Woody plant phenological responses are strongly associated with key functional traits

Deirdre Loughnan¹, Faith A M Jones¹, Geoffrey Legault¹, Mira Garner², Darwin Sodhi³, Daniel Buonaiuto⁴, Catherine Chamberlain⁵, Ignacio Morales Castilla ⁶, Ailene Ettinger⁷, and E M Wolkovich¹

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Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, 2424
Main Mall Vancouver, BC Canada V6T 1Z4.
Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;
Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;
XXXX
SXXXX
Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain
XXXX
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Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca

24 1 Summary

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$_{\scriptscriptstyle 6}$ 2 Introduction

- Invasive plants are shaping plant communities worldwide, filling vacant niches and displacing native plants through the novel community landscapes and changes in resource availability.
- 1. many studies have tried to predict species invasive potential based on functional traits and the links between traits, resource use, and growth strategies
- 2. the same traits we associate with native plants tracking changes in climate may also allow invasive species greater fitness and adaptive advantage to invasive species
 - 3. traits that promote earlier growth in the spring = priority effects and less competitive temporal niche
- 4. understanding the links between species traits', climate, and temporal niche will provide greater insight into likely responses of species fitness and community dynamics in response to climate change
- 1. Functional traits: decades of work associating easy to measure traits related to growth and competition
- 2. drawing bread generalizable trends independent of species
 - (a) Early vs late expect species like many invasive, with fast growth strategies, all along fast axes = high sea, high photosynthesis (LNC), small seeds
- 3. Phenology is similarity a well studied traits not included in broader framework
- 4. invasives fill empty niche early in the growing season
- 5. studies of woody plants focus on how app are responding to changes in climate and the effect of key abiotic cues on growth and phenology
- 6. In woody plants there are 3 key cues chilling, forcing, photoperiod
- 7. We assume these cues would relate to broader growth strategies
 - (a) Particularly tradeoff in resource investment and chilling
 - (b) Forcing vs risk frost
 - (c) Photoperiod and photosynthetic potential
- 8. Relate cues to traits
- 9. Predictions, limitations of previous work
- 54 10. Our aims

5 Some text for intro and methods...

- 56 A major goal of trait ecology has been to predict species-level characteristics by their traits alone; to
- 57 do this, we need to be able to replace species distinctions in models with species' traits. To that aim,
- our models are designed to attribute phenological variation (days to budburst) to species' trait values,
- ⁵⁹ while allowing for residual variation explained by species (partially-pooled). When traits explain a

- significant portion of variation, species will explain only a small amount, and suggest we may be able to predict species for which we only have trait values.
- While phenology in observational data is often considered highly variable, it is actually highly pre-
- dictable in experiments where the major cues (forcing, chilling, photoperiod) are known and thus we
- 64 focus on cues here.

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$_{\scriptscriptstyle 5}$ 3 Predictions

- 1. Chilling Species with high chilling requirements will have traits associated with greater protection from harsh conditions and higher competitive abilities, but requiring longer periods to accumulate chilling and days to budburst.
 - (a) SLA should positively correlate with increasing chill requirements since leaves with large SLA are less frost tolerant
 - (b) Height should positively correlate since there will be more competition for light
 - (c) Seed mass may negatively correlate, as later species have less time for seed development
 - 2. Forcing Species with low forcing requirements will express traits related to frost tolerance and high productivity through faster resource acquisition.
 - (a) Leaves should have smaller SLA because smaller, thicker leaves are more frost tolerant •
 - (b) Shorter in height, as there is less competition for light prior to canopy closure
 - (c) Seed mass may be greater as there is more time for seed development
 - (d) LNC will be greater and is a proxy for photosynthetic rates
 - 3. Photoperiod Species with high photoperiod requirements will budburst later and should have traits associated with greater competitive abilities.
 - (a) SLA should positively correlate with increasing photoperiod requirements
 - (b) Height should positively correlate since there will be more competition for light
 - (c) LNC will be lower in later budbursting species

$_{ iny 4}$ m Methods

$_{ ilde{5}}$ 5 Results

- 1. Quick overview of models again ... (but try not to repeat ourselves from methods)
 - (a) Our models jointly estimated species traits and the phenological cues that predict phenological variation in days to budburst to understand connections between phenology and other plant traits.
 - (b) Because we drew on large trait databases for our analyses we partitioned trait variation due to species versus study-level effects. We then used the species-level estimates of traits (ie., estimates of species with study removed) to examine how traits predicted phenological cues, which in turn predict budburst, while allowing for residual variation in cues to be explained by a species effect.
 - (c) (Probably move to methods): This model is a departure from current efforts in several ways: first, while these steps would normally be done separately, our models allow them to be jointly estimated at once. This allows separating out the trait versus residual species effect; second, we focus on phenological cues as predictors for day of budburst and thus allow traits to influence each cue.

- 2. Review of trait model part ... comparing study variation to species level variation
 - (a) Across our models, we found important study-level variation across traits.
 - (b) In our height model, study level variation was greater (7.5) than species level variation (7.5) (Fig. 1).
 - (c) In contrast, study level variation in our SLA model was approximately half the value of the species level variations (7.8 and 3.3 respectivley).
 - (d) In the seed mass and LNC models it was considerably less than that of the species level variation (seed mass: 1.6, 1; LNC: 7.8, 3.3 for species and study level variation respectively) (Fig. 1).
- 3. Very short paragraph reminding audience of the model and connecting figure on cue-trait relationships.
 - (a) We next combined these trait-level estimates (Fig. 2) with data on forcing, chilling and photoperiod values from a large meta-analysis of experiments to test if traits (height, SLA, seed mass, LNC) related to phenological cues and species budburst dates (Fig. 3).
 - (b) For some traits we found much of the variation in phenological cues across species could be explained by trait variation (see panel a-f in Fig 2), while for others traits were weak predictors (see g-i in Fig 2).
- 4. Discuss how Height and SLA were partially in line with predictions
 - (a) Across traits, height and SLA showed the greatest responses to changes in cues level, though the direction of responses were not consistent across cues for either trait (Fig. 2 a-f).
 - (b) Taller species had extremely weak responses to forcing (0.2 m per standardized forcing; -0.1, 0.5).
 - (c) However, as we predicted, taller species had larger 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, two cues that would generally lead to later budburst and fit within an overall conservative strategy.
 - (d) High SLA species, which produce thin leaves with a relatively lower investment in 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
 - (e) But stronger photoperiod cues (-0.2 mm²/mg per standardized photoperiod; -0.4, 0)
- 5. ...But Seed mass and LNC were not
 - (a) In contrast to height and SLA, seed mass and LNC had very weak responses (Fig. 2 g-m).
 - (b) As we predicted, we found that species that produce leaves with high nitrogen content, which reflects high photosynthetic rates, showed weak trait responses, and weak 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
 - (c) Contrary to our predictions, 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))

6 Discussion

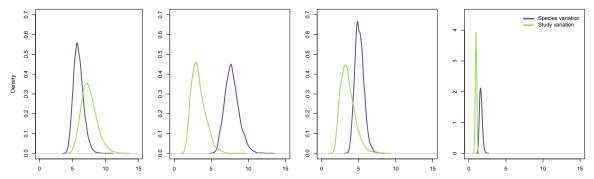


Figure 1: Comparison of the posterior densities for the species level variation and study level variation of a. height, b. SLA, c. LNC, and d. seed mass.

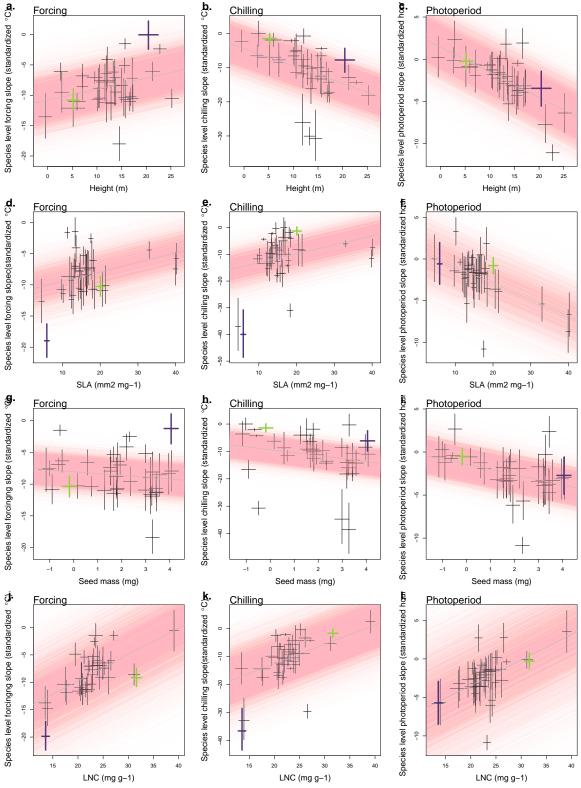


Figure 2: Estimated trait values for height (a-c) and SLA (d-f) traits, correlated against species level cue responses to forcing (a & d), chilling (b & e), and photoperiod cues (c & f). Parameters were estimated using our joint trait-phenology model, with the grey line depicting the mean linear relationship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

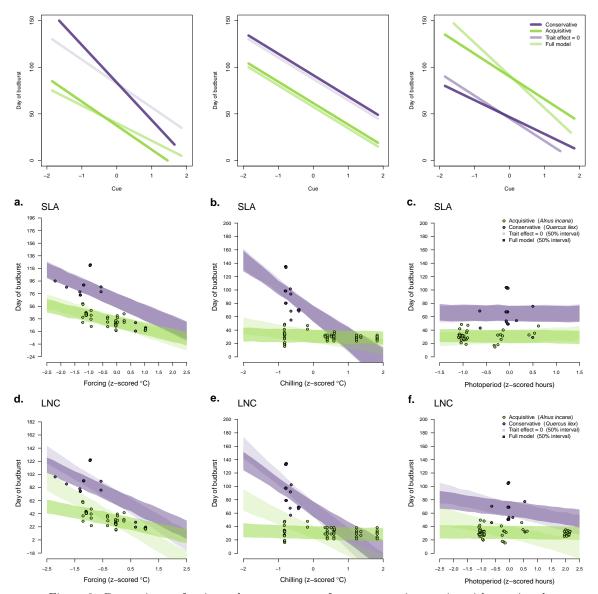


Figure 3: Comparisons of estimated cue responses of a representative species with a trait value associated with acquisitive growth strategies, shown in green, or conservative growth strategies, shown in purple. Some traits strongly predicted phenological responses to cues, as seen by comparing the model estimates including trait (darker bands epresent the 50% uncertainty interval for the posterior cue estimates for the full model) versus without (lighter bands represent the 50% uncertainty interval interval for the posterior cue estimates with a trait effect of zero), which is especially obvious in the species with the higher trait value. Points represent the raw budburst data for each respective species. We show the full range of all treatment values (x axis) though most species cover only a portion.

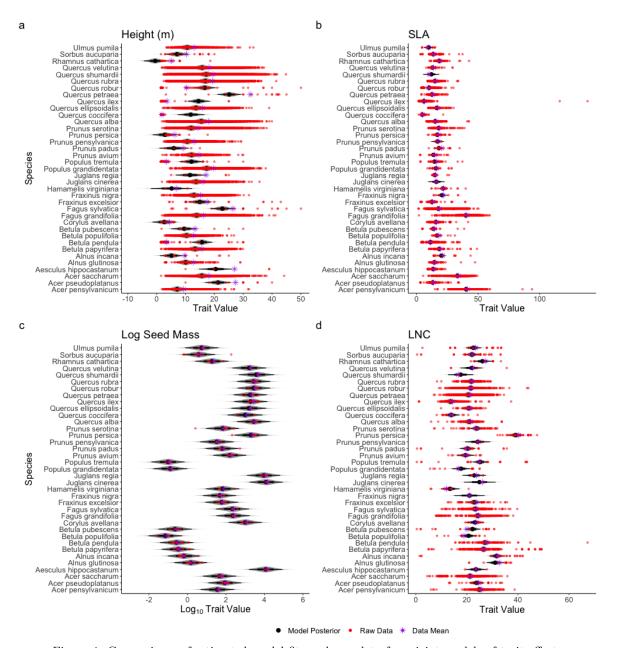


Figure 4: Comparisons of estimated model fits and raw data from joint models of trait effects on budburst phenological cues for 37 species of woody deciduous plants. Four functional traits – a. height, b. SLA, c. seed mass, and d. LNC – were modelled individually, with the calculated trait value being 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.