

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

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32 Summary

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

54

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
58 dynamics. Spring phenology, for example, defines the start and overall length of the growing season—
59 shaping forest carbon storage and species interactions (Cleland et al., 2007; Beard et al., 2019; Gu
60 et al., 2022). As climate change has caused spring growth to advance in many systems (Menzel et al.,
61 2006; Vitasse et al., 2021), there is growing concern over how these changes may impact communities
62 and ecosystems.

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

73 At the ultimate level, our predictions for why phenologies vary generally stem from our understanding
74 of how selective pressures change across the growing season. Species that start growth early often risk
75 high tissue loss—due to frost damage (Sakai and Larcher, 1987; Augspurger, 2009) or high herbivore
76 apparentness (Wainwright et al., 2012)—but benefit from higher resource availability (Rathcke and Lacey,
77 1985; Hufkens et al., 2012). In contrast, later species face greater biotic pressures, especially from high
78 competition for resources (Lopez et al., 2008; Wolkovich and Ettinger, 2014).

79

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

86 In plants, leaf and wood traits co-vary along gradients that range from acquisitive (fast) growth strate-
 87 gies to more conservative (slow) growth strategies (S1) (Westoby, 1998; Westoby and Wright, 2006;
 88 Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016). These global relationships are the foundation
 89 of the leaf economic spectrum and the wood economic spectrum (Wright et al., 2004; Chave et al.,
 90 2009), but are limited in their ability to predict how variable traits are (Viole et al., 2012). As a
 91 result, highly variable traits like phenology are often excluded from trait studies, leaving the relation-
 92 ships between broader trait syndromes and phenology largely unknown, while many studies simply
 93 assume this variability to be negligible (Grime, 2006; Pau et al., 2011)

94

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

106

107 Spring phenology in temperate forests may provide the best opportunity to integrate phenology into
 108 functional trait research, given the strong gradients in selective environments that occur early ver-
 109 sus later in the spring. As in other systems, early season species trade-off high access to resources
 110 (greater soil resources and light availability) with risks of tissue loss and damage, while late season
 111 species experience a highly competitive but less risky environment. Based on these trade-offs, we
 112 predict that acquisitive species, to be shorter, with leaf traits favourable to higher light availability
 113 and tolerance of late spring frost (high specific leaf area (SLA) and leaf nitrogen content (LNC)) S1.
 114 Such species should exhibit early phenology, with weak cue responses, especially to chilling and pho-
 115 toperiod. Canopy species that budburst later—when competition for soil resources is greatest—would
 116 have traits associated with conservative growth; being taller with denser wood (Laughlin et al., 2010),
 117 with leaf traits suited for more variable light (low SLA and LNC) S1. This delayed phenology should
 118 be reflected in their higher cue responses. Seed size may similarly be predicted from this acquisitive
 119 to conservative continuum, as acquisitive species produce smaller seeds that germinate quickly and
 120 conservative species produce larger, better provisioned, seeds S1.

121

122 Testing these predictions requires a reliable way to define early to late phenology, as phenology varies
 123 strongly across sites and years. The underlying cues that predict gradients in phenology, however, do
 124 not vary strongly across space and time (Chuine and Cour, 1999; Harrington and Gould, 2015; Flynn
 125 and Wolkovich, 2018). Early species generally have weak (small in magnitude) responses to all three
 126 major cues of spring leafout: warm spring temperatures (forcing), cool winter temperatures (chilling)
 127 and daylength (photoperiod). In contrast, later species have stronger (larger) responses to chilling
 128 and/or photoperiod (Laube et al., 2014; Flynn and Wolkovich, 2018), and we predict to also have
 129 higher forcing as well .

130

131 To test these predictions of associations between budburst responses to environmental cues and com-

mon functional traits, 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. We focus on woody species, initially considering six commonly measured traits—SLA, leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC. We further removed SSD and LDMC from our focal traits, as they correlated strongly with height and SLA respectively (see supplementary material).

138

To better understand the relationships between phenology and other traits, we analyzed this novel and encompassing trait-phenology dataset with a hierarchical Bayesian joint model. This analytical approach allows us to predict phenological responses to cues 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 will explain only a small amount, which would allow us to use trait values to predict species growth strategies and phenological responses, while providing new insights into the effects of traits on phenological cues.

147

148 Methods

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

153

154 Trait data was obtained from TRY and BIEN—two large trait databases compiling plant trait data
 155 across many individuals, species, and studies. We obtained data from both databases on 5 December,
 156 2018, with an updated version of the TRY data obtained 10 April, 2019. We focused our search for
 157 trait data on the subset of 234 OSPREE species used in Morales-Castilla et al. (in prep), which rep-
 158 resents well studied species with good phenology and phylogenetic data. Using the BIEN R package
 159 (Maitner et al., 2018), we downloaded trait data for the 94 available species for 13 traits. The TRY
 160 database included 96 of our focal species with ten functional traits (Kattge et al., 2020). Only trait
 161 data from adult individuals with a minimum height of 1.42 m was included in our analyses and we
 162 removed all data from experiments or from plants growing in non-natural habitats. We also grouped
 163 trait values where appropriate, for example categorizing trait values for SLA, SLA with petioles, and
 164 SLA without petioles as simply SLA in our analysis (Table S1). Duplicated data in both the TRY and
 165 BIEN datasets were also removed ($n = 434905$).

166

167 For our analysis, we aimed to only include species for which we had a complete trait profile, subsetting
 168 the phenology and trait data to include only species for which we had at least one measurement for
 169 each trait. We used a principle component analysis to understand trait correlations and adjusted which
 170 traits we included. A PCA of our six initial traits identified high correlations between SLA and leaf dry
 171 matter content (LDMC), and between height and stem specific density (SSD) (see Supplementary ma-
 172 terial). In this analysis, the principal component explained 32% of variation while the second explained
 173 24.2% of the variation (Fig. S1). By excluding one trait from each of these pairs (specifically LDMC
 174 and SSD) we increased the number of species in our dataset from the 26 species with six traits, to 37
 175 species for which we had complete datasets for four traits. The data for these 37 species was from 24
 176 unique studies (height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n = 7656$). We subsampled
 177 height measurements to reduce the influence the 13 most frequently measured tree species had on our
 178 height model (discussed below). These species were measured on average 19 times more frequently
 179 than other species in our dataset and therefore we randomly sampled 3000 height measurements for
 180 each of these species.

181

182 **Joint model of trait and phenology**

183 To understand connections between phenology and other species traits, we built a joint model for
 184 each trait (height, SLA, LNC, and seed mass) with the major phenological cues (forcing, chilling, and
 185 photoperiod) to predict day of year of budburst.
 186 The joint model includes a hierarchical linear model to partition variation for individual observations
 187 (i) of a given trait value ($y_{\text{trait}[i]}$) to the effects of species (sp id), study ($study$ id), and residual
 188 variation (σ_{trait} , also called ‘measurement error’).

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

189 It estimates a separate value for each species ($\alpha_{\text{sp[sp id]}}$), and study ($\alpha_{\text{study[study id]}}$), while partially
 190 pooling across species and studies to yield overall estimates of variance across each ($\sigma_{\alpha_{\text{sp}}}$ and $\sigma_{\alpha_{\text{study}}}$,
 191 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:

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

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

197 Results

198 We combined the species-level trait estimates with data on forcing, chilling and photoperiod values
 199 from the OSPREE database of phenological experiments in order to test if traits (height, SLA, seed
 200 mass, LNC) related to phenological cues and species budburst dates (Fig. S3). For some traits we
 201 did find traits to relate to variation in phenological cues across species, with some species exhibiting
 202 stronger or weaker responses (as illustrated conceptually in Fig S3a and c), while traits were weak
 203 predictors for other species (Fig S3b).

204
 205 Across traits, height, SLA, and LNC strongly predicted responses to different cue-levels ($(\beta_{chill[sp]},$
 $\beta_{force[sp]},$ and $\beta_{photo[sp]}$, Fig S4 a-i), but only showed consistent directions of responses across cues for
 206 LNC (Fig. S4 j-l). As we predicted, height was related to chilling and photoperiod cues, with taller
 207 species having larger responses with stronger cues (-0.5 m per standardized chilling; 90% uncertainty
 208 interval (UI): -1, -0.1 and -0.2 m per standardized photoperiod; 90% UI: -0.5, 0, Fig S4 a-c). As illus-
 209 trated for the characteristically acquisitive species, *Alnus incana*, and conservative species, (*Aesculus*
 210 *hippocastanum*) (Fig 3), this response to chilling and photoperiod cues leads to later budburst (μ_{pheno}),
 211 and therefore fits within an overall conservative growth strategy. Seed mass, however, had the weakest
 212 responses, with no considerable relationship between seed mass and cues across the three cues (Fig.
 213 S4 g-i & Fig 3).

214
 215 Of our leaf traits, we found species SLA to relate to photoperiod (-0.2 mm²/mg per standardized
 216 photoperiod; 90% UI: -0.4, 0.0, Fig. S4 f), but did not strongly predict responses to chilling or forcing
 217 (Fig. S4 d and e). Thus, species with more acquisitive growth strategies (thin leaves and a lower
 218 investment in leaf mass that leads to high SLA values), had larger responses to photoperiod cues,
 219 contrary to our predictions (Fig. S4 d and e). For LNC, we found that species that produce leaves
 220 with high nitrogen content, which relates generally to high photosynthetic rates and acquisitive growth,
 221 show weak responses to cues (Fig. S4 j-i). These findings are in line with our predictions that high
 222 LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g per standardized chilling; 90%
 223 UI: 0.3, 1.2), but we found similar responses to photoperiod (0.3 mg/g per standardized photoperiod;
 224 90% UI: 0, 0.6) and to forcing cues (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig S4 j-i).
 225 Across our models, we found species-level variation across traits ($\sigma_{sp[sp id]}$) was comparable with or
 226 greater than variation across studies ($\sigma_{study[study id]}$, Fig S2). Variation across studies was greatest for
 227 height (7.5 m compared to 5.9 m species-level variation, Fig S2a). For seed mass and LNC study-level
 228 variation was less than that of the species-level variation (seed mass study-level variation: 1 mg; versus
 229 species-level variation: 1.6 mg; LNC study-level variation 3.6 mg g⁻¹ versus species-level variation: 5.1
 230 mg g⁻¹; Fig S2c and d). At the lowest end, study-level variation in SLA was approximately half the
 231 value of the species-level variation (and 3.3 mm² mg⁻¹ versus 7.8 mm² mg⁻¹, respectively, Fig S2b).
 232 The magnitude of study-level variation we observed suggests that models using large trait databases
 233 that fail to separate out study from species-level variation may poorly estimate species' traits.

234
 235

236 Discussion

237 Species traits influenced the timing of budburst in response to three primary cues for spring phenology
 238 (chilling, forcing and photoperiod). Whether these trait effects were associated with earlier or later
 239 phenology was correlated with well known gradients in traits, that vary from acquisitive to conservative
 240 growth strategies. We found the greatest budburst responses for traits related to resource acquisition
 241 and structure, with SLA, LNC, and height all depicting strong responses across our three cues. In con-
 242 trast, our one reproductive trait—seed mass—showed a weak response. Despite finding these general
 243 trends in trait relationships to phenology, we also found considerable variation across studies, often at
 244 a magnitude comparable to the differences observed across species .

245

246 Gradients in phenology generally followed similar gradients in traits we associate with fast growing,
 247 acquisitive species to conservative, slower growth strategies. Phenologically earlier species had traits
 248 that inferred faster return on resource investments (Grime, 1977; Westoby, 1998; Chave et al., 2009).
 249 In contrast, phenologically late species filled different trait space (Fig. S4), exhibiting a phenotype
 250 that infers greater competitive abilities and slower growth (Grime, 1977; Westoby, 1998; Chave et al.,
 251 2009). Our findings suggest the assembly of communities results from varying selective pressures, such
 252 as strong abiotic filters early in the growing season, and greater biotic pressures later in the season.
 253 By including phenology in the trait framework, we can identify the interactions across traits and cues
 254 and tease apart the underlying mechanisms shaping species' phenology across communities.

255

256 Effects of phenology-trait relationships on community assembly

257 In our study of temperate forest communities, the relationships between budburst phenology and other
 258 plant traits provided insights into the mechanisms that shape species phenotypes. Earlier budbursting
 259 species had traits, such as shorter heights and low LNC, that allow them to grow quickly and benefit
 260 from greater light availability in the open canopy of many early-spring temperate forests. This pheno-
 261 type can be linked to other ecological processes and species characteristics, such as species successional
 262 position, as illustrated by the differences between early and late successional species, like *Alnus incana*
 263 and *Quercus rubra* (Fig S4). Our results may also be useful to help predict communities' potential for
 264 invasion, as communities with similar phenologies and suites of traits, appear more susceptible to fast
 265 growing, non-native species (Wolkovich and Cleland, 2011; Alexander and Levine, 2019; Schuster et al.,
 266 2021). In identifying the trait syndromes of native forest communities and the interactions between
 267 traits and environmental cues, we can better predict how changes in environmental cues will alter
 268 species growth strategies and productivity, identifying species most likely to be negatively impacted
 269 by future climates and in need of mitigation and conservation efforts.

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

280

281 Phenology-trait relationships under future climates

282 Incorporating phenology within broader trait syndromes is necessary to accurately predict species re-
 283 sponds to climate change. Recent phenological shifts are well documented, but there remains a high
 284 degree of unexplained variation across species and populations (Vitasse et al., 2009; Wolkovich and
 285 Ettinger, 2014; Zohner and Renner, 2014; Vitasse et al., 2018). Our findings demonstrate that the same
 286 environmental cues driving phenological traits also relate to leaf and structural traits and thus sug-
 287 gest that warming that favors species with certain phenological cues, can favor specific trait syndromes.

288

289 In temperate forests, warming may favor species with weak chilling and photoperiod requirements,
 290 as these requirements may allow phenology to shift more with warming. Our results suggest that
 291 these low cue requirements co-vary with acquisitive growth strategies. Thus, future forests may be
 292 dominated by species with lower chill and photoperiod cues and with traits that allow them to grow

293 faster and rapidly acquire resources, while also being more vulnerable to late-season frosts, when they
294 do occur. In contrast, conservative species with high chilling and photoperiod requirements, could
295 face greater abiotic stress. Rising winter temperatures could result in insufficient chilling, while strong
296 photoperiod cues could limit species ability to also advance in response to warmer spring conditions
297 (Guy, 2014). Species that are less able to advance phenologically might experience more competition
298 (Carter et al., 2018; Alexander and Levine, 2019), as species that begin growth earlier in the season
299 deplete resources. Growing under warmer summer conditions could also result in greater drought stress
300 (Frelich and Reich, 2010). In addition to altering the timing and interactions between species within a
301 season, species trait syndromes have the potential to define the environmental conditions under which
302 growth occurs.

303

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

318

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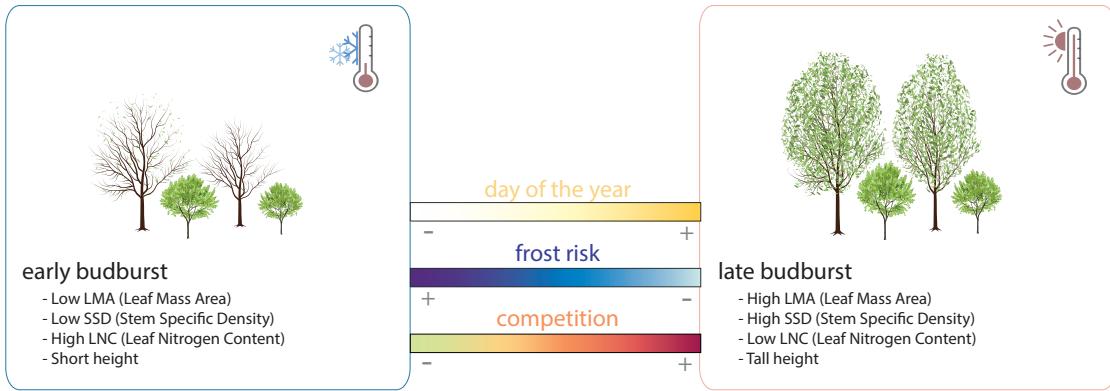


Figure S1: Conceptual fig

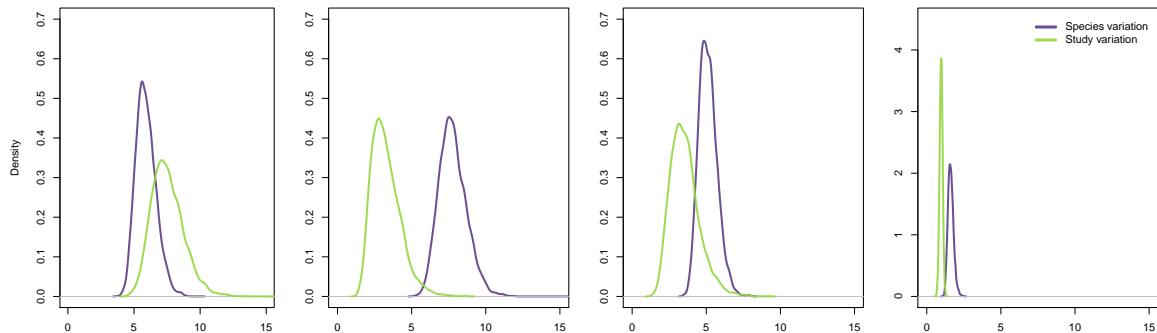


Figure S2: Comparison of the posterior densities for the species-level variation and study-level variation of a. height, b. specific leaf area, c. leaf nitrogen content, and d. seed mass.

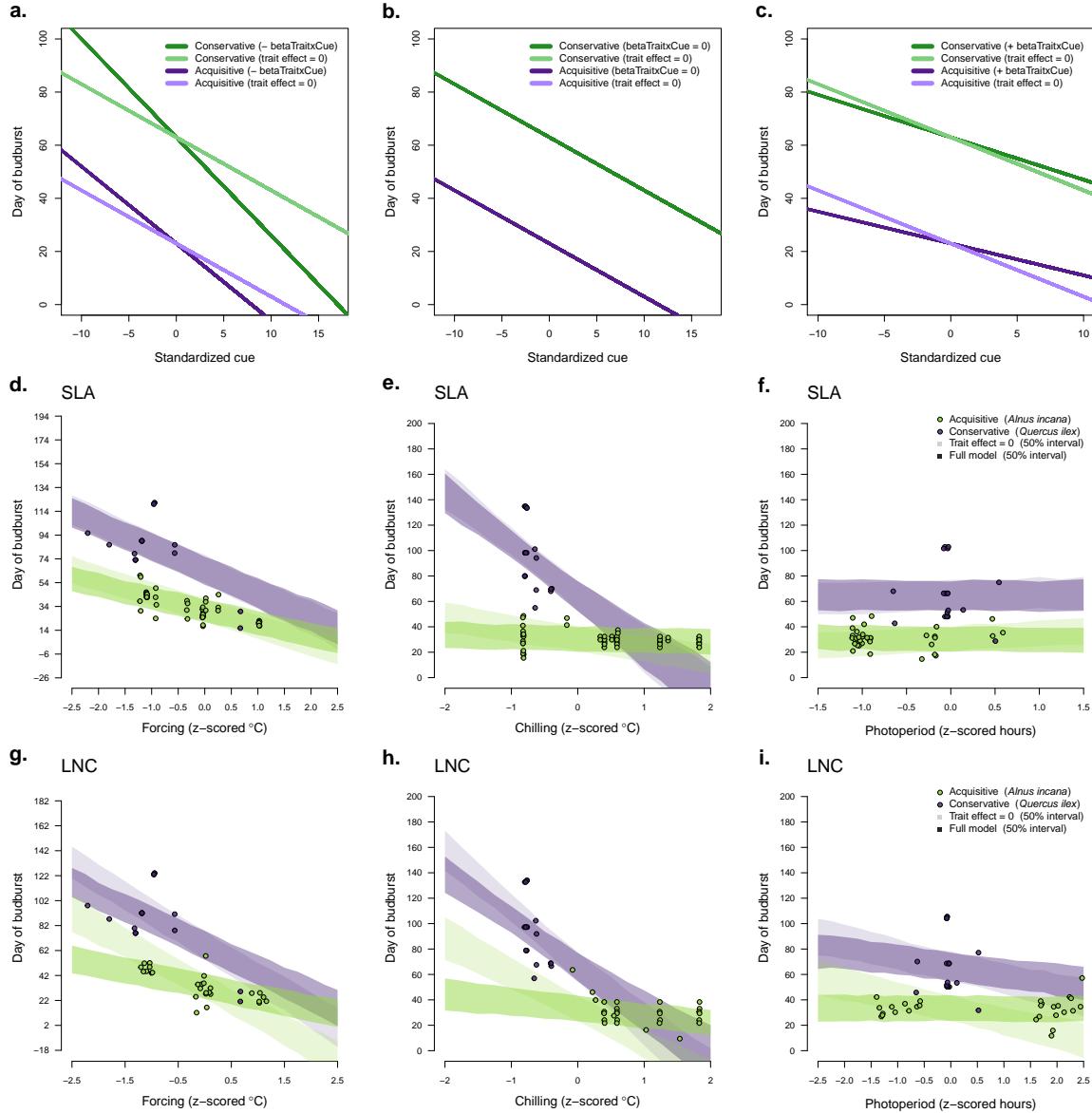


Figure S3: Functional traits may contribute to the species responses to forcing, chilling, or photoperiod cues in several ways. a) If traits are also responding to the environmental cue and lead to stronger phenological responses (larger in magnitude) then budburst will be earlier with increasing chilling, 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.

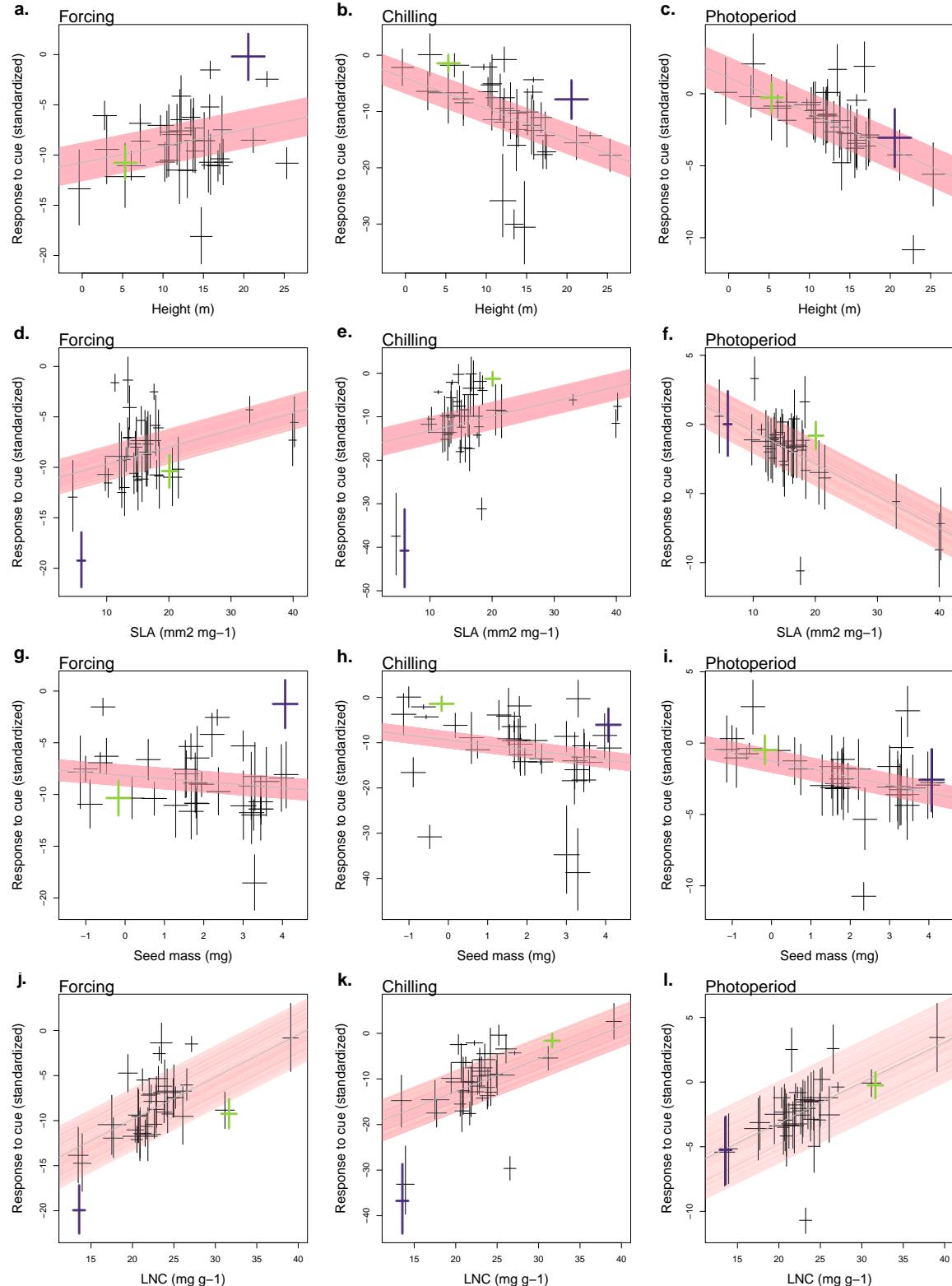


Figure S4: Estimated trait values for height (a-c), SLA (d-f), log₁₀ Seed mass (g-i), and LNC (j-l), correlated against species-level cue responses to standardized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using a joint trait-phenology 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 species depicted in Fig S3 colored in each panel, with the acquisitive species, such as *Alnus incana* shown in green, and the conservative species, such as *Quercus ilex* (a-c & j-l) or *Aesculus hippocastanum* (d-i), shown in purple.