Woody plant phenological responses are strongly associated with key functional traits

Deirdre Loughnan[1], Faith A M Jones[1], Geoffrey Legault[1], Mira Garner[2],
Darwin Sodhi[3], Daniel Buonaiuto[4], Catherine Chamberlain[5], Ignacio Morales Castilla [6],
Ailene Ettinger[7], and E M Wolkovich[1]

May 18, 2023

[1] Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, 2424 Main Mall Vancouver, BC Canada V6T 1Z4.

[2] Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

[3] Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;

Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca

Summary

Key Words: Budburst phenology, functional traits, Trees, climate change

Introduction

The timing of life history events—phenology—can shape both ecosystem services and community dynamics. The timing of spring plant growth, for example, defines the start and overall length of the growing season in many systems—shaping forest carbon storage and species interactions (Cleland et al., 2007; Beard et al., 2019; Gu et al., 2022). As climate change advances spring in many systems (Menzel et al., 2006; Vitasse et al., 2021) there is growing concern over how these advances may impact communities and ecosystems.

Predicting these changes requires understanding the drivers of phenology both at a proximate scale—the environmental triggers of phenology, such as temperature and daylength—and at a more ultimate scale, of how timing may assemble species within a community (CITES). At the proximate level, changing environmental conditions across the late winter and spring cause species to start growth at different times. Recent advances in our understanding of leafout phenology of woody species (which have been heavily studied) underscore this and have identified important trends across species (Laube et al., 2014; Flynn and Wolkovich, 2018). But this work has provided limited reasons for species differences (Laube et al., 2014; Chuine et al., 2016; Flynn and Wolkovich, 2018).

At the ultimate level, predictions for why species vary may come from considering how selective pressures change as the early season progresses. Species that start growth first often risk high tissues loss, for example, due to frost damage or high herbivore apparency (WainwrightCITE), but they often benefit from higher resource availability (Rathcke and Lacey, 1985; Hufkens et al., 2012). In contrast, later species have greater selection from many biotic pressures, especially high competition for resources (Lopez et al., 2008; Wolkovich and Ettinger, 2014).

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

Decades of research on plant trait ecology has identified certain traits as species-level proxies for characteristics that predict patterns in growth strategies and interactions (McGill et al., 2006). Many leaf and wood traits follow predictable gradients in species trait values, having associations that range from acquisitive (fast) growth strategies to more conservative (slow) growth strategies (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Díaz et al., 2016). Collectively, these trait relationships led to the development of the leaf economic spectrum and the wood economic spectrum (Wright et al., 2004; Chave et al., 2009).

These functional trait spectra—or frameworks—have been built into decades of research linking functional traits to species responses to abiotic and biotic factors and community assembly, but they have limitations. One concern is their limited ability to predict how variable traits are (Violle et al., 2012), a reason sometimes given for why phenology is excluded from studies of functional traits. Including phenology with other functional traits could both advance the functional trait framework and help explain why species phenologies differ.

Integrating plant phenology into functional traits may be especially tractable when considering the early-late selective environment of spring temperate forests. As in other systems, early season species trade off high access to resources (greater soil resources and light availability) with risks of tissue loss

and damage while late season species trade off a highly competitive but less risky environment. These trade-offs would predict that shrub and woody understory species that budburst early (Donnelly and Yu, 2019) would have traits associated with acquisitive growth; they thus would 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)). Canopy species that budburst later—when competition for soil resources is greatest—would have traits associated with conservative growth; being taller with denser wood (Laughlin et al., 2010), with leaf traits suited for more variable light (low SLA and LNC). Increasing seed size may similarly be predicted from this acquisitive to conservative continuum from early to late budbursting species.

Testing these predictions requires a reliable way to define early to late phenology, however, as phenology varies strongly across sites. The underlying cues that predict early to late phenology, however, generally do not vary strongly (CITES). Early species generally have weak (small) 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 chill and/or photoperiod, and likely higher forcing as well (Laube et al., 2014; Flynn and Wolkovich, 2018). To test these predictions of associations between budburst responses to environmental cues and common functional traits, we merged available data from trait databases (BIEN and TRY) with budburst data from the OSPREE database of controlled environment studies. We focus on woody species, considering four commonly measured traits—SLA, LNC, height, and seed mass with the cues of forcing, chilling, and photoperiod.

To combine these diverse and messy datasets we present a new hierarchical Bayesian joint model that predicts phenological responces to cues based on species-level trait values. Our model attributes phenological variation to species' trait values while including residual variation from species (partial-pooling). When traits explain a significant portion of the variation, species will explain only a small amount, which may allow us to predict species growth strategies and phenological responses from trait values.

1   Methods

Our analysis combines phenological data from the OSPREE database (Ettinger et al., 2020) with functional trait data from the TRY (Kattge et al., 2020) and BIEN (Maitner et al., 2018) trait databases. The OSPREE database contains phenological data for woody, deciduous species from experiments of phenological cues. We updated OSPREE since its initial publication, using the original search terms:

- (budburst OR leaf-out) AND (photoperiod OR daylength) AND temperature* (yielded additional 623 publications since previous OSPREE publication)

- (budburst OR leaf-out) AND dorman* (yielded additional 270 publications since previous OSPREE publication).

In updating the database, we added an additional 12 papers that met selection criteria for inclusion in OSPREE see Ettinger2020 for more details).

Trait data was obtained from TRY and BIEN - two large trait databases compiling plant trait data across many individuals, species, and studies that we obtained on XX date, and thus were last updated... XX
We began by searching for all available trait data for the 234 woody species with budburst data in the OSPREE database. The TRY database included 96 of these species for ten functional traits (Table S1 - table of requested traits for each database). Using the BIEN R package (?), we downloaded trait

data for 94 species for 13 traits. All trait data were requested or downloaded in December 2018. Only trait data from adult individuals with a minimum height of 1.42 m was included in our analyses and we removed all data from experiments or from plants growing in non-natural habitats. Traits were also grouped where appropriate, for example, with traits denoted as SLA, SLA with petioles, and SLA without petioles all categorized as simply SLA in our analysis (see Table S1). Duplicated data in both the TRY and BIEN datasets were also removed (n = 434905). Finally, we subsetted the data to include only species for which we had a complete dataset for each species and trait, which resulted in a dataset of only 26 species and six functional traits. After performing a PCA, we further refined our trait selection, and only included traits that did not show strong correlations. In this analysis, the principal component explained 32% of variation while the second explained 24.2% of the variation (Fig. **??**). Due to strong association between specific leaf area (SLA) and leaf dry matter content (LDMC), and between stem specific density (SSD) and height, we 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 with at least one trait measurement per trait to 37 species with data from 24 studies (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. This was done to reduce the effect of trait values from these frequently measured species from overwhelming the partial pooling effect in our model. In addition, we excluded the single seed mass observation from the HE Marx dataset from BIEN, as it was difficult to include include the study-level effect in our model.

Joint model of trait and phenology

To understand connections between phenology and other species traits, we built a joint model for each trait (height, SLA, LNC, and seed mass) with the major phenological cues (forcing, chilling, and photoperiod) to predict day of year of budburst. This approach allowed us to jointly estimate species trait effects and responses to phenological cues in one model, carrying through all uncertainty across varying datasets and approaches (e.g., TRY and BIEN observational databases of traits and the database of experiments in plant phenology, OSPREE). As phenological cues are the most proximate drivers of variation in budburst (cite Ettinger2020), and appear to represent different strategies along a continuum from acquisitive to conservative, our model allows traits to influence each cue separately (cite slopes (current Fig 3)).

The joint model includes a hierarchical linear model to partition variation in observed trait values ($y_{\text{trait}[i]}$) to the effects of species, study, and residual variation (σ_{trait}, sometimes called 'measurement error').

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

It estimates a separate value for each species ($\alpha_{\text{sp[sp]}}$), and study ($\alpha_{\text{study[study id]}}$), while partially pooling across species and studies to yield overall estimates of variance across each ($\sigma_{\alpha_{\text{sp}}}$ and $\sigma_{\alpha_{\text{study}}}$, respectively). This partial pooling (often called 'random effects') controls for variation in sample size and variability to yield more accurate estimates for each species.

These species-level estimates of traits ($\alpha_{\text{trait sp[sp id]}}$) were then used as predictors of species-level

estimates of each phenological cue ($\beta_{\text{force[sp]}}$, $\beta_{\text{chill[sp]}}$, $\beta_{\text{photo[sp]}}$)

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

148 This model allows an overall effect of each trait—estimated across species—on each phenological cue
149 ($\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$), while also allowing for species-level variation in cues that is not
150 explained by traits ($\alpha_{\text{chill}[sp]}$, $\alpha_{\text{force}[sp]}$, $\alpha_{\text{photo}[sp]}$; this importantly means that variation across species
151 is not forced onto the trait effect). Thus the model tests the power of traits to predict species-level
152 differences.
153

Days to budburst ($y_{\text{pheno[i]}}$) is then predicted by the phenological cues and variation across experi-
ments in chilling, forcing and photoperiod levels (C_i, F_i, P_i, respectively, which we z-scored to allow
direct comparison of cues), with residual variation allowed across species ($\alpha_{\text{pheno[sp]}}$) and observations
(σ_{pheno}):

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

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

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

154 We chose weakly informative priors, and validated them using a series of prior predictive checks.
155 The model was coded in the Stan programming language (Stan citation), fit using the rstan package
156 (version, citation) with 1,000 iterations per chain across 4 chain (4,000 total sampling iterations), and
157 all models met basic diagnostic checks, including no divergences, high effective sample size (n_eff),
158 and $\hat{R}$ close to 1.

2 Results

160 Our approach used models that jointly estimated species traits and phenological cues to understand
161 the connections between phenology, with a focus on days to budburst, and other plant traits. Since
162 our trait data was from large trait databases, which combine data across many studies, our analysis
163 partitioned the trait variation due to species from the study-level effects. Then using the species-level
164 estimates of traits (ie. species-level estimates with effects of study removed), we examined how traits
165 predicted phenological cues, which in turn predicted budburst, while allowing for residual variation in
166 cues to be explained by a species effect.
167

168 Across our models, we found study-level variation across traits was comparable with or greater than
169 variation across species. Variation across studies was greatest for height (7.5 m compared to 5.9 m
170 species-level variation, Fig. 1). For seed mass and LNC study-level variation was less than that of the
171 species-level variation (seed mass study-level variation: 1 mg; versus species-level variation: 1.6 mg;
172 LNC study-level variation 3.6 mg g^{-1} versus species-level variation: 5.1 mg g^{-1}) (Fig. 1). At the lowest
173 end, study-level variation in SLA was approximately half the value of the species-level variations (and
174 3.3 mm^2 mg^{-1} versus 7.8 mm^2 mg^{-1}, respectively). The magnitude of study-level variation we observed
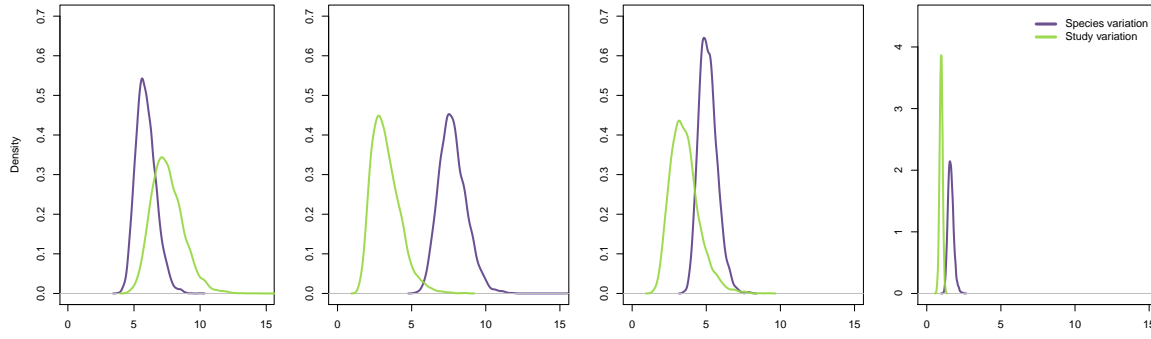
Figure 1: Comparison of the posterior densities for the species-level variation and study-level variation of a. height, b. SLA, c. LNC, and d. seed mass.

suggests that models using large trait databases that fail to separate out study from species-level variation may misestimate species' traits.

We next combined the species-level trait estimates with data on forcing, chilling and photoperiod values from the OSPREE database of phenological experiments in order to test if traits (height, SLA, seed mass, LNC) related to phenological cues and species budburst dates (Fig. 2). For some traits we found much of the variation in phenological cues across species could be explained by trait variation (see panel a-f and j-l in Fig 3), while other traits were weak predictors (see g-i in Fig 3).

Across traits, height, SLA, and LNC strongly predicted responses to different cue-levels (forcing, chilling, photoperiod), with a consistent direction of responses across cues for only LNC and not height or SLA (Fig. 3 a-f and j-l). Taller species had small responses to forcing (0.2 m per standardized forcing; 90% uncertainty interval: -0.2, 0.5). But as we predicted, taller species had larger responses to chilling (-0.5 m per standardized chilling; 90% uncertainty interval: -1, -0.1)) and photoperiod (-0.2 m per standardized photoperiod; 90% uncertainty interval: -0.5, 0), both of which are cues that would generally lead to later budburst and fit within an overall conservative growth strategy.

Species' SLA did not strongly predict responses to chilling (0.3 mm^2/mg per standardized chilling; 90% uncertainty interval: -0.1, 0.7, Fig. 2 b). However, SLA did relate strongly to photoperiod (-0.2 mm^2/mg per standardized photoperiod; -0.4, 0). Thus, species with more acquisitive growth strategies (thin leaves and a lower investment in leaf mass that leads to high SLA values), had larger responses to photoperiod cues, contrary to our predictions. In line with our predictions, species with high SLA values (acquisitive strategy) had a smaller response to forcing cues (0.2 mm^2/mg per standardized forcing; 90% uncertainty interval: -0.1, 0.4), with low SLA species being more responsive to forcing (Fig. 3 d).

For LNC, we found that species that produce leaves with high nitrogen content, which relate to high photosynthetic rates and acquisitive growth, were less responsive to cues (Fig. 3 j-i)). These findings are in line with our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g per standardized chilling; 90% uncertainty interval: 0.3, 1.2), with similar responses to photoperiod (0.3 mg/g per standardized photoperiod; 90% uncertainty interval: 0, 0.6) and to forcing cues (0.5 mg/g per standardized forcing; 90% uncertainty interval: 0.1, 0.9).

Of our four traits, seed mass had the weakest responses across the three cues (Fig. 3 g-i). While the direction of the species responses were in line without predictions, we did not find a considerable
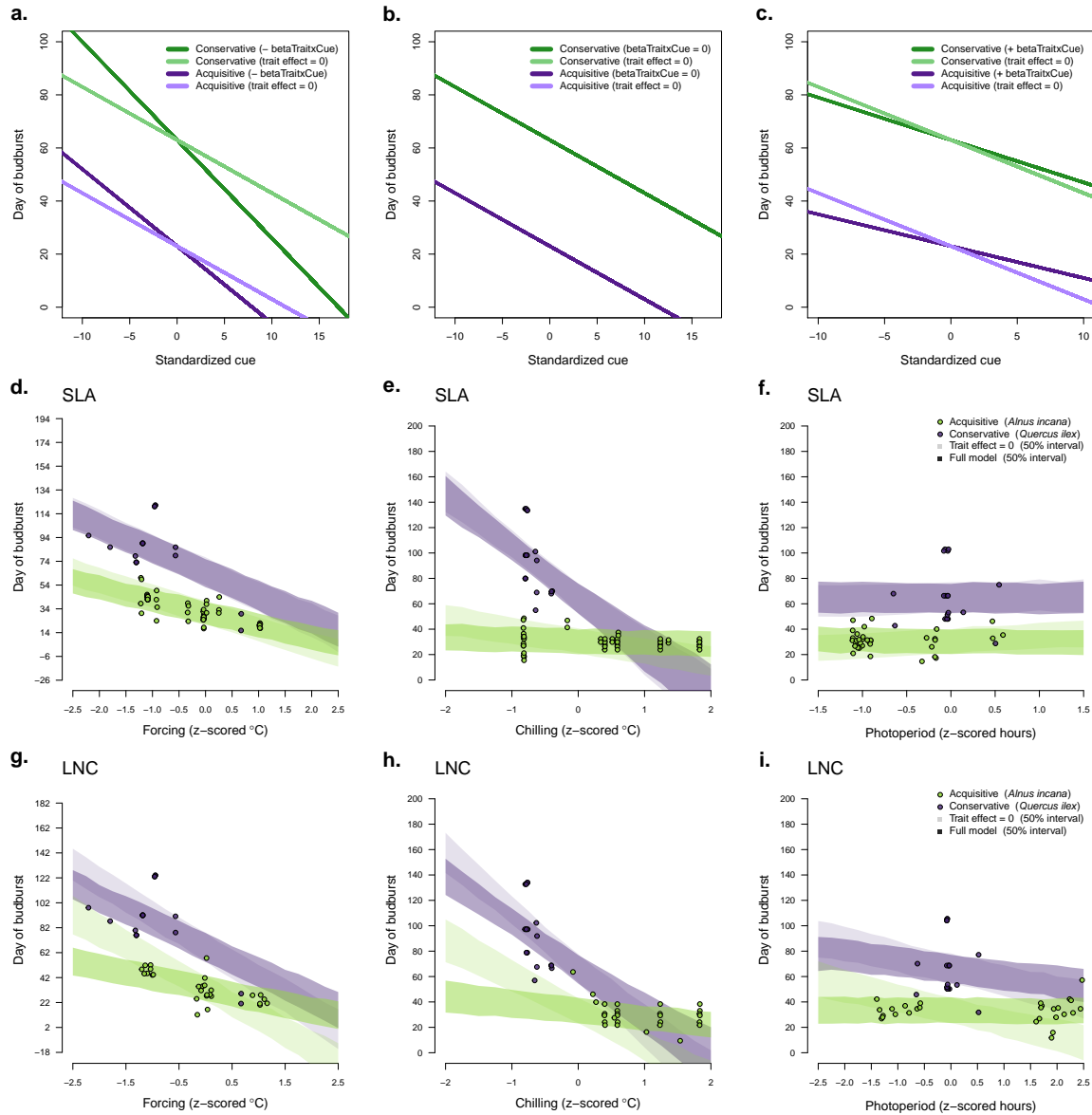
Figure 2: Functional traits may contribute to the species responses to forcing, chilling, or photoperiod cues in several ways. a) If traits are contributing negatively to the timing of phenological events, we expect the phenological response to be stronger and budburst earlier with increasing cue values. b) But if traits have no effects on the timing of budburst, then cue responses will be zero and equivalent to the cue only model estimates. c) Traits that have a positive contribution to the timing of phenological events produce weaker responses with later budburst dates. A delay in day of budburst due to trait effects was found for both SLA and LNC in response to forcing and chilling cues and for LNC in response to photoperiod cues (panel d, e, g, h, and i). Only in response to photoperiod cues does the effect of SLA lead to stronger cue responses and slightly earlier budburst with longer photoperiods. Species with conservative traits are shown in purple and species with acquisitive growth shown in green. Bands represent the 50% uncertainty intervals of the model estimates.

210   relationship between seed mass and cue responses for forcing (-0.3 mg per standardized forcing; -1.4,

0.9) or photoperiod or chilling (-1.1 mg per standardized chilling; -2.8, 0.7). -0.6 mg per standardized photoperiod; -1.6, 0.3).

3   Discussion

1. Timing of plant phenological events define species' temporal niche = the partitioning of resources across species over time (Gotelli & Granves 1996 - ch5).

2. temporal niche differences determine the abiotic environment during growth and biotic interactions – for example, competitive landscape and pressures from herbivory/disease.

3. Distribution of temporal niche within community influences its potential invasibility— invasive spp tend to be early bb with the can fill vacant niche space early in the season.

4. you can save your point about 'traits are often pretty distal to the processes they are supposed to capture' for the discussion

5. Despite the lack of integration between functional trait and phenological research, both are likely to shape species growth strategies

6. more constant light compensates for their slower overall growth rates.

7. Associations are intuitive but few studies have tested for similar gradients in growth strategies in phenological events across diverse species

References

Beard, K. H., K. C. Kelsey, A. J. Leffler, and J. M. Welker. 2019. The Missing Angle : Ecosystem Consequences of Phenological Mismatch. Trends in Ecology and Evolution 34:885–888.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366.

Chuine, I., M. Bonhomme, J. M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. Global change biology 22:3444–3460.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. Trends in Ecology and Evolution 22:357–365.

Díaz, S., J. Kattge, J. H. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet Ev, H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function. Nature 529:167–171.

Donnelly, A., and R. Yu. 2019. Temperate deciduous shrub phenology : the overlooked forest layer. International Journal of Biometeorology 65:343–355.

Ettinger, A. K., C. J. Chamberlain, I. Morales-Castilla, D. M. Buonaiuto, D. F. Flynn, T. Savas, J. A. Samaha, and E. M. Wolkovich. 2020. Winter temperatures predominate in spring phenological responses to warming. Nature Climate Change 10:1137–1142.

Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. New Phytologist 219:1353–1362.

Gorné, L. D., S. Díaz, V. Minden, Y. Onoda, K. Kramer, C. Muir, S. T. Michaletz, S. Lavorel, J. Sharpe, S. Jansen, M. Slot, E. Chacon, and G. Boenisch. 2020. The acquisitive–conservative axis of leaf trait variation emerges even in homogeneous environments. Annals of Botany .

Gu, H., Y. Qiao, Z. Xi, S. Rossi, N. G. Smith, J. Liu, and L. Chen. 2022. Warming-induced increase in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. Nature Communications 13:1–8.

Hufkens, K., M. A. Friedl, T. F. Keenan, O. Sonnentag, A. Bailey, J. O'keefe, and A. D. Richardson. 2012. Ecological impacts of a widespread frost event following early spring leaf-out. Global Change Biology 18:2365–2377.

Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, S. Tautenhahn, G. D. Werner, T. Aakala, M. Abedi, A. T. Acosta, G. C. Adamidis, K. Adamson, M. Aiba, C. H. Albert, J. M. Alcántara, C. Alcázar C, I. Aleixo, H. Ali, B. Amiaud, C. Ammer, M. M. Amoroso, M. Anand, C. Anderson, N. Anten, J. Antos, D. M. G. Apgaua, T. L. Ashman, D. H. Asmara, G. P. Asner, M. Aspinwall, O. Atkin, I. Aubin, L. Baastrup-Spohr, K. Bahalkeh, M. Bahn, T. Baker, W. J. Baker, J. P. Bakker, D. Baldocchi, J. Baltzer, A. Banerjee, A. Baranger, J. Barlow, D. R. Barneche, Z. Baruch, D. Bastianelli, J. Battles, W. Bauerle, M. Bauters, E. Bazzato, M. Beckmann, H. Beeckman, C. Beierkuhnlein, R. Bekker, G. Belfry, M. Belluau, M. Beloiu, R. Benavides, L. Benomar, M. L. Berdugo-Lattke, E. Berenguer, R. Bergamin, J. Bergmann, M. Bergmann Carlucci, L. Berner, M. Bernhardt-Römermann, C. Bigler, A. D. Bjorkman, C. Blackman, C. Blanco, B. Blonder, D. Blumenthal, K. T. Bocanegra-González, P. Boeckx, S. Bohlman, K. Böhning-Gaese, L. Boisvert-Marsh, W. Bond, B. Bond-Lamberty, A. Boom, C. C. Boonman, K. Bordin, E. H. Boughton, V. Boukili,

D. M. Bowman, S. Bravo, M. R. Brendel, M. R. Broadley, K. A. Brown, H. Bruelheide, F. Brumnich, H. H. Bruun, D. Bruy, S. W. Buchanan, S. F. Bucher, N. Buchmann, R. Buitenwerf, D. E. Bunker, J. Bürger, S. Burrascano, D. F. Burslem, B. J. Butterfield, C. Byun, M. Marques, M. C. Scalon, M. Caccianiga, M. Cadotte, M. Cailleret, J. Camac, J. J. Camarero, C. Campany, G. Campetella, J. A. Campos, L. Cano-Arboleda, R. Canullo, M. Carbognani, F. Carvalho, F. Casanoves, B. Castagneyrol, J. A. Catford, J. Cavender-Bares, B. E. Cerabolini, M. Cervellini, E. Chacón-Madrigal, K. Chapin, F. S. Chapin, S. Chelli, S. C. Chen, A. Chen, P. Cherubini, F. Chianucci, B. Choat, K. S. Chung, M. Chytrý, D. Ciccarelli, L. Coll, C. G. Collins, L. Conti, D. Coomes, J. H. Cornelissen, W. K. Cornwell, P. Corona, M. Coyea, J. Craine, D. Craven, J. P. Cromsigt, A. Csecserits, K. Cufar, M. Cuntz, A. C. da Silva, K. M. Dahlin, M. Dainese, I. Dalke, M. Dalle Fratte, A. T. Dang-Le, J. Danihelka, M. Dannoura, S. Dawson, A. J. de Beer, A. De Frutos, J. R. De Long, B. Dechant, S. Delagrange, N. Delpierre, G. Derroire, A. S. Dias, M. H. Diaz-Toribio, P. G. Dimitrakopoulos, M. Dobrowolski, D. Doktor, P. Dřevojan, N. Dong, J. Dransfield, S. Dressler, L. Duarte, E. Ducouret, S. Dullinger, W. Durka, R. Duursma, O. Dymova, A. E-Vojtkó, R. L. Eckstein, H. Ejtehadi, J. Elser, T. Emilio, K. Engemann, M. B. Erfanian, A. Erfmeier, A. Esquivel-Muelbert, G. Esser, M. Estiarte, T. F. Domingues, W. F. Fagan, J. Fagúndez, D. S. Falster, Y. Fan, J. Fang, E. Farris, F. Fazlioglu, Y. Feng, F. Fernandez-Mendez, C. Ferrara, J. Ferreira, A. Fidelis, B. Finegan, J. Firn, T. J. Flowers, D. F. Flynn, V. Fontana, E. Forey, C. Forgiarini, L. François, M. Frangipani, D. Frank, C. Frenette-Dussault, G. T. Freschet, E. L. Fry, N. M. Fyllas, G. G. Mazzochini, S. Gachet, R. Gallagher, G. Ganade, F. Ganga, P. García-Palacios, V. Gargaglione, E. Garnier, J. L. Garrido, A. L. de Gasper, G. Gea-Izquierdo, D. Gibson, A. N. Gillison, A. Giroldo, M. C. Glasenhardt, S. Gleason, M. Gliesch, E. Goldberg, B. Göldel, E. Gonzalez-Akre, J. L. Gonzalez-Andujar, A. González-Melo, A. González-Robles, B. J. Graae, E. Granda, S. Graves, W. A. Green, T. Gregor, N. Gross, G. R. Guerin, A. Günther, A. G. Gutiérrez, L. Haddock, A. Haines, J. Hall, A. Hambuckers, W. Han, S. P. Harrison, W. Hattingh, J. E. Hawes, T. He, P. He, J. M. Heberling, A. Helm, S. Hempel, J. Hentschel, B. Hérault, A. M. Hereş, K. Herz, M. Heuertz, T. Hickler, P. Hietz, P. Higuchi, A. L. Hipp, A. Hirons, M. Hock, J. A. Hogan, K. Holl, O. Honnay, D. Hornstein, E. Hou, N. Hough-Snee, K. A. Hovstad, T. Ichie, B. Igić, E. Illa, M. Isaac, M. Ishihara, L. Ivanov, L. Ivanova, C. M. Iversen, J. Izquierdo, R. B. Jackson, B. Jackson, H. Jactel, A. M. Jagodzinski, U. Jandt, S. Jansen, T. Jenkins, A. Jentsch, J. R. P. Jespersen, G. F. Jiang, J. L. Johansen, D. Johnson, E. J. Jokela, C. A. Joly, G. J. Jordan, G. S. Joseph, D. Junaedi, R. R. Junker, E. Justes, R. Kabzems, J. Kane, Z. Kaplan, T. Kattenborn, L. Kavelenova, E. Kearsley, A. Kempel, T. Kenzo, A. Kerkhoff, M. I. Khalil, N. L. Kinlock, W. D. Kissling, K. Kitajima, T. Kitzberger, R. Kjøller, T. Klein, M. Kleyer, J. Klimešová, J. Klipel, B. Kloeppel, S. Klotz, J. M. Knops, T. Kohyama, F. Koike, J. Kollmann, B. Komac, K. Komatsu, C. König, N. J. Kraft, K. Kramer, H. Kreft, I. Kühn, D. Kumarathunge, J. Kuppler, H. Kurokawa, Y. Kurosawa, S. Kuyah, J. P. Laclau, B. Lafleur, E. Lallai, E. Lamb, A. Lamprecht, D. J. Larkin, D. Laughlin, Y. Le Bagousse-Pinguet, G. le Maire, P. C. le Roux, E. le Roux, T. Lee, F. Lens, S. L. Lewis, B. Lhotsky, Y. Li, X. Li, J. W. Lichstein, M. Liebergesell, J. Y. Lim, Y. S. Lin, J. C. Linares, C. Liu, D. Liu, U. Liu, S. Livingstone, J. Llusià, M. Lohbeck, Á. López-García, G. Lopez-Gonzalez, Z. Lososová, F. Louault, B. A. Lukács, P. Lukeš, Y. Luo, M. Lussu, S. Ma, C. Maciel Rabelo Pereira, M. Mack, V. Maire, A. Mäkelä, H. Mäkinen, A. C. M. Malhado, A. Mallik, P. Manning, S. Manzoni, Z. Marchetti, L. Marchino, V. Marcilio-Silva, E. Marcon, M. Marignani, L. Markesteijn, A. Martin, C. Martínez-Garza, J. Martínez-Vilalta, T. Mašková, K. Mason, N. Mason, T. J. Massad, J. Masse, I. Mayrose, J. McCarthy, M. L. McCormack, K. McCulloh, I. R. McFadden, B. J. McGill, M. Y. McPartland, J. S. Medeiros, B. Medlyn, P. Meerts, Z. Mehrabi, P. Meir, F. P. Melo, M. Mencuccini, C. Meredieu, J. Messier, I. Mészáros, J. Metsaranta, S. T. Michaletz, C. Michelaki, S. Migalina, R. Milla, J. E. Miller, V. Minden, R. Ming, K. Mokany, A. T. Moles, A. Molnár, J. Molofsky, M. Molz, R. A. Montgomery, A. Monty, L. Moravcová, A. Moreno-Martínez, M. Moretti, A. S. Mori, S. Mori, D. Morris, J. Morrison, L. Mucina, S. Mueller, C. D. Muir, S. C. Müller, F. Munoz, I. H. Myers-Smith, R. W. Myster, M. Nagano, S. Naidu, A. Narayanan, B. Natesan, L. Negoita, A. S. Nelson, E. L. Neuschulz, J. Ni, G. Niedrist, J. Nieto, Ü. Niinemets, R. Nolan, H. Nottebrock, Y. Nouvellon, A. Novakovskiy, K. O. Nystuen,

A. O'Grady, K. O'Hara, A. O'Reilly-Nugent, S. Oakley, W. Oberhuber, T. Ohtsuka, R. Oliveira, K. Öllerer, M. E. Olson, V. Onipchenko, Y. Onoda, R. E. Onstein, J. C. Ordonez, N. Osada, I. Ostonen, G. Ottaviani, S. Otto, G. E. Overbeck, W. A. Ozinga, A. T. Pahl, C. E. Paine, R. J. Pakeman, A. C. Papageorgiou, E. Parfionova, M. Pärtel, M. Patacca, S. Paula, J. Paule, H. Pauli, J. G. Pausas, B. Peco, J. Penuelas, A. Perea, P. L. Peri, A. C. Petisco-Souza, A. Petraglia, A. M. Petritan, O. L. Phillips, S. Pierce, V. D. Pillar, J. Pisek, A. Pomogaybin, H. Poorter, A. Portsmuth, P. Poschlod, C. Potvin, D. Pounds, A. S. Powell, S. A. Power, A. Prinzing, G. Puglielli, P. Pyšek, V. Raevel, A. Rammig, J. Ransijn, C. A. Ray, P. B. Reich, M. Reichstein, D. E. Reid, M. Réjou-Méchain, V. R. de Dios, S. Ribeiro, S. Richardson, K. Riibak, M. C. Rillig, F. Riviera, E. M. Robert, S. Roberts, B. Robroek, A. Roddy, A. V. Rodrigues, A. Rogers, E. Rollinson, V. Rolo, C. Römermann, D. Ronzhina, C. Roscher, J. A. Rosell, M. F. Rosenfield, C. Rossi, D. B. Roy, S. Royer-Tardif, N. Rüger, R. Ruiz-Peinado, S. B. Rumpf, G. M. Rusch, M. Ryo, L. Sack, A. Saldaña, B. Salgado-Negret, R. Salguero-Gomez, I. Santa-Regina, A. C. Santacruz-García, J. Santos, J. Sardans, B. Schamp, M. Scherer-Lorenzen, M. Schleuning, B. Schmid, M. Schmidt, S. Schmitt, J. V. Schneider, S. D. Schowanek, J. Schrader, F. Schrodt, B. Schuldt, F. Schurr, G. Selaya Garvizu, M. Semchenko, C. Seymour, J. C. Sfair, J. M. Sharpe, C. S. Sheppard, S. Sheremetiev, S. Shiodera, B. Shipley, T. A. Shovon, A. Siebenkäs, C. Sierra, V. Silva, M. Silva, T. Sitzia, H. Sjöman, M. Slot, N. G. Smith, D. Sodhi, P. Soltis, D. Soltis, B. Somers, G. Sonnier, M. V. Sørensen, E. E. Sosinski, N. A. Soudzilovskaia, A. F. Souza, M. Spasojevic, M. G. Sperandii, A. B. Stan, J. Stegen, K. Steinbauer, J. G. Stephan, F. Sterck, D. B. Stojanovic, T. Strydom, M. L. Suarez, J. C. Svenning, I. Svitková, M. Svitok, M. Svoboda, E. Swaine, N. Swenson, M. Tabarelli, K. Takagi, U. Tappeiner, R. Tarifa, S. Tauugourdeau, C. Tavsanoglu, M. te Beest, L. Tedersoo, N. Thiffault, D. Thom, E. Thomas, K. Thompson, P. E. Thornton, W. Thuiller, L. Tichý, D. Tissue, M. G. Tjoelker, D. Y. P. Tng, J. Tobias, P. Török, T. Tarin, J. M. Torres-Ruiz, B. Tóthmérész, M. Treurnicht, V. Trivellone, F. Trolliet, V. Trotsiuk, J. L. Tsakalos, I. Tsiripidis, N. Tysklind, T. Umehara, V. Usoltsev, M. Vadeboncoeur, J. Vaezi, F. Valladares, J. Vamosi, P. M. van Bodegom, M. van Breugel, E. Van Cleemput, M. van de Weg, S. van der Merwe, F. van der Plas, M. T. van der Sande, M. van Kleunen, K. Van Meerbeek, M. Vanderwel, K. A. Vanselow, A. Vårhammar, L. Varone, M. Y. Vasquez Valderrama, K. Vassilev, M. Vellend, E. J. Veneklaas, H. Verbeeck, K. Verheyen, A. Vibrans, I. Vieira, J. Villacís, C. Violle, P. Vivek, K. Wagner, M. Waldram, A. Waldron, A. P. Walker, M. Waller, G. Walther, H. Wang, F. Wang, W. Wang, H. Watkins, J. Watkins, U. Weber, J. T. Weedon, L. Wei, P. Weigelt, E. Weiher, A. W. Wells, C. Wellstein, E. Wenk, M. Westoby, A. Westwood, P. J. White, M. Whitten, M. Williams, D. E. Winkler, K. Winter, C. Womack, I. J. Wright, S. J. Wright, J. Wright, B. X. Pinho, F. Ximenes, T. Yamada, K. Yamaji, R. Yanai, N. Yankov, B. Yguel, K. J. Zanini, A. E. Zanne, D. Zelený, Y. P. Zhao, J. Zheng, J. Zheng, K. Ziemińska, C. R. Zirbel, G. Zizka, I. C. Zo-Bi, G. Zotz, and C. Wirth. 2020. TRY plant trait database – enhanced coverage and open access. Global Change Biology 26:119–188.

Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. Global Change Biology 20:170–182.

Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. Functional Ecology 24:493–501.

Lopez, O. R., K. Farris-Lopez, R. A. Montgomery, and T. J. Givnish. 2008. Leaf phenology in relation to canopy closure in southern Appalachian trees. American Journal of Botany 95:1395–1407.

Maitner, B. S., B. Boyle, N. Casler, R. Condit, J. Donoghue, S. M. Durán, D. Guaderrama, C. E. Hinchliff, P. M. Jørgensen, N. J. Kraft, B. McGill, C. Merow, N. Morueta-Holme, R. K. Peet, B. Sandel, M. Schildhauer, S. A. Smith, J. C. Svenning, B. Thiers, C. Violle, S. Wiser, and B. J. Enquist. 2018. The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. Methods in Ecology and Evolution 9:373–379.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aaasa, R. Ahas, K. Alm-Kübler, P. Bissolli, O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatczak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová, H. Scheifinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12:1969–1976.

Rathcke, B., and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16:179–214.

Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman. 1999. Generality of leaf trait relationships: A test across six biomes. Ecology 80:1955–1969.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: Intraspecific variability in community ecology. Trends in Ecology and Evolution 27:244–252.

Vitasse, Y., S. Ursenbacher, G. Klein, T. Bohnenstengel, Y. Chittaro, A. Delestrade, C. Monnerat, M. Rebetez, C. Rixen, N. Strebel, B. R. Schmidt, S. Wipf, T. Wohlgemuth, N. G. Yoccoz, and J. Lenoir. 2021. Phenological and elevational shifts of plants , animals and fungi under climate change in the European Alps. Biological Reviews 96:1816–1835.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199:213–227.

Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. Trends in Ecology and Evolution 21:261–268.

Wolkovich, E. M., and A. K. Ettinger. 2014. Back to the future for plant phenology research. New Phytologist 203:1021–1024.

Wright, I. J., M. Westoby, P. B. Reich, J. Oleksyn, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornellissen, M. Diemer, J. Flexas, J. Gulias, E. Garnier, M. L. Navas, C. Roumet, P. K. Groom, B. B. Lamont, K. Hikosaka, T. Lee, W. Lee, C. Lusk, J. J. Midgley, Ü. Niinemets, H. Osada, H. Poorter, P. Pool, E. J. Veneklaas, L. Prior, V. I. Pyankov, S. C. Thomas, M. G. Tjoelker, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.
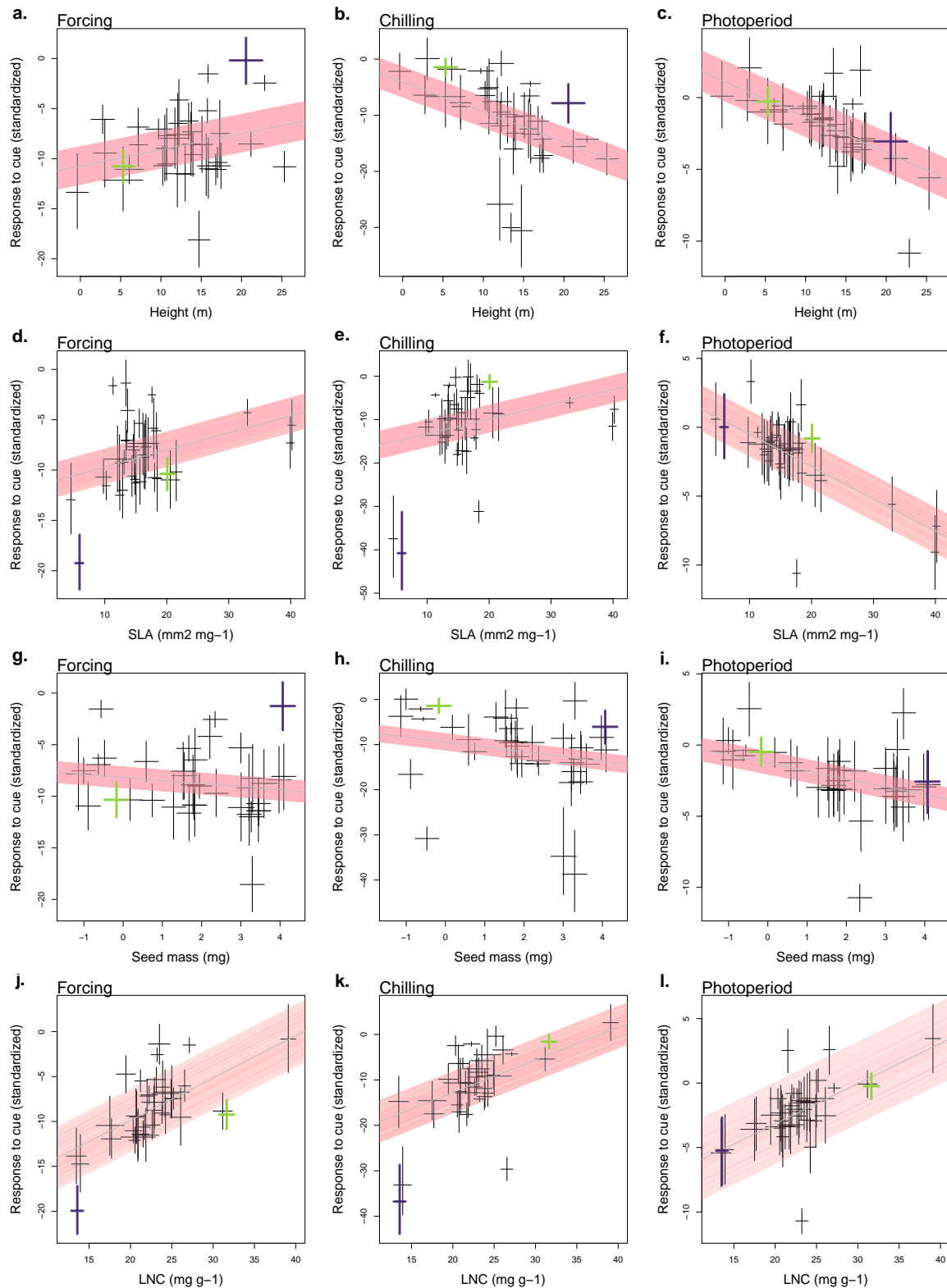
Figure 3: Estimated trait values for height (a-c), SLA (d-f), log10 Seed mass (g-i), and LNC (j-l), correlated against species-level cue responses to standardized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using our joint trait-phenology model, with the grey line depicting the mean linear relationship between estimated trait effects and the slope of the cue response and the pink band the 50% confidence interval. The species depicted in Fig 2 are highlighted in each panel, with the acquisitive species, such as *Alnus incana* shown in green, and the conservative species, such as *Quercus ilex* (a-c & j-l) or *Aesculus hippocastanum* (d-i), shown in purple.