Cue responses in woody plants of North America

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

October 20, 2022

[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

1 Research questions:

1. How do species in deciduous forests across North America respond to varying chilling, forcing, and photoperiod cues?
2. Do we see similar trends when we compare species eastern deciduous forests to western deciduous forests communities?
3. How do shrub species differ from tree species in their cue use?

2 Results

1. General Survival and germination success from the western transect experiment
   (a) Of the 2285 samples that went into chilling, 2458 survived the duration of the experiment, with only 7% 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 full model, estimates for the forcing x photoperiod interactions is considerably different, while the estimates and interactions for Manning Park, and the interaction with Manning Park and both chilling and photoperiod are considerably different.
2. General findings...
   (a) Species cue responses were strongly phylogenetically structured (with a lambda 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 the two eastern sites and between chilling and the two eastern sites.
   (e) As illustrated for our St. Hippolyte site in Fig. 2 b and c), eastern sites has weaker responses to forcing and chilling cues, budbursting earlier than western species in response to both cues.
   (f) 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 (Fig. 2 d).
   (g) While there are some differences across sites, they are weak when site effects are accounted for (Fig. **??**)
   (h) We also did not observe differences across different plant architectures (Fig. **??**)

3. We found different trends in cue use when comparing the timing of first lateral budburst and 50% lateral budburst for our western species.
   (a) In comparison to our model of the timing of first budburst, the timing of lateral budburst had stronger responses to chilling, with 50% lateral budburst having almost equivalent responses to forcing and chilling.
   (b) However, lateral budburst also experienced a strong interaction between forcing and chilling cues as well as between forcing and photoperiod for the timing of the fist lateral budburst.
   (c) Our more southern site in our western transect, Manning Park, showed delayed budburst relative to our more northern Smithers sites.
   (d) While we do observe weak interactions between photoperiod and Manning Park and chilling and Manning park, a strong advancing interactions occurred between forcing and Manning Park.

4. 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 imporatnce of each cue, with thier own unique temporal niche.
   (b) Weak trends for each cue, with later budburst in species with stronger responses to high chilling, forcong and photoperiod cues (8) - This should be tested quantitiatively
   (c) understory species, such as Corsto had both weak chilling and forcing cues, while tree speces such as quevel had stroner chilling and forcing cues as well as photoperiod
   (d) faggra ahd the strongest photoperiod response, but surprisingly symalb (a shrub had the strongest chilling response).

3 Tables and figures

4 Supplementary Material

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
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

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
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

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
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, speices 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
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

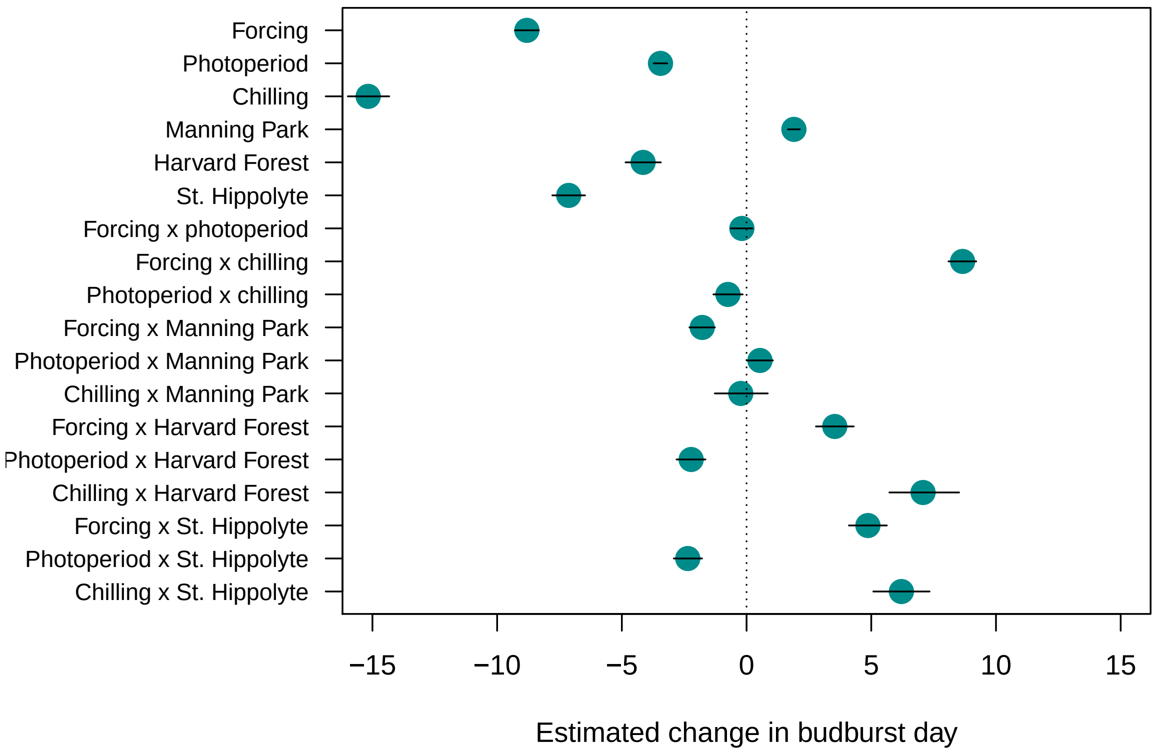

Figure 1: Estimated mean responses in budburst date of first bud to varying forcing, chilling, and photoperiod cues for 47 deciduous woody species across North America. Points represent mean budburst dates, while bars depict the 50% uncertainty interval. Negative responses represent advances budburst,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

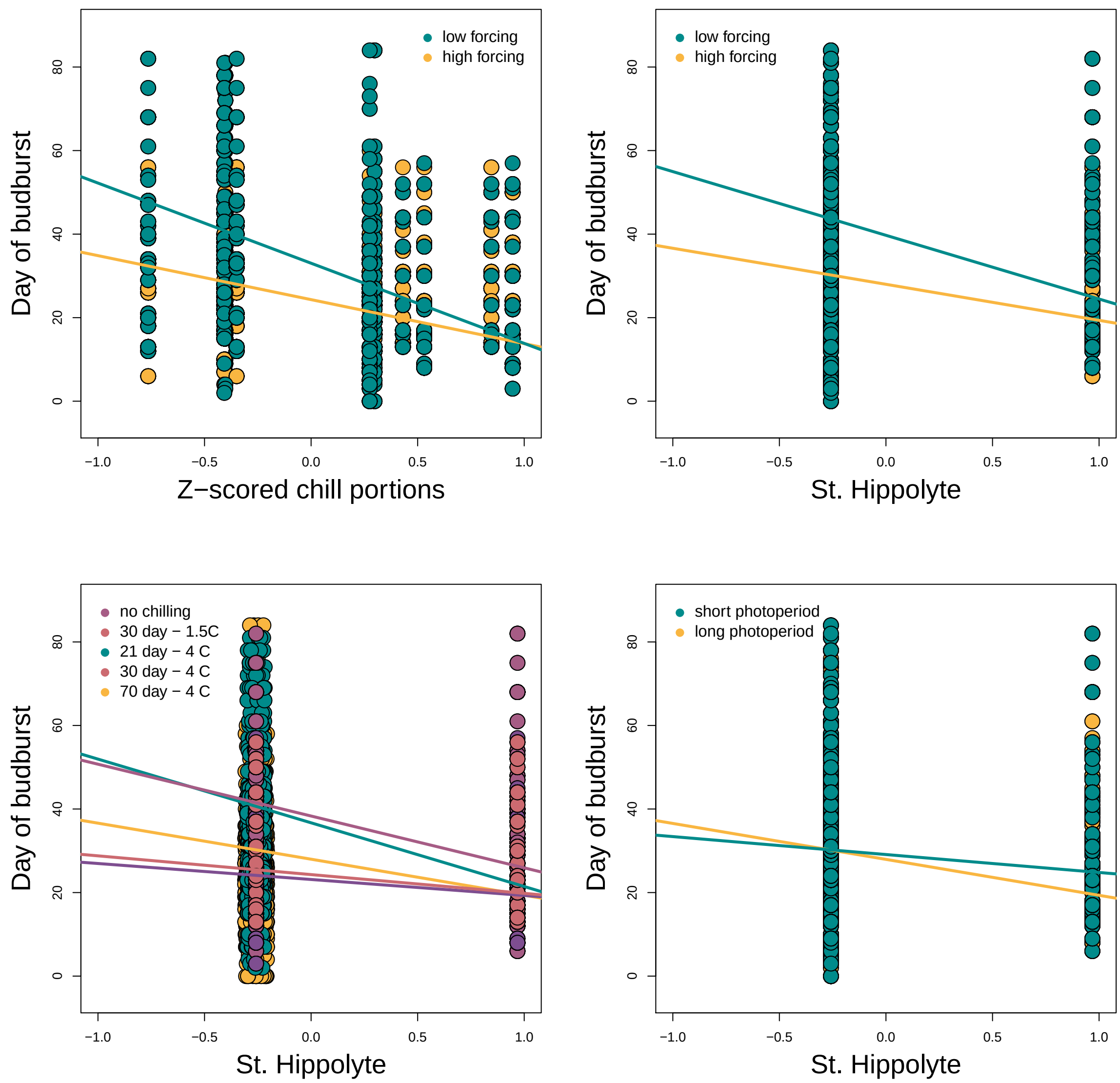

Figure 2: Interaction plots of day of budburst of first bud in response a) chill portions and forcing, b) forcing cues for species sampled from St. Hippolyte, c) chilling cues for species sampled from St. Hippolyte, and d) photoperiod cues and species sampled from St. Hippolyte.

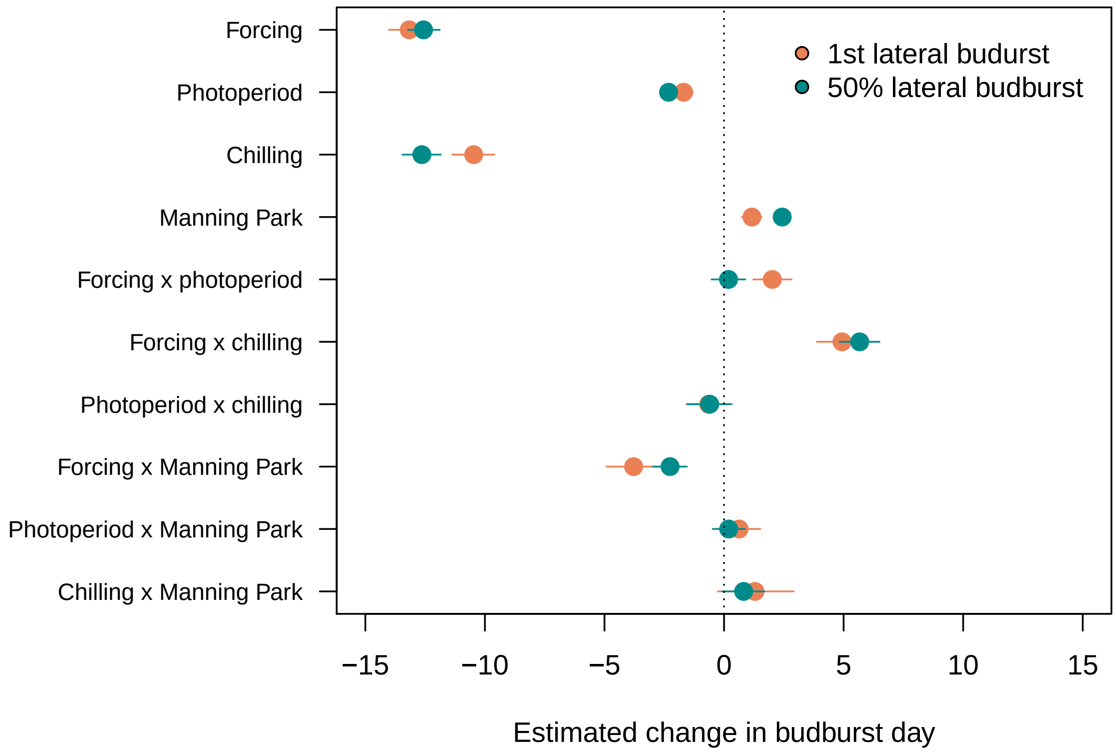

Figure 3: Estimated mean responses in lateral budburst date to varying environmental cues for 21 deciduous woody species in British Columbia. Points represent mean budburst dates, while bars depict the 50% uncertainty interval. Negative responses represent advances budburst, while positive values represent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

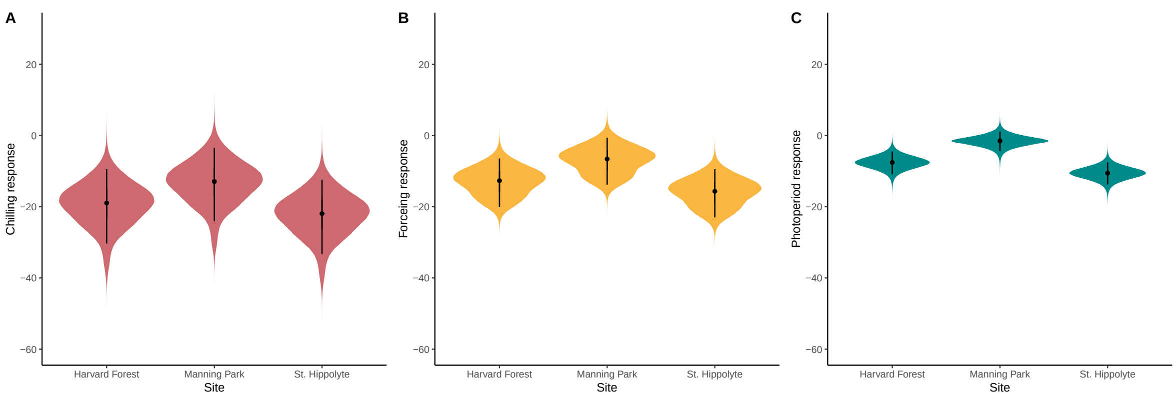

Figure 4: Posterior distributions of estimated cue responses with site level effects for individual sites, depicting a) chilling, b) forcing, and c) photoperiod cue responses. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution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

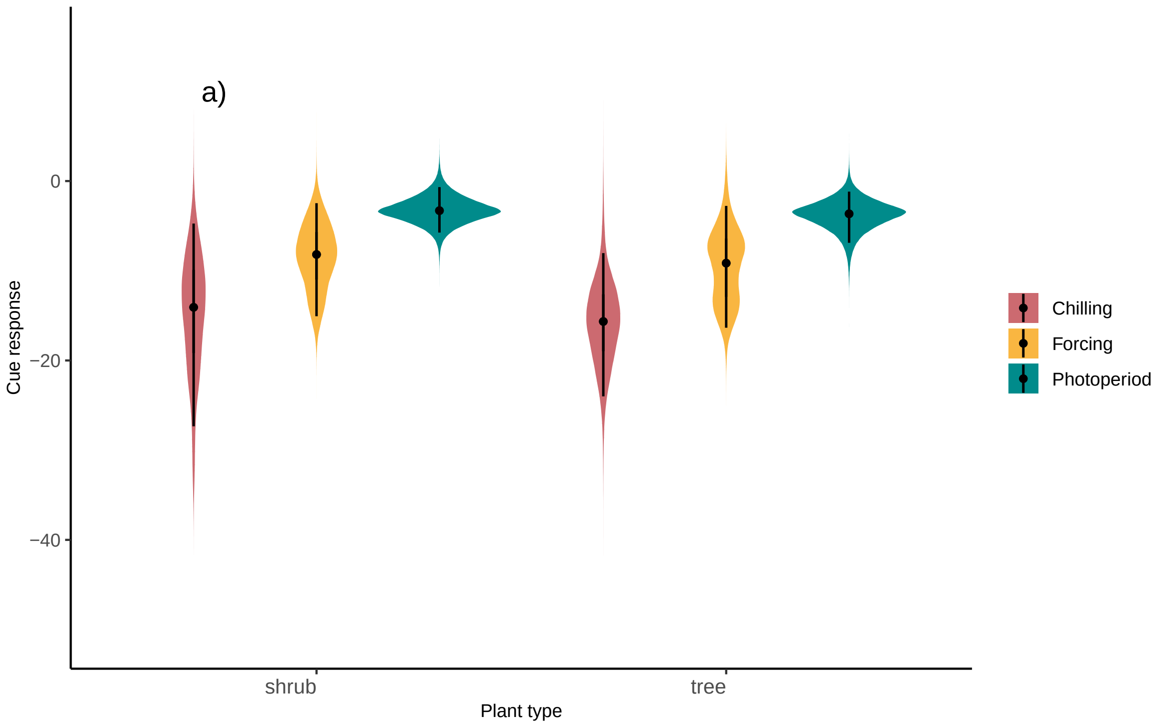

Figure 5: Comparisons of posterior distributions for cues estimates between shrub and tree species. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution is the the posterior density of the posteriors of the cue responses for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

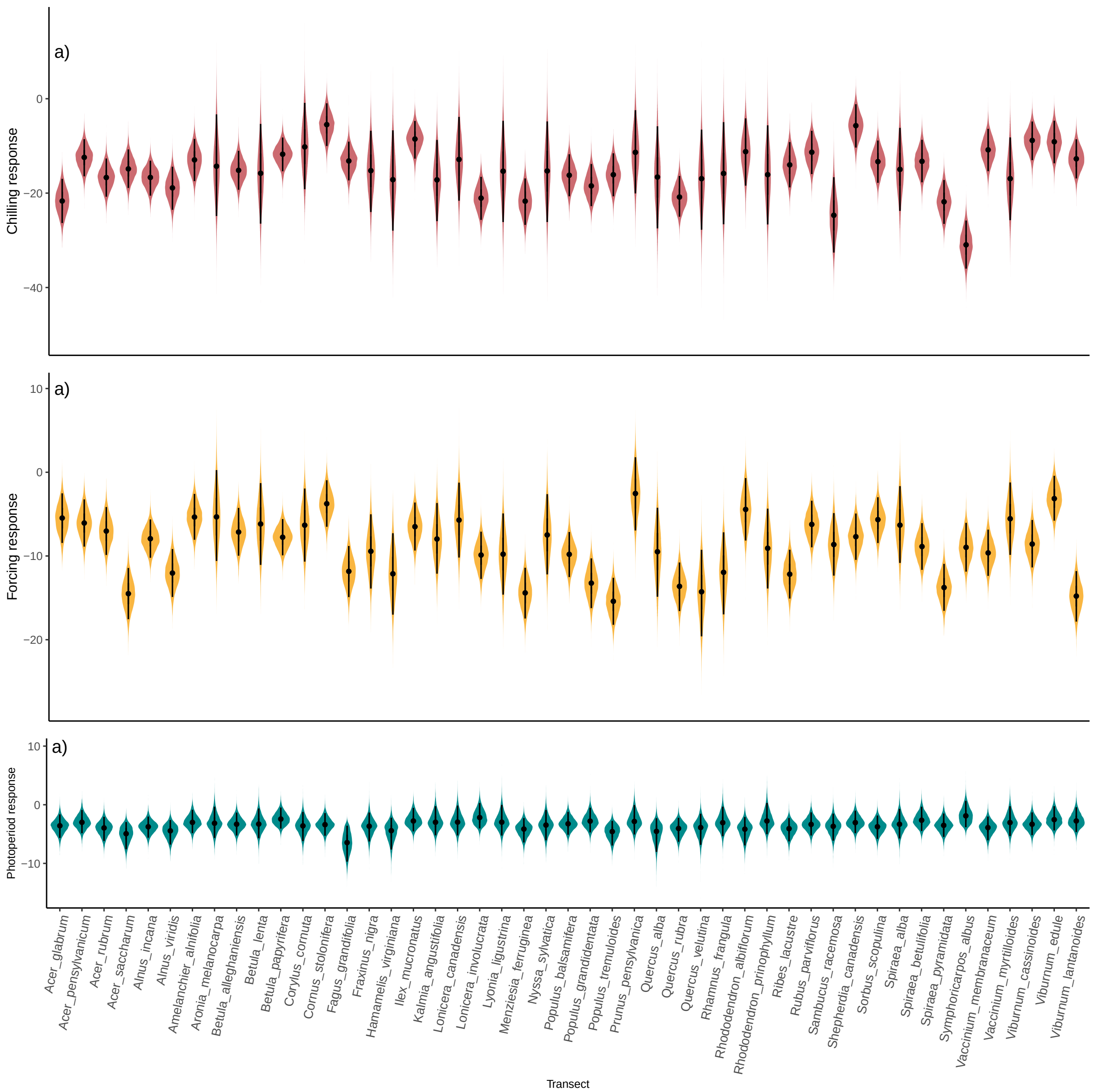

Figure 6: Species differences in cue estimate posterior distributions, comparing species differences across a) chilling, b) forcing, and c) photoperiod cues. The median cue response is illustrated by the black circle, while the 90% quantile interval is illustrated by the black line. The coloured distribution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

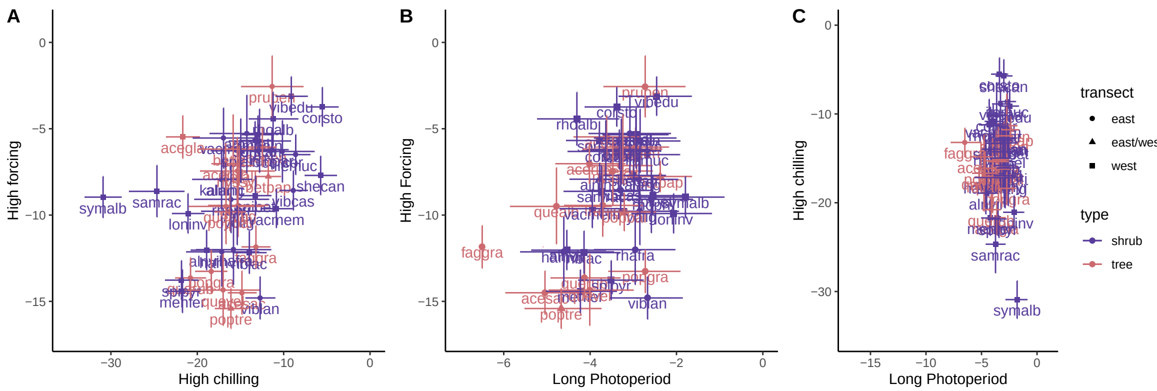

Figure 7: Species responses to a) warming compared to longer chilling, b) warming compared to longer photoperiods, and c) longer chilling compared to longer photoperiod

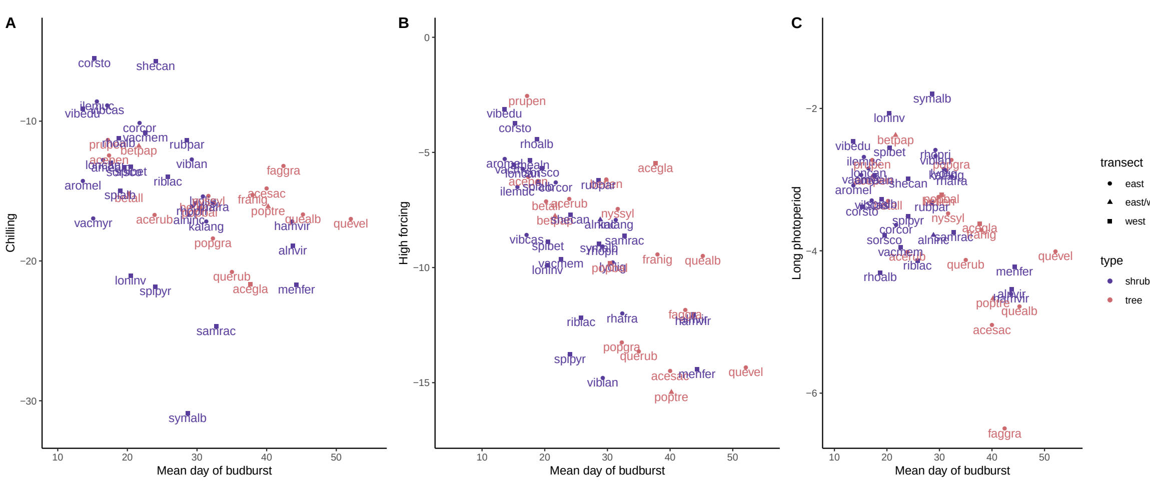

Figure 8: Trends in budburst date in relation to species-level a) chill responses, b) high forcing temperatures, and c) long photoperiod cues

Table 5: Mean budburst dates across all treatments from raw data for 47 species at our two western sites, E.C. Manning Park and Smither 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: Proporation 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