

<sup>1</sup> Woody plant phenological responses are strongly associated  
<sup>2</sup> with key functional traits

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## <sup>32</sup> Summary

<sup>33</sup> Species-level variation in phenology—the timing of recurring life history events—can vary seasonally  
<sup>34</sup> with changes in abiotic risks, light, and nutrients. This favours acquisitive growth strategies early in  
<sup>35</sup> the spring season and conservative growth strategies under the more benign, but competitive, envi-  
<sup>36</sup> ronment later in the season. This framework infers suites of traits that may co-vary with phenologies,  
<sup>37</sup> but high trait variability across environments makes this challenging to test. Using a joint model  
<sup>38</sup> to accommodate this variability, we performed a meta-analysis using budburst data from controlled  
<sup>39</sup> environment experiments and plant traits to test the relationships between traits and cues. Earlier  
<sup>40</sup> species were shorter with denser, lower nitrogen leaves, but showed no relationship in terms of seed  
<sup>41</sup> mass. In general, leafout fit within the common trait framework, and can improve predictions of how  
<sup>42</sup> species growth strategies and phenologies may shift with climate change.

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<sup>44</sup> Key Words: Budburst, spring phenology, functional traits, trees, climate change, forest communities

## <sup>45</sup> Introduction

<sup>46</sup> The timing of life history events—phenology—can shape both ecosystem services and community  
<sup>47</sup> dynamics. Spring phenology, for example, defines the start and overall length of the growing season—  
<sup>48</sup> shaping forest carbon storage and species interactions (Cleland et al., 2007; Beard et al., 2019; Gu  
<sup>49</sup> et al., 2022). Shifts in phenology with climate change across systems (Menzel et al., 2006; Vitasse  
<sup>50</sup> et al., 2021) have thus led to growing concerns over their possible impacts.

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<sup>52</sup> Predicting these changes requires understanding the drivers of phenology both at a proximate scale—  
<sup>53</sup> the environmental triggers of phenology each year, such as temperature and daylength—and at an  
<sup>54</sup> ultimate scale, where long-term environmental pressures may select for the different phenologies across  
<sup>55</sup> species (e.g., certain species are early or late relative to other species each year, Ovaskainen et al.,  
<sup>56</sup> 2013; Wolkovich and Donahue, 2021). At the proximate level, environmental conditions across the  
<sup>57</sup> winter and spring cause species to start growth at different times, and is well documented for the start  
<sup>58</sup> of growth in woody plants each year (Laube et al., 2014; Flynn and Wolkovich, 2018). Similar trends  
<sup>59</sup> are also observed for spring phenological events across taxa, including in the timing of egg laying in  
<sup>60</sup> birds (Crick et al., 1997; D'Alba et al., 2010) and the advance of spawning in amphibians (Tryjanowski  
<sup>61</sup> et al., 2003; Kusano and Inoue, 2008), but current work provides limited insights into the drivers of  
<sup>62</sup> species differences (Laube et al., 2014; Chuine et al., 2016; Flynn and Wolkovich, 2018).

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<sup>64</sup> At the ultimate level, species phenologies may vary due to changing pressures across the growing  
<sup>65</sup> season. Species that start growth early often risk high tissue loss—due to frost damage (Sakai and  
<sup>66</sup> Larcher, 1987; Augspurger, 2009) or high herbivore apparency (Wainwright et al., 2012)—but benefit  
<sup>67</sup> from higher resource availability (Rathcke and Lacey, 1985; Hufkens et al., 2012). In contrast, later  
<sup>68</sup> species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008;  
<sup>69</sup> Wolkovich and Ettlinger, 2014). For plants, this variation in early to late season growth, may mirror  
<sup>70</sup> the stressors from early to late successional communities, and may similarly shape phenology (Laube  
<sup>71</sup> et al., 2014).

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<sup>73</sup> Different pressures could shape a number of species attributes related to their growth strategies, in-  
<sup>74</sup> cluding phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced  
<sup>75</sup> if damaged (Reich et al., 1999), while species with later phenology may benefit from investing in tissues  
<sup>76</sup> that infer greater resource retention (Gorné et al., 2020). These differences in traits, and trade-offs in  
<sup>77</sup> allocation of resources to growth and tissue quality, can be related to a broader framework of species  
<sup>78</sup> growth strategies and functional traits (Fig. 1, Wolkovich and Ettlinger, 2014), where species range  
<sup>79</sup> from acquisitive (fast) to more conservative (slow) growth (Wright et al., 2004; Chave et al., 2009).

Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation of the leaf economic and the wood economic spectra (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016), but they can make limited predictions of trait variability (Viole et al., 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving the relationships between broader trait syndromes and phenology largely unknown. Understanding these relationships is critical to forecasting community dynamics and responses to climate change. To date, studies have generally only examined the relationship between traits and phenology within a single site (reviewed in Wolkovich and Cleland, 2014; Wolkovich and Donahue, 2021), where the problem of proximate drivers causing phenological variation can be more easily ignored. Adding phenology to broader trait frameworks becomes more complex when high levels of variation occurs across large spatial and temporal ranges.

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

Studies of spring phenology in temperate forests may provide the best opportunity to integrate phenology into functional trait research, given their cues are well understood and the strong gradients in selective environments that occur over the spring season. Based on trade-offs between early and late spring phenologies, we predict acquisitive species to be shorter, with leaf traits favourable to higher light availability and tolerance of late spring frost (high specific leaf area, SLA, and leaf nitrogen content, LNC; Fig 1). Such species should exhibit early phenology, with small cue responses. Canopy species that budburst later via larger cue responses, when competition for soil resources is greater, would then have traits associated with conservative growth—taller with denser wood (Laughlin et al., 2010)—with leaf traits suited for more variable light (low SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative continuum, as acquisitive species produce smaller seeds and conservative species produce larger—better provisioned—seeds (Fig 1).

To test our predicted relationships between budburst responses to environmental cues and common functional traits (height, SLA, seed mass, and LNC), 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 (Ettinger et al., 2020). We developed a hierarchical Bayesian joint model that predicts phenological responses to forcing, chilling and photoperiod treatments 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 identity will explain only a small amount), which could help forecast species phenological responses based on trait values alone.

## Methods

We merged three major databases for our analysis. We gathered phenological data from the OSPREE database (Ettinger et al., 2020), which contains budburst data for woody, deciduous species from experiments of forcing, chilling and photoperiod. We updated this database since its initial publication, the methods of which are discussed by Morales-Castilla et al. (in prep). We gathered trait data from TRY and BIEN (Maitner et al., 2018; Kattge et al., 2020), both of which are large trait databases

that include plant trait data across many individuals, species, and studies (Table S1). We obtained data from both databases on 5 December, 2018, with an updated version of the TRY data obtained 10 April, 2019. We focused our search for trait data on the subset of 234 OSPREE species used in Morales-Castilla et al. (in prep), which represents well studied species with good phenology and phylogenetic data. Using the BIEN R package, version 1.2.5 (Maitner et al., 2018), we downloaded trait data for the 94 species available, for which there were 13 traits. The TRY database included data for 10 traits for 96 of our focal species (Kattge et al., 2020). Given our focus on phenology of adult trees, we included trait data from adult individuals with a minimum height of 1.38 m. We further removed all data from experiments or from plants growing in non-natural habitats. We also grouped trait values where appropriate, for example categorizing trait values for “SLA”, “SLA with petioles”, and “SLA without petioles” as simply “SLA” in our analysis (see Table S1). Duplicated data in both the TRY and BIEN datasets were also removed ( $n = 434905$ ). Based on our selection criteria, our final dataset included data for 11 traits from 91 of the species also represented in the OSPREE database, with each species differing in the number and types of traits measured.

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

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## 159 Joint model of trait and phenology

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

### 168 Trait sub-model

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

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

with

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

where  $\alpha_{\text{trait}_i}$  and  $\alpha_{\text{study}_j}$  are elements of the normal random vectors:

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

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

## Phenology sub-model

The phenology sub-model describes the processes that determine phenological observations for 1 to  $n$  species, specifically the timing (day of year) of budburst from the updated OSPREE dataset. We assume that an observation of budburst day for species  $k$  under set  $g$  of chilling, forcing, and photoperiod treatments (which we  $z$ -scored to allow direct comparison of cues),  $(c_g, f_g, p_g)$ ,  $Y_{\text{pheno}_{k,g}}$ , 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

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

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:

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

Parameter  $\alpha_{\text{pheno},k}$  represents the day of budburst for species  $k$  without the influence of chilling, forcing, or photoperiod treatments. Average day of budburst (independent of treatments) is  $\mu_{\text{pheno}}$ , and  $\sigma_{\text{pheno}}^2$  is the variance across species. The parameters  $\alpha_{\text{chill},k}$ ,  $\alpha_{\text{force},k}$ , and  $\alpha_{\text{photo},k}$  represent the trait-independent responses of species  $k$  to chilling, forcing, and photoperiod treatments respectively, each with an associated mean ( $\mu_{\text{chill}}$ ,  $\mu_{\text{force}}$ ,  $\mu_{\text{photo}}$ ) and variance ( $\sigma_{\text{chill}}^2$ ,  $\sigma_{\text{force}}^2$ ,  $\sigma_{\text{photo}}^2$ ) across species. The effect of the species trait value,  $\alpha_{\text{trait},k}$  (parameter shared with trait sub-model above), on its responses to chilling, forcing, and photoperiod are described by parameters  $\beta_{\text{trait.chill}}$ ,  $\beta_{\text{trait.force}}$ ,  $\beta_{\text{trait.photo}}$ . Finally,  $\sigma_d^2$  is the variance arising from measurement error.

193

194 We chose weakly informative priors, and validated them using a series of prior predictive checks.  
 195 The model was coded in the Stan programming language, fit using the rstan package version 3.3.6  
 196 (Stan Development Team, 2018), with 1,000 iterations per chain across 4 chains (4,000 total sampling  
 197 iterations), and all models met basic diagnostic checks, including no divergences, high effective sample  
 198 size ( $n_{eff}$ ), and  $\hat{R}$  close to 1, fitting the data well (Fig S2). Here we present our model estiamtes as  
 199 the means and 90% posterior uncertainty intervals.

## 200 Results

201 Across traits, height, SLA, and LNC strongly related to chilling, forcing and photoperiod treatments  
 202 ( $\beta_{chill[k]}$ ,  $\beta_{force[k]}$ , and  $\beta_{photo[k]}$ , Fig 2 a-f & j-l), but the direction of these relationships only showed  
 203 consistent trends for LNC (Fig. 2 j-l). As we predicted, height was related to chilling ( $\beta_{chill[k]}$ ) and  
 204 photoperiod ( $\beta_{photo[k]}$ ), with taller species having larger responses to cues (-0.5 m per standardized  
 205 chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized photoperiod; 90% UI:  
 206 -0.5, 0.0, Fig 2 a-c, Table S2). As illustrated for one characteristically acquisitive species, *Alnus in-*  
 207 *cana*, and one characteristically conservative species, *Quercus robur* (Fig S3), the cue relationships  
 208 with height led to generally later budburst ( $\mu_{k,g}$ ), and fit within our predictions for acquisitive versus  
 209 conservative growth strategies (Fig. 3). In contrast, seed mass had the smallest responses, with no  
 210 relationship between seed mass and any cue (Fig. 2 g-i, Fig 3 d-f, & Table S3).

211  
 212 Of our leaf traits, we found that species SLA related to photoperiod ( $\beta_{photo[k]}$ , -0.2 mm<sup>2</sup>/mg per stan-  
 213 dardized photoperiod; 90% UI: -0.4, 0.0, Fig. 2 f, Table S4), but did not strongly predict responses to  
 214 chilling ( $\beta_{chill[k]}$ ) or forcing treatments ( $\beta_{force[k]}$ , Fig. 2 d and e). Thus, species with more acquisitive  
 215 growth strategies (thin leaves and a lower investment in leaf mass that leads to large SLA values),  
 216 had larger responses to photoperiod, contrary to our predictions (Fig. 2 f). For LNC, we found that  
 217 species that produce leaves with high nitrogen content, which relates generally to high photosynthetic  
 218 rates and acquisitive growth, show smaller responses to cues (Fig. 2 j-l). These findings are in line  
 219 with our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g  
 220 per standardized chilling; 90% UI: 0.3, 1.2, Table S5), but we also found high LNC species to be less  
 221 responsive to photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0, 0.6) and to forcing (0.5  
 222 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig 2 j-l & Fig S3 d-f).

223  
 224 Across our models, we found species-level variation across traits ( $\sigma_{trait}^2$ ) were comparable to or greater  
 225 than variation across studies ( $\sigma_{study}^2$ , Fig 4). The magnitude of study-level variation ( $\sigma_{study}^2$ ) that we  
 226 found, however, suggests that models using large trait databases that fail to separate out study from  
 227 species-level variation ( $\sigma_{trait}^2$ ) may poorly estimate species traits. Variation across studies was greatest  
 228 for height (with  $\sigma_{study}^2$  of 7.5m compared to 5.9 m for  $\sigma_{trait}^2$ , Fig 4a). For seed mass and LNC study-  
 229 level variation was less than that of the species-level variation, with estimates of 1 mg for study-level  
 230 variation versus 1.6 for species-level variation in seed mass and estimates of 3.6 mg g<sup>-1</sup> for study-level  
 231 variation and 5.1 mg g<sup>-1</sup> for the species-level variation in LNC (Fig 4c and d). At the lowest end,  
 232 study-level variation in SLA was approximately half the value of the species-level variation (3.3 mm<sup>2</sup>  
 233 mg<sup>-1</sup> versus 7.8 mm<sup>2</sup> mg<sup>-1</sup> for  $\sigma_{study}^2$  and  $\sigma_{trait}^2$ , respectively, Fig 4b).

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

had traits associated with conservative, slower strategies. We found the largest budburst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and height all showing large responses across our three cues. In contrast, our one reproductive trait—seed mass—showed a smaller response. Our results provide a major step forward in integrating phenology into broader trait syndromes that shape species growth strategies, and support previous findings from more local scales that found strong relationships between height and species phenology (Sun and Frelich, 2011; Sporbert et al., 2022; Segrestin et al., 2020). Our findings also suggest other traits—such as seed mass—show no relationship with phenology in our more global analysis.

249

## 250 Effects of phenology-trait relationships on community assembly

251 Early budbursting species with shorter heights and low LNC , grow quickly and benefit from greater  
 252 light availability in the open canopy of many temperate forests in the early spring.  
 253 Our findings suggest the changing selective pressures across the early growing season may affect the  
 254 temporal assembly of communities, with strong abiotic pressures early in the season associated with  
 255 early acquisitive species while greater biotic pressures later were associated with later conservative  
 256 species. Early budbursting species with shorter heights and low LNC , grow quickly and benefit from  
 257 greater light availability in the open canopy of many temperate forests in the early spring. We found  
 258 phenologically earlier species had traits that allow for faster return on resource investments (Grime,  
 259 1977; Westoby, 1998; Chave et al., 2009) and thus their tissues may be easier to replace if lost to  
 260 frost or other abiotic disturbances. In contrast, phenologically later species had traits associated with  
 261 greater competitive abilities and slower growth (Fig. 2, Grime, 1977; Westoby, 1998; Chave et al.,  
 262 2009), which may be necessary to compete for soil and light resources when most other species are  
 263 already growing. These traits can be linked to other ecological processes and species characteristics,  
 264 such as species successional position, as illustrated by the differences between early and late succes-  
 265 sional species, like *Alnus incana* and *Quercus robur* (Fig 2).

266

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

278

## 279 Phenology-trait relationships under future climates

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

289 the potential for invasion, as communities with similar phenologies and suites of traits, appear more  
290 susceptible to fast growing, phenologically more responsive invasive species (Wolkovich and Cleland,  
291 2011; Alexander and Levine, 2019; Schuster et al., 2021).

292

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

309

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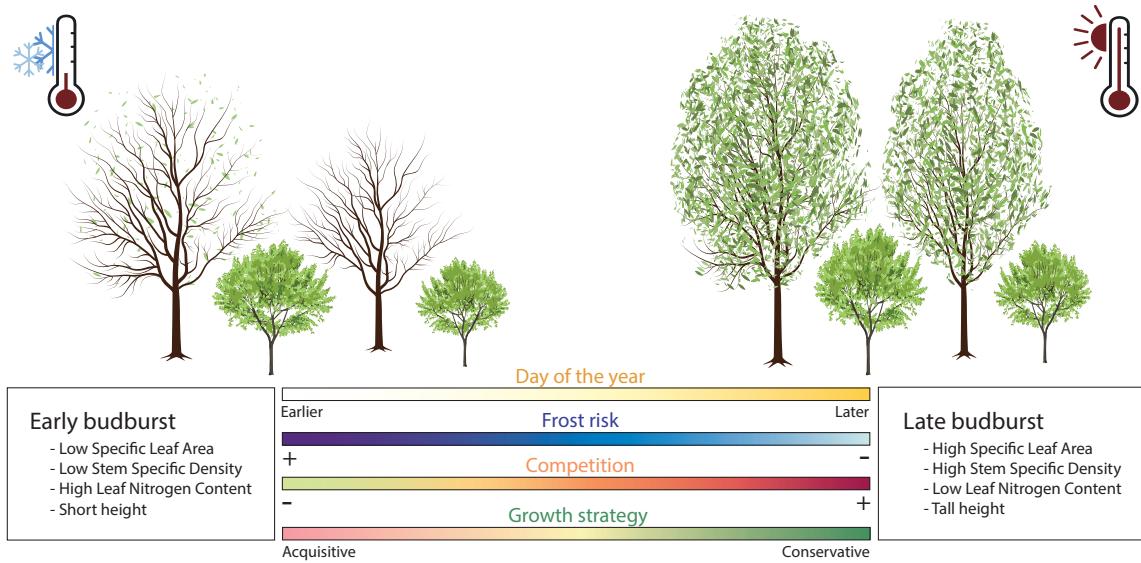


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species to exhibit traits associated with acquisitive growth, as they are more apt to experience greater risk of frost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

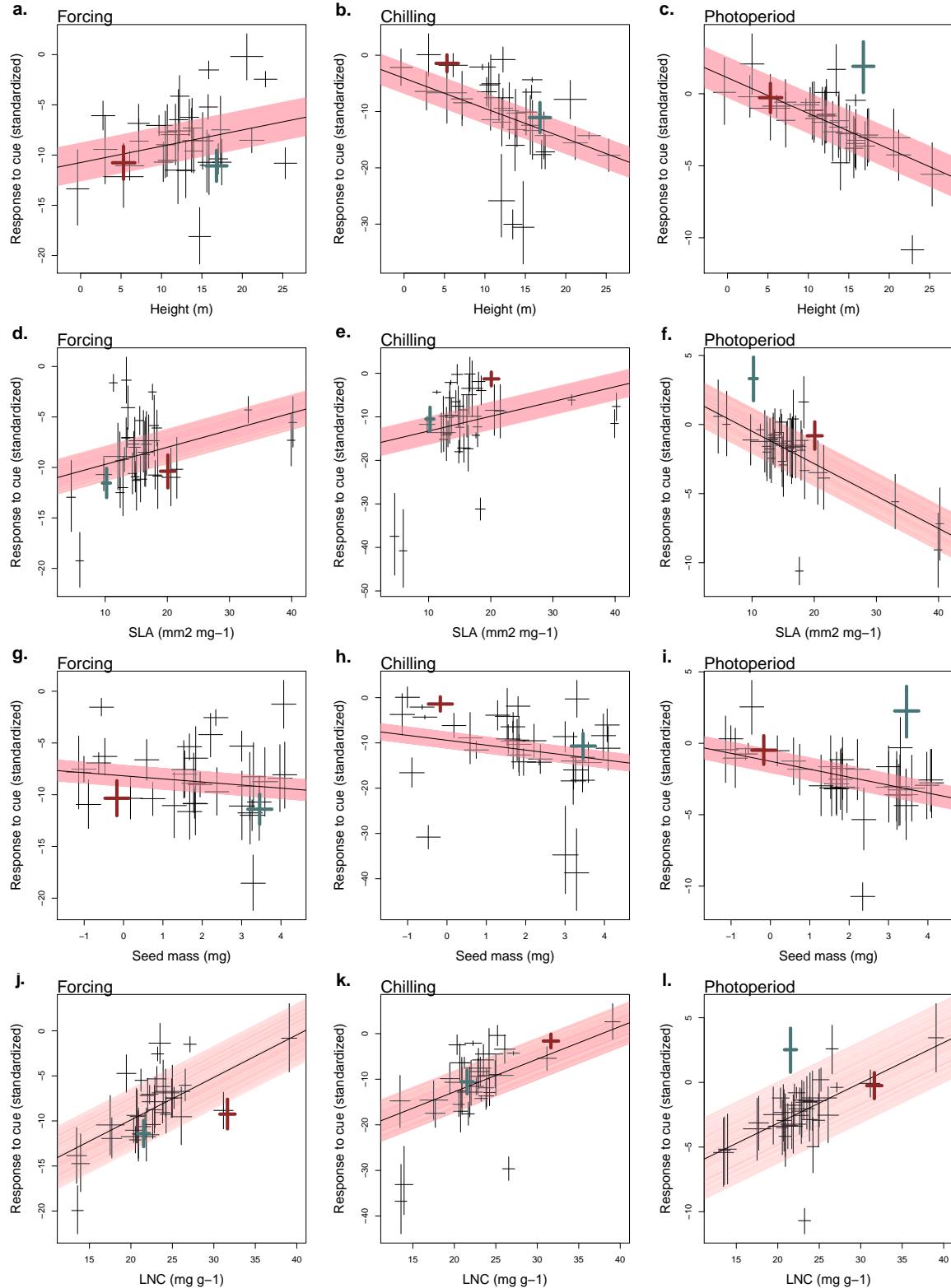


Figure 2: Estimated species-level cue responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third 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.

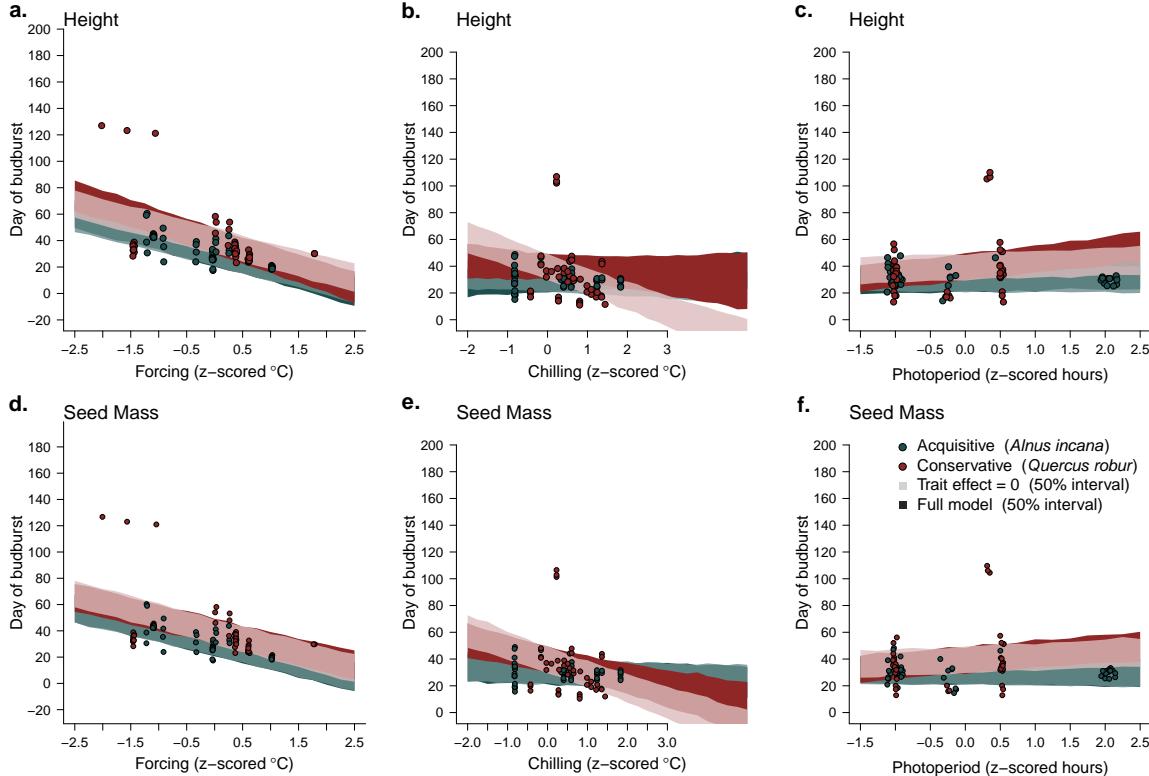


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with height (**a-c**) and seed mass (**d-f**) for an acquisitive species, *Alnus incana* shown in red, and a conservative species, *Quercus robur*, shown in blue. **a**, The effect of height on phenological cue responses was weaker in response to forcing cues, but stronger in response to both **b**, chilling and **c**, photoperiod. In contrast, seed mass has a negligible effect on **d**, forcing and **f**, photoperiod cue responses, **e**, but a greater response with chilling. Band represent the 50% uncertainty intervals of the model estimates. The coloured bands represent the 50% uncertainty intervals of the model estimates and points individual trait measurements.

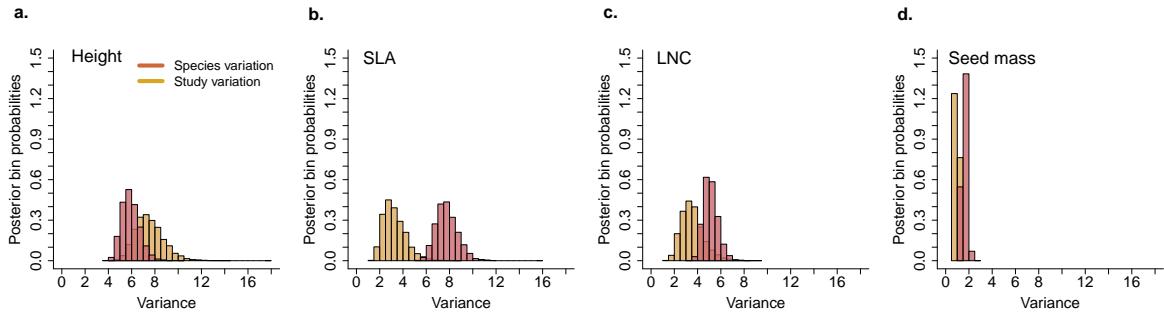


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation, with only a. the height model estimating greater study-level variation than species-level, while our b. specific leaf area, c. leaf nitrogen content, and d. seed mass models all estimated higher species-level 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.