Woody plant phenological responses are strongly associated with key functional traits- Outline

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Climate change is altering the timing of species phenologies, with changes in temporal niches reshaping ecological communities and interactions between species. In temperate systems, the observed advances in plant phenological events, such as budburst, leafout, and flowering times, are associated with changes in seasonal temperatures, particularly warming winter and spring conditions (**??**). But despite this strong general trend, phenological responses vary across species and geographically, and we have yet to fully understand the underlying mechanisms driving observed differences (**??**). As the effects of climate change become more pronounced, understanding these relationships is of increasing importance if we are to predict and preserve the diversity and services found in temperate forest ecosystems.

While we have yet to identify all drivers of selection on phenologies, considerable work has shown the importance of three abiotic cues – chilling, forcing, and photoperiod – as the primary drivers of budburst and

leafout in temperate deciduous species (**????**). For budburst to occur, species must experience extended period of cold temperatures to break dormancy (**?**), where species with higher chill requirements budburst later in the season. Spring forcing temperatures, or the temperatures needed to cue species to initiate growth after dormancy release, are also changing as temperatures warm and the timing at which suitable temperature thresholds are met occur earlier within the season (citation). Photoperiod cues can also determine a species ability to initiate growth (**??**). Species with strong photoperiod requirements are, however, expected to be more constrained in their ability to track changes in temperature and may face fitness costs and novel species interactions as a result (**??**). Previous studies support the general trend of advancing budburst in response to each cue, but with considerable variation in the relative importance of different cues across species (**??**). Some woody plant species, for example, require less forcing to budburst after experiencing a cool winter with more chilling, while also having the ability to compensate for low chilling with high forcing conditions or longer photoperiods (**??????**). Evidence for the role of photoperiod is largely species specific (**????**), with few studies testing for its importance across species in a community (but see **?**). Species that are less dependent on photoperiod cues and able to track trends in temperatures may benefit from greater intra-annual phenotypic plasticity resulting in greater fitness outcomes under increasingly variable climates (citation?). Despite the insights that identifying these proximate drivers have provided, we still lack a generalizable and mechanistic understanding of why species and populations differ in their cue use that. Further insight on this topic is needed to predict future changes in species sensitivities and community structure.

In our efforts to understand variation in spring phenological timing, researchers have tested several potential mechanisms to identify the drivers of species cue responses. Work exploring drivers of intraspecific cue use, for example, has found age or the development stage of woody plants to be important. Younger life stages, including both seedlings and younger understory trees, budburst earlier than mature individuals in the canopy (**??**). These trends reflect both differences in the temperature sensitivities across life stages and effects of ontogenic changes as trees mature (**??**). Interspecific differences in cues, however, have been studied in relation to species' phylogenetic relatedness. Work on this topic has found strong evidence for events like flowering-time and budburst to be consistent within taxonomic families, suggesting conservatism in the genetic and physiological mechanisms that determine species phenologies (**???**). Studies of woody plant phenologies across species ranges have also highlighted the importance of local adaptations, with the presence of gradients in phenological responses and presumably cue use at northern range limits (**???**). In temperate systems for example, greater temperature variation in North America was associated with higher chilling requirements and more conservative phenological responses (**?**). Studies testing for trends in cues responses across species latitudinal ranges have also observed stronger responses to photoperiod cues at lower latitudes (**?**). Exploring these potential drivers of plant phenologies have illustrated the nuanced nature of

phenology in shaping diverse communities, but they are still limited in the degree to which they explain the variation we observe across species and ecosystems.

Taking a functional trait approach to phenological research could help explain the variation in cue use across species and geographically (??). Early work on functional traits used trait data from diverse global assemblages of deciduous plants to identify associations between traits, common growth strategies, and different niche space (???). The resulting leaf-height-seed scheme and the more extensive leaf economic spectrum found direct associations between several trait values and gradients in species growth rates and competitive abilities (?????). While reproductive phenological traits have been identified as ecologically important for many years (??), few studies have explored their role in the larger trait framework. Spring phenological traits, such as budburst and leafout, define the beginning of the growing season and period of photosynthesis, and therefore also have the potential to correlate with established growth strategies. Support for the existence of trade-offs in budburst dates and traits related to growth and resource use have been observed across plant functional groups and habitat types in a handful of studies. For example, several studies have found deciduous woody species with smaller vessel diameters and diffuse or semi-ring-porous xylem structures to leaf out earlier than species with larger vessels, as this anatomy reduces the risk of embolism during freezing events (??). In testing relationships between budburst and leaf traits of deciduous tree species in Japan, (?) found positive correlations between budburst date and leaf area, leaf mass, and nitrogen content by both mass and area, while (?) found deciduous species with high leaf mass per area (a trait that is the inverse of specific leaf area) to budburst earlier in deciduous oak forests in eastern China. Variation in leafout can also relate to species heights, both intraspecifically and across functional groups, with shorter individuals or understory species leafing out earlier than taller individuals or canopy species (??). To date, however, research in this area has focused on individuals at local scales, or few traits for a small number of species, limiting our ability to draw more general and causal inferences. There is also a lack of studies linking traits directly to cue sensitivity rather than phenological date. The likely associations between cue sensitivity, phenological events, and growth strategies may allow for more generalizable trends across species and sites, and better account for species variability in key environmental cue use.

To date, there have been numerous studies investigating the relationships between climate and functional traits and a wealth of literature on the separate effects of climate cues as drivers of phenology. However, the selective pressures shaping species traits under variable temperatures are also likely to act on species responses to phenological cues and define a species temporal niche. Species with a more acquisitive life-strategy have shorter rates of return on resource investments and the ability to take advantage of the greater abundance of soil nutrients and light early in the growing season. Such species face a lesser cost in initiating

phenological events too early, as they can recover from early season damage (cite Cat's paper?). For example, some acquisitive species produce leaves with high leaf nitrogen content and Specific Leaf Area (SLA) and can take advantage of greater light availability by having higher rates of photosynthesis (**??**), while also limiting the costs of tissue production (**???**). Acquisitive-strategy species also invest less in their wood structure, having shorter heights and lower stem densities (**?**). Species that budburst earlier in the growing season require less spring forcing and winter chilling, and shorter photoperiods (**?**), allowing them to grow under less competition for light and soil resources. The suite of traits of acquisitive species contrasts with more conservative life-strategy species that exhibit slower, more competitive growth strategies that benefit from slower rates of return on resource investment and the longer retention of leaf tissue. A greater requirement for cue unit accumulation to trigger phenological events should align with a more conservative life-strategy as such species seek to avoid damage due to premature development.

In this study, we test for associations between plant phenological responses to environmental cues and common functional traits. Budburst data for tree species in controlled environmental studies was selected from the Observed Spring Phenology Response in Experimental Environments (OSPREE) database and paired with functional trait data from the TRY and BIEN databases. This data was used to explicitly test for the relative differences in functional traits and the timing of budburst in response to experimental forcing, chilling, and photoperiod cues. Drawing on previous work and the broader trait literature, we predict that species that respond less strongly to chilling, forcing, and photoperiod conditions are more likely to have traits associated with acquisitive growth but low competitiveness, as reflected by high SLA, high leaf nitrogen content per mass (LNC), shorter heights, and lower seed mass. In contrast, species that are more responsive to chilling, forcing and photoperiods will have traits more associated with conservative growth and higher competitive abilities, such as low SLA, low LNC, greater heights and heavier seeds.
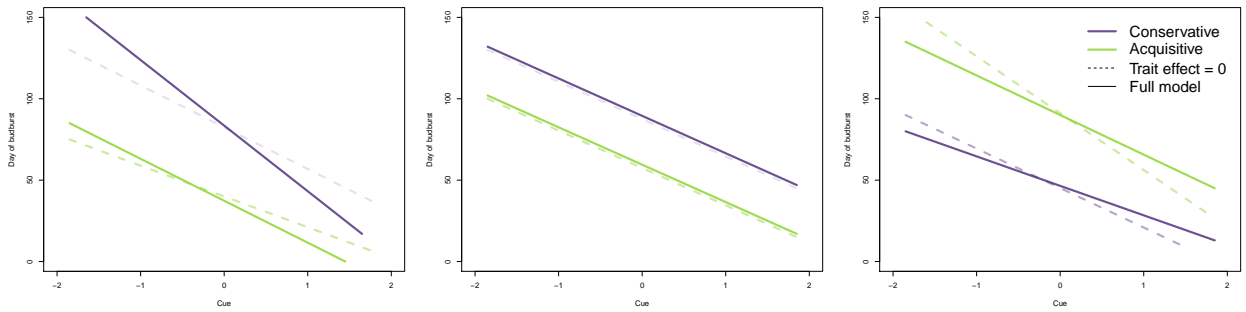

Figure 1: Conceptual figures

Using tree height as an illustrative example, we predict taller trees to be more conservative in their growth strategies and shorter species to budburst earlier and exhibit a more acquisitive growth strategy. Previous

work on cue responses in woody species have consistently observed negative responses to stronger cues, resulting in advanced budburst, and therefore we expect that the estimated cue responses from our models would all be negative. Under this assumption, there could be three possible trends in the relationships between cue and trait effects on budburst date. If phenological responses align with trait variation associated axes of acquisitive to conservative growth, we predict there to be a negative trait effect, resulting in a steeper negative slope in the cue response, and a stronger cue response and advance in budburst dates with higher cues 1. This is illustrated by the steeper slope of the solid lines for both the conservative and acquisitive species in 1. If the more conservative species have later budburst dates than the more acquisitive species, we should also observe a negative correlation between the trait effect and the cue slopes. It is important to note that the smaller differences in slope estimates for when the trait effect is zero and the full model observed for species with low traits is due to the magnitude of the trait value and not a difference in strength of the response. If functional traits have no relation to budburst phenology, the trait effect will be estimated as zero and we could expect to see no difference in the slopes of full model and cue only model 1. Finally, if our model estimates a positive trait effect, potentially as a result of a trade-off in selection for budburst phenology and resource use or competitiveness, we predict the slopes of our full model to be less steep than the cue only model 1.

1 Methods

For our analysis, we combined phenological data from the OSPREE database (?) with functional trait data from the TRY(cite) and BIEN (cite) trait databases.

The OSPREE database contains woody, deciduous species phenological data for which experimental data on phenological cues is available, and the phylogenetic relationship is well estimated. First published in 2019, this database has since been updated, and now includes the review of an additional 623 and 270 new publications from each of the following search terms:

- (budburst OR leaf-out) AND (photoperiod OR daylength) AND temperature*

- (budburst OR leaf-out) AND dorman*.

From this subsequent review, we an additional 12 papers met our selection criteria. For additional information on the construction of the OSPREE database and methods of cue estimates, see (?). Our analysis used all available budburst data for our 37 focal species, with the data originating from 28 unique studies.

Both TRY and BIEN are large databases compiling plant trait data across many individuals, species, and

studies. Initially, we began by searching both databases for all available trait data for all 234 species repre-sented in the OSPREE database.

Data was also obtained from the BIEN database using the BIEN R package (**?**). Data were requested or downloaded in December 2018. Our full trait datasets included data on 96 species and ten traits from the TRY database and 34 species and seven traits from the BIEN database. For our analysis, however, we only included trait data from adult individuals with a minimum height of 1.42 m and we removed all data from experiments or growing in non-natural habitats. Traits were also grouped where appropriate, for example, separate entries for SLA values with petioles, without petioles, and for which no petiole presence was specified were all categorized as a single trait in our analysis (see Table S1). Duplicated data across the datasets were removed (n= 434905). Finally, we subsetted the data to include only species for which we had a complete dataset for each species and trait. This resulted in a dataset of only 26 species and six functional traits. To test for correlations in our six traits and further refine our trait selection, we applied a PCA. The principle component explained 32.2% of variation while the second explained 23.4% of the variation (Fig. S1). Given the strong association between the SLA and LDMC leaf traits, and similarly between stem specific density (SSD) and height, we further reduced the number of traits in our analysis to include only height, seed mass, LNC, and SLA. By including only these four traits, we were able to increase the number of species we could include in our analysis as we had had at least one trait measurement for 37 species (height n = 47781, seed mass n = 281, LNC n = 3853, SLA n = 7656). Given the abundance of height data and overrepresentation of height measurements for six of our focal species, we randomly sampled 3000 height measurements for each of these species to include in our analysis (n = 27318). This reduces the effect of trait values from these frequently measured species from overwhelming the partial pooling effect in our model. In addition we excluded seed mass data from the HE Marx dataset from BIEN, as it consisted of only one value, making it challenging to include the study level effect in our model

Joint model of trait and phenology

To understand the implications of linking traits directly to cue responses, we developed a joint hierarchical Bayesian model. Our model is composed of two sub-models, a trait model and a phenology model, that are co-estimated and linked by a shared parameter. Since each trait varied in the number of studies in which it is included as well as the number of individuals for which it is measured, we chose to model each trait separately. The first part of the model is a hierarchical intercept only model where the response variable $Y_{i,j}$ is the observed trait value of species i from study j, and is assumed to be normally distributed. We further assume that the observed trait value is composed of a "grand" species trait value $\alpha_{\text{trait},i}$ that is shared

across all individuals of a species and that is independent of environment, a hierarchical grouping term on the intercept for study, $\alpha_{\text{study},j}$, to account for study-level differences in environment or observation methods, and random error. This results in the following sub-model for each trait:

$$Y_{i,j} \sim \mathcal{N}(\mu_{i,j}, \sigma_{\text{trait}}) \tag{1}$$

where σ_{trait} represents random error in the trait value (i.e., independent of study or species) and:

$$\mu_{i,j} = \alpha_{\text{trait},i} + \alpha_{\text{study},j} \tag{2}$$

with:

$$\boldsymbol{\alpha}_{\text{trait}} = \{\alpha_{\text{trait},1}, \ldots, \alpha_{\text{trait},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{trait}} \sim \mathcal{N}(\mu_{\alpha_{\text{trait}}}, \sigma_{\alpha_{\text{trait}}}) \tag{3}$$

$$\boldsymbol{\alpha}_{\text{study}} = \{\alpha_{\text{study},1}, \ldots, \alpha_{\text{study},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \mathcal{N}(0, \sigma_{\alpha_{\text{study}}})$$

Parameters $\mu_{\alpha_{\text{trait}}}$ and $\sigma_{\alpha_{\text{trait}}}$ represent the mean trait value across all species and the standard deviation in trait values between species, respectively. The mean effect of study is assumed to be centered at 0 with standard deviation $\sigma_{\alpha_{\text{study}}}$.

The second part of the joint model is a hierarchical linear model where the normally distributed response variable $Z_{i,k}$ is the day of budburst for species i experiencing forcing (F_k), chilling (C_k), and photoperiod (P_k). This sub-model is linked to the trait sub-model via the shared parameters $\alpha_{\text{trait},i}$, representing the "grand" trait values of species that are independent of study. The overall structure of the phenology sub-model is similar to that of Ettinger et al. (https://doi.org/10.1038/s41558-020-00917-3), except species' responses to forcing ($\beta_{\text{force},i}$), chilling ($\beta_{\text{chill},i}$), and photoperiod ($\beta_{\text{photo},i}$) are treated not as single parameters but as a combination of parameters, a species-specific response that is independent of its trait value (e.g., $\alpha_{\text{force},i}$) and an effect of its trait value (e.g., $\beta_{\text{trait.force}}$) that is multiplied by $\alpha_{\text{trait},i}$ and does not differ between species. In other words, species responses to cues interact with their "grand" trait values, and we assume this interaction is independent of species identity. The phenology sub-model can thus be written as:

$$Z_{i,k} \sim \mathcal{N}(\mu_{i,k}, \sigma_{\text{pheno}}) \tag{4}$$

where σ_{pheno} represents random error in budburst day and:

$$\mu_{i,k} = \alpha_{\text{pheno},i} + \beta_{\text{force},i} \times F_k + \beta_{\text{chill},i} \times C_k + \beta_{\text{photo},i} \times P_k \tag{5}$$

with:

$$\beta_{\text{force},i} = \alpha_{\text{force},i} + \beta_{\text{trait.force}} \times \alpha_{\text{trait},i} \tag{6}$$

$$\beta_{\text{chill},i} = \alpha_{\text{chill},i} + \beta_{\text{trait.chill}} \times \alpha_{\text{trait},i}$$

$$\beta_{\text{photo},i} = \alpha_{\text{photo},i} + \beta_{\text{trait.photo}} \times \alpha_{\text{trait},i}$$

and all species-specific parameters are, as in the trait sub-model, given hierarchical structure whereby:

$$\boldsymbol{\alpha}_{\text{pheno}} = \{\alpha_{\text{pheno},1}, \ldots, \alpha_{\text{pheno},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \mathcal{N}(\mu_{\alpha_{\text{pheno}}}, \sigma_{\alpha_{\text{pheno}}}) \tag{7}$$

$$\boldsymbol{\alpha}_{\text{force}} = \{\alpha_{\text{force},1}, \ldots, \alpha_{\text{force},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{force}} \sim \mathcal{N}(\mu_{\alpha_{\text{force}}}, \sigma_{\alpha_{\text{force}}})$$

$$\boldsymbol{\alpha}_{\text{chill}} = \{\alpha_{\text{chill},1}, \ldots, \alpha_{\text{chill},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chill}} \sim \mathcal{N}(\mu_{\alpha_{\text{chill}}}, \sigma_{\alpha_{\text{chill}}})$$

$$\boldsymbol{\alpha}_{\text{photo}} = \{\alpha_{\text{photo},1}, \ldots, \alpha_{\text{photo},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photo}} \sim \mathcal{N}(\mu_{\alpha_{\text{photo}}}, \sigma_{\alpha_{\text{photo}}})$$

Parameters $\mu_{\alpha_{\text{pheno}}}$, $\mu_{\alpha_{\text{force}}}$, $\mu_{\alpha_{\text{chill}}}$, $\mu_{\alpha_{\text{photo}}}$ represent the mean budburst day, response to forcing, response to chilling, and response to photo period across all species, respectively. Parameters $\sigma_{\alpha_{\text{pheno}}}$, $\sigma_{\alpha_{\text{force}}}$, $\sigma_{\alpha_{\text{chill}}}$, $\sigma_{\alpha_{\text{photo}}}$ are the standard deviations between species.

Forcing, chilling, and photoperiod (F_k, C_k, P_k) were z-scored to account for differences in the scale of predictors across studies (**?**), as well as differences in the natural units for the cues. We assumed parameters had weakly informative prior distributions (generally normal or half-normal distributions) that we obtained from a series of prior predictive checks where the objective was to produce a wide but also plausible range of trait and phenology values (e.g., budburst dates between days $0 - 365$). The joint model was coded in the Stan programming language (Stan citation) and fit to the trait and phenology data (see above) using using the rstan package (version, citation). For all traits, model fits were deemed valid based on *Stan's* diagnostic metrics, including no divergences across 1000 iterations, high effective sample size (*n_eff*), and scale reduction factor $\hat{R}$ close to 1 across 4 chains.

Finally, we used a phylogenetic generalized least-squares regression model (PGLS) to test the relationship between day of budburst and individual traits. This analysis allowed us to test for phylogenetic non-independence in the phenology-trait relationship (**?**). We obtained a rooted phylogenetic tree by pruning the tree developed by (**?**) and performed the PGLS analysis using the mean trait values and mean posterior estimates of the cue responses from our joint model. The PGLS was run using the "Caper" package in R (**?**).

2   Results

We estimated mean height as 14m (90% uncertainty intervals: 11m, 17m). Species height values were distributed with a variance of 6 (90% uncertainty intervals: 5m, 7m), and study height values were distributed with a variance of 7m (90% uncertainty intervals: 6m, 9m). The highest estimated mean species height estimate in our dataset was 26m (90% uncertainty intervals: 22m,29m) for *Quercus petraea*, and the lowest estimated mean height value was 0.7m (90% uncertainty intervals: -2m,4m) for *Rhamnus cathartica*.

Mean LNC was estimated as 23 (90% uncertainty intervals: 20, 25). Species LNC values were distributed with a variance of 5 (90% uncertainty intervals: 4, 7), and study LNC values were distributed with a variance of 4 (90% uncertainty intervals: 2, 5). The highest estimated mean species LNC estimate in our dataset was 39 (90% uncertainty intervals: 37,41) for *Prunus persica*, and the lowest estimated mean LNC estimate was 14(90% uncertainty intervals: 10,17) for *Hamamelis virginiana*.

Mean $\log_{10}$ seed mass was estimated as 2.0 (90% uncertainty intervals:1.5, 2.4), which translates as a seed mass of approximately 104mg. Species $\log_{10}$ seed mass values were distributed with a variance of 1.6 (90% uncertainty intervals: 1.3, 1.9), and study $\log_{10}$ seed mass values were distributed with a variance of 0.5 (90% uncertainty intervals: 0.3, 0.6). The highest estimated mean species $\log_{10}$ seed mass estimate in our dataset was 4.2 (90% uncertainty intervals: 3.9, 4.6) for *Juglans cinerea*, which translates as a seed mass of approximately 18000mg. The lowest estimated mean $\log_{10}$ seed mass estimate was -1(90% uncertainty intervals: -1.4,-0.6) for *Betula populifolia*, which translates as a seed mass of approximately 0.1mg.

We estimated mean SLA as 16.8 (90% uncertainty intervals:15, 19). Species SLA estimates were distributed with a variance of 8.1 (90% uncertainty intervals: 6.6, 9.6), and study SLA estimates were distributed with a variance of 3.3 (90% uncertainty intervals: 1.8, 4.8). The highest estimated mean species SLA estimate in our dataset was 4.9 (90% uncertainty intervals: 2.9, 6.5) for *Acer pensylvanicum*, and the lowest estimated mean LNC estimate was -1(90% uncertainty intervals: -1.4,-0.6) for *Quercus coccifera*.

In most cases, the simple geometric mean for each species-trait combination fell within the posterior estimations from our models (Fig. 2). There were a limited number of species in the height model were the simple geometric mean fell outside of predicted species species means after accounting for the effect of study, for example *Quercus ilex*, *Quercus petraea*, *Quercus coccifera*, and *Aesculus hippocastanum*.

We found a negative relationship between SLA and each cue response 3, meaning that as SLA increased, responses to each cue became more negative. Chilling was most strongly influenced by a SLA (interaction parameter: -9.3: 90% uncertainty interval: -17.9, -18.1). Species' responses to forcing were also negatively correlated with SLA values (interaction parameter:-7.8, 90% uncertainty interval: -14.5, -10.5), as were responses to photoperiod (interaction parameter:-2.0, 90% uncertainty interval: -11.1, -11.6). At high SLA values, for example leaves from *Fagus grandifolia*, this negative trait effect produced a more negative slope in the full model relative to the slope when the trait effect is set to zero. There is a much smaller difference in the slopes of species with leaves with low SLA, such as *Quercus ilex* **??**. The relatively small trait effect of photoperiod is reflected in the smaller difference in the slopes between the full model and the model without the effect of trait **??**.

In modeling relationship between species height and cue responses, we found that as tree height increased cue responses became more negative. Chilling had the largest trait slope in response to height at -9.6 (90%
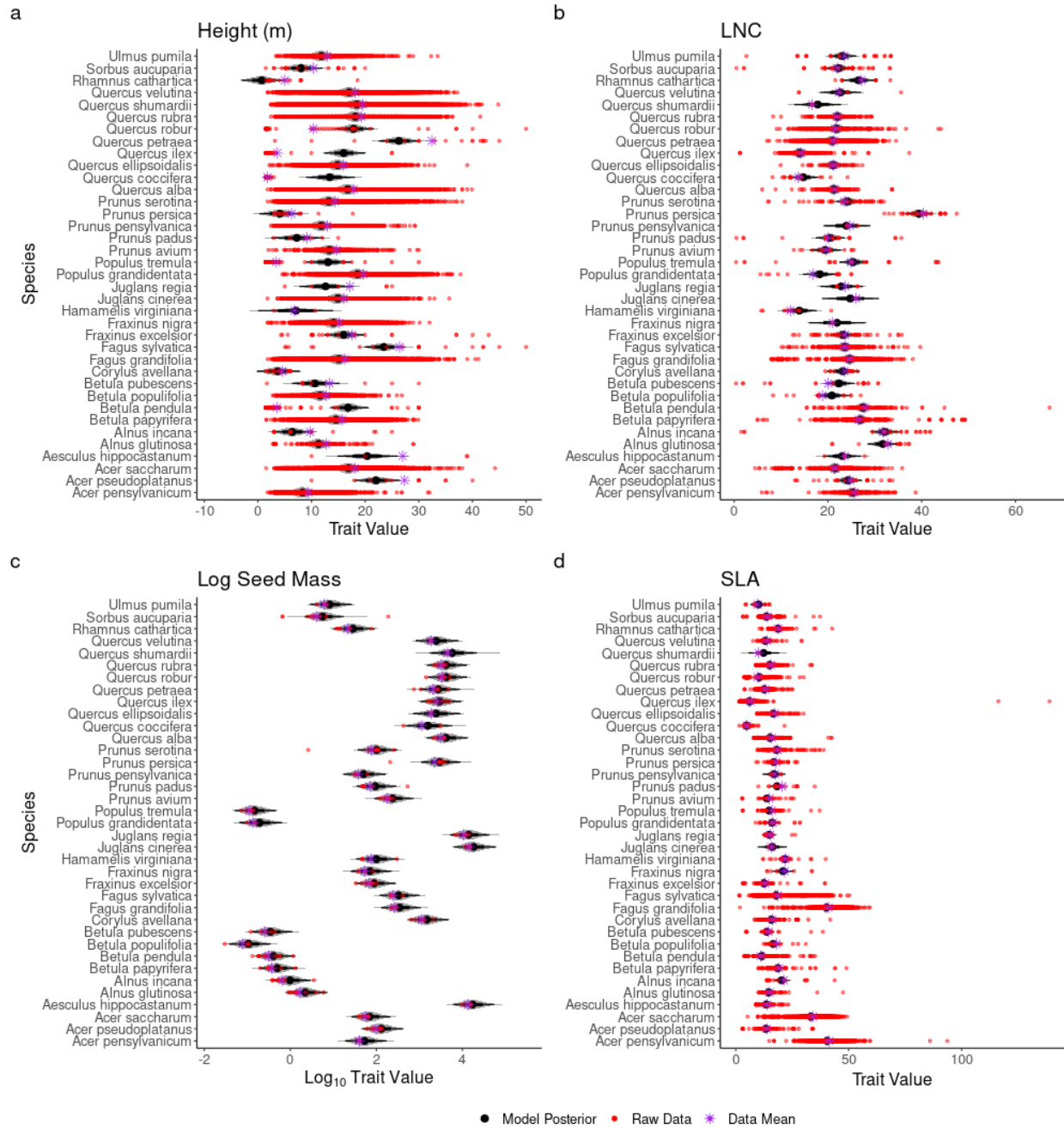
Figure 2: Raw data and posterior esti.

uncertainty interval: -14.6, -20.8), followed by the forcing slope at -7.5 (90% uncertainty interval: -12.1, -10.7), the photoperiod slope at -2.3 (90% uncertainty interval: -7.8, -12.4). This means that the estimated slopes for a tall tree, such as *Acer pseudoplantanus*, could change from having a positive slope when the trait effect is zero, to having a negative slope in response to chilling and forcing cues 5. The change in slope in

response to photoperiod is follows a similar trend, becoming more negative when the trait effect is included, but is more moderate in magnitude. In general, taller tree species, for which there is a greater estimated trait effect, also have more negative estimated slopes for each of the three cues 3.

In our model of LNC, we found species that produce leaves with hight LNC also had increasingly negative cue responses. Chilling had the largest trait slope in response to LNC at -9.6 (90% uncertainty interval: -16, -19.1), followed by the forcing slope at -8.1 (90% uncertainty interval: -12.9, -10.7), the photoperiod slope at -1.7 (90% uncertainty interval: -8.2, -12.3). Species like *Alnus glutinosa* that have high LNC would have a more negative slope in response to increasing forcing and chilling cues, while species with low LNC like *Quercus ilex* experience a much smaller decrease in their slopes 5. The model estimated trait effect of LNC for photoperiod is relatively negligible, producing no noticeable differences between the cue only slopes and full model slope. The effects of LNC and estimated model slopes were negatively correlated for each of the cues, indicating that species with higher LNC have a stronger negative response to increasing cues 3.

Finally, we found that species with increasingly large seeds also had more negative responses to cues when trait effects were incorporated. Chilling had the largest trait slope in response to seed mass at -10 (90% uncertainty interval: -15.3, -19.4), followed by the forcing slope at -8 (90% uncertainty interval: -12.2, -10.3), the photoperiod slope at -2.2 (90% uncertainty interval: -7.9, -12.2). Our model estimates for the model cue slopes were all negative, however, given the nature of the log10 transformation of the seed mass data, the modelled response has a positive slope for species with large seeds. This is shown for *Aesculus hippocastanum* in 5, where we found the negative effect of seed mass to make the slopes more negative for each of the cues. The magnitude of the differences between the cue only slopes and full model slopes are much greater for forcing and chilling cues and relatively moderate for photoperiod. As we observed for the other traits, species with larger seeds had larger trail effects, which were again negatively correlated with the estimates cue slopes 3

PGLS suggests there are no strong phylogenetic effects for most of our cue trait relationships, with the exception of .... This suggests there is a phylogenetic effect influencing the cue response of species for these traits. Given the complexity of our model, however, we were not able to fully incorporate these phylogenetic effects into our current analysis.

3 Discussion

Discuss the DF paper again

Geoff : "Overall, we found that conservative species, which generally had high traits values for SLA, Height,

etc., shifted their phenology more and earlier in response to forcing, chilling, and photoperiod, than acquisitive species with low trait values. This responsiveness is linked to later budbursting - earlier sp have lower slopes bc they require less cues in general, having a lower intercept"

- What do our results suggest for the relationship between cue use and traits? - Species responses to forcing, chilling, and photoperiod cues are influenced by species functional traits. - generally in line with previous studies of phenological cues, cue responses were all negative leading to strong advances in bb date

  - Do we find relationships between cues and traits? - yes, with the exception of LNC and photoperiod, all traits had an effect of the response of species to cues
  - Do these trends agree with an acquisitive/conservative tradeoff? - yes, with the exception of seed mass, species with traits associated with acquisitive growth strategies did budburst earlier

- How do our results relate to previous studies? Huang et al. 2018 - found several growth strategies - all combinations of early- fast, early-slow, late-fast etc - but looked at flowering Osada 2017 - bb later for sp with greater LMA, thickness, Narea – driven by differences across deciduous and evergreen spp; Deciduous alone: bb positively correlated with leaf mass, area, vessel diam in cross spp comparisons

- What do our results suggest for the bigger picture? Sun, S., D. Jin, and R. Li. 2006. LMA neg correl with leafout; larger LMA = earlier

  - How might traits constrain/facilitate future shifts in phenology? - our findings do partially (maybe not LNC and Seedmass) support the idea that phenology is an important functional trait
  - How might ecosystem functioning shift if species track temperature? How to our results relate to seasonality and frost risk?
  - What does it mean if more competitive/invasive species respond to warming and start bb earlier - outcompete species and lead to compressed temporal niche?
  - Relate our results to invasion success

- Limitations/strengths?

  - we assume stronger cues mean earlier bb but really it's more complicated than this
  - broad approach means lose detail and compromise - traits come from different populations to the phenology data
  - disconnect between trait data - observational - and phenology data that is in a controlled environment

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- limited data may have reduced diversity of traits/strategies - may not be enough to detect predicted trends – reframe this as less of a limitation and more of a future direction

- Why we think mean height values were different from geometric mean values for some species. Talk about the influence of accounting for the study effect.
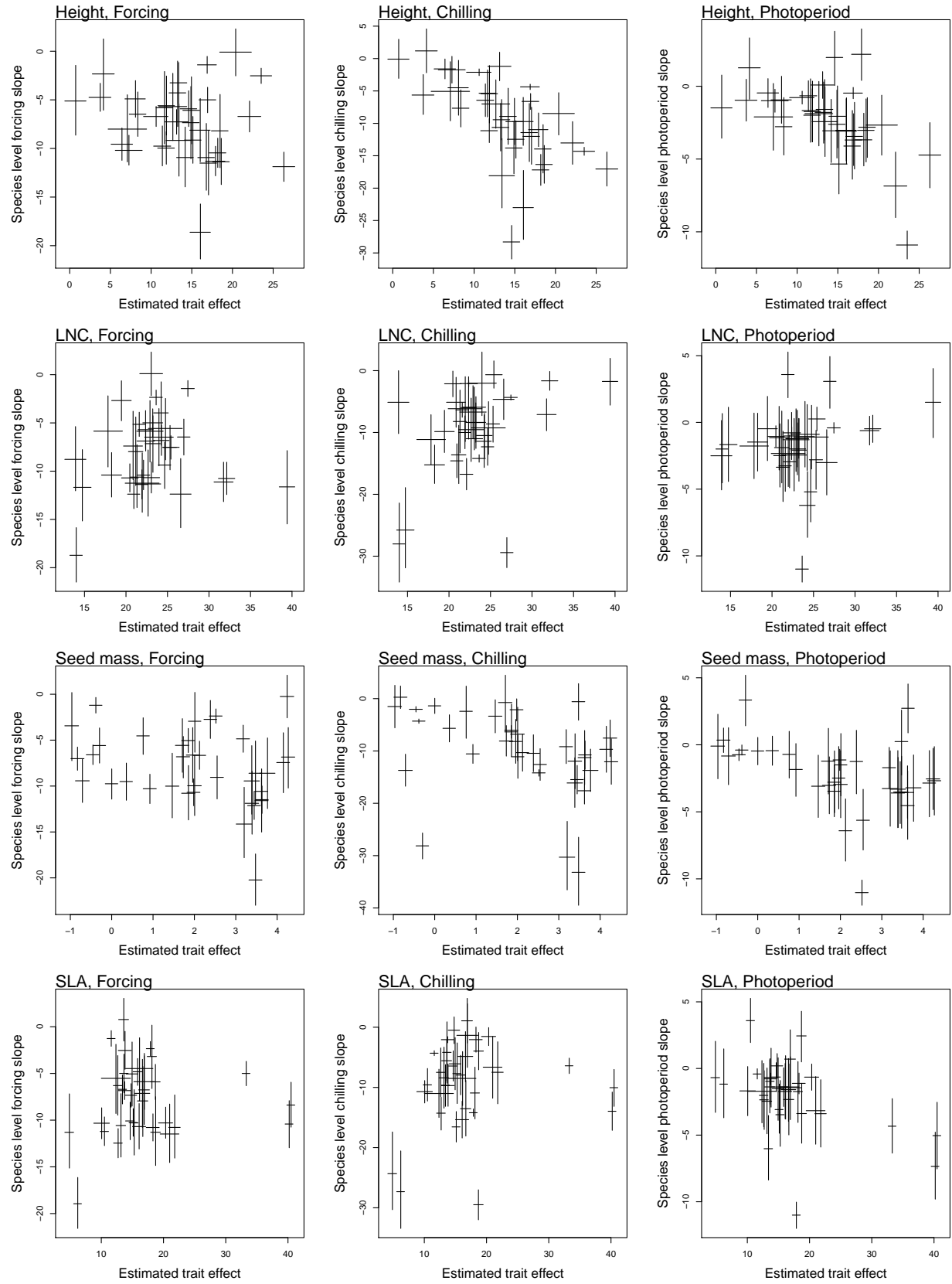
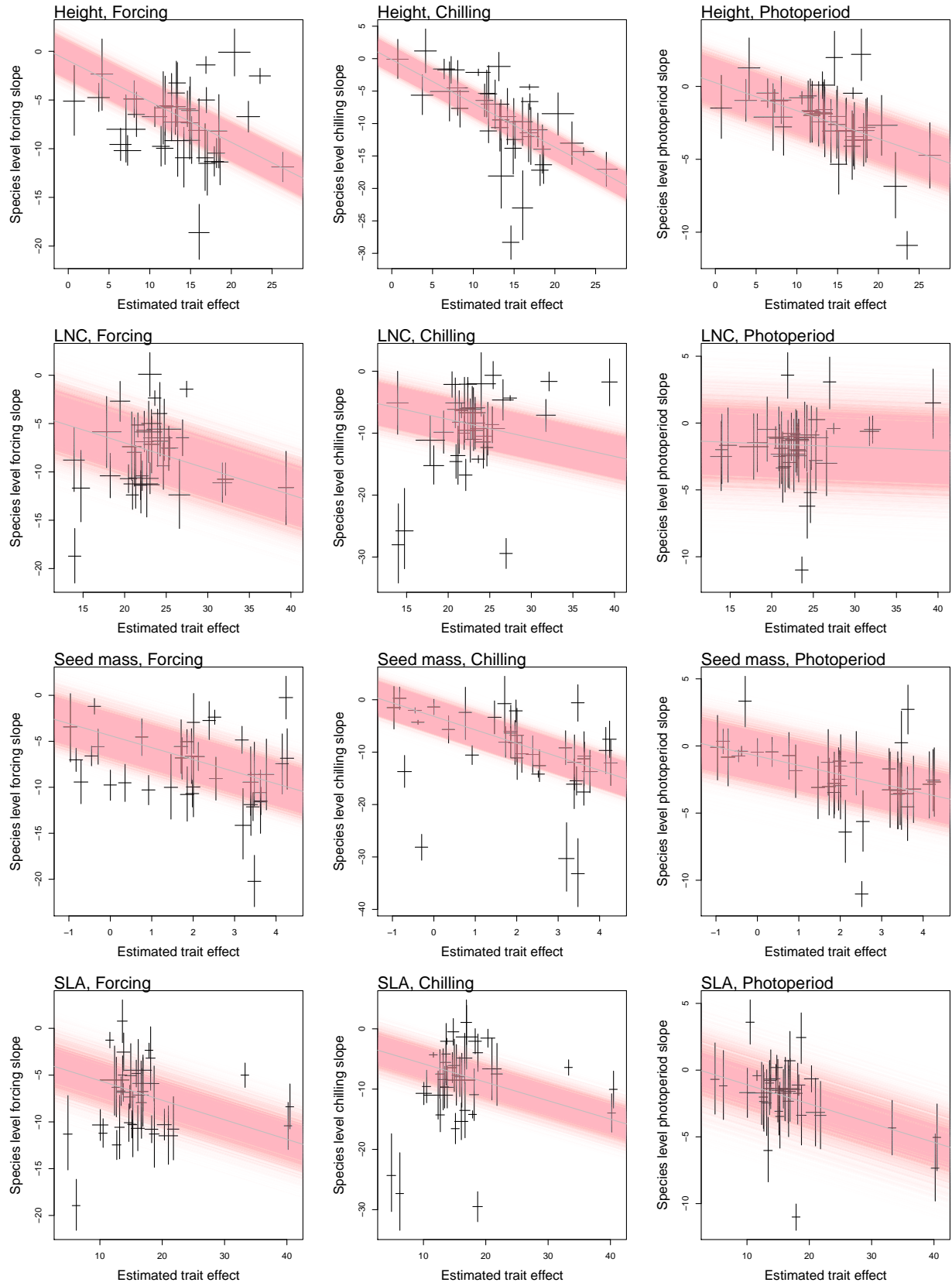Figure 3: Trait relationships with cue slopes
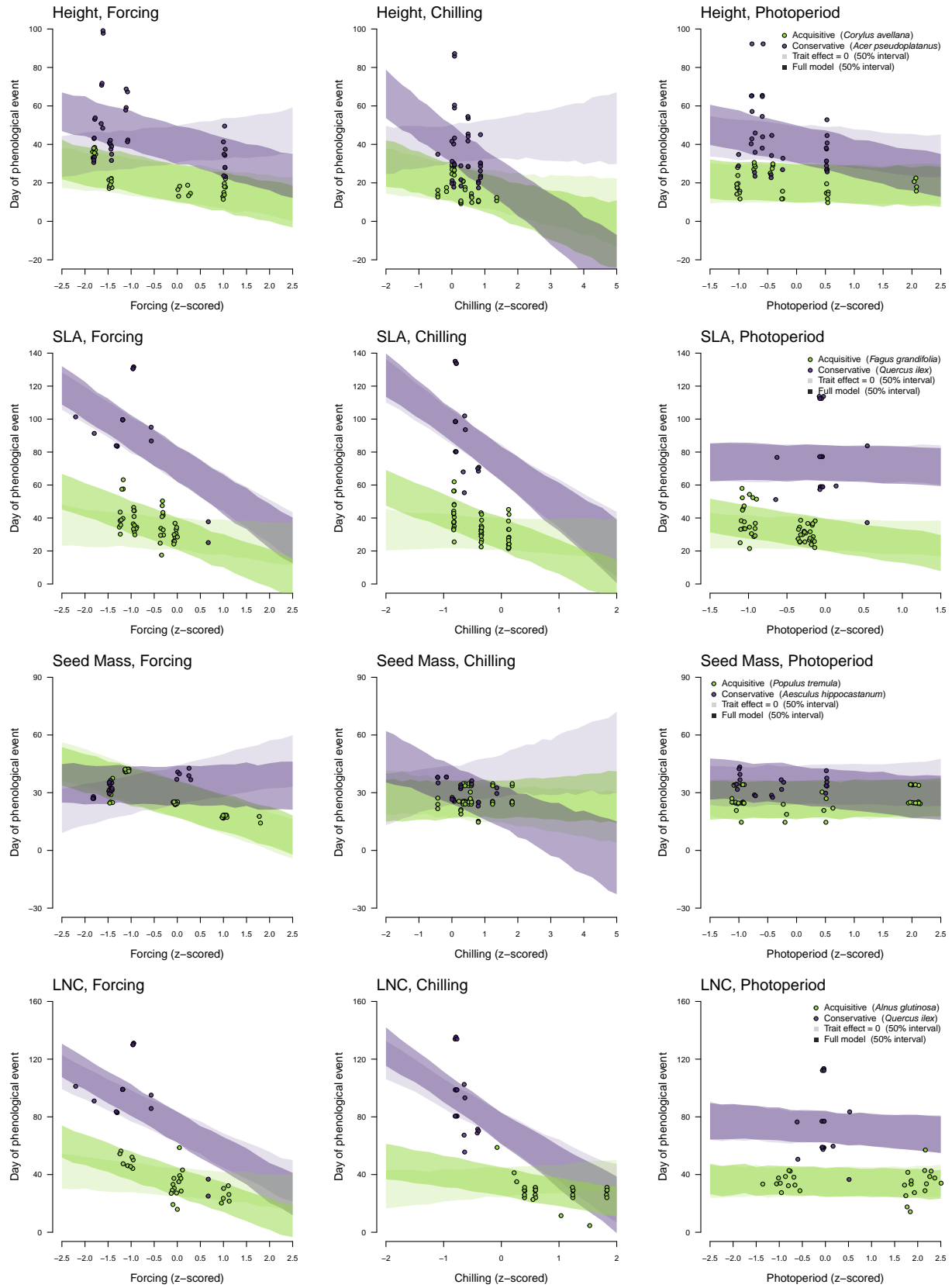
Figure 4: Trait relationships with cue slopes

Figure 5: Estimated cue responses for acquisitive and conservative spp.