

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 Buonaiuto³,
Catherine Chamberlain⁴, Ailene Ettinger⁵, Mira Garner⁶, Ignacio Morales-Castilla ^{7,8},
Darwin Sodhi¹, and E M Wolkovich^{1,9,10}

⁴ May 18, 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 Sciences,
⁸ 901 83 Umeå, Sweden

⁹ ³ Department of Environmental Conservation, University of Massachusetts, Amherst, 160 Holdsworth
¹⁰ Way, Amherst, MA, USA

¹¹ ⁴ The Nature Conservancy, 334 Blackwell St Ste 300, Durham, NC, USA

¹² ⁵ The Nature Conservancy of Washington, 74 Wall Street, Seattle, WA USA

¹³ ⁶ Mira's new affiliation

¹⁴ ⁷ GloCEE—Global Change Ecology and Evolution Group, Department of Life Sciences, University of
¹⁵ Alcalá, Alcalá de Henares, Spain

¹⁶ ⁸ Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

¹⁷ ⁹ Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

¹⁸ ¹⁰ Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts,
¹⁹ USA;

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

³² **Summary**

³³ Species phenologies—the timing of recurring life history events—can vary substantially with environmental variation. While climate change has triggered shifts in phenology and changed proximate drivers like temperature, the ultimate drivers of species-level variation are still poorly understood. Across species, variation in phenology result from difference in selection between early season conditions—with trade-offs between risks of tissue loss to frost versus the availability of nutrients and light that favour acquisitive growth—and late season conditions like more benign temperatures but greater competition that favour conservative growth strategies. Drawing on the framework of plant growth strategies from the leaf economic spectrum, we can infer suites of traits that may co-vary with phenologies. But the high variability in traits across environments, and especially phenology, have made testing the role of phenology within a trait framework challenging. Here, we developed a robust modelling framework to account for this variability and performed a meta-analysis using phenological data from controlled environment experiments and plant traits to test the relationships between traits and budburst phenological cues. We found height, specific leaf area (SLA), and leaf nitrogen content (LNC) to have strong relationships with cue responses and budburst, but differences in the direction of these relationships between cue. The conservative, more competitive, phenotype of tall trees with low LNC both showed the strongest responses to chilling, photoperiod and impacts on phenology. Cues, however, varied in their relationship to SLA, with low SLA species responding to forcing, but not photoperiod. Our findings demonstrate important relationships between phenological cues and broader trait phenotypes, showing that spring leafout phenology generally fits within a functional trait framework of acquisitive to conservative growth strategies, allowing us to better predict the cues shaping species phenotypes and their influence on community dynamics.

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⁵⁵ Key Words: Budburst phenology, functional traits, Trees, climate change

⁵⁶ **Introduction**

⁵⁷ The timing of life history events—phenology—can shape both ecosystem services and community dynamics. Spring phenology, for example, defines the start and overall length of the growing season—shaping forest carbon storage and species interactions (Cleland et al., 2007; Beard et al., 2019; Gu et al., 2022). As climate change has caused spring growth to advance in many systems (Menzel et al., 2006; Vitasse et al., 2021), there is growing concern over how these changes may impact communities and ecosystems.

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⁶⁴ Predicting these changes requires understanding the drivers of phenology both at a proximate scale—the environmental triggers of phenology, such as temperature and daylength—and at an ultimate scale, of how timing may assemble species within a community (Ovaskainen et al., 2013; Wolkovich and Donahue, 2021). At the proximate level, changing environmental conditions across the winter and spring cause species to start growth at different times. This has been especially well documented for the start of growth in woody plants each year (Laube et al., 2014; Flynn and Wolkovich, 2018), with similar trends observed for spring phenological events across taxa, including in the timing of egg laying in birds (Crick et al., 1997; D’Alba et al., 2010) and the advance of spawning in amphibians (Tryjanowski et al., 2003; Kusano and Inoue, 2008). But this work has provided limited insights into the drivers of species differences (Laube et al., 2014; Chuine et al., 2016; Flynn and Wolkovich, 2018).

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⁷⁵ At the ultimate level, our predictions for why phenologies vary generally stem from our understanding of how selective pressures change across the growing season. Species that start growth early often risk high tissue loss—due to frost damage (Sakai and Larcher, 1987; Augspurger, 2009) or high herbivore apparentency (Wainwright et al., 2012)—but benefit from higher resource availability (Rathcke and Lacey, 1985; Hufkens et al., 2012). In contrast, later species face greater biotic pressures, especially from high

competition for resources (Lopez et al., 2008; Wolkovich and Ettinger, 2014).

Differences in the timing of selective pressures within the growing season could shape a number of species attributes. Species with earlier growth may produce cheaper tissues that can be more easily replaced if damaged (Reich et al., 1999). But later species would benefit from investing in tissues that infer greater resource retention (Gorné et al., 2020). These differences in traits, and trade-offs in allocation of resources to growth and tissue quality can be related to a broader framework of species growth strategies and functional traits (Wolkovich and Ettinger, 2014).

In plants, leaf and wood traits co-vary along gradients that range from acquisitive (fast) growth strategies to more conservative (slow) growth strategies (1) (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016). These global relationships are the foundation of the leaf economic spectrum and the wood economic spectrum (Wright et al., 2004; Chave et al., 2009), but are limited in their ability to predict how variable traits are (Violle et al., 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving the relationships between broader trait syndromes and phenology largely unknown, while many studies simply assume this variability to be negligible (Grime, 2006; Pau et al., 2011)

What research has been done to explore the relationship between phenology and broader trait syndromes has mostly focused on intra-specific trait variability within a growing season. This work highlights the importance of accounting for phenology when collecting trait data, demonstrating the potential for traits—and correlations between traits—to vary within a growing season relative to phenological stages (McKown et al., 2013; Fajardo and Siefert, 2016). But only a handful of studies have explicitly examined phenology-trait relationships in the context of phenological responses to climate change or environmental cues. Recent work by Sporbert et al. (Sporbert et al. 2022) conducted across European botanical gardens, however, found evidence of relationships between woody plant vegetative stages and traits such as height and leaf area, with taller trees exhibiting delays in phenology relative to short species. But the generality of these trends and whether they persist under natural conditions, is less clear.

Studies of spring phenology in temperate forests may provide the best opportunity to integrate phenology into functional trait research, given the strong gradients in selective environments that occur early versus later in the spring. 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 late 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 weak cue responses, especially to chilling and photoperiod. Canopy species that budburst later—when competition for soil resources is greatest—would have traits associated with conservative growth; being taller with denser wood (Laughlin et al., 2010), with leaf traits suited for more variable light (low SLA and LNC, Fig 1). This delayed phenology should be reflected in their higher cue responses. Seed size may similarly be predicted from this acquisitive to conservative continuum, as acquisitive species produce smaller seeds that germinate quickly and conservative species produce larger—better provisioned—seeds (Fig 1).

Testing these predictions requires a reliable way to define early to late phenology, as phenology varies strongly across sites and years. The underlying cues that predict gradients in phenology, however, do not vary strongly across space and time (Chuine and Cour, 1999; Harrington and Gould, 2015; Flynn and Wolkovich, 2018). 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 we predict to have higher

132 forcing as well .

133
134 To test these predictions of associations between budburst responses to environmental cues and com-
135 mon functional traits, we merged available data from trait databases (BIEN, Maitner et al. (2018) and
136 TRY, Kattge et al. (2020)) with budburst data from the OSPREE database of controlled environment
137 studies. We focus on woody species, initially considering six commonly measured traits—SLA, leaf dry
138 matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC. We further removed
139 SSD and LMDC from our focal traits, as they correlated strongly with height and SLA respectively
140 (see supplementary material).

141
142 To better understand the relationships between phenology and other traits, we analyzed this novel
143 and encompassing trait-phenology dataset with a hierarchical Bayesian joint model. This analytical
144 approach allows us to predict phenological responses to cues based on species-level trait values, while
145 allowing additional variation due to species. This approach takes a step towards predicting variation
146 via species traits instead of species identity. When traits explain a significant portion of the variation,
147 species will explain only a small amount, which would allow us to use trait values to predict species
148 growth strategies and phenological responses, while providing new insights into the effects of traits on
149 phenological cues.

150

151 Methods

152 For our analysis we used phenological data from the OSPREE database (Ettinger et al., 2020). The
153 OSPREE database contains phenological data for woody, deciduous species from experiments of phe-
154 nological cues. We updated the database since its initial publication, for details on the methods used
155 see Morales-Castilla et al. (in prep).

156

157 Trait data was obtained from TRY and BIEN ((Maitner et al., 2018; Kattge et al., 2020)—two large
158 trait databases compiling plant trait data across many individuals, species, and studies. We obtained
159 data from both databases on 5 December, 2018, with an updated version of the TRY data obtained
160 10 April, 2019. We focused our search for trait data on the subset of 234 OSPREE species used in
161 Morales-Castilla et al. (in prep), which represents well studied species with good phenology and phy-
162 logenetic data. Using the BIEN R package (Maitner et al., 2018), we downloaded trait data for the 94
163 available species for 13 traits. The TRY database included 96 of our focal species with ten functional
164 traits (Kattge et al., 2020). Only trait data from adult individuals with a minimum height of 1.42
165 m was included in our analyses and we removed all data from experiments or from plants growing in
166 non-natural habitats. We also grouped trait values where appropriate, for example categorizing trait
167 values for SLA, SLA with petioles, and SLA without petioles as simply SLA in our analysis (Table
168 SS1). Duplicated data in both the TRY and BIEN datasets were also removed ($n = 434905$).

169

170 For our analysis, we aimed to only include species for which we had a complete trait profile, subsetting
171 the phenology and trait data to include only species for which we had at least one measurement for
172 each trait. We used a principle component analysis to understand trait correlations and adjusted which
173 traits we included. A PCA of our six initial traits identified high correlations between SLA and leaf
174 dry matter content (LDMC), and between height and stem specific density (SSD, see Supplementary
175 material). In this analysis, the principal component explained 32% of variation while the second ex-
176 plained 24.2% of the variation (Fig. SS1). By excluding one trait from each of these pairs (specifically
177 LDMC and SSD) we increased the number of species in our dataset from the 26 species with six traits,
178 to 37 species for which we had complete datasets for four traits. The data for these 37 species was
179 from 24 unique studies (height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n = 7656$). We
180 subsampled height measurements to reduce the influence the 13 most frequently measured tree species

had on our height model. These species were measured on average 19 times more frequently than other species in our dataset and therefore we randomly sampled 3000 height measurements for each of these species.

184

185 Joint model of trait and phenology

186 To understand connections between phenology and other species traits, we built a joint model for
 187 each trait (height, SLA, LNC, and seed mass) with the major phenological cues (forcing, chilling, and
 188 photoperiod) to predict day of year of budburst.

189

190 The joint model includes a hierarchical linear model to partition variation for individual observations
 191 (i) of a given trait value ($y_{\text{trait}[i]}$) to the effects of species (*sp id*), study (*study id*), and residual
 192 variation (σ_{trait} , also called ‘measurement error’).

$$\begin{aligned} \mu_{\text{trait}} &= \alpha_{\text{grand trait}} + \alpha_{\text{sp[sp id]}} + \alpha_{\text{study[study id]}} \\ \alpha_{\text{trait sp[sp id]}} &\sim \text{normal}(0, \sigma_{\alpha_{\text{sp}}}) \\ \alpha_{\text{study[study id]}} &\sim \text{normal}(0, \sigma_{\alpha_{\text{study}}}) \\ y_{\text{trait}[i]} &\sim \text{normal}(\mu_{\text{trait}}, \sigma_{\text{trait}}) \end{aligned} \quad (1)$$

193 It estimates a separate value for each species ($\alpha_{\text{sp[sp id]}}$), and study ($\alpha_{\text{study[study id]}}$), while partially
 194 pooling across species and studies to yield overall estimates of variance across each ($\sigma_{\alpha_{\text{sp}}}$ and $\sigma_{\alpha_{\text{study}}}$,
 195 respectively).

These species-level estimates of traits ($\alpha_{\text{trait sp[sp id]}}$) were then used as predictors of species-level
 estimates of each phenological cue ($\beta_{\text{force[sp]}}$, $\beta_{\text{chill[sp]}}$, $\beta_{\text{photo[sp]}}$)

$$\begin{aligned} \beta_{\text{chill[sp]}} &= \alpha_{\text{chill[sp]}} + \beta_{\text{trait.chill}} \times \alpha_{\text{trait sp[sp]}} \\ \beta_{\text{force[sp]}} &= \alpha_{\text{force[sp]}} + \beta_{\text{trait.force}} \times \alpha_{\text{trait sp[sp]}} \\ \beta_{\text{photo[sp]}} &= \alpha_{\text{photo[sp]}} + \beta_{\text{trait.photo}} \times \alpha_{\text{trait sp[sp]}} \end{aligned} \quad (2)$$

Days to budburst ($y_{\text{pheno}[i]}$) is then predicted by the phenological cues and variation across experiments
 in chilling, forcing and photoperiod levels (C_i , F_i , P_i , respectively, which we z -scored to allow direct
 comparison of cues), with residual variation estimated across species ($\alpha_{\text{pheno[sp]}}$) and observations
 (σ_{pheno}):

$$\begin{aligned} \mu_{\text{pheno}} &= \alpha_{\text{pheno[sp]}} + \beta_{\text{chill[sp]}} \times C_i + \beta_{\text{force[sp]}} \times F_i + \beta_{\text{photo[sp]}} \times P_i \\ y_{\text{pheno}[i]} &\sim \text{normal}(\mu_{\text{pheno}}, \sigma_{\text{pheno}}) \end{aligned} \quad (3)$$

The model includes partial pooling for residual variation in days to budburst across species and variation
 in each phenological cue not attributed to the trait:

$$\begin{aligned} \alpha_{\text{pheno}} &\sim \text{normal}(\mu_{\alpha_{\text{pheno}}}, \sigma_{\alpha_{\text{pheno}}}) \\ \alpha_{\text{force}} &\sim \text{normal}(\mu_{\alpha_{\text{force}}}, \sigma_{\alpha_{\text{force}}}) \\ \alpha_{\text{chill}} &\sim \text{normal}(\mu_{\alpha_{\text{chill}}}, \sigma_{\alpha_{\text{chill}}}) \\ \alpha_{\text{photo}} &\sim \text{normal}(\mu_{\alpha_{\text{photo}}}, \sigma_{\alpha_{\text{photo}}}) \end{aligned} \quad (4)$$

196 We chose weakly informative priors, and validated them using a series of prior predictive checks. The
 197 model was coded in the Stan programming language, fit using the rstan package (Stan Development
 198 Team, 2018), with 1,000 iterations per chain across 4 chain (4,000 total sampling iterations), and all
 199 models met basic diagnostic checks, including no divergences, high effective sample size (n_{eff}), and
 200 \hat{R} close to 1.

201 Results

202 We combined the species-level trait estimates with data on forcing, chilling and photoperiod values
 203 from the OSPREE database of phenological experiments in order to test if traits (height, SLA, seed
 204 mass, LNC) related to phenological cues and species budburst dates (Fig. 3). For some traits we
 205 did find traits to relate to variation in phenological cues across species, with some species exhibiting
 206 stronger or weaker responses (as illustrated conceptually in Fig 3a and c), while traits were weak pre-
 207 dictors for other species (Fig 3b).

208 Across traits, height, SLA, and LNC strongly predicted responses to different cue-levels ($(\beta_{chill[sp]},$
 209 $\beta_{force[sp]},$ and $\beta_{photo[sp]}$, Fig 4 a-i), but only showed consistent directions of responses across cues for
 210 LNC (Fig. 4 j-l). As we predicted, height was related to chilling and photoperiod cues, with taller
 211 species having larger responses with stronger cues (-0.5 m per standardized chilling; 90% uncertainty
 212 interval (UI): -1, -0.1 and -0.2 m per standardized photoperiod; 90% UI: -0.5, 0, Fig 4 a-c). As illus-
 213 trated for the characteristically acquisitive species, *Alnus incana*, and conservative species, (*Quercus*
 214 *robur*) (Fig S3), this gradient in their response to chilling and photoperiod cues leads to delayed bud-
 215 burst (μ_{pheno}), and therefore fits within an overall gradients in growth strategy. Seed mass, however,
 216 had the weakest responses, with no considerable relationship between seed mass and cues across the
 217 three cues (Fig. 4 g-i & Fig S3).

218
 219 Of our leaf traits, we found species SLA to relate to photoperiod (-0.2 mm²/mg per standardized
 220 photoperiod; 90% UI: -0.4, 0.0, Fig. 4 f), but did not strongly predict responses to chilling or forcing
 221 (Fig. 4 d and e). Thus, species with more acquisitive growth strategies (thin leaves and a lower
 222 investment in leaf mass that leads to high SLA values), had larger responses to photoperiod cues,
 223 contrary to our predictions (Fig. 4 d and e). For LNC, we found that species that produce leaves with
 224 high nitrogen content, which relates generally to high photosynthetic rates and acquisitive growth,
 225 show weak responses to cues (Fig. 4 j-i). These findings are in line with our predictions that high
 226 LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g per standardized chilling;
 227 90% UI: 0.3, 1.2), but we found similar responses to photoperiod (0.3 mg/g per standardized photope-
 228 rioid; 90% UI: 0, 0.6) and to forcing cues (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig 4 j-i).

229
 230 Across our models, we found species-level variation across traits ($\sigma_{sp[sp id]}$) was comparable with or
 231 greater than variation across studies ($\sigma_{study[study id]}$, Fig 2). Variation across studies was greatest for
 232 height (7.5 m compared to 5.9 m species-level variation, Fig 2a). For seed mass and LNC study-
 233 level variation was less than that of the species-level variation (seed mass study-level variation: 1 mg;
 234 versus species-level variation: 1.6 mg; LNC study-level variation 3.6 mg g⁻¹ versus species-level vari-
 235 ation: 5.1 mg g⁻¹; Fig 2c and d). At the lowest end, study-level variation in SLA was approximately
 236 half the value of the species-level variation (and 3.3 mm² mg⁻¹ versus 7.8 mm² mg⁻¹, respectively,
 237 Fig 2b). The magnitude of study-level variation we observed suggests that models using large trait
 238 databases that fail to separate out study from species-level variation may poorly estimate species traits.
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240

241 Discussion

242 We found species traits influenced the timing of budburst in response to three primary cues for spring
 243 phenology (chilling, forcing and photoperiod). Whether these trait effects were associated with earlier
 244 or later phenology was correlated with well known gradients in traits, that vary from acquisitive to
 245 conservative growth strategies. The greatest budburst responses occurred for traits related to resource
 246 acquisition and structure, with SLA, LNC, and height all depicting strong responses across our three
 247 cues. In contrast, our one reproductive trait—seed mass—showed a weak response. Despite finding
 248 these general trends in trait relationships to phenology, we also found considerable variation across

²⁴⁹ studies, often at a magnitude comparable to the differences observed across species.

²⁵⁰

²⁵¹ Gradients in phenology generally followed similar gradients in traits varied from fast and acquisitive
²⁵² to conservative, slower growth strategies. Phenologically earlier species had traits that inferred faster
²⁵³ return on resource investments (Grime, 1977; Westoby, 1998; Chave et al., 2009). In contrast, phe-
²⁵⁴ nologically late species filled different trait space (Fig. 4), exhibiting a phenotype that infers greater
²⁵⁵ competitive abilities and slower growth (Grime, 1977; Westoby, 1998; Chave et al., 2009). Our findings
²⁵⁶ suggest the assembly of communities results from varying selective pressures, such as strong abiotic
²⁵⁷ filters early in the growing season, and greater biotic pressures later in the season. By including phe-
²⁵⁸ nology in the trait framework, we can identify these interactions across traits and cues and tease apart
²⁵⁹ the underlying mechanisms shaping species' phenology across communities.

²⁶⁰

²⁶¹ Effects of phenology-trait relationships on community assembly

²⁶² In our study of temperate forest communities, the relationships between budburst phenology and other
²⁶³ plant traits provided insights into the mechanisms that shape species phenotypes. Earlier budbursting
²⁶⁴ species had traits, such as shorter heights and low LNC, that allow them to grow quickly and benefit
²⁶⁵ from greater light availability in the open canopy of many early-spring temperate forests. This phe-
²⁶⁶ notype can be linked to other ecological processes and species characteristics, such as species successional
²⁶⁷ position, as illustrated by the differences between early and late successional species, like *Alnus incana*
²⁶⁸ and *Quercus robur* (Fig 4). Our results may also be useful to help predict the potential for invasion,
²⁶⁹ as communities with similar phenologies and suites of traits, appear more susceptible to fast growing,
²⁷⁰ non-native species (Wolkovich and Cleland, 2011; Alexander and Levine, 2019; Schuster et al., 2021).
²⁷¹ In identifying the trait syndromes of native forest communities and the interactions between traits and
²⁷² environmental cues, we can better predict the changes in environmental cues that will alter species
²⁷³ growth strategies and productivity, and help identify which species are most likely to be negatively
²⁷⁴ impacted under future climates, thus informing mitigation and conservation efforts.

²⁷⁵

²⁷⁶ The traits with cue responses that deviated from our expectations also offer novel insights into the
²⁷⁷ tradeoffs between traits and environmental cues. All of our traits are associated with numerous aspects
²⁷⁸ of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our
²⁷⁹ predictions, we found strong forcing cues for short trees, which could prevent frost damage or xylem
²⁸⁰ cavitation under a late spring frost (Clements et al., 1972; Marquis et al., 2020) and influence annual
²⁸¹ cambial meristem growth (Lenz et al., 2016). Similarly, the lack of chilling or forcing responses by
²⁸² high SLA individuals' could be driven by other trait attributes and environmental cues—selecting for
²⁸³ species relative growth rates or leaf longevity—and not photosynthetic potential (Westoby, 1998; Re-
²⁸⁴ ich, 2014). These findings highlight the complexity of determining the drivers of species trait profiles,
²⁸⁵ offering novel insights into how traits affect community dynamics under variable environments.

²⁸⁶

²⁸⁷ Phenology-trait relationships under future climates

²⁸⁸ Incorporating phenology within broader trait syndromes is necessary to accurately predict species re-
²⁸⁹ sponses to climate change. Recent phenological shifts are well documented, but there remains a high
²⁹⁰ degree of unexplained variation across species and populations (Vitasse et al., 2009; Wolkovich and
²⁹¹ Ettinger, 2014; Zohner and Renner, 2014; Vitasse et al., 2018). Our findings demonstrate that the
²⁹² same environmental cues driving phenological traits also relate to leaf and structural traits and thus
²⁹³ suggest that warming that favors species with certain phenological cues, and can select for specific
²⁹⁴ trait syndromes.

²⁹⁵

296 In temperate forests, warming may favor species with weak chilling and photoperiod requirements,
297 as these requirements may allow phenology to shift more with warming. Our results suggest that
298 these low cue requirements co-vary with acquisitive growth strategies. Thus, future forests may be
299 dominated by species with lower chill and photoperiod cues and with traits that allow them to grow
300 faster and rapidly acquire resources, while also being more vulnerable to late-season frosts, when they
301 do occur. In contrast, conservative species with high chilling and photoperiod requirements, could
302 face greater abiotic stress. Rising winter temperatures could result in insufficient chilling, while strong
303 photoperiod cues could limit species ability to advance in response to warmer spring conditions (Guy,
304 2014). Species that are less able to advance phenologically might experience more competition (Carter
305 et al., 2018; Alexander and Levine, 2019), as species that begin growth earlier in the season deplete
306 resources. Growing under warmer summer conditions could also expose species to greater drought
307 stress (Frelich and Reich, 2010). In addition to altering the timing and interactions between species
308 within a season, species trait syndromes have the potential to redefine the environmental conditions
309 under which growth occurs.

310

311 Our study is one of the first to jointly model budburst cues and timing with other trait relationships.
312 Using this approach we identified trends in phenological cues based on species-level trait variation,
313 while accounting for the high degree of uncertainty that arises when combining datasets of diverse
314 communities. While the available data limited the number of species, our dataset represents the most
315 comprehensive trait syndrome available, making it an important first step to identify general trends
316 that scale across populations and species. We have demonstrated that species' traits and phenologies
317 are inextricably linked to varying survival strategies, such as strong abiotic filters early in the growing
318 season, and greater biotic pressures later in the season, producing varying selective pressures that may
319 shape the assembly of communities. By including phenology in the existing trait framework, we can
320 identify the key interactions across traits and cues and tease apart the underlying mechanisms shaping
321 species phenology across communities. In doing so, we can address the complex interactions shaping
322 communities, and implement a more holistic approach to better forecast future changes, as species
323 phenologies respond to climate change and impact processes of community assembly and productivity
324 of diverse ecological communities.

325

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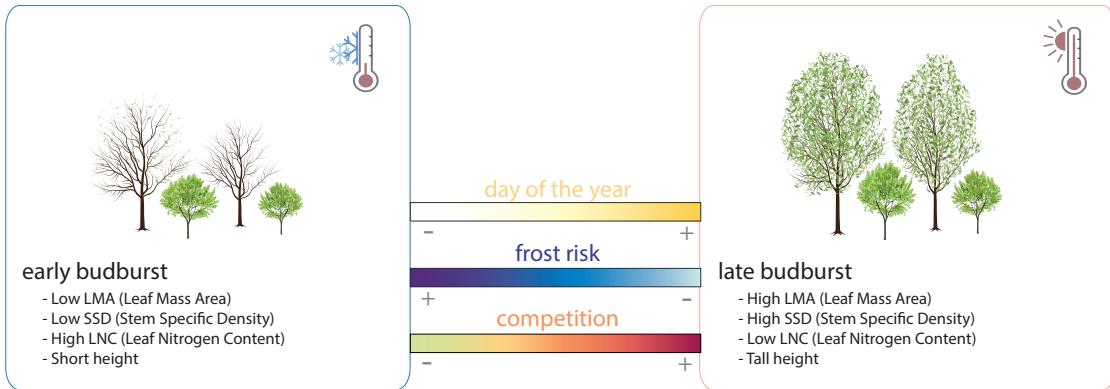


Figure 1: Leaf and wood trait are known to follow gradients that vary from acquisitive versus conservative growth strategies. Less clear, however, is how well this variation corresponds to phenology. We expect phenologically early species to exhibit traits associated with acquisitive, as they are more apt to experience greater risk of frost but reduced competition. In contrast, phenologically delayed species should exhibit traits related to conservative growth, as they experience greater competition but a more benign environment.

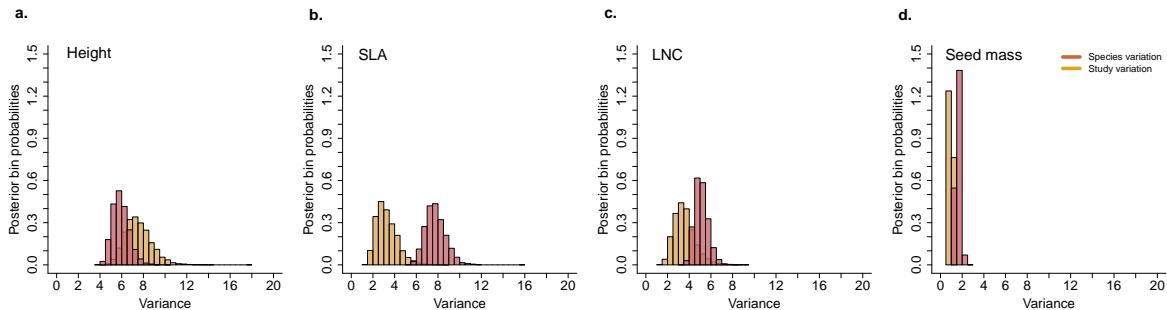


Figure 2: Comparison of the posterior densities for the species-level variation and study-level variation of a. height, b. specific leaf area, c. leaf nitrogen content, and d. seed mass.

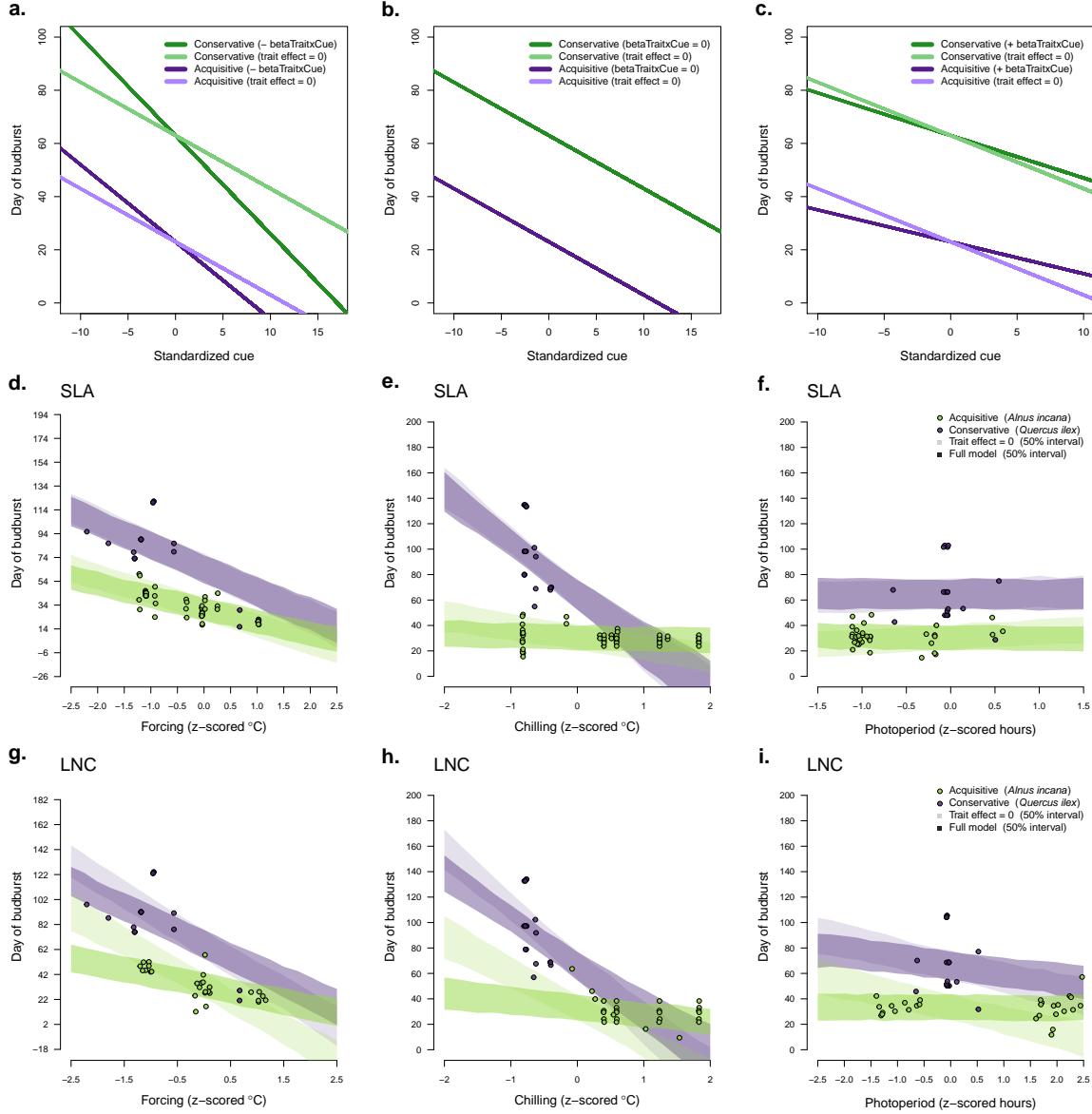


Figure 3: Functional traits may contribute to the species responses to forcing, chilling, or photoperiod cues in several ways. a) If traits are also responding to the environmental cue and lead to stronger phenological responses (larger in magnitude) then budburst will be earlier with increasing chilling, forcing and photoperiod. b) But if traits have no effect on the timing of budburst, then phenological responses will be equivalent to the cue only model estimates. c) Traits that have an opposing relationship to cues will produce weaker phenological responses (smaller in magnitude) and produce later budburst dates. A delay in day of budburst due to trait effects was found for both SLA and LNC in response to forcing and chilling cues and for LNC in response to photoperiod cues (panel d, e, g, h, and i). Only in response to photoperiod does the effect of SLA lead to stronger phenological responses and slightly earlier budburst with longer photoperiods. Species with conservative traits are shown in purple and species with acquisitive growth shown in green. Bands represent the 50% uncertainty intervals of the model estimates.

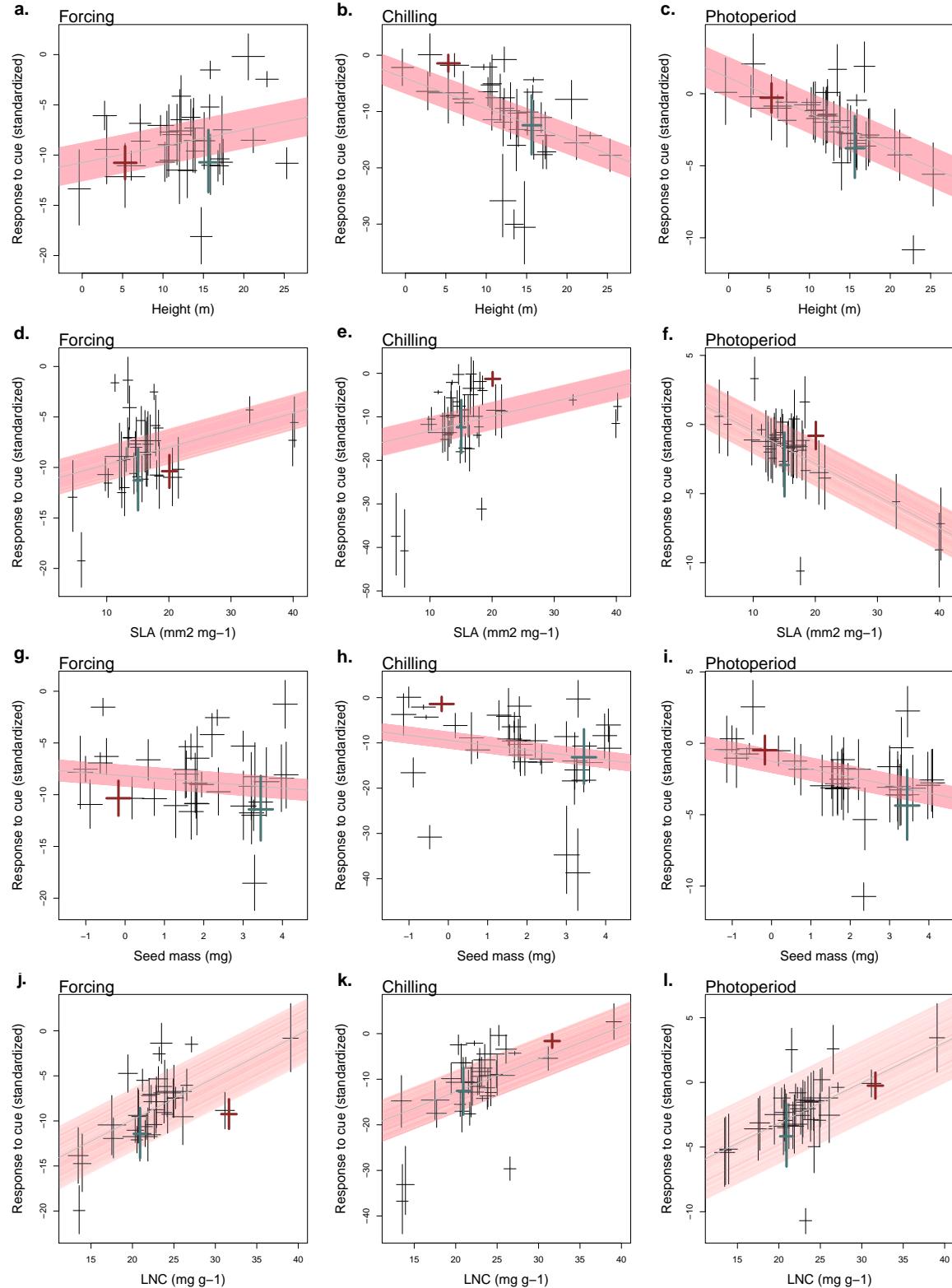


Figure 4: Estimated trait values for height (a-c), SLA (d-f), log₁₀ Seed mass (g-i), and LNC (j-l), correlated against species-level cue responses to standardized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using a joint trait-phenology 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% confidence interval. Each set of crossed lines represents one species, with the acquisitive species, such as *Alnus incana* shown in red, and the conservative species, such as *Quercus robur*, shown in blue.