species having larger responses to high chilling and longer photoperiod conditions (-0.5
243 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized
244 photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). These large responses in the timing of budburst
245 (as estimated by $\mu_{k,g}$), in response to chilling and photoperiod treatments likely reflect that taller tree
246 species require more chilling and forcing to budburst (conditions that are often met later in the growing
247 season), while shorter species budburst earlier, under the lower chilling and photoperiod conditions
248 that occur earlier in the spring. In contrast, seed mass had a negligible relationship with budburst and
249 all three cues (Fig. 2 g-i & Table S3).

250

251 Of the studied leaf traits, we found that SLA related to photoperiod ($\beta_{\text{photoperiod}_k}$, -0.2 mm²/mg per
252 standardized photoperiod; 90% UI: -0.5, 0.0, Table S4), but with larger responses to longer photope-
253 riods for high SLA species (Fig. 2 f). But we did not find strong responses to chilling ($\beta_{\text{chilling}_k}$) or
254 forcing treatments (β_{forcing_k} , Fig. 2 d & e). The relationship between LNC and budburst cues, was

in line with our predictions, with high LNC species being less responsive to chilling (0.7 mg/g per standardized chilling; 90% UI: 0.2, 1.2, Table S5), forcing (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.8), and photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6, Fig 2 j-l). This suggests that species that produce leaves with high nitrogen content, which relates generally to high photosynthetic rates and acquisitive growth, are likely to budburst under early spring conditions (based on the relationships between this trait and environmental cues).

261

We found that the species-level variance across traits were comparable to, or greater than, variance across studies (using our model that partitions the measurement error in the trait values from variance from species and study-level effects; Fig 3). For height, variance across studies (σ_{study}^2) was greater (7.5 m; 90% UI: 5.7, 9.8), than the variance caused by species ($\sigma_{\text{species}}^2$, 6 m; 90% UI: 4.9, 7.3, Fig 3a). For seed mass and LNC, study-level variance was less than that of the species-level variance, with variance in seed mass observations of 1 mg (90% UI: 0.8, 1.1) and 1.6 mg (90% UI: 0.8, 1.1) for study-level and species-level variance respectively and for LNC 3.6 mg g⁻¹ (90% UI: 2.2, 5.3) for study-level variance and 5.1 mg g⁻¹ for the species-level variance (90% UI: 2.2, 5.3, Fig 3c and d). The difference between species and study-level variance was greatest for SLA, with the estimate of 3.3 mm² mg⁻¹ (90% UI: 2, 5.1) for study-level variance being approximately half that of the estimated species-level variance of 7.8 mm² mg⁻¹ (90% UI: 6.4, 9.4, Fig 3b).

273

274 Discussion

We found several species traits influenced the timing of budburst in response to one or more of the three primary cues of spring phenology. In general, early species (those with smaller responses to chilling, forcing and photoperiod in experiments Flynn & Wolkovich, 2018; Laube *et al.*, 2014), had relationships with several traits associated with fast and acquisitive growth strategies. Later budbursting species (those with larger responses to chilling, forcing and photoperiod in experiments Flynn & Wolkovich, 2018; Laube *et al.*, 2014), however, had traits indicative of conservative, slower growth strategies. Specifically, the trait effects of height and LNC on the timing of budburst followed well-established gradients in growth strategies predicted by functional trait frameworks (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004). But in the case of SLA, its relationship to spring phenological cues was opposite of our predictions. Species with high SLA—as a result of having the larger, thin leaves, with low investment in leaf mass, and generally indicative of acquisitive growth strategies—had larger responses to photoperiod. Seed mass, which was our one reproductive trait, showed the weakest response to all three cues, suggesting no connection

288 between seed mass and spring phenology. Our results are in line with previous studies conducted
289 at more local scales that found large relationships between height and species phenology (Osada &
290 Hiura, 2019; Seiwa, 1999), as well as findings from large-scale research which found no relationship
291 between phenology and seed mass in woody plants (Bolmgren & D. Cowan, 2008; Ettinger *et al.*, 2018).

292

293 In addition to identifying trait-phenology relationships shaping the timing of spring budburst, our
294 results provide further insights into the use of data from large databases to estimate ecological pro-
295 cesses. By partitioning the different sources of variation that contribute to observed trait values, we
296 found study-level variance made a considerable contribution to the overall variance. Such study-level
297 variance is likely the result of several factors, including differences across sites, observer error, and
298 differences in methodologies, that are present in any dataset that pools data from diverse sources. We
299 found a particularly strong effect in our height data, as the variance due to study differences exceeded
300 the estimated species-level variance. This suggests that models using large trait databases that fail to
301 separate out study from species-level variance may poorly estimate species traits, especially for species
302 observed in a single study.

303

304 Effects of phenology-trait relationships on community assembly

305 Our findings suggest that changing pressures across the early growing season may affect the temporal
306 assembly of communities. Early-active species had traits indicative of acquisitive growth strategies
307 that allow faster return on resource investments, like shorter heights and high LNC (Chave *et al.*,
308 2009; Grime, 1977; Westoby, 1998). In deciduous forests, these traits would allow early-budbursting
309 species to benefit from greater light availability in the open forest canopy in the early spring and
310 to withstand the low light conditions later in the season. In contrast, later-budbursting species had
311 traits associated with slower, more conservative, growth (Chave *et al.*, 2009; Grime, 1977; Westoby,
312 1998), which may help them compete for the more limited soil and light resources later in the grow-
313 ing season. Similar trait-phenology relationships have also been linked to other ecological processes
314 and species characteristics that define community structure and diversity, such as species successional
315 position (Laube *et al.*, 2014), leading to the differences we observed for height and LNC in our exam-
316 ple comparing *Alnus incana* (a pioneer species) and *Quercus rubra* (a later successional species; Fig 2).

317

318 While our study focuses mainly on early versus later spring phenology, our approach and findings may
319 provide insights into potential trade-offs between traits and the phenological cues that underlie early
320 versus late budburst timing. In particular the relationships between traits and specific phenological

321 cues that deviated from our expectations may offer novel insights. This is the case for tree height,
322 which is related to mechanical strength and water transport (Chave *et al.*, 2009). Our finding that tree
323 height was associated with chilling and photoperiod cues (but not forcing) suggests that species use of
324 these two cues may be tied to preventing frost damage or xylem cavitation under a late spring frost
325 (Clements *et al.*, 1972; Marquis *et al.*, 2020). Similarly, the lack of a relationship between SLA and
326 temperature cues (chilling and forcing) was surprising, given that differences in leaf area can also affect
327 heat transfer, such that thicker leaves with higher SLA may have an increased risk of frost damage
328 (Lusk *et al.*, 2018). Further, many different traits may contribute to decreasing the risk of frost dam-
329 age (e.g., trichome density, cuticle type, Sakai & Larcher (1987)) and thus a composite of many traits
330 may give better insights into links between traits and frost damage. Well-studied traits, such as SLA,
331 often reflect multiple aspects of growth and function (Maynard *et al.*, 2022), and may be adaptive for
332 reasons other than those we predicted. Variation in SLA, for example, can also capture differences
333 in species relative growth rates or leaf longevity, and not just photosynthetic potential (Reich, 2014;
334 Westoby, 1998).

335

336 Our findings highlight the complexity and challenges in determining the drivers of species trait profiles
337 to understand how phenology fits within a functional trait framework, but expanding to more diverse
338 species and ecosystems could help. Major trait frameworks today, such as the leaf and wood economic
339 spectra, generally emerged from studies across highly different ecosystems (Chave *et al.*, 2009; Díaz
340 *et al.*, 2016), while relationships within certain habitats or regions often show much weaker relation-
341 ships (Funk & Cornwell, 2013; Messier *et al.*, 2017). Our focus on budburst timing for temperate
342 woody species leverages the largest databases of traits and phenological experiments, but it still has a
343 limited sample size of species and focuses on only one major ecosystem, which is primarily controlled
344 by temperature (Chapin *et al.*, 2011; Kattge *et al.*, 2020b). Extending into other types of plant com-
345 munities controlled by other factors, such as in savannas or tropical forests, which may be shaped by
346 cues other than light or seasonal temperatures, could greatly expand how we understand the role of
347 phenology within trait syndromes.

348

349 Future outlook and applications

350 Incorporating phenology within broader trait syndromes could aid in forecasting species and commu-
351 nity responses to climate change. Decades of research have documented phenological advances with
352 anthropogenic climate change (Fitter & Fitter, 2002; Menzel *et al.*, 2006), however, increasing research
353 suggests a potential benefit to advancing, as plant species that shift their phenology with warming also

354 perform better (Cleland *et al.*, 2012). Our results suggest phenology-performance relationships could
355 be driven in part by a suite of traits that covary with phenology to determine how responsive species
356 are to warming. Our results suggest that early-active species—which other studies have found to also
357 be those that advance more with warming (Fuccillo Battle *et al.*, 2022; Menzel *et al.*, 2020)—are likely
358 to have acquisitive traits (such as shorter heights and high LNC) that allow them to grow quickly, ac-
359 cumulate resources faster and possibly have greater carbon sequestration over a longer growing season.
360 How much these relationships continue in the future also depends on how warming in the winter and
361 spring continues, and the complexities of exactly how chilling and photoperiod cues operate, which is
362 an area of active debate. Studies to date suggest chilling may decrease in most places with warming
363 (Guy, 2014; Wang *et al.*, 2022) while research on photoperiod has variously suggested photoperiod cues
364 could stall responses for some later-active species (Ettinger *et al.*, 2021) or have at most a relatively
365 small effect (Ettinger *et al.*, 2021, 2020).

366

367 The insight that understanding trait-phenology relationships provides into how climate change may
368 alter species coexistence and create novel species assemblages across communities (Rudolf, 2019;
369 Wolkovich & Donahue, 2021) could have important implication for restoration ecology, including for
370 pollinator communities and invasive plant management. For example, applying our approach to flower
371 and fruit traits may help link plant phenology to pollinator communities, with the opportunity to better
372 predict shifts in phenology and pollination services with climate change (Leclerc *et al.*, 2024; Pareja-
373 Bonilla *et al.*, 2025). Opportunities to better manage invasive plants may come from their tendency
374 to have earlier phenologies (Alexander & Levine, 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019)
375 and traits that facilitate fast growth (Fridley *et al.*, 2022). By identifying the trait-cue relationships
376 that shape phenology, we could use existing trait data from invasive species to better predict whether
377 they are likely to out-compete native species by growing earlier in the season and drawing down soil
378 nutrients and/or light resources that later-active native species may rely on (CITES?). This could
379 lead to better identifying which species may be of most concern and thus lead to effective management
380 practices that protect native plant communities under future climate conditions.

381 **References**

- 382 Aitken, S.N. & Bemmels, J.B. (2016) Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications* **9**, 271–290.
- 384 Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violette, C. (2011) When and how should
385 intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology,
386 Evolution and Systematics* **13**, 217–225.
- 387 Alexander, J.M. & Levine, J.M. (2019) Earlier phenology of a nonnative plant increases impacts on
388 native competitors. *PNAS* **116**, 6199–6204.
- 389 Augspurger, C.K. (2009) Spring 2007 warmth and frost : phenology , damage and refoliation in a
390 temperate deciduous forest. *Functional Ecology* **23**, 1031–1039.
- 391 Beard, K.H., Kelsey, K.C., Leffler, A.J. & Welker, J.M. (2019) The Missing Angle : Ecosystem Con-
392 sequences of Phenological Mismatch. *Trends in Ecology and Evolution* **34**, 885–888.
- 393 Bolmgren, K. & D. Cowan, P. (2008) Time – size tradeoffs: a phylogenetic comparative study of
394 flowering time, plant height and seed mass in a north-temperate flora. *Oikos* **117**, 424–429.
- 395 Chapin, F.S., Matson, P.A. & Vitousek, P.M. (2011) *Principles of Terrestrial Ecosystem Ecology*.
396 Springer New York, New York, NY.
- 397 Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a
398 worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.
- 399 Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A. &
400 Améglio, T. (2016) Can phenological models predict tree phenology accurately in the future? The
401 unrevealed hurdle of endodormancy break. *Global change biology* **22**, 3444–3460.
- 402 Chuine, I. & Cour, P. (1999) Climatic determinants of budburst seasonality in four temperate-zone
403 tree species. *New Phytologist* **143**, 339–349.
- 404 Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S.
405 & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate
406 change.pdf. *Ecology* **93**, 1765–1771.
- 407 Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology
408 in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.
- 409 Clements, J.R., Fraser, J. W. & Yeatman, C.W. (1972) Frost Damage to White Spruce Buds. *Canadian
410 Journal of Forest Research* **2**, 62–63.

- 411 Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource Availability and Plant Antiherbivore Defense.
412 *Science* **230**, 895–899.
- 413 Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth,
414 C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T.,
415 Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel,
416 H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S.,
417 Günther, A., Falcuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of
418 plant form and function. *Nature* **529**, 167–171.
- 419 Ettinger, A.K., Buonaiuto, D.M., Chamberlain, C.J., Morales-Castilla, I. & Wolkovich, E.M. (2021)
420 Spatial and temporal shifts in photoperiod with climate change. *New Phytologist* **230**, 462–474.
- 421 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F., Savas, T.,
422 Samaha, J.A. & Wolkovich, E.M. (2020) Winter temperatures predominate in spring phenological
423 responses to warming. *Nature Climate Change* **10**, 1137–1142.
- 424 Ettinger, A.K., Gee, S. & Wolkovich, E.M. (2018) Phenological sequences: how early-season events
425 define those that follow. *American Journal of Botany* **105**, 1771–1780.
- 426 Fitter, A.H. & Fitter, R.S.R. (2002) Rapid Changes in Flowering Time in British Plants. *Science* **296**,
427 1689–1691.
- 428 Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across
429 all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.
- 430 Fridley, J.D., Bauerle, T.L., Craddock, A., Ebert, A.R., Frank, D.A., Heberling, J.M., Hinman, E.D.,
431 Jo, I., Martinez, K.A., Smith, M.S., Woolhiser, L.J. & Yin, J. (2022) Fast but steady: An integrated
432 leaf-stem-root trait syndrome for woody forest invaders. *Ecology Letters* **25**, 900–912.
- 433 Fuccillo Battle, K., Duhon, A., Vispo, C.R., Crimmins, T.M., Rosenstiel, T.N., Armstrong-Davies,
434 L.L. & De Rivera, C.E. (2022) Citizen science across two centuries reveals phenological change
435 among plant species and functional groups in the Northeastern <span style="font-variant:small-
436 caps;">US. *Journal of Ecology* **110**, 1757–1774.
- 437 Funk, J.L. & Cornwell, W.K. (2013) Leaf traits within communities: Context may affect the mapping
438 of traits to function. *Ecology* **94**, 1893–1897.
- 439 Grime, J.P. (1977) Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance
440 to Ecological and Evolutionary Theory Author (s): J . P . Grime Source : The American Naturalist

- 441 , Vol . 111 , No . 982 (Nov . - Dec ., 1977), pp . 1169-1194 Published. *The American Naturalist*
442 **111**, 1169–1194.
- 443 Gu, H., Qiao, Y., Xi, Z., Rossi, S., Smith, N.G., Liu, J. & Chen, L. (2022) Warming-induced in-
444 crease in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. *Nature*
445 *Communications* **13**, 1–8.
- 446 Guy, R.D. (2014) The early bud gets to warm. *New Phytologist* **202**, 7–9.
- 447 Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying dormancy
448 requirements for Pacific Northwest tree species. *Frontiers in Plant Science* **6**, 1–12.
- 449 Horbach, S., Rauschkolb, R. & Römermann, C. (2023) Flowering and leaf phenology are more variable
450 and stronger associated to functional traits in herbaceous compared to tree species. *Flora* **300**, 1–9.
- 451 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O’keefe, J. & Richardson, A.D.
452 (2012) Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change
453 Biology* **18**, 2365–2377.
- 454 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C. & et al. (2020a) TRY plant trait database
455 – enhanced coverage and open access. *Global Change Biology* **26**, 119–188.
- 456 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. & Tautenhahn, e.a. (2020b)
457 TRY plant trait database – enhanced coverage and open access. *Global Change Biology* **26**, 119–188.
- 458 Laube, J., Sparks, T.H., Estrella, N., Höfner, J., Ankerst, D.P. & Menzel, A. (2014) Chilling outweighs
459 photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- 460 Laughlin, D.C., Leppert, J.J., Moore, M.M. & Sieg, C.H. (2010) A multi-trait test of the leaf-height-
461 seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* **24**, 493–501.
- 462 Leclerc, M.A.J., Gibernau, M. & Pincebourde, S. (2024) Pollination-related plant traits under environ-
463 mental changes: Seasonal and daily mismatches produce temporal constraints. *Functional Ecology*
464 pp. 1365–2435.14674.
- 465 Lenz, A., Hoch, G., Vitasse, Y. & Körner, C. (2013) European deciduous trees exhibit similar safety
466 margins against damage by spring freeze events along elevational gradients. *New Phytologist* **200**,
467 1166–1175.
- 468 Lopez, O.R., Farris-Lopez, K., Montgomery, R.A. & Givnish, T.J. (2008) Leaf phenology in relation
469 to canopy closure in southern Appalachian trees. *American Journal of Botany* **95**, 1395–1407.

- 470 Lusk, C.H., Clearwater, M.J., Laughlin, D.C., Harrison, S.P., Prentice, I.C., Nordenstahl, M. & Smith,
471 B. (2018) Frost and leaf-size gradients in forests: global patterns and experimental evidence. *New*
472 *Phytologist* **219**, 565–573.
- 473 Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S.M., Guaderrama, D., Hinchliff,
474 C.E., Jørgensen, P.M., Kraft, N.J., McGill, B., Merow, C., Morueta-Holme, N., Peet, R.K., Sandel,
475 B., Schildhauer, M., Smith, S.A., Svenning, J.C., Thiers, B., Violle, C., Wiser, S. & Enquist, B.J.
476 (2018) The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN)
477 database. *Methods in Ecology and Evolution* **9**, 373–379.
- 478 Marquis, B., Bergeron, Y., Simard, M. & Tremblay, F. (2020) Growing-season frost is a better predictor
479 of tree growth than mean annual temperature in boreal mixedwood forest plantations. *Global Change*
480 *Biology* **26**, 6537–6554.
- 481 Maynard, D.S., Bialic-Murphy, L., Zohner, C.M., Averill, C., Van Den Hoogen, J., Ma, H., Mo, L.,
482 Smith, G.R., Acosta, A.T.R., Aubin, I., Berenguer, E., Boonman, C.C.F., Catford, J.A., Cerabolini,
483 B.E.L., Dias, A.S., González-Melo, A., Hietz, P., Lusk, C.H., Mori, A.S., Niinemets, Ü., Pillar, V.D.,
484 Pinho, B.X., Rosell, J.A., Schurr, F.M., Sheremetev, S.N., Da Silva, A.C., Sosinski, É., Van Bode-
485 gom, P.M., Weiher, E., Bönisch, G., Kattge, J. & Crowther, T.W. (2022) Global relationships in
486 tree functional traits. *Nature Communications* **13**, 3185.
- 487 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P.,
488 Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C.,
489 Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P.,
490 Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J., Wielgolaski, F.E., Zach, S. &
491 Zust, A. (2006) European phenological response to climate change matches the warming pattern.
492 *Global Change Biology* **12**, 1969–1976.
- 493 Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R. & Estrella, N. (2020) Climate
494 change fingerprints in recent European plant phenology. *Global Change Biology* **26**, 2599–2612.
- 495 Messier, J., Lechowicz, M.J., McGill, B.J., Violle, C. & Enquist, B.J. (2017) Interspecific integration
496 of trait dimensions at local scales: the plant phenotype as an integrated network. *Journal of Ecology*
497 **105**, 1775–1790.
- 498 Morales-Castilla, I., Davies, T.J., Legault, G., Buonaiuto, D.M., Chamberlain, C.J., Ettinger, A.K.,
499 Garner, M., Jones, F.A.M., Loughnan, D., Pearse, W.D., Sodhi, D. & Wolkovich, E.M. (2024)
500 Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate*
501 *Change* **14**, 989–995.

- 502 Natural Resources Canada (2020) Forestry glossary: Sapling.
- 503 Osada, N. & Hiura, T. (2019) Intraspecific differences in spring leaf phenology in relation to tree size
504 in temperate deciduous trees. *Tree Physiology* **39**, 782–791.
- 505 Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N.,
506 Shcherbakov, A., Meyke, E. & del Mar Delgado, M. (2013) Community-level phenological response
507 to climate change. *PNAS* **110**, 13434–13439.
- 508 Pareja-Bonilla, D., Ortiz, P.L., Morellato, L.P.C. & Arista, M. (2025) Functional traits predict changes
509 in floral phenology under climate change in a highly diverse Mediterranean community. *Functional
510 Ecology* pp. 1365–2435.70062.
- 511 Polgar, C., Gallinat, A. & Primack, R.B. (2014) Drivers of leaf-out phenology and their implications
512 for species invasions: insights from thoreau's concord. *New Phytologist* **202**, 106–115.
- 513 R Development Core Team (2017) R: A language and environment for statistical computing. *R Foundation
514 for Statistical Computing*, Vienna, Austria .
- 515 Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology
516 and Systematics* **16**, 179–214.
- 517 Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka,
518 D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F.,
519 Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M.,
520 Stevens, A.D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg,
521 M., Knickmann, B., Nordt, B., Wirth, C. & Römermann, C. (2024) Spatial variability in herbaceous
522 plant phenology is mostly explained by variability in temperature but also by photoperiod and
523 functional traits. *International Journal of Biometeorology* **68**, 761–775.
- 524 Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal
525 of Ecology* **102**, 275–301.
- 526 Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in
527 plant functioning. *Proceedings of the National Academy of Sciences* **94**, 13730–13734.
- 528 Rudolf, V.H.W. (2019) The role of seasonal timing and phenological shifts for species coexistence.
529 *Ecology Letters* **22**, 1324–1338.
- 530 Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants: Responses and adaptation to freezing stress*.
531 Springer-Verlag, Berlin, Heidelberg.

- 532 Seiwa, K. (1999) Changes in leaf phenology are dependent on tree height in Acer mono, a deciduous
533 broad-leaved tree. *Annals of Botany* **83**, 355–361.
- 534 Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Bar-
535 aloto, C., Carlucci, M.B., Cianciaruso, M.V., De L. Dantas, V., De Bello, F., Duarte, L.D.S., Fonseca,
536 C.R., Freschet, G.T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama,
537 C., Katabuchi, M., Kembel, S.W., Kichenin, E., Kraft, N.J.B., Lagerström, A., Bagousse-Pinguet,
538 Y.L., Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J.M., Peltzer, D.A., Pérez-Ramos,
539 I.M., Pillar, V.D., Prentice, H.C., Richardson, S., Sasaki, T., Schamp, B.S., Schöb, C., Shipley, B.,
540 Sundqvist, M., Sykes, M.T., Vandewalle, M. & Wardle, D.A. (2015) A global meta-analysis of the
541 relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**, 1406–1419.
- 542 Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., Konig, A., Nordt, B.,
543 Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstadter, A., Maskova, T., Primack,
544 R., Rosche, C., Shah, M.A., Stevens, A.D., Teilborger, K., Trager, S., Wirth, C. & Romermann,
545 C. (2022) Functional traits influence patterns in vegetative and reproductive plant phenology – a
546 multi-botanical garden study. *New Phytologist* **235**, 2199–2210.
- 547 Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3.
- 548 Stan Development Team (2024) Stan reference manual, v2.36.0.
- 549 Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J.
550 (2012) The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology
551 and Evolution* **27**, 244–252.
- 552 Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the
553 concept of trait be functional! *Oikos* **116**, 882–892.
- 554 Vitasse, Y. (2013) Ontogenetic changes rather than difference in temperature cause understory trees to
555 leaf out earlier. *New Phytologist* **198**, 149–155.
- 556 Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat,
557 C., Rebetez, M., Rixen, C., Strelbel, N., Schmidt, B.R., Wipf, S., Wohlgemuth, T., Yoccoz, N.G.
558 & Lenoir, J. (2021) Phenological and elevational shifts of plants , animals and fungi under climate
559 change in the European Alps. *Biological Reviews* **96**, 1816–1835.
- 560 Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2012) Seasonal priority effects : implications for
561 invasion and restoration in a semi-arid system. *Journal of Applied Ecology* **49**, 234–241.

- 562 Wang, H., Dai, J., Peñuelas, J., Ge, Q., Fu, Y.H. & Wu, C. (2022) Winter warming offsets one half of
563 the spring warming effects on leaf unfolding. *Global Change Biology* **28**, 6033–6049.
- 564 Wang, L., Han, X., Yin, Q., Wang, G., Xu, J., Chai, Y. & Yue, M. (2021) Differences in leaf phenological
565 traits between trees and shrubs are closely related to functional traits in a temperate forest. *Acta
566 Oecologica* **112**, 103760.
- 567 Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**,
568 213–227.
- 569 Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in
570 Ecology & Evolution* **21**, 261–268.
- 571 Wolkovich, E.M. & Cleland, E.E. (2014) Phenological niches and the future of invaded ecosystems
572 with climate change. *AoB PLANTS* **6**, 1–16.
- 573 Wolkovich, E.M. & Donahue, M.J. (2021) How phenological tracking shapes species and communities
574 in non-stationary environments. *Biological Reviews* **96**, 2810–2827.
- 575 Wolkovich, E.M. & Ettinger, A.K. (2014) Back to the future for plant phenology research. *New Phy-
576 tologist* **203**, 1021–1024.
- 577 Wright, I.J., Westoby, M., Reich, P.B., Oleksyn, J., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-
578 Bares, J., Chapin, T., Cornellissen, J.H.C., Diemer, M., Flexas, J., Gulias, J., Garnier, E., Navas,
579 M.L., Roumet, C., Groom, P.K., Lamont, B.B., Hikosaka, K., Lee, T., Lee, W., Lusk, C., Midgley,
580 J.J., Niinemets, Ü., Osada, H., Poorter, H., Pool, P., Veneklaas, E.J., Prior, L., Pyankov, V.I.,
581 Thomas, S.C., Tjoelker, M.G. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*
582 **428**, 821–827.
- 583 Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology
584 on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* **107**, 22151–22156.
- 585 Zeng, Z.A. & Wolkovich, E.M. (2024) Weak evidence of provenance effects in spring phenology across
586 Europe and North America. *New Phytologist* **242**, 1957–1964.
- 587 Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019) Phenology in a warming world: differences
588 between native and non-native plant species. *Ecology Letters* **22**, 1253–1263.
- 589 Zuleta, D., Muller-Landau, H.C., Duque, A., Caro, N., Cardenas, D., Castaño, N., León-Peláez, J.D.
590 & Feeley, K.J. (2022) Interspecific and intraspecific variation of tree branch, leaf and stomatal traits
591 in relation to topography in an aseasonal Amazon forest. *Functional Ecology* **36**, 2955–2968.

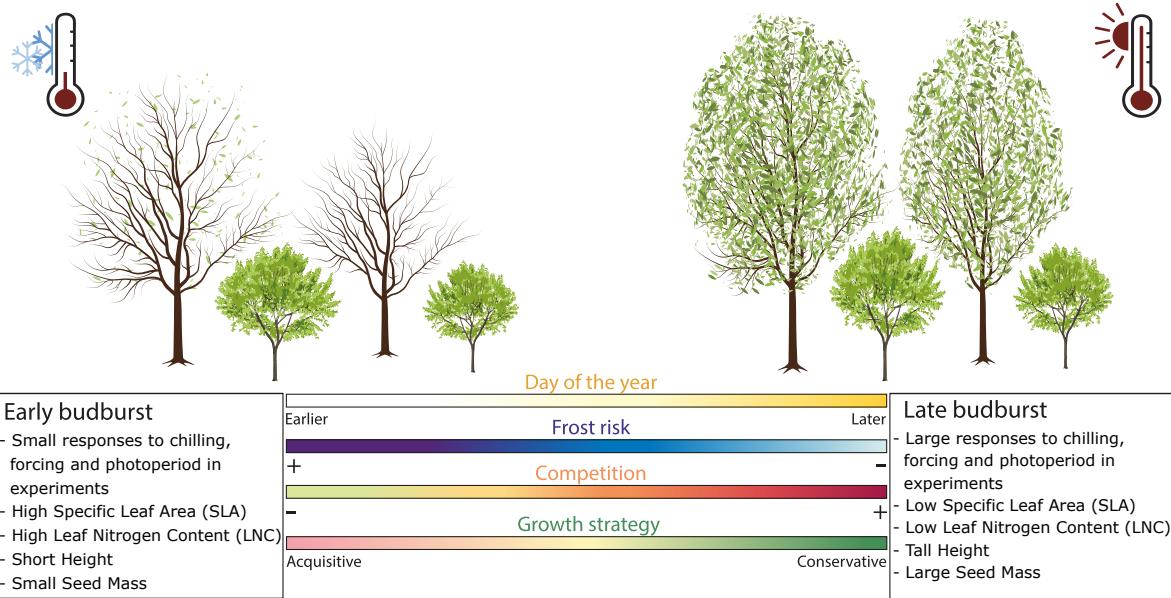


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies (Chave *et al.*, 2009; Westoby & Wright, 2006; Wright *et al.*, 2004), which may also include phenology. Drawing on previous research in plants, we predicted that early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater abiotic and biotic risk but reduced competition. In contrast, we expected later-budbursting species would have traits associated with conservative growth, as they are more likely to experience greater competition but a more climatically benign environment. Previous studies looking at different phenological events, such as flowering, or suites of non-woody species, have found varying relationships between traits and phenology, highlighting the complexity that may shape species timings.

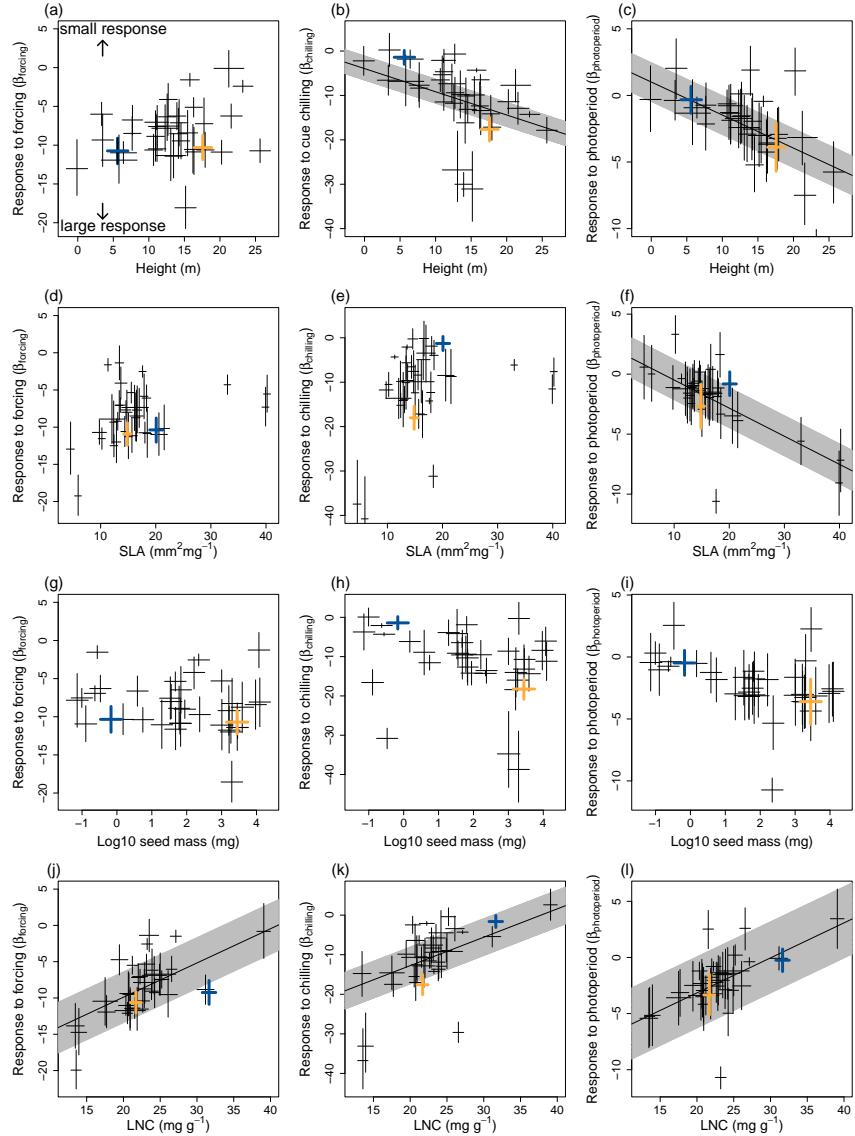


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the solid black lines showing the relationship between estimated trait effects and the responses to phenological cues (either β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$ for each trait, shown only where this relationship does not include zero within the 90% UI) with the gray band the 50% uncertainty interval. As illustrated by the arrows in panel a, species with smaller responses to cues (chilling, forcing, photoperiod) have more positive values, while species with larger responses to cues have more negative values. Each set of crossed lines represents one species (with each line spanning the 50% uncertainty interval), depicting how well our model fits the data across all species. To illustrate the relationship between traits and the three phenological cues, we highlight two example species that differ greatly in their growth forms and life history. *Alnus incana*, shown in blue,²² a shorter, shrubby tree species with a growth strategy characteristic of an acquisitive species and *Quercus rubra*, shown in yellow, a taller and characteristically conservative species.

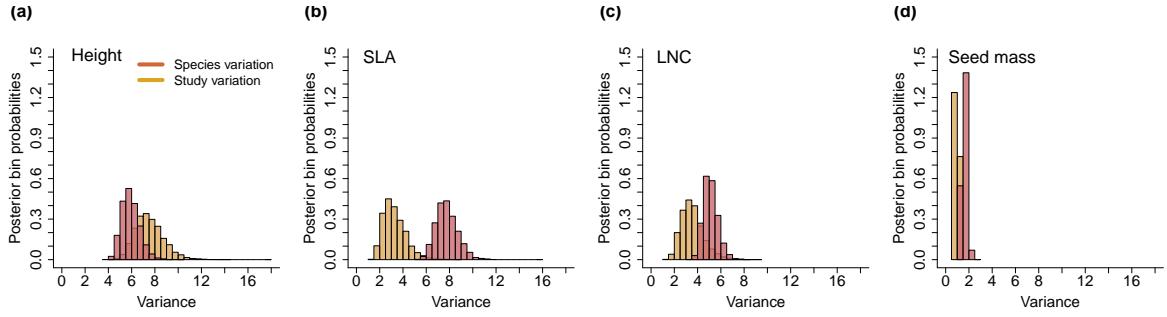


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only (a) the height model estimating greater study-level variation than species-level, while our (b) specific leaf area, (c) leaf nitrogen 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.