Species differences in budburst responses in woody plants of North America

Deirdre Loughnan[1] and E M Wolkovich[1]

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

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

Introduction

1. Plant phenology is changing with climate change:
    (a) Timing of spring bb is changing with anthropogenic climate change
    (b) But changes are not uniform with some regions experience greater warming than others.
    (c) Responses are also species specific and highly variable
    (d) Important to understand and predict the drivers and extent of biogeographic trends, as changes in spring phenology determines—growing season length, carbon cycle, species interactions
2. Variation in bb phenology:
    (a) To date, most work has been devoted to understanding how environmental cues shape phenology and what drives the high variation in budburst we observe
    (b) Differences in budburst responses are likely to exist both within communities, as understory spp tend to bb earlier than canopy species, likely reflecting overarching differences in traits.
    (c) But few studies have explored how cue use may differ across populations of the same species and the role of local adaptation.
3. Cues that shape bb
    (a) For woody plants, we know there are three important cues for bb:
        i. Forcing: spring temperatures
        ii. Photoperiod/daylength
        iii. Chilling: winter length and temperatures
    (b) But these cues interact—forcing can offset low chilling—photoperiod offsets weak forcing (Heide1993, Chuine2000, Caffarra2011, Flynn2018)
    (c) The consistency and strength of these interactions across populations is unclear.
4. Understanding species specific responses to cues is critical for predicting future climate change impacts across forest communities and for the species within them.

(a) In many ecosystems winter and spring temperatures are increasing with climate change = faster accumulation of chilling and forcing (Guy2014)

(b) Spp with strong photoperiod cues would be limited in their ability to advance (Korner2010)

(c) Knowing whether there are geographic trends in species responses will allow us to predict how local changes in climate will effect species phenology and ultimately species coexistence

5. In this study we:

(a) Combined results from two growth chamber studies of woody plant phenological cues

(b) Data from four population, from eastern to western North America and a range of 4-6° latitude

(c) Allows us to detect general trends in how bb of N Am. woody plants respond to forcing, chilling, photoperiod

(d) But also community specific responses—detect differences between Western and Eastern forest communities, and at different latitudes

1 Methods

Research questions

(a) Are species responses to chilling, forcing and photoperiod phylogenetically structured?

(b) How do species in deciduous forests communities across North America respond differently to varying cues?

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Results + figures

1. Budburst responses and interactions...

(a) On average, species budburst 28 days after the start of forcing, but some species budburst as early as day 14 for *Aronia melanocarpa* and as late as day 52 for *Quercus velutina*

(b) Species budburst = strongly phylogenetically structured (λ of 0.8, UI: 0.9, 0.6)

(c) All cues did lead to an advance in budburst date, chilling being strongest (-15.2, UI: -17.3, -13.2) and photoperiod weakest (-3.6, UI: -4.3, -3.0, Fig. 1)

(d) But we observed strong interactions between cues and between cues and populations.

(e) Forcing by chilling (9.1, UI: 7.6, 10.5) = delaying effect = low chilling offset by high forcing (Fig. 2 and see Table 1 for model output).

2. Transition between overall and sites with message: overall, population effects were small compared to differences between cues

(a) Across all species, we observed considerable overlap in the responses of our four populations (Fig. 1)

(b) Overall: Low forcing, chilling, and shorter photoperiods resulted in later estimated budburst dates than higher temperature and longer photoperiod treatments across all populations (Fig. 3 a-c)

   (c) However, populations did differ in their their overall budburst dates ... Between the two transects estimated budburst dates were earlier for our eastern populations under our baseline condition (34.1, UI: 40.7, 27.1) compared to our western populations (46.5, UI: 52.7, 39.4, see also Table 1 for model output).
   (d) But individual cue responses were similar across populations and transects (Fig. 3, see Table 1 for model output).

3. Individual species show distinct differences in their timing of bb and relative importance of cues.
   (a) Both chilling and forcing responses varied with budburst, with later bbing species having slightly stronger responses to each cue respectively (Fig. 4).
   (b) But these differences are not due to plant architecture — shrubs and trees = very similar responses overall (Fig. S3)
   (c) Many of our earliest bb species are shrub species, e.g. *Cornus stolonifera* — fits our predicted profile of weak chilling and forcing
   (d) But other shrub species do not — e.g. *Menziesia ferruginea* and *Symphoricarpos alba* = latest bb, but also higher chill and forcing estimates (Fig. S3).
   (e) Tree species = no strong trends, but e.g. *Quercus velutina* = stronger chilling and photoperiod responses as predicted, and *Fagus grandifolia* = strongest photoperiod response

4. Results show the relative importance of phenological cues to variation across species, but suggest they are not the primary drivers of budburst differences across species.
   (a) We observed relatively weak gradients in species' responses across the period of budburst (Fig. 4)
   (b) Species level differences (intercept) explain considerable portion of bb (Fig. 5)
   (c) For our western species, 60.6% of the estimated bb was due to the species intercept, while 67% of the estimated bb of eastern species was due to their species intercepts (Fig. 5).

Discussion

1. Across all species, relative importance of cue = varied = unique temporal niches (Fig. S2)
2. Large portion of bb due to spp differences - need more research to understand this, if not cues what causes it? Could introduce traits and foreshadow the third chapter
3. The experimental design (which is impressive) combined with your models means that most other things some models would assign to the intercept are assigned to site, species, chill, force etc. here... and still the intercept is big. Wow!!
4. Suggests factors other than species cues and architectural growth driving budburst.

2 Tables and figures

Table 1: Summary output from a phylogenetic Bayesian model in which species are partially pooled and phylogeny is included on the intercept. The model includes photoperiod and site as dummy variables, while the forcing and chilling effect is included as continuous. Parameter estimates were used to etimate day of budburst for sites under low cue conditions and for Smithers only when relevant.

	mean	sd	5%	95%
Intercept	12.51	3.14	7.40	17.60
Phylogenetic effect	0.79	0.12	0.60	0.90
Forcing	-9.55	0.74	-10.70	-8.30
Photoperiod	-3.62	0.41	-4.30	-3.00
Chilling	-15.21	1.25	-17.30	-13.20
Manning Park	2.09	0.36	1.50	2.70
Harvard Forest	-6.04	1.03	-7.80	-4.40
St. Hippolyte	-8.71	0.97	-10.30	-7.10
Forcing x photoperiod	0.23	0.71	-1.00	1.40
Forcing x chilling	9.06	0.90	7.60	10.50
Photoperiod x chilling	-0.67	0.90	-2.20	0.80
Forcing x Manning Park	-1.76	0.77	-3.00	-0.50
Photoperiod x Manning Park	0.58	0.79	-0.70	1.90
Chilling x Manning Park	-0.36	1.60	-3.00	2.20
Forcing x Harvard Forest	3.81	1.22	1.80	5.80
Photoperiod x Harvard Forest	-1.96	0.86	-3.30	-0.60
Chilling x Harvard Forest	9.97	2.03	6.60	13.40
Forcing x St. Hippolyte	5.25	1.19	3.20	7.20
Photoperiod x St. Hippolyte	-2.13	0.84	-3.50	-0.70
Chilling x St. Hippolyte	8.65	1.70	5.90	11.50

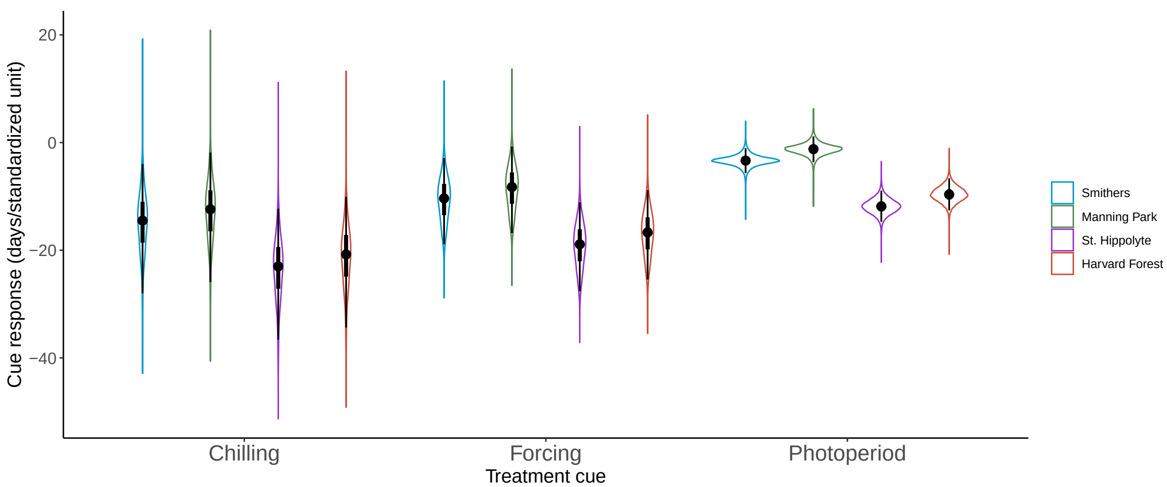

Figure 1: Posterior distributions of estimated chilling, forcing, and photoperiod responses with site level effects for individual populations. Black circles represent the median cue response, thicker black lines the 50% uncertainty interval, while the thinner black line the 90% uncertainty interval. The y-axis spans the entire range of the data. Cues were z-scored using two standard deviations.

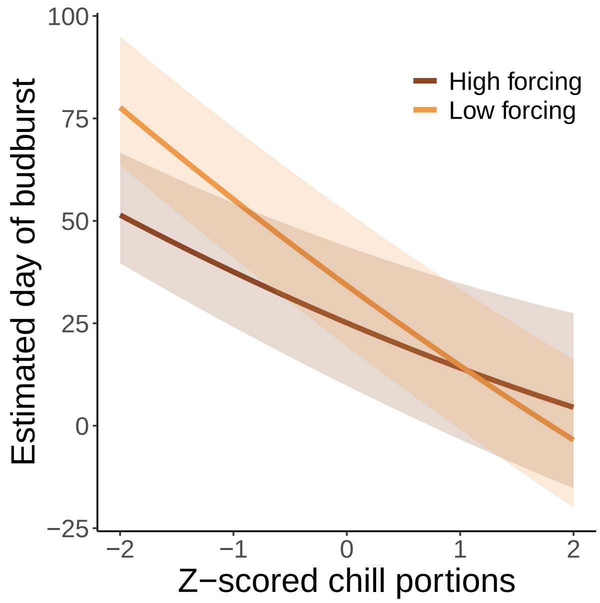

Figure 2: Estimated day of budburst of first bud in response to chill portions and forcing, estimated for our defined baseline conditions.

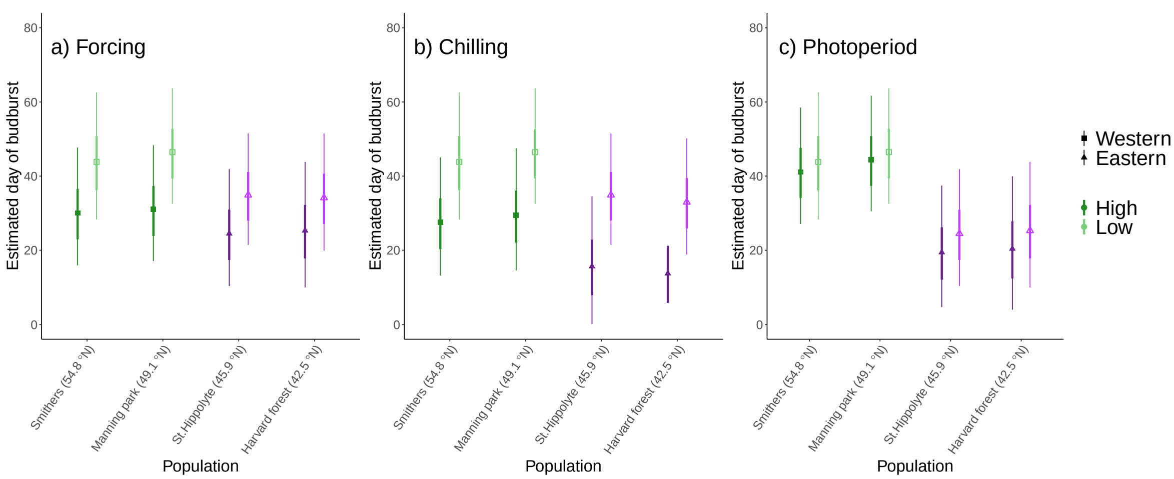

Figure 3: Estimated day of budburst of first bud in response to (a) forcing across populations under low chilling conditions and short photoperiods, (b) chilling across populations under low forcing and short photoperiods, and (c) across photoperiods under our baseline forcing and chilling conditions for species sampled from our four populations. The thin error bars represent the 90% uncertainty interval, while the thicker error bars represent the 50% uncertainty interval.

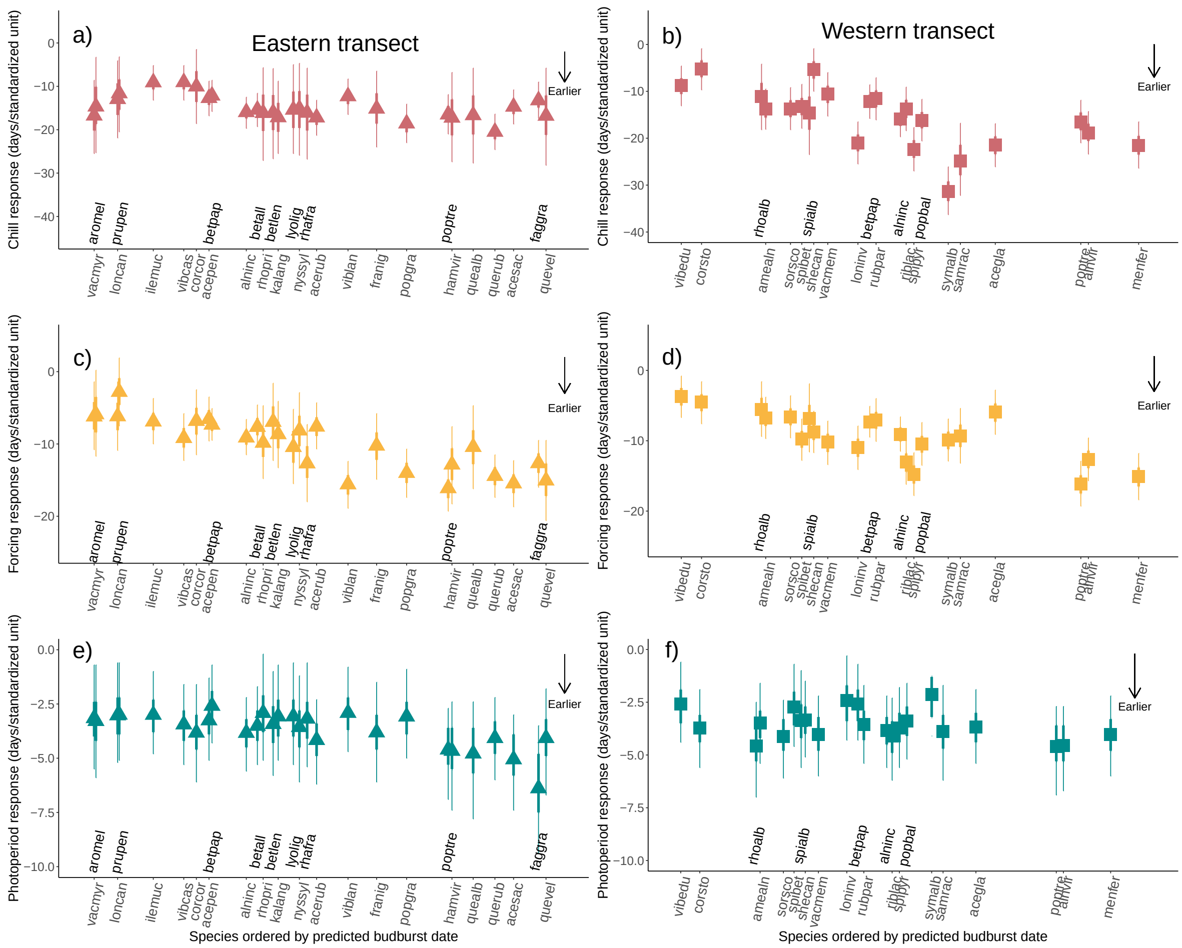

Figure 4: Estimated species' chilling (a,b), forcing (c,d) and photoperiod (e,f) responses ranked by increasing estimated budburst dates for both the eastern (a, c, e) and western (b, d, f) populations. Cues are plotted on differing y-axis to better depict species differences. For each species, the thiner error bars represent the 90% uncertainty interval, and thicker bars represent the 50% uncertainty interval. Each cue was z-scored, using two standard deviations.

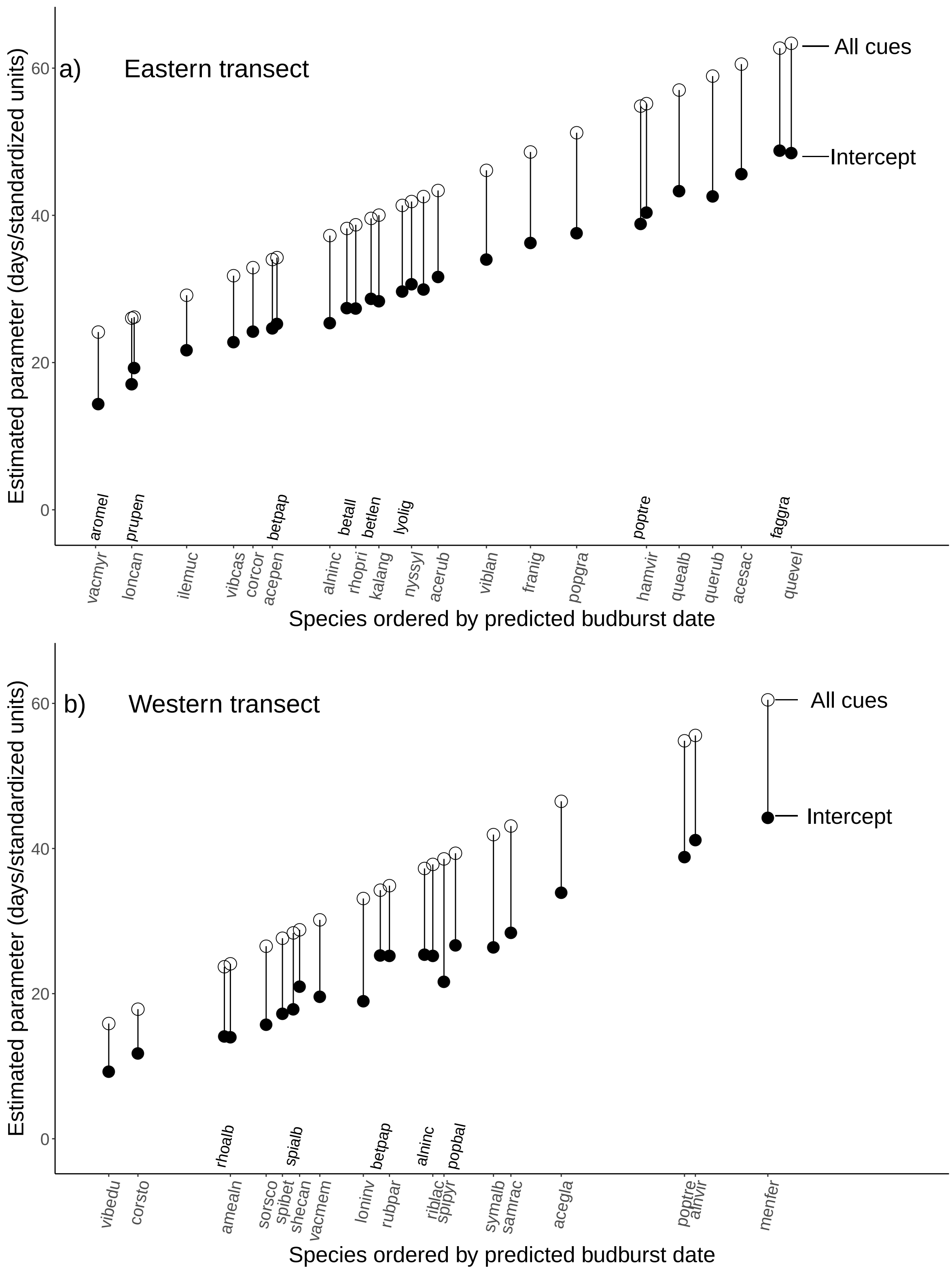

Figure 5: Estimated budburst, shown in blue, and species intercepts, shown in red, ranked by increasing budburst dates for both the eastern (a) and western (b) populations.