

Reconciling competing hypotheses regarding flower-leaf sequences in temperate forests for fundamental and global change biology

Daniel Buonaiuto, Nacho, Lizzie

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Abstract

It is not only individual phenological events that affect organism fitness, but also the relationship between events. Deciduous woody plants exhibit considerable variation in the relative order of their reproductive and vegetative events, or their flower-leaf sequence (FLS). Research suggests that FLSs are adaptive, and several competing hypotheses may explain their function. Reconciling these hypotheses has been impeded by our conceptual orientation towards them. Classically, FLSs are treated as discrete categories at the species level, obscuring important inter-specific differences and ignoring substantial intra-specific variation. Here, we develop existing hypotheses to account for the inter- and intra-specific FLS variation seen in nature and evaluate these hypotheses with four case studies. Our inquiry provides three major insights towards a new framework for understanding FLSs. First, we find concurrent support for multiple hypotheses. Future research should allow for overlapping hypotheses and test individual hypotheses in smaller sub-groupings. Second, support for FLS hypotheses is highly sensitive to how FLSs are defined. Researchers should move away from categorization and use continuous measures of FLS. Finally, researchers should use an intra-specific approach to evaluate fitness consequences of FLS variation to help predict how climate-related alterations to FLSs will affect plant communities.

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 shown that it is not only individual phenological stages that affect these processes, but also the relationships between them (Ettinger *et al.*, 2018).

One phenological relationship that has long received scientific interest (see Robertson, 1895), and recently, increased attention in the literature (Savage, 2019; Gougherty & Gougherty, 2018) is the flower-leaf phenological sequence (FLS) of deciduous woody plants. In a typical model of plant life-history, vegetative growth precedes reproduction. However, for many species in the 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 suggests that this FLS has adaptive significance (Rathcke & Lacey, 1985).

A deep inquiry into the nature of this phenological pattern is necessary and particularly timely now because anthropogenic climate change is altering FLSs (Fig. 1). For the three European tree species we examined, the number of days between flowering and leafout have increased as a result of climate change, but the rate of change differs among them. If, as suggested, optimum not FLS patterning is an important component of fitness, this differential FLS sensitivity to climate change may influence which species will persist under altered climate conditions.

Despite recent advances in characterizing the evolution and underlying physiology of FLS (Gougherty & Gougherty, 2018; Savage, 2019), a major challenge to predicting how FLS patterns will shift in response to climate change is that we do not have a solid baseline understanding of variability in FLS. While some authors present general correlations 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 not only improve our ability to predict how FLS patterns will change in the future, but also allow for a more biologically relevant evaluation of the current FLS hypotheses, revealing avenues for future, direct hypothesis testing.

Here we 1) Review the hypotheses of woody plant FLSs and their respective predictions, 2) Evaluate variation in FLSs, and explore how FLS variation within species, populations and individuals alters the predictions of the hypotheses, 3) Show how the incorporation of variation reveals consistencies and anomalies in support for FLS hypotheses using several case studies from temperate forests, and 4) make recommendations for future study of FLSs.

Defining FLS

Flower-leaf sequences have traditionally been classified into qualitative categories that are almost always defined at the species level. The terms hysteroanthous, protoanthous, proteranthous or precocious flowering describe plants that produce flowers before their leaves. Synanthous describes species whose flowering period overlaps their leaf development and seranthous describes plants whose flowers open after their leaves emerge (Lamont & Downes, 2011; Heinig, 1899). But applying these categories is not so straightforward, and the ambiguity impedes hypothesis testing.

Both flowering and leaf phenological sequences consist of multiple sub-stages, and this introduces significant ambiguity into how we interpret qualitative FLS descriptions. Consider a species with the following FLS:

Flower budburst → leaf budburst → flower open → leafout

Phenological observers might classify this species as hysteroanthous because flower budburst proceeds leaf budburst. They would also be justified if they called this species synanthous because flowers open during the time between leaf budburst and leafout. But they could just as easily categorize this species as seranthous because flowers open after leaf budburst. If a species is called hysteroanthous in one data set and synanthous in another, we have no way of knowing whether this discrepancy reflects temporal or geographic variability in FLSs or is simply an artifact of observer decision-making.

Further, it is not clear that there is any biological significance to these particular FLS determinations. When we consider selection on FLS variation, we have no *a priori* reason to expect that a species whose flowers open two days after leaf budburst would be more similar to another species that flowers two weeks after leaf budburst than to a species whose flowers open two days before, though the first two would both be classified as synanthous and the later as hysteroanthous.

This uncertainty hampers our ability to accurately test the existing FLS hypotheses because any statistical relationship between FLS and other traits is biased by the subjectivity of the original observer.

In order to begin to for the traditional inter-specific categorical approach to FLSs to be useful for identifying the evolutionary significance of FLS variation, we must consider FLS patterns in the biological context of the various FLS hypotheses. The biological mechanisms underlying each hypothesis make different predictions the degrees of overlap between vegetative and floral phenophases, which is instructive for how to group or divide FLS patterns for hypothesis testing.

Below, we review the current FLS hypotheses, identify the underlying biology of each, and clarify how much overlap between flowering and vegetative growth they predict.

Wind pollination

The most prevalent FLS hypothesis suggests that hysteresis 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 leaves create 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, we expect that trees that flower during the early stages of leaf expansion would gain similar mechanical advantage to those who complete their flowering before any leaf activity. We see that in Harvard Forest, while wind-pollinated species flower both before and after bud burst, they all flower before their leaves reach 75% of their final size (Fig. 2). 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 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 asserts there is a significant cost to maintaining floral structures during any stage of leaf activity, and therefore only species whose flowering occurs 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 vegetative phenophases. Species that are not drought tolerant gain no advantage from flowering first, so in these species FLSs should be random.

Early flowering

A third possibility is that the 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 hysteresis vs. seranthous, as long as the absolute flowering time of the contrasting FLSs is the same. However, recent work from Savage (2019) has demonstrated that floral hydration is primarily maintained by the phloem rather than the xylem. With leaf phenology constrained by the timing of xylem re-growth, selection for early-season reproduction could drive flowering into the early season when xylem function is still suppressed, producing the hysteresis FLS. This might explain why hysteresis species tend to be the earliest species to flower (Fig. 2). Here, we expect longer time between flowering and leafing to be associated with earlier flowering phenology in general, and we expect more phenological overlap or a switch to seranthous in later flowering species. For

hysteranthly, we might also expect to see strong associations with other early flowering traits such as seed mass, dispersal season or cold tolerance, but the hypothesis does not exclusively require the selective driver of early flowering to be one of these traits (Savage, 2019). This hypothesis predicts that early flowering times should be strongly associated with flowering-first FLSs. It also is likely there would be a relationship between this FLS and other early flowering traits, but the absence of these associations does not invalidate the hypothesis.

Phylogenetics

Finally, it is also possible that FLSs are highly conserved traits, and the preponderance of hysteranthly in the temperate zone is a product of phylogenetic representation of the region rather than an adaptive aspect of the trait. In this framework, a species' FLS is under very weak or no selection so there are no expectations regarding the degree of overlap between flower and leaf phenological activity. This hypothesis predicts strong phylogenetic patterning in the FLS with no correlation with other traits.

A second problem

This approach can increase the utility of FLS categorization by helping researchers determine which categories should be separated or grouped given each hypothesis; however we must address a second problematic assumption of the classification system. We find that there is substantial intra-specific differences in FLS, and this variation has become even more obvious as climate changes (Fig. 1). Yet, FLS categories are always applied at the species level, and intra-specific variation has never been broadly assessed (Gougherty & Gougherty, 2018). Intra-specific variation is the engine of natural selection, and if it is substantial in FLS patterns, we can infer much about the origins of this trait as well as its trajectory as the climate changes.

Variation in FLS

We investigated individual FLS variation in the Harvard Forest data (O'Keefe, 2015), and found that the time between flowering and leaf activity varied by as much as several weeks for most species. This variability is lost completely in the classic framework of categorization. For example, for *Q. rubra*, a species classically listed as flowering and leafing in synanthly, there are some years in which flower budburst is more than a week before leaf budburst, and other years in which leaf buds burst weeks prior to floral budburst (Fig. 3). We also found significant population-level variation in FLS, using the Pan European phenological database PEP725 (Templ *et al.*, 2018), with the average time between flowering and leafing varying between sites by a week or more.

Given the variability of FLSs at the individual and population level, it is clear that considering FLS variability at only higher taxonomic levels obscures 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

Pollination syndrome is generally treated as a species-level trait, considered to be fairly immutable across ecological time and space. Because of this, we would not expect significant variation in FLS across populations or individuals because we 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. The pollination efficiency advantage from flowering-first diminishes as the canopy fills in, but we do not know at what point during leaf expansion pollination would become significantly encumbered. It is possible that interannual and population-level variation in the timing between flowering and leaf out for hysteranthous and synanthous individuals 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 this hypothesis.

Water dynamics

If FLS's are driven by water dynamics, we would expect there to be significant population-level variation in FLSs. Populations growing in drier habitats should flower earlier relative to their leaf activity than their counterparts growing in wetter areas that experience weaker selection for minimizing phenological overlap. Therefore, increased time between flowering and leafing should be negatively correlated with average soil moisture. Water availability may also drive interannual FLS variation, with drought years increasing hysteranthy, and wetter years permitting more FLS overlap. Because plants have many other physiological mechanisms for dealing with occasional drought, we only expect to see a signal for the association between drought tolerance and hysteranthy for observations of populations in consistently dry regions.

Early flowering

This hypothesis predicts some variation on the population level based on local adaptation. We would expect populations in which selection for earlier phenology is stronger, perhaps those in regions with shorter growing seasons, to flower earlier relative to their

leaf development. 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 more sensitive response to environment in flowering time resulting in FLS variation. This hypothesis predicts that early flowering years or populations should be associated with an increase in the time between flowering and leafing for hysteranthous species. It also predicts a tighter temporal correlation between flowering and leafing for seranthous species or those with mixed buds in which flower timing is constrained by leaf budburst.

Phylogenetics

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

Available evidence for FLS hypotheses in temperate woody species

Direct tests of these hypotheses are relatively rare in the literature, and—when tested—support for them is mixed. Many studies only test a single hypothesis, making comparison between them difficult. For example, the primary evidence for 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 hypotheses. We are aware of no direct tests that have tried and distinguish selection for hysteranthous from selection for 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, traits associated with early flowering in general. This raises the distinct possibility that hysteranthous may simply be one component of a larger suite of early flowering traits. We are also unaware of any studies that have mechanistically evaluated the water dynamics hypothesis, though observations of flowering in the dry tropics suggest that the timing of flowering in hysteranthous taxa is associated with a plant water status recovery due to leaf drop (Borchert, 1983; Reich & Borchert, 1984). Only recently has it even been

suggested that this hypothesis might be relevant in the temperate zone as well, as we would not expect that water status would limit biological activity in the wet springs of the temperate zone (Gougherty & Gougherty, 2018).

In contrast, studies testing multiple hypotheses have generally found support for more than one evolutionary driver of hysteresis. One study by Bolmgren *et al.* (2003) showed that wind-pollinated species tend to also be earlier flowering than their biotically-pollinated sister taxa, suggesting a relationship between the early flowering and wind pollination hypotheses. A recent study by Gougherty & Gougherty (2018) tested multiple hypotheses by modeling associations between species' trait and FLS patterns in the Great Lakes region. They found strong support for both the water dynamics and early flowering (flower timing and seed characteristics) hypotheses along with strong phylogenetic clustering.

In all of these cases, variability in FLS below the species-level was not addressed. Yet, there are datasets widely available that allow for testing these several hysteresis hypotheses concurrently, and at multiple taxonomic levels. To address this gap, we supplement our literature review with several analyses. First, we test all hypotheses at once with species-level datasets (previously-used in other analyses of FLS). Next, we leverage additional datasets to test how support for these hypotheses varies across the inter- to intra-specific levels.

We evaluated hysteresis in four phenological datasets, spanning species, population and individual-level data on a total of XX woody species. 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 two 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 above by measuring the time between several different floral and leaf phenophases. From the Pan European Phenological Database (PEP725) (Templ *et al.*, 2018) we obtained spatially and temporally explicit, quantitative flowering and leaf phenology for four common European tree species. This allows us to evaluate FLSs only at the intra-specific level, but permits us to address variability among populations.

In considering all data sets in tandem two clear trend emerge: First, in accordance with the recent literature, we found support for multiple hypotheses (figure 4. There was generally strong support for the early flowering and wind pollination hypotheses, poor support for the water dynamics hypothesis, and the phylogenetic signal was usually strong but highly variable (table ??). But we also found that relative importance of each predictor, and therefore, the strength of the support for each hypothesis, changed significantly depending on how we defined hysternanthy in the data set. Using continuous measures of FLS stabilized removed instability in parameter methods (across definitions), but increased the uncertainty around the estimates, suggesting categorical data may be over-simplifying trait relationships and providing inaccurately high levels of certainty.

We used our intra-specific datasets to test some of the predictions we made about intra-specific variability in the water dynamics and early flower hypotheses. Contrary to our prediction, we found that dry years correlate with a decrease in time between flowering and leafing for hysternanthous species, largely due to delayed flowering. When we examined the relationship between 30 year soil moisture records (DWD, 2019) and population level variation in FLS timing across Germany, we found a weak negative association between average soil moisture levels and time between flowering and leafing as predicted by the water dynamics hypothesis. However, when we incorporated other predictors, such as flowering time into our analysis, the association disappeared, and early flowering was the only predictor of hysternanthy (Fig. 4, PEP725 estimates).

In accordance with our predictions for the early flowering hypothesis, we found that for hysternanthous species, FLS variation is much more tightly correlated with variation in flowering timing than in leafing timing, but this contrast is far less stark in seranthous *Aesculus hippocastum* (table ??). Though our intra-specific data set is species limited, we can refine our prediction to say that plasticity in the first phenophase of the season (flowering for hysternanthous species and leafing for seranthous species) seems to drive variability in FLSs, but this observation should be tested more rigorously and explicitly in future work.

While the inter- and intra-specific case studies are not perfectly comparable (ie the wind pollination hypothesis cannot be evaluated on the intra-specific level), the general insights from our intra-specific studies supports the relationships found in the inter-specific case studies and provide novel, higher resolution insights of their own.

Future

Perhaps more important than the results of all of our specific case studies themselves, is that in considering them together, we gain a more comprehensive picture of where our understanding of this phenological trait is currently, and where it needs to go. Below we highlight five characteristics of FLS that should be incorporated into future research.

Multiple hypotheses explain FLSs

Our results underscore other lines of evidence that show multiple hypotheses should be starting point for all future FLS research. While there is certainly value to broad taxonomic studies, and future large-scale analyses should continue, the consistent support for multiple hypotheses shows there are limits to the utility of these kinds of studies. We suggest that it is better to explore the evolutionary dynamics of hysteresis 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 hysteresis among biotically-pollinated taxa? It certainly is not wind pollination efficiency. Or, what factors accounts for variability in hysteresis among wind-pollinated taxa? Incorporating a more explicit phylo-biogeographic approach would be instructive at this level, for example: are their phylo-geographic commonalities between the few biotically-pollinated hysteresis species in Eastern flora?

Even with drilling down to sub-groupings, interspecific trait-association models can only take us so far. One reality of these kinds of studies is that we never know that 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 inter-specific models, to represent the water dynamics hypothesis. Is this really a good proxy for drought tolerance? Further, species evolve a suite of traits for any function, and unmeasured traits might bias our results (Davies *et al.*, 2019). For example, wind-pollinated species could compensate for pollen intercepted by a synanthous or seranthous FLS by over-producing pollen or through self-pollination. To really understand FLS across large taxonomic space, one would have to compare species across an unfeasibly large, N-dimensional trait space, suggesting we will need to utilize other, complementary approaches.

Intra-specific variation in FLS

In this paper, we have shown that FLSs can be highly variable at the intra-specific level. This variation can be leveraged through carefully designed research to overcome many of the limitations of larger trait-correlation models. Unlike with inter-specific approaches, focusing on FLS variation within species holds most other traits relatively equal, avoiding the problem of tradeoffs with latent unmeasured traits. Evolutionary theory predicts that intra-specific variation should follow the same trends as inter-specific variation, and consistent agreement between inter- and intra-specific, as we found in our analysis, will help narrow in on certain hypotheses.

The FLS is a quantitative trait

Treating FLS observations as continuous variables are the most accurate way to describe these data. Our modeling work shows that this is an important step towards reducing observer bias and revealing important inter-specific differences that are masked by categorization. Quantitative measure of phenology (e.g. the BBCH scale, Finn *et al.*, 2007), standardize data across time and space, observer, and analyst. Adopting such measurements in the study of phenological sequences would allow for FLS patterns to be compared across larger temporal, geographic and taxonomic scales, giving researchers more power to accurately address questions about FLS variation.

FLS and fitness

While trait associations point to past selection, fitness is the driver of trait evolution, and at the core of each FLS hypothesis is a fitness prediction. By utilizing intra-specific comparisons and continuous measurements of FLS, we can move beyond trait associations and test the fitness consequences of FLS variation.

Variability in hysteresis should lead to variability into fitness outcome at the intra-specific level. For example, the wind pollination hypothesis predicts that with all else equal, years with increased time between flowering and leafing should correlate with more pollination success. The water dynamics hypothesis suggests hysteranthous populations with a consistently large time between flowering and leafing should better tolerate drought. These predictions could be directly assessed through well-designed experiments and field studies.

FLS and physiology

Decades of research suggests that both floral and vegetative phenological events are cued by temperature and photoperiod (Forrest & Miller-Rushing, 2010; Flynn & Wolkovich, 2018), suggesting they are under shared genetic and physiological control. But to yield the FLS variation seen in nature, there must be systematic differences in reproductive and vegetative phenological responses to the environment. Researchers can use intra-specific variation in FLS to identify which cues dominate each phenological process and better understand the underlying genetic and physiological constraints that structure phenological sequences.

Our proposed framework provides a path to understand the multivariate drivers of FLSs in woody plants. Through examining FLS variation in more targeted taxonomic assemblages and using quantitative data with mechanistic metrics, we can refine the existing FLS hypotheses and better comprehend the causes and consequences of FLS variation at multiple taxonomic scales. This is an essential step towards a more complete

understanding of the fundamental biology of temperate woody plants, and for predicting the fate of these species as global climate continues to change.

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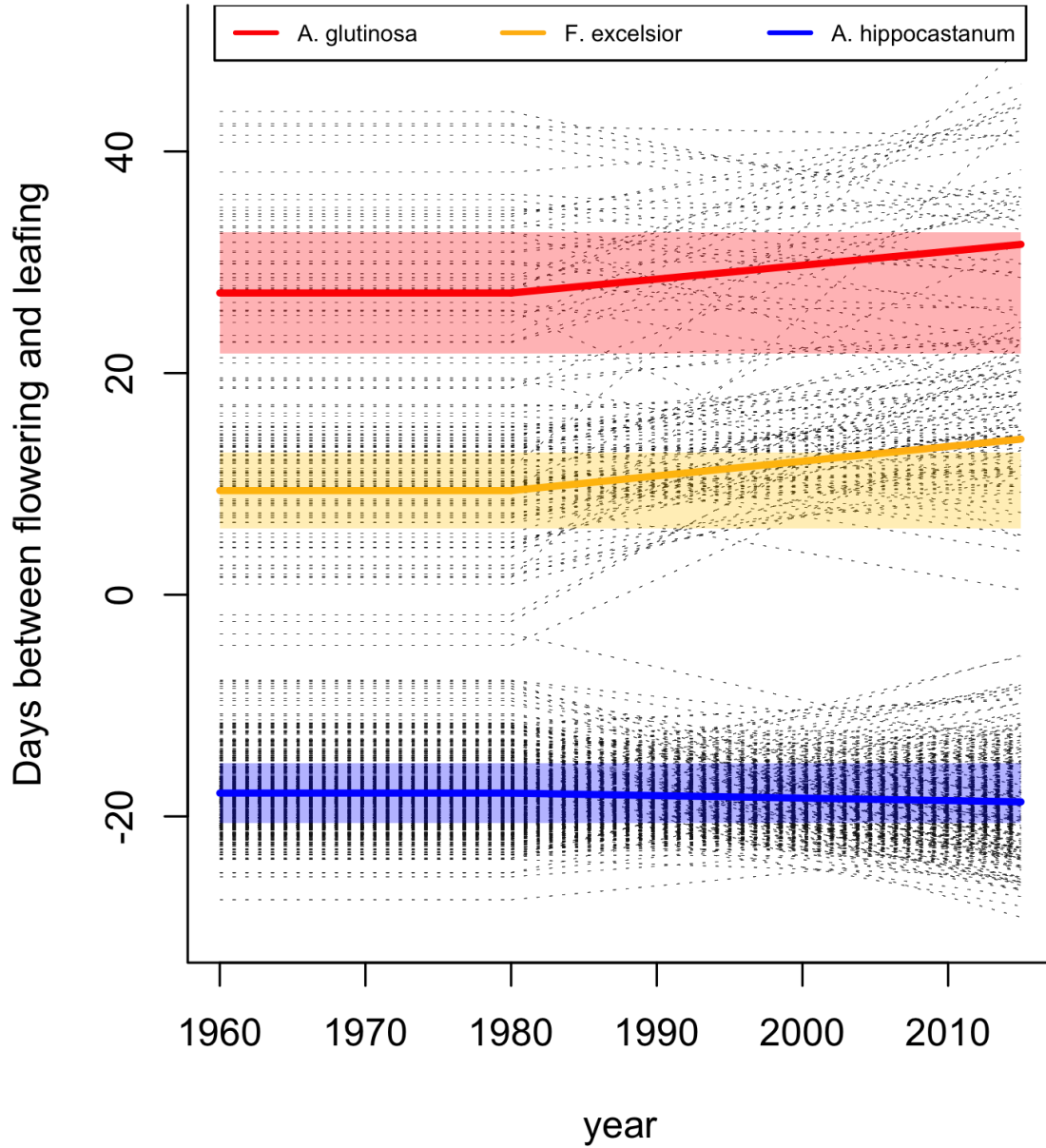


Figure 1: Trends in average FLS offset across Europe for three tree species from 1960 to 2015. Highlighted regions indicate historic range of FLS variability. For all species, the time between flowering and leafing is increasing but the rate of change differs between species and sites

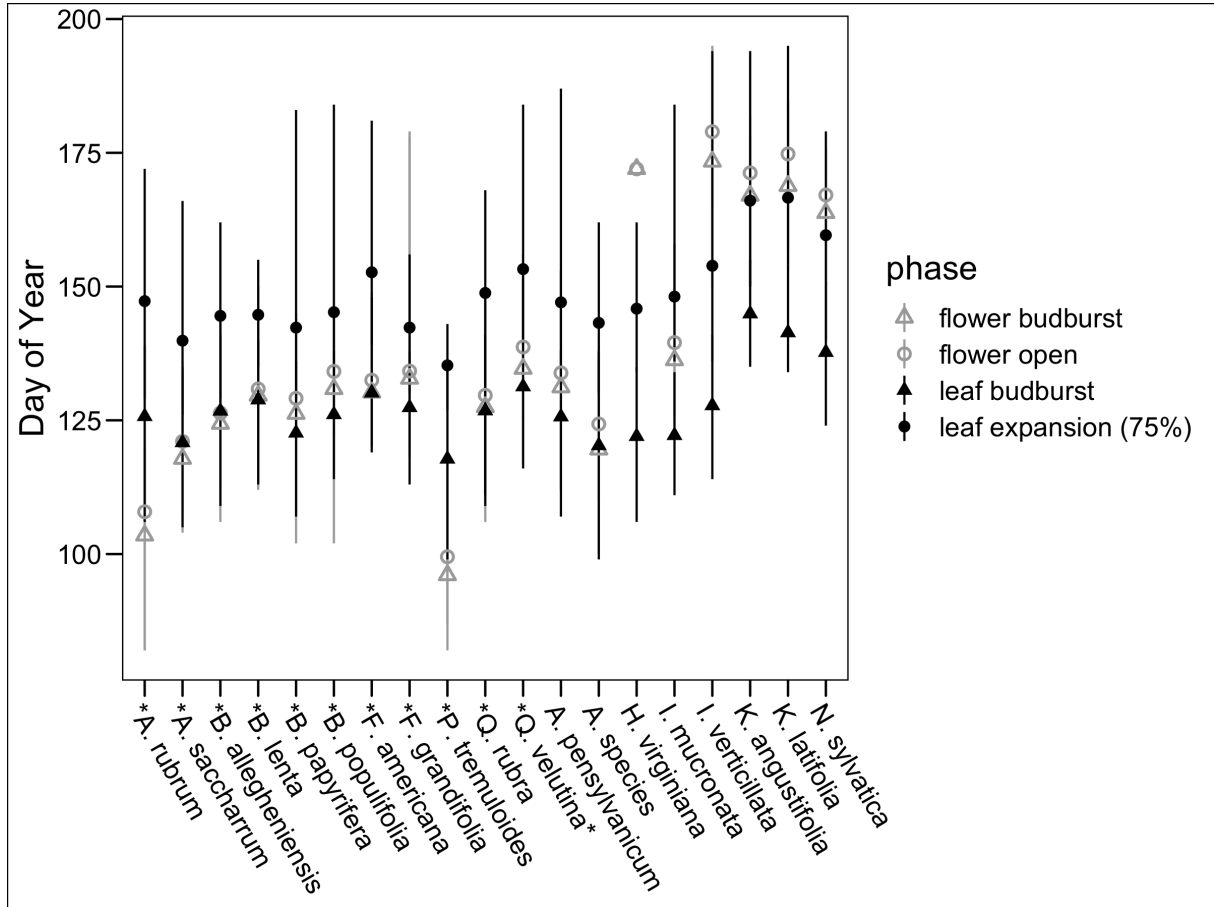


Figure 2: Average day of phenological events for woody plant species at Harvard Forest in Petersham, MA from 1990-2015. This community displays all major FLS patterns, but because of overlapping floral and vegetative development and interannual variability in phenology, it is difficult to neatly assign all species to a FLS category. Other notable patterns relevant to the FLS hypotheses can be seen. For example, as predicted by the early flowering hypothesis, the earliest species to initiate spring phenology are hysteroanthous and as predicted by the pollination syndrome hypothesis, wind-pollinated species (indicated with a *) may vary in whether their flowers or vegetative buds break first, but all open their flowers before leaves expand to 75%.

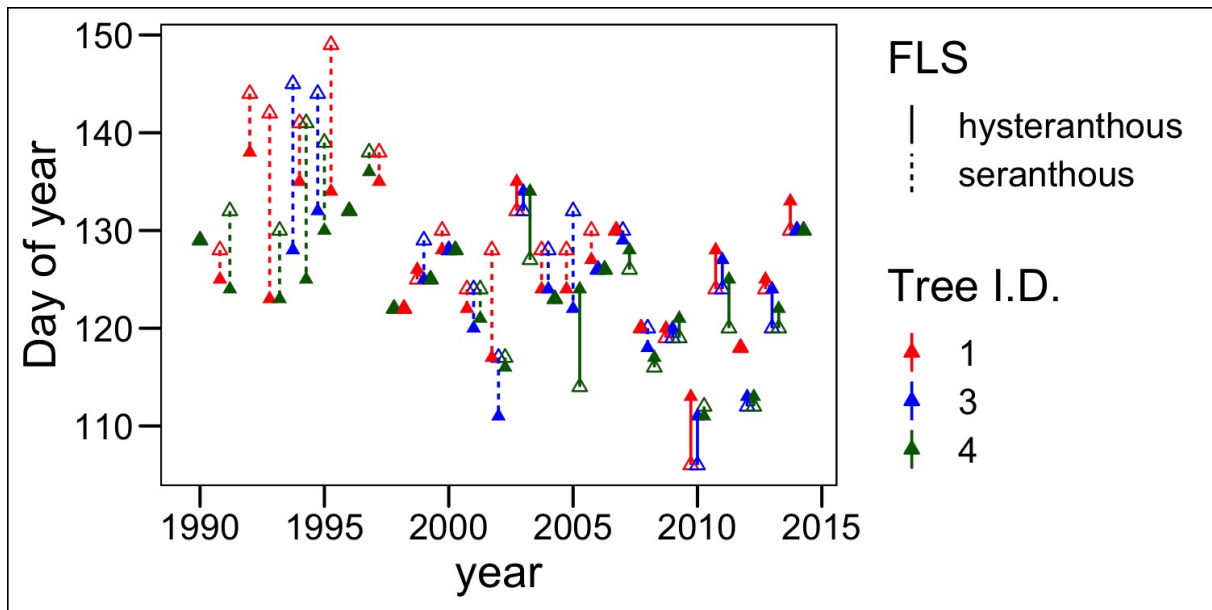


Figure 3: FLS variability among years and within a population of *Quercus rubra* at Harvard Forest. While this species is typically reported as flowering and leafing in tandem, the order of flower and leaf bud break, and the time between them varies considerably within the community in a give year, and within an individual across year.

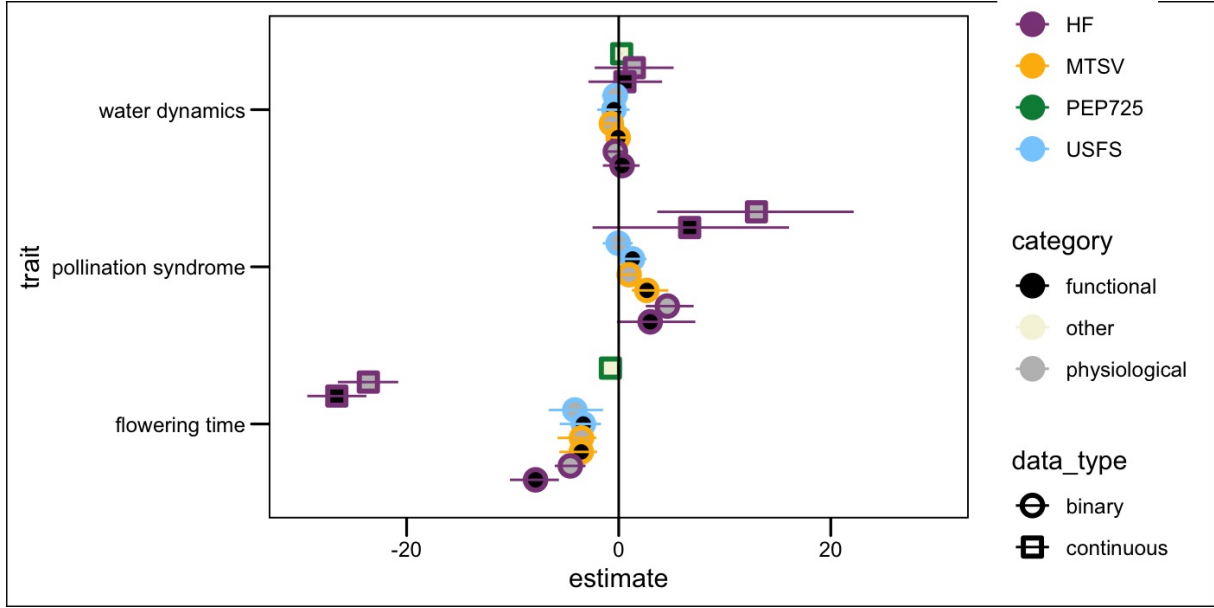


Figure 4: Estimated effects of water dynamics (minimum precipitation across species range or average soil moisture), pollination syndrome, and flowering time on FLS patterns across four case studies. We used phylogenetic adjustments and standardized units to make a basic comparison of four datasets of different taxonomic scopes (intra-vs. interspecific variation) data types (categorical and continuous) and definitions of FLS. While absolute parameter estimates should not be directly compared due to scaling inconsistencies between models and different modeling approaches for differing data structure, all models support the consensus that wind pollination and early flowering is associated with a flowering first FLS, and there is little effect of measures of water dynamics. Lines represent 95% bootstrap or credible intervals depending on the modeling framework.