

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

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Abstract

Phenology is a major component of an organism's fitness. While individual phenological events affect fitness, growing evidence suggests that the relationship between events may be equally or more important. This may explain why deciduous woody plants exhibit considerable variation in the order of reproductive and vegetative events, or flower-leaf sequences (FLSs). Research suggests that FLSs are adaptive, with several competing hypotheses to explain their function. Here, we augment the existing framework for the study of FLS to incorporate FLS variation at multiple taxonomic scales and reconcile the existing hypotheses with detailed case studies from temperate forests. Using this novel approach, we found concurrent support for multiple hypotheses that reflect the complicated history of migration and community assembly in the temperate zone. We highlight how adopting a quantitative, intra-specific approach generates new hypotheses and avenues for evaluating fitness consequences of FLS variation and provides cascading benefits to improving predictions of how climate change will alter FLSs and thereby re-shape plant communities and ecosystems.

Introduction

Phenology, the timing of seasonal life cycle events, allows organisms to synchronize 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 (and other temperate regions of the Northern Hemisphere), 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 forests, and its prevalence suggests that this FLS has adaptive significance (Rathcke & Lacey, 1985).

Understanding this phenological pattern is timely because anthropogenic climate change is altering FLSs. Long-term observations show the number of days between flowering and leafout is increasing as a result of climate change, but the rate of change differs up to five-fold among species (Fig. S1). If FLSs are indeed an important component of woody plant fitness, this inter-specific variation will exacerbate fitness differences between species, influencing which species will persist under altered climate conditions.

Long-term data also highlight high within-species variability in FLSs. Despite recent advances in understanding the physiology and evolution of FLSs (Gougherty & Gougherty, 2018; Savage, 2019), most research has not addressed this variability—potentially stymieing efforts to predict how FLS patterns will respond to climate change. While some authors present general correlations between flowering and leafing phenology (Lechowicz, 1995; Ettinger *et al.*, 2018), the high-resolution dynamics of this variability have not been thoroughly evaluated (Gougherty & Gougherty, 2018). We suggest that characterizing intra-specific variation in FLSs is critical to understanding this important phenological sequence. We propose a new conceptual framework for the study of FLSs built on continuous measures of both inter- and intra-specific FLS variation. This shift will improve our ability to predict how FLS patterns will change in the future, and reveal novel avenues for direct hypothesis testing to better understand the fundamental biology of this important phenological sequence.

Here we 1) review the hypotheses of the origins of FLSs and their respective predictions, 2) compare the biological basis of the current, inter-specific categorical FLS framework to our proposed intra-specific, quantitative approach 3) test our framework with a detailed case study of long-term phenology records from Harvard Forest in Petersham, MA, and 4) identify avenues for future FLS research.

FLS hypotheses and their predictions

Hypotheses of FLS

Wind pollination

The most prevalent FLS hypothesis suggests that flowering-first is an adaptation for wind-pollination, with leafless flowering allowing for more efficient pollen transfer (Whitehead, 1969; Stephen H. Spurr, 1980; Friedman & Barrett, 2009). The primary evidence for this hypothesis comes from pollen diffusion studies (e.g., particle movement through closed and open canopies, Niklas, 1985; Nathan & Katul, 2005; Milleron *et al.*, 2012) and suggests canopy structure encumbers pollen movement. This hypothesis predicts a strong association between FLS and pollination syndrome.

Water dynamics

Another hypothesis suggests that flowering before leaf development is an adaptation to reduce water stress caused by concurrently maintaining floral hydration and leaf transpiration. (Franklin, 2016). Observations of flowering in the dry tropics where this FLS pattern is also common confirm that the timing of flowering in these taxa is associated with a water status recovery due to leaf drop (Borchert, 1983; Reich & Borchert, 1984), and recent analysis of temperate flora has also yielded support for this hypothesis despite that fact that temperate forests are rarely water-limited during the spring flushing season (Gougherty & Gougherty, 2018). This hypothesis predicts a strong relationship between FLS and metrics of hydraulic demand.

Early flowering

A third possibility is that the flowering-first FLS is a physiological byproduct of selection for early flowering (Primack, 1987). Here, there is no functional advantage to a species flowering before or after leafing; all that matters is its absolute flowering time. Primack (1987) notes that flowering-first 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 possibility that this FLS may simply be one component of a larger suite of early flowering traits. Recent work from Savage (2019) demonstrated that spring flower phenology is less constrained by prior phenological events than leaf phenology, which would allow selection to drive flowering into the early

season, producing the the flowering-first FLS. Given this hypothesis, we would expect a strong relationship between a flowering-first FLS and early flowering in general.

Phylogenetics

Finally, it is also possible that FLSs are highly conserved traits for which FLS variation reflects macro-evolutionary relationships among taxa rather than selection. If this is the case, the preponderance of flowering-first in the temperate zone is a product of phylogenetic representation of the region rather than an adaptive aspect of the trait. In a recent analysis, Gougherty & Gougherty (2018) found strong phylogenetic clustering in FLS variation. Given this hypothesis, we would expect to see a strong phylogenetic signal for FLS variation.

While decades of inquiry have advanced each of these hypotheses independently, there is no clear consensus regarding their comparative merits. This is in part, because the aim of most FLS studies was to thoroughly test a single hypothesis, rather than make broad comparisons between them. Studies designed to compare hypotheses have generally found support for multiple hypotheses (see Bolmgren *et al.*, 2003; Gougherty & Gougherty, 2018), but understanding the relative importance of each hypothesis and the relationships between them requires further exploration, which may be limited by the very way in which FLS patterns are generally described.

We argue that a satisfying reconciliation of these hypotheses is possible with a shift to a new conceptual framework for the study of FLSs. Under the current framework, FLSs are described qualitatively, and defined at the species level. We suggest that quantitative, intra-specific measures of FLS are more compatible with the biological processes underlying the very FLS variation that research aims to understand. Below we present an overview of the classic approach to describing FLSs and highlight some of the challenges that can arise when using it for data analysis. We then identify two major assumptions about FLS variation in this current framework and discuss how they compare to the observed phenological patterns in natural systems.

The current FLS framework

Describing FLSs

The current framework describes three main FLS categories: flowers before leaves (hysteranthly, proteranthly, precocious flowering); flowers with leaves (synanthly); and flowers after leaves (seranthly) (Lamont & Downes, 2011; Heinig, 1899). Some data sources (e.g. Burns *et al.*, 1990; Barnes & Wagner, 1981,2004) include additional categories: “flowers before/with leaves” and “flowers with/after leaves”, but it is unclear whether these categories describe intermediate FLS patterns or FLS variability in these species. While these categories are conceptually reasonable, applying them to real phenological sequences is not always so straightforward.

Both reproductive and vegetative 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** → **first flowers open** → **leafout** → **peak flowering** → **end of leaf expansion**

Observers could justifiably classify this species as: 1) Hysteranthous because flower budburst proceeds leaf budburst, 2) Synanthous because flowers open during the budburst-leafout inter-phase, 3) Seranthous because

peak flowering occurs after leafout. This problem extends beyond this simple example to real datasets, (e.g. O’Keefe, 2015) where the same ambiguities exist (Fig S3). Not surprisingly then, different sources may classify the same species differently. We compared species-level FLS descriptions in two of the most comprehensive records of FLS, Michigan Trees and its companion volume Michigan Shrubs and Vines (MTSV) (Barnes & Wagner, 1981,2004; Burton V. Barnes, Christopher W. Dick, 2016) with The USFS Silvics Manual Volume II (Burns *et al.*, 1990). Of the 49 overlapping species, 30% were classified differently. Such different classifications could reflect interesting temporal or geographic variability in FLSs, but—given current definitions—they could equally be an artifact of observer classification decisions.

Categorization can often introduce biases in analyses (Naggara *et al.*, 2011; Royston *et al.*, 2006). In the case of FLSs, the hypotheses themselves may suggest different boundaries than the ones prescribed by the traditional framework. We illustrate this below by contrasting the biological mechanisms underlying two of the major adaptive hypotheses.

The wind pollination hypothesis hinges on the fact that leaves create a substantial physical disruption to pollen transfer, a premise that would not necessarily be true for the early stages of leaf expansion when tiny leaf primordia would have little impact on environmental structure. Rather, trees that flower during the early stages of leaf expansion should gain similar advantage to those who complete their flowering before any leaf activity. Alternatively, because transpiration intensifies as soon as leaves begin to expand (Breda & Granier, 1996; Wang *et al.*, 2018), the water dynamics hypothesis asserts there should a cost to maintaining floral structures during any stage of leaf activity. Here, only species whose flowering occurs before any leaf expansion should gain a hydraulic advantage.

Given the differences in biological processes underlying these hypotheses, statistical relationships between FLS and traits will fluctuate depending on where category boundaries are drawn. For the example presented above, we would expect to see the strongest signal of the wind-pollination hypothesis when the category of hysteranthly includes species that flower before and with early leaf development. The strongest signal for the water dynamics hypothesis should occur when hysteranthly is restricted to only species that flower before any leaf activity. If these hypotheses require different categorization schemes to accurately capture the underlying biology, it becomes very difficult to compare them in the same modeling framework.

We compared associations between FLS variation and traits related to each FLS hypothesis in both the USFS and MTSV datasets. To evaluate categorization bias, we applied two alternative FLS categorizations; physiological hysteranthly, which allowed for no overlap between floral and leaf phenophases, and functional hysteranthly, which allowed for a degree of overlap. We found that for both datasets, the strength of associations between FLS and predictors and the phylogenetic signal were highly sensitive to how FLSs were defined (Fig: S2, e.g. pollination syndrome, Fig: S4). This is because alternate categorization boundaries re-shuffle the species included in each classification, affecting both the trait distributions within each category and the phylogenetic patterning across the tree (Fig. S5). These findings suggests that this categorical approach is inherently picking up substantial bias along with biology.

Inter-specific variation in the current framework

According to the current framework, species are classified simply based on sequence alone. Biology, however, has continually shown that the duration of and time between phases also matters (Inouye *et al.*, 2019). We quantified the timing between reproductive and vegetative events for several species at Harvard Forest (O’Keefe, 2015), and found that, when considering measures of time, FLSs of species within each category can be quite different (Fig. 1a). This substantial inter-specific variation, previously obscured by categorization, could in reality be the fingerprint of selection on FLSs.

Intra-specific variation in the current framework

In the current framework, FLS categories are assigned at the species level, however, if there is substantial variation in FLS below the species level, understanding what drives this variation may be a critical step in linking FLSs and performance under altered climate conditions. By re-analyzing the long-term phenology records from Harvard Forest (O’Keefe, 2015), we found that the time between flowering and leaf activity varied by as much as several weeks between individuals and years, and in some species the sequence itself regularly switched across years and individuals (Fig. 1b). As far as we know, this is the first time intra-specific variation in FLSs has been quantified, and the magnitude of variation at this level suggests that considering FLSs at finer taxonomic resolution—i.e. intra-specifically—has the potential to clarify the mechanisms underlying inter-specific differences.

A new framework for FLSs

There are other ways to approach FLSs that relax the assumptions of the current framework, increase the precision of FLS descriptions, and capture important biological variation that could be leveraged to better understand this phenological syndrome. We propose a shift from categorical, species-level descriptions of FLS to continuous individual-level quantification, i.e. reporting the number of days between specific phenophases. This approach eliminates categorization bias, reduces the noise associated with unmeasured variation, and offers novel avenues for fine-tuning FLS hypotheses.

Quantitative measures of FLS across multiple taxonomic scales should improve FLS-trait association models like the ones presented above by allowing researchers to explicitly incorporate the multiple levels of FLS variation into such models (i.e. through hierarchical modeling). Quantitative measures of phenology (e.g. the BBCH scale, Finn *et al.*, 2007) also 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. Conversely, since phenology information is often taxonomically and geographically biased (Wolkovich *et al.*, 2014; Willis *et al.*, 2017), combining information from multiple levels may provide important insights to the nature of this trait.

An intra-specific FLS framework augments the existing FLS hypotheses and generates new, testable predictions. One of the challenges of inter-specific comparisons that may be mitigated by an intra-specific approach is that species evolve a suite of traits for any function, and unmeasured traits might bias results (Davies *et al.*, 2019). For example, wind-pollinated species could compensate for pollen intercepted by a seranthous FLS by over-producing pollen or through self-pollination, and omitting such trade-offs from analyses would bias inter-specific comparisons. Focusing on FLS variation within species holds most other traits relatively equal, which will allow researchers to move beyond simple FLS-trait correlation analyses and begin to make predictions and evaluate the performance consequences of FLS variation, which, importantly, could help anticipate the fitness effects of changing FLS patterns with climate change.

Testing the new framework

To test our proposed framework, we modeled the associations between FLS and traits related to the FLS hypotheses using both the classic, categorical FLS framework and our new, quantitative one using long-term phenological records for woody species at Harvard Forest (O’Keefe, 2015). With the classic approach, we

found strongest support for the early flowering hypothesis, some support for the wind pollination hypothesis and poor support for the water dynamics hypothesis, with no substantial interactions between predictors and a strong phylogenetic structure to FLS variation (Fig. 2, Fig. S4 panel f.). These results are qualitatively similar to models from two other large categorical FLS datasets (Fig. S2).

The quantitative version of the model paints a more complex picture of the function of FLSs, highlighting key biological insights obscured by categorization. As in the categorical model, we found strong effects of flowering time, pollination syndrome and phylogeny on FLS variation (Fig. 2, Fig. S4). However, in the quantitative model we also detected a signal for the water dynamics hypothesis. Most significantly, in this model we identified strong interactions between predictors. While early flowering is associated with hysteranthly in all species, this effect was even more pronounced in wind-pollinated taxa. (Fig. 2). Further, we also found that water dynamics were associated with increased time between flowering and leafing in biotically-pollinated taxa but not wind-pollinated taxa (Fig. 3).

These systematic differences between pollination syndromes are informative. Many of the biotically-pollinated species of the temperate forests trace their bio-geographic origins to the same tropical regions (Daubenmire, 1972) in which the water dynamics hypothesis originated (Janzen, 1967; Franklin, 2016). In particular, many biotically-pollinated, hysteranthous species in the temperate zone are geographic outliers from largely tropical clades (e.g. *Fabaceae*, *Lauraceae*, *Annonaceae*). It may be that for these taxa, hysteranthly developed in a warmer, drier selection environment and bears no functional similarity to hysteranthous flowering in wind-pollinated species that predominately evolved in the temperate zone. While beyond the scope of this analysis, the bio-geography behind our findings suggests a more complex story of convergent evolution, migration history, and community assembly in hysteranthous flowering than can be encompassed by any single FLS hypothesis.

While it may be surprising that there is a relationship between hydraulic demand and FLSs in the temperate zone where water tends to be abundant in the spring season (Polgar & Primack, 2011), it may be that hysteranthly in biotically-pollinated species in the temperate zone is maintained because there is no strong selection against it, or it has come to serve a different function. Hysteranthous flowering may expand species' temporal niches and partition inter-specific competition for pollinators, or it may be a useful tool for attracting them (Janzen, 1967). For example, there is some evidence that hysteranthous species invest less in floral resources than seranthous sister taxa (Gunatilleke & Gunatilleke, 1984), suggesting that perhaps their flowers are easier for pollinators to locate. While these explanations are still speculative, they are readily testable under the new framework.

Our findings suggest that the tendency for previous studies to find support for multiple hypotheses (Bolmgren *et al.*, 2003; Gougherty & Gougherty, 2018; Savage, 2019) is consistent with the biological processes that shape FLSs. Using available data, we have demonstrated the advantages of a new conceptual framework for the study of FLSs based on quantitative measures of individual variation in FLS patterns. Using these methods, we found that in accordance with previous work, flowering time and pollination syndrome are important drivers of hysteranthly (Gougherty & Gougherty, 2018). We also found support for the water dynamics hypothesis in the evolutionary history of biotically-pollinated taxa, and identified several new, testable hypotheses regarding the biological nuances of FLSs. Together, these results provide a more comprehensive picture of where our understanding of this phenological trait is currently, and where it needs to go. Below we highlight four characteristics of FLS that we suggest, utilizing this new framework, could be incorporated into future research to improve our fundamental knowledge about this important life-history trait and better predict how alterations to FLSs will impact species in an era of global change.

The Future of FLS:

Multiple hypotheses explain FLSs

Our results underscore other lines of evidence that show multiple hypotheses should be the starting point for 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. A better understanding about the mechanisms leading to FLS variation may result from pattern deconstruction (i.e. grouping of species according to trait commonalities or their geographic or phylogenetic distributions) (Terribile *et al.*, 2009). For example, we know that wind-pollination efficiency is not driving hysteranthous flowering among biotically-pollinated taxa, so considering this group of species alone rules out one major FLS hypothesis and would allow for a better evaluation of alternative hypotheses.

FLS, performance and fitness

Even with focused work on sub-groupings of species, inter-specific trait-association models can only take us so far. As in most other areas of plant biology examining traits, research is hampered by the difficulty of knowing which are the “right” traits (Violle *et al.*, 2007). 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, but we have no way of knowing for certain that this is actually a good proxy for hydraulic demand or drought tolerance.

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 performance consequences of FLS variation. As we discussed above, variability in hysteresis should lead to variability in performance outcomes at the intra-specific level. For example, the wind pollination hypothesis predicts that years with increased time between flowering and leafing should correlate with more pollination success. The water dynamics hypothesis suggests hysteranthous populations with a consistently larger time between flowering and leafing should better tolerate drought. These predictions could be directly assessed through well-designed experiments and field studies, providing a new avenue to test the existing hypotheses and better understand how variability in performance may or may not ultimately translate into differential fitness as FLSs continue to shift due to climate change.

FLS and physiology

Decades of research shows 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.

Linking individual phenophases and sequences

In this paper, we reviewed and evaluated a century of research interrogating how selection operates on flower-leaf sequences in woody plants. By contrast, much of research on the evolution of plant phenology has sought to understand the selective forces operating on specific phenophases (e.g. Savage & Cavender-Bares, 2013; Ollerton & Lack, 1992). With growing evidence that adaptation drives both the absolute timing of individual phenophases and the relative timing between them we must continue to developing analytical tools that improve our understanding of the drivers of phenology holistically. Our treatment of FLSs here is a small part of this work, but understanding how selection shapes phenology both throughout the whole growing season and across years remains an exciting frontier for the study of phenology (Wolkovich & Ettinger, 2014).

Conclusions: Our proposed framework provides a path to understanding the 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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⁴¹⁷ Figures

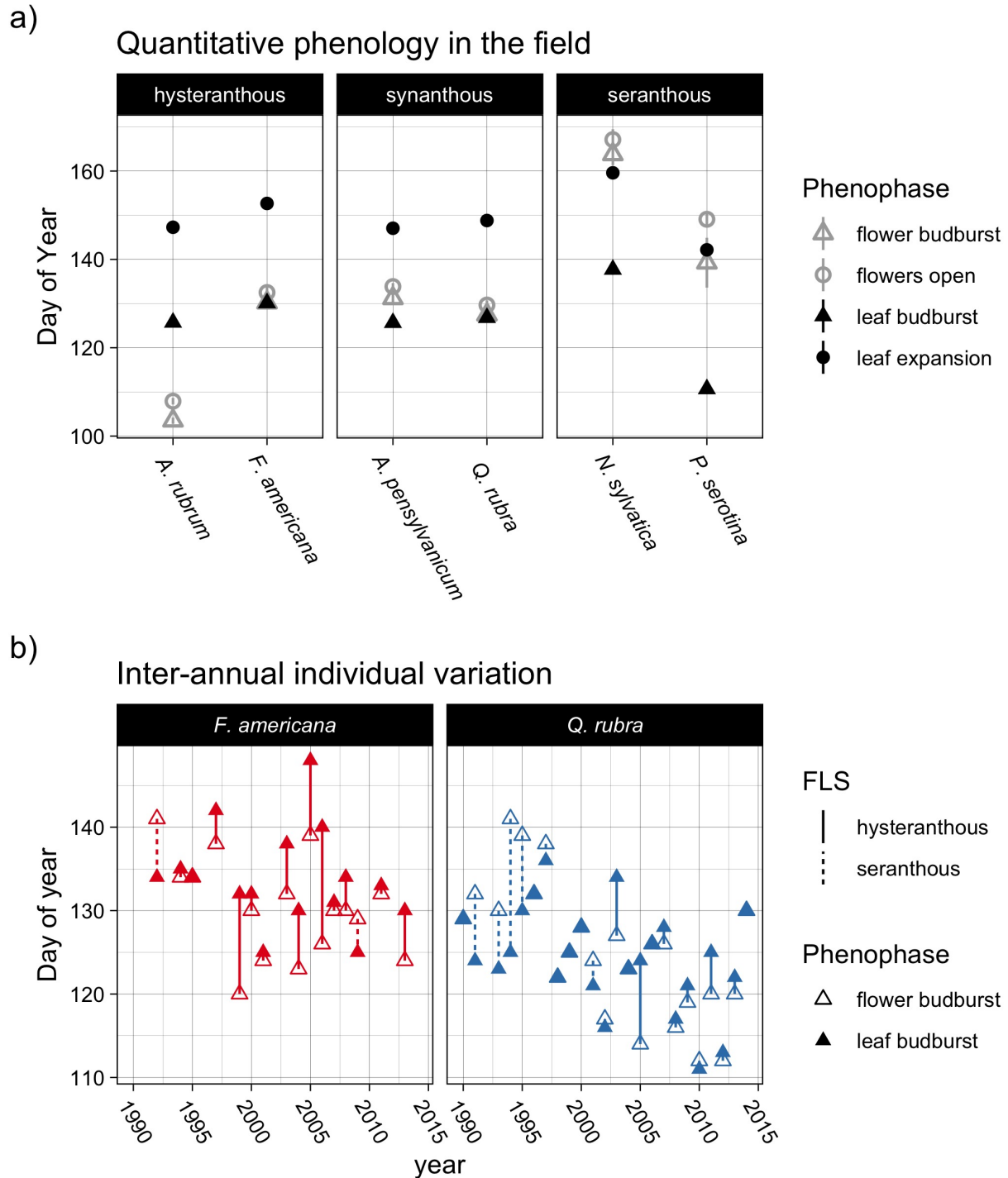


Figure 1: **The shift from categorical/inter-specific descriptions to quantitative/intra-specific measures of FLS reveals substantial, previously unrecognized variation.** Under the current framework, species are assigned to FLS categories by the order of phenophases alone. However, observations from Harvard Forest in Petersham, MA demonstrate that measuring the time between phenophases reveals substantial differences among species within each category **a)**, previously obscured by categorization. These records also show that below the species level, the time between flowering and leaf activity can vary by as much as several weeks for an individual across years and, in some species, an individual's sequence itself regularly switches across time **b)**. This inter- and intra- specific variation is key understanding the function of FLS variation in deciduous, woody plants.

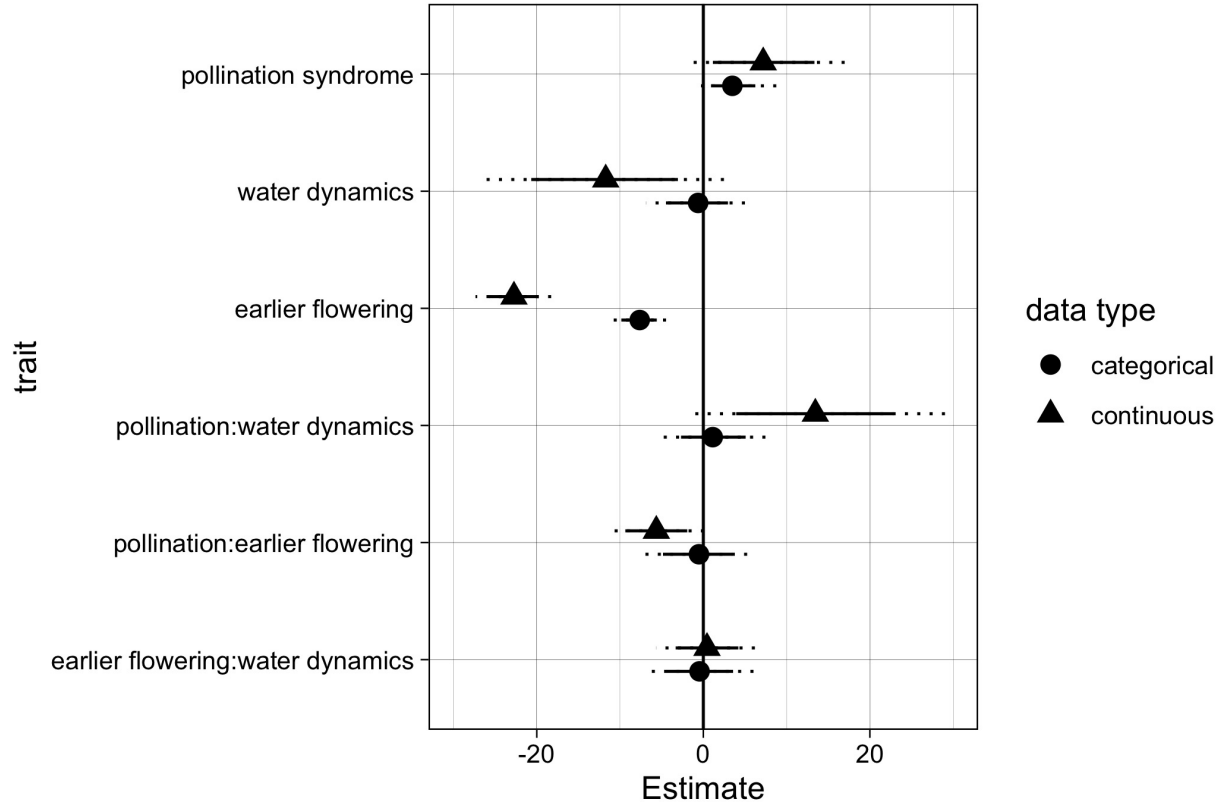


Figure 2: Mean estimates of the effects of FLS predictors on the timing between flowering and leaf expansion for individual woody plants at Harvard Forest between 1990-2015 reveal important differences between categorical and quantitative frameworks of FLS. With the categorical approach, there is a strong effect of flowering time and pollination syndrome on FLS variability, with no detectable effect of water dynamics or interactions between the predictors. However, with quantitative measures of FLS, we find increased support for the water dynamics hypothesis, and strong interactions between pollination syndrome and both flowering time and water dynamics. This interactions suggest multiple drivers of FLS variability in the temperate zone. Both models use a Bayesian, phylogenetic mixed modeling approach with standardized predictors to allow for comparisons between them. Symbols represent mean estimated effect of each predictor, with solid and dotted lines representing 50 and 95% credible intervals respectively.

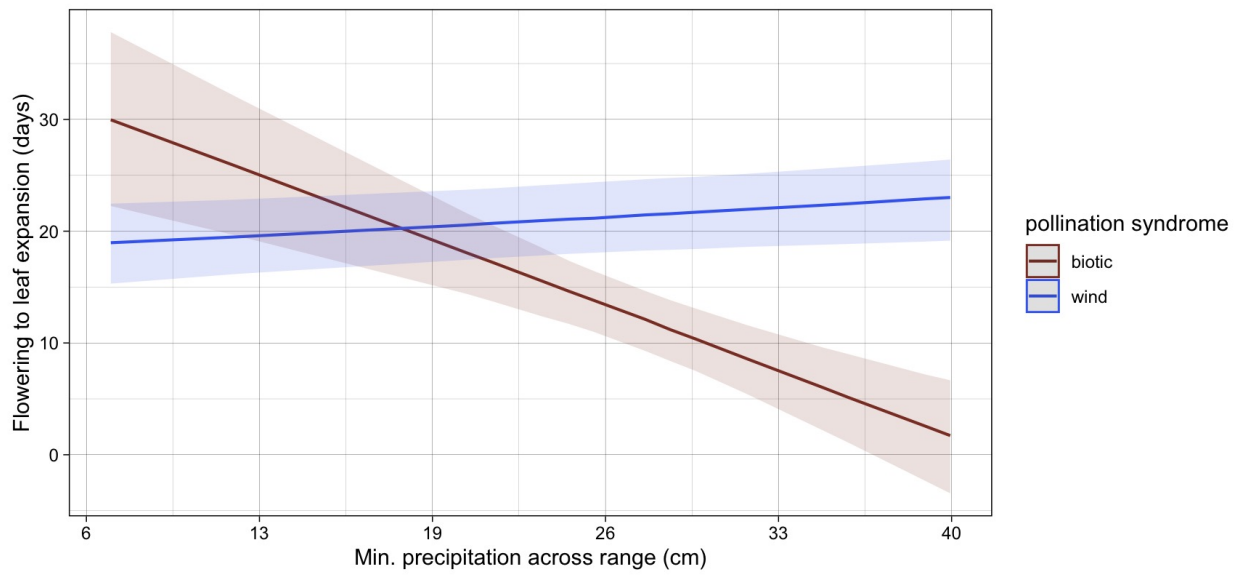


Figure 3: **For individuals flowering in early May, marginal effects from our quantitative FLS model suggest that water dynamics may be a driver of hysteresis in biotically-pollinated but not in wind-pollinated taxa.** These systematic differences in drivers of FLS could reflect greater differences in the bio-geographic histories of the wind and biotically-pollinated taxa of temperate forest communities.