

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

3 Deirdre Loughnan¹, Faith A M Jones¹, Geoffrey Legault¹, Mira Garner²,
Darwin Sodhi³, Daniel Buonaiuto⁴, Catherine Chamberlain⁵, Ignacio Morales Castilla⁶,
Ailene Ettinger⁷, and E M Wolkovich¹

4 June 16, 2022

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

7
8 ² Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

9
10
11 ³ Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts,
12 USA;

13
14 ⁴ XXXX

15
16 ⁵ XXXX

17
18 ⁶ Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

19
20 ⁷ XXXX

21
22 Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca
23

1 Summary

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

2 Introduction

3 Methods

4 Results

1. Our models jointly estimated species traits and phenological cues from large databases, while accounting for significant variation.
 - (a) Across our trait models, we found important study-level variation across traits. Study level variation in our SLA model was approximately half the value of the species level variations (7.78 and 3.27 respectively), while study level variation in seed mass and LNC was proportionally less than that of the species level variation (seed mass: 1.62, 0.97; LNC: 7.78, 3.27 for species and study level variation respectively) (??, ??, ??). Our height model, however, had greater study level variation (7.51) than species level variation (7.51) ??.
 - (b) ...provided estimates of species-level traits with lower uncertainty than simply using the raw data (Fig 3). DL: what do you mean by this? Report the muSp and CI for species that we have good estimates for and for species we have bad estimates for?
 - (c) We combined these trait-level estimates with estimates of forcing, chilling and photoperiod cues from a large meta-analysis of experiments where cues were generally independently manipulated (fig 1). [We can work on updating the caption of fig 1 later to explain this more I think.]
 - (d) Together this joint model produced estimates of how species-level traits may predict species-level phenological cues.
2. Traits differed in whether they led to greater advances and earlier budburst with increasing cues.
 - (a) Height and SLA showed the greatest responses to changes in cues level, while seed mass and LNC had the smallest responses.
 - (b) Taller species had extremely weak responses with forcing (0.2 m per standardized forcing; -0.1, 0.5).
 - (c) But as predicted, these taller species also had larger cue responses to chilling (-0.5 m per standardized chilling; 90% uncertainty interval interval: -1, -0.1) and photoperiod (-0.3 m per standardized photoperiod; -0.6, 0).
 - (d) We did not find a relationship between seed mass and cue responses for any of our three cues (-1.1 mg per standardized chilling; -2.8, 0.7, -0.6 mg per standardized photoperiod; -1.6, 0.4, (-0.3 mg per standardized forcing; -1.4, 0.8))
 - (e) High SLA species, that produced thin leaves with a greater surface area or relatively lower investment to leaf mass, had weaker forcing and chilling cues (0.2 mm²/mg per standardized forcing; -0.1, 0.4, 0.3 mm²/mg per standardized chilling; -0.1, 0.7
 - (f) But stronger photoperiod cues (-0.2 mm²/mg per standardized photoperiod; -0.4, 0)
 - (g) As we predicted, species that produce leaves with high nitrogen content, which reflects high photosynthetic rates, showed weak trait responses, with small responses to both forcing and chilling cues at 0.5 mg/g per standardized forcing; 0.1, 0.9) and (0.7 mg/g per standardized chilling; 0.2, 1.2, and 0.3 mg/g per standardized photoperiod; 0, 0.7 for each cue respectively

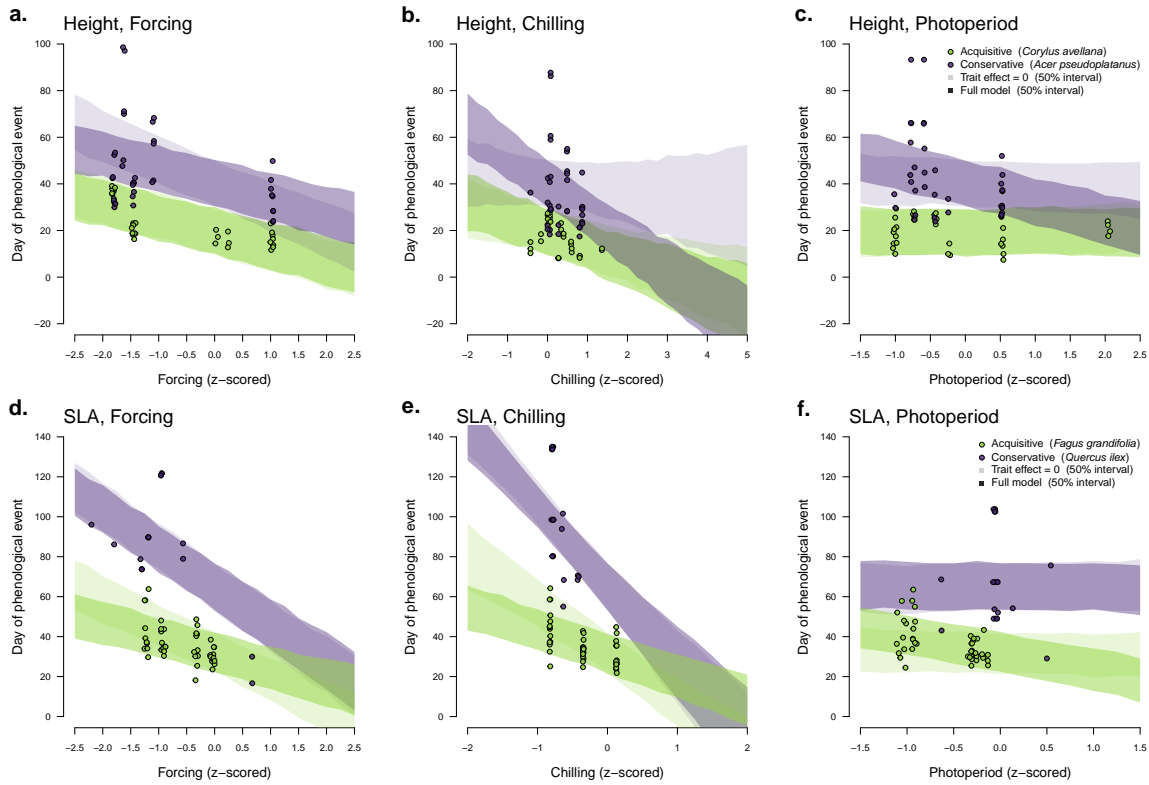


Figure 1: Comparisons of estimated cue responses of a representative species with a trait value associated with acquisitive growth strategies, shown in green, or conservative growth strategies, shown in purple. Points represent the raw budburst data for each respective species. Dark bands represent the 50% uncertainty interval for the posterior cue estimates for the full model, while opaque bands represent the 50% uncertainty interval interval for the posterior cue estimates with a trait effect of zero.

65 5 Discussion

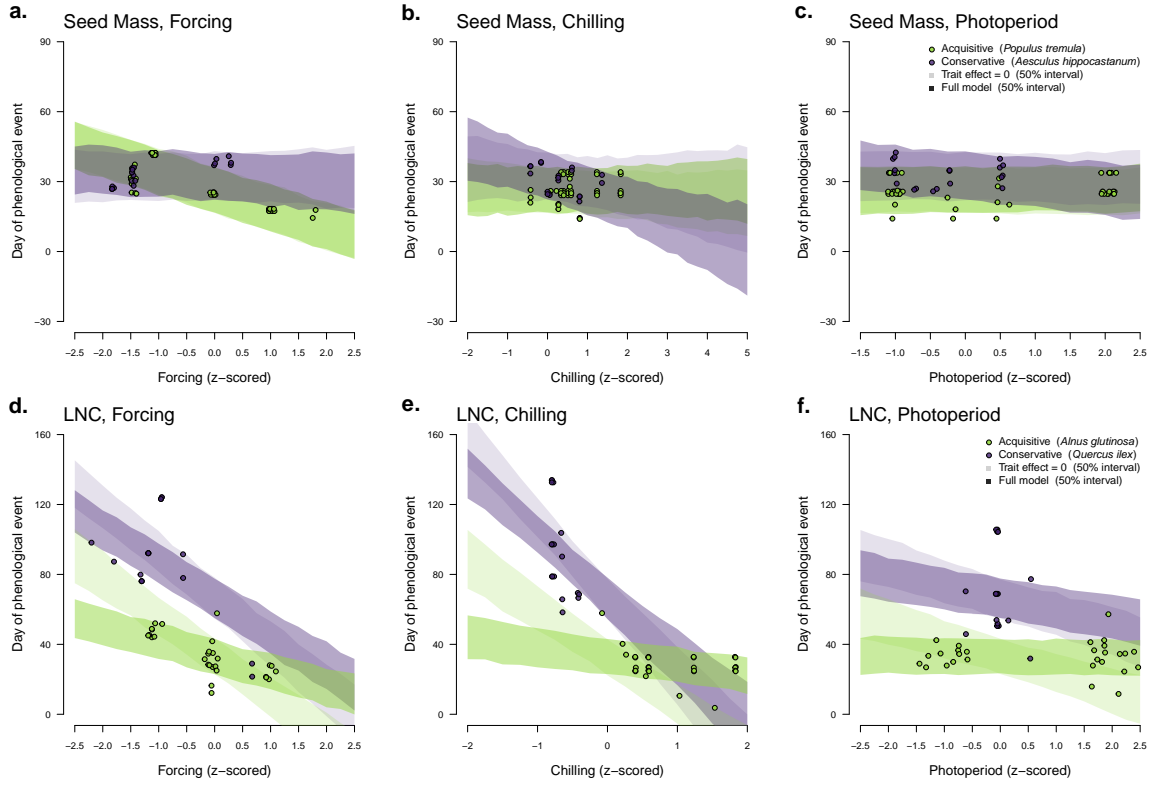


Figure 2: Comparisons of estimated cue responses of a species with an trait value associated with acquisitive growth strategies, shown in green, or conservative growth strategies, shown in purple. Associations between seed mass and forcing, chilling, and photoperiod are depicted on panels a to c and associations between LNC and each cue in panel d to f. The green points represent the budburst data for *Populus tremula*, a relatively small seeded species, while the purple points are budburst data of the large seeded species, *Aesculus hippocastanum*. Dark bands represent the 50% credible interval for the posterior cue estimates for the full model. Opaque bands represent the 50% credible interval for the posterior cue estimates with a trait effect of zero. The negative value of the seed mass model's slope for each cue produces a more negative effect on the day of budburst when seed mass is included in the model. This suggests that trees that produce large seeds advance their budburst dates at a higher rate to increasing cues (a-c). The effect of seed mass however, is relatively small compared to that observed from other traits. Estimates of the cue responses in our LNC model were all positive and produced more positive slopes in the full model. This indicates that high SLA values are less responsive in their budburst to increasing forcing, chilling, and photoperiod values (d to f). The greater effect of slopes on taller trees and high SLA species is an artifact of the trait value itself being larger and not a reflection on the magnitude of the response.

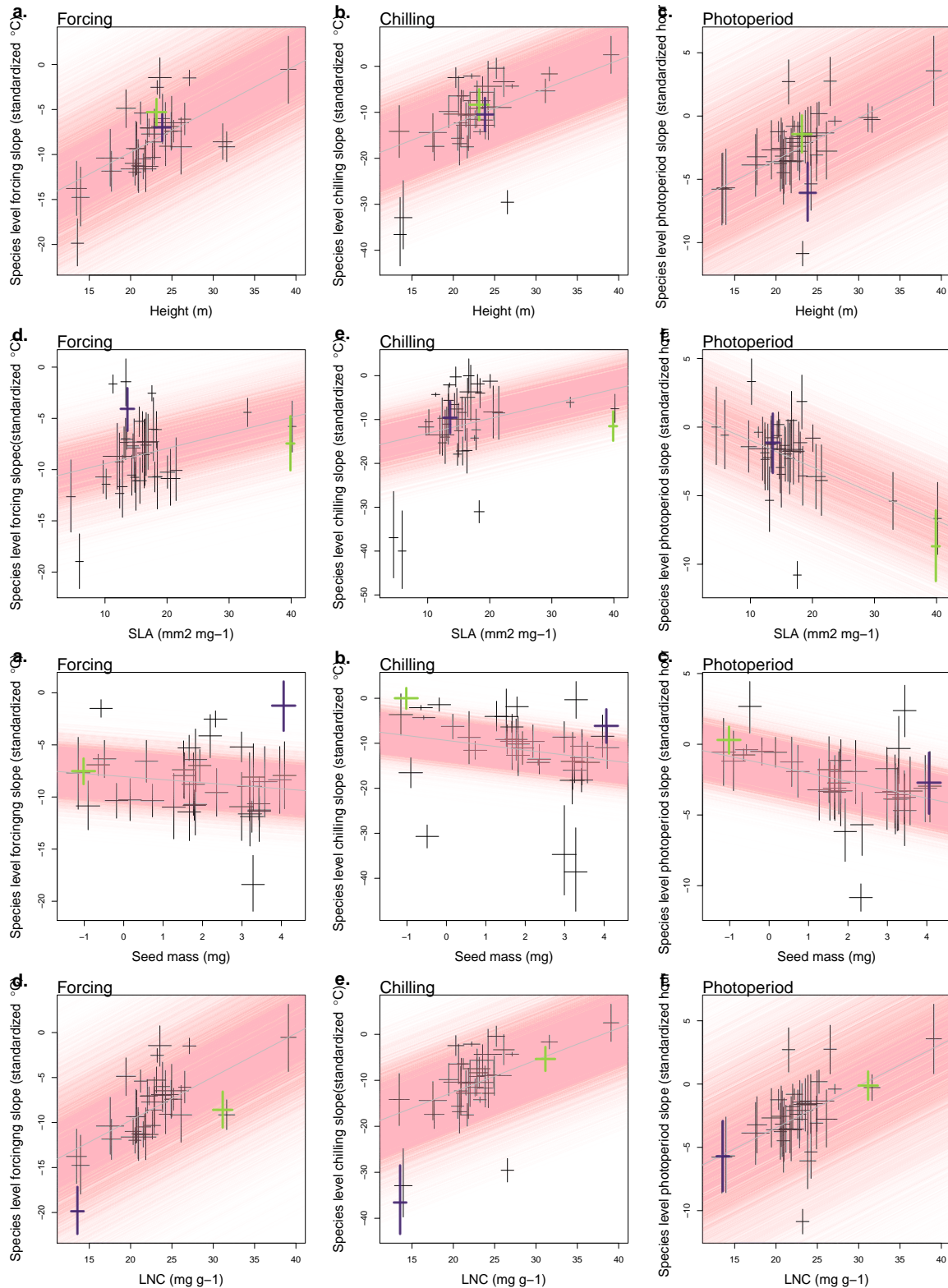


Figure 3: Estimated trait values for height (a-c) and SLA (d-f) traits, correlated against species level cue responses to forcing (a & d), chilling (b & e), and photoperiod cues (c & f). Parameters were estimated using our joint trait-phenology model, with the grey line depicting the mean linear relationship between estimated trait effects and the slope of the cue response. The pink shading represents the distribution of the posterior estimates. The species depicted in Fig 2 are highlighted in each panel, with the acquisitive species shown in green, and the conservative species, shown in purple.

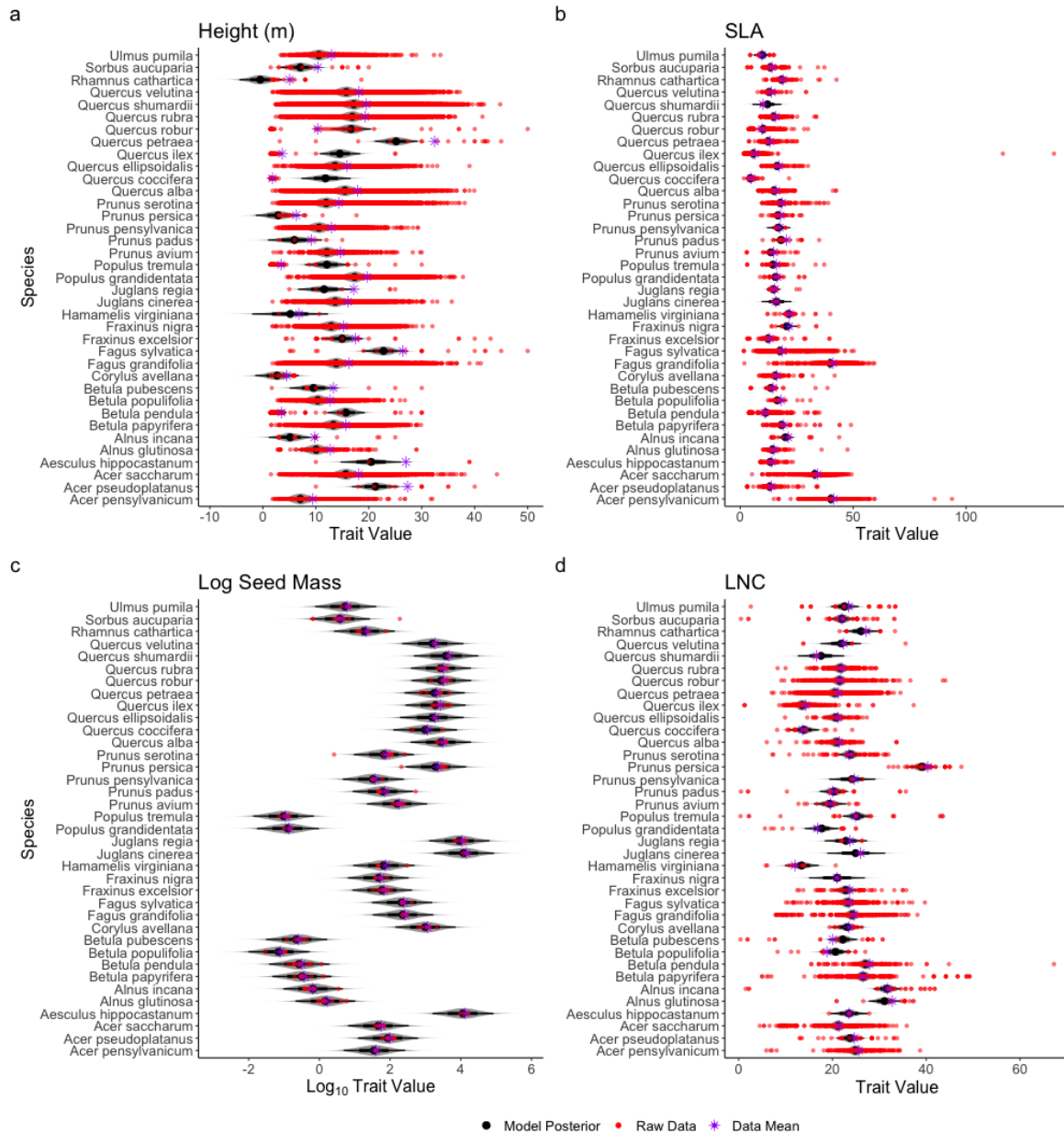


Figure 4: Comparisons of estimated model fits and raw data from joint models of trait effects on budburst phenological cues for 37 species of woody deciduous plants. Four functional traits – a. height, b. SLA, c. seed mass, and d. LNC – were modelled individually, with the calculated trait value being used to jointly model species responses to standardized chilling, forcing, and photoperiod cues. Model posteriors are shown in black, with the thicker line depicting the 66% interval and the thinner black line the 97% interval. Overall species level model posterior distributions were well aligned with the raw data, shown in red, and the species level means from the raw data, denoted as a purple stars.

