

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

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³³ **Summary**

³⁴ 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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⁵⁶ Key Words: Budburst phenology, functional traits, Trees, climate change

⁵⁷ **Introduction**

⁵⁸ 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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⁶⁵ 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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⁷⁶ 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

133 forcing as well .

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

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

151

152 Methods

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

157

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

170

171 For our analysis, we aimed to only include species for which we had a complete trait profile, subsetting
 172 the phenology and trait data to include only species for which we had at least one measurement for
 173 each trait. We used a principle component analysis to understand trait correlations and adjusted which
 174 traits we included. A PCA of our six initial traits identified high correlations between SLA and leaf
 175 dry matter content (LDMC), and between height and stem specific density (SSD, see Supplementary
 176 material). In this analysis, the principal component explained 32% of variation while the second ex-
 177 plained 24.2% of the variation (Fig. SS1). By excluding one trait from each of these pairs (specifically
 178 LDMC and SSD) we increased the number of species in our dataset from the 26 species with six traits,
 179 to 37 species for which we had complete datasets for four traits. The data for these 37 species was
 180 from 24 unique studies (height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n = 7656$). We
 181 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.

185

186 Joint model of trait and phenology

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

190

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

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

194 It estimates a separate value for each species ($\alpha_{\text{sp[sp id]}}$), and study ($\alpha_{\text{study[study id]}}$), while partially
 195 pooling across species and studies to yield overall estimates of variance across each ($\sigma_{\alpha_{\text{sp}}}$ and $\sigma_{\alpha_{\text{study}}}$,
 196 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:

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

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

202 Results

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

209

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

220

221 Of our leaf traits, we found species SLA to relate to photoperiod (-0.2 mm²/mg per standardized
 222 photoperiod; 90% UI: -0.4, 0.0, Fig. 4 f), but did not strongly predict responses to chilling or forcing
 223 (Fig. 4 d and e). Thus, species with more acquisitive growth strategies (thin leaves and a lower
 224 investment in leaf mass that leads to high SLA values), had larger responses to photoperiod cues,
 225 contrary to our predictions (Fig. 4 d and e). For LNC, we found that species that produce leaves with
 226 high nitrogen content, which relates generally to high photosynthetic rates and acquisitive growth,
 227 show weak responses to cues (Fig. 4 j-i). These findings are in line with our predictions that high
 228 LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g per standardized chilling;
 229 90% UI: 0.3, 1.2), but we found similar responses to photoperiod (0.3 mg/g per standardized photope-
 230 riod; 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).

231

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

241

242 Discussion

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

250 variation across studies, often at a magnitude comparable to the differences observed across species.
 251

252 Effects of phenology-trait relationships on community assembly

253 The relationships between traits and phenological cues provide insight into how proximate drivers of
 254 phenology can impact process, like community assembly, at ultimate scales. Phenologically earlier
 255 species had traits that inferred faster return on resource investments (Grime, 1977; Westoby, 1998;
 256 Chave et al., 2009). In contrast, phenologically late species filled different trait space (Fig. 4), exhibiting
 257 a phenotype that infers greater competitive abilities and slower growth (Grime, 1977; Westoby,
 258 1998; Chave et al., 2009). Our findings suggest the temporal assembly of communities results from
 259 varying selective pressures, with strong abiotic filters acting early in the growing season, versus greater
 260 biotic pressures later in the season. By including phenology in the trait framework, we can identify
 261 these interactions across traits and cues and tease apart the underlying mechanisms shaping species'
 262 phenology and communities.

263
 264 In our study of temperate forest communities, the relationships between budburst phenology and other
 265 plant traits allowed us to better understand the mechanisms that shape woody species phenotypes.
 266 Earlier budbursting species had traits, such as shorter heights and low LNC, that allow them to grow
 267 quickly and benefit from greater light availability in the open canopy of many early-spring temperate
 268 forests. This phenotype can be linked to other ecological processes and species characteristics, such
 269 as species successional position, as illustrated by the differences between early and late successional
 270 species, like *Alnus incana* and *Quercus robur* (Fig 4).

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

282
 283 Our analytical approach and results can be used to help forecast future changes in forest communities
 284 and productivity. Understanding how phenology relates to species broader trait syndromes allows
 285 us to better predict the potential for invasion, as communities with similar phenologies and suites
 286 of traits, appear more susceptible to fast growing, non-native species (Wolkovich and Cleland, 2011;
 287 Alexander and Levine, 2019; Schuster et al., 2021). By identifying the trait syndromes of native forest
 288 communities and the interactions between traits and environmental cues, we can better predict how
 289 climate change will alter species growth and productivity, identify which species are most likely to be
 290 negatively impacted under future climates, and develop better strategies for climate change mitigation
 291 and conservation.

293 Phenology-trait relationships under future climates

294 Incorporating phenology within broader trait syndromes is necessary to accurately predict species re-
 295 sponds to climate change. Recent phenological shifts are well documented, but there remains a high
 296 degree of unexplained variation across species and populations (Vitasse et al., 2009; Wolkovich and
 297 Ettinger, 2014; Zohner and Renner, 2014; Vitasse et al., 2018). Our findings demonstrate that the

298 same environmental cues driving phenological traits also relate to leaf and structural traits and thus
299 suggest that warming that favors species with certain phenological cues, and can select for specific
300 trait syndromes.

301

302 In temperate forests, warming may favor species with weak chilling and photoperiod requirements,
303 as these requirements may allow phenology to shift more with warming. Our results suggest that
304 these low cue requirements co-vary with acquisitive growth strategies. Thus, future forests may be
305 dominated by species with lower chill and photoperiod cues and with traits that allow them to grow
306 faster and rapidly acquire resources, while also being more vulnerable to late-season frosts, when they
307 do occur. In contrast, conservative species with high chilling and photoperiod requirements, could
308 face greater abiotic stress. Rising winter temperatures could result in insufficient chilling, while strong
309 photoperiod cues could limit species ability to advance in response to warmer spring conditions (Guy,
310 2014). Species that are less able to advance phenologically might experience more competition (Carter
311 et al., 2018; Alexander and Levine, 2019), as species that begin growth earlier in the season deplete
312 resources. Growing under warmer summer conditions could also expose species to greater drought
313 stress (Frelich and Reich, 2010). In addition to altering the timing and interactions between species
314 within a season, species trait syndromes have the potential to redefine the environmental conditions
315 under which growth occurs.

316

317 Our study is one of the first to jointly model budburst cues and timing with other trait relationships.
318 Using this approach we identified trends in phenological cues based on species-level trait variation,
319 while accounting for the high degree of uncertainty that arises when combining datasets of diverse
320 communities. Despite the diversity within our dataset being limited by the availability of data, our
321 dataset represents the most comprehensive trait syndrome available, making it an important first step
322 to identify general trends that scale across populations and species. Further, our findings demonstrate
323 how traits and phenologies are inextricably linked to varying strategies for growth, with gradients from
324 strong abiotic filters early in the growing season to greater biotic pressures later in the season, produc-
325 ing varying selective pressures that may shape the assembly of communities. By including phenology
326 in the existing trait framework, we identified the key interactions across traits and cues and can tease
327 apart the underlying mechanisms shaping species phenology across communities. Our work highlights
328 the complexity of interactions shaping communities, and represents holistic approach to better forecast
329 future changes in phenologies, community assembly, and productivity of diverse ecological communities.

330

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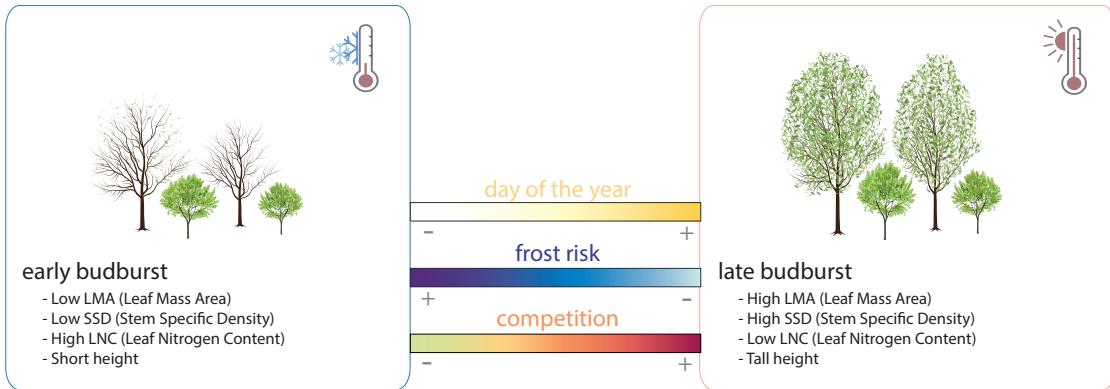


Figure 1: Leaf and wood trait are known to follow gradients that vary from acquisitive versus conservative growth strategies. Less clear, however, is how well this variation corresponds to phenology. We expect phenologically early species to exhibit traits associated with acquisitive, as they are more 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.

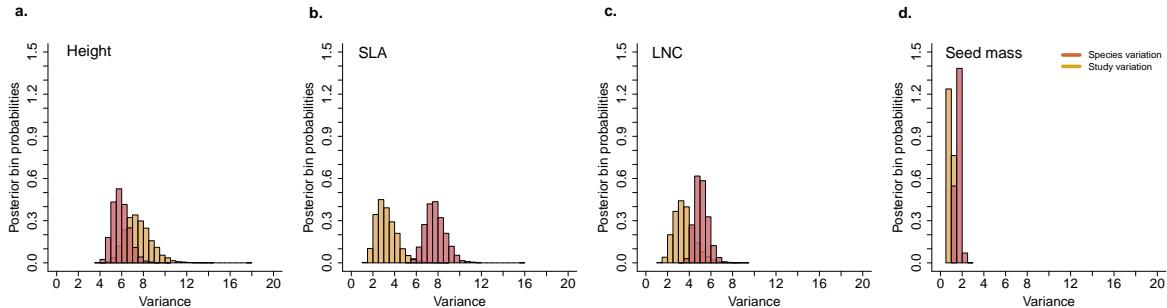


Figure 2: Comparison of the posterior densities for the species-level variation and study-level variation of a. height, b. specific leaf area, c. leaf nitrogen content, and d. seed mass.

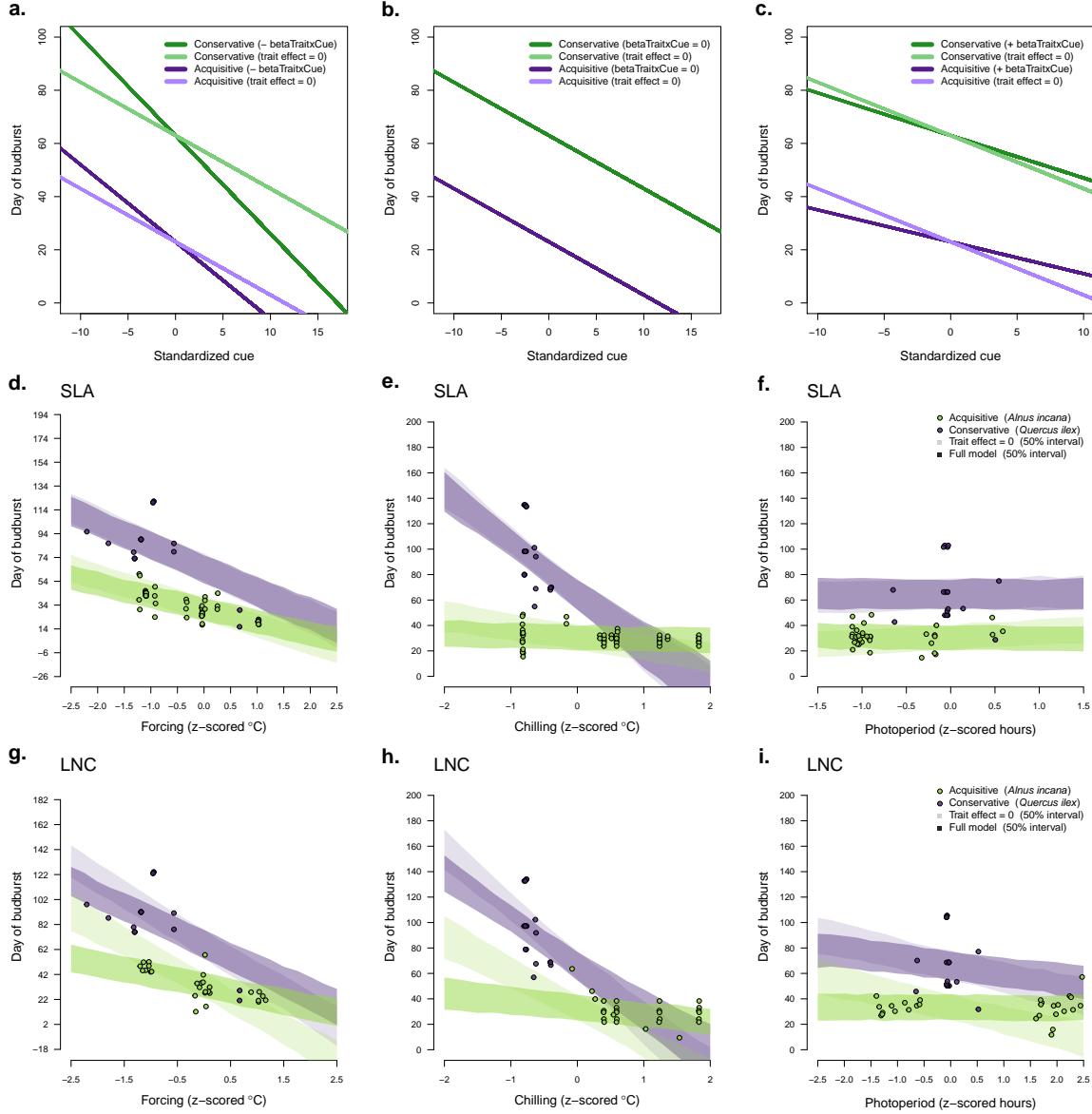


Figure 3: Functional traits may contribute to the species responses to forcing, chilling, or photoperiod cues in several ways. a) If traits are also responding to the environmental cue and lead to stronger phenological responses (larger in magnitude) then budburst will be earlier with increasing chilling, 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.

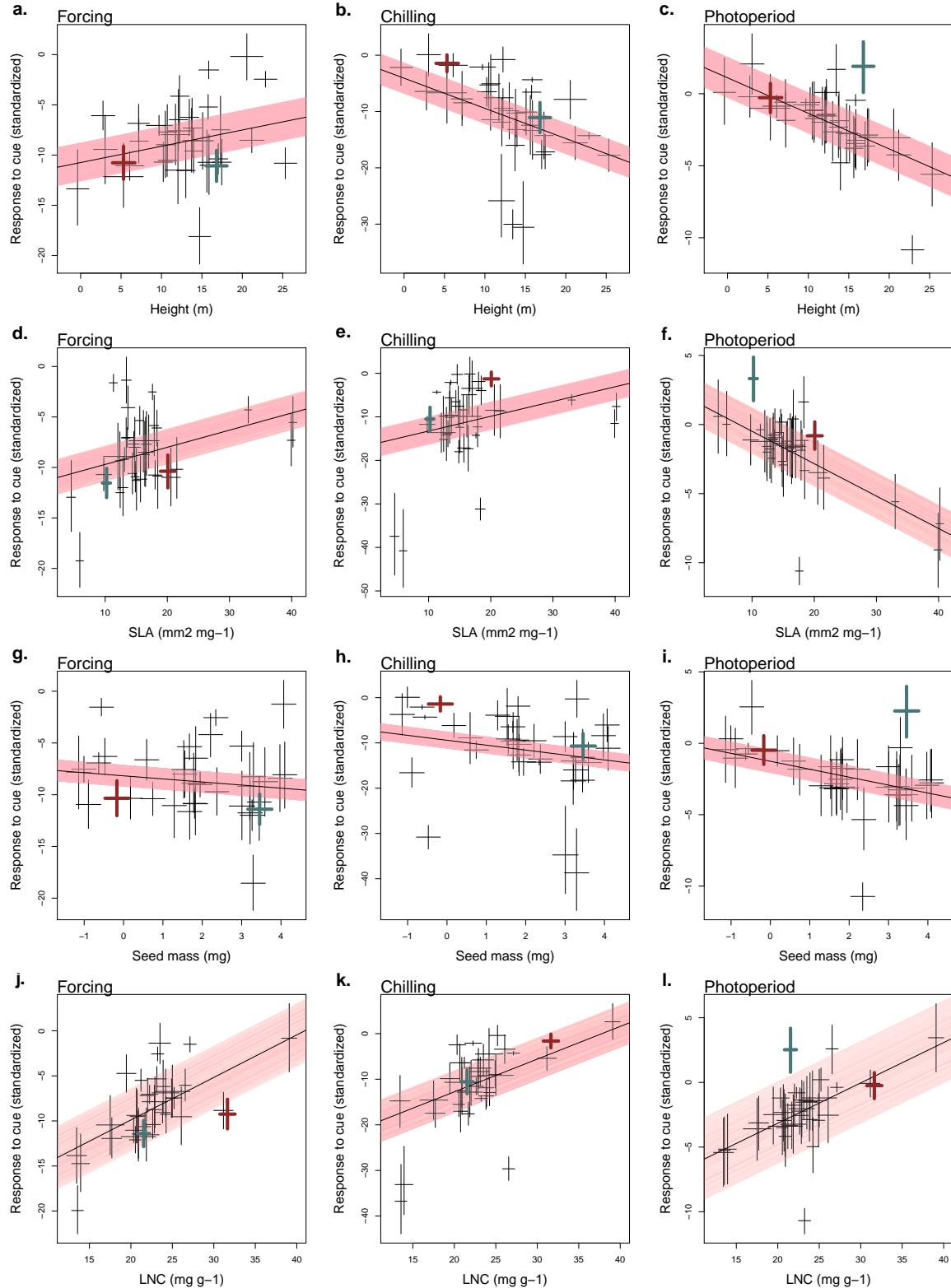


Figure 4: Estimated trait values for height (a-c), SLA (d-f), log₁₀ Seed mass (g-i), and LNC (j-l), correlated against species-level cue responses to standardized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using a joint trait-phenology 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 species⁵ with the species depicted in Fig 3 colored in each panel, with the acquisitive species, such as *Alnus incana* shown in red, and the conservative species, such as *Quercus robur*, shown in blue.