

Concept paper outline:

Green is the color of spring (?), but any keen observer walking the Eastern deciduous forests early in the season would readily notice that it is often the subtle reds and yellows of emerging tree flowers that are the first harbingers of the season. Why do some tree species seasonally flower before leafing out? What benefit might a species gain by engaging in the costly process of reproduction at a time when the current year's photosynthesis is unavailable to them, and stored energy is at a seasonal low (cite missy's paper)? This trait, known as hysteresis, is a feature common to deciduous forests, and is apparent in many commercially and ecologically important woody plant species. This flowering behavior has long been noted by botanists (?) and several hypotheses have been put forth suggesting that this temporal trait is critical for the reproductive success of these species, but there has been little empirical investigation into the origins or significance of this pattern. While hysteresis is reported to be common in temperate deciduous forests, as far as we know, there have been no attempts to quantify the prevalence of this trait, or to evaluate it in either a phylogenetic or community context. Further, while the study of phenology, the timing of seasonal lifecycle events, has received increased attention in the past decades for its link to anthropogenic climate change, floral and leaf phenology have long been treated as disparate processes, and have been rarely observed in tandem (?). As a result, it is even difficult conclusively to classify hysteranthous species.

It has been shown that interactions between temperature and day length are cues for both floral and foliar phenology in trees (cite lots of people). Significant shifts in phenology due to anthropogenic climate change have already been observed, (cite a lot of people), but there is little baseline data for evaluating if and how hysteresis has been altered (cite Lechowicz 1995). This gap in the literature is particularly alarming, as seasonal temperatures are projected to continue to change dramatically as a result of human industrial activity (cite any reasonable climate science). If hysteresis is indeed affected by climate change, this could have negative reproductive, and ultimately demographic consequences for many important woody species. In this paper we will:

- Present and evaluate the current hypotheses relating to the origins and significance of hysteresis
- Develop an empirical framework for identifying hysteranthous species
- Characterize the prevalence of hysteresis in Eastern North American temperate forests, investigate the phylogenetic signal of the trait, and identify other biological trait predictors associated with hysteresis.
- Discuss the implications of hysteranthous flowering for forest demography in a changing climate, and present future research directions.

A History of Hysteranthous Hypotheses

Descriptions of hysteranthous flowering in trees seems to have entered the scientific literature in the mid 1890's (Robertson 1985), but has been used imprecisely (?), and other terms to describe this pattern have been used overtime, making it difficult to trace the study of this trait through the literature. The term hysteranthly also appears prior to the 20th century, coming from the Greek *husteros* (after) and *anthos* (flower), and is most succinctly defined as a plant producing leaves after the flowers have formed (?). The very same phenological pattern can also be described by its linguistic opposite proteranthly or protanthly, coming from the Greek prefix *pro* (before) defined as plants flowering before the foliage leaves appear (?). Others have attempted to differentiate between hysteranthly and proteranthly, defining hysteranthly more broadly as flowering during the leafless season and ascribing to proteranthly a temporal component where flowering occurs seasonally prior to budburst (?). A third synonym, precocious flowering, comes from the Latin *praecox*, meaning premature(?). However, precocious flowering is more widely used to describe species or individuals that flower early in their ontogeny, and using it to describe leafless flowering produces unnecessary confusion. Additionally, many sources describing species hysteranthous flowering do not use any of these terms but rather rely on verbal descriptions of the phenological pattern. To allow for a more robust study of this trait to emerge in the future, we suggest that researchers adopt the term hysteranthly moving forward, eliminating confusing synonyms and allowing for comparison with other systems where flowering in the leafless season is common such as the dry deciduous tropics(?) and Mediterranean geophyte communities(?).

Despite the infrequent and ambiguous descriptions of hysteranthly in the literature, several hypotheses for the origins and significance of the trait have emerged. These hypotheses can be broadly classified into two categories: functional and physiological. Functional hypotheses posit that the hysteranthous pattern confers, in and of itself, a fitness advantage on a species, while physiological hypotheses posit that the hysteranthous pattern emerges due to physiological constraint within a species.

Perhaps the most common explanation for the seemingly high rate of occurrence of hysteranthly in temperate deciduous species is that this phenological pattern is an adaptation critical for wind pollination (anemophily), with leafless flowering allowing for more efficient pollen dispersal and transfer (???). While we are unaware of any studies that have tested this anemophily efficiency hypotheses directly, there are several studies that provide tangential support. Simplistically, pollen dispersal is a function of the terminal velocity of pollen grains and the wind intensity(?). Vegetation structure and canopy closure reduce particle diffusion through a forest(?), and that wind velocities in forest are considerably higher in the leafless season than when a canopy is full (?). As such, flowering during the leafless period would increase the possibility of long distance pollen transfer.

Several studies have shown that there is significant filtration of pollen by leaves (??). A particularly relevant study Tauber (1967), demonstrated high rates of pollen transfer in the trunk space of forest canopies, and

quantified the amount of pollen impacted on non-floral structures like branches and leaves. In this study, the author reports pollen counts on a single bare twig, and, on 20 twigs with leaves, of a grey willow *Salix cinerea*., with 40,000 grains impacted on the bare branch, and 1,687,600 grains on the 20 branches with leaves (Tauber 1967: Table IV). Simple arithmetic allow us to estimate that a single branch with leaves would be expected to intercept 84,400 pollen grains, more than double than what was impacted on the bare branch. This finding suggests that flowering during the leafless season significantly reduces the amount of pollen filtration by non-floral plant tissue, decreasing the likelihood of pollen limitation for these taxa. Pollen limitation has been show to be more common in trees than other plant taxa (?), but studies of pollen limitation in wind pollinated taxa are limited (?). Recently, several studies have suggested the pollen and dispersal limitation in wind pollinated taxa may be more prevelant than once thought (?). While research is beginning to address the relationship between phenology, pollen limitation and reproductive output in wind pollinated species (???), but these studies tend to focus on the duration of the flowering season, rather than the timing of flowering relative to leaf phenology. A comparative study of the frequency of pollen limitation in hysternanthous and non-hysternanthous taxa would be instructive, but such studies are conceptually difficult because it is difficult to control for other differences in pollination syndrome between taxa. One possibility would be to utalize the interannual variation in hysternanthy an test whether pollen limitation increased in years where the leafless flowering window was reduced.

While our discussion of hysternanthy will be primarily focuses on the temperate decidious forests, hysternanthous flowering is also reported to be common in the dry-deciduous tropics (?). In this system where the vast majority of woody plants species are biotically pollinated, a similar, pollination effeciency hypothesis has emerged, stating that hysternanthous flowering is an adaptation for increased pollinator visibility (?). To our knowledge there have been no direct test of this hypothesis. One study by Gunatilleke and Gunatilleke (1984) compared the floral of biology of three species in the genus *Cornus*, and found that the hysternanthous *Cornus mas* allotted less invenstment in their floral display and attractant than two other *Cornus* species that flowered with or after leafing out suggesting increased visibility in the leafless season compensated for this reduced investment. One possibily approach to testing the pollination effeciency hypothesis would be to follow this comparative morphology approach for a broader range of hysternanthous and non-hysternanthous species. Another option would be to perform pollinator choice trials (cite) between closely related hysternanthous and non-hysternanthous taxa, or remove the leaves from non-hysternanthous species and compare their visitation rates to unaltered controls.

A third functional hypothesis which we refer to as the "differential selection hypothesis" comes out of an application of life history theory. Phenological plasticity allows organisms to match life cycle events to the appropriate environmental conditions. For species in the temperate zones, the optimal timing for phenological events such as flowering and leaf out tradeoff between advancing to maximize the length of the growing season, and delaying to minimize exposure to last season frost events. One possible explanation for hyster-

anthous flowering patterns is that these selection pressures operate upon foliar and floral phenology with different strength. It has been shown that long lived perennials such as trees and shrubs invest primary in growth and survival (foliar resources), rather than reproduction (floral resources) (cite the paper). It follows that floral tissues would be more expendable than leaf tissue. Frost damage to developing leaves has been shown to reduce primary productivity significantly for up to two years (cite something), while it is unlikely that sporadic pollination droughts from losing a cohort of flowers would make a significant difference in the lifetime fitness of long lived organisms such as trees (?). This difference in criticalness of tissue could allow for some species to employ a riskier strategy with floral phenology than leaf phenology. For these species the benefits of early flowering, whether they be pollination efficiency or increased time to develop and disperse fruit (cite someone) outweigh the risk of late season frost exposure. This is less true for the more critical leaf tissue, and thus a more conservative, delayed phenological strategy is employed. This differential selection pressure on flower and leaf timing produces the hysteranthous pattern. Support for this interpretation of hysteranthy comes from other comparative studies between floral and leaf tissue. Caradonna (XXXX) found that leaf tissue had higher frost resistance than floral tissue in alpine perennials. MORE IF POSSIBLE.

We must emphasize that for all of these functional hypotheses, species must exhibit physiological independence between flowering and leafing, which is certainly not the case in all temperate woody species, such as species with floral phenologies constrained by the requirement to build flower tissue from the current year's photosynthate, or species with flower buds contained within leaf buds. But there is also the possibility that hysteranthy itself is the product of biological constraints. We refer to this suggestion as the physiological hypotheses of hysteranthy.

The main physiological hypothesis suggests that hysteranthous flowering evolved in areas prone to water stress. This hypothesis suggests that species cannot maintain hydration in their flowers while transpiration is occurring through their leaves, so flowering is temporally allocated to the leafless season. This hypothesis is generally presented as an alternative to the insect visibility hypothesis of the dry tropics, and to our knowledge has not been widely discussed in the context of temperate forests, although extremely early spring flowering species may experience where flower sizes are generally reduced compared to their tropical kin.

It is also possible that hysteranthy is a highly conserved trait, and the preponderance of this phenological pattern in the temperate zone has more to do with the phylogenetic representation of the region rather than an adaptive quality to the trait. In this paper, we explore the phylogenetic signal of hysteranthy in the eastern temperate forests of North America, but more work should be done to understand distribution and evolutionary history of hysteranthy in other ecosystems and globally.

It is important to acknowledge that none of these hypotheses are mutually exclusive. Flowering on bare branches in the dry tropics may reduce water stress and increase pollinator visibility, and selection for hysteranthy in the temperate zone favoring.....

Towards an Empirical Definition of Hysteranthy

Given the lack of explicit research attention in the literature, the most detailed descriptions of hysteranthous flowering come from regional Flora, botanial guidebooks and species monographs. In these sources, hysteranthy information is given as verbal description such as *"Flowers: March-April before the leaves."* or *"Flowers: May, when leaves are half grown."*. These kinds verbal descriptors are inheirantly ambiguous and incompatible with our current, more quantitative observations standards like the BBCH scale (?) displayed in the suppliment. Does the description "Flowers before leaves" mean that a plant's flower buds burst before the leaf buds? (bbch 55 before 09)? Does it mean that one flower is open before one individual leaf begins to expand (bbch 60 before 15)? Does it mean peak flowering occurs before most of a tree's leaves are approaching full size (bbch 65 before 17)? The answer to this question would radically change which species are categorized as hysteranthous. For example, using phenological observations from Harvard Forest from 1990-2015 (cite O'Keefe) we see that if our criteria for hysteranthous classification is flower budburst before leaf budburst, only three species in the community could be classified as hysteranthous, while if we use the criteria of flowers open before leave expansion reaches 75 percent of full size, most of the species community would be considered to be hysteranthous (see figure 1). We suggest that an appropriate empirical definition of hysteranthy is largely dependent on which catagory of hypotheses are of interest. For the pollination efficiency, functional hypotheses developed for temperate flora, we suggest that species that have open flowers during the early part of leaf expansion ((bbch 60-65 before 15 or 17) should be considered hysteranthous.

If researchers are more interested in the physiological hypotheses developed for the dry tropics, a more conservation definition, flowers between leaf drop and new leaf budburst (bbch 55-65 after and 97 before 09) would be more appropriate. Because the focus of this paper is on temperate forests communities, we have elected to primarily adopt a functional definition of hysteranthy.

Predicting hysteranthy

While direct tests of each of the hysteranthy hypotheses should still be pursued, we can deduce much about the strength of the hypotheses by examining the relationship between hysteranthy and other relevant plant traits. We used published descriptions of hysteranthous species to model the association between hysteranthy and several other biological and phenological traits pertanent to the fuctional hypotheses of hysteranthy.

For our analysis we obtained species level descriptions of floral-foliate sequences from the regional guidebook Michigan Trees (?) and its companion volume Michigan Shrubs and Vines (?) hereafter MTSV. We investigated several other floras and monographs for possible inclusion in our analysis, but we found no other with comperably high levels of completeness of phenological descriptions. The complete list of sources can be found in the Suppliment. While MTSV describes woody plants found in Michigan, these comunites bear

a strong resemblance to forest communities of the Northeastern United States in generally, and can serve as a reasonable model for the whole region.

We coded hysteranthly as binary trait based on verbal phenological descriptions. In keeping with our functional definition of hysteranthly, Entries "*flowers: before the leaves*", "*flowers: before or with leaves*" and "*flowers: with leaves*" were coded as hysteranthous while entries "*flowers with or after leaves*" and "*flowering after leaf development*" were coded as non-hysteranthous. Using the same data source, we obtained descriptions of several other traits that we determined to be biologically relevant to the various hypotheses relating to the prevalence of hysteranthly including pollination syndrome, maximum height, shade tolerance, and flowering and fruiting phenology . We coded pollination syndrome as binary trait (wind or animal pollinated). We also condensed verbal descriptions of shade tolerance to binary, collapsing descriptions "moderately, or medium shade tolerant", "tolerant" and "very tolerant" to "tolerant". In the text, flowering and fruiting phenology are described a range of months. For both phenological entries, we calculated the average of the time span described, and coded it numerically in our dataset. In total, 194 woody species were included in our analysis. To investigate the phylogenetic signal of hysteranthly and control for phylogenetic structure in our dataset, we used a published angiosperm phylogenetic tree (?) pruned to match the species list from the MTSV data. Species that obtained in the trait dataset but not in the original phylogenetic tree were added to the pruned tree at the genus level root. In total 32 species were added to the generic roots. To assess the phylogenetic structure in the trait of hysteranthly, we used Caper packaged () to calculate a phylogenetic D statistic (?). To test the hypotheses regarding the trait associations of hysteranthly, we used phylogenetic generalized linear model framework (?) to build a logistical regression model corrected for phylogenetic structure using the R package phyloglm (). The model was run with 50 bootstrapped re-sampling iterations for each dataset. Continuous predictors were centered and re-scaled by subtracting the mean and dividing by two standard deviations to allow for a reasonable comparison of effect sizes between the binary and continuous predictors in this model (?).

To illustrate that our analysis is sensitive to how hysteranthly is defined, we also built a model using a physiological definition of hysteranthly in which only the descriptor "*flowers: before leaves*" was coded as hysteranthous and all other descriptors were coded as non-hysteranthous. The results from this model can be found in the Supplement.

Our primary analysis suggested that 101 out of 194 species should be classified as hysteranthous (see figure 2). We found that the phylogenetic signal for hysteranthly was relatively low. The D statistic, for hysteranthly in the MTSV data was 0.06, suggesting a very weak phylogenetic structuring for this trait. We found that average timing of flowering was the strongest predictor of hysteranthly, with the likelihood of hysteranthly increasing substantially with earlier flowering. Pollination syndrome also had a strong effect, with the likelihood of hysteranthly increasing in wind pollinated taxa. None of the other predictors has substantial effect sizes.

One challenge to interpreting these results is that since hysteroanthous species must flower before their leaves, they can never flower late in the season. This begs the question, do hysteroanthous species indeed flower earlier than early flowering non-hysteroanthous species? To address this question we re-did our analysis excluding all species which that flowered after the median flowering time, re-running our on a restricted dataset only including species that flowered between mid-March and mid-May. We found that even among early flowering species only, the likelihood of hysteroanthous still increased substantially with earlier flowering (see figure).

The large effect size of pollination syndrome on the likelihood of hysteroanthous gives credence to anemophily efficiency hypothesis, and supports the long held observation that hysteroanthous is associated with wind pollination in the temperate zone. The substantial effect of earlier seasonal flowering on the likelihood of hysteroanthous observed in both our full and restricted data set provide support for the differential selection hypothesis in demonstrating that the earliest flowering species are indeed hysteroanthous. To illustrate the effect this with average predictive comparisons, we find that with all other traits equal, a species that is wind pollinated is 38 percent more likely to be hysteroanthous than an insect pollinated species and a species flowering in April is 22 percent more likely to be hysteroanthous than one flowering in May. These findings suggest that hysteroanthous is indeed associated with wind pollination and/or extremely early flowering in the temperate deciduous forest of eastern North America.

Hysteroanthous and Climate Change

The pollination efficiency hypotheses of hysteroanthous that seems to predominate the literature and find support in our model suggest that the leafless period of flowering is critical for the reproductive success of hysteroanthous species. With many reported cases of phenological shifts in plants due to anthropogenic climate changes, it is certainly possible that hysteroanthous flowering pattern may be altered by changing seasonal conditions. Any substantial shifts in timing or duration of the hysteroanthous period could have significant effects on the reproductive success of these species. As stated above, foliar and floral phenology both respond to complex interactions between cold winter vernalization temperatures, warm spring forcing temperatures, and day length. However, we have little understanding of the comparative strength of the cues on different phenophases such as flowering and leafing within one organism. Several studies have found temperature to be the driving phenological cue for leaf out and classify many woody species as "photoperiod insensitive" with regard to their foliar phenology Basler. At the same time, much of the classic work with regards to flowering suggests that the importance of photoperiod (long day/short day) in determining flowering phenology is Beverly. With global climate change, both winter and spring temperature are projected to be warmer on average while photoperiod will remain unchanged. If floral and foliate phenologies respond with proportionate sensitivity to these cues, we may observe overall shifts in phenology but the relative timing between the phenophases

would be maintained (figure 3a). However, if flowering and leafing are differentially sensitive to these cues, we would expect that the timing relative to the other may shift. This could result in an extension or contraction (figure 3b,3c) of the hysteranthous period, or even a loss of it entirely (figure 3d). A contraction or loss of the hysteranthous period could result in increased pollen limitation or restricted pollen dispersal, endangering the long term demographic viability of hysteranthous species.

Climate change is also likely to affect the life history tradeoff inherent to the differential selection hypothesis, which also found support in our analysis. It has been shown that warming spring temperatures tend to advance flowering, though this effect may be muted by the inverse effect of warmer winters (Lizzies's paper). Advancing phenology and changing spring climate patterns could push hysteranthous flowering deeper into the unstable climate period of late winter and early spring, and may increase the risk of exposure to late season frost. If the return interval on late season frost damage becomes more frequent or severe, the reward of early flowering in frost free years may no longer offset the detrimental effects of years with frost episodes. This may give more conservative, later flowering species a demographic advantage over the hysteranthous opportunists. To begin to understand the likelihood and severity of these scenarios, it is clear that future phenological and climate change research must pay attention to flowering and the intra-phenophase constraints in general. Below we outline several important lines of inquiry for future research.

Future Directions

Hysteranthous reaction norms Clines? Population differences? Scope of interannual variation?

Independence and Constraint between phenophases Pathways, Coordinated cues.

Direct tests for functional hypotheses

Hysteranthous and reproductive variability We know there is variability in pollen production, flowering, and seed production. Does hysteranthous interact with this variability. Offsetting or enabling.

Hysteranthous in Other Systems

Figures