

¹ Woody plant phenological responses are strongly associated
² with key functional traits

³ Deirdre Loughnan¹, Faith A M Jones^{1,2}, Geoffrey Legault¹, Daniel Buonaiuto^{3,4,5},
Catherine Chamberlain^{3,4,6}, Ailene Ettinger⁷, Mira Garner¹, Ignacio Morales-Castilla^{8,9},
Darwin Sodhi¹, and E M Wolkovich^{1,3,4}

⁴ July 28, 2024

⁵ ¹ Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, 2424
⁶ Main Mall Vancouver, BC Canada V6T 1Z4.

⁷ ² Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sci-
⁸ ences, 901 83 Umeå, Sweden

⁹ ³ Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

¹⁰ ⁴ Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts,
¹¹ USA;

¹² ⁵ Department of Environmental Conservation, University of Massachusetts, Amherst, 160 Holdsworth
¹³ Way, Amherst, MA, USA

¹⁴ ⁶ The Nature Conservancy, 334 Blackwell St Ste 300, Durham, NC, USA

¹⁵ ⁷ The Nature Conservancy of Washington, 74 Wall Street, Seattle, WA USA

¹⁶ ⁸ GloCEE—Global Change Ecology and Evolution Group, Department of Life Sciences, University of
¹⁷ Alcalá, Alcalá de Henares, Spain

¹⁸ ⁹ Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

²⁰ Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca

²¹ Running title: Budburst responses associated with traits

³² Summary

³³ Species-level variation in phenology—the timing of recurring life history events—can vary seasonally
³⁴ with changes in abiotic risks, light, and nutrients. This favours acquisitive growth strategies early in
³⁵ the spring season and conservative growth strategies under the more benign, but competitive, envi-
³⁶ ronment later in the season. This framework infers suites of traits that may co-vary with phenologies,
³⁷ but high trait variability across environments makes this challenging to test. Using a joint model
³⁸ to accommodates this variability, we performed a meta-analysis using budburst data from controlled
³⁹ environment experiments and plant traits to test the relationships between traits and cues. Earlier
⁴⁰ species (with smaller cues) were shorter with denser, lower nitrogen leaves, but showed no relationship
⁴¹ in terms of seed mass. In general, leafout fit within the common trait framework, and can improve
⁴² predictions of how species growth strategies and phenologies may shift with climate change.

⁴³

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

⁴⁵ Introduction

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

⁵¹

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

⁶³

⁶⁴ At the ultimate level, species phenologies may vary due to changing pressures across the growing
⁶⁵ season. Species that start growth early often risk high tissue loss—due to frost damage (Sakai and
⁶⁶ Larcher, 1987; Augspurger, 2009) or high herbivore apparency (Wainwright et al., 2012)—but benefit
⁶⁷ from higher resource availability (Rathcke and Lacey, 1985; Hufkens et al., 2012). In contrast, later
⁶⁸ species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008;
⁶⁹ Wolkovich and Ettlinger, 2014). For plants, this variation in early to late season growth, may mirror
⁷⁰ the stressors from early to late successional communities, and may similarly shape phenology (Laube
⁷¹ et al., 2014).

⁷²

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

80

Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation of the leaf economic and the wood economic spectra (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016), but they can make limited predictions of trait variability (Viole et al., 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving the relationships between broader trait syndromes and phenology largely unknown. Understanding these relationships is critical to forecasting community dynamics and responses to climate change. To date, studies have generally only examined the relationship between traits and phenology within a single site (reviewed in Wolkovich and Cleland, 2014; Wolkovich and Donahue, 2021), where the problem of proximate drivers causing phenological variation can be more easily ignored. Adding phenology to broader trait frameworks requires finding a way to deal with the high levels of variation in the calendar dates of phenology when measured across sites and years.

92

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

100

Studies of spring phenology in temperate forests may provide the best opportunity to integrate phenology into functional trait research, given their cues are well understood and the strong gradients in selective environments that occur over the spring season. As in other systems, early season species trade-off high access to resources (greater soil resources and light availability) with risks of tissue loss and damage, while later season species experience a highly competitive but less risky environment. Based on these trade-offs, we predict acquisitive species to be shorter, with leaf traits favourable to higher light availability and tolerance of late spring frost (high specific leaf area, SLA, and leaf nitrogen content, LNC; Fig 1). Such species should exhibit early phenology, with small cue responses, especially to chilling and photoperiod. Canopy species that budburst later via larger cue responses, when competition for soil resources is greater, would then have traits associated with conservative growth—taller with denser wood (Laughlin et al., 2010)—with leaf traits suited for more variable light (low SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative continuum, as acquisitive species produce smaller seeds and conservative species produce larger—better provisioned—seeds (Fig 1).

115

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

125

126 Methods

127 We merged three major databases for our analysis. We gathered phenological data from the OSPREE
128 database (Ettinger et al., 2020), which contains budburst data for woody, deciduous species from ex-

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

146
 147 For our analysis, we aimed to only include species for which we had a complete trait profile (i.e.,
 148 all traits measured for all species). We initially considered six commonly measured traits—SLA, leaf
 149 dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26
 150 species had at least one trait measurement for each trait. We then used a principle component analysis
 151 to understand trait correlations and adjusted which traits we included. A PCA of our six initial traits
 152 identified high correlations between SLA and LDMC, and between height and SSD (see Supplementary
 153 material). The first principal component explained 32% of variation while the second explained 24.2%
 154 of the variation (Fig. S1). By excluding one trait from each of these highly correlated pairs of traits
 155 (specifically LDMC and SSD) we increased the number of species in our dataset from the 26 species
 156 with six traits, to 37 species for which we had complete datasets for four traits. The data for these 37
 157 species were from 24 unique studies (height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n =$
 158 7656). We subsampled height measurements to reduce the influence the 13 most frequently measured
 159 tree species had on our height model. Since these 13 species were measured 19 times more frequently
 160 than other species, for each species, we randomly sampled 3000 height measurements.

161

162 Joint model of trait and phenology

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

171 Trait sub-model

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

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

with

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

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

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

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

Phenology sub-model

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

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

with

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

and

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

where $\alpha_{\text{pheno},k}$, $\alpha_{\text{chill},k}$, $\alpha_{\text{force},k}$, and $\alpha_{\text{photo},k}$ are elements of the normal random vectors:

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

Parameter $\alpha_{\text{pheno},k}$ represents the day of budburst for species k without the influence of chilling, forcing, or photoperiod treatments. Average day of budburst (independent of treatments) is μ_{pheno} , and σ_{pheno}^2 is the variance across species. The parameters $\alpha_{\text{chill},k}$, $\alpha_{\text{force},k}$, and $\alpha_{\text{photo},k}$ represent the trait-independent responses of species k to chilling, forcing, and photoperiod treatments respectively, each with an associated mean (μ_{chill} , μ_{force} , μ_{photo}) and variance (σ_{chill}^2 , σ_{force}^2 , σ_{photo}^2) across species. The

193 effect of the species trait value, $\alpha_{\text{trait},k}$ (parameter shared with trait sub-model above), on its responses
 194 to chilling, forcing, and photoperiod are described by parameters $\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$. Finally,
 195 σ_d^2 is the variance arising from measurement error.

196

197 We chose weakly informative priors, and validated them using a series of prior predictive checks.
 198 The model was coded in the Stan programming language, fit using the rstan package version 3.3.6
 199 (Stan Development Team, 2018), with 1,000 iterations per chain across 4 chains (4,000 total sampling
 200 iterations), and all models met basic diagnostic checks, including no divergences, high effective sample
 201 size (n_{eff}), and \hat{R} close to 1. Here we present our model estimates as the means and 90% posterior
 202 uncertainty intervals.

203 Results

204 Across traits, height, SLA, and LNC strongly related to chilling, forcing and photoperiod treatments
 205 ($\beta_{\text{chill}[k]}$, $\beta_{\text{force}[k]}$, and $\beta_{\text{photo}[k]}$, Fig 4 a-i), but the direction of these relationships only showed con-
 206 sistent trends for LNC (Fig. 4 j-l). As we predicted, height was related to chilling ($\beta_{\text{chill}[k]}$) and
 207 photoperiod ($\beta_{\text{photo}[k]}$), with taller species having larger responses to cues (-0.5 m per standardized
 208 chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized photoperiod; 90% UI:
 209 -0.5, 0.0, Fig 4 a-c). As illustrated for one characteristically acquisitive species, *Alnus incana*, and one
 210 characteristically conservative species, *Quercus robur* (Fig S3), these responses led to generally later
 211 budburst ($\mu_{k,g}$), and fit within our predictions for acquisitive versus conservative growth strategies.
 212 Seed mass, however, had the smallest responses, with no relationship between seed mass and any cue
 213 (Fig. 4 g-i & Fig S3).

214

215 Of our leaf traits, we found that species SLA related to photoperiod ($\beta_{\text{photo}[k]}$, -0.2 mm²/mg per stan-
 216 dardized photoperiod; 90% UI: -0.4, 0.0, Fig. 4 f), but did not strongly predict responses to chilling
 217 ($\beta_{\text{chill}[k]}$) or forcing treatments ($\beta_{\text{force}[k]}$, Fig. 4 d and e). Thus, species with more acquisitive growth
 218 strategies (thin leaves and a lower investment in leaf mass that leads to large SLA values), had larger
 219 responses to photoperiod, contrary to our predictions (Fig. 4 d and e). For LNC, we found that species
 220 that produce leaves with high nitrogen content, which relates generally to high photosynthetic rates
 221 and acquisitive growth, show smaller responses to cues (Fig. 4 j-i). These findings are in line with
 222 our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g per
 223 standardized chilling; 90% UI: 0.3, 1.2), but we also found high LNC species to be less responsive to
 224 photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0, 0.6) and to forcing (0.5 mg/g per
 225 standardized forcing; 90% UI: 0.1, 0.9, Fig 4 j-i).

226

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

237

238 Discussion

239 We found species traits influenced the timing of budburst in response to the three primary cues of
 240 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or
 241 later phenology following well-established gradients in growth strategies predicted by functional traits
 242 (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016):
 243 early species tended to have traits associated with fast and acquisitive strategies while later species
 244 had traits associated with conservative, slower strategies. We found the largest budburst responses oc-
 245 curred for traits related to resource acquisition and structure, with SLA, LNC, and height all showing
 246 large responses across our three cues. In contrast, our one reproductive trait—seed mass—showed a
 247 smaller response. Our results provide a major step forward in integrating phenology into broader trait
 248 syndromes that shape species growth strategies, and support previous findings from more local scales
 249 that found strong relationships between height and species phenology (Sun and Frelich, 2011; Sporbert
 250 et al., 2022; Segrestin et al., 2020). Our findings also suggest other traits—such as seed mass—show
 251 no relationship with phenology in our more global analysis.

252

253 Effects of phenology-trait relationships on community assembly

254 Our findings suggest the changing selective pressures across the early growing season may effect the
 255 temporal assembly of communities, with strong abiotic pressures early in the season associated with
 256 early acquisitive species while greater biotic pressures later were associated with later conservative
 257 species. These traits of early budbursting species, such as shorter heights and low LNC, would allow
 258 them to grow quickly and benefit from greater light availability in the open canopy of many early-
 259 spring temperate forests. We found phenologically earlier species had traits that inferred faster return
 260 on resource investments (Grime, 1977; Westoby, 1998; Chave et al., 2009) and thus their tissues may be
 261 easier to replace if lost to frost or other abiotic disturbances. In contrast, phenologically later species
 262 had traits associated with greater competitive abilities and slower growth (Fig. 4, Grime, 1977; West-
 263 oby, 1998; Chave et al., 2009), which may be necessary to compete for soil and light resources when
 264 most other species are already growing. These traits can be linked to other ecological processes and
 265 species characteristics, such as species successional position, as illustrated by the differences between
 266 early and late successional species, like *Alnus incana* and *Quercus robur* (Fig 4).

267

268 The traits with cue responses that deviated from our expectations also offer novel insights into the
 269 tradeoffs between traits and environmental cues. All of our traits are associated with numerous aspects
 270 of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our
 271 predictions, we found large responses to forcing for short trees, which could prevent frost damage or
 272 xylem cavitation under a late spring frost (Clements et al., 1972; Marquis et al., 2020) and influence
 273 annual cambial meristem growth (Lenz et al., 2016). Similarly, the lack of a response to chilling or
 274 forcing by high SLA individuals could be driven by other trait attributes and environmental cues—
 275 selecting for species relative growth rates or leaf longevity—and not photosynthetic potential (Westoby,
 276 1998; Reich, 2014). These findings highlight the complexity of determining the drivers of species trait
 277 profiles, offering novel insights into how traits affect community dynamics under variable environments.

278

279 Phenology-trait relationships under future climates

280 Incorporating phenology within broader trait syndromes could aid forecasting species and community
 281 responses to climate change. While decades of research have documented phenological shifts with an-
 282 thropogenic climate change, increasing research suggests a potential connection between phenological
 283 responses to warming and performance with warming, where species that shift more with phenology
 284 appear to perform better (Cleland et al., 2012; Macgregor et al., 2019). Our results suggest this

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

292
293 Our analytical approach and results may be especially useful to help forecast changes in forest dy-
294 namics. By identifying the trait syndromes of forest communities and the interactions between traits
295 and environmental cues, we can make predictions about how climate change will alter species growth
296 and productivity, identify which species are most likely to be negatively impacted under future cli-
297 mates, and develop better strategies for climate change mitigation and conservation. For example,
298 our results suggest that, by favoring more phenologically responsive species (i.e., with small chilling
299 and photoperiod requirements), warming may also favor species with acquisitive growth strategies. In
300 contrast, conservative species, which appear less phenologically responsive (due to larger chilling and
301 photoperiod requirements) could therefore face greater abiotic and biotic stress (Guy, 2014). Species
302 that fail to advance phenologically with warming might experience more competition (Carter et al.,
303 2018; Alexander and Levine, 2019), as species that begin growth earlier in the season have more time
304 to deplete resources. Growing under warmer summer conditions could also expose species to greater
305 drought stress (Frelich and Reich, 2010). In addition to altering the timing and interactions between
306 species within a season, species trait syndromes have the potential to redefine the environmental con-
307 ditions under which growth occurs, and as a result, shape community assembly, and productivity of
308 diverse ecological communities.

309

310 References

- 311 Alexander, J. M., and J. M. Levine. 2019. Earlier phenology of a nonnative plant increases impacts
312 on native competitors. *PNAS* 116:6199–6204.
- 313 Augspurger, C. K. 2009. Spring 2007 warmth and frost : phenology , damage and refoliation in a
314 temperate deciduous forest. *Functional Ecology* 23:1031–1039.
- 315 Beard, K. H., K. C. Kelsey, A. J. Leffler, and J. M. Welker. 2019. The Missing Angle : Ecosystem
316 Consequences of Phenological Mismatch. *Trends in Ecology and Evolution* 34:885–888.
- 317 Carter, S. K., D. Saenz, and V. H. Rudolf. 2018. Shifts in phenological distributions reshape interaction
318 potential in natural communities. *Ecology Letters* 21:1143–1151.
- 319 Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a
320 worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- 321 Chuine, I., M. Bonhomme, J. M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and
322 T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The
323 unrevealed hurdle of endodormancy break. *Global change biology* 22:3444–3460.
- 324 Chuine, I., and P. Cour. 1999. Climatic determinants of budburst seasonality in four temperate-zone
325 tree species. *New Phytologist* 143:339–349.
- 326 Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta,
327 and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate
328 change.pdf. *Ecology* 93:1765–1771.
- 329 Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology
330 in response to global change. *Trends in Ecology and Evolution* 22:357–365.
- 331 Clements, J. R., W. Fraser, J, and C. W. Yeatman. 1972. Frost Damage to White Spruce Buds.
332 Canadian Journal of Forest Research 2:62–63.
- 333 Crick, H., C. Dudley, D. E. Glue, and D. L. Thomson. 1997. UK birds are laying eggs earlier. *Nature*
334 388:526–527.
- 335 D'Alba, L., P. Monaghan, and R. G. Nager. 2010. Advances in laying date and increasing population
336 size suggest positive responses to climate change in Common Eiders *Somateria mollissima* in Iceland.
337 International Journal of Avian Science 152:19–28.
- 338 Díaz, S., J. Kattge, J. H. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth,
339 I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie,
340 A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet Ev, H. Jactel, C. Baraloto,
341 B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falcuk,
342 N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function.
343 *Nature* 529:167–171.
- 344 Ettinger, A. K., C. J. Chamberlain, I. Morales-Castilla, D. M. Buonaiuto, D. F. Flynn, T. Savas,
345 J. A. Samaha, and E. M. Wolkovich. 2020. Winter temperatures predominate in spring phenological
346 responses to warming. *Nature Climate Change* 10:1137–1142.
- 347 Fajardo, A., and A. Siefert. 2016. Phenological variation of leaf functional traits within species.
348 *Oecologia* 180:951–959.
- 349 Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology
350 across all species in a temperate forest community. *New Phytologist* 219:1353–1362.

- 351 Frelich, L. E., and P. B. Reich. 2010. Will environmental changes reinforce the impact of global
352 warming on the prairie – forest border of central North America? *Frontiers in Ecology and the
353 Environment* 8:371–378.
- 354 Gorné, L. D., S. Díaz, V. Minden, Y. Onoda, K. Kramer, C. Muir, S. T. Michaletz, S. Lavorel,
355 J. Sharpe, S. Jansen, M. Slot, E. Chacon, and G. Boenisch. 2020. The acquisitive–conservative axis
356 of leaf trait variation emerges even in homogeneous environments. *Annals of Botany* .
- 357 Grime, J. P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance
358 to Ecological and Evolutionary Theory Author (s): J . P . Grime Source : The American Naturalist
359 , Vol . 111 , No . 982 (Nov . - Dec ., 1977), pp . 1169-1194 Published. The American Naturalist
360 111:1169–1194.
- 361 Gu, H., Y. Qiao, Z. Xi, S. Rossi, N. G. Smith, J. Liu, and L. Chen. 2022. Warming-induced increase
362 in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. *Nature
363 Communications* 13:1–8.
- 364 Guy, R. D. 2014. The early bud gets to warm. *New Phytologist* 202:7–9.
- 365 Harrington, C. A., and P. J. Gould. 2015. Tradeoffs between chilling and forcing in satisfying dormancy
366 requirements for Pacific Northwest tree species. *Frontiers in Plant Science* 6:1–12.
- 367 Hufkens, K., M. A. Friedl, T. F. Keenan, O. Sonnentag, A. Bailey, J. O'keefe, and A. D. Richardson.
368 2012. Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change
369 Biology* 18:2365–2377.
- 370 Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I. C. Prentice, and et al. 2020. TRY plant trait database
371 – enhanced coverage and open access. *Global Change Biology* 26:119–188.
- 372 König, P., S. Tautenhahn, J. H. C. Cornelissen, J. Kattge, G. Bönisch, and C. Römermann. 2018.
373 Advances in flowering phenology across the Northern Hemisphere are explained by functional traits.
374 *Global Ecology and Biogeography* 27:310–321.
- 375 Kusano, T., and M. Inoue. 2008. Long-Term Trends toward Earlier Breeding of Japanese Amphibians.
376 *Journal of Herpetology* 42:608–614.
- 377 Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs
378 photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- 379 Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf-
380 height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*
381 24:493–501.
- 382 Lenz, A., G. Hoch, C. Körner, and Y. Vitasse. 2016. Convergence of leaf-out towards minimum risk
383 of freezing damage in temperate trees. *Functional Ecology* 30:1480–1490.
- 384 Lopez, O. R., K. Farris-Lopez, R. A. Montgomery, and T. J. Givnish. 2008. Leaf phenology in relation
385 to canopy closure in southern Appalachian trees. *American Journal of Botany* 95:1395–1407.
- 386 Macgregor, C. J., C. D. Thomas, D. B. Roy, M. A. Beaumont, J. R. Bell, T. Brereton, J. R. Bridle,
387 C. Dytham, R. Fox, K. Gotthard, A. A. Hoffmann, G. Martin, I. Middlebrook, S. Nylin, P. J.
388 Platts, R. Rasteiro, I. J. Saccheri, R. Villoutreix, C. W. Wheat, and J. K. Hill. 2019. Climate-
389 induced phenology shifts linked to range expansions in species with multiple reproductive cycles per
390 year. *Nature Communications* 10:1–10.

- 391 Maitner, B. S., B. Boyle, N. Casler, R. Condit, J. Donoghue, S. M. Durán, D. Guaderrama, C. E.
392 Hinchliff, P. M. Jørgensen, N. J. Kraft, B. McGill, C. Merow, N. Morueta-Holme, R. K. Peet,
393 B. Sandel, M. Schildhauer, S. A. Smith, J. C. Svenning, B. Thiers, C. Viole, S. Wiser, and B. J.
394 Enquist. 2018. The bien r package: A tool to access the Botanical Information and Ecology Network
395 (BIEN) database. *Methods in Ecology and Evolution* 9:373–379.
- 396 Marquis, B., Y. Bergeron, M. Simard, and F. Tremblay. 2020. Growing-season frost is a better predictor
397 of tree growth than mean annual temperature in boreal mixedwood forest plantations. *Global Change
398 Biology* 26:6537–6554.
- 399 Mckown, A. D., R. D. Guy, M. S. Azam, E. C. Drewes, and L. K. Quamme. 2013. Seasonality and
400 phenology alter functional leaf traits. *Oecologia* 172:653–665.
- 401 Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kübler, P. Bissolli,
402 O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Don-
403 nnelly, Y. Filella, K. Jatczak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová,
404 H. Scheifinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Zust. 2006.
405 European phenological response to climate change matches the warming pattern. *Global Change
406 Biology* 12:1969–1976.
- 407 Morales-Castilla, I., T. J. Davies, G. Legault, D. M. Buonaiuto, C. J. Chamberlain, A. K. Ettinger,
408 M. Garner, F. A. M. Jones, D. Loughnan, W. D. Pearse, D. Sodhi, and E. M. Wolkovich. in prep.
409 Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate
410 Change* .
- 411 Ovaskainen, O., S. Skorokhodova, M. Yakovleva, A. Sukhov, A. Kutenkov, N. Kutenkova,
412 A. Shcherbakov, E. Meyke, and M. del Mar Delgado. 2013. Community-level phenological response
413 to climate change. *PNAS* 110:13434–13439.
- 414 Rathcke, B., and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of
415 Ecology and Systematics* 16:179–214.
- 416 Reich, P. B. 2014. The world-wide ‘fast – slow’ plant economics spectrum : a traits manifesto. *Journal of
417 Ecology* 102:275–301.
- 418 Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman.
419 1999. Generality of leaf trait relationships: A test across six biomes. *Ecology* 80:1955–1969.
- 420 Sakai, A., and W. Larcher. 1987. Frost Survival of Plants: Responses and adaptation to freezing stress.
421 Springer-Verlag, Berlin, Heidelberg.
- 422 Schuster, M. J., P. D. Wragg, and P. B. Reich. 2021. Phenological niche overlap between invasive buck-
423 thorn (*Rhamnus cathartica*) and native woody species. *Forest Ecology and Management* 498:119568.
- 424 Segrestin, J., M.-l. Navas, and E. Garnier. 2020. Reproductive phenology as a dimension of the
425 phenotypic space in 139 plant species from the Mediterranean. *New Phytologist* 225:740–753.
- 426 Sporbert, M., D. Jakubka, S. F. Bucher, I. Hensen, M. Freiberg, K. Heubach, A. Konig, B. Nordt,
427 C. Plos, I. Blinova, A. Bonn, B. Knickmann, T. Koubek, A. Linstdater, T. Maskova, R. Primack,
428 C. Rosche, M. A. Shah, A.-D. Stevens, K. Teilborger, S. Trager, C. Wirth, and C. Romermann.
429 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-
430 botanical garden study. *New Phytologist* 235:2199–2210.
- 431 Stan Development Team. 2018. RStan: the R interface to Stan. R package version 2.17.3.
- 432 Sun, S., and L. E. Frelich. 2011. Flowering phenology and height growth pattern are associated with
433 maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland
434 species. *Journal of Ecology* 99:991–1000.

- 435 Tryjanowski, P., M. Rybacki, and T. Sparks. 2003. Changes in the first spawning dates of common
436 frogs and common toads in western Poland in 1978-2002. *Annales Zoologici Fennici* 40:459–464.
- 437 Violette, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier.
438 2012. The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology
439 and Evolution* 27:244–252.
- 440 Vitasse, Y., S. Ursenbacher, G. Klein, T. Bohnenstengel, Y. Chittaro, A. Delestrade, C. Monnerat,
441 M. Rebetez, C. Rixen, N. Strelbel, B. R. Schmidt, S. Wipf, T. Wohlgemuth, N. G. Yoccoz, and
442 J. Lenoir. 2021. Phenological and elevational shifts of plants , animals and fungi under climate
443 change in the European Alps. *Biological Reviews* 96:1816–1835.
- 444 Wainwright, C. E., E. M. Wolkovich, and E. E. Cleland. 2012. Seasonal priority effects : implications
445 for invasion and restoration in a semi-arid system. *Journal of Applied Ecology* 49:234–241.
- 446 Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- 447 Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in
448 Ecology and Evolution* 21:261–268.
- 449 Wolkovich, E. M., and E. E. Cleland. 2011. The phenology of plant invasions: A community ecology
450 perspective. *Frontiers in Ecology and the Environment* 9:287–294.
- 451 ———. 2014. Phenological niches and the future of invaded ecosystems with climate change. *AoB
452 PLANTS* 6:1–16.
- 453 Wolkovich, E. M., and M. J. Donahue. 2021. How phenological tracking shapes species and communities
454 in non-stationary environments. *Biological Reviews* 96:2810–2827.
- 455 Wolkovich, E. M., and A. K. Ettinger. 2014. Back to the future for plant phenology research. *New
456 Phytologist* 203:1021–1024.
- 457 Wright, I. J., M. Westoby, P. B. Reich, J. Oleksyn, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-
458 Bares, T. Chapin, J. H. C. Cornellissen, M. Diemer, J. Flexas, J. Gulias, E. Garnier, M. L. Navas,
459 C. Roumet, P. K. Groom, B. B. Lamont, K. Hikosaka, T. Lee, W. Lee, C. Lusk, J. J. Midgley,
460 Ü. Niinemets, H. Osada, H. Poorter, P. Pool, E. J. Veneklaas, L. Prior, V. I. Pyankov, S. C. Thomas,
461 M. G. Tjoelker, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.

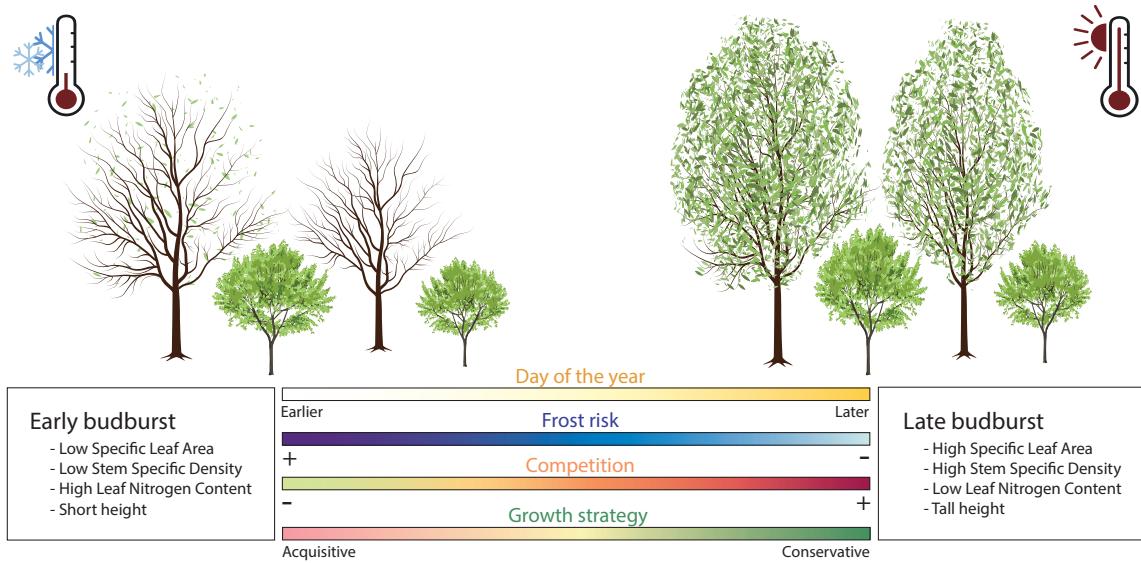


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species to exhibit traits associated with acquisitive growth, as they are more apt to experience greater risk of frost but reduced competition. In contrast, we expect later-budbursting species to exhibit traits related to conservative growth, as they experience greater competition but a more benign environment.

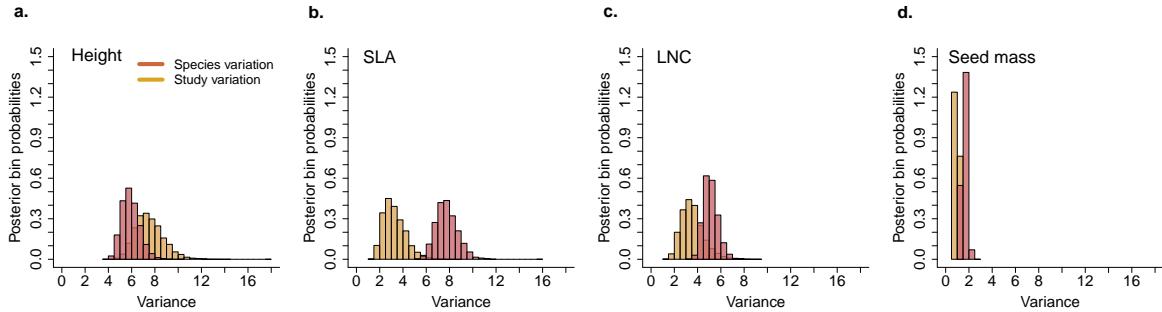


Figure 2: Traits differed in the relative magnitude of their species-level and study-level variation, with only a. the height model estimating greater study-level variation than species-level, while our b. specific leaf area, c. leaf nitrogen content, and d. seed mass models all estimated higher species-level variation. Shown here are the posterior densities for the species-level variation, shown in red, and study-level variation, shown in yellow. For comparison, we show all x-axes spanning the minimum to maximum variances across all four traits, and we show histograms for which we have normalized each bin by the total count.

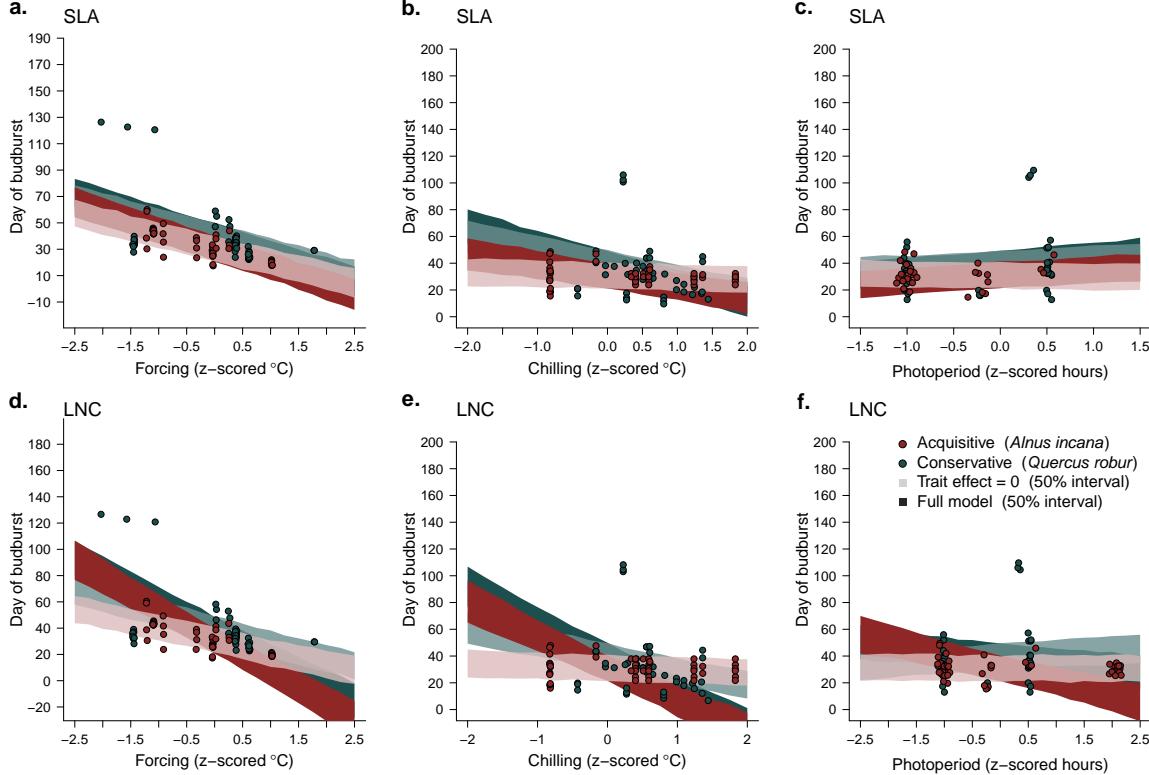


Figure 3: We expected species with traits associated with acquisitive (e.g., low SLA and LNC) versus conservative (e.g., high SLA and LNC) growth strategies would have different budburst responses to phenological cues. Our joint model allows traits of species to influence their responses to cues. We show an example here with an acquisitive species, *Alnus incana* shown in red, and a conservative species, *Quercus robur* shown in blue, for specific leaf area (SLA) and leaf nitrogen content (LNC). Our joint model estimated later budburst due to trait effects for both SLA and LNC in response to forcing and chilling and for LNC in response to photoperiod (panel d, e, g, h, and i). Only in response to photoperiod did we estimate the effect of SLA to lead to slightly earlier budburst with longer photoperiods. Bands represent the 50% uncertainty intervals of the model estimates.

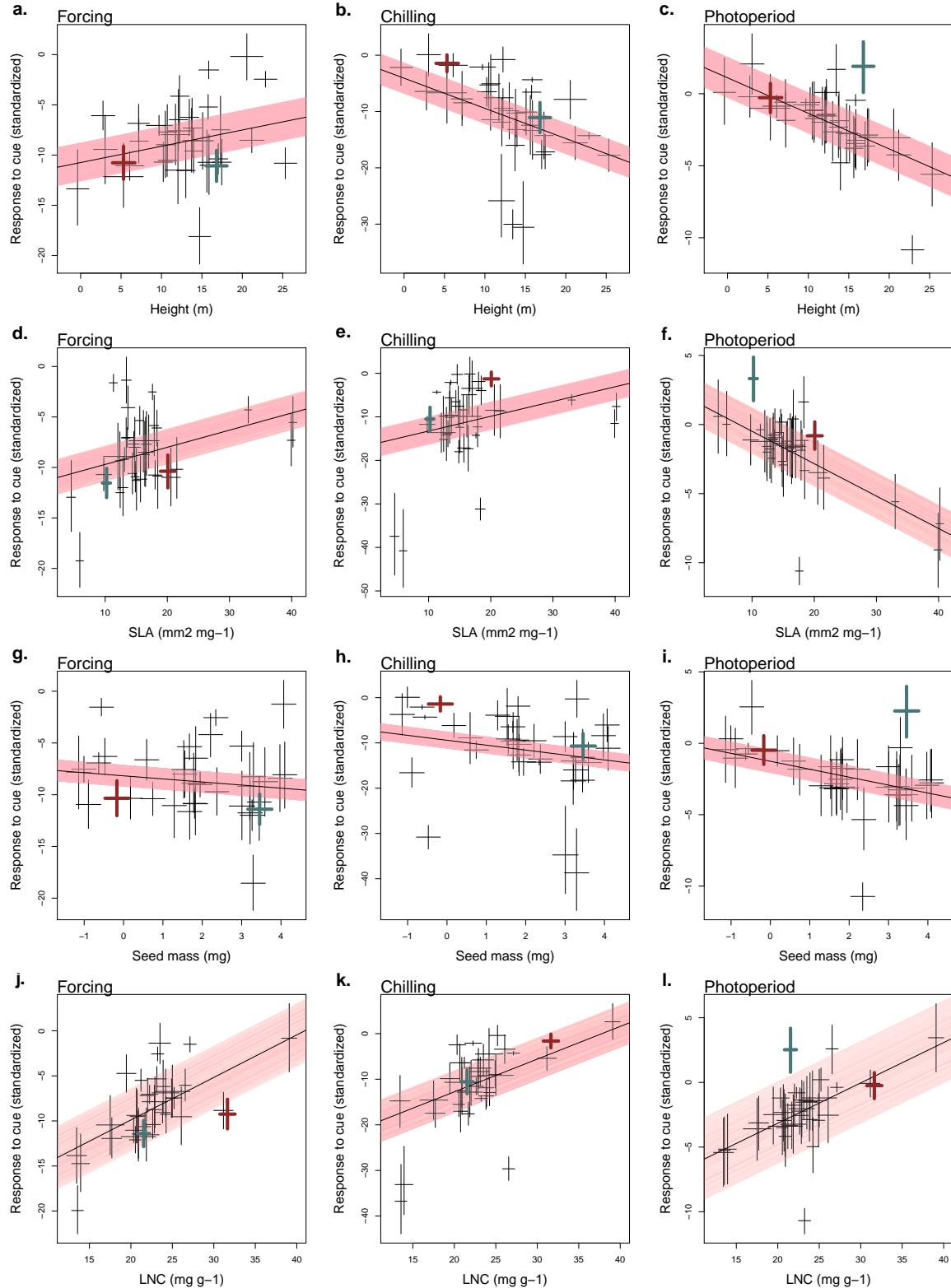


Figure 4: Estimated species-level cue responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the grey line depicting the mean linear relationship between estimated trait effects and the slope of the cue response and the pink band the 50% uncertainty interval. Each set of crossed lines represents one species, with the acquisitive species (*Alnus incana*) shown in red, and the conservative species (*Quercus robur*) shown in blue.