# Cue responses in woody plants of North America

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October 20, 2022

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## 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 the model with all species, estimates are considerably differetn 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. 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 more (Fig. 2 d).

(g) While there are some differences across cue responses across sites, they are weak when site effects are accounted for (Fig. 4)

(h) We also did not observe differences across different plant architectures, with both shrubs and trees having very similar cue responses (Fig. **??**)

3. We found different trends in cue responses 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) Budburst was delayed for the Manning Park community, budbursting later than those sampled in Smithers b.C..

(d) Lateral budburst dates also show weak interactions between photoperiod and Manning Park and chilling and Manning park, but a strong advancing interactions 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, 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 ues, with *Fagus grandifolia* having the strongest photoperiod response, but surprisingly the shrub *Symphoricarpos alba* 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 |

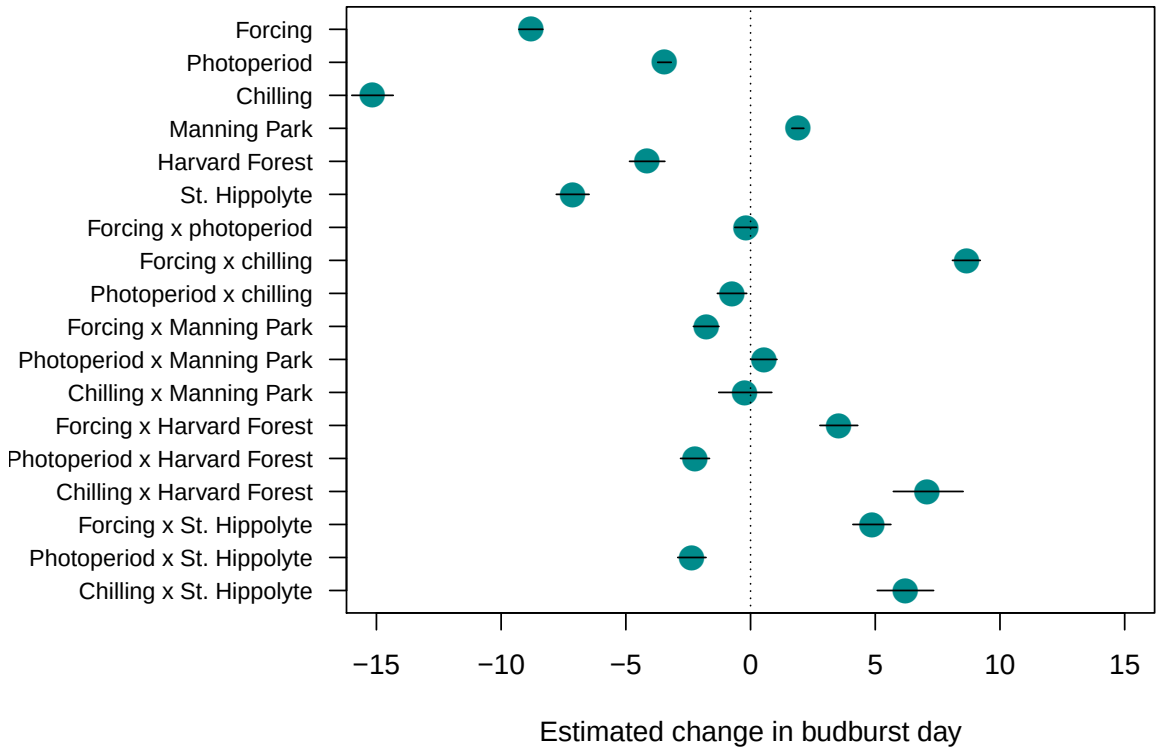


Figure 1: Estimated mean responses in budburst date of first bud to varying forcing, chilling, and photoperiod cues for 47 deciduous woody species across North America. Points represent mean budburst dates, while bars depict the 50% uncertainty interval. Negative responses represent advances budburst,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

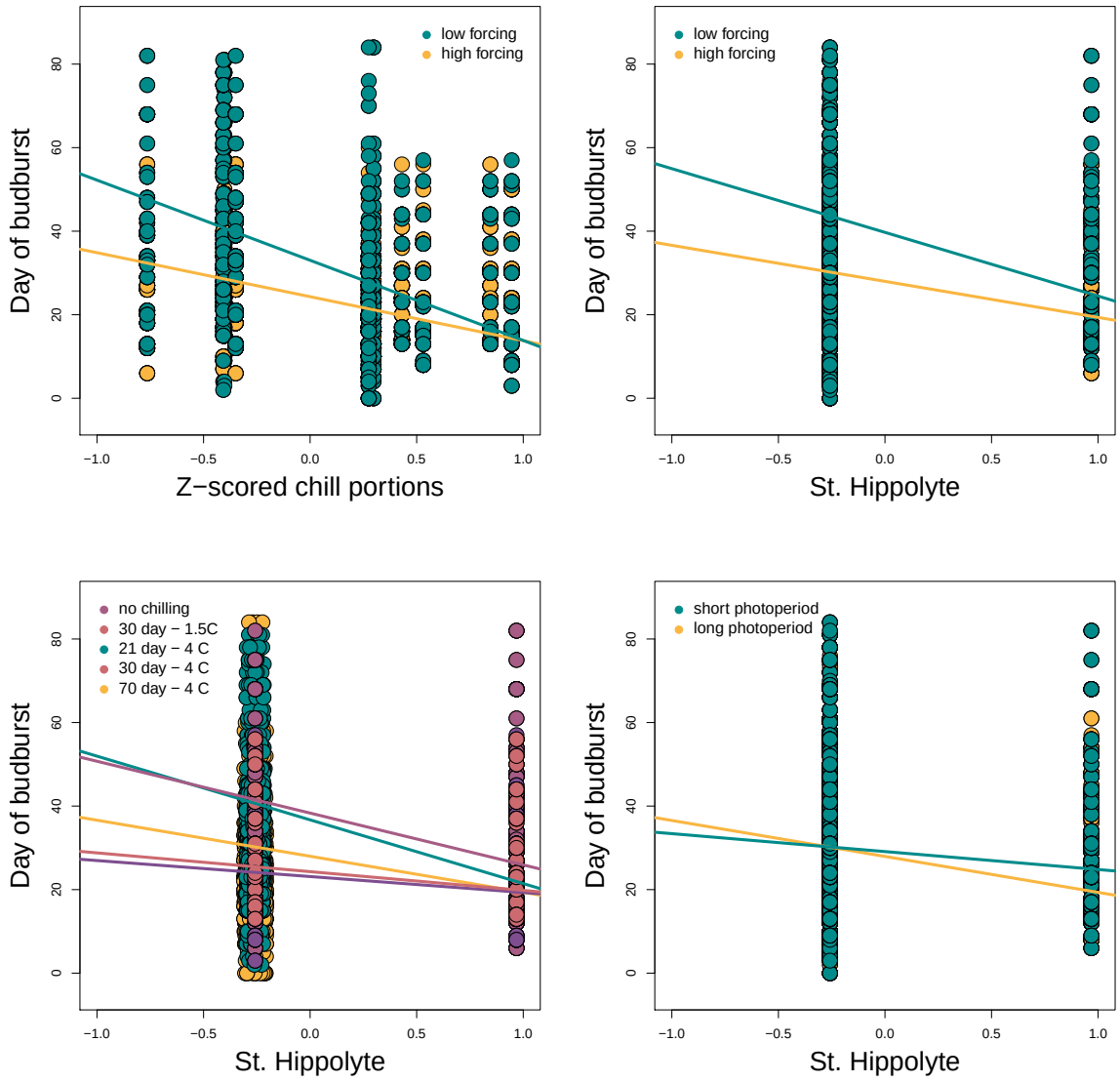


Figure 2: Interaction plots of day of budburst of first bud in response a) chill portions and forcing, b) forcing cues for species sampled from St. Hippolyte, c) chilling cues for species sampled from St. Hippolyte, and d) photoperiod cues and species sampled from St. Hippolyte.

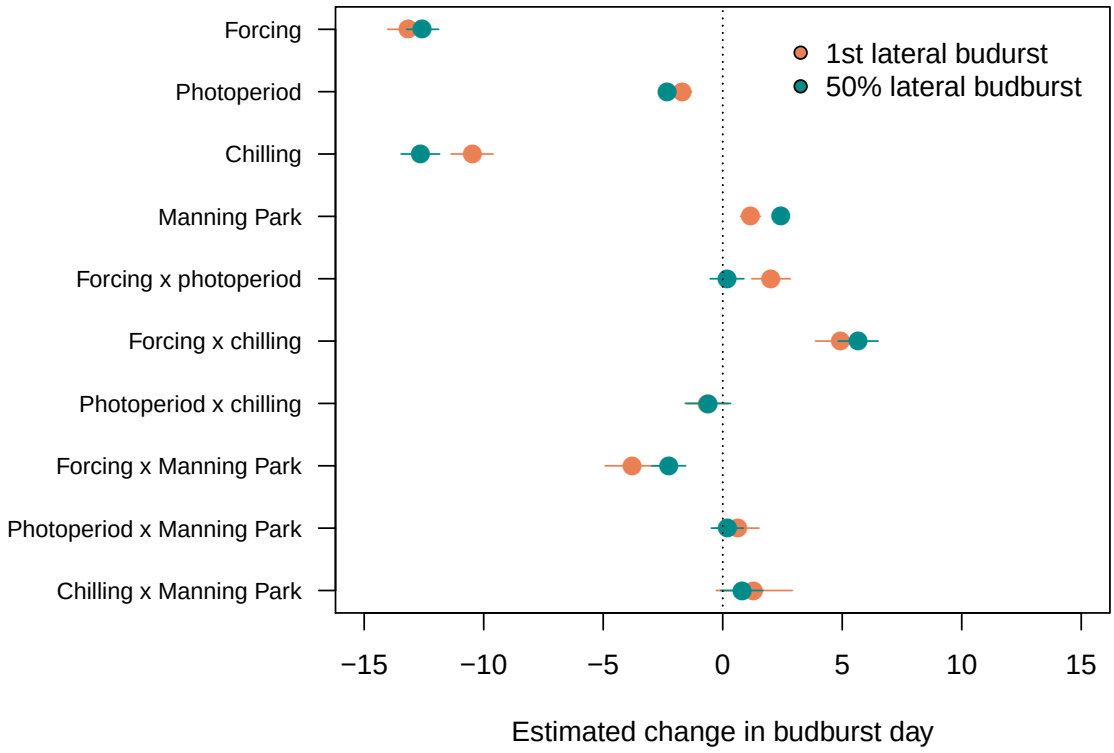


Figure 3: Estimated mean responses in lateral budburst date to varying environmental cues for 21 deciduous woody species in British Columbia. Points represent mean budburst dates, while bars depict the 50% uncertainty interval. Negative responses represent advances budburst, while positive values represent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

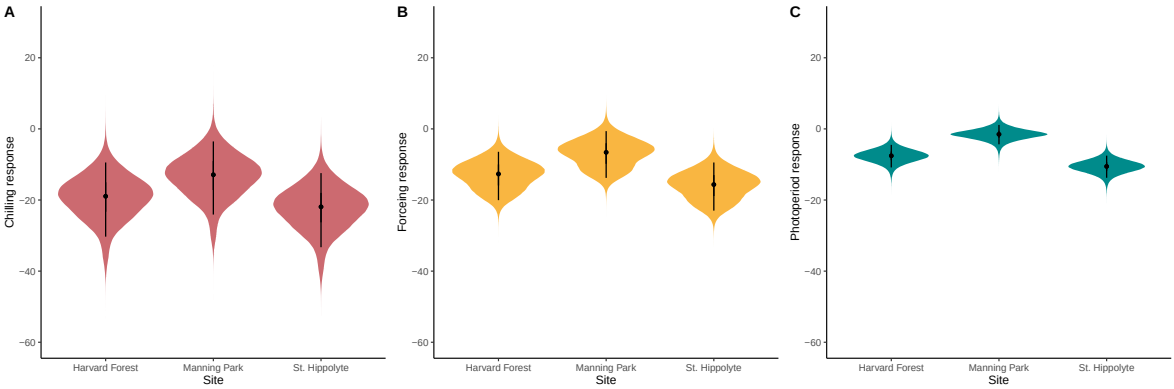


Figure 4: Posterior distributions of estimated cue responses with site level effects for individual sites, depicting a) chilling, b) forcing, and c) photoperiod cue responses. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution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

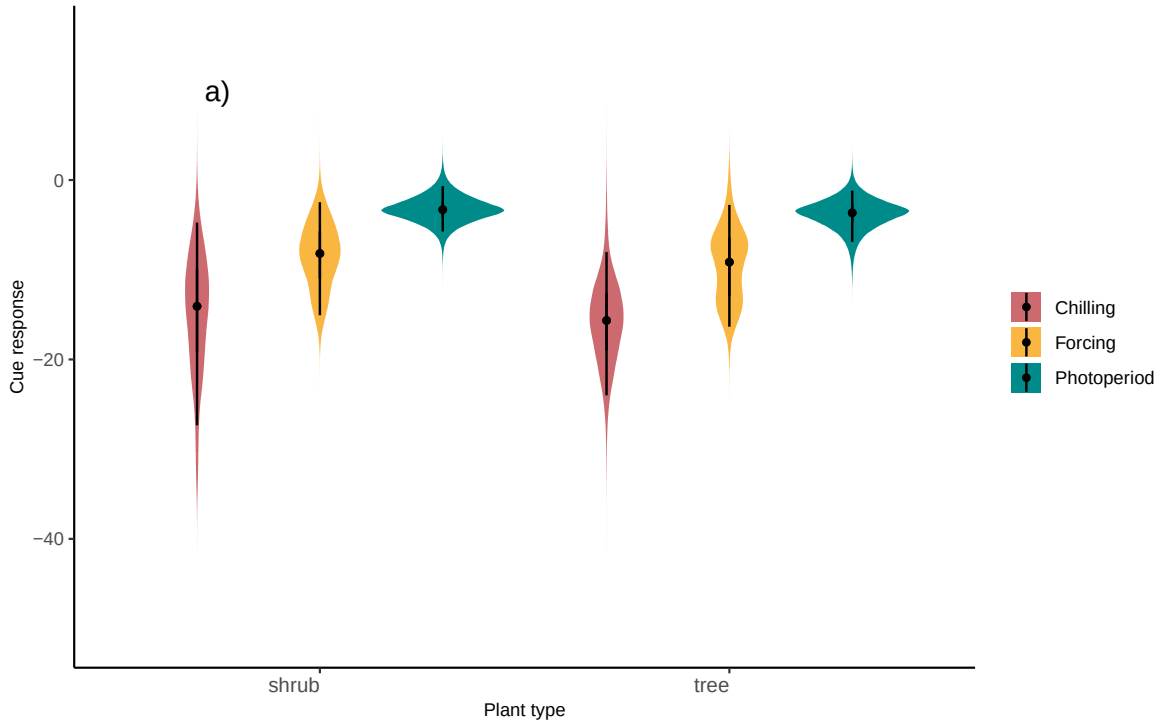


Figure 5: Comparisons of posterior distributions for cues estimates between shrub and tree species. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution is the the posterior density of the posteriors of the cue responses for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

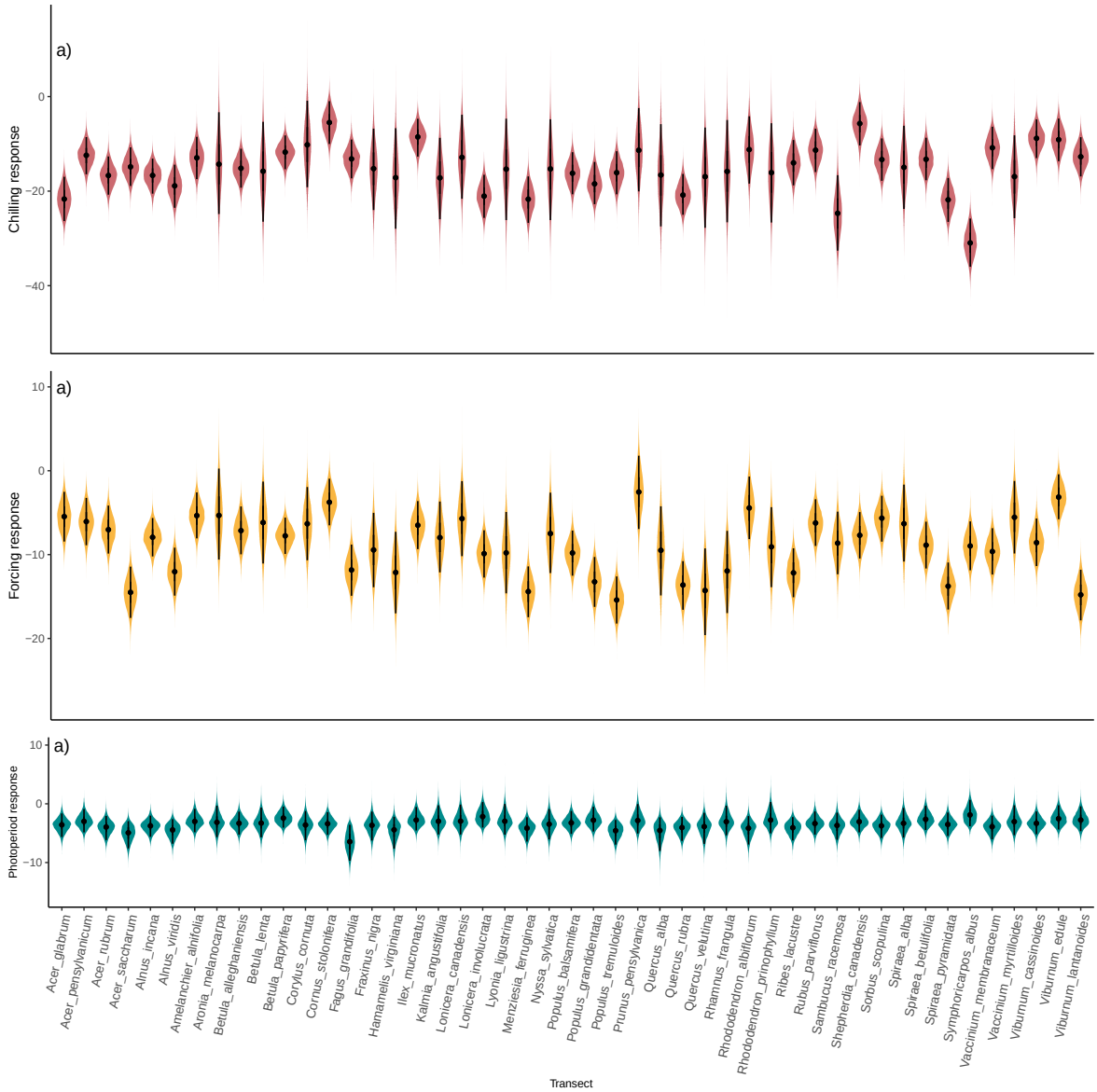


Figure 6: Species differences in cue estimate posterior distributions, comparing species differences across a) chilling, b) forcing, and c) photoperiod cues. The median cue response is illustrated by the black circle, while the 90% quantile interval is illustrated by the black line. The coloured distribution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

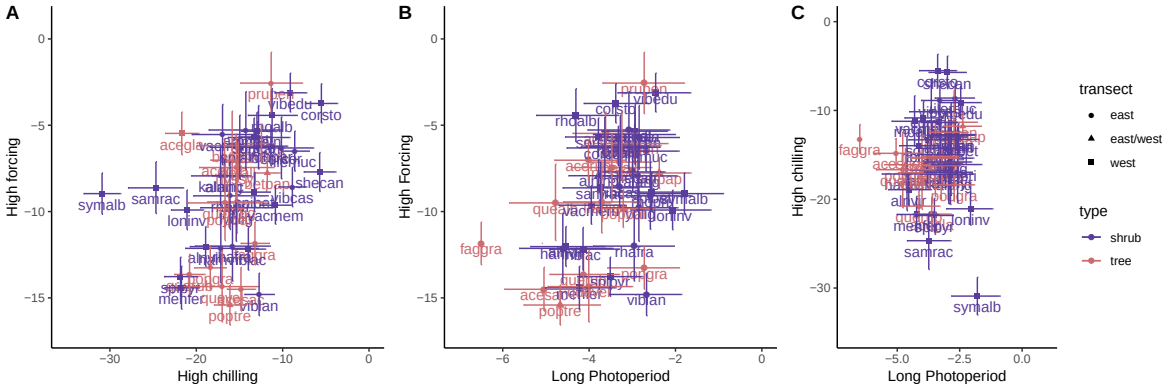


Figure 7: Species responses to a) warming compared to longer chilling, b) warming compared to longer photoperiods, and c) longer chilling compared to longer photoperiod

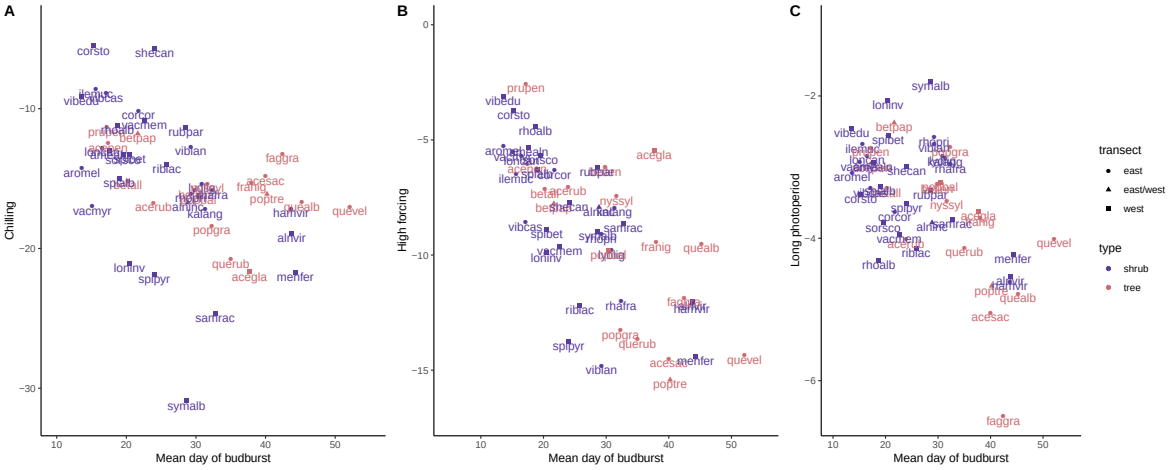


Figure 8: Trends in budburst date in relation to species-level a) chill responses, b) high forcing temperatures, and c) long photoperiod cues

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 |