Species differences in cue responses in woody plants of North America

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

May 13, 2023

[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) Important to understand and predict these changes as spring phenology determines—growing season length, carbon cycle, species interactions
   (c) But responses are species specific and highly variable
2. Variation in bb phenology:
   (a) Decades of work has been devoted to understanding how environmental cues shape phenology and what drives the high variation in budburst we observe
   (b) Understory spp tend to bb earlier than canopy species, likely in response to overarching differences in traits, but also environmental cues.
   (c) But few studies have explored how cue use may differ acoss populations of the same species and the role of local adapation.
3. Cues that shape bb
   (a) Decades of work has demonstrated the importance of three 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)
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) As winter and spring temperatures increase 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) Potential to alter species coexistence and synchrony on trophic interactions

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
6. Important to consider not just spp but communities as a whole—understand role phenology in shaping spp assemblages, community dynamics, and ecoystem services (Cleland2007).

Research questions

(a) Are species responses to chilling, forcing and photoperiod cues phylogenetically structured?
(b) How do species in deciduous forests communities across North America respond differently to varying cues?

Results + figures

1. Cue responses and interactions...
   (a) On average, species budburst on the 28.1 day after the start of forcing, but ranged from 13.6 for *Aronia melanocarpa* to 52.1 for *Quercus velutina*
   (b) Species budburst = strongly phylogenetically structured (λ of 0.8, UI: 0.6, 1, root trait value of 12.5, UI: 7.3, 17.5.
   (c) All cues did lead to an advance in budburst date, chilling being strongest (-15.2, UI: -17.8, -12.9) and photoperiod weakest (-3.6, UI: -4.4, -2.8)
   (d) But with interactions between cues and between cues and sites.
   (e) Forcing by chilling (9.1, UI: 7.3, 10.8) = delaying effect = low chilling offset by high forcing (Fig. S2 a).
2. Populations differed in their their overall budburst dates, but interacted with cues — effects were clearly divided between eastern and western populations.
   (a) Overall: Low forcing, chilling, and shorter photoperiods resulted in later budburst dates than higher temperature and longer photoperiod treatments across all sites (Fig. 1b-d)
   (b) Between the two transects eastern budburst dates were consistently earlier(-6, UI: -8.1, -4.1 and -8.7, UI: -10.7, -6.8 for Harvard Forest and St. Hippolyte respectively), although not by a considerable amount. Western sites produced a postive response (2.1, UI:1.4, 2.8), with similar budburst dates between the two sites (Fig. 1).
   (c) Lower latitude site in eastern transect was less responsive to forcing 3.8, UI: 1.4, 6.2) = slightly later bb than high latitude site 5.2, UI: 2.9, 7.6) — but western sites were only slightly later under low forcing (Fig. 1b)

(d) This latitudinal effect was not found for chilling — chilling responses were similar across the eastern transects (10, UI: 1.4, 6.2 for Harvard Forest and 8.6, UI: 5.4, 12 for St. Hippolyte) = prodcuing later bb for the low chilling treatment than the high chilling treatment — western transect = advances in bb with greater chilling but not the 95% uncertainty interval crosses zero (-0.4, UI: -3.5, 2.6) (Fig. 1c).

(e) Photoperiod effects = greatest in eastern populations and weak in western populations — low latitude site had slightly later bb in eastern transect (-2, UI: -3.6, -0.3 for Harvard Forest and -2.1, UI: -3.8, -0.5 for St. Hippolyte), but negligible photoperiod response in the west, with estimates 95% uncertianty interval spanning zero (0.6, UI:-0.9, 2.1). (Fig. 1d)

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 gradients were not as strong as expected (Fig. 3 and Fig. 4)
   (c) Species level differences (intercept) explain considerable portion of bb, explaining 60.6% of the estimated bb for western species and 67% of the estimated bb for eastern species (Fig. 3)

4. Species differences are not due to plant architecture — shrubs and trees = very similar responses overall (Fig. **??**)
   (a) Many of our earliest bb species are shrub species, e.g. *Cornus stolonifera* — fits our predicted profile of weak chilling and forcing cues
   (b) But other shrub species do not — e.g. *Menziesia ferruginea* and *Symphoricarpos alba* = latest bb, but also higher chill and forcing cue estimates (Fig. S2).
   (c) Tree species = no strong trends, but e.g. *Quercus velutina* = stronger chilling and photoperiod cues as predicted, and *Fagus grandifolia* = strongest photoperiod response
   (d) Unexpected spp responses are partially due to having stronger cue responses, but also driven by large spp intercepts — suggests factors other than species architectural growth driving diff cue responses

Discussion

1. Across all species, relative importance of cue = varied = unique temporal niches (Fig. **??**)
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!!

1 Tables and figures

Table 1: Summary output from a phylogenetic mixed-effect 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.

	mean	sd	2.5%	50%	97.5%	n_eff	Rhat
Forcing	-9.55	0.74	-10.98	-9.55	-8.07	1391.78	1.00
Photoperiod	-3.62	0.41	-4.44	-3.62	-2.82	3089.29	1.00
Chilling	-15.21	1.25	-17.77	-15.19	-12.88	2142.42	1.00
Manning Park	2.09	0.36	1.37	2.09	2.79	4061.13	1.00
Harvard Forest	-6.04	1.03	-8.10	-6.02	-4.11	486.95	1.01
St. Hippolyte	-8.71	0.97	-10.65	-8.70	-6.83	485.37	1.01
Forcing x photoperiod	0.23	0.71	-1.21	0.24	1.66	3698.87	1.00
Forcing x chilling	9.06	0.90	7.30	9.06	10.81	3005.09	1.00
Photoperiod x chilling	-0.67	0.90	-2.42	-0.66	1.09	2690.36	1.00
Forcing x Manning Park	-1.76	0.77	-3.27	-1.74	-0.28	3836.43	1.00
Photoperiod x Manning Park	0.58	0.79	-0.93	0.57	2.14	3375.92	1.00
Chilling x Manning Park	-0.36	1.60	-3.55	-0.31	2.63	1714.08	1.00
Forcing x Harvard Forest	3.81	1.22	1.43	3.80	6.22	1752.75	1.00
Photoperiod x Harvard Forest	-1.96	0.86	-3.64	-1.96	-0.28	2877.96	1.00
Chilling x Harvard Forest	9.97	2.03	5.99	9.97	14.05	911.46	1.01
Forcing x St. Hippolyte	5.25	1.19	2.85	5.25	7.60	1659.45	1.00
Photoperiod x St. Hippolyte	-2.13	0.84	-3.78	-2.14	-0.46	2606.20	1.00
Chilling x St. Hippolyte	8.65	1.70	5.39	8.63	12.03	1021.36	1.01

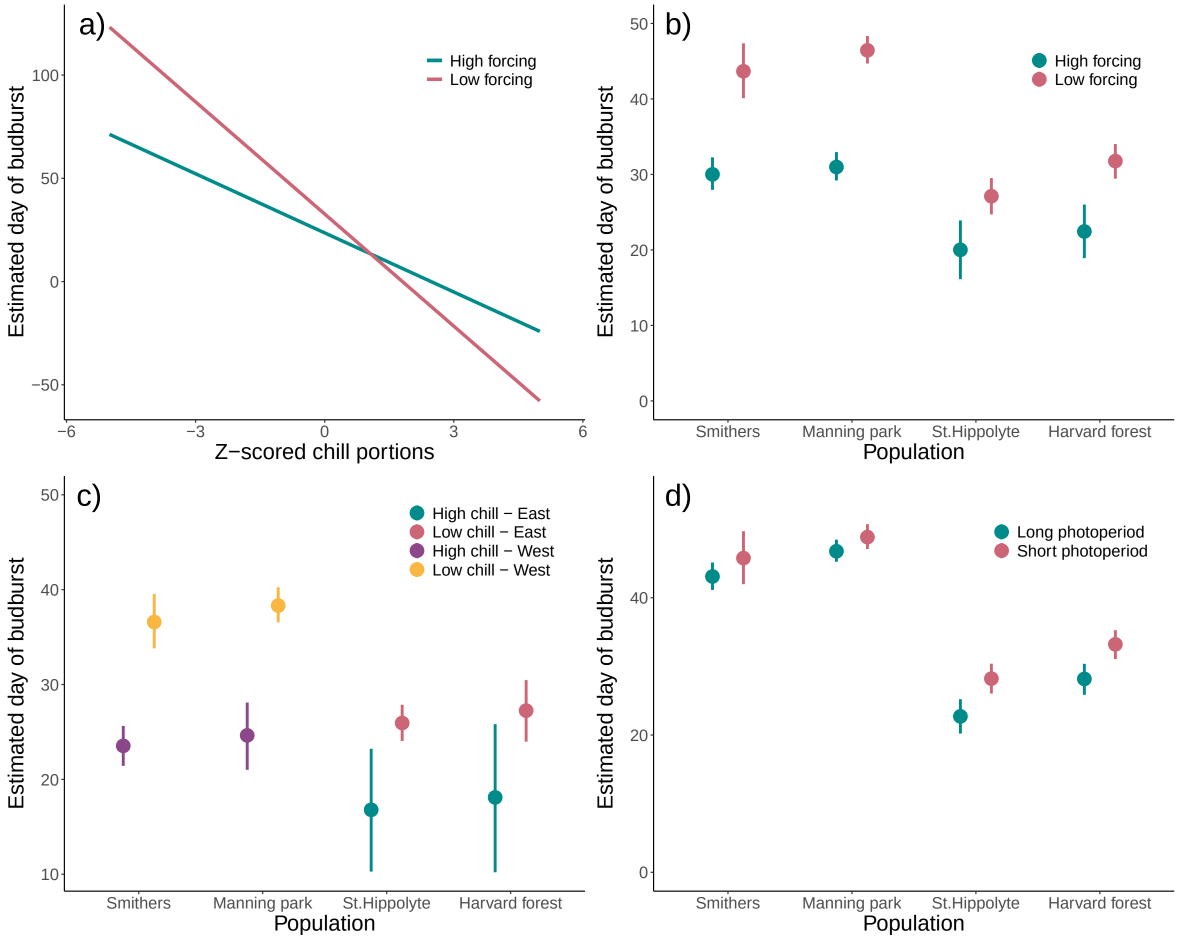

Figure 1: Interaction plots of day of budburst of first bud in response chill portions and forcing (a), forcing cues(b), chilling cues (c), and photoperiod cues (d) and species sampled from St. Hippolyte, Harvard Forest, Manning park, and Smithers.

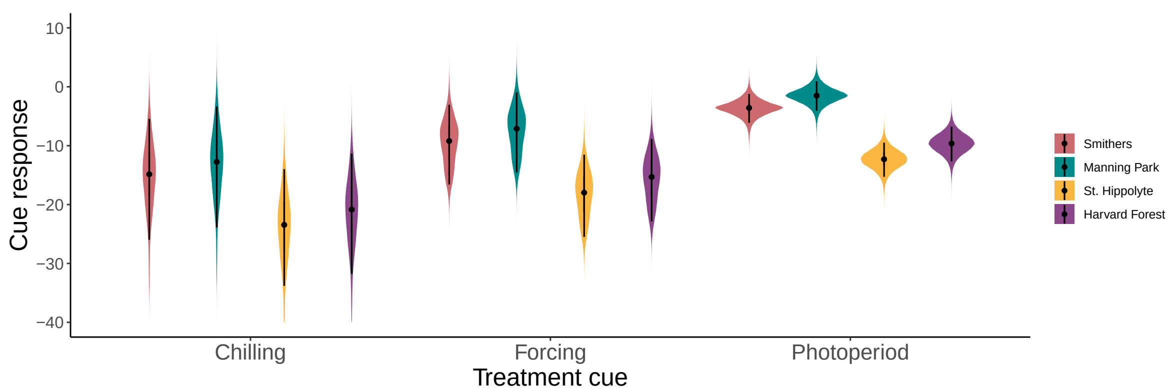

Figure 2: Posterior distributions of estimated cue responses with site level effects for individual sites, depicting a) chilling, b) forcing, and c) photoperiod cue responses. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution is the the posterior density of the posteriors of the cue responses and site level responses for all species at a given site. The y-axis spans the entire range of the data.

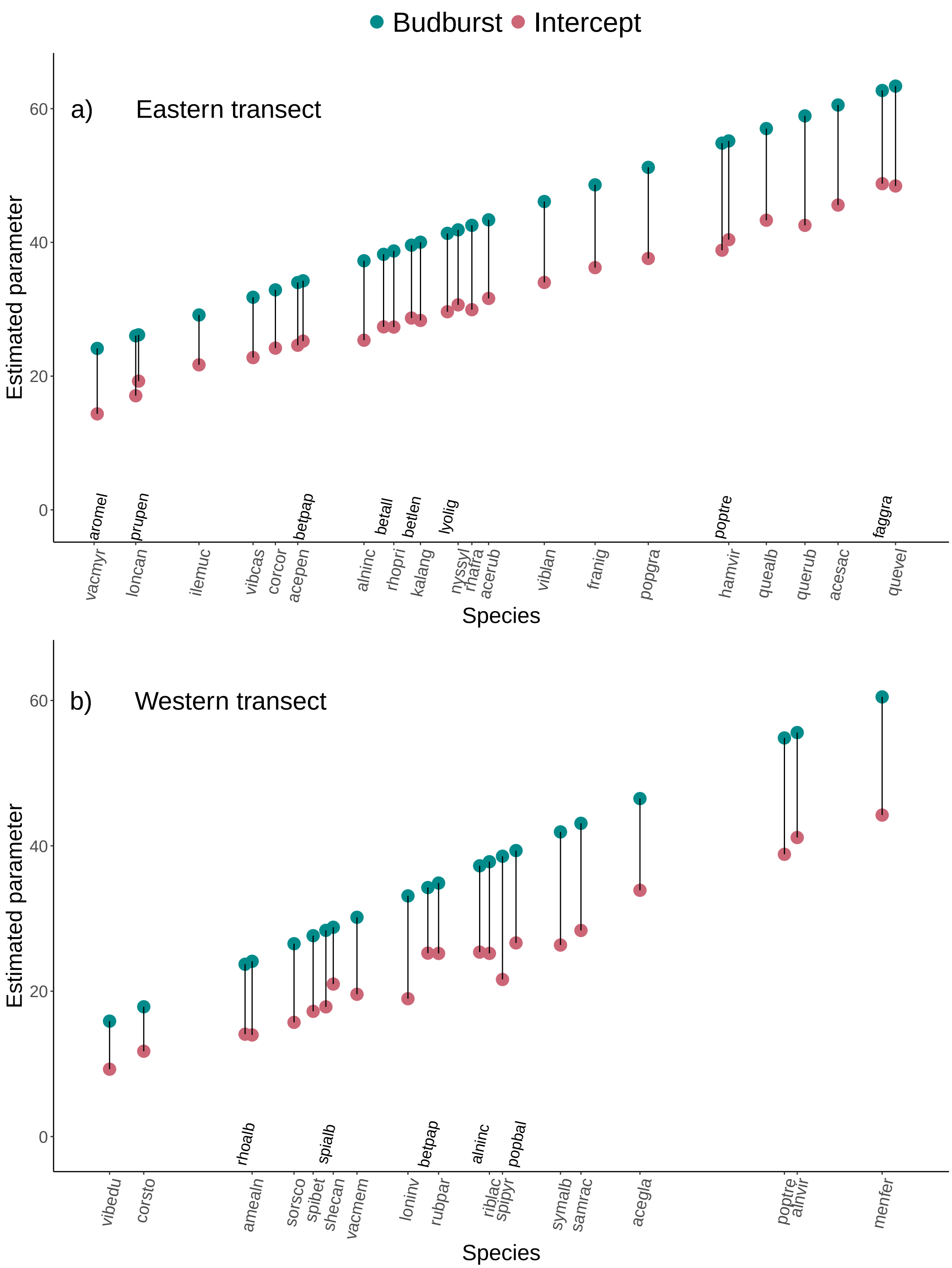

Figure 3: Estimated budburst, shown in blue, and species intercepts, shown in red, ranked by budburst dates for both the eastern (a) and western (b) transects.

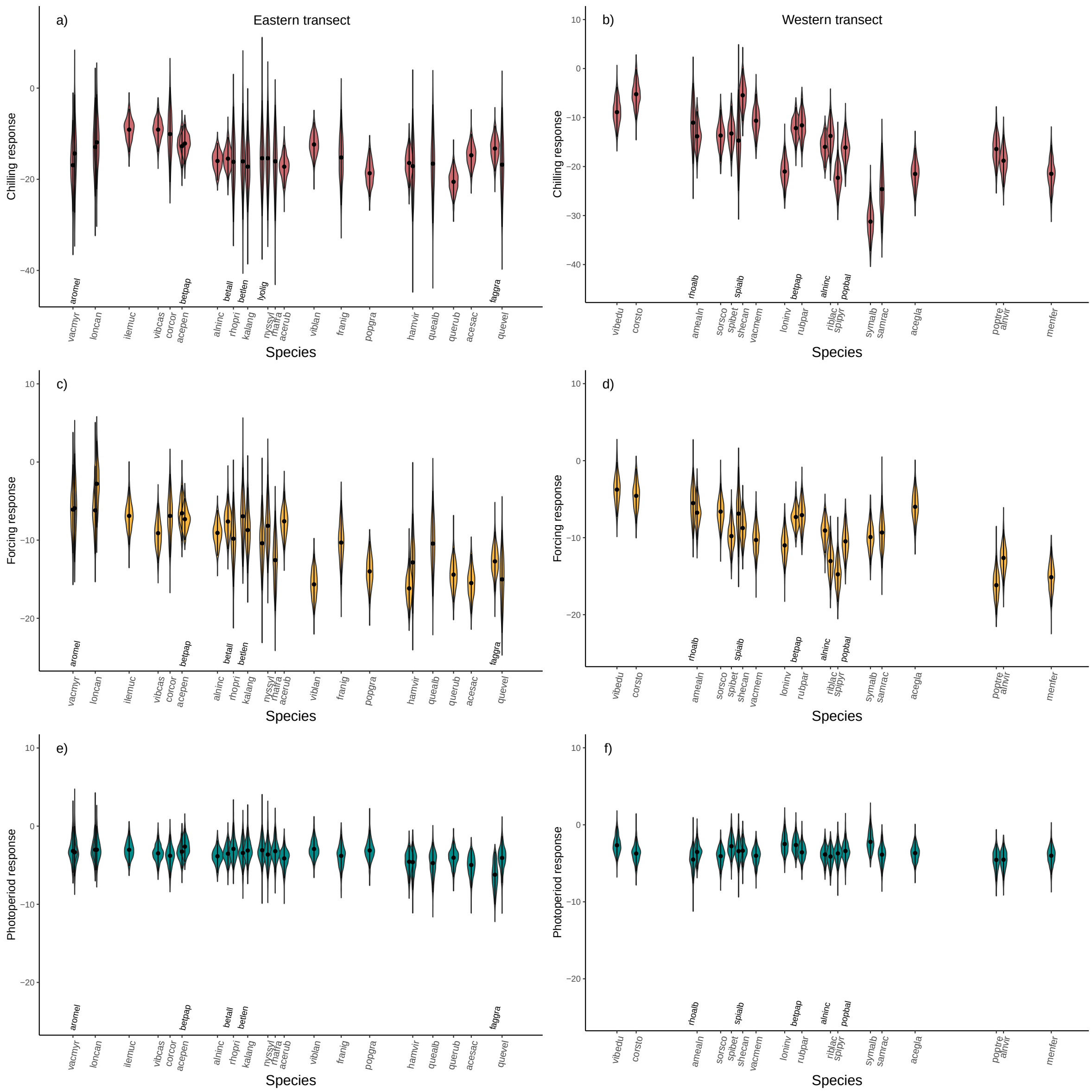

Figure 4: Species' chilling (a,b), forcing (c,d) and photoperiod (e,f) cue responses ranked by estimated budburst dates for both the eastern (a, c, e) and western (b, d, f) transects.