

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.

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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 (Viole *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
78 variation occur across larger spatial and temporal scales.

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

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

111

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

121

122 Methods

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

130

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

133

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

141

142 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020a; Maitner
143 *et al.*, 2018), both of which are large trait databases that include plant trait observations across many
144 individuals, species, and studies (Table S1) and are available through slightly different mechanisms.
145 BIEN is accessible via the BIEN R package (here we used v. 1.2.5, Maitner *et al.*, 2018), and TRY
146 is requested. **We obtained data from the BIEN databases on 5 December 2018 and the TRY data**
147 **on 10 April 2019.** We initially searched for trait data on the subset of 234 OSPREE species used
148 in Morales-Castilla *et al.* (2024). From BIEN, this resulted in 94 of the 234 species available in the
149 database, for which there were 13 unique traits. From the TRY database we received data for 10
150 unique traits for 96 of the 234 requested species (Kattge *et al.*, 2020a). As we were interested in the
151 trait-phenology relationships of adult trees we subsetted the available data to **remove any observations**
152 **denoted as being from juvenile individuals or with heights less than 2 m (following Natural Resources**
153 **Canada, 2020, we assume this removes most individuals that were saplings when measured; analyses**
154 **using an alternative cut-off of 1.37 m showed similar results).** We further removed all data from ma-
155 nipulative experiments or from plants growing in non-natural habitats. We then grouped trait values
156 where appropriate, for example pooling trait values for specific leaf area (SLA) with those denoted as
157 ‘SLA with petioles’, and ‘SLA without petioles’ in our analysis (see Table S1). We also removed data
158 that was duplicated in both the TRY and BIEN datasets ($n = 434,905$). For a full depiction of our
159 data cleaning process and decisions see Fig. S2.

160

161 For our analysis, we only included species for which we had a complete trait profile (i.e., all traits
162 measured for all species). For this profile, **we initially considered six commonly measured traits: SLA,**
163 **leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC.** There were
164 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. S3). 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 (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:

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

195 with

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

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

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

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

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

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

204 Phenology sub-model

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

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

211 with

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

²¹² and

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

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

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

²¹³ 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)

²¹⁴ The model partitions day of budburst for species (k) as a combination of the overall mean day of
²¹⁵ budburst without the influence of chilling, forcing, or photoperiod treatments ($\alpha_{\text{pheno},k}$, normally dis-
²¹⁶ tributed with a mean of μ_{pheno} and variance σ_{pheno}^2) combined with the effects of treatments both
²¹⁷ dependent and independent of trait values. The parameters $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$
²¹⁸ represent the trait-independent responses of species k to chilling, forcing, and photoperiod treat-
²¹⁹ ments respectively, each with an associated mean (μ_{chilling} , μ_{forcing} , $\mu_{\text{photoperiod}}$) and variance ($\sigma_{\text{chilling}}^2$,
²²⁰ $\sigma_{\text{forcing}}^2$, $\sigma_{\text{photoperiod}}^2$) across species. The shared parameter between the trait and phenology sub-model,
²²¹ α_{trait_k} , represents the effect of the species trait value on its responses to chilling ($\beta_{\text{trait.chilling}}$), forcing
²²² ($\beta_{\text{trait.forcing}}$), and photoperiod ($\beta_{\text{trait.photoperiod}}$). Finally, our model provides an estimate of σ_d^2 , which

223 is the variance arising from measurement error for the observed day of budburst.

224

225 The model was coded in the Stan (Stan Development Team, 2024), which is a probabilistic program-
226 ming language for building Bayesian models. We used the rstan package (Stan Development Team,
227 2018) to interface with and run the Stan code in R version 3.3.6 (R Development Core Team, 2017).
228 For our model, we chose weakly informative priors, and validated them using a series of prior predictive
229 checks. The model was fit with 1,000 iterations per chain across 4 chains (4,000 total sampling iter-
230 ations), and all models met basic diagnostic checks, including no divergences, high effective sample size
231 (n_{eff}), and \hat{R} close to 1, fitting the data well (Fig S4). In our discussion of the results we present our
232 model estimates as the means and 90% posterior uncertainty intervals (UI), with the 50% UI depicted
233 in the figures and both the 90% and 50% UI included in the supplementary tables to allow assessing
234 and comparing the strength of relationships. We consider parameters with a 90% UI that overlap to
235 be similar to each other and those that cross zero in the 90% UI to have no effect.

236 Results

237 Across traits, height, SLA, and LNC were related to one or more environmental cue ($\beta_{chilling_k}$, $\beta_{forcing_k}$,
238 or $\beta_{photoperiod_k}$, Fig 2 a-f & j-l), with only LNC showing a relationship with all three cues (Fig. 2 j-l).
239 As we predicted, height was negatively related to chilling ($\beta_{chilling_k}$) and photoperiod ($\beta_{photoperiod_k}$),
240 with taller species having larger responses to high chilling and longer photoperiod conditions (-0.5
241 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized
242 photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). These large responses in the timing of budburst
243 (as estimated by $\mu_{k,g}$), in response to chilling and photoperiod treatments likely reflect that taller tree
244 species require more chilling and forcing to budburst (conditions that are often met later in the growing
245 season), while shorter species budburst earlier, under the lower chilling and photoperiod conditions
246 that occur earlier in the spring . In contrast, seed mass had a negligible relationship with budburst
247 and all three cues (Fig. 2 g-i & Table S4).

248

249 Of the studied leaf traits, we found that SLA related to photoperiod ($\beta_{photoperiod_k}$, -0.2 mm²/mg per
250 standardized photoperiod; 90% UI: -0.5, 0.0, Table S3), but with larger responses to longer photope-
251 riodes for high SLA species (Fig. 2 f). But we did not find strong responses to chilling ($\beta_{chilling_k}$) or
252 forcing treatments ($\beta_{forcing_k}$, Fig. 2 d & e). The relationship between LNC and budburst cues, was
253 in line with our predictions, with high LNC species being less responsive to chilling (0.7 mg/g per
254 standardized chilling; 90% UI: 0.2, 1.2, Table S5), forcing (0.5 mg/g per standardized forcing; 90%
255 UI: 0.1, 0.8), and photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6, Fig 2 j-l).

256 This suggests that species that produce leaves with high nitrogen content, which relates generally to
257 high photosynthetic rates and acquisitive growth, are likely to budburst under early spring conditions
258 (based on the relationships between this trait and environmental cues).

259

260 We found that the species-level variance across traits were comparable to, or greater than, variance
261 across studies (using our model that partitions the measurement error in the trait values from variance
262 from species and study-level effects; Fig 3). For height, variance across studies (σ_{study}^2) was greater (7.5
263 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
264 seed mass and LNC, study-level variance was less than that of the species-level variance, with variance
265 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
266 species-level variance respectively and for LNC 3.6 mg g⁻¹ (90% UI: 2.2, 5.3) for study-level variance
267 and 5.1 mg g⁻¹ for the species-level variance (90% UI: 2.2, 5.3, Fig 3c and d). The difference between
268 species and study-level variance was greatest for SLA, with the estimate of 3.3 mm² mg⁻¹ (90% UI: 2,
269 5.1) for study-level variance being approximately half that of the estimated species-level variance of
270 7.8 mm² mg⁻¹ (90% UI: 6.4, 9.4, Fig 3b).

271

272 Discussion

273 We found several species traits influenced the timing of budburst in response to one or more of the
274 three primary cues of spring phenology. In general, early species (those with smaller responses to
275 chilling, forcing and photoperiod in experiments Flynn & Wolkovich, 2018; Laube *et al.*, 2014), had
276 relationships with several traits associated with fast and acquisitive growth strategies. Later bud-
277 bursting species (those with larger responses to chilling, forcing and photoperiod in experiments Flynn
278 & Wolkovich, 2018; Laube *et al.*, 2014), however, had traits indicative of conservative, slower growth
279 strategies. Specifically, the trait effects of height and LNC on the timing of budburst followed well-
280 established gradients in growth strategies predicted by functional trait frameworks (Chave *et al.*, 2009;
281 Díaz *et al.*, 2016; Westoby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004). But in the case of
282 SLA, its relationship to spring phenological cues was opposite of our predictions. Species with high
283 SLA—as a result of having the larger, thin leaves, with low investment in leaf mass, and generally
284 indicative of acquisitive growth strategies—had larger responses to photoperiod. Seed mass, which was
285 our one reproductive trait, showed the weakest response to all three cues, suggesting no connection
286 between seed mass and spring phenology. Our results are in line with previous studies conducted
287 at more local scales that found large relationships between height and species phenology (Osada &
288 Hiura, 2019; Seiwa, 1999), as well as findings from large-scale research which found no relationship

289 between phenology and seed mass in woody plants (Bolmgren & D. Cowan, 2008; Ettinger *et al.*, 2018).

290

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

301

302 Effects of phenology-trait relationships on community assembly

303 Our findings suggest that changing pressures across the early growing season may affect the temporal
304 assembly of communities. Early-active species had traits indicative of acquisitive growth strategies
305 that allow faster return on resource investments, like shorter heights and high LNC (Chave *et al.*,
306 2009; Grime, 1977; Westoby, 1998). **In deciduous forests**, these traits would allow early-budbursting
307 species to benefit from greater light availability in the open forest canopy in the early spring and
308 to withstand the low light conditions later in the season. In contrast, later-budbursting species had
309 traits associated with slower, more conservative, growth (Chave *et al.*, 2009; Grime, 1977; Westoby,
310 1998), which may help them compete for the more limited soil and light resources later in the growing
311 season. Similar trait-phenology relationships have also been linked to other ecological processes and
312 species characteristics that define community structure and diversity, such as species successional
313 position (Laube *et al.*, 2014), leading to the differences we observed for height and LNC in our example
314 comparing *Alnus incana* (a pioneer species) and *Quercus rubra* (a later successional species; Fig 2).
315 While our study focuses mainly on early versus later spring phenology, our approach and findings may
316 provide insights into potential trade-offs between traits and the phenological cues that underlie early
317 versus late budburst timing. In particular the relationships between traits and specific phenological
318 cues that deviated from our expectations may offer novel insights. This is the case for tree height,
319 which is related to mechanical strength and water transport (Chave *et al.*, 2009). **Our finding that tree**
320 **height was associated with chilling and photoperiod cues (but not forcing)**suggests that species use of
321 these two cues may be tied to preventing frost damage or xylem cavitation under a late spring frost

322 (Clements *et al.*, 1972; Marquis *et al.*, 2020). Similarly, the lack of a relationship between SLA and
323 temperature cues (chilling and forcing) was surprising, given that differences in leaf area can also affect
324 heat transfer, such that thicker leaves with higher SLA may have an increased risk of frost damage
325 (Lusk *et al.*, 2018). Further, many different traits may contribute to decreasing the risk of frost damage
326 (e.g., trichome density, cuticle type, Sakai & Larcher (1987)) and thus a composite of many traits may
327 give better insights into links between traits and frost damage. Well-studied traits, such as SLA, often
328 reflect multiple aspects of growth and function (Maynard *et al.*, 2022), and may be adaptive for reasons
329 other than those we predicted. . Variation SLA, for example, can also capture differences in species
330 relative growth rates or leaf longevity, and not just photosynthetic potential(Reich, 2014; Westoby,
331 1998).

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

344

345 Future outlook and applications

346 Incorporating phenology within broader trait syndromes could aid in forecasting species and commu-
347 nity responses to climate change. Decades of research have documented phenological advances with
348 anthropogenic climate change (Fitter & Fitter, 2002; Menzel *et al.*, 2006), however, increasing research
349 suggests a potential benefit to advancing, as plant species that shift their phenology with warming also
350 perform better (Cleland *et al.*, 2012). Our results suggest phenology-performance relationships could
351 be driven in part by a suite of traits that covary with phenology to determine how responsive species
352 are to warming. Our results suggest that early-active species—which other studies have found to also
353 be those that advance more with warming (Fuccillo Battle *et al.*, 2022; Menzel *et al.*, 2020)—are likely
354 to have acquisitive traits (such as shorter heights and high LNC) that allow them to grow quickly,

355 accumulate resources more quickly and possibly greater carbon sequestration over a longer growing
356 season. How much these relationships continue in the future also depends on how warming in the
357 winter and spring continues and complexities of exactly how chilling and photoperiod cues operate,
358 which is an area of active debate. Studies to date suggest chilling may decrease in most places with
359 warming (Guy, 2014; Wang *et al.*, 2022) while research on photoperiod has variously suggested pho-
360 toperiod cues could stall responses for some later-active species (Ettinger *et al.*, 2021) or have at most
361 a relatively small effect (Ettinger *et al.*, 2021, 2020).

362
363 The insight that understanding trait-phenology relationships provides into how climate change may
364 alter species coexistence and create novel species assemblages across communities (Rudolf, 2019;
365 Wolkovich & Donahue, 2021) could have important implication for restoration ecology, including for
366 pollinator communities and invasive plant management. For example, applying our approach to flower
367 and fruit traits may help link plant phenology to pollinator communities, with the opportunity to better
368 predict shifts in phenology and pollination services with climate change (Leclerc *et al.*, 2024; Pareja-
369 Bonilla *et al.*, 2025). Opportunities to better manage invasive plants may come from their tendency
370 to have earlier phenologies (Alexander & Levine, 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019)
371 and traits that facilitate fast growth (Fridley *et al.*, 2022). By identifying the trait-cue relationships
372 that shape phenology, we could use existing trait data from invasive species to better predict whether
373 they are likely to out-compete native species by growing earlier in the season and drawing down soil
374 nutrients and/or light resources that later-active native species may rely on (CITES?). This could
375 lead to better identifying which species may be of most concern and thus lead to effective management
376 practices that protect native plant communities under future climate conditions.

377 **References**

- 378 Aitken, S.N. & Bemmels, J.B. (2016) Time to get moving: assisted gene flow of forest trees. *Evolu-*
379 *tionary Applications* **9**, 271–290.
- 380 Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violette, C. (2011) When and how should
381 intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology,*
382 *Evolution and Systematics* **13**, 217–225.
- 383 Alexander, J.M. & Levine, J.M. (2019) Earlier phenology of a nonnative plant increases impacts on
384 native competitors. *PNAS* **116**, 6199–6204.
- 385 Augspurger, C.K. (2009) Spring 2007 warmth and frost : phenology , damage and refoliation in a
386 temperate deciduous forest. *Functional Ecology* **23**, 1031–1039.
- 387 Beard, K.H., Kelsey, K.C., Leffler, A.J. & Welker, J.M. (2019) The Missing Angle : Ecosystem Con-
388 sequences of Phenological Mismatch. *Trends in Ecology and Evolution* **34**, 885–888.
- 389 Bolmgren, K. & D. Cowan, P. (2008) Time – size tradeoffs: a phylogenetic comparative study of
390 flowering time, plant height and seed mass in a north-temperate flora. *Oikos* **117**, 424–429.
- 391 Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a
392 worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.
- 393 Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A. &
394 Améglio, T. (2016) Can phenological models predict tree phenology accurately in the future? The
395 unrevealed hurdle of endodormancy break. *Global change biology* **22**, 3444–3460.
- 396 Chuine, I. & Cour, P. (1999) Climatic determinants of budburst seasonality in four temperate-zone
397 tree species. *New Phytologist* **143**, 339–349.
- 398 Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S.
399 & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate
400 change.pdf. *Ecology* **93**, 1765–1771.
- 401 Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology
402 in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.
- 403 Clements, J.R., Fraser, J. W. & Yeatman, C.W. (1972) Frost Damage to White Spruce Buds. *Canadian*
404 *Journal of Forest Research* **2**, 62–63.
- 405 Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource Availability and Plant Antiherbivore Defense.
406 *Science* **230**, 895–899.

- 407 Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth,
408 C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T.,
409 Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel,
410 H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S.,
411 Günther, A., Falcuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of
412 plant form and function. *Nature* **529**, 167–171.
- 413 Ettinger, A.K., Buonaiuto, D.M., Chamberlain, C.J., Morales-Castilla, I. & Wolkovich, E.M. (2021)
414 Spatial and temporal shifts in photoperiod with climate change. *New Phytologist* **230**, 462–474.
- 415 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F., Savas, T.,
416 Samaha, J.A. & Wolkovich, E.M. (2020) Winter temperatures predominate in spring phenological
417 responses to warming. *Nature Climate Change* **10**, 1137–1142.
- 418 Ettinger, A.K., Gee, S. & Wolkovich, E.M. (2018) Phenological sequences: how early-season events
419 define those that follow. *American Journal of Botany* **105**, 1771–1780.
- 420 Fitter, A.H. & Fitter, R.S.R. (2002) Rapid Changes in Flowering Time in British Plants. *Science* **296**,
421 1689–1691.
- 422 Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across
423 all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.
- 424 Fridley, J.D., Bauerle, T.L., Craddock, A., Ebert, A.R., Frank, D.A., Heberling, J.M., Hinman, E.D.,
425 Jo, I., Martinez, K.A., Smith, M.S., Woolhiser, L.J. & Yin, J. (2022) Fast but steady: An integrated
426 leaf-stem-root trait syndrome for woody forest invaders. *Ecology Letters* **25**, 900–912.
- 427 Fuccillo Battle, K., Duhon, A., Vispo, C.R., Crimmins, T.M., Rosenstiel, T.N., Armstrong-Davies,
428 L.L. & De Rivera, C.E. (2022) Citizen science across two centuries reveals phenological change
429 among plant species and functional groups in the Northeastern US. *Journal of Ecology* **110**, 1757–1774.
- 431 Funk, J.L. & Cornwell, W.K. (2013) Leaf traits within communities: Context may affect the mapping
432 of traits to function. *Ecology* **94**, 1893–1897.
- 433 Grime, J.P. (1977) Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance
434 to Ecological and Evolutionary Theory Author (s): J . P . Grime Source : The American Naturalist
435 , Vol . 111 , No . 982 (Nov . - Dec ., 1977), pp . 1169-1194 Published. *The American Naturalist*
436 **111**, 1169–1194.

- 437 Gu, H., Qiao, Y., Xi, Z., Rossi, S., Smith, N.G., Liu, J. & Chen, L. (2022) Warming-induced in-
438 crease in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. *Nature*
439 *Communications* **13**, 1–8.
- 440 Guy, R.D. (2014) The early bud gets to warm. *New Phytologist* **202**, 7–9.
- 441 Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying dormancy
442 requirements for Pacific Northwest tree species. *Frontiers in Plant Science* **6**, 1–12.
- 443 Horbach, S., Rauschkolb, R. & Römermann, C. (2023) Flowering and leaf phenology are more variable
444 and stronger associated to functional traits in herbaceous compared to tree species. *Flora* **300**, 1–9.
- 445 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'keefe, J. & Richardson, A.D.
446 (2012) Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change
447 Biology* **18**, 2365–2377.
- 448 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C. & et al. (2020a) TRY plant trait database
449 – enhanced coverage and open access. *Global Change Biology* **26**, 119–188.
- 450 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner,
451 G.D., Aakala, T., Abedi, M., Acosta, A.T., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H.,
452 Alcántara, J.M., Alcázar C, C., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M.M., Anand,
453 M., Anderson, C., Anten, N., Antos, J., Apgaua, D.M.G., Ashman, T.L., Asmara, D.H., Asner, G.P.,
454 Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker,
455 W.J., Bakker, J.P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche,
456 D.R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann,
457 M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides,
458 R., Benomar, L., Berdugo-Lattke, M.L., Berenguer, E., Bergamin, R., Bergmann, J., Bergmann
459 Carlucci, M., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A.D., Blackman, C.,
460 Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K.T., Boeckx, P., Bohlman, S.,
461 Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C.C.,
462 Bordin, K., Boughton, E.H., Boukili, V., Bowman, D.M., Bravo, S., Brendel, M.R., Broadley, M.R.,
463 Brown, K.A., Bruelheide, H., Brummich, F., Bruun, H.H., Bruy, D., Buchanan, S.W., Bucher, S.F.,
464 Buchmann, N., Buitenwerf, R., Bunker, D.E., Bürger, J., Burrascano, S., Burslem, D.F., Butterfield,
465 B.J., Byun, C., Marques, M., Scalon, M.C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J.,
466 Camarero, J.J., Campany, C., Campetella, G., Campos, J.A., Cano-Arboleda, L., Canullo, R.,
467 Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J.A., Cavender-Bares, J.,
468 Cerabolini, B.E., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F.S., Chelli, S., Chen,

469 S.C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.S., Chytrý, M., Ciccarelli, D.,
470 Coll, L., Collins, C.G., Conti, L., Coomes, D., Cornelissen, J.H., Cornwell, W.K., Corona, P., Coyea,
471 M., Craine, J., Craven, D., Cromsigt, J.P., Csecserits, A., Cufar, K., Cuntz, M., da Silva, A.C.,
472 Dahlin, K.M., Dainese, M., Dalke, I., Dalle Fratte, M., Dang-Le, A.T., Danihelka, J., Dannoura,
473 M., Dawson, S., de Beer, A.J., De Frutos, A., De Long, J.R., Dechant, B., Delagrange, S., Delpierre,
474 N., Derroire, G., Dias, A.S., Diaz-Toribio, M.H., Dimitrakopoulos, P.G., Dobrowolski, M., Doktor,
475 D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S.,
476 Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R.L., Ejtehadi, H., Elser, J., Emilio,
477 T., Engemann, K., Erfanian, M.B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M.,
478 Domingues, T.F., Fagan, W.F., Fagúndez, J., Falster, D.S., Fan, Y., Fang, J., Farris, E., Fazlioglu,
479 F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J.,
480 Flowers, T.J., Flynn, D.F., Fontana, V., Forey, E., Forgiarini, C., Fran ois, L., Frangipani, M.,
481 Frank, D., Frenette-Dussault, C., Freschet, G.T., Fry, E.L., Fyllas, N.M., Mazzochini, G.G., Gachet,
482 S., Gallagher, R., Ganade, G., Ganga, F., Garc a-Palacios, P., Gargaglione, V., Garnier, E., Garrido,
483 J.L., de Gasper, A.L., Gea-Izquierdo, G., Gibson, D., Gillison, A.N., Giroldo, A., Glasenhardt,
484 M.C., Gleason, S., Gliesch, M., Goldberg, E., G odel, B., Gonzalez-Akre, E., Gonzalez-Andujar,
485 J.L., Gonz lez-Melo, A., Gonz lez-Robles, A., Graae, B.J., Granda, E., Graves, S., Green, W.A.,
486 Gregor, T., Gross, N., Guerin, G.R., G nther, A., Guti rez, A.G., Haddock, L., Haines, A., Hall,
487 J., Hambuckers, A., Han, W., Harrison, S.P., Hattingh, W., Hawes, J.E., He, T., He, P., Heberling,
488 J.M., Helm, A., Hempel, S., Hentschel, J., H rault, B., Her s, A.M., Herz, K., Heuertz, M., Hickler,
489 T., Hietz, P., Higuchi, P., Hipp, A.L., Hirons, A., Hock, M., Hogan, J.A., Holl, K., Honnay, O.,
490 Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K.A., Ichie, T., Igi , B., Illa, E., Isaac, M.,
491 Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C.M., Izquierdo, J., Jackson, R.B., Jackson, B., Jactel,
492 H., Jagodzinski, A.M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J.R.P., Jiang, G.F.,
493 Johansen, J.L., Johnson, D., Jokela, E.J., Joly, C.A., Jordan, G.J., Joseph, G.S., Junaedi, D., Junker,
494 R.R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E.,
495 Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M.I., Kinlock, N.L., Kissling, W.D., Kitajima, K.,
496 Kitzberger, T., Kj ller, R., Klein, T., Kleyer, M., Klime ov , J., Klipel, J., Kloepel, B., Klotz, S.,
497 Knops, J.M., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., K nig, C., Kraft,
498 N.J., Kramer, K., Kreft, H., K hn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa,
499 Y., Kuyah, S., Laclau, J.P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D.J., Laughlin,
500 D., Le Bagousse-Pinguet, Y., le Maire, G., le Roux, P.C., le Roux, E., Lee, T., Lens, F., Lewis,
501 S.L., Lhotsky, B., Li, Y., Li, X., Lichstein, J.W., Liebergesell, M., Lim, J.Y., Lin, Y.S., Linares,
502 J.C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusi , J., Lohbeck, M., L pez-Garc a,  ., Lopez-
503 Gonzalez, G., Lososov , Z., Louault, F., Luk cs, B.A., Luke , P., Luo, Y., Lussu, M., Ma, S., Maciel

504 Rabelo Pereira, C., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A.C.M., Mallik, A.,
505 Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani,
506 M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K.,
507 Mason, N., Massad, T.J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M.L., McCulloh, K.,
508 McFadden, I.R., McGill, B.J., McPartland, M.Y., Medeiros, J.S., Medlyn, B., Meerts, P., Mehrabi,
509 Z., Meir, P., Melo, F.P., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J.,
510 Michaletz, S.T., Michelaki, C., Migalina, S., Milla, R., Miller, J.E., Minden, V., Ming, R., Mokany,
511 K., Moles, A.T., Molnár, A., Molofsky, J., Molz, M., Montgomery, R.A., Monty, A., Moravcová,
512 L., Moreno-Martínez, A., Moretti, M., Mori, A.S., Mori, S., Morris, D., Morrison, J., Mucina,
513 L., Mueller, S., Muir, C.D., Müller, S.C., Munoz, F., Myers-Smith, I.H., Myster, R.W., Nagano,
514 M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A.S., Neuschulz, E.L., Ni, J.,
515 Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A.,
516 Nystuen, K.O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka,
517 T., Oliveira, R., Öllerer, K., Olson, M.E., Onipchenko, V., Onoda, Y., Onstein, R.E., Ordonez,
518 J.C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G.E., Ozinga, W.A., Pahl, A.T.,
519 Paine, C.E., Pakeman, R.J., Papageorgiou, A.C., Parfionova, E., Pärtel, M., Patacca, M., Paula,
520 S., Paule, J., Pauli, H., Pausas, J.G., Peco, B., Penuelas, J., Perea, A., Peri, P.L., Petisco-Souza,
521 A.C., Petraglia, A., Petritan, A.M., Phillips, O.L., Pierce, S., Pillar, V.D., Pisek, J., Pomogaybin,
522 A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A.S., Power, S.A.,
523 Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C.A., Reich, P.B.,
524 Reichstein, M., Reid, D.E., Réjou-Méchain, M., de Dios, V.R., Ribeiro, S., Richardson, S., Riibak,
525 K., Rillig, M.C., Riviera, F., Robert, E.M., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A.V.,
526 Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J.A.,
527 Rosenfield, M.F., Rossi, C., Roy, D.B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S.B.,
528 Rusch, G.M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina,
529 I., Santacruz-García, A.C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning,
530 M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J.V., Schowanek, S.D., Schrader, J., Schrödt,
531 F., Schuldt, B., Schurr, F., Selaya Garvizu, G., Semchenko, M., Seymour, C., Sfair, J.C., Sharpe,
532 J.M., Sheppard, C.S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T.A., Siebenkäs, A., Sierra,
533 C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N.G., Sodhi, D., Soltis, P., Soltis,
534 D., Somers, B., Sonnier, G., Sørensen, M.V., Sosinski, E.E., Soudzilovskaia, N.A., Souza, A.F.,
535 Spasojevic, M., Sperandii, M.G., Stan, A.B., Stegen, J., Steinbauer, K., Stephan, J.G., Sterck, F.,
536 Stojanovic, D.B., Strydom, T., Suarez, M.L., Svenning, J.C., Svitková, I., Svitok, M., Svoboda,
537 M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau,
538 S., Tavsanoglu, C., te Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson,

- 539 K., Thornton, P.E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M.G., Tng, D.Y.P., Tobias, J.,
540 Török, P., Tarin, T., Torres-Ruiz, J.M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F.,
541 Trotsiuk, V., Tsakalos, J.L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadéboncoeur,
542 M., Vaezi, J., Valladares, F., Vamosi, J., van Bodegom, P.M., van Breugel, M., Van Cleemput, E.,
543 van de Weg, M., van der Merwe, S., van der Plas, F., van der Sande, M.T., van Kleunen, M., Van
544 Meerbeek, K., Vanderwel, M., Vanselow, K.A., Vårhammar, A., Varone, L., Vasquez Valderrama,
545 M.Y., Vassilev, K., Vellend, M., Veneklaas, E.J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I.,
546 Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A.P., Waller, M.,
547 Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J.T.,
548 Wei, L., Weigelt, P., Weiher, E., Wells, A.W., Wellstein, C., Wenk, E., Westoby, M., Westwood,
549 A., White, P.J., Whitten, M., Williams, M., Winkler, D.E., Winter, K., Womack, C., Wright, I.J.,
550 Wright, S.J., Wright, J., Pinho, B.X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov,
551 N., Yguel, B., Zanini, K.J., Zanne, A.E., Zelený, D., Zhao, Y.P., Zheng, J., Zheng, J., Ziemińska,
552 K., Zirbel, C.R., Zizka, G., Zo-Bi, I.C., Zottz, G. & Wirth, C. (2020b) TRY plant trait database –
553 enhanced coverage and open access. *Global Change Biology* **26**, 119–188.
- 554 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014) Chilling outweighs
555 photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- 556 Laughlin, D.C., Leppert, J.J., Moore, M.M. & Sieg, C.H. (2010) A multi-trait test of the leaf-height-
557 seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* **24**, 493–501.
- 558 Leclerc, M.A.J., Gibernau, M. & Pincebourde, S. (2024) Pollination-related plant traits under environ-
559 mental changes: Seasonal and daily mismatches produce temporal constraints. *Functional Ecology*
560 pp. 1365–2435.14674.
- 561 Lenz, A., Hoch, G., Vitasse, Y. & Körner, C. (2013) European deciduous trees exhibit similar safety
562 margins against damage by spring freeze events along elevational gradients. *New Phytologist* **200**,
563 1166–1175.
- 564 Lopez, O.R., Farris-Lopez, K., Montgomery, R.A. & Givnish, T.J. (2008) Leaf phenology in relation
565 to canopy closure in southern Appalachian trees. *American Journal of Botany* **95**, 1395–1407.
- 566 Lusk, C.H., Clearwater, M.J., Laughlin, D.C., Harrison, S.P., Prentice, I.C., Nordenstahl, M. & Smith,
567 B. (2018) Frost and leaf-size gradients in forests: global patterns and experimental evidence. *New
568 Phytologist* **219**, 565–573.
- 569 Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S.M., Guaderrama, D., Hinchliff,
570 C.E., Jørgensen, P.M., Kraft, N.J., McGill, B., Merow, C., Morueta-Holme, N., Peet, R.K., Sandel,

- 571 B., Schildhauer, M., Smith, S.A., Svenning, J.C., Thiers, B., Violle, C., Wiser, S. & Enquist, B.J.
572 (2018) The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN)
573 database. *Methods in Ecology and Evolution* **9**, 373–379.
- 574 Marquis, B., Bergeron, Y., Simard, M. & Tremblay, F. (2020) Growing-season frost is a better predictor
575 of tree growth than mean annual temperature in boreal mixedwood forest plantations. *Global Change
576 Biology* **26**, 6537–6554.
- 577 Maynard, D.S., Bialic-Murphy, L., Zohner, C.M., Averill, C., Van Den Hoogen, J., Ma, H., Mo, L.,
578 Smith, G.R., Acosta, A.T.R., Aubin, I., Berenguer, E., Boonman, C.C.F., Catford, J.A., Cerabolini,
579 B.E.L., Dias, A.S., González-Melo, A., Hietz, P., Lusk, C.H., Mori, A.S., Niinemets, Ü., Pillar, V.D.,
580 Pinho, B.X., Rosell, J.A., Schurr, F.M., Sheremetev, S.N., Da Silva, A.C., Sosinski, É., Van Bode-
581 gom, P.M., Weiher, E., Bönisch, G., Kattge, J. & Crowther, T.W. (2022) Global relationships in
582 tree functional traits. *Nature Communications* **13**, 3185.
- 583 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P.,
584 Bráslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C.,
585 Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P.,
586 Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J., Wielgolaski, F.E., Zach, S. &
587 Zust, A. (2006) European phenological response to climate change matches the warming pattern.
588 *Global Change Biology* **12**, 1969–1976.
- 589 Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R. & Estrella, N. (2020) Climate
590 change fingerprints in recent European plant phenology. *Global Change Biology* **26**, 2599–2612.
- 591 Messier, J., Lechowicz, M.J., McGill, B.J., Violle, C. & Enquist, B.J. (2017) Interspecific integration
592 of trait dimensions at local scales: the plant phenotype as an integrated network. *Journal of Ecology*
593 **105**, 1775–1790.
- 594 Morales-Castilla, I., Davies, T.J., Legault, G., Buonaiuto, D.M., Chamberlain, C.J., Ettinger, A.K.,
595 Garner, M., Jones, F.A.M., Loughnan, D., Pearse, W.D., Sodhi, D. & Wolkovich, E.M. (2024)
596 Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate
597 Change* **14**, 989–995.
- 598 Natural Resources Canada (2020) Forestry glossary: Sapling.
- 599 Osada, N. & Hiura, T. (2019) Intraspecific differences in spring leaf phenology in relation to tree size
600 in temperate deciduous trees. *Tree Physiology* **39**, 782–791.

- 601 Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N.,
602 Shcherbakov, A., Meyke, E. & del Mar Delgado, M. (2013) Community-level phenological response
603 to climate change. *PNAS* **110**, 13434–13439.
- 604 Pareja-Bonilla, D., Ortiz, P.L., Morellato, L.P.C. & Arista, M. (2025) Functional traits predict changes
605 in floral phenology under climate change in a highly diverse Mediterranean community. *Functional
606 Ecology* pp. 1365–2435.70062.
- 607 Polgar, C., Gallinat, A. & Primack, R.B. (2014) Drivers of leaf-out phenology and their implications
608 for species invasions: insights from thoreau's concord. *New Phytologist* **202**, 106–115.
- 609 R Development Core Team (2017) R: A language and environment for statistical computing. *R Foun-
610 dation for Statistical Computing, Vienna, Austria* .
- 611 Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology
612 and Systematics* **16**, 179–214.
- 613 Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka,
614 D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F.,
615 Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M.,
616 Stevens, A.D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg,
617 M., Knickmann, B., Nordt, B., Wirth, C. & Römermann, C. (2024) Spatial variability in herbaceous
618 plant phenology is mostly explained by variability in temperature but also by photoperiod and
619 functional traits. *International Journal of Biometeorology* **68**, 761–775.
- 620 Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal
621 of Ecology* **102**, 275–301.
- 622 Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in
623 plant functioning. *Proceedings of the National Academy of Sciences* **94**, 13730–13734.
- 624 Rudolf, V.H.W. (2019) The role of seasonal timing and phenological shifts for species coexistence.
625 *Ecology Letters* **22**, 1324–1338.
- 626 Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants: Responses and adaptation to freezing stress*.
627 Springer-Verlag, Berlin, Heidelberg.
- 628 Seiwa, K. (1999) Changes in leaf phenology are dependent on tree height in Acer mono, a deciduous
629 broad-leaved tree. *Annals of Botany* **83**, 355–361.

- 630 Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Bar-
631 aloto, C., Carlucci, M.B., Cianciaruso, M.V., De L. Dantas, V., De Bello, F., Duarte, L.D.S., Fonseca,
632 C.R., Freschet, G.T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama,
633 C., Katabuchi, M., Kembel, S.W., Kichenin, E., Kraft, N.J.B., Lagerström, A., Bagousse-Pinguet,
634 Y.L., Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J.M., Peltzer, D.A., Pérez-Ramos,
635 I.M., Pillar, V.D., Prentice, H.C., Richardson, S., Sasaki, T., Schamp, B.S., Schöb, C., Shipley, B.,
636 Sundqvist, M., Sykes, M.T., Vandewalle, M. & Wardle, D.A. (2015) A global meta-analysis of the
637 relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**, 1406–1419.
- 638 Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., Konig, A., Nordt, B.,
639 Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstadter, A., Maskova, T., Primack,
640 R., Rosche, C., Shah, M.A., Stevens, A.D., Teilborger, K., Trager, S., Wirth, C. & Romermann,
641 C. (2022) Functional traits influence patterns in vegetative and reproductive plant phenology – a
642 multi-botanical garden study. *New Phytologist* **235**, 2199–2210.
- 643 Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3.
- 644 Stan Development Team (2024) Stan reference manual, v2.36.0.
- 645 Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J.
646 (2012) The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology
647 and Evolution* **27**, 244–252.
- 648 Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the
649 concept of trait be functional! *Oikos* **116**, 882–892.
- 650 Vitasse, Y. (2013) Ontogenetic changes rather than difference in temperature cause understory trees to
651 leaf out earlier. *New Phytologist* **198**, 149–155.
- 652 Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat,
653 C., Rebetez, M., Rixen, C., Strelbel, N., Schmidt, B.R., Wipf, S., Wohlgemuth, T., Yoccoz, N.G.
654 & Lenoir, J. (2021) Phenological and elevational shifts of plants , animals and fungi under climate
655 change in the European Alps. *Biological Reviews* **96**, 1816–1835.
- 656 Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2012) Seasonal priority effects : implications for
657 invasion and restoration in a semi-arid system. *Journal of Applied Ecology* **49**, 234–241.
- 658 Wang, H., Dai, J., Peñuelas, J., Ge, Q., Fu, Y.H. & Wu, C. (2022) Winter warming offsets one half of
659 the spring warming effects on leaf unfolding. *Global Change Biology* **28**, 6033–6049.

- 660 Wang, L., Han, X., Yin, Q., Wang, G., Xu, J., Chai, Y. & Yue, M. (2021) Differences in leaf phenological
661 traits between trees and shrubs are closely related to functional traits in a temperate forest. *Acta*
662 *Oecologica* **112**, 103760.
- 663 Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**,
664 213–227.
- 665 Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in*
666 *Ecology & Evolution* **21**, 261–268.
- 667 Wolkovich, E.M. & Cleland, E.E. (2014) Phenological niches and the future of invaded ecosystems
668 with climate change. *AoB PLANTS* **6**, 1–16.
- 669 Wolkovich, E.M. & Donahue, M.J. (2021) How phenological tracking shapes species and communities
670 in non-stationary environments. *Biological Reviews* **96**, 2810–2827.
- 671 Wolkovich, E.M. & Ettinger, A.K. (2014) Back to the future for plant phenology research. *New Phy-*
672 *tologist* **203**, 1021–1024.
- 673 Wright, I.J., Westoby, M., Reich, P.B., Oleksyn, J., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-
674 Bares, J., Chapin, T., Cornellissen, J.H.C., Diemer, M., Flexas, J., Gulias, J., Garnier, E., Navas,
675 M.L., Roumet, C., Groom, P.K., Lamont, B.B., Hikosaka, K., Lee, T., Lee, W., Lusk, C., Midgley,
676 J.J., Niinemets, Ü., Osada, H., Poorter, H., Pool, P., Veneklaas, E.J., Prior, L., Pyankov, V.I.,
677 Thomas, S.C., Tjoelker, M.G. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*
678 **428**, 821–827.
- 679 Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology
680 on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* **107**, 22151–22156.
- 681 Zeng, Z.A. & Wolkovich, E.M. (2024) Weak evidence of provenance effects in spring phenology across
682 Europe and North America. *New Phytologist* **242**, 1957–1964.
- 683 Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019) Phenology in a warming world: differences
684 between native and non-native plant species. *Ecology Letters* **22**, 1253–1263.
- 685 Zuleta, D., Muller-Landau, H.C., Duque, A., Caro, N., Cardenas, D., Castaño, N., León-Peláez, J.D.
686 & Feeley, K.J. (2022) Interspecific and intraspecific variation of tree branch, leaf and stomatal traits
687 in relation to topography in an aseasonal Amazon forest. *Functional Ecology* **36**, 2955–2968.

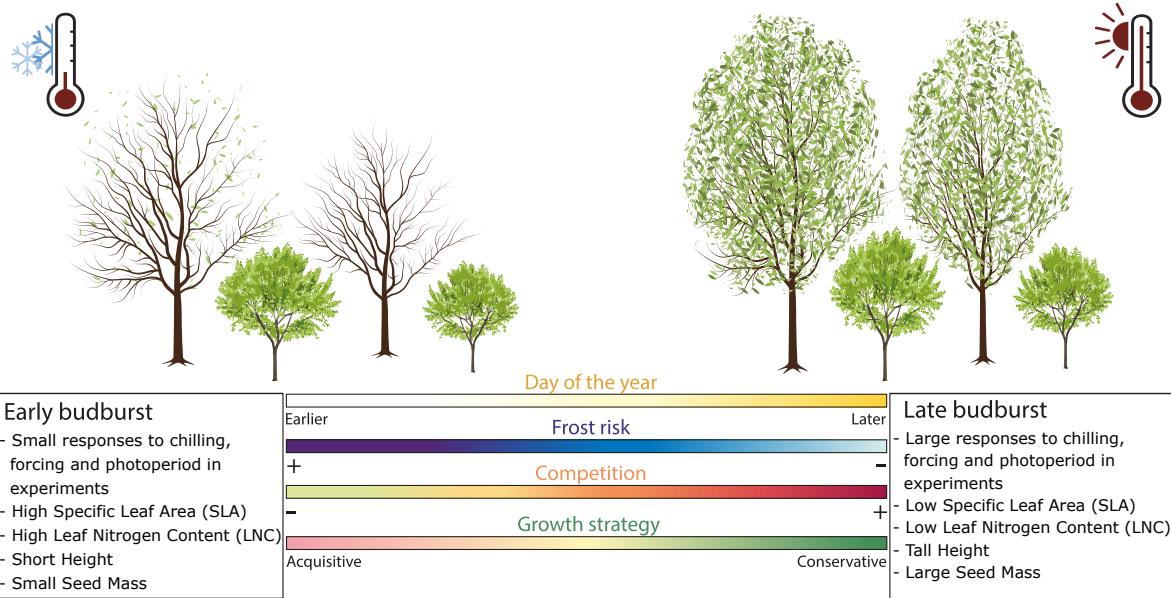


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies (Chave *et al.*, 2009; Westoby & Wright, 2006; Wright *et al.*, 2004), which may also include phenology. Drawing on previous research in plants, we predicted that early-budbursting species 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.

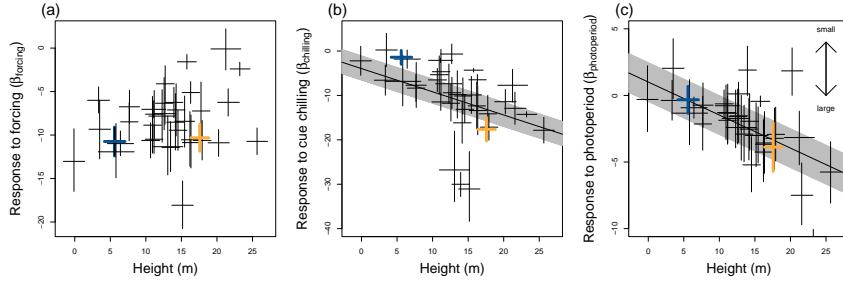


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third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

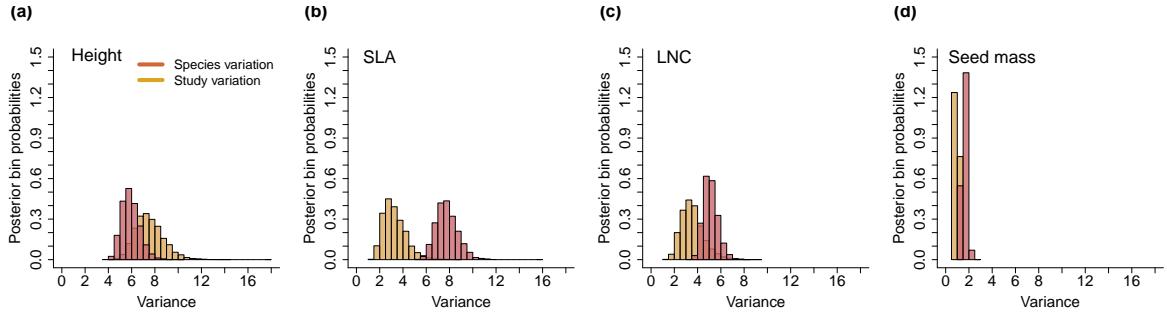


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only (a) the height model estimating greater study-level variation than species-level, while our (b) specific leaf area, (c) leaf nitrogen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