

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

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34 **Summary**

35 Phenologies—the timing of recurring life history events—can vary substantially in different environments
36 and for different species. While climate change has changed the proximate drivers of phenology—
37 such as temperature—causing it to shift, changes in the ultimate drivers that select for species-level
38 variation in phenology remain poorly explained. Theory suggests that species-level variation in phe-
39 nology can result from selection favoring different strategies across the early (spring) growing season.
40 During early season conditions, risks of tissue loss to frost combined with the availability of nutrients
41 and light should favour acquisitive growth strategies, transitioning to favouring conservative growth
42 strategies as the season progresses, and as more benign temperatures but greater competition occur.
43 From this we can infer suites of traits that may co-vary with species phenologies, but the high variabil-
44 ity in traits—and especially phenology—across environments, have made testing the role of phenology
45 within a trait framework challenging. Using a modelling framework that accommodates this variability
46 we performed a meta-analysis using phenological data from controlled environment experiments and
47 plant traits to test the relationships between traits and cues for tree budburst (forcing, chilling, and
48 photoperiod). We found that earlier species (with small responses to all cues) are shorter with denser,
49 lower nitrogen leaves, while later-active species (with large responses to chilling and photoperiod) were
50 taller with low nitrogen leaves. How budburst timing related to leaf density, however, was less in line
51 with our predictions, as species with denser leaves had large responses to only some cues. Our findings
52 show how spring leafout phenology fits within a functional trait framework of acquisitive to conserv-
53 ative growth strategies, and better predicts how communities may shift in their growth strategies
54 alongside changing phenology with climate change.

55
56 Key Words: Budburst, spring phenology, functional traits, trees, climate change, forest communities

57 **Introduction**

58 The timing of life history events—phenology—can shape both ecosystem services and community
59 dynamics. Spring phenology, for example, defines the start and overall length of the growing season—
60 shaping forest carbon storage and species interactions (Cleland et al., 2007; Beard et al., 2019; Gu
61 et al., 2022). Climate change has caused spring growth to advance in many systems (Menzel et al.,
62 2006; Vitasse et al., 2021), leading to growing concern over the impacts these changes will have.

63
64 Predicting these changes requires understanding the drivers of phenology both at a proximate scale—
65 the environmental triggers of phenology each year, such as temperature and daylength—and at an
66 ultimate scale, where long-term environmental pressures select for the different phenologies across
67 species (e.g., certain species are early or late relative to other species each year Ovaskainen et al., 2013;
68 Wolkovich and Donahue, 2021). At the proximate level, environmental conditions across the winter
69 and spring cause species to start growth at different times. This is well documented for the start of
70 growth in woody plants each year (Laube et al., 2014; Flynn and Wolkovich, 2018). Similar trends
71 are also observed for spring phenological events across taxa, including in the timing of egg laying in
72 birds (Crick et al., 1997; D'Alba et al., 2010) and the advance of spawning in amphibians (Tryjanowski
73 et al., 2003; Kusano and Inoue, 2008). But current work provides limited insights into the drivers of
74 species differences (Laube et al., 2014; Chuine et al., 2016; Flynn and Wolkovich, 2018).

75
76 At the ultimate level, species phenologies may vary due to changing selective pressures across the grow-
77 ing season. Species that start growth early often risk high tissue loss—due to frost damage (Sakai and
78 Larcher, 1987; Augspurger, 2009) or high herbivore apperency (Wainwright et al., 2012)—but benefit
79 from higher resource availability (Rathcke and Lacey, 1985; Hufkens et al., 2012). In contrast, later
80 species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008;
81 Wolkovich and Ettlinger, 2014). For plants, this variation in early to late season growth, may mirror

82 the stressors from early to late successional communities, and may similarly shape phenology (Laube
83 et al., 2014).

84
85 Different selective pressures could shape a number of species attributes related to their growth strate-
86 gies, including phenology. Species with earlier phenology may produce cheaper tissues that are easily
87 replaced if damaged (Reich et al., 1999). Species with later phenology would benefit from investing
88 in tissues that infer greater resource retention (Gorné et al., 2020). These differences in traits, and
89 trade-offs in allocation of resources to growth and tissue quality, can be related to a broader framework
90 of species growth strategies and functional traits (Fig. 1, Wolkovich and Ettinger, 2014), where species
91 range from acquisitive (fast) to more conservative (slow) growth strategies (Wright et al., 2004; Chave
92 et al., 2009).

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

104
105 Consistently defining early to late phenology is possible using the underlying cues that predict gradients
106 in phenology, which do not vary strongly across space and time (Chuine and Cour, 1999; Harrington and
107 Gould, 2015; Flynn and Wolkovich, 2018). For many plants, early species generally have weak (small
108 in magnitude) responses to all three major cues of spring leafout: warm spring temperatures (forc-
109 ing), cool winter temperatures (chilling) and daylength (photoperiod). In contrast, later species have
110 stronger (larger) responses to chilling and/or photoperiod (Laube et al., 2014; Flynn and Wolkovich,
111 2018), and we predict to have higher forcing requirements as well.

112
113 Research exploring the relationships between phenology and plant traits has demonstrated how traits
114 vary within a growing season relative to phenological stages (Mckown et al., 2013; Fajardo and Siefert,
115 2016) and across species (König et al., 2018; Sporbert et al., 2022). At the community scale, this work
116 has found plant phenologies relate to traits such as height and leaf area, with taller plants exhibiting
117 delayed phenology relative to short species. But how other trait values relate to the underlying cues
118 of phenology remains unclear.

119
120 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-
121 nology into functional trait research, given their cues are well understood and the strong gradients in
122 selective environments that occur over the spring season. As in other systems, early season species
123 trade-off high access to resources (greater soil resources and light availability) with risks of tissue loss
124 and damage, while late season species experience a highly competitive but less risky environment.
125 Based on these trade-offs, we predict acquisitive species to be shorter, with leaf traits favourable to
126 higher light availability and tolerance of late spring frost (high specific leaf area, SLA, and leaf nitrogen
127 content, LNC; Fig 1). Such species should exhibit early phenology, with weak cue responses, especially
128 to chilling and photoperiod. Canopy species that budburst later, when competition for soil resources is
129 greater, would then have traits associated with conservative growth—taller with denser wood (Laughlin
130 et al., 2010)—with leaf traits suited for more variable light (low SLA and LNC, Fig 1). This delayed
131 phenology should be reflected in their higher cue responses. Seed size may similarly be predicted from
132 this acquisitive to conservative continuum, as acquisitive species produce smaller seeds and conserva-
133 tive species produce larger—better provisioned—seeds (Fig 1).

134

135 To test these predictions of associations between budburst responses to environmental cues and com-
 136 mon functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases
 137 (BIEN, Maitner et al. (2018) and TRY, Kattge et al. (2020)) with budburst data from the OSPREE
 138 database of controlled environment studies (Ettinger et al., 2020). We developed a hierarchical Bayesian
 139 joint model that predicts phenological responses to forcing, chilling and photoperiod treatments based
 140 on species-level trait values, while allowing additional variation due to species. This approach takes
 141 a step towards predicting variation via species traits instead of species identity—when traits explain
 142 a significant portion of the variation, species will explain only a small amount—and forecast species
 143 phenological responses to cues based on trait values alone. We expected acquisitive versus conservative
 144 species to exhibit different responses to phenological cues estimated from chilling forcing and photope-
 145 rioid treatments (as illustrated conceptually in Fig 3a-c for one acquisitive and one conservative species).

146

147 Methods

148 We merged three major databases for our analysis. We gathered phenological data from the OSPREE
 149 database (Ettinger et al., 2020), which contains budburst data for woody, deciduous species from
 150 experiments of forcing, chilling and photoperiod, which we updated since its initial publication, for
 151 details on the methods used see Morales-Castilla et al. (in prep). We obtained from TRY and BIEN
 152 ((Maitner et al., 2018; Kattge et al., 2020)—two large trait databases compiling plant trait data across
 153 many individuals, species, and studies. We obtained data from both databases on 5 December, 2018,
 154 with an updated version of the TRY data obtained 10 April, 2019. We focused our search for trait
 155 data on the subset of 234 OSPREE species used in Morales-Castilla et al. (in prep), which represents
 156 well studied species with good phenology and phylogenetic data. Using the BIEN R package (Maitner
 157 et al., 2018), we downloaded trait data for the 94 available species for 13 traits. The TRY database
 158 included 96 of our focal species with 10 functional traits (Kattge et al., 2020). Only trait data from
 159 adult individuals with a minimum height of 1.38 m were included in our analyses and we removed all
 160 data from experiments or from plants growing in non-natural habitats. We also grouped trait values
 161 where appropriate, for example categorizing trait values for SLA, SLA with petioles, and SLA without
 162 petioles as simply SLA in our analysis (see Table S1). Duplicated data in both the TRY and BIEN
 163 datasets were also removed ($n = 434905$). Based on our selection criteria, our final dataset included
 164 data for 11 traits from 91 of the species also represented in the OSPREE database, but each species
 165 differs in the number and types of traits measured.

166

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

182

¹⁸³ **Joint model of trait and phenology**

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

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

¹⁸⁹ This part of the model estimates a separate value for each species ($\alpha_{\text{sp[sp id]}}$), and study ($\alpha_{\text{study[study id]}}$),
¹⁹⁰ while partially pooling across species and studies to yield overall estimates of variance across each ($\sigma_{\alpha_{\text{sp}}}$
¹⁹¹ and $\sigma_{\alpha_{\text{study}}}$, respectively). This partial pooling (often called ‘random effects’) accounts for variation in
¹⁹² sample size and variability to yield more accurate estimates for each species.

¹⁹³ 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 ($\beta_{\text{force[sp]}}$, $\beta_{\text{chill[sp]}}$, $\beta_{\text{photo[sp]}}$)

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

These phenological cues predict days to budburst ($y_{\text{pheno[i]}}$) across experiments that varied in chilling,
forcing and photoperiod treatments (C_i , F_i , P_i , respectively, which we *z*-scored to allow direct com-
parison of cues), with residual variation estimated across species ($\alpha_{\text{pheno[sp]}}$) and observations (σ_{pheno}):

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

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

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

¹⁹⁴ We chose weakly informative priors, and validated them using a series of prior predictive checks. The
¹⁹⁵ model was coded in the Stan programming language, fit using the rstan package (Stan Development
¹⁹⁶ Team, 2018), with 1,000 iterations per chain across 4 chain (4,000 total sampling iterations), and all
¹⁹⁷ models met basic diagnostic checks, including no divergences, high effective sample size (n_{eff}), and
¹⁹⁸ \hat{R} close to 1.

¹⁹⁹ **Results**

²⁰⁰ Across traits, height, SLA, and LNC strongly related to chilling, forcing and photoperiod treatments
²⁰¹ ($\beta_{\text{chill[sp]}}$, $\beta_{\text{force[sp]}}$, and $\beta_{\text{photo[sp]}}$, Fig 4 a-i), but the direction of these relationships only showed con-
²⁰² sistent trends for LNC (Fig. 4 j-l). As we predicted, height was related to chilling ($\beta_{\text{chill[sp]}}$) and

203 photoperiod ($\beta_{\text{photo[sp]}}$), with taller species having larger responses to cues (-0.5 m per standardized
 204 chilling; 90% uncertainty interval (UI): -1, -0.1 and -0.2 m per standardized photoperiod; 90% UI:
 205 -0.5, 0, Fig 4 a-c). As illustrated for one characteristically acquisitive species, *Alnus incana*, and one
 206 characteristically conservative species (*Quercus robur*) (Fig S3), these responses lead to generally later
 207 budburst (μ_{pheno}), and fit within our predictions for acquisitive versus conservative growth strategies.
 208 Seed mass, however, had the weakest responses, with no relationship between seed mass and any cue
 209 (Fig. 4 g-i & Fig S3).

210

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

222

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

234

235 Discussion

236 We found species traits influenced the timing of budburst in response to the three primary cues of
 237 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or
 238 later phenology following well-established gradients in growth strategies predicted by functional traits
 239 (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016):
 240 early species tended to have traits associated with fast and acquisitive strategies while later species
 241 had traits associated with conservative, slower strategies. We found the largest budburst responses oc-
 242 curred for traits related to resource acquisition and structure, with SLA, LNC, and height all showing
 243 strong responses across our three cues. In contrast, our one reproductive trait—seed mass—showed
 244 a weak response. Our results support previous findings highlighting the importance of broader trait
 245 syndromes to shaping species growth strategies. Similarly to studies conducted at single sites and
 246 regionally, we also found strong relationships between height and species phenology (Sun and Frelich,
 247 2011; Sporbert et al., 2022; Segrestin et al., 2020), while other traits—such as seed mass—showed no
 248 relationships with phenology in our more global analysis.

249

250 Effects of phenology-trait relationships on community assembly

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

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

277 Phenology-trait relationships under future climates

278 Incorporating phenology within broader trait syndromes could aid forecasting species and community
 279 responses to climate change. While decades of research have documented phenological shifts with an-
 280 thropogenic climate change, increasing research suggests a potential connection between phenological
 281 responses to warming and performance with warming, where species that shift more with phenology
 282 appear to perform better (Cleland et al., 2012; Macgregor et al., 2019). Our results suggest this
 283 phenology-performance relationship could be driven in part by a suite of traits that covary with phe-
 284 nological cues to determine how responsive species are to warming. As species with smaller responses
 285 to all cues, especially chilling and photoperiod, would tend to advance more with warming, our re-
 286 sults suggest these species may also grow more quickly. These results could further aid predicting
 287 the potential for invasion, as communities with similar phenologies and suites of traits, appear more
 288 susceptible to fast growing, phenologically more responsive non-native species (Wolkovich and Cleland,
 289 2011; Alexander and Levine, 2019; Schuster et al., 2021).

290 Our analytical approach and results may be especially useful to help forecast changes in forest dynam-
 291 ics. By identifying the trait syndromes of forest communities and the interactions between traits and
 292 environmental cues, we can make predictions about how climate change will alter species growth and
 293 productivity, identify which species are most likely to be negatively impacted under future climates,
 294 and develop better strategies for climate change mitigation and conservation. For example, our results
 295 suggest warming may favor species with weak chilling and photoperiod requirements, which are often
 296 species with acquisitive growth strategies. In contrast, conservative species with high chilling and
 297 photoperiod requirements could face greater abiotic and biotic stress (Guy, 2014). Species that fail to

299 advance phenologically with warming might experience more competition (Carter et al., 2018; Alexander
300 and Levine, 2019), as species that begin growth earlier in the season have more time to deplete
301 resources. Growing under warmer summer conditions could also expose species to greater drought
302 stress (Frelich and Reich, 2010). In addition to altering the timing and interactions between species
303 within a season, species trait syndromes have the potential to redefine the environmental conditions
304 under which growth occurs.

305

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

320

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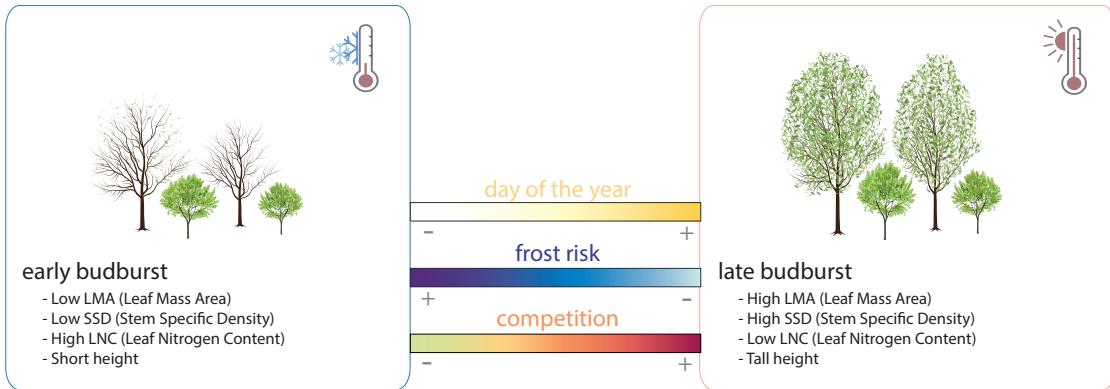


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies. Less clear, however, is how well this variation corresponds to phenology. We expect phenologically early species to exhibit traits associated with acquisitive growth, as they are more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

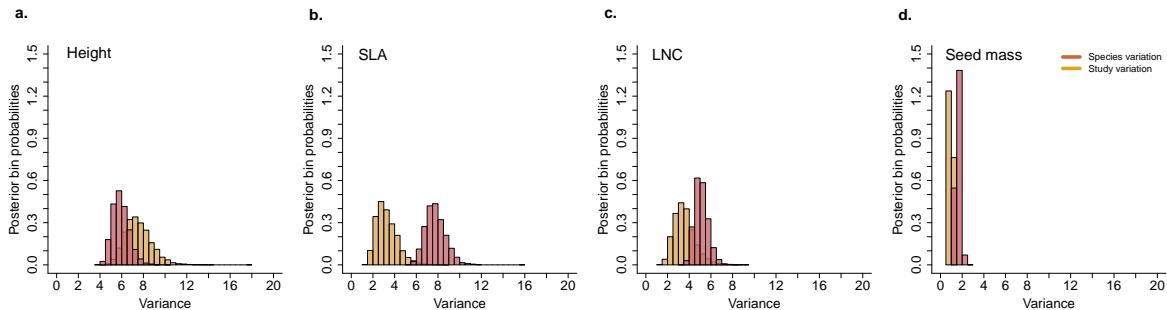


Figure 2: Traits differed in the relative magnitude of their species-level and study-level variation, with only a. the height model estimating greater study-level variation than species-level, while our b. specific leaf area, c. leaf nitrogen content, and d. seed mass models all estimated higher species-level variation. Shown here are the of the posterior densities for the species-level variation, shown in red, and study-level variation, shown in yellow.

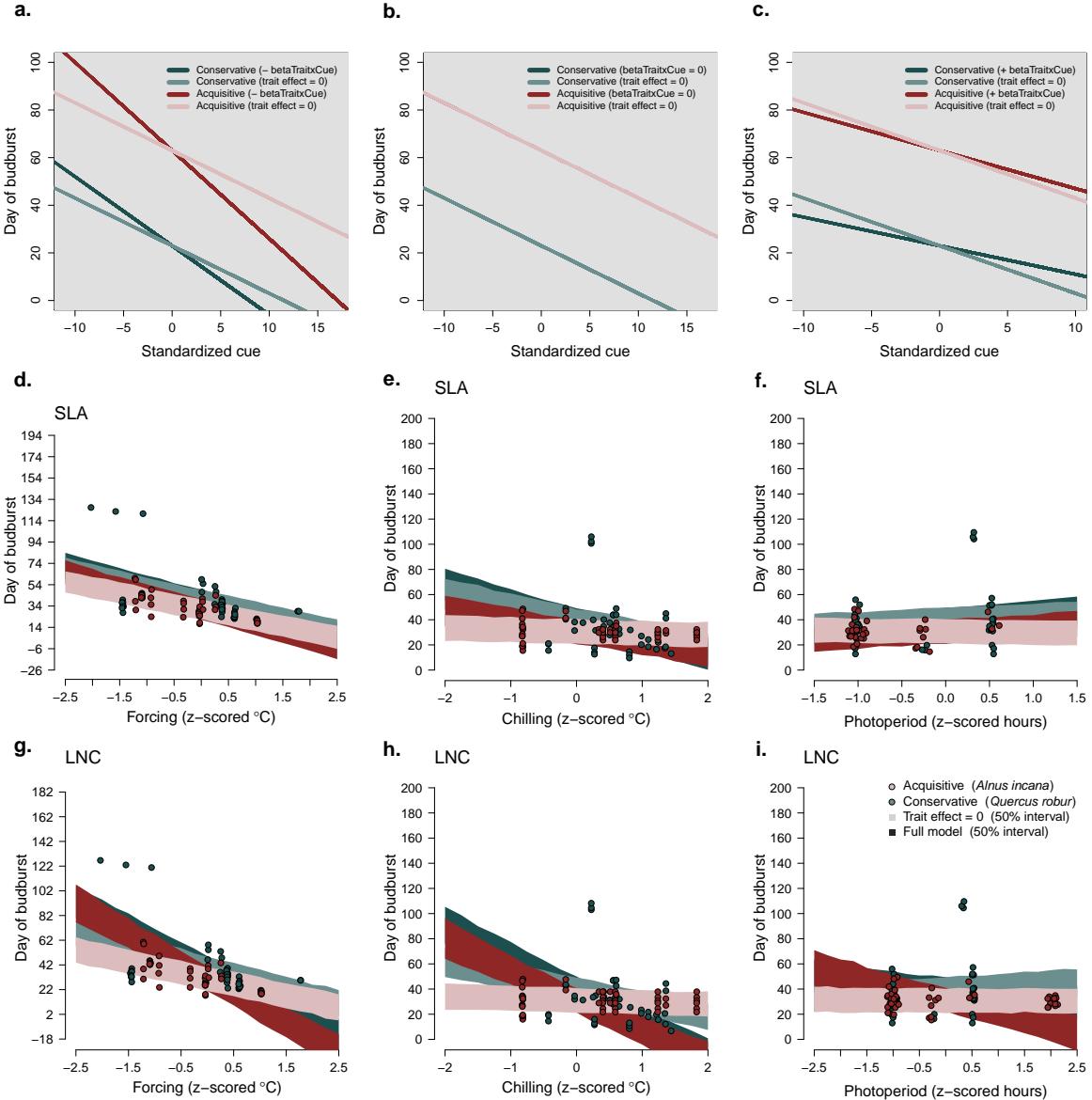


Figure 3: We expected species with traits associated with acquisitive (e.g., low SLA and LNC) versus conservative (e.g., high SLA and LNC) growth strategies would have different budburst responses to phenological cues. We designed a joint model to test this while also allowing species to intrinsically vary in different budburst responses to phenological cues. Under this conceptual model if: a. higher trait values predict larger budburst responses to cues, then budburst will be earlier with increasing cues. b. But if traits have no effect on the timing of budburst, then budburst responses will be equivalent to the cue only model estimates. c. If higher trait values predict weak budburst responses to cues, then budburst will be later with increasing cues. Our model estimated later budburst due to trait effects were found for both SLA and LNC in response to forcing and chilling and for LNC in response to photoperiod (panel d, e, g, h, and i). Only in response to photoperiod did we estimate the effect of SLA lead to larger phenological responses and slightly earlier budburst with longer photoperiods. Species with acquisitive growth shown in red and species with conservative traits are shown in blue. Bands represent the 50% uncertainty intervals of the model estimates.

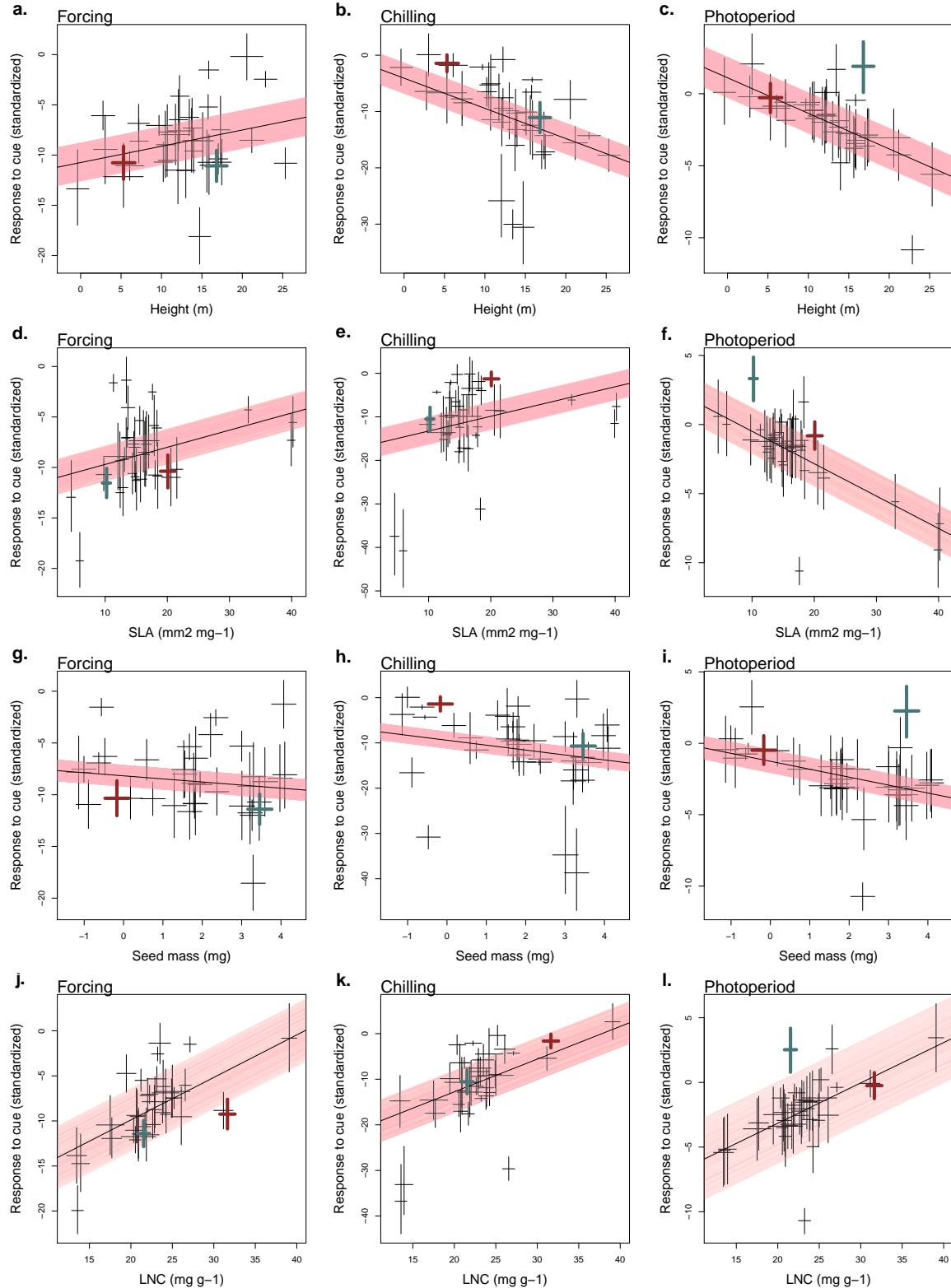


Figure 4: Estimated species-level cue responses to standardized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod treatments (c, f, i & l) predicted by estimated trait values for height (a-c), SLA (d-f), log10 Seed mass (g-i), and LNC (j-l). We estimated parameters using a joint trait-phenology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