Species differences in cue responses in woody plants of North America

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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 cue 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 cue 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 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 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, root trait value of 12.5, UI: 17.6, 7.4).
   (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, Fig. 1)
   (d) But interactions between cues and between cues and sites .
   (e) Forcing by chilling (9.1, UI: 7.6, 10.5) = delaying effect = low chilling offset by high forcing (Fig. 2).
2. Transition between overall and sites with message: overall, site effects were small compared to differences between cues
   (a) Across all species, we observed considerable overlap in the cue responses of our four sites (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 sites (Fig. 3a-c)

   (c) However, populations differed in their their overall budburst dates ... Between the two transects eastern budburst dates were consistently earlier(-6, UI: -7.8, -4.4 and -8.7, UI: -7.1, -10.3 for Harvard Forest and St. Hippolyte respectively). Budburst of individuals from Manning park had a delayed response (2.1, UI:1.5, 2.7), although both western sites were similar in the estimated day of budburst across treatments (producing highly overlapping bars between the high cue treatments across populations, Fig. 3).

3. Site effects were generally divided between populations in eastern and western transects.
   (a) Lower latitude site in eastern transect was less responsive to forcing (3.8, UI: 1.8, 5.8) = slightly later bb than high latitude site (5.2, UI: 3.2, 7.2) — but budburst for our low latitude western sites advanced more under high forcing conditions (-1.8, UI: -3, -0.5).
   (b) This latitudinal effect was not found for chilling — chilling responses were similar across the eastern transects (10, UI: 6.6, 13.4 for Harvard Forest and 8.6, UI: 5.9, 11.5 for St. Hippolyte) = prodcuing later bb for the low chilling treatment than the high chilling treatment — western transect = showed no differences in their budburst responses to greater chilling (-0.4, UI: -3, 2.2) (Fig. 3b).
   (c) After adjusting for the covariation in photoperiod and forcing temperatures in the eastern species' responses, photoperiod effects = greatest in eastern populations, but low latitude site had slightly later bb in the eastern transect (-2.1, -3.5, -0.7 for St. Hippolyte and -2, -3.3, -0.6 for Harvard Forest); while photoperiod effects were negligible in Manning Park (0.6, -0.7, 1.9).
4. 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 cues
   (d) But other shrub species do not — e.g. *Menziesia ferruginea* and *Symphoricarpos alba* = latest bb, but also higher chill and forcing cue estimates (Fig. S3).
   (e) Tree species = no strong trends, but e.g. *Quercus velutina* = stronger chilling and photoperiod cues as predicted, and *Fagus grandifolia* = strongest photoperiod response
5. Results show the relative importance of phenological cues and variation across species, but the gradients were not strong
   (a) We observed relatively weak gradients in species cue 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 species level differences, while 67% of the estimated bb of eastern species was due to species (Fig. 5).
   (d) Suggests factors other than species cues and architectural growth driving budburst.

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!!

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.

	mean	sd	2.5%	50%	97.5%	n_eff	Rhat
Root trait value	12.51	3.14	6.44	12.56	18.68	3183.32	1.00
Phylogenetic effect	0.79	0.12	0.50	0.81	0.95	2156.20	1.00
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

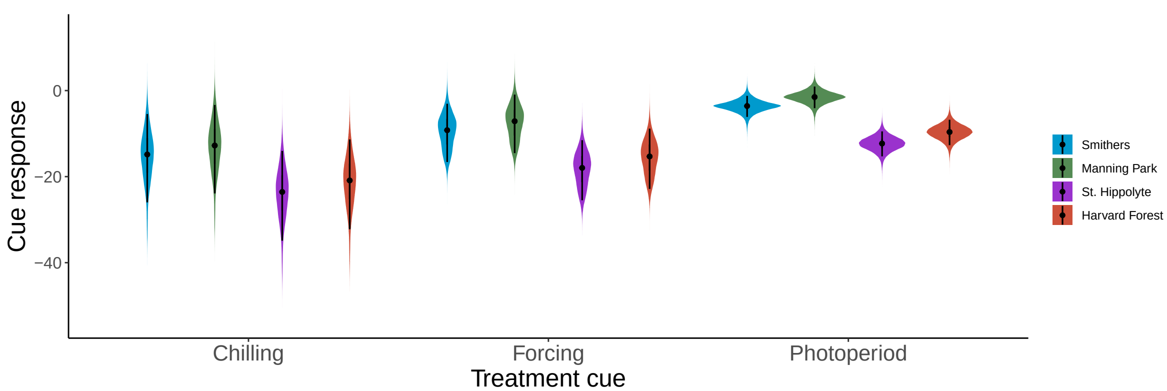


Figure 1: Posterior distributions of estimated chilling, forcing, and photoperiod cue responses with site level effects for individual sites. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The y-axis spans the entire range of the data.

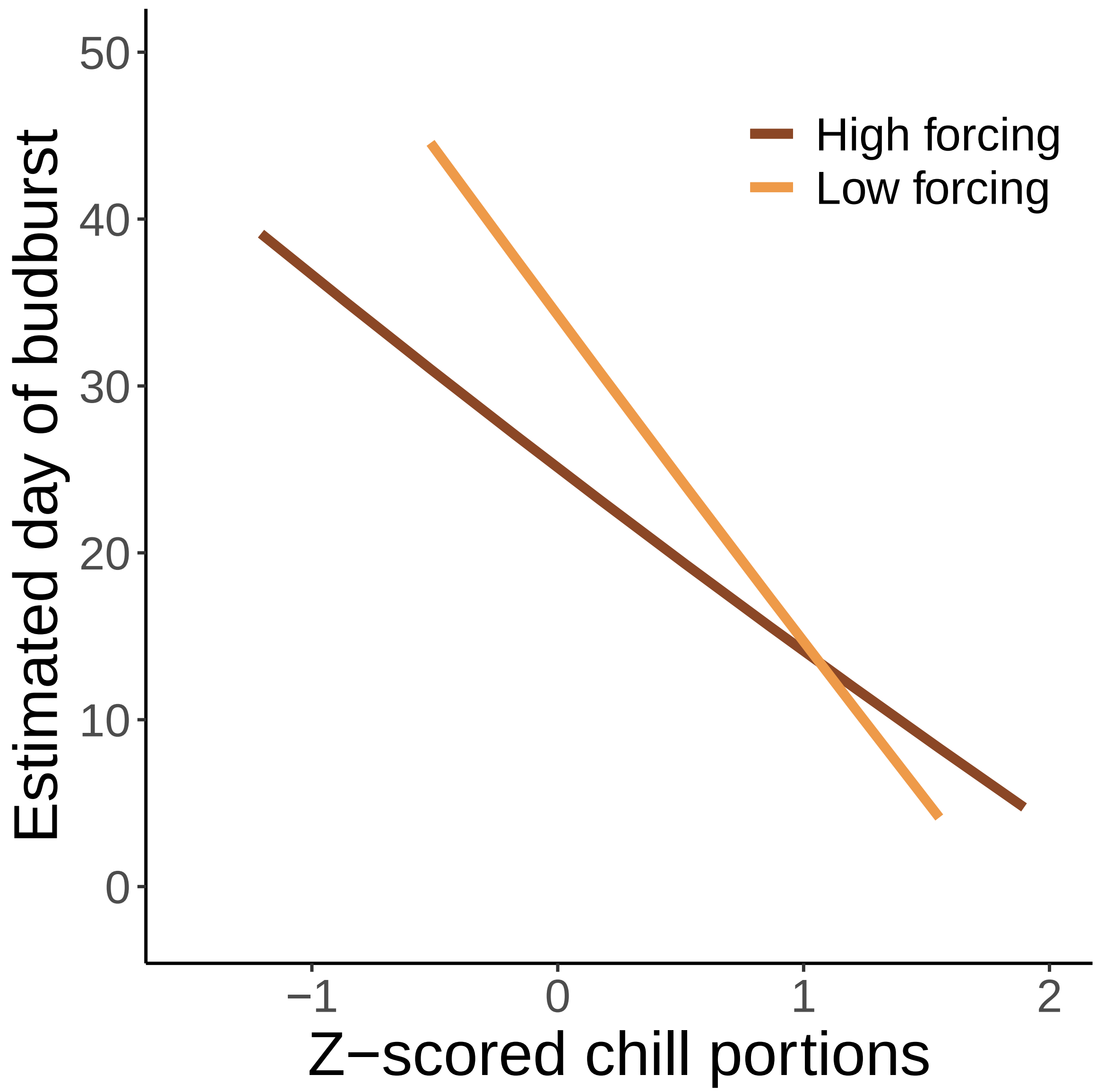


Figure 2: Estimated day of budburst of first bud in response to chill portions and forcing, estimated for our defined baseline conditions.

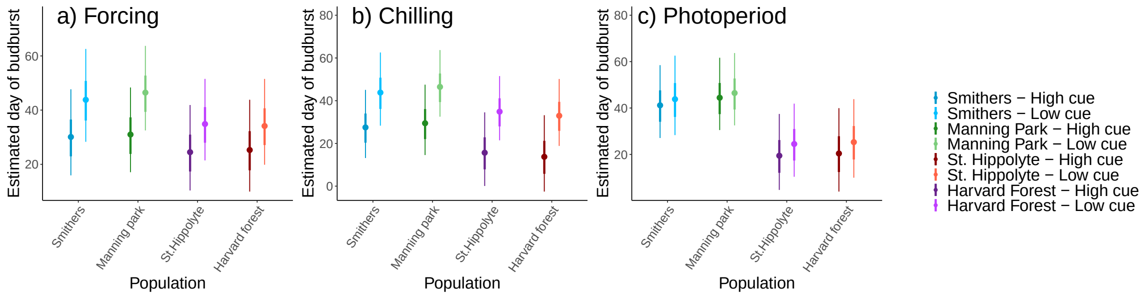


Figure 3: Estimated day of budburst of first bud in response to (a) forcing cues across sites under low chilling conditions and short photoperiods, (b) chilling cues across sites under low forcing and short photoperiods, and (c) across photoperiod cues under our baseline forcing and chilling conditions for species sampled from our four populations.

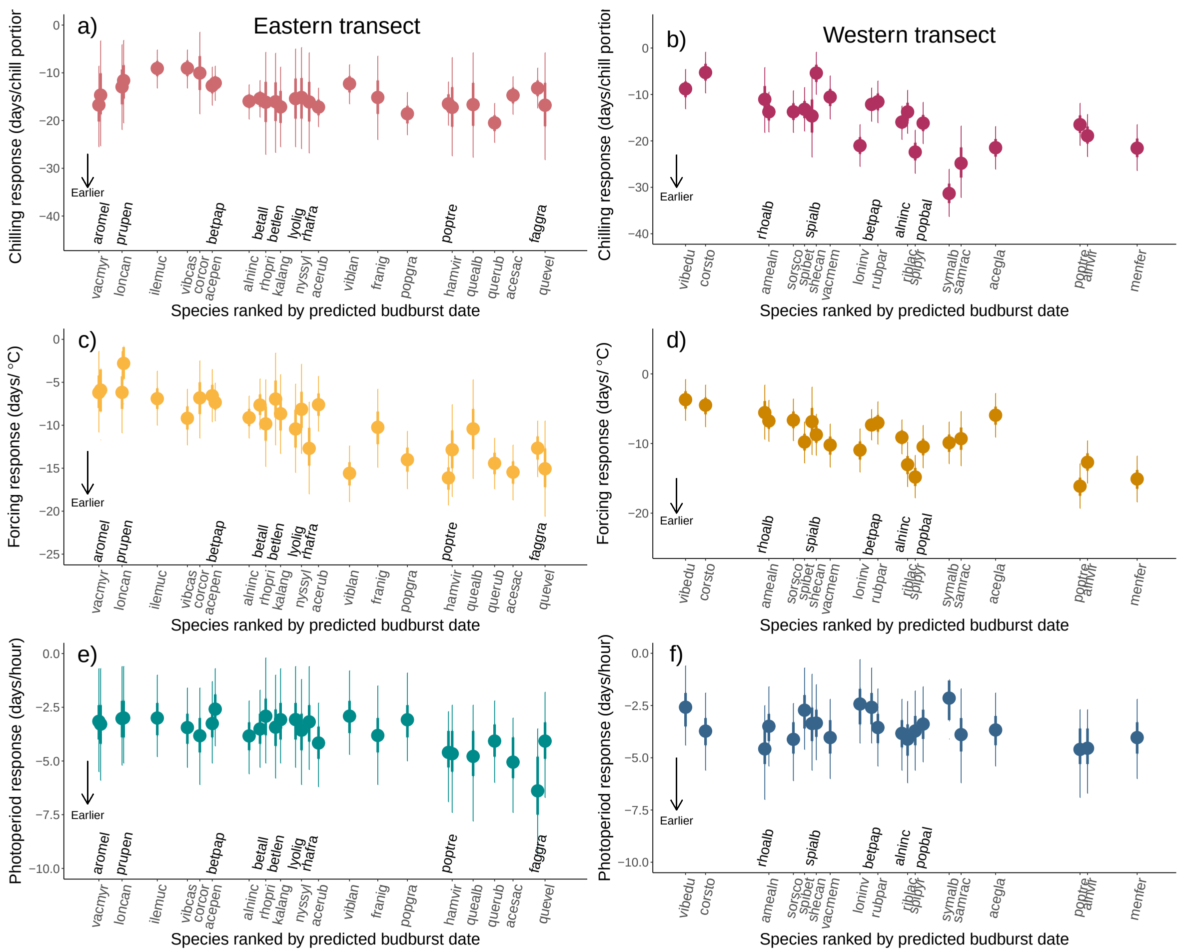
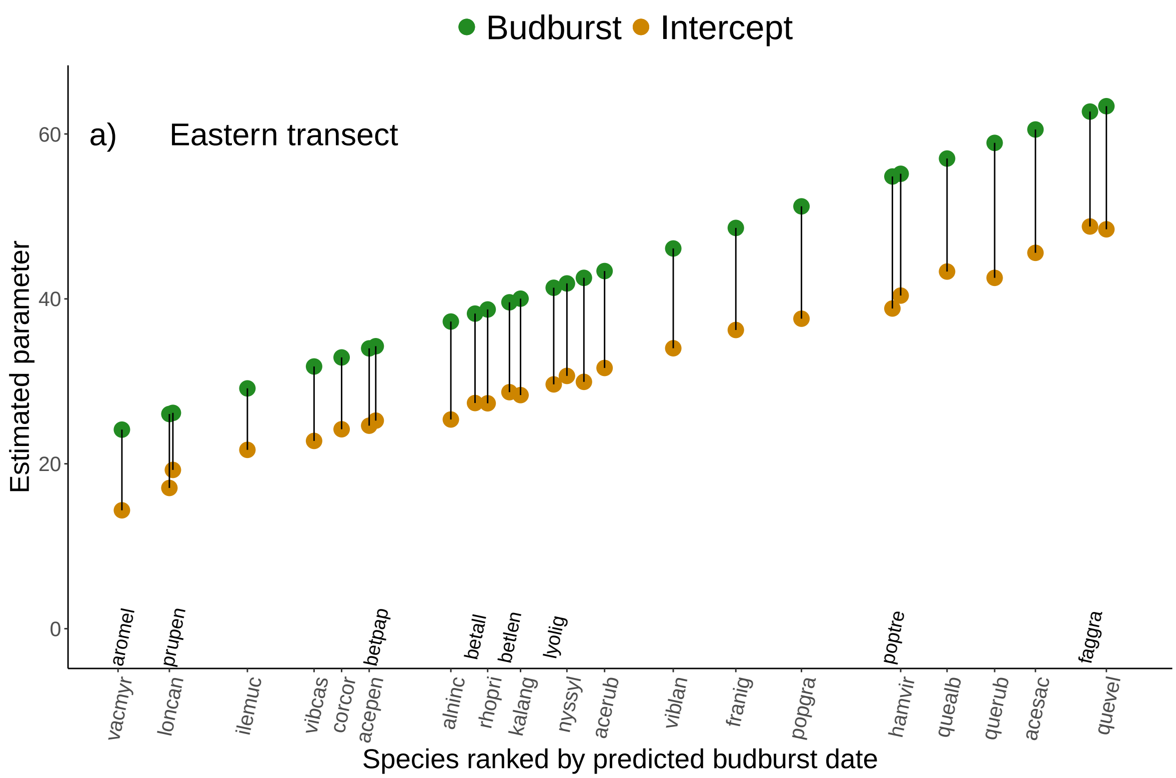


Figure 4: Estimated species' chilling (a,b), forcing (c,d) and photoperiod (e,f) cue responses ranked by increasing estimated budburst dates for both the eastern (a, c, e) and western (b, d, f) transects. Cues are plotted on differing y-axis to better depict species differences.



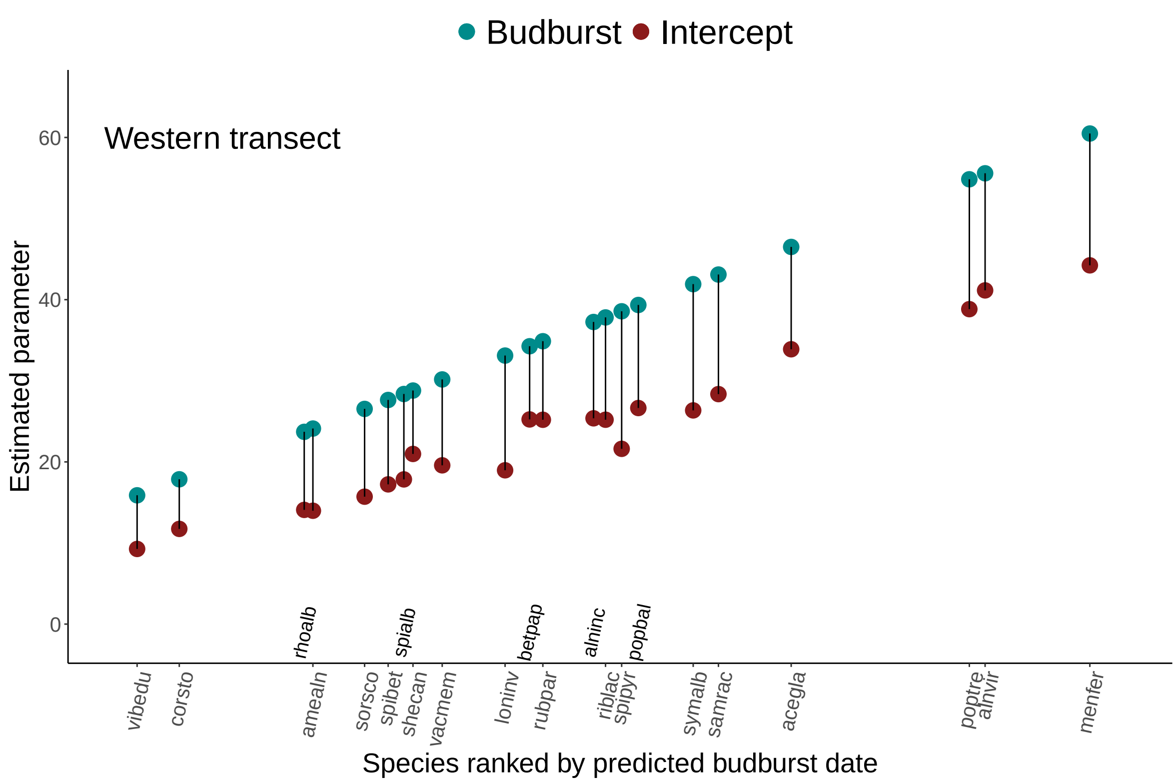


Figure 5: Estimated budburst, shown in blue, and species intercepts, shown in red, ranked by increasing budburst dates for both the eastern (a) and western (b) transects.