Cue 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

Analyeses - ranked by DL

1. Species differences in cue use
2. Phylogeny
3. shrubs vs trees - tied into traits (shrubs acquisitive growth, trees conservative)
4. Cue use - east vs west
5. Lateral bud cue use

General thoughts/concerns/responses to comments on prev outline

1. I think Smithers is technically boreal forest, it is in the sub-boreal spruce BEC zone
2. The tree shrub work would fit better with the traits paper - since traits seem to strongly fall along this axis
3. I am unsure how to manage the differences in sampling method (if we are missing local adaptation by sampling western sp earlier) and the fact that we have so many more shrubs in our western vs eastern transect
4. Because of the differences in the sampling (ie field chilling), avoid drawing comparisons between east vs west and just purely compare spp?
5. Should I discuss the survival/sucesses of my study and just cite the Flynn study, or present both in the same manner (ie with all 47 spp in the tables, averages of mortality and success across all spp).

Paper 1: Cue responses of western spp in terminal vs lateral budburst

Research questions

1. What is the relative importance of chilling, forcing, and photoperiod cues for budburst phenology in woody plant communities in Western Canada?
2. How might cue use differ for the timing of first budburst in comparison to canopy budburst (50% budburst)?

Results + figures

1. General Survival and germination success from the western transect experiment
   (a) Of the 2560 samples that went into chilling, 2458 survived the duration of the experiment, with only 4% percent mortality occurring.
   (b) We also had considerable success in the percentage of budburst, with only 7% of the surviving samples exhibiting no budburst at all.
   (c) Terminal buds failed to open for 15.7% of samples, most of which were *Vaccinium membranaceum*, *Rubus parviflorus*, and *Ribes lacustre*.
   (d) Overall budburst was lowest for *Acer glabrum*, *Ribes lacustre*, *Menziesia ferruginea*, *Symphoricarpos albus*.
   (e) Removing these four western species does change several of the model estimates. While most parameter estimates are within 15% of the model with all species, estimates are considerably different for the forcing x photoperiod interactions, the site estimate for Manning Park, and the interaction with Manning Park and both chilling and photoperiod respectively.
2. Section on bb cues of western species only - very similar to below
3. Comparing lateral to terminal? Or first bb to lateral 50% (canopy level bb)
   (a) We found different trends in cue responses when comparing the timing of first lateral budburst and 50% lateral budburst for our western species.
   (b) In comparison to our model of the timing of first budburst, the timing of lateral budburst had stronger responses to chilling (b_{chill}), with 50% lateral budburst having almost equivalent responses to forcing and chilling (b_{force} and b_{chill}).
   (c) However, lateral budburst also experienced a strong interaction between forcing and chilling cues ($b_{forcexchill}$) as well as between forcing and photoperiod ($b_{forcexphoto}$) for the timing of the fist lateral budburst.
   (d) Budburst was delayed for the Manning Park community (b_{site2}), budbursting later than those sampled in Smithers b.C..
   (e) Lateral budburst dates also show weak interactions between photoperiod and Manning Park ($b_{photoxsite2}$) and between chilling and Manning park ($b_{chillxsite2}$), but a strong advancing interactions between forcing and Manning Park ($b_{forcexsite2}$).

Paper 2: Species differences in cue use across North America + phylogeny

Research questions

1. Are species responses to chilling, forcing and photoperiod cues phylogenetically structured?

2. How do species in deciduous forests across North America to these varying cues?
3. Optional: Do we see differences across shrub and tree species?

0.1 Results + figures

1. General findings...
    (a) Species budburst was strongly phylogenetically structured (with a λ of 0.8 (90% uncertainty interval: 0.6, 1), with a root trait value of 12.3 (90% uncertainty interval: 7.2, 17.3).
    (b) While all cues did lead to an advance in budburst date, there were strong interactions between cues and between cues and sites.
    (c) Forcing and chilling cues produced a strong delaying effect, with low chilling being offset by high forcing conditions(Fig. 2 a).
    (d) Similar delaying interactions occur between forcing and St.Hippolyte ($b_{forcexsite3}$), forcing and Harvard forest ($b_{forcexsite4}$), and for the chilling by St. Hippolyte ($b_{chillxsite3}$) and chilling by Harvard forest interactions ($b_{chillxsite4}$).
    (e) As illustrated in Fig. 2 b and c), sites experienced unique cue responses, with St. Hippolyte having earlier budburst than out western sites, with high forcing leading to earlier budburst. Harvard Forest, however, had later budburst than our Smithers site at low forcing, but a greater response to high forcing, resulting in earlier budburst. Finally, the response in Manning park was surprising, with earlier budburst at low forcing, but delayed budburst under high forcing conditions.
    (f) At each site, low amounts of chilling lead to advances in budburst dates, with the strongest response occurring at St. Hippolyte, which also advanced their budburst at high chilling. However, chilling at both Harvard forest and Manning park had delayed budburst relative to the response of species in Smithers. Suggesting that latitudinal differences might be imporant in shaping chilling cue responses.
    (g) The interaction between photoperiod and our eastern sites in contrast, support a moderate advancing effect, with longer photoperiods at our eastern sites causing budburst dates to advance more, while short photoperiods had a negligible response. A similar but weaker trend was also found for Harvard Forest. But Manning park exhibited the opposite and stronger responses, with low and high chilling converging, with short photoperiod cues leading to earlier budburst than the response of species at Smithers and long photoperiods causing species to have slightly delayed budburst. (Fig. 2 d).
    (h) While there are some differences across cue responses across sites, they are weak when site effects are accounted for (Fig. 4)
    (i) We also did not observe differences across different plant architectures, with both shrubs and trees having very similar cue responses (Fig. 5)
2. Individual species show more distinct trends
    (a) Across all our focal species, cue responses were strongest for chilling and forcing compared to photoperiod, but species varied in the relative importance of each cue, producing unique temporal niches (8)
    (b) We do not find strong evidence of generalizable trends in species cue responses across the transects or between tree and shrub species.
    (c) While some understory species, such as *Cornus stolonifera* had both weak chilling and forcing cues, others like *Menziesia ferruginea* exhibit strong responses to all three cues (Fig. 8.

(d) Tree species similarly to not show strong trends, with *(*Quercus velutina) having stronger chilling and forcing cues as well as photoperiod as we would predict, but other trees like *Prunus pensylvanica* having consistently weak cue responses (Fig. 8.

(e) Our model estimates do support previously identified trends in cue uses, with *Fagus grandifolia* having the strongest photoperiod response, but surprisingly the shrub *Symphoricarpos alba* had the strongest chilling response).

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, forcing, and site as dummy variables, while the chilling effect is included as continuous chill portions.

	mean	sd	2.5%	50%	97.5%	n_eff	Rhat
Root trait intercept	12.31	3.09	6.28	12.31	18.40	9887.59	1.00
Lambda	0.78	0.12	0.48	0.81	0.95	7760.47	1.00
Forcing	-8.81	0.72	-10.23	-8.80	-7.38	9931.87	1.00
Photoperiod	-3.45	0.41	-4.25	-3.45	-2.63	8418.40	1.00
Chilling	-15.17	1.27	-17.71	-15.16	-12.66	5282.13	1.00
Manning Park	1.90	0.35	1.22	1.90	2.60	13833.47	1.00
Harvard Forest	-4.15	1.06	-6.26	-4.14	-2.12	1330.94	1.00
St. Hippolyte	-7.13	0.99	-9.10	-7.13	-5.23	1329.89	1.00
Forcing x photoperiod	-0.19	0.65	-1.43	-0.19	1.11	12000.48	1.00
Forcing x chilling	8.66	0.86	7.00	8.65	10.39	7759.42	1.00
Photoperiod x chilling	-0.75	0.90	-2.55	-0.75	1.01	6849.85	1.00
Forcing x Manning Park	-1.78	0.77	-3.27	-1.78	-0.25	11224.65	1.00
Photoperiod x Manning Park	0.54	0.78	-0.99	0.54	2.04	9557.53	1.00
Chilling x Manning Park	-0.23	1.63	-3.51	-0.20	2.94	5942.76	1.00
Forcing x Harvard Forest	3.54	1.14	1.31	3.52	5.82	3930.17	1.00
Photoperiod x Harvard Forest	-2.22	0.87	-3.91	-2.23	-0.50	8263.34	1.00
Chilling x Harvard Forest	7.08	2.11	2.80	7.14	11.06	2838.67	1.00
Forcing x St. Hippolyte	4.86	1.15	2.59	4.86	7.14	4048.10	1.00
Photoperiod x St. Hippolyte	-2.36	0.85	-4.02	-2.37	-0.69	7814.44	1.00
Chilling x St. Hippolyte	6.21	1.72	2.76	6.24	9.57	3335.24	1.00

2 Supplementary Material

Table 2: Summary output from a phylogenetic mixed-effect model for the day of budburst of the first lateral bud for western species. In this model, species are partially pooled and phylogeny is included on the intercept. The model includes photoperiod, forcing, and site as dummy variables, while the chilling effect is included as continuous chill portions.

	mean	sd	25%	50%	75%	n_eff	Rhat
Root trait intercept	6.89	1.00	6.22	6.89	7.56	7493.22	1.00
Lambda	0.67	0.08	0.61	0.67	0.73	8201.76	1.00
Forcing	-12.55	0.99	-13.17	-12.54	-11.91	2286.03	1.00
Photoperiod	-2.29	0.57	-2.66	-2.28	-1.93	3873.11	1.00
Chilling	-12.54	1.26	-13.39	-12.55	-11.70	4735.75	1.00
Manning Park	2.44	0.45	2.13	2.43	2.74	7934.30	1.00
Forcing x photoperiod	0.16	1.05	-0.54	0.16	0.83	4950.07	1.00
Forcing x chilling	5.62	1.30	4.78	5.61	6.47	3921.71	1.00
Photoperiod x chilling	-0.62	1.50	-1.61	-0.59	0.39	2753.68	1.00
Forcing x Manning Park	-2.22	1.13	-2.97	-2.21	-1.46	4797.06	1.00
Photoperiod x Manning Park	0.15	1.01	-0.53	0.14	0.82	7029.58	1.00
Chilling x Manning Park	0.88	1.40	-0.04	0.87	1.77	3742.14	1.00

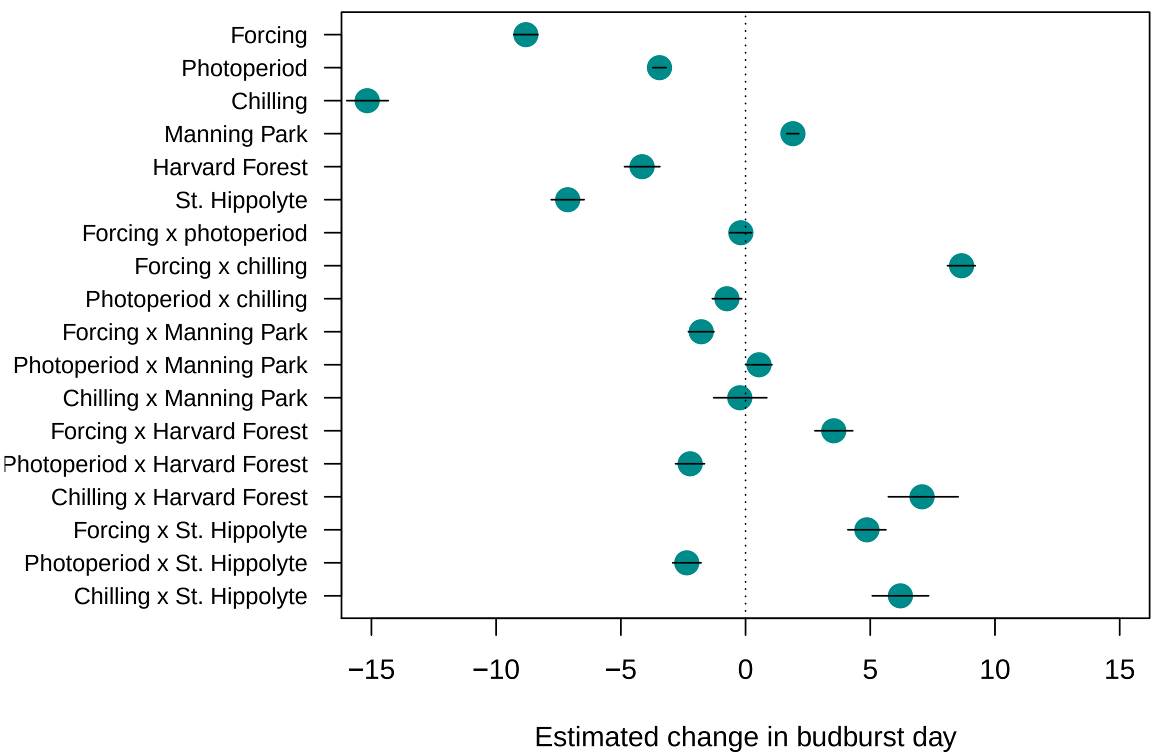

Figure 1: Estimated mean responses in budburst date of first bud to varying forcing, chilling, and photoperiod cues for 47 deciduous woody species across North America. Points represent mean budburst dates, while bars depict the 50% uncertainty interval. Negative responses represent advances budburst, while positive values represent delaying effects.

Table 3: Summary output from a phylogenetic mixed-effect model for the day of 50 percent lateral budburst of species from our western transect. In this model, species are partially pooled and phylogeny is included on the intercept. The model includes photoperiod, forcing, and site as dummy variables, while the chilling effect is included as continuous chill portions.

	mean	sd	25%	50%	75%	n_eff	Rhat
Root trait intercept	6.89	1.01	6.25	6.91	7.56	9968.43	1.00
Lambda	0.69	0.08	0.64	0.70	0.75	9150.28	1.00
Forcing	-13.16	1.29	-14.01	-13.17	-12.33	2179.45	1.00
Photoperiod	-1.69	0.61	-2.09	-1.70	-1.30	6774.36	1.00
Chilling	-10.47	1.33	-11.37	-10.49	-9.61	5047.62	1.00
Manning Park	1.17	0.60	0.75	1.18	1.58	7519.30	1.00
Forcing x photoperiod	2.02	1.18	1.22	2.03	2.83	6463.12	1.00
Forcing x chilling	4.93	1.63	3.88	4.96	5.98	3690.31	1.00
Photoperiod x chilling	-0.64	1.44	-1.57	-0.67	0.24	4810.07	1.00
Forcing x Manning Park	-3.78	1.75	-4.92	-3.79	-2.64	4200.16	1.00
Photoperiod x Manning Park	0.63	1.41	-0.31	0.61	1.52	4991.98	1.00
Chilling x Manning Park	1.29	2.50	-0.27	1.23	2.91	2181.64	1.00

Table 4: Summary output from a phylogenetic mixed-effect model in which the four species with the lowest budburst success was excluded. In this model, species are partially pooled and phylogeny is included on the intercept. The model includes photoperiod, forcing, and site as dummy variables, while the chilling effect is included as continuous chill portions.

	mean	sd	2.5%	50%	97.5%	n_eff	Rhat
Root trait intercept	11.88	3.11	5.77	11.89	17.92	14378.92	1.00
Lambda	0.70	0.15	0.33	0.73	0.93	12911.08	1.00
Forcing	-8.34	0.76	-9.84	-8.35	-6.82	14251.06	1.00
Photoperiod	-3.58	0.45	-4.47	-3.57	-2.68	11193.77	1.00
Chilling	-14.16	1.19	-16.54	-14.14	-11.83	7044.06	1.00
Manning Park	2.49	0.35	1.80	2.49	3.16	17995.43	1.00
Harvard Forest	-4.60	1.06	-6.71	-4.60	-2.56	1874.34	1.00
St. Hippolyte	-7.66	0.99	-9.61	-7.66	-5.73	1897.45	1.00
Forcing x photoperiod	0.45	0.59	-0.70	0.44	1.62	19780.25	1.00
Forcing x chilling	8.87	1.01	6.91	8.87	10.89	8903.33	1.00
Photoperiod x chilling	-0.66	0.77	-2.21	-0.65	0.84	12887.94	1.00
Forcing x Manning Park	-1.95	0.80	-3.49	-1.95	-0.33	14571.36	1.00
Photoperiod x Manning Park	0.68	0.84	-1.01	0.68	2.32	12357.84	1.00
Chilling x Manning Park	-0.74	1.72	-4.28	-0.69	2.52	8029.51	1.00
Forcing x Harvard Forest	3.39	1.19	1.04	3.39	5.73	6397.33	1.00
Photoperiod x Harvard Forest	-2.15	0.92	-3.96	-2.16	-0.33	10185.41	1.00
Chilling x Harvard Forest	6.14	2.15	1.87	6.18	10.28	5263.90	1.00
Forcing x St. Hippolyte	4.74	1.21	2.37	4.74	7.13	6110.36	1.00
Photoperiod x St. Hippolyte	-2.29	0.91	-4.08	-2.29	-0.50	10540.06	1.00
Chilling x St. Hippolyte	5.44	1.71	2.07	5.45	8.73	6644.03	1.00

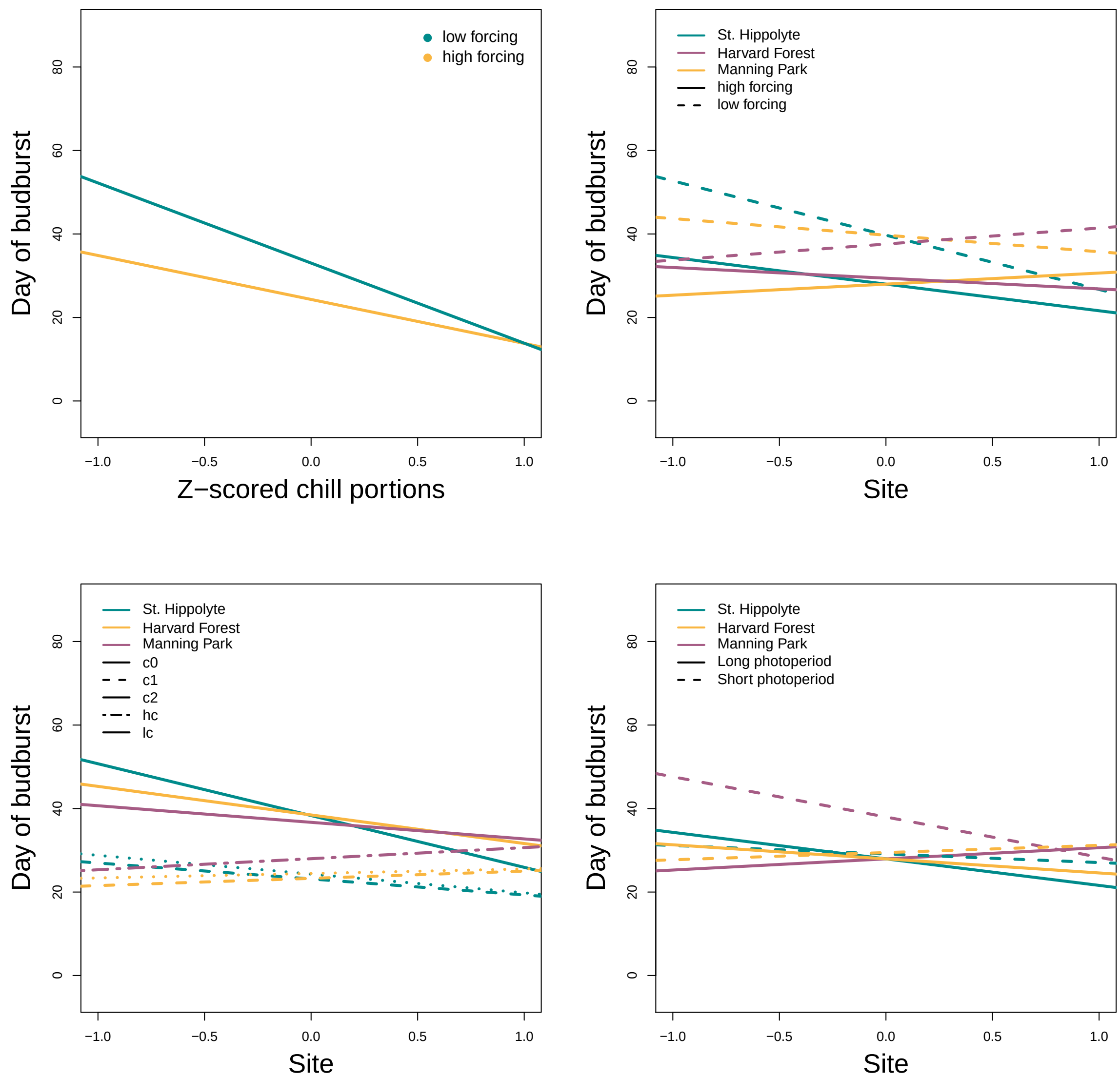

Figure 2: Interaction plots of day of budburst of first bud in response a) chill portions and forcing, b) forcing cues, c) chilling cues, and d) photoperiod cues and species sampled from St. Hippolyte, Harvard Forest, and Manning park.

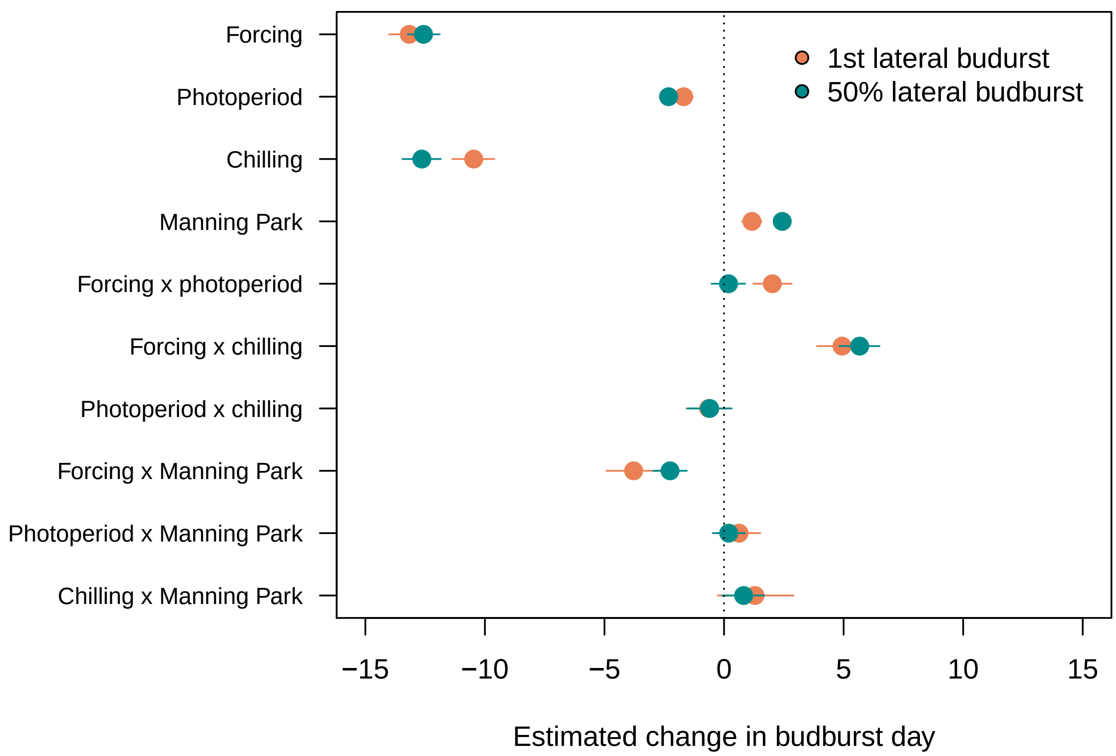

Figure 3: Estimated mean responses in lateral budburst date to varying environmental cues for 21 deciduous woody species in British Columbia. Points represent mean budburst dates, while bars depict the 50% uncertainty interval. Negative responses represent advances budburst, while positive values represent delaying effects.

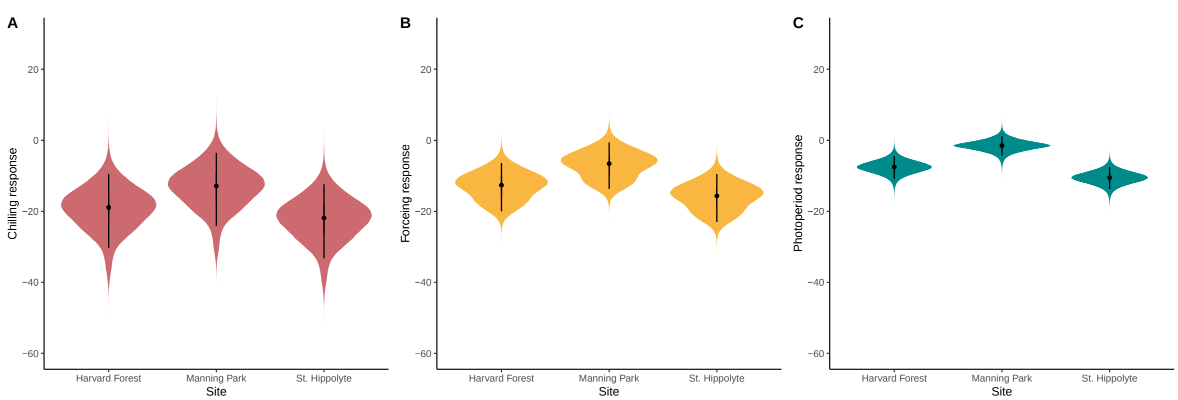

Figure 4: Posterior distributions of estimated cue responses with site level effects for individual sites, depicting a) chilling, b) forcing, and c) photoperiod cue responses. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution 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.

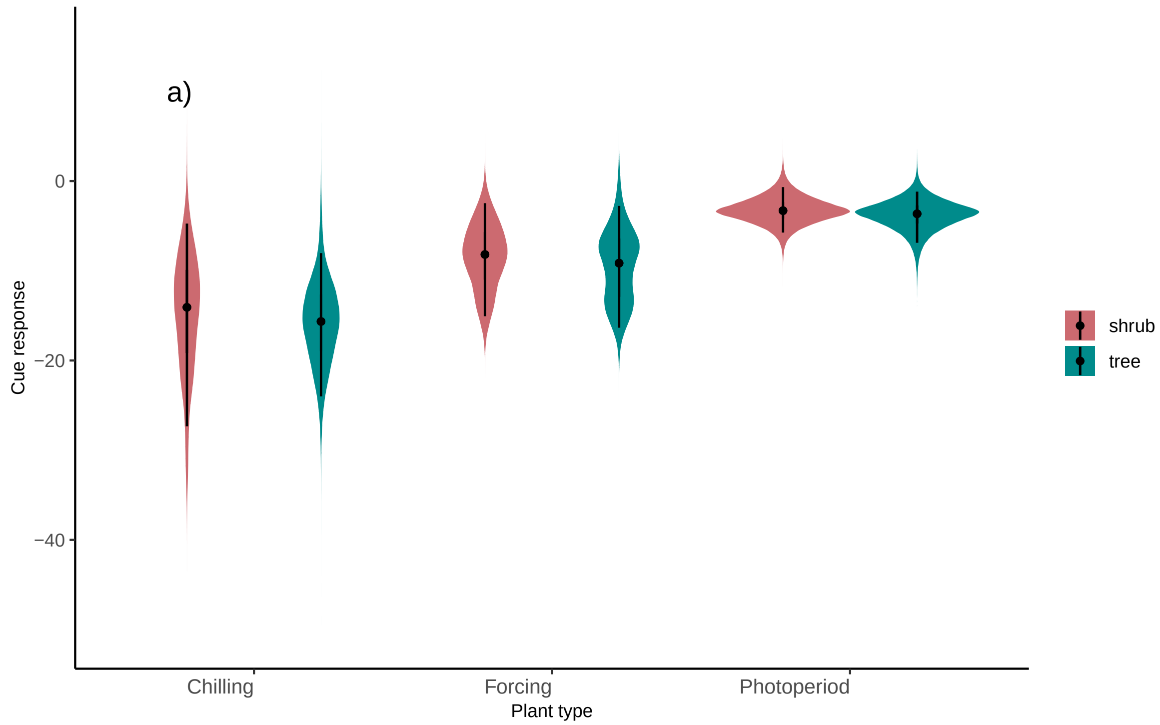

Figure 5: Comparisons of posterior distributions for cues estimates between shrub and tree species. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution is the the posterior density of the posteriors of the cue responses for all species within a given architectural type. The y-axis spans the entire range of the data.

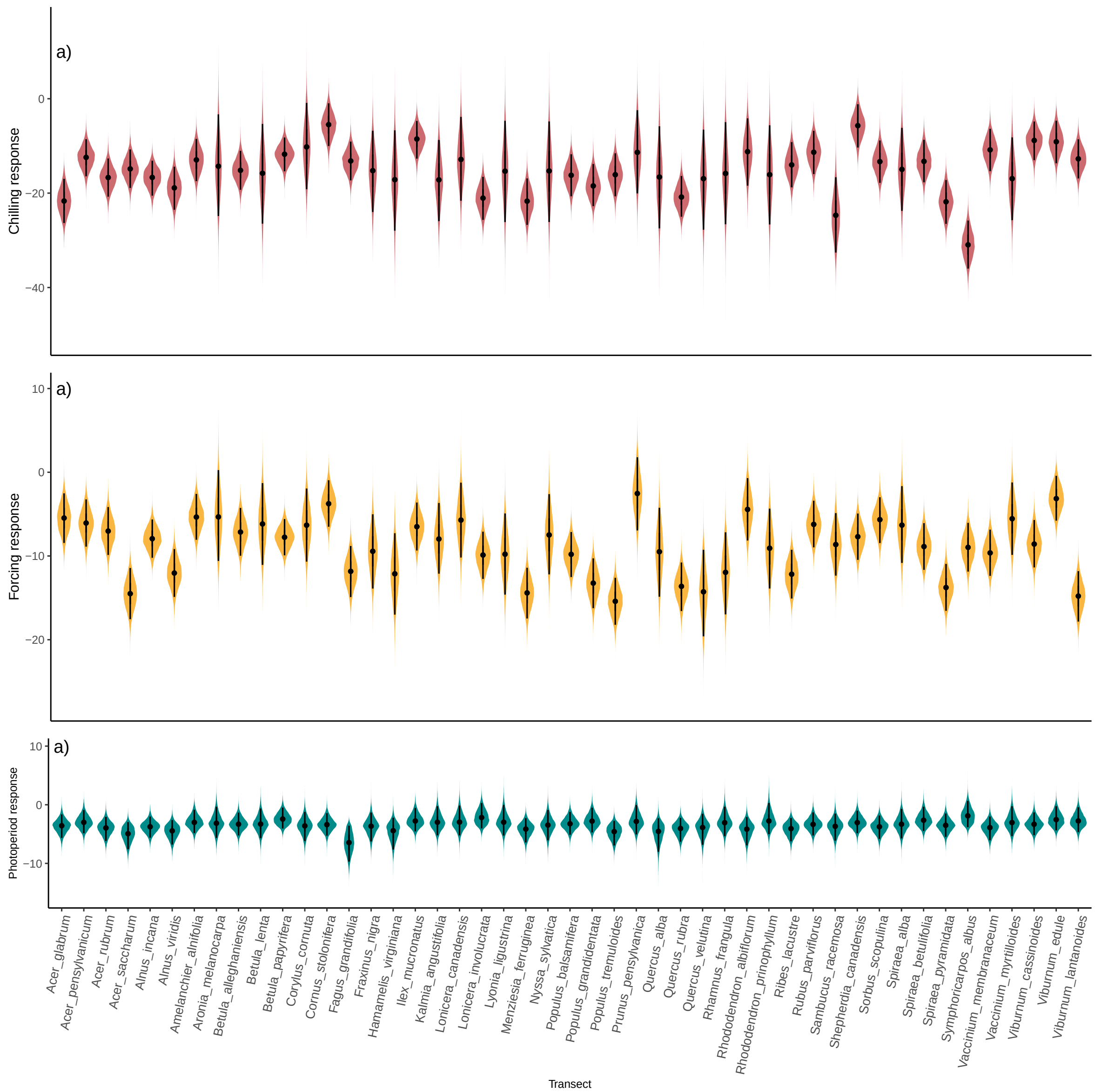

Figure 6: Species differences in cue estimate posterior distributions, comparing species differences across a) chilling, b) forcing, and c) photoperiod cues. The median cue response is illustrated by the black circle, while the 90% quantile interval is illustrated by the black line. The coloured distribution depicts the shape of the posterior density for all samples of a given species.

Figure 7: Species responses to a) warming compared to longer chilling, b) warming compared to longer photoperiods, and c) longer chilling compared to longer photoperiod

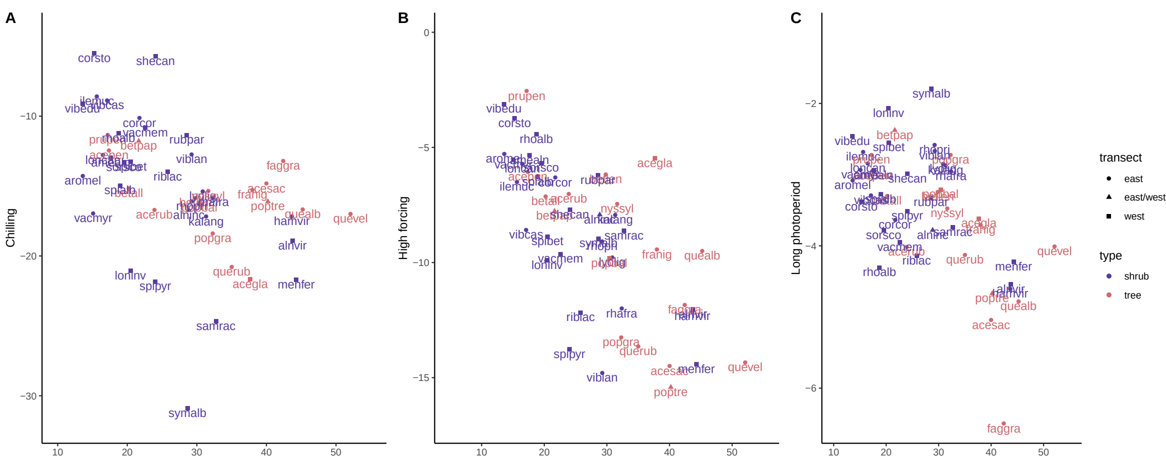

Figure 8: Trends in budburst date in relation to species-level a) chill responses, b) high forcing temperatures, and c) long photoperiod cues

Table 5: Mean budburst dates across all treatments from raw data for 47 species at our two western sites, E.C. Manning Park and Smithers B.C., and our two eastern sites, Harvard Forest (HF) USA and St. Hippolyte (SH) Canada.

Species	Harvard Forest	St. Hippoltye	Manning Park	Smithers
Acer glabrum			36.00	39.00
Acer pensylvanicum	16.00	18.00		
Acer rubrum	22.00	25.00		
Acer saccharum	45.00	36.00		
Alnus incana			28.00	30.00
Alnus incana	33.00	25.00		
Alnus viridis			44.00	43.00
Amelanchier alnifolia			18.00	17.00
Aronia melanocarpa	14.00			
Betula alleghaniensis	20.00	21.00		
Betula lenta	30.00			
Betula papyrifera				30.00
Betula papyrifera	17.00	18.00		
Corylus cornuta	25.00	19.00		
Cornus stolonifera			14.00	16.00
Fagus grandifolia	42.00	43.00		
Fraxinus nigra	38.00	38.00		
Hamamelis virginiana	44.00			
Ilex mucronatus	16.00	15.00		
Kalmia angustifolia	30.00	32.00		
Lonicera canadensis	17.00	16.00		
Lonicera involucrata			22.00	19.00
Lyonia ligustrina	31.00			
Menziesia ferruginea			43.00	46.00
Nyssa sylvatica	32.00			
Populus balsamifera			30.00	31.00
Populus grandidentata	33.00	31.00		
Populus tremuloides			46.00	35.00
Prunus pensylvanica	18.00	16.00		
Quercus alba	45.00			
Quercus rubra	36.00	34.00		
Quercus velutina	52.00			
Rhamnus frangula	32.00			
Rhododendron albiflorum			19.00	
Rhododendron prinophyllum	29.00			
Ribes lacustre			29.00	23.00
Rubus parviflorus			28.00	29.00
Sambucus racemosa			33.00	
Shepherdia canadensis			25.00	23.00
Sorbus scopulina			21.00	18.00
Spiraea alba	18.00	20.00		
Spiraea betulifolia			24.00	18.00
Spiraea pyramidata			26.00	22.00
Symphoricarpos albus			26.00	31.00
Vaccinium membranaceum			22.00	23.00
Vaccinium myrtilloides	13.00	17.00		
Viburnum cassinoides	15.00	18.00		
Viburnum edule			19.00	8.00
Viburnum lantanoides	31.00	28.00		

Table 6: Chill units from our two western sites, E.C. Manning Park and Smithers B.C., and our two eastern sites, Harvard Forest (HF) USA and St. Hippolyte(SH) Canada.

Population	Chilling.treatment	Chilling.Hours	Utah.Model	Chill.Portions
Harvard forest	Field chilling	892	814.50	56.62
Harvard forest	Field chilling + 30 d at 4 degree C	2140	2062.50	94.06
Harvard forest	Field chilling + 30 d at 1.5 degree C	2140	1702.50	91.17
St. Hippoltye	Field chilling	682	599.50	44.63
St. Hippoltye	Field chilling + 30 d at 4 degree C	1930	1847.50	82.06
St. Hippoltye	Field chilling + 30 d at 1.5 degree C	1930	1487.50	79.18
Smithers	Field chilling + 30 d at 4 degree C	1965	2016.00	74.67
Smithers	Field chilling + 70 d at 4 degree C	1317	1368.00	54.95
Manning Park	Field chilling + 30 d at 4 degree C	1861	2025.00	75.33
Manning Park	Field chilling + 70 d at 4 degree C	1213	1377.00	55.09

Table 7: Proportion of samples with budburst per species

Species name	Proportion budburst	Plant type
Acer glabrum	0.83	tree
Alnus incana	1.00	shrub
Alnus viridis	0.92	shrub
Amelanchier alnifolia	0.99	shrub
Betula papyrifera	1.00	tree
Cornus stolonifera	0.99	shrub
Lonicera involucrata	0.87	shrub
Menziesia ferruginea	0.80	shrub
Populus balsamifera	0.98	tree
Populus tremuloides	0.90	tree
Rhododendron albiflorum	1.00	shrub
Ribes lacustre	0.82	shrub
Rubus parviflorus	0.94	shrub
Sambucus racemosa	0.95	shrub
Shepherdia canadensis	1.00	shrub
Sorbus scopulina	0.99	shrub
Spiraea betulifolia	0.94	shrub
Spiraea pyramidata	0.92	shrub
Symphoricarpos albus	0.84	shrub
Vaccinium membranaceum	0.90	shrub
Viburnum edule	1.00	shrub