

Species differences in cue responses in woody plants of North America

Deirdre Loughnan¹ and E M Wolkovich¹

December 5, 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

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?

0.1 Results + figures

1. General findings...

- (a) Species budburst was strongly phylogenetically structured (with a λ of
- (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 important 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

2 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
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

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

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

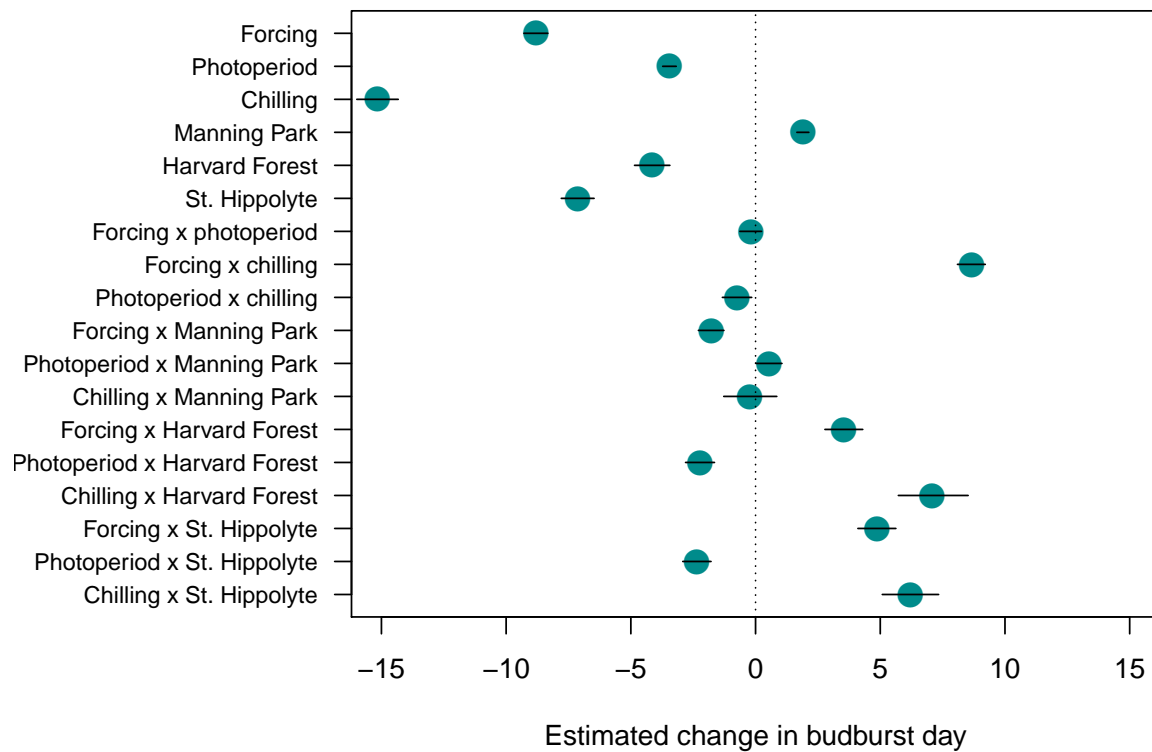


Figure 1: Estimated mean responses in budburst date of first bud to varying forcing, chilling, and photoperiod cues for 47 deciduous woody species across North America. Points represent mean budburst dates, while bars depict the 50% uncertainty interval. Negative responses represent advances budburst,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

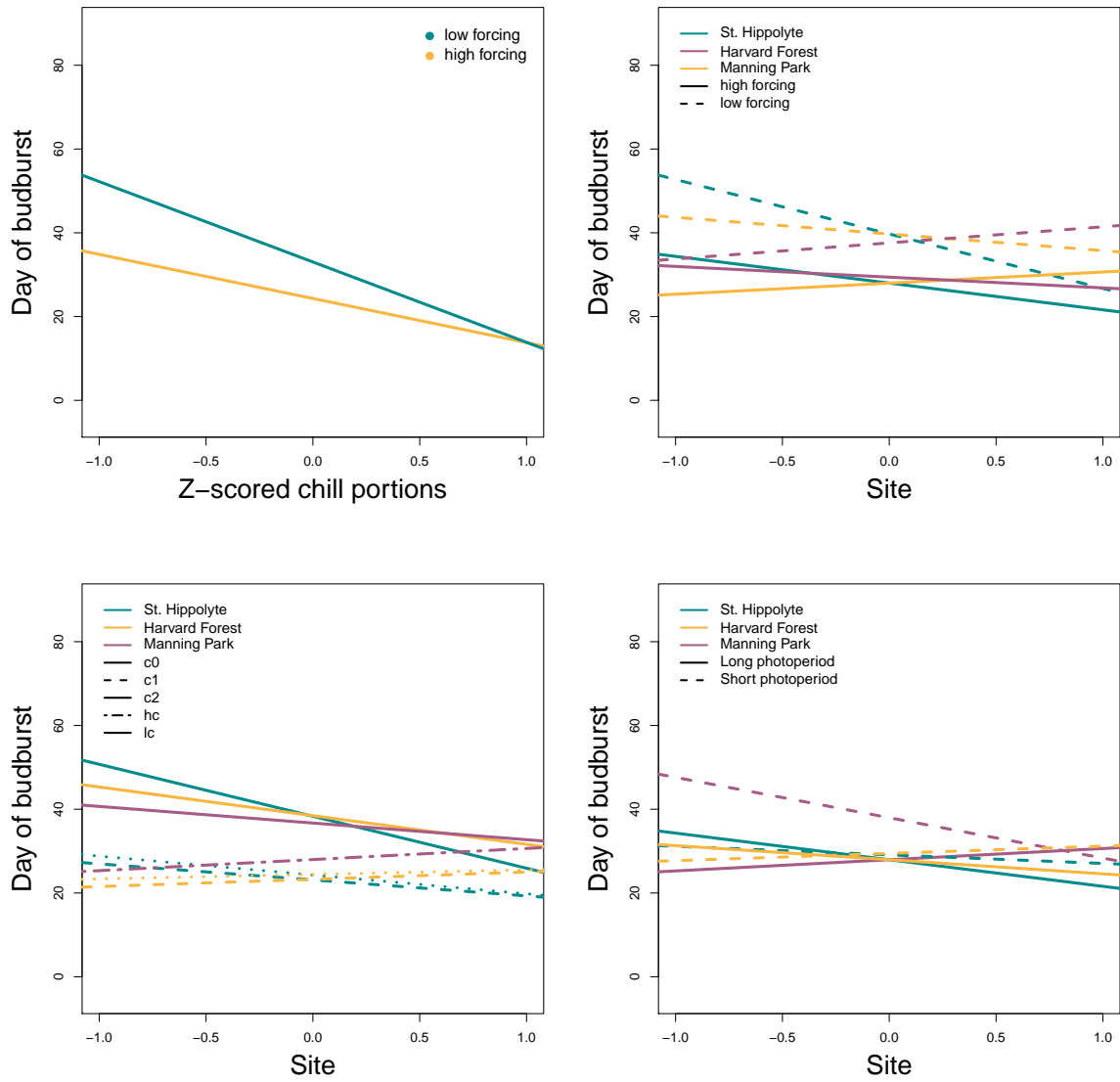


Figure 2: Interaction plots of day of budburst of first bud in response a) chill portions and forcing, b) forcing cues, c) chilling cues, and d) photoperiod cues and species sampled from St. Hippolyte, Harvard Forest, and Manning park.

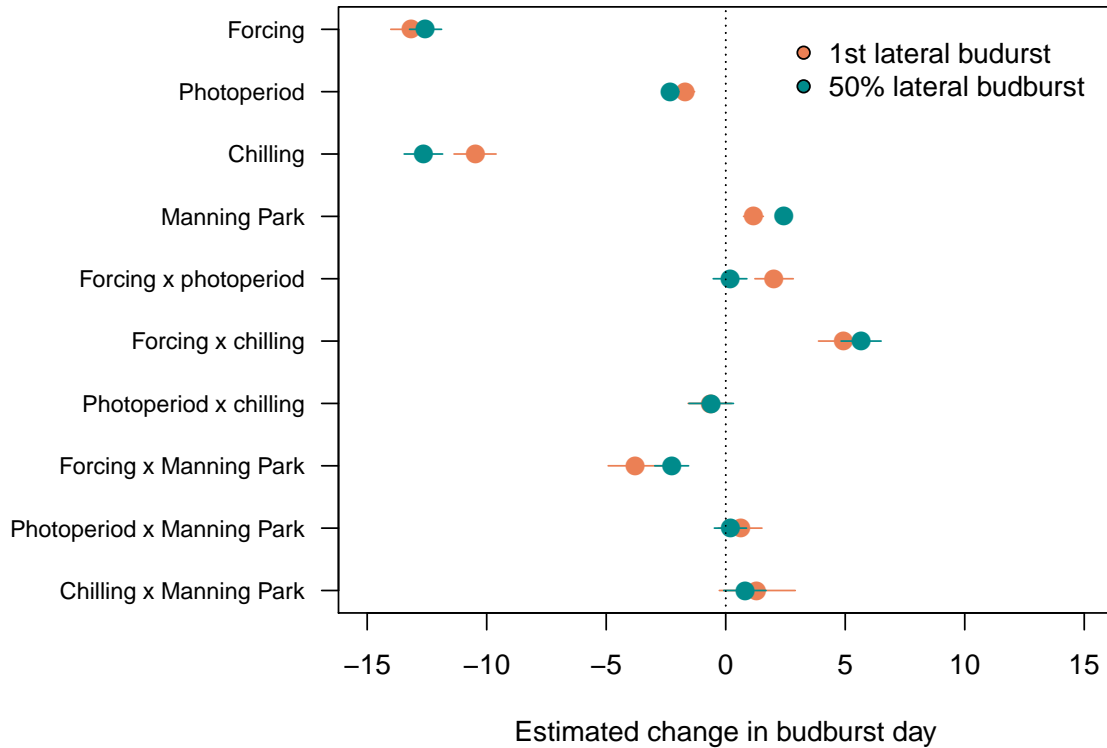


Figure 3: Estimated mean responses in lateral budburst date to varying environmental cues for 21 deciduous woody species in British Columbia. Points represent mean budburst dates, while bars depict the 50% uncertainty interval. Negative responses represent advances budburst, while positive values represent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

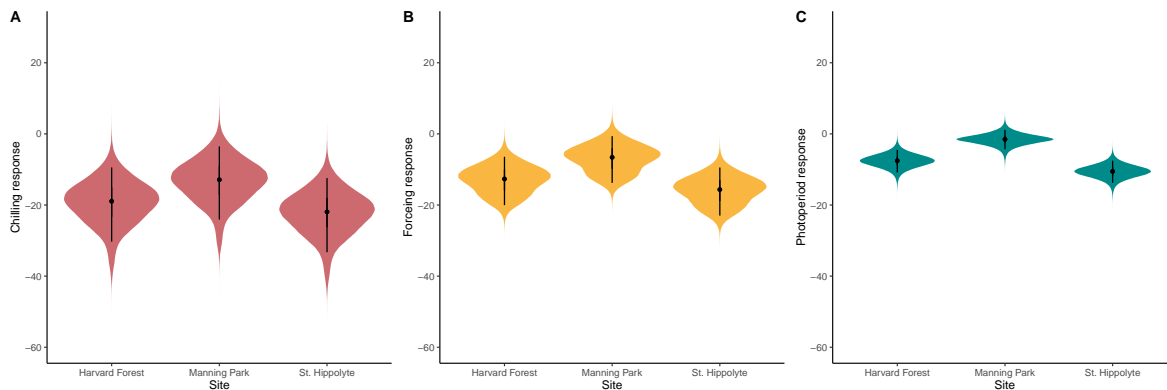


Figure 4: Posterior distributions of estimated cue responses with site level effects for individual sites, depicting a) chilling, b) forcing, and c) photoperiod cue responses. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution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

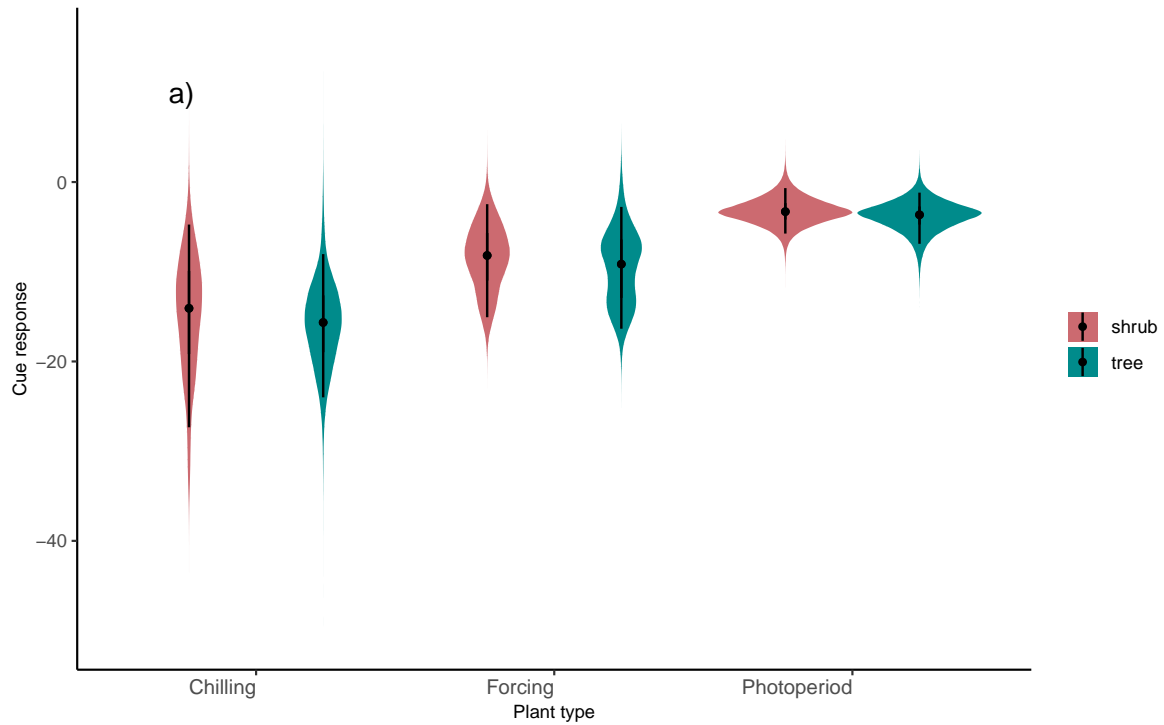


Figure 5: Comparisons of posterior distributions for cues estimates between shrub and tree species. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution is the the posterior density of the posteriors of the cue responses for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

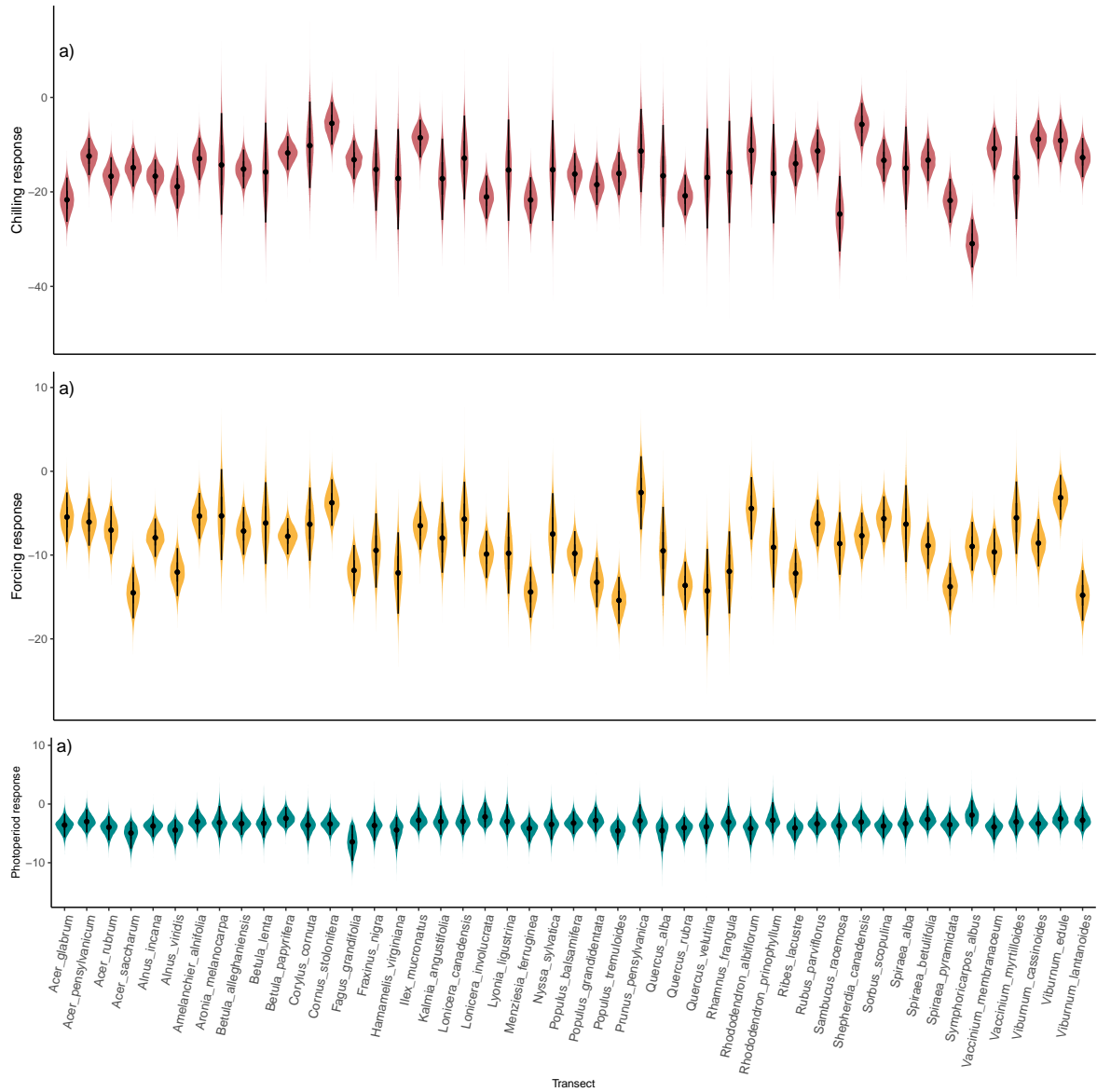


Figure 6: Species differences in cue estimate posterior distributions, comparing species differences across a) chilling, b) forcing, and c) photoperiod cues. The median cue response is illustrated by the black circle, while the 90% quantile interval is illustrated by the black line. The coloured distribution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

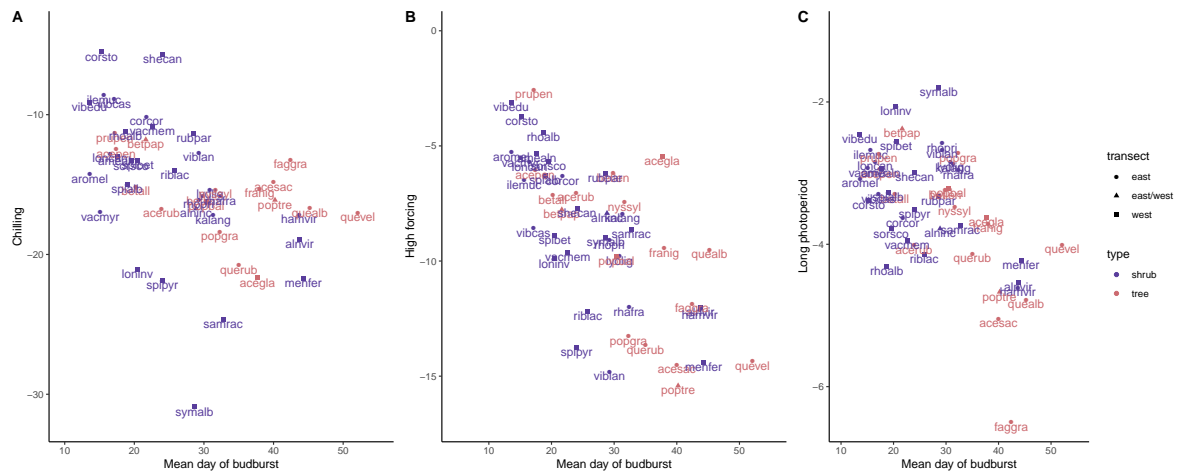


Figure 8: Trends in budburst date in relation to species-level a) chill responses, b) high forcing temperatures, and c) long photoperiod cues

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. Hippolyte	Manning Park	Smithers
<i>Acer glabrum</i>			36.00	39.00
<i>Acer pensylvanicum</i>	16.00	18.00		
<i>Acer rubrum</i>	22.00	25.00		
<i>Acer saccharum</i>	45.00	36.00		
<i>Alnus incana</i>			28.00	30.00
<i>Alnus incana</i>	33.00	25.00		
<i>Alnus viridis</i>			44.00	43.00
<i>Amelanchier alnifolia</i>			18.00	17.00
<i>Aronia melanocarpa</i>	14.00			
<i>Betula alleghaniensis</i>	20.00	21.00		
<i>Betula lenta</i>	30.00			
<i>Betula papyrifera</i>				30.00
<i>Betula papyrifera</i>	17.00	18.00		
<i>Corylus cornuta</i>	25.00	19.00		
<i>Cornus stolonifera</i>			14.00	16.00
<i>Fagus grandifolia</i>	42.00	43.00		
<i>Fraxinus nigra</i>	38.00	38.00		
<i>Hamamelis virginiana</i>	44.00			
<i>Ilex mucronatus</i>	16.00	15.00		
<i>Kalmia angustifolia</i>	30.00	32.00		
<i>Lonicera canadensis</i>	17.00	16.00		
<i>Lonicera involucrata</i>			22.00	19.00
<i>Lyonia ligustrina</i>	31.00			
<i>Menziesia ferruginea</i>			43.00	46.00
<i>Nyssa sylvatica</i>	32.00			
<i>Populus balsamifera</i>			30.00	31.00
<i>Populus grandidentata</i>	33.00	31.00		
<i>Populus tremuloides</i>			46.00	35.00
<i>Prunus pensylvanica</i>	18.00	16.00		
<i>Quercus alba</i>	45.00			
<i>Quercus rubra</i>	36.00	34.00		
<i>Quercus velutina</i>	52.00			
<i>Rhamnus frangula</i>	32.00			
<i>Rhododendron albiflorum</i>			19.00	
<i>Rhododendron prinophyllum</i>	29.00			
<i>Ribes lacustre</i>			29.00	23.00
<i>Rubus parviflorus</i>			28.00	29.00
<i>Sambucus racemosa</i>			33.00	
<i>Shepherdia canadensis</i>			25.00	23.00
<i>Sorbus scopulina</i>			21.00	18.00
<i>Spiraea alba</i>	18.00	20.00		
<i>Spiraea betulifolia</i>			24.00	18.00
<i>Spiraea pyramidata</i>			26.00	22.00
<i>Symphoricarpos albus</i>			26.00	31.00
<i>Vaccinium membranaceum</i>			22.00	23.00
<i>Vaccinium myrtilloides</i>	13.00	17.00		
<i>Viburnum cassinoides</i>	15.00	18.00		
<i>Viburnum edule</i>			19.00	8.00
<i>Viburnum lantanoides</i>	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. Hippolyte	Field chilling	682	599.50	44.63
St. Hippolyte	Field chilling + 30 d at 4 degree C	1930	1847.50	82.06
St. Hippolyte	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