

Introduction

Shifts in phenology, or the annual timing of life cycle events, is a well documented organismic response to anthropogenically induced global change. As the effects of global change become more pronounced in the coming decades, it is likely that many of the temporal patterns of ecological communities, long considered to be relatively fixed in order, will become uncoupled. Take for example, the phenophases of early spring, budburst, leaf expansion, and flowering. We understand that individual species in a given plant community occupy their own temporal niche, and while the absolute timing of phenophases with relation to the gregorian calendar may shift depending on seasonal conditions, the relative timing of phenophases between species tend to follow fixed patterns— for example, the leaves of maple trees (*Acer spp.*) consistently emerging before the walnuts (*Juglans spp.*). However, recent studies have established that the phenology of individual species is dictated by different combinations of environmental cues, most significantly winter chilling temperatures, spring warming temperatures, and photoperiod. As winter and spring temperatures rise in the coming decades, it is likely that the reliable patterns of spring may be altered, resulting in a loss of many species interaction and the genesis of other, novel ones.

Pattern shifts are not only likely at the community level, but it is also conceivable that climate change may effect the internal temporal patterns of individuals as well. The flowering and leafout phenophases of temperate woody plants show relatively fixed order, with some species consistently flowering before leafout, and others producing leaves before flowers. While floral and foliate phenophases may appear to be disparate, and have long been treated as such in the study of phenology, the temporal ordering and offset between them, may confer a unique fitness advantage upon the species. For example, it is widely believed that many canopy trees in temperate regions flower before leafing out to maximize the efficiency of anemophilous pollination due increased windflow and minimal obstructions to pollen transfer associated with open canopy conditions. The floral-leaf ordering of plants species are describe by life history trait classifications of proteranthly (flowers before leaves), synanthly (leaves and flowers together), and seranthly (flowers after leaves). Will these traits remain fixed as climate conditions change? These internal relationships between floral and foliate phenophases, have been poorly studied, but must be better understood to better understand and predict the demographics and composition of forest communities in an era of climate change.

At its core, the afore mentioned question hinged on another one: are individuals responding to the same environmental cues to initiate their floral and foliate phenophases? The following section briefly describes a preliminary study addressing this questions, and highlights the importance of continuing this work.

Pilot Study

Using data generated in the Wolkovich lab (experimental methods will be explained in a later document), I compared the leafout and flowering phenology for cuttings of three temperate, woody shrubs in a growth chamber experiment, where cutting were exposed to combinations of warm and cool forcing temperatures and short and long photoperiod.

As can be seen in the following figure, it appears that the floral and foliate phenophases were indeed dependent on differing environmental cues.

Using multiway ANOVA, I determined the photoperiod and forcing temperature treatment effects on flowering and leafout for each species. I then determined the temperature and photoperiod sensitivities of each species, by dividing the effect size by the number of hours or degrees celcius between each treatment level (4 hours and 5 degrees respectively.) The results can be found in Figure 2.

Analysis

From these data, it appears that each of the observed species have differing responses. In *Corylus cornuta*, flowering is more strongly controlled by photoperiod, though neither variable was shown to have a statistically significant effect. *C. cornuta* is typically proteranthous under field conditions, with shorter photoperiods accelerating flowering, but to a significantly less degree than the acceleration of leafout due to increased forcing temperature. This relationship indicates that as spring warming accelerates, it is possible that leafout could overtake flowering, and the species may lose its proteranthous character, which would have detrimental demographic consequences due to a decrease in pollination efficiency.

In *Prunus pensylvanica* we see a different trend. Both flowering and leaf out seem to be most strongly influenced by forcing temperature but with different effect size. Flowering time appears to be 2x more sensitive than leafout. *P. pensylvanica* is classified as synanthous in the USFS Silvics manual and appears seranthous in our data set. Perhaps under warmer conditions this species will shift toward proteranthous.

In *Ilex mucronata*, forcing temperature also seems to be the dominant cue for both flowering and leaf out. In this species, both phenophases show relatively equal sensitivities, indicating it is likely the seranthous character of the species will be maintained.

Conclusion and Future Directions

It appears from this pilot study that the cue coordination between floral and foliate phenophases differs in different species. These differences indicate that the internal sequence and patterns of phenology we ascribe to individual species may not be as fixed as once believed as climate change continues to alter the abiotic environment in the coming decades. While it is difficult to draw conclusions based on a limited examination of just three species, the results of this study lend merit to the question, and the experiment should be repeated on a more broad scale. Furthermore, it would be useful (for me), to evaluate the average lag time between these phenophases under field conditions. Then, using my sensitivity calculations planted into model climate projection, determine whether proteranthous switches are indeed plausible under different climate change scenarios.

There are many other questions related to proteranthous that must be addressed.

1. How common is proteranthous? Is there a phylogenetic signal for it? Is it associated with other traits?
2. Does proteranthous truly facilitate pollination under open canopy conditions?
3. What are the fitness benefits associated with this life history trait?

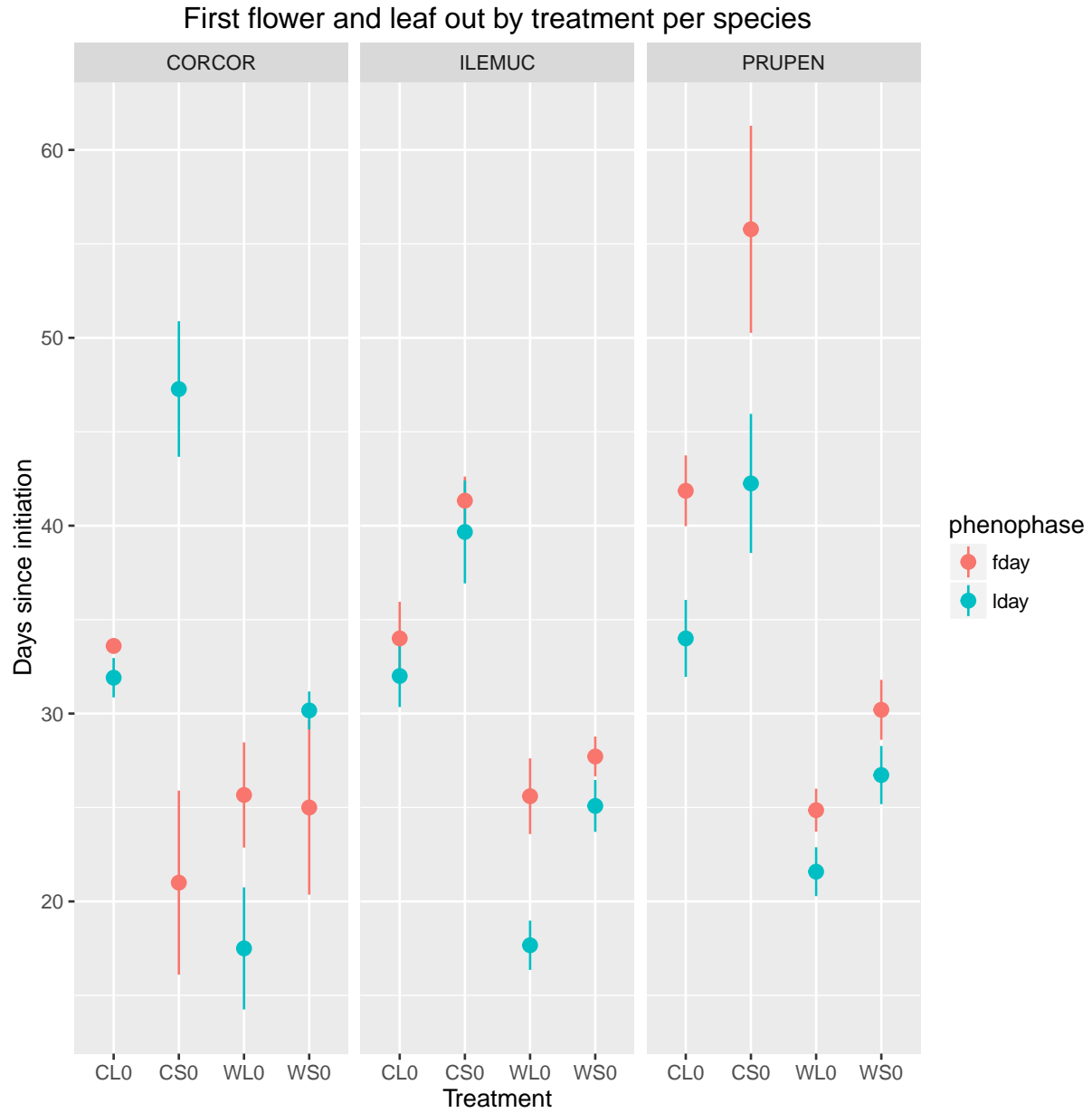


Figure 1: Mean flowering and leafout date for forcing and photoperiod treatments for three temperate shrubs

Species	Flower forcing sensitiv- ity	Flower photo. sensitiv- ity	Leaf forcing sensitivity	Leaf photo sensitivity
CORCOR	-0.6111	1.5821	-3.1638	-3.5052
PRUPEN	-4.2213	-2.5676	-2.7870	-1.6829
ILEMUC	-2.2460	-1.1901	-2.8917	-1.8854

Figure 2: Sensitivity to photoperiod and forcing temperature on flowering and leafout of three temperate shrub species

Figure 3: Appendix with ANOVA outputs for all species

```
##
## Call:
## aov(formula = fday ~ warm + photo, data = CORCOR)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -14.409  -5.245   1.591   5.755  12.920
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  20.6453    14.9469   1.381   0.182
## warm         -0.6111     0.7409  -0.825   0.419
## photo        1.5821     0.9408   1.682   0.108
##
## Residual standard error: 8.638 on 20 degrees of freedom
## (25 observations deleted due to missingness)
## Multiple R-squared:  0.1336, Adjusted R-squared:  0.04697
## F-statistic: 1.542 on 2 and 20 DF,  p-value: 0.2383
##
## Call:
## aov(formula = lday ~ warm + photo, data = CORCOR)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -13.601  -3.987  -1.181   3.218  21.399
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept) 122.1002    10.7089  11.402 2.72e-14 ***
## warm         -3.1638     0.4858  -6.513 8.07e-08 ***
## photo        -3.5052     0.6079  -5.767 9.29e-07 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 8.047 on 41 degrees of freedom
## (4 observations deleted due to missingness)
## Multiple R-squared:  0.6385, Adjusted R-squared:  0.6208
## F-statistic: 36.2 on 2 and 41 DF,  p-value: 8.756e-10
```

```
##
## Call:
## aov(formula = fday ~ warm + photo, data = PRUPEN)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -33.181  -5.122   0.926   3.419  13.819
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept) 138.0410    15.4745   8.921 3.05e-09 ***
## warm        -4.2213     0.7819  -5.399 1.33e-05 ***
## photo       -2.5676     0.9673  -2.654  0.0136 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 10.13 on 25 degrees of freedom
## (28 observations deleted due to missingness)
## Multiple R-squared:  0.6223, Adjusted R-squared:  0.5921
## F-statistic: 20.59 on 2 and 25 DF,  p-value: 5.18e-06
##
## Call:
## aov(formula = lday ~ warm + photo, data = PRUPEN)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -14.759  -2.824  -2.491   5.176  26.509
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  96.7593    10.1104   9.570 2.54e-12 ***
## warm        -2.7870     0.4721  -5.904 4.67e-07 ***
## photo       -1.6829     0.5901  -2.852  0.0066 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 8.087 on 44 degrees of freedom
## (9 observations deleted due to missingness)
## Multiple R-squared:  0.4985, Adjusted R-squared:  0.4757
## F-statistic: 21.87 on 2 and 44 DF,  p-value: 2.543e-07
```

```
##
## Call:
## aov(formula = fday ~ warm + photo, data = ILEMUC2)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -6.286 -2.067 -1.167  1.953  7.714
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  83.2582     7.2927  11.417 1.81e-10 ***
## warm        -2.2460     0.3259  -6.892 8.24e-07 ***
## photo       -1.1901     0.4088  -2.911 0.00835 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 3.978 on 21 degrees of freedom
## (24 observations deleted due to missingness)
## Multiple R-squared:  0.7162, Adjusted R-squared:  0.6891
## F-statistic: 26.49 on 2 and 21 DF,  p-value: 1.809e-06
##
## Call:
## aov(formula = lday ~ warm + photo, data = ILEMUC2)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -12.0625  -3.4479  -0.0625   1.8542  28.3958
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  98.0625     7.9635  12.314 5.21e-16 ***
## warm        -2.8917     0.3678  -7.862 5.48e-10 ***
## photo       -1.8854     0.4598  -4.101 0.00017 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 6.371 on 45 degrees of freedom
## Multiple R-squared:  0.636, Adjusted R-squared:  0.6198
## F-statistic: 39.31 on 2 and 45 DF,  p-value: 1.334e-10
```