

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

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34 Summary

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

45
 46 Key Words: Budburst, spring phenology, functional traits, trees, climate change, forest communities

47 Introduction

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

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

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

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

82 2009).

83
84 Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation
85 of the leaf economic and the wood economic spectra (Westoby, 1998; Westoby and Wright, 2006;
86 Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016), but they are limited in predicting trait
87 variability (Violette et al., 2012). As a result, highly variable traits like phenology are often excluded
88 from trait studies, leaving the relationships between broader trait syndromes and phenology largely
89 unknown. But understanding these relationships is critical to forecasting community dynamics and
90 responses to climate change. To date, studies have generally only examined the relationship between
91 traits and phenology within a single site (reviewed in Wolkovich and Cleland, 2014; Wolkovich and
92 Donahue, 2021), where the problem of proximate drivers causing phenological variation can be more
93 easily ignored. But adding phenology to broader trait frameworks requires finding a way to deal with
94 the high levels of variation in the calendar dates of phenology when measured across sites and years.

95
96 Consistently defining early to late phenology is possible using the underlying cues that predict gradients
97 in phenology (which do not vary strongly across space and time, Chuine and Cour, 1999; Harrington and
98 Gould, 2015; Flynn and Wolkovich, 2018). For many plants, early species generally have weak (small
99 in magnitude) responses to all three major cues of spring leafout: warm spring temperatures (forcing),
100 cool winter temperatures (chilling) and daylength (photoperiod). In contrast, later species have
101 stronger (larger) responses to chilling and/or photoperiod (Laube et al., 2014; Flynn and Wolkovich,
102 2018), and larger forcing requirements.

103
104 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phenology
105 into functional trait research, given their cues are well understood and the strong gradients in
106 selective environments that occur over the spring season. As in other systems, early season species
107 trade-off high access to resources (greater soil resources and light availability) with risks of tissue loss
108 and damage, while later season species experience a highly competitive but less risky environment.
109 Based on these trade-offs, we predict acquisitive species to be shorter, with leaf traits favourable to
110 higher light availability and tolerance of late spring frost (high specific leaf area, SLA, and leaf ni-
111 tragen content, LNC; Fig 1). Such species should exhibit early phenology, with small cue responses,
112 especially to chilling and photoperiod. Canopy species that budburst later via larger cue responses,
113 when competition for soil resources is greater, would then have traits associated with conservative
114 growth—taller with denser wood (Laughlin et al., 2010)—with leaf traits suited for more variable light
115 (low SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative
116 continuum, as acquisitive species produce smaller seeds and conservative species produce larger—better
117 provisioned—seeds (Fig 1).

118
119 To test our predicted relationships between budburst responses to environmental cues and common
120 functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases
121 (BIEN, Maitner et al. (2018) and TRY, Kattge et al. (2020)) with budburst data from the OSPREE
122 database of controlled environment studies (Ettinger et al., 2020). We developed a hierarchical Bayesian
123 joint model that predicts phenological responses to forcing, chilling and photoperiod treatments based
124 on species-level trait values, while allowing additional variation due to species. This approach takes
125 a step towards predicting variation via species traits instead of species identity (when traits explain
126 a significant portion of the variation, species identity will explain only a small amount), which could
127 help forecast species phenological responses based on trait values alone.

128

129 Methods

130 We merged three major databases for our analysis. We gathered phenological data from the OSPREE
 131 database (Ettinger et al., 2020), which contains budburst data for woody, deciduous species
 132 from experiments of forcing, chilling and photoperiod, which we updated since its initial publication,
 133 for details on the methods used see Morales-Castilla et al. (in prep). We gathered trait data from
 134 TRY and BIEN ((Maitner et al., 2018; Kattge et al., 2020)—two large databases that include plant
 135 trait data across many individuals, species, and studies. We obtained data from both databases on 5
 136 December, 2018, with an updated version of the TRY data obtained 10 April, 2019. We focused our
 137 search for trait data on the subset of 234 OSPREE species used in Morales-Castilla et al. (in prep),
 138 which represents well studied species with good phenology and phylogenetic data. Using the BIEN
 139 R package (Maitner et al., 2018), we downloaded trait data for the 94 available species for 13 traits.
 140 The TRY database included 96 of our focal species with 10 functional traits (Kattge et al., 2020).
 141 Given our focus on phenology of adult trees, we included trait data from adult individuals with a
 142 minimum height of 1.38 m. We further removed all data from experiments or from plants growing in
 143 non-natural habitats. We also grouped trait values where appropriate, for example categorizing trait
 144 values for SLA, SLA with petioles, and SLA without petioles as simply SLA in our analysis (see Table
 145 S1). Duplicated data in both the TRY and BIEN datasets were also removed ($n = 434905$). Based
 146 on our selection criteria, our final dataset included data for 11 traits from 91 of the species also repre-
 147 sented in the OSPREE database, but each species differs in the number and types of traits measured.
 148

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

164

165 Joint model of trait and phenology

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

¹⁷⁴ **Trait sub-model**

¹⁷⁵ The trait sub-model describes the processes that determine trait observations for 1 to n species across
¹⁷⁶ each of the 1 to m studies in the trait part of our dataset (TRY and BIEN data). We use hierarchical
¹⁷⁷ modeling to partitions trait variation by measurement error, species identity, and study identity. In
¹⁷⁸ particular, we assume that a trait observation for species i from study j , $Y_{\text{trait}_{i,j}}$, has the following
¹⁷⁹ normal distribution:

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

with

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

¹⁸⁰ where α_{trait_i} and α_{study_j} are elements of the normal random vectors:

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

¹⁸¹ The latent parameter $\alpha_{\text{grand trait}}$ represents a trait value that is independent of study and species,
¹⁸² $\alpha_{\text{species},i}$ and $\alpha_{\text{study},j}$ are species- and study-level offsets from that trait value, σ_m^2 is measurement error,
¹⁸³ and σ_{trait}^2 and σ_{study}^2 represent species and study-level variances in trait values. Of these parameters,
¹⁸⁴ $\boldsymbol{\alpha}_{\text{trait}}$ are shared by the phenology sub-model.

¹⁸⁵ **Phenology sub-model**

¹⁸⁶ The phenology sub-model describes the processes that determine phenological observations for 1 to n
¹⁸⁷ species, specifically the timing (day of year) of budburst from the updated OSPREE dataset. We as-
¹⁸⁸ sume that an observation of budburst day for species k under set g of chilling, forcing, and photoperiod
¹⁸⁹ treatments, (c_g, f_g, p_g) , $Y_{\text{pheno}_{k,g}}$, has the following normal distribution:

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

with

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

and

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

¹⁹⁰ where $\alpha_{\text{pheno},k}$, $\alpha_{\text{chill},k}$, $\alpha_{\text{force},k}$, and $\alpha_{\text{photo},k}$ are elements of the normal random vectors:

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

191 Parameter $\alpha_{\text{pheno},k}$ represents the day of budburst for species k without the influence of chilling,
 192 forcing, or photoperiod treatments. Average day of budburst (independent of treatments) is μ_{pheno} , and
 193 σ_{pheno}^2 is the variance across species. The parameters $\alpha_{\text{chill},k}$, $\alpha_{\text{force},k}$, and $\alpha_{\text{photo},k}$ represent the trait-
 194 independent responses of species k to chilling, forcing, and photoperiod treatments respectively, each
 195 with an associated mean (μ_{chill} , μ_{force} , μ_{photo}) and variance (σ_{chill}^2 , σ_{force}^2 , σ_{photo}^2) across species. The
 196 effect of the species trait value, $\alpha_{\text{trait},k}$ (parameter shared with trait sub-model above), on its responses
 197 to chilling, forcing, and photoperiod are described by parameters $\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$.
 198 Finally, σ_d^2 is the variance arising from measurement error.
 199 We chose weakly informative priors, and validated them using a series of prior predictive checks. The
 200 model was coded in the Stan programming language, fit using the rstan package (Stan Development
 201 Team, 2018), with 1,000 iterations per chain across 4 chains (4,000 total sampling iterations), and all
 202 models met basic diagnostic checks, including no divergences, high effective sample size (n_{eff}), and
 203 \hat{R} close to 1.

204 Results

205 Across traits, height, SLA, and LNC strongly related to chilling, forcing and photoperiod treatments
 206 ($\beta_{\text{chill[sp]}}$, $\beta_{\text{force[sp]}}$, and $\beta_{\text{photo[sp]}}$, Fig 4 a-i), but the direction of these relationships only showed con-
 207 sistent trends for LNC (Fig. 4 j-l). As we predicted, height was related to chilling ($\beta_{\text{chill[sp]}}$) and
 208 photoperiod ($\beta_{\text{photo[sp]}}$), with taller species having larger responses to cues (-0.5 m per standardized
 209 chilling; 90% uncertainty interval (UI): -1, -0.1 and -0.2 m per standardized photoperiod; 90% UI:
 210 -0.5, 0, Fig 4 a-c). As illustrated for one characteristically acquisitive species, *Alnus incana*, and one
 211 characteristically conservative species (*Quercus robur*) (Fig S3), these responses lead to generally later
 212 budburst (μ_{pheno}), and fit within our predictions for acquisitive versus conservative growth strategies.
 213 Seed mass, however, had the smallest responses, with no relationship between seed mass and any cue
 214 (Fig. 4 g-i & Fig S3).

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

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

239

240 Discussion

241 We found species traits influenced the timing of budburst in response to the three primary cues of
 242 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or
 243 later phenology following well-established gradients in growth strategies predicted by functional traits
 244 (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016):
 245 early species tended to have traits associated with fast and acquisitive strategies while later species
 246 had traits associated with conservative, slower strategies. We found the largest budburst responses
 247 occurred for traits related to resource acquisition and structure, with SLA, LNC, and height all showing
 248 large responses across our three cues. In contrast, our one reproductive trait—seed mass—showed
 249 a smaller response. Our results provide a major step forward in integrating phenology into broader
 250 trait syndromes that shape species growth strategies, and support some previous findings from more
 251 local scales that found strong relationships between height and species phenology (Sun and Frelich,
 252 2011; Sporbert et al., 2022; Segrestin et al., 2020), while other traits—such as seed mass—showed no
 253 relationships with phenology in our more global analysis.

254

255 Effects of phenology-trait relationships on community assembly

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

269

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 large responses to forcing for short trees, which could prevent frost damage or
 274 xylem cavitation under a late spring frost (Clements et al., 1972; Marquis et al., 2020) and influence
 275 annual cambial meristem growth (Lenz et al., 2016). Similarly, the lack of a response to chilling or
 276 forcing by high SLA individuals' could be driven by other trait attributes and environmental cues—
 277 selecting for species relative growth rates or leaf longevity—and not photosynthetic potential (Westoby,
 278 1998; Reich, 2014). These findings highlight the complexity of determining the drivers of species trait
 279 profiles, 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 could aid forecasting species and community
 283 responses to climate change. While decades of research have documented phenological shifts with an-
 284 thropogenic climate change, increasing research suggests a potential connection between phenological
 285 responses to warming and performance with warming, where species that shift more with phenology
 286 appear to perform better (Cleland et al., 2012; Macgregor et al., 2019). Our results suggest this

287 phenology-performance relationship could be driven in part by a suite of traits that covary with phe-
288 nological cues to determine how responsive species are to warming. As species with smaller responses
289 to all cues, especially chilling and photoperiod, would tend to advance more with warming, our re-
290 sults suggest these species may also grow more quickly. These results could further aid predicting
291 the potential for invasion, as communities with similar phenologies and suites of traits, appear more
292 susceptible to fast growing, phenologically more responsive non-native species (Wolkovich and Cleland,
293 2011; Alexander and Levine, 2019; Schuster et al., 2021).

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

310

311 References

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

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

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

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

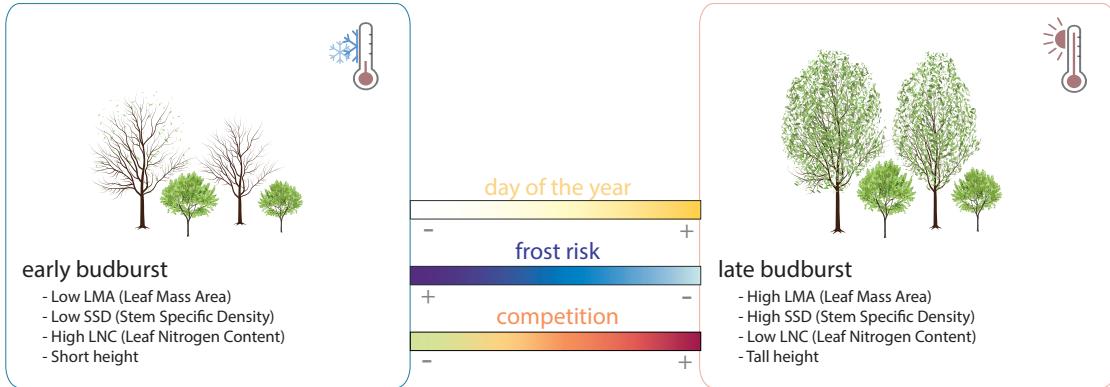


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species to exhibit traits associated with acquisitive growth, as they are more apt to experience greater risk of frost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

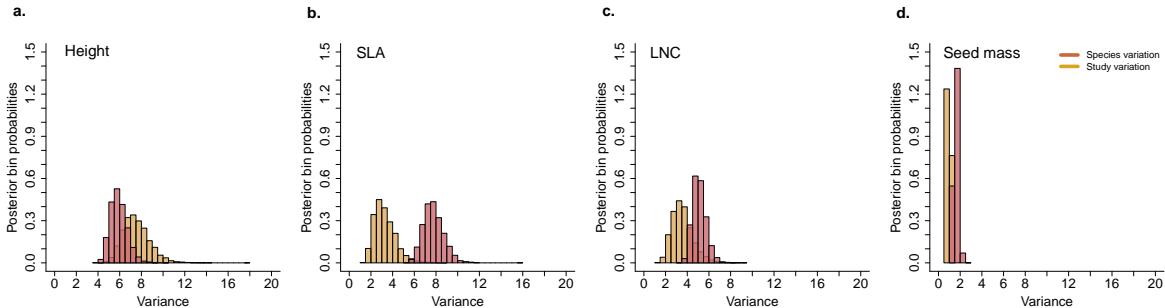


Figure 2: Traits differed in the relative magnitude of their species-level and study-level variation, with only a. the height model estimating greater study-level variation than species-level, while our b. specific leaf area, c. leaf nitrogen content, and d. seed mass models all estimated higher species-level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

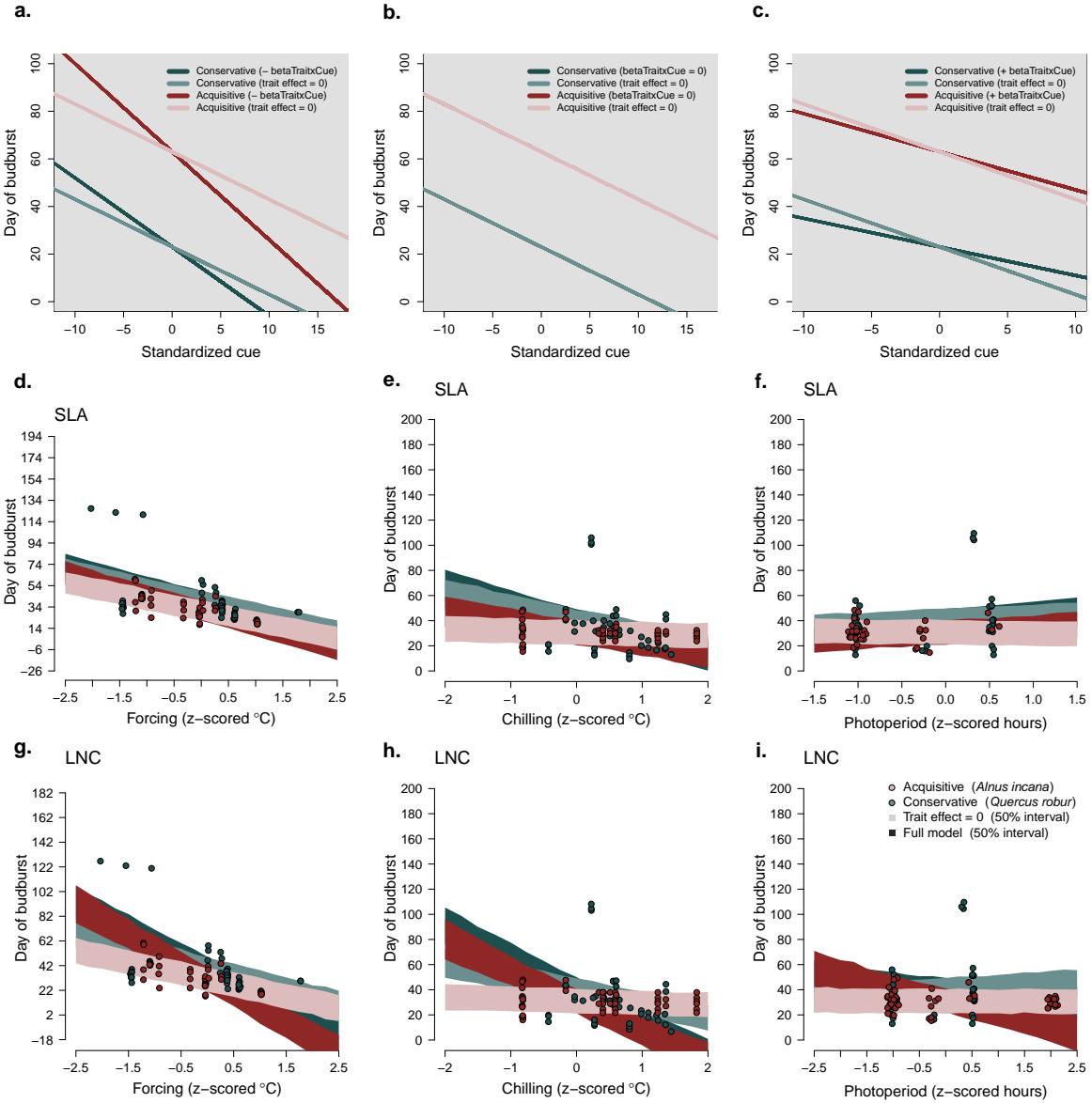


Figure 3: We expected species with traits associated with acquisitive (e.g., low SLA and LNC) versus conservative (e.g., high SLA and LNC) growth strategies would have different budburst responses to phenological cues. Our joint model allows traits of species to influence their responses to cues. We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

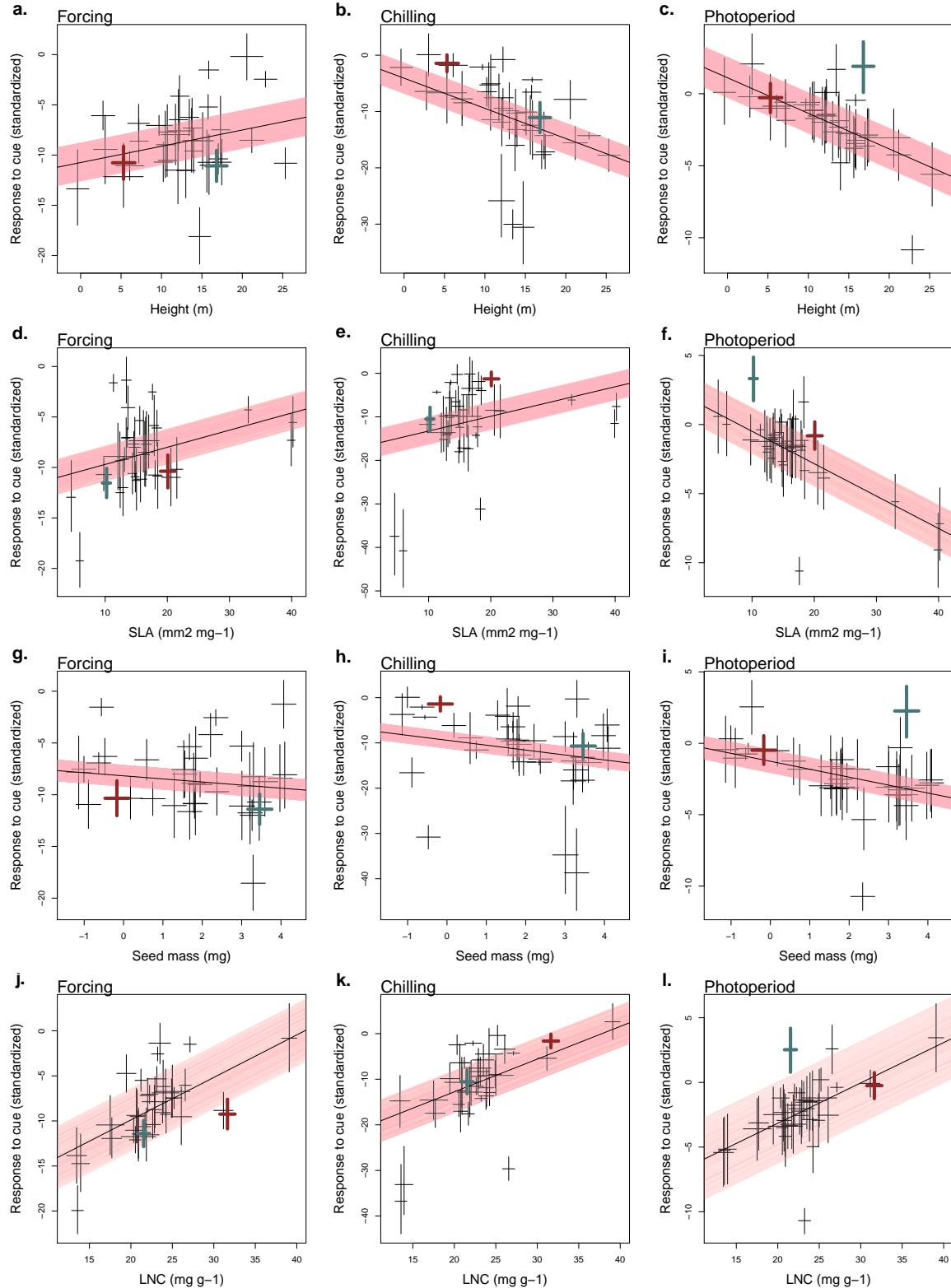


Figure 4: Estimated species-level cue responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third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