

Intra-specific variation in flower and leaf emergence: New directions for the study of phenological sequences in temperate forests

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To Do:

1. Supplement
2. Bayesian models for MTSV and USFS
3. Include figures for intra-annual pepmodels
4. Remake all figures to look better (possibly grey scale), standardize themes.

Abstract

As the the study of phenology has developed overtime, it has become increasing clear that it is not only individual phenological stages that affect organism fitness and ecological functioning, but also the relationship between stages. Of these phenological relationships, the flower-leaf phenological sequence (FLS) of deciduous woody plants have recieved particular treatment. The high incidence of a flowering-first species in the temperate zone has lead to the suggestion that FLS's are adaptive, and several hypotheses have been put forth to explain their evolution and function.

Classically, FLS's have been treated catagorically and assigned at the species level. However, long-term phenological data suggest that not only are there substantial diffrences between species' FLS thatare masked by catagorization, there is also considerable intraspecific variaton in FLS, at both the population and individual level. These observations suggest that the existing conceptual framework my be impeding our understanding of this phenological trait, and a new framework is needed.

In this paper, we first review the existing FLS hypotheses, and discuss of the existance of singificant intraspecific variation would modify the hypotheses. We then present four case studies from temperature forest species which demonstrate that multiple hypotheses

seem to be supported, and highlight that inference regarding the FLS hypotheses is highly sensitive to how FLS's are defined.

The review and case studies provide three major insights towards a new conceptual framework for the study of FLS. First, future research should allow for the coincidence of multiple hypotheses which can be achieved both by allowing for overlapping hypotheses in large community models and by testing individual hypotheses in smaller subgroupings that control for other trait variation. Secondly, FLS's are better treated as continuous variables and the classic categorization of FLS should be abandoned as continuous measures of FLS reduce the impact of observer bias, and allow for stronger inference regarding FLS variability both among and within species. Finally, researchers should move beyond hypothesis testing through trait associations and use intra-specific measure of FLS to test actually test for fitness consequences in FLS variation.

Introduction

Phenology, the timing of seasonal life cycle events, allows organisms to synchronize important life history transitions with optimum environmental conditions (Forrest & Miller-Rushing, 2010), and is a critical component of ecosystem structure and function (Cleland *et al.*, 2007; Piao *et al.*, 2007). Recent work in woody plant phenology has begun to show that it is not only individual phenological stages that affect these processes, but also the relationship between them (Ettinger *et al.*, 2018). One phenological relationship that has received increased attention in the literature is the flower-leaf phenological sequence (FLS). In a typical model of plant life history, vegetative growth precedes reproduction. However, for many species in the deciduous forests of Eastern North America, it is not the green tips of new shoots that mark the commencement of the growing season, but the subtle, reds, and yellows of their flowers. This flowering-first FLS is common in these regions, and its prevalence has led to the suggestion that this FLS has adaptive significance (Rathcke & Lacey, 1985). While recent advances have been in characterizing the evolution and physiology of FLS (Gougherty & Gougherty, 2018; Savage, 2019), our understanding of this phenological trait remains in its infancy.

This is alarming, because as can be seen in 1, anthropogenic climate change is altering FLS, but the FLS response to climate change differs among species. In our comparison of three European tree species, all species increase the offset between flowering and leaf phenophases, but the rate of change varied between species. In fact, the mean FLS offset for one species, *Fraxinus excelsior* has already exceeded its historic range of variability, while *Aesculus hippocastanum* FLS shows a more muted response. Depending on the function of FLS, this differential FLS sensitivity to climate change may have implications for community composition and population demography in the future.

As the study of phenology has matured as a discipline, it has become clear that measures of synchrony and variability are key components to understand the fitness benefits

of distinct phenological syndromes (). It would be expected this would hold true for phenological sequences as well. However, while some have found general correlation between flowering and leafing phenology (Lechowicz, 1995; Ettinger *et al.*, 2018), fine scale FLS variability has never been evaluated. We suggest that characterizing FLS variation among individuals and populations will allow for a more biologically relevant evaluation of the current FLS hypotheses as well as reveal avenues for future direct hypothesis testing.

After providing a more thorough definition of FLS patterns, we will: 1) Review the adaptive hypotheses of FLS and their respective predictions, 2) Evaluate variation in FLS, and explore how FLS variation within species populations and individuals alter the predictions of the hypotheses, 3) Provide four case study analyses of FLS in temperate trees that demonstrate how the incorporation of variation alters which hypotheses are supported from statistical models, and 4) make recommendations for future study of FLS.

Defining FLS

Flower-leaf sequences have traditionally been classified into distinct qualitative categories that are almost always defined at the species level. The terms hysteroanthous, proteranthous or precocious flowering describe plants which produce flowers before leaves (). A classic example of this FLS is *Acer rubrum*, which, as seen in figure 2 reaches peak flowering weeks before any sign of leaf development. These species tend to exhibit a degree of physiological specialization, such as the separation of flower and leaf buds.

Seranthous, considered the null FLS and embodied in figure 2 by the species *Nyssa sylvatica*, describes species in which flowers begin to open after leaves are approach this full size. These species may still differentiate flower buds in the previous season, but may rely less on stored energy than flowering-first taxa.

But what about species whose FLS separation is less clear? It is possible to describe all species whose flowering period overlaps their leaf development as synanthous, but this third category may obscure important interspecific differences. Furthermore, both the flowering and leaf growth periods consist of several sub-stages making it difficult to fit FLS patterns neatly into these categories.

Take *Betula alleghaniensis* from figure 2 for example: One would be justified in classifying this species as hysteroanthous because its flower buds tend to burst before its leaf buds, or as synanthous for the fact the its open flowers overlap the beginning of leaf growth Can we really put this species in the same category as *Acer rubrum*, whose flowers open weeks before the leaves? Conversely, is this species truly similar to figure 2's *Acer pensylvanicum* whose flowers do not open until leaves are further along in their expansion? These decisions are best guided with a focus on their implications for the FLS hypotheses, which we will discuss in detail below.

Hypotheses of FLS and their predictions

Wind pollination

The most prevalent FLS hypothesis associates hysteranthous flowering with pollination syndrome, suggesting that it is an adaptation critical for effective wind pollination, with leafless flowering allowing for more efficient pollen dispersal and transfer (Whitehead, 1969; Stephen H. Spurr, 1980; Friedman & Barrett, 2009). This hypothesis hinges on the fact that the presence of leaves results in a substantial physical disruption to pollen transfer, a premise that we would not necessarily expect to be true for the early stages of leaf expansion, when tiny leaf primordia would have little impact on environmental structure. In this framework, trees that flower during the early stages of leaf expansion would be expected to gain similar mechanical advantage to those who complete their flowering before any leaf activity. Therefore, this hypothesis predicts that wind pollinated species should flower before or with their leaves, while in animal pollinated species, FLS should be random or co-vary with pollinator activities.

Water dynamics

Another hysteranthous hypothesis, emerging from the dry deciduous tropics where flowering during the leafless season is also common (Janzen, 1967), suggests that flowering before leaf development is an adaptation to reduce water stress associated with maintaining floral hydration while leaves are transpiring (Franklin, 2016). This hypothesis suggests that there would be a significant cost to maintaining flower structure during any stage of leaf activity, and as such, it would be expected only species whose flowering occurred before any leaf expansion would gain this drought advantage. This hypothesis predicts that species that are drought tolerant should flower before leafing out, with minimal overlap between the floral and foliate phenophases. Species that are not drought tolerant get no real advantage from flowering first, so in these species FLS should be random.

Early flowering

A third possibility is flowering-first FLS is a physiological byproduct of selection for early flowering (Primack, 1987). Within this framework, there is no advantage to a species being hysteranthous vs. seranthous, as long as the absolute flowering time of the contrasting FLS's were the same. However, this equivalency may simply be a physiological impossibility. Recent work from Savage (2019) has demonstrated that flowers are primarily hydrated by the phloem and therefore are independent of xylem re-geneses, which is not the case for the xylem maintained leaf tissue. With physiological constraints on leaf phenology but not on flowering, selection for early flowering would drive the hysteranthous. This would explain why hysteranthous species tend to be the earliest species to flower. Here, we would expect increased FLS offset (time between flowering and leaf out) to be

associated with generally earlier flowering phenology. We also would expect associations with other early flowering traits such as seed mass, dispersal season, cold tolerance etc to be more pronounced. However, this hypothesis does not require the selective driver of early flowering to be exclusively be one of these trait and pollination syndrome or drought tolerance may still play a role in driving the early flowering.

This hypothesis predicts that species' flowering times should be strongly associate with flowering-first FLS. It also is likely there would be relationship between this FLS and other early flowering traits, but an additional association with pollination or drought syndromes is acceptable.

Phylogenetics

Finally, it is also possible that FLS's are highly conserved traits, and the preponderance of hysternanthy in the temperate zone is a product of phylogenetic representation of the region rather than an adaptive quality to the trait. There is no biology here to suggest differences between species that flower well in advance of the leaves or just prior to their emergence, but considering but extra categories may help see the patterning across the tree. This hypothesis predicts strong phylogenetic patterning in the FLS with no correlation with other traits to be expected.

Variation in FLS

All of the above hypotheses assume that FLS's are a consistent species level trait, however, this assumption has not been well examined in the literature (Gougherty & Gougherty, 2018). We investigated individual FLS variation using a long term phenological data set collected at Harvard Forest in Petersham, Massachusetts (O'Keefe, 2015). There was substantial variation in FLS offset among years, with offset values varying by up to several weeks for most species. This variability can significantly blur FLS categorization. AS seen in 3 *Q. rubra*, a species classically listed as flowering and leafing in synanthy, there are some years in which flower bud bust is over a week before leaf bud burst, and other years, in which leaf buds burst weeks prior to floral bud bust. We also found there to significant population level variation in FLS, using the Pan European phenological database PEP725(Templ *et al.*, 2018), with some populations differing in their mean FLS offset by a week or more.

Given the variability of FLS at the individual and population level, it is clear that considering FLS variability only higher taxonomic levels may obscure important realities about the biology of this phenological trait. Below, we discuss how the observed variation below the species level may alter the existing FLS hypotheses.

How FLS variation alters predictions

Wind pollination

It is well accepted that pollination syndrome is a species level trait, considered to be fairly immutable across ecological time and space. One would not expect significant variation in FLS across population or individuals because one would not expect variation in pollination syndrome. However, as discussed above, a tree with no overlap between flowering and leafing phenology does not necessarily gain a significant pollen transfer advantage over an individual with some overlap. It is clear the the pollination efficiency advantage from flowering first diminishes as the canopy fills in, but the dynamics of this impact are not well characterized. We do not know at what point in the leaf expansion progress pollination would become significantly encumbered, so it is possible, that interannual and population level variation in hysteranthous FLS could maintain a wind pollination advantage, as long as the overlap did not cross a certain unknown threshold. Therefore, based on the wind pollination efficiency hypothesis, we would not expect high levels of population or individual variation in FLS, but the detection of some FLS variability at these levels, does not inherently challenge the plausibility of the hypothesis.

Water dynamics

If FLS's are driven by water dynamics, we would expect there to be significant population level variation in FLS. Populations growing in drier habitats would be expected to show a stronger hysteranthous pattern than their counterparts growing in wetter habitats where there would be more relaxed selection for minimizing phenological overlap. Therefore, we would predict a strong correlation between FLS and average soil moisture. This hypothesis also suggests that water availability may drive interannual FLS variation, with drought year increasing an hysteranth, and wetter years permitting more FLS overlap. We might only expect to see a signal for the association between a drought tolerance and hysteranth if the phenological observations for the species came from populations in drought prone regions.

Early flowering

This hypothesis predicts some variation on the population level based on local adaptation. Populations in which selection for earlier phenology is stronger, perhaps those in regions with shorter growing seasons, would be expected to show a higher degree of hysteranth. At the individual level, FLS variability could be driven by interannual variability in spring conditions. Both flowering and leaf phenology are strongly cued to temperature and photoperiod (Flynn & Wolkovich, 2018; Rathcke & Lacey, 1985), but with leaf phenology constrained by xylem activity and flowering phenology relatively independent of it, we would expect a stronger response in to environment in flowering time resulting in FLS variation. With the greater sensitivity to environment of flowering than leafing, we

would expect FLS variation to be positively associated with flowering phenology variation. Below the species level, this hypothesis predicts that early flowering years or populations are associated with increased FLS offset for hysteranthous species.

Phylogenetics

With the lack of treatment of FLS variability in the literature below the species level, we have no strong basis for asserting whether the apparent variability in FLS is a product of genetic or environmental controls. If there is a strong genetic component to FLS as has been shown in other phenophases (Wilczek *et al.*, 2010), some population level variation could be driven by reproductive isolation. With strong genetic control to FLS, we might also see consistent genotypic differences in FLS among individuals within a population, but would not predict high levels of interannual variation in FLS.

Available evidence for FLS hypotheses in temperate woody species

Despite a strong conceptual basis, direct tests of these hypotheses of hysteranthly in the literature are relatively rare, and support for them is mixed. Many studies only test a single hypothesis at once, making comparison between them difficult. For example, the primary evidence supporting the wind pollination hypotheses comes from pollen diffusion studies, e.g., particle movement through closed and open canopies (Niklas, 1985; Nathan & Katul, 2005; Milleron *et al.*, 2012), which provide no framework for comparatively evaluating the other hysteranthly hypotheses. We are aware of no direct test to try and distinguish hysteranthly from selection early flowering, but Primack (1987) notes that hysteranthous wind pollinated species tend to also have large seed mass, and lack primary seed dormancy for germination. These are traits associated with early flowering in general, making the case that hysteranthly may simply be one component of a larger suite of early flowering traits. We are also aware of no studies that have mechanistically evaluated the water dynamics hypothesis, though observations of flowering in the dry tropics by Borchert (1983); Reich & Borchert (1984) suggest that the timing of flowering in hysteranthous taxa is associated with a plant water status recovery due to leaf drop. Only recently has it even been suggested that this hypothesis might be relevant in the temperate zone as well, as it is not expected that water status would limit biological activity in the wet spring months of the temperate zone (Gougherty & Gougherty, 2018).

In contrast, studies testing multiple hypotheses have generally found support for more than one evolutionary driver of hysteranthly. One study by Bolmgren *et al.* (2003) showed that wind pollinated species tend to also be earlier flowering than their biotocally pollinated sister taxa, suggesting an interaction between the early flowering and wind pol-

lination hypotheses. A recent study by Gougherty & Gougherty (2018) tested multiple hypotheses by modeling associations between species' trait and FLS patterns in the Great Lakes regions. They found strong support for both the water dynamics and early flowering (flower timing and seed characteristics) hypotheses, and found strong phylogenetic clustering for FLS.

In all of these cases, variability in FLS below the species level isn't addressed. Yet, there are datasets widely available that would allow for concurrently testing these several hysteresis hypotheses concurrently, and at multiple taxonomic levels. To address this gap, we supplement our literature review by re-testing some previously-used datasets to examine all hypotheses, and we leverage several widely-available datasets to test how support for these hypotheses varies across the inter- to Intra-specific levels.

We evaluated hysteresis in four phenological datasets. Michigan Trees and its companion volume Michigan Shrubs and Vines (Barnes & Wagner, 1981,2004; Burton V. Barnes, Christopher W. Dick, 2016) (MTSV) contains categorical FLS information for 195 Woody plant species. The USFS Silvics manual volume II (Burns *et al.*, 1990) contains categorical FLS descriptions for 81 woody species. These data can be used to test Inter-specific FLS variation. Within these datasets, we applied 2 alternative FLS classification schemes; physiological hysteresis, which allowed for no overlap between floral and leaf phenophases, and functional hysteresis, which allowed for a degree of overlap as predicted by the wind pollination hypotheses. The Harvard Forest data set (HF) contains quantitative flowering and leaf phenology measurements for individuals of 24 woody species over a 15 year period, allowing for both inter- and intra-specific comparisons (O'Keefe, 2015). In this data set, we approximated the two hysteresis classification schemes mentioned by measuring the temporal offset between different floral and leaf phenophases. From the Pan European Phenological Database (PEP725) (look up citation) we obtained spatially and temporally explicit, quantitative flowering and leaf phenology for 3 European hysteresis species. This allows for test only at the intra-specific level, but unlike the other datasets, it allows for population level variability to be assessed.

Results of sorts, and ideas about them

In considering each data set separately and in tandem two clear trends emerge: One, in accordance with the recent literature, we found that in our re-analyses, multiple hypotheses were supported. There was generally a strong support for the early flowering and wind pollination hypotheses, poor support for the water dynamics hypothesis, and the phylogenetic signal was variable. The support for multiple hypotheses is not terribly surprising. We wouldn't expect the wind pollination hypothesis to explain hysteresis in biotically pollinated taxa. Further, given the almost constant non-equilibrium state of temperate forest communities due to glacial cycles over the last 10,000 years (Stephen

H. Spurr, 1980), it is not surprising our flora consists of species with radically different bio-geographic histories that may have evolved hysteranthous flower under very different selection environments. The second clear signature from our analysis was that relative importance of each the predictors changed significantly depending on how hysteranthty was defined. This effect was minimized when continuous measure of FLS were used over categorical. But perhaps more important that the results of these specific model themselves, is that through considering them together, we are provided a more comprehensive picture of where our understanding of this phenological trait is currently, and where it needs to go.

Future

Our analysis reveals the clear advantages of treating hysteranthty as a continuous trait. As mentioned above, continuous data minimizes the observer bias that comes with categorization. It also reveals important inter-specific differences that are masked by categorization. For example, two categorically hysteranthous species may have dramatically different FLS offsets. Through working with continuous measures of hysteranthty, substantial intra-specific differences in FLS emerge, and as will be discussed more below, these will be valuable for hypothesis testing. All and all, our work shows categorizing hysteranthty into groups is biased and biologically problematic; future studies about phenological sequences should avoid these categories when possible and treat FLS as continuous traits whenever possible.

Another main outgrowth of our analysis is the realization that it is instructive to test questions of hysteranthty at many scales. Because trait modeling in large community level datasets seem to support multiple hypotheses and are confounded by species' identities and observer bias, the utility of these data can only take us so far. While there is certainly value to broad taxonomic studies, and future large-scale analyses should continue, it is possible the evolutionary dynamics of hysteranthty may be better explored with a more mechanistic approach, which may mean utilizing a more taxonomically restricted focus.

One option is to look within the hypotheses to address sub-grouping of taxa in which overlap between hypotheses could be controlled. For example, what drives hysteranthty among biotically pollinated taxa? It certain isn't wind pollination efficiency. Or, what factors accounts for variability in hysteranthty among wind pollinated taxa? Incorporating a more explicit phylo-biogeographic approach would probably be instructive at this level, for example: are their phylogeographic commonalities between Bionically pollinated hysteranthous species in Eastern flora?

But even with drilling down to sub-groupings, interspecific trait association models can only can take us so far. One reality of these kind of studies is that we never know we are picking the right traits. For example we used minimum precipitation across a species' range, one of the only available quantitative drought metrics at the scale of large interspecific models, to represent the water dynamics hypothesis. Is this really a good

proxy for drought tolerance? Further, species evolve a suit of traits for any function, and unmeasured traits might bias our results (Davies *et al.*, 2019). For example, wind pollinated species could compensate for a lack of hysteranthly by over producing pollen or through self-pollination. To really understand this trait across large taxonomic space, you would have to compare species across an unfeasibly large, N-dimensional trait space.

Considering hysteranthly variation at the intra-specific level overcomes many of these limitations, and is the the next frontier in testing the evolutionary and ecological significance of FLS. Evolutionary theory predicts that Intra-specific variation should follow the same trends as interspecific variation. The agreement between our intra- and interspecific models supports this, and may suggests that we are narrowing in on certain hypotheses. Further, though our datasets were taxonomically and geographically limited, they demonstrate that FLS variability is significant over time and space. Looking within species holds most other traits relatively equal, avoiding the problem of latent tradeoffs with unmeasured traits.

With this equalizing nature of intra-specific comparison we can now, move beyond trait associations and actually begin to to look at fitness consequences of FLS variation through experimental manipulations and observations. This next step is intuitive because fitness actually drives trait evolution, and the hysteranthly hypotheses themselves make fitness predictions. It is tough to tease these apart at the interspecific level because of the N-dimensional trait axis mentioned above, but the hypotheses predict that variability in hysteranthly would lead to variability into fitness outcome at the intra-specific level. For example, the wind pollination hypothesis predicts that years with increased hysteranthly should correlate with more pollination success. The water dynamics hypothesis suggests more hysteranthous populations should better tolerate drought. These predictions could be directly assessed through well designed experiments.

Looking at fitness consequences will not only help clarify basic scientific hypotheses, but is essential for understanding how global change induced alterations to hysteranthly will impact species demographics. For example, if hysteranthly is driven by pollination efficiency, increased hysteranthly with climate change might favor hysteranthous species. Or, if climate changes reduces FLS offset, hysteranthous species may be at greater risk for reproductive failure. If there really is strong selection on early-flowering what is predicted next (lots of cites you could add here). A better understanding of consequences of variation in hysteranthly is essential both for understanding the evolutionary origins of this trait, and for predicting the fate of species with this Phenological syndrome as global climate continues to change.

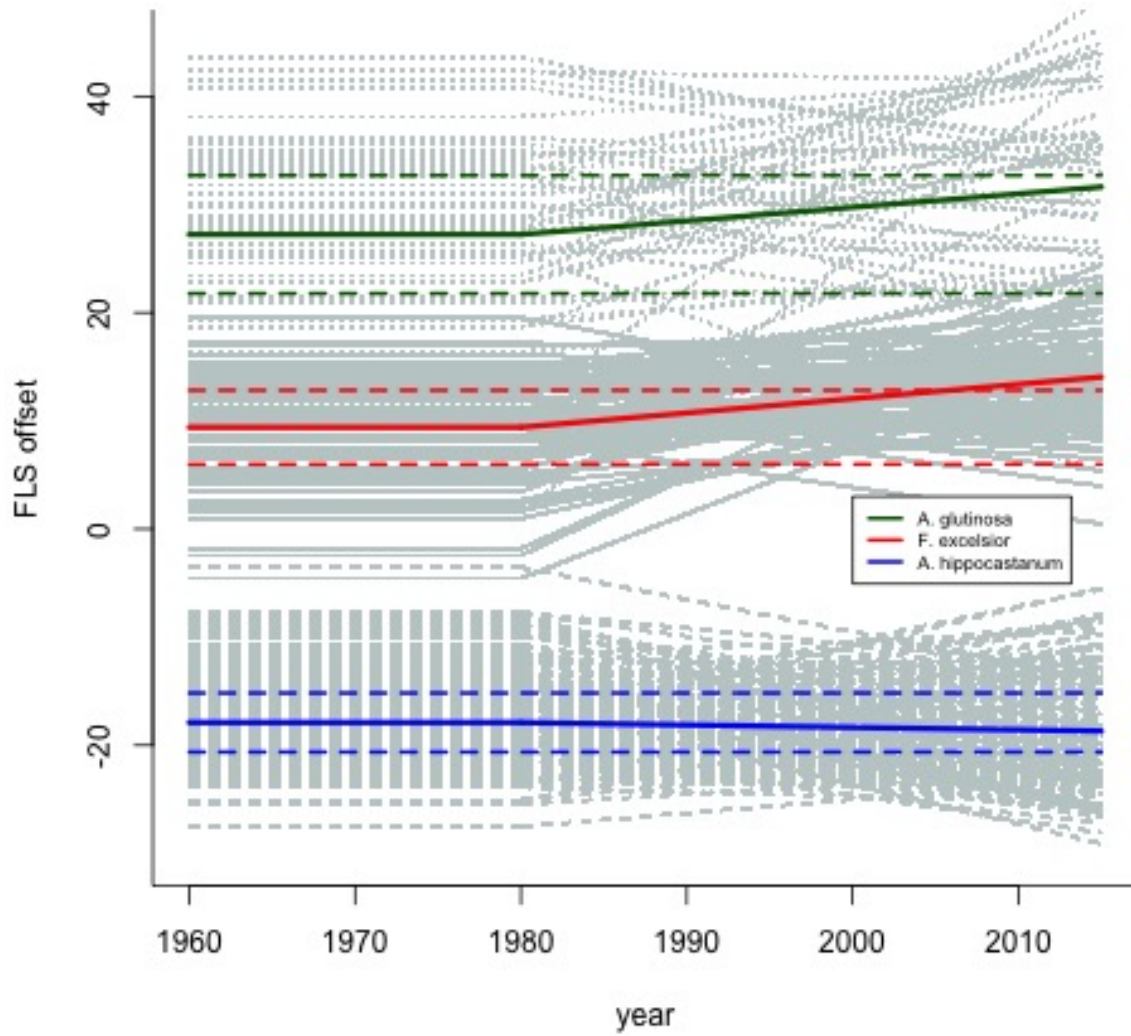


Figure 1: Trends in average FLS offset across Europe for 3 tree species from 1960 to 2015. Dashed lines indicate historic range of FLS variability. All species are increasing their offset, but the rate of change differs between species and sites

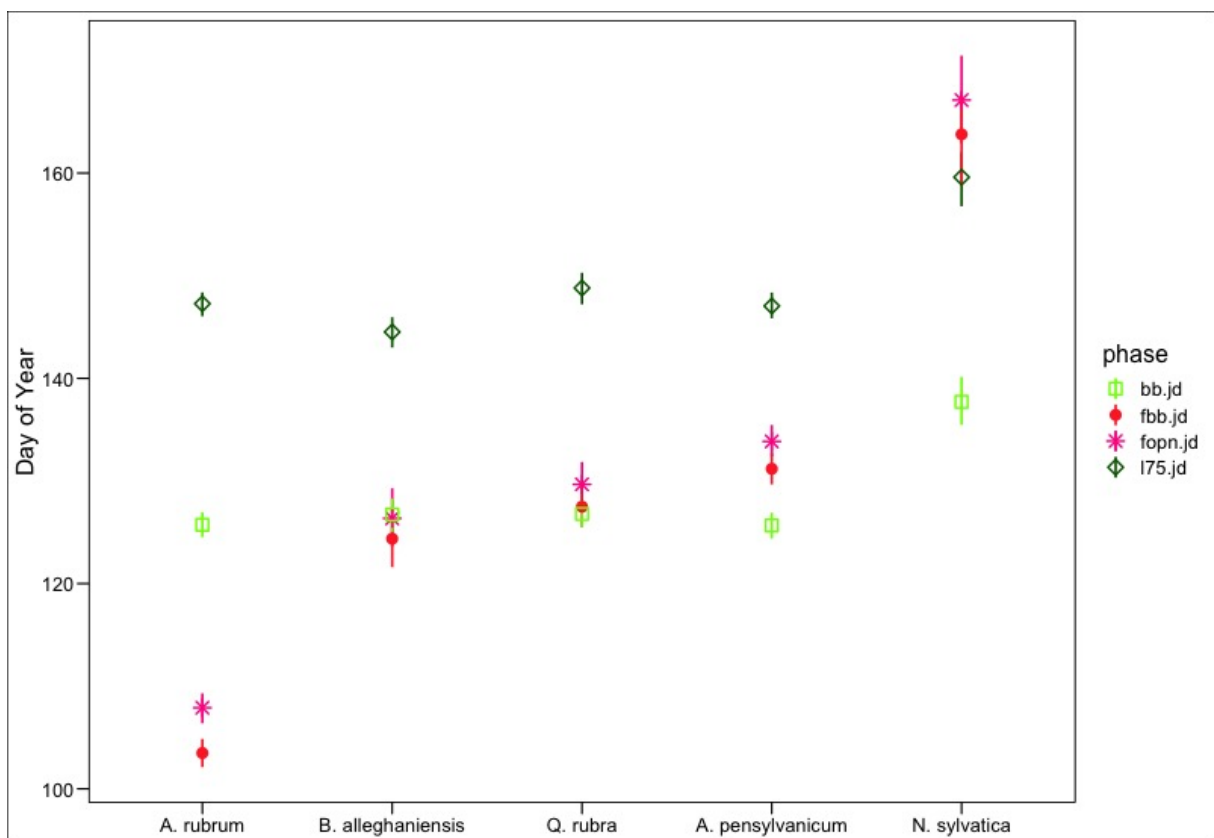


Figure 2: Average day of phenological events for highlighted woody plant species at Havard Forest in Petersham, MA from 1990-2015

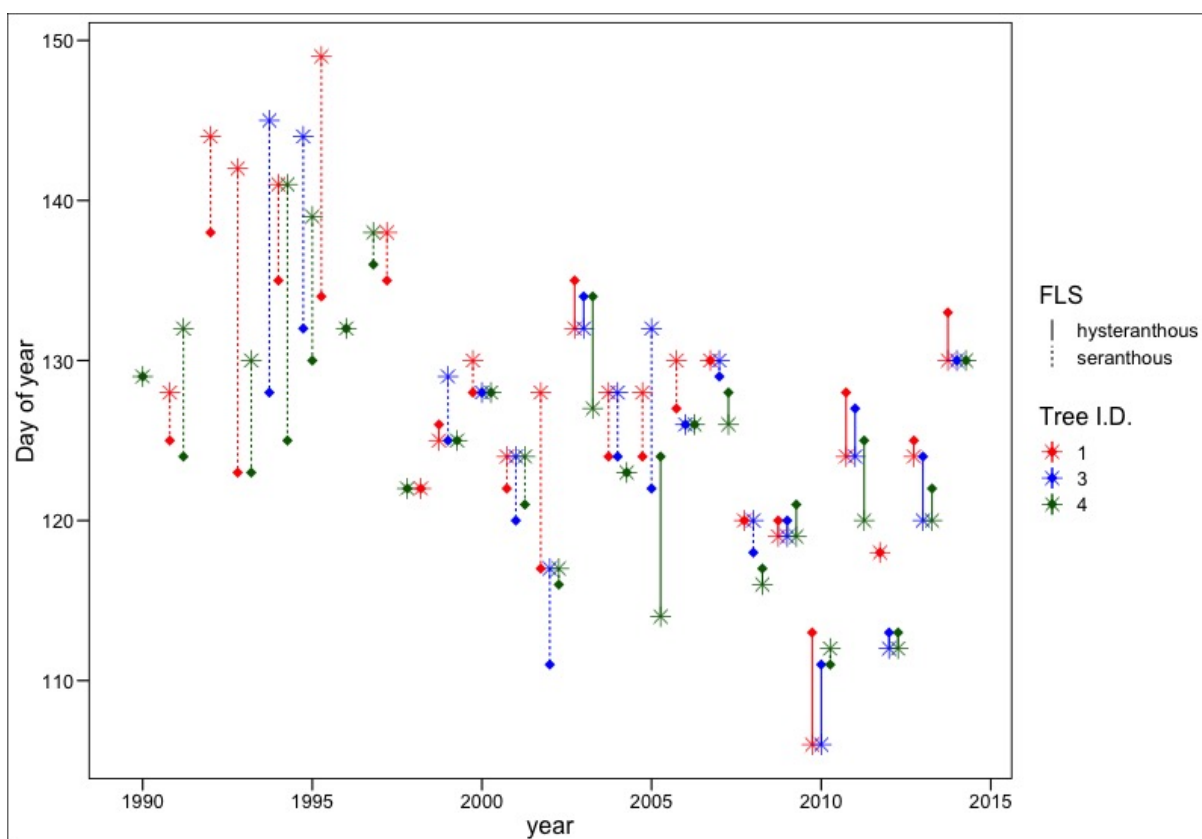


Figure 3: FLS variability among years and within a population of *Quercus rubra* at Harvard forest.

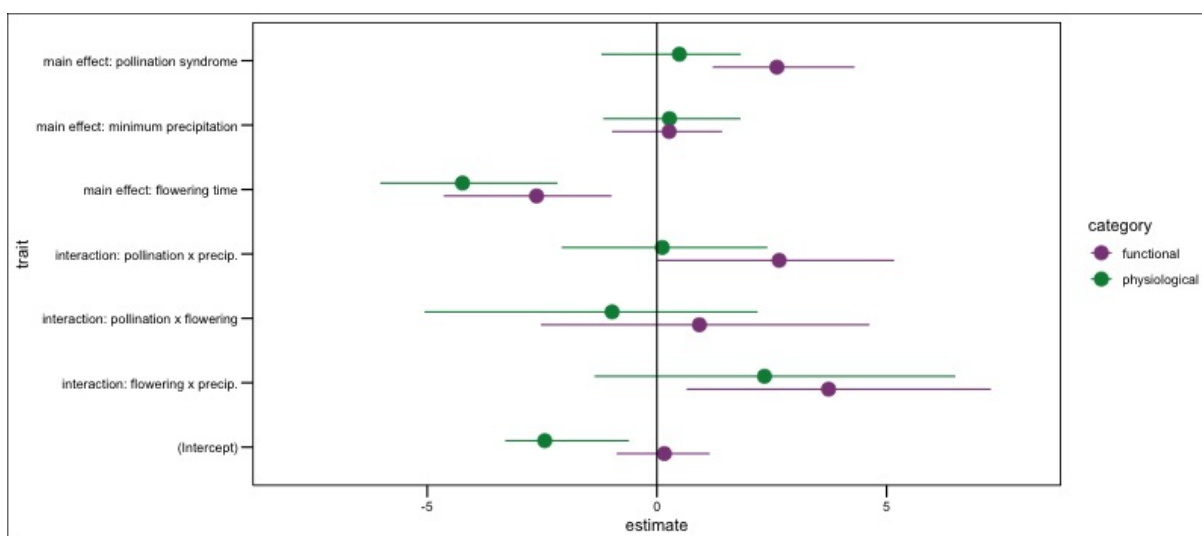


Figure 4: MTSV Effect size and 95% bootstrapping intervals estimates

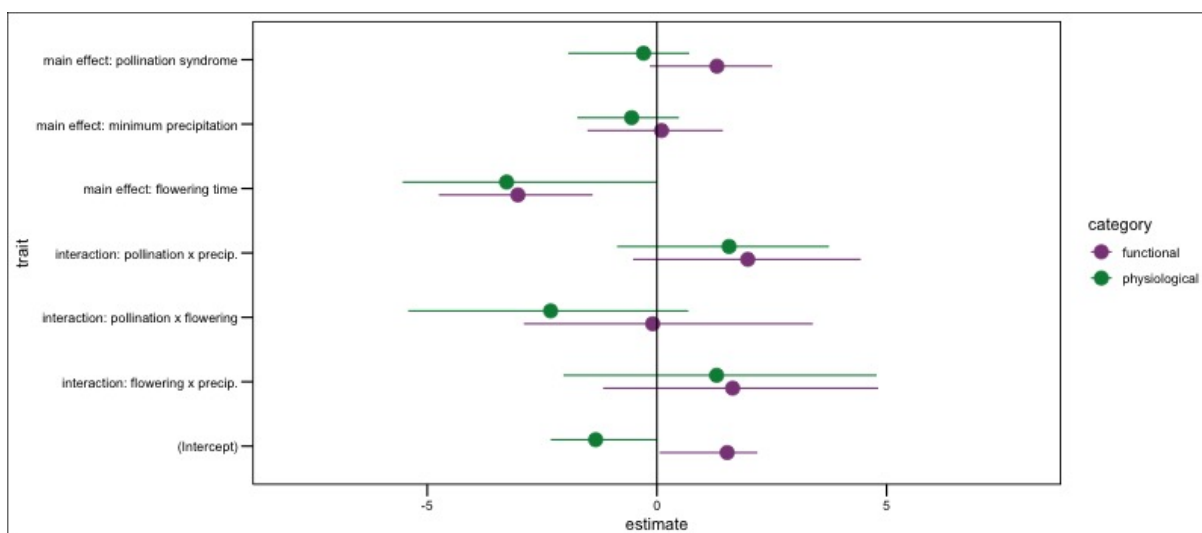


Figure 5: USFS Estimates 95% bootstrapping intervals depicted

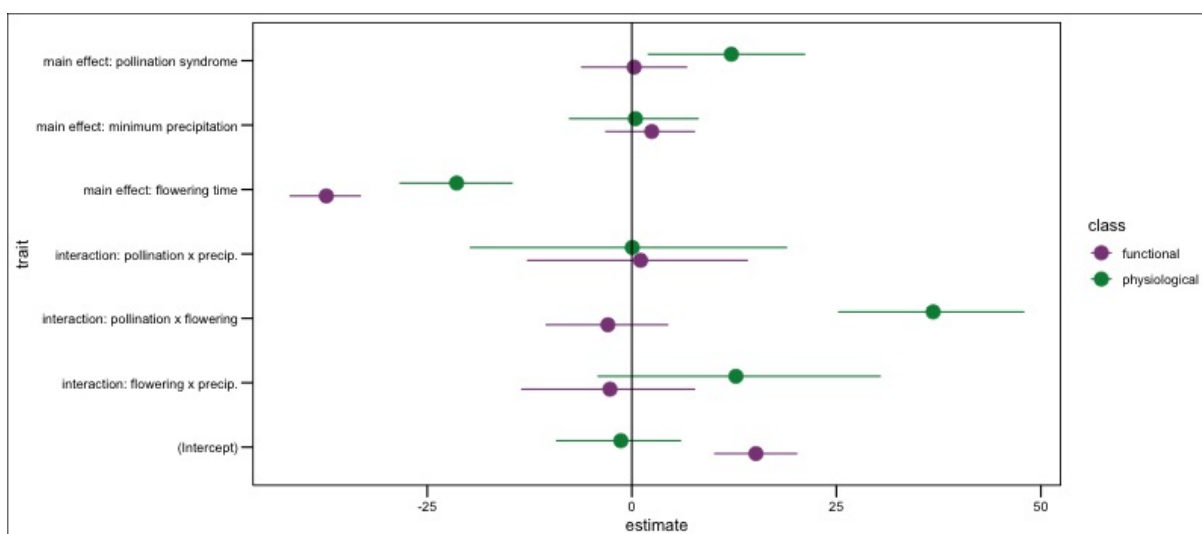


Figure 6: Harvard forest continuous . Estimates, 95% bootstrapping intervals depicted

References

- Barnes, B.V. & Wagner, W.H.J. (1981,2004) *Michigan Trees: A guide to the Trees of the Great Lakes Region*. University of Michigan Press.
- Bolmgren, K., Eriksson, O. & Linder, H.P. (2003) Contrasting flowering phenology and species richness in abiotically and biotically pollinated angiosperms. *Evolution* **57**, 2001–2011.
- Borchert, R. (1983) PHENOLOGY AND CONTROL OF FLOWERING IN TROPICAL TREES. *BIOTROPICA* **15**, 81–89.
- Burns, R.M., Honkala, B.H. & coordinators], T. (1990) *Silvics of north america: Volume 2. hardwoods*. Tech. rep., United States Department of Agriculture (USDA), Forest Service.
- Burton V. Barnes, Christopher W. Dick, M.E.G. (2016) *Michigan Shrubs Vines: A guide to species of the Great Lakes Region*. University of Michigan Press.
- Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology Evolution* **22**, 357 – 365.
- Davies, T.J., Regetz, J., Wolkovich, E.M. & McGill, B.J. (2019) Phylogenetically weighted regression: A method for modelling non-stationarity on evolutionary trees. *Global Ecology and Biogeography* **28**, 275–285.
- Ettinger, A., Gee, S. & M. Wolkovich, E. (2018) Phenological sequences: how earlyseason events define those that follow. *American Journal of Botany* **105**.
- Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.
- Forrest, J. & Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3101–3112.
- Franklin, D.C. (2016) Flowering while leafless in the seasonal tropics need not be cued by leaf drop: evidence from the woody genus brachychiton (malvaceae). *Plant Ecology and Evolution* **149**, 272–279.
- Friedman, J. & Barrett, S.C.H. (2009) Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. *Annals of Botany* **103**, 1515–1527.

- Gougherty, A.V. & Gougherty, S.W. (2018) Sequence of flower and leaf emergence in deciduous trees is linked to ecological traits, phylogenetics, and climate. *New Phytologist* **220**, 121–131.
- Janzen, D.H. (1967) Synchronization of sexual reproduction of trees within the dry season in central america **21**, 620–637.
- Lechowicz, M.J. (1995) Seasonality of flowering and fruiting in temperate forest trees. *Canadian Journal of Botany* **73**, 175–182.
- Milleron, M., Lopez de Heredia, U., Lorenzo, Z., Perea, R., Dounavi, A., Alonso, J., Gil, L. & Nanos, N. (2012) Effect of canopy closure on pollen dispersal in a wind-pollinated species (*Fagus sylvatica* L.). *PLANT ECOLOGY* **213**, 1715–1728.
- Nathan, R. & Katul, G. (2005) Foliage shedding in deciduous forests lifts up long-distance seed dispersal by wind. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA* **102**, 8251–8256.
- Niklas, K.J. (1985) The aerodynamics of wind pollination **51**, 328–386.
- O’Keefe, J. (2015) Phenology of woody species at harvard forest since 1990.
- Piao, S., Friedlingstein, P., Ciais, P., Viovy, N. & Demarty, J. (2007) Growing season extension and its impact on terrestrial carbon cycle in the northern hemisphere over the past 2 decades. *Global Biogeochemical Cycles* **21**.
- Primack, R.B. (1987) Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* **18**, 409–430.
- Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**, 179–214.
- Reich, P. & Borchert, R. (1984) WATER-STRESS AND TREE PHENOLOGY IN A TROPICAL DRY FOREST IN THE LOWLANDS OF COSTA-RICA. *JOURNAL OF ECOLOGY* **72**, 61–74.
- Savage, J.A. (2019) A temporal shift in resource allocation facilitates flowering before leaf out and spring vessel maturation in precocious species. *AMERICAN JOURNAL OF BOTANY* **106**, 113–122.
- Stephen H. Spurr, B.V.B. (1980) *Forest Ecology*. John Wiley Sons, 3rd edn.
- Templ, B., Koch, E., K.Bolmgren, Ungersböck, M., Paul, A., Scheifinger, H. & et al. (2018) Pan european phenological database (pep725): a single point of access for european data. *Int. J. Biometeorology* .

Whitehead, D.R. (1969) Wind pollination in the angiosperms: Evolutionary and environmental considerations **23**, 28–35.

Wilczek, A.M., Burghardt, L.T., Cobb, A.R., Cooper, M.D., Welch, S.M. & Schmitt, J. (2010) Genetic and physiological bases for phenological responses to current and predicted climates. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**, 3129–3147.

Suppliment

Methods

Climate change projections

Case studies

MTSV and USFS: For these two, catagorical, species level case studies, we converted verbal descriptions of flower-leaf sequences into a binary response variable. For our more inclusive "functional" definition of hysternanthy, we included species entries with descriptions "*flowers before the leaves*", "*flowers before or with leaves*" and textit"flowers with leaves" as hysternanthous. Our more restrictive "physiological" hysternanthy definition only included species described as "*flowers before the leaves*" as hysternanthous.

For modeling trait associates we chose three predictors to represent the three major FLS hypothesis; pollination syndrome, average flowering time and minimum precipitation levels across the species range. Pollination syndrome and average flowering time we obtained directly from the data sources, and estimates of minimum precipitation came from the USDA/NRCS Conservation plants characteristics (). We coded pollination syndrome as binary, biotic or wind pollinated, with known ambophilous species in the genus *Salix* assigned to the ancestral, biotic pollinated, state of angiosperms. Flowering time was the average of the range of months reported in each data source.

HF For each species in the HF dataset, we calculated a continuous mean off FLS "offset" defined here as the average foliate day of the year - average floral day of the year. We approximated our "physiological" FLS characterizaton be defining offset as (day of leaf budburst-day of flower bud burst) and our "functional" FLS catagorization by defining offset as (day of leaf expansion to 75% of final size- day of first flower open). We also recoded the HF continuous offset variables as continuous with postive offset values coded as hysternanthous and negative values as seranthous.

For all species-level case studies (USFS MTSV and HF), associations between hysternanthy and the trait predictors were modeled with logistical regressions in phylogenetic generalized linear modeling framework (?) using the R package phylolm (?). Our models incorporated a published angiosperm phylogenetic tree (?) pruned to match the species

list for each case study. Species found 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 for the MTSV dataset . We The models were run with 599 bootstrapped re-sampling iterations for each dataset (?). Continuous predictors were rescaled 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 assess the phylogenetic structure of hysteranthous flowering, we used the Caper package (?) to calculate a phylogenetic D statistic.

Phylogenetic signal

Dataset	Physiological	Functional
MTSV	0.22	0.07
USFS	0.13	0.65
HF	0.01	0.27

Figure 7: Phylo.D estimates for hysteranthous flowering in three case studies

Phylogenies

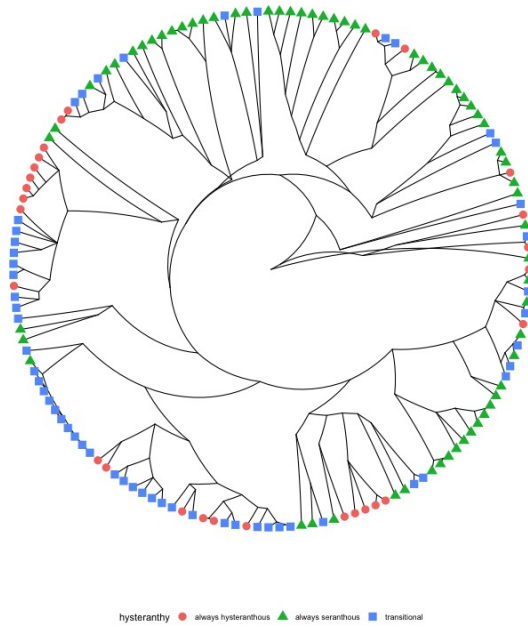


Figure 8: MTSV phylogeny

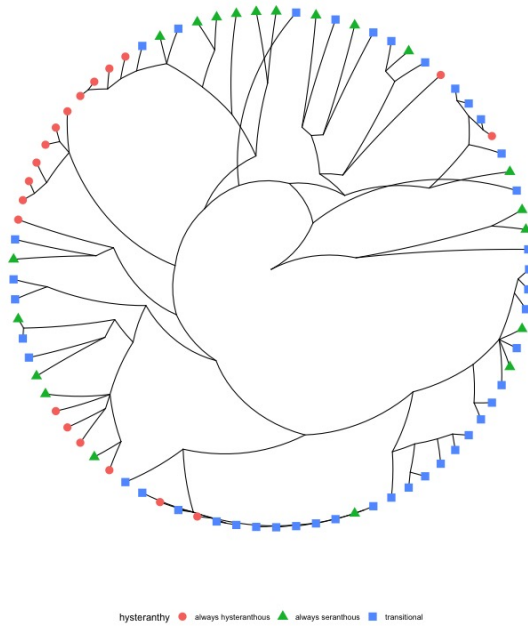


Figure 9: USFS Phylogeny

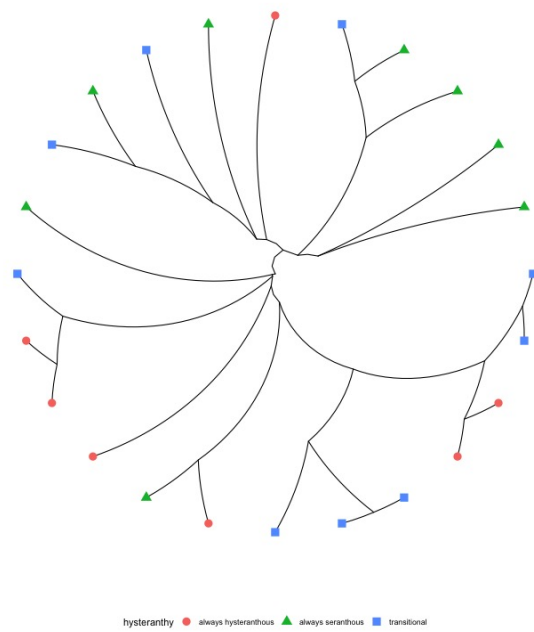


Figure 10: HF Phylogeny