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, 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).

Understanding this phenological pattern is necessary and timely because anthropogenic climate change is altering FLSs (Fig. 1). 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. 1). 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.

These long-term data also highlight high —within species— variability in FLSs. Despite recent advances in understanding the physiology and evolution of FLS (Gougherty & Gougherty, 2018; Savage, 2019), most research has ignored 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), fine-scale FLS variability has never been evaluated. We suggest that characterizing intra-specific variation in FLS 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) compare the biological basis of the current FLS framework to our proposed framework based on intra-specific, quantitiatve measures of FLS, 3) Test our framework with a detailed case study of long-term phenology records from Harvard Forest, in Petersham, MA 4) make recommendations to improve future study of FLSs.

FLS hypotheses and their predictions

Hypotheses of FLS

Wind pollination

The most prevalent FLS hypothesis suggests that hysteranthy 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 pollen movement is indeed encoubered by the maturing leaves. Given this hypothesis, we would expect a strong association between FLS and pollination syndrome, with wind-pollination associated with flowering-first.

Water dynamics

Another hypothesis suggests that flowering before leaf development is an adaptation to reduce water stress from maintaining floral hydration with transpiring leaves (Franklin, 2016). We are unaware of any studies that have mechanistically evaluated the water dynamics hypothesis, though observations of flowering in the dry tropics where this FLS pattern is also common suggest that the timing of flowering in these taxa is associated with a water status recovery due to leaf drop (Borchert, 1983; Reich & Borchert, 1984). Given this hypothesis, we would expect a strong relationship between FLS and metrics of drought tolerance, with drought tolerance associated with a flowering-first FLS.

Early flowering

A third possibility is that the flowering-first FLS is a physiological byproduct of selection for early flowering Despite decades of inquiry, only limited progress has been made towards any consensus for these hypotheses. Many studies only test a single hypothesis, making comparison between them difficult. In contrast, studies testing multiple hypotheses have generally found support for multiple hypotheses (see Bolmgren *et al.*, 2003; Gougherty & Gougherty, 2018). We argue that this lack of resolution stems from the fact that the current way that FLS patterns are conceptualized is not compatable with the biological processes underlying FLS variation that research aims to test.

The current FLS framework and its limitations

Under the current framework, FLSs are described qualitatively, and defined at the species level. This inherently introduces observer and interpreter bias into FLS data, and fails to capture underlying biology that structures FLS. Below, we highlight three main spurious assumptions of the current FLS framework and suggest more appropriate alternatives for describing FLS patterns.

Assumption I: FLS patterns are simple to describe and biologically meaningful:

In the current framework, there are three main FLS categories; flowers before leaves (hysteranthy, proteranthy, precocious flowering) flowers with leaves (synanthy) and flowers after leaves (seranthy) (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 straight forward.

The biological reality:

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 interphase 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. S2). Not surprisingly then, different sources (e.g.,

floras) 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 these 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 decision-making.

Given that the most complete FLS datasets currently come from regional guide books and floras, FLS categories were likely determined to aid with plant identification rather than to detail biological processes. Such categorization can often introduce biases in analyses (), and in this case, the FLS hypotheses themselves may suggest different boundaries. For example, the wind-pollination 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. 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), there should a cost to maintaining floral structures during any stage of leaf activity, and only species whose flowering occurs before any leaf expansion would gain a drought advantage. Given the biological processes underlying these hypotheses, we would expect statistical relationships between FLS and traits to fluctuate depending on where catagory boundiaries are defined. Important association may be missed entirely if, as in the case of the current categories, the imposed boundary does not match the biological process.

Assumption II: There are no meaningful differences within FLS categories

Consider two temperate taxa depicted in figure (Fig. 2a). According to the current framework, both would be classified as hysteranthous despite substantial differences in timing between reproductive and vegetative events.

The biological reality:

These species are classified the same simply based on sequence, but this ignores any other measure of time. Biology, however, has continual shown that the length of time also matters(Inouye *et al.*, 2019). This assumption obscures substantial inter-specific variation that could in reality be the fingerprint of selection of FLS. This inter-specific variation should be leveraged for more biologically reasonable hypothesis testing.

Assumption III: FLS variation is a species level trait

In the current framework, FLS categories are assigned at the species level.

The biological reality:

We investigated individual FLS variation at Harvard Forest (O'Keefe, 2015), and found that the time between flowering and leaf activity varied by as much as several weeks within species, between indiviudals and years. We also found similar levels of population level FLS variation accross Europe (Templ *et al.*, 2018). This variability is lost completely in the classic framework of categorization. For example, in the synanthous*Quercus rubra*, there are some years in which flower budburst is more than a week before leaf budburst, and other years in which leaf buds burst almost three weeks prior to floral budburst (Fig. **??** b). Given the variability of FLSs at the individual level, it is clear that considering FLS variability at only higher taxonomic levels obscures important realities about the biology of this phenological trait that may be instrumental for better tests of the FLS hypotheses.

Under the current framework, any statistical relationship between FLS and other traits is biased by the subjectivity of the original observer, the modeler, and the possibility that the associations being tested do not reflect the biology processes that shape FLS. We compared traits associated with hysteranthy in the USFS and MTSV datasets. We applied two alternative FLS catagorizations; physiological hysteranthy, which allowed for no overlap between floral and leaf phenophases, and functional hysteranthy, which allowed for a degree of overlap. We found the strength of associations between FLS and predictors is highly sensitive to how FLSs were defined **??**Fig:fig: muplots.USMT Supliment,e.g. pollination syndrome). With the current framework, any similar analyses would be subject to these biases, and inferences from them are tenuous.

A new framework for FLS

The shortcomings of the current FLS framework can be easily rectified with a shift from categorical, species-level descriptions of FLS to continuous individual-level quantification. The primary reason for this shift is logical; if researchers seek to understand the *biological* processes driving FLS patterns, we will be the most successful if we use the most *biologically* relevant measures. Making this change should improve and clarify inferences from traits association models like the ones presented above. Additionally a qunatitive, intra-specific framework offers secondary advantages and novel avenues for fine-tuning FLS hypotheses.

In addition to addressing substantial inter-specific differnces in FLS, quantitative measures 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.

Additionally, one of the challenges of inter-specific comparisons that can be mitigated by an intra-specific approach is that 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 seranthous FLS by over-producing pollen or through self-pollination. To truly understand FLS at the species level, one would have to compare species across an unfeasible, N-dimensional trait space. Focusing on FLS variation within species holds most other traits relatively equal, avoiding this problem of tradeoffs with latent, unmeasured traits.

Testing the new framework

To date, FLS variability below the species-level have not been addressed. To address this gap, we supplement our literature review with several analyses. We tested associations between hypothesis-releveant traits and FLS using the phenological records from Harvard Forest with both the classic FLS catagories and our new proposed framework. The results from the categorical version of our Harvard Forest model(**??**a) reflect the MTSV USFS model results (Fig. **??**). We found strongest support for the early flowering hypothesis, good support for the wind pollination hypothesis and poor support for the water dynamics hypothesis. We detected no substantial interactions between predictors and found X phylogenetic structure to FLS.

The results form our quantitative version of the model highlight key biological insights obscured by categorization. With quantitative model, we detected a signal for the water dynamics hypothesis, implying that while drought tolerance may not play a major role in determining whether or not flowering happens before leaf expansion, it may contribute to determining the time between these phenophases.

Most significantly, in this model we identify strong interactions between predictors. While early flowering is associated with hysteranthy in all species, this effect is even more pronounced in wind pollinated-taxa. Average predictive comparisons from this model demonstrate that water dynamics drive FLS patterns of biotically-pollinated taxa but not wind-pollinated taxa (3). These systematic differences between pollination sydromes are informative. Many of the biotically-pollinated species of the temperature forests trace their biogeographic origins to the tropical regions (**?**) where the water dynamics hypothesis originated(Janzen, 1967; Franklin, 2016). In particular, we see many of the biotically-pollinated, hysteranthous species in the temperate zone are geographic outlyers from largely tropical clades (e.g. *(*Fabaceae),*(*Lauraceae),*(*Annonaceae). It may be that for these taxa, hysteranthy developed in this warmer, drier selection environment and bears no functional similarity to hysteranthous flowering in wind-pollinated species that prodominately evolved in the temperate zone. While beyond the scope of this analysis, the biogeopgraphy behind our findings suggests a more complex story of parallel evolution, biogeographic history, and community assembly in hysteranthous flowering than can be encompased any single FLS hypothesis.

We leveraged the inter-annual FLS variation at Harvard Forest to investigate other signals of the water dynamics hypothesis that may be have been missed in larger inter-specific inquiries. As predicted by the hypothesis, we found a negative association between FLS variation and annual precipitation at Harvard Forest, however, we estimated it would take a change of apporximately 100 centimeters in annual precipitation to drive a day differnce in FLS. This suggests that even if water dynamics shaped FLS in some temperate taxa on the evolutionary time-scale, it does not appear to be a major driver of FLS variation on an ecological one. Given this, it may be that hysteranthy 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 fuction. Hysteranthous flowering may expand the temporal niches available to species, partitioning inter-specific competition for pollinators, or it may be a useful tool for attracting them. 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 to locate. While these explainations are still purely speculative, they are readily testible with our new framework as will be discussed below.

findings suggest that the fact that previous studies tend to find support for multiple hypotheses is not simply a methodological artifact but rather a result consistant with the biolocial processes that shape FLS. 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 have identified several biological nuances to advance our understanding of this phenological trait and provided a more comprehensive picture of where our understanding of this phenological trait is currently, and where it needs to go. Below we highlight three characteristics of FLS that we suggest, utilizing this new framework, should 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 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 hysteranthy with a more mechanistic approach, which may mean utilizing a more taxonomically-restricted focus. The significance of interaction terms in some of our models suggest that a promising option is to look within the

hypotheses to address sub-grouping of taxa in which overlap between hypotheses could be controlled. For example, we know that wind-pollination efficiency is not driving hysteranthous flowering among biotically-pollinated taxa, so if we consider this group of species alone, we may be able to detect stronger signals from other traits that support other competing hypotheses. Incorporating a more explicit phylo-biogeographic approach would be instructive at this level; there are phylo-geographic commonalities between the few biotically-pollinated hysteranthous species in Eastern flora, we might better understand the function of FLS variation in these species by investigating FLS variation in their sister-taxa in their regions of origin.

FLS and fitness

Even with focused work on sub-groupings of species, interspecific trait-association models can only can 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 (). 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 really a good proxy for 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 fitness consequences of FLS variation. Variability in hysteranthy 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 larger 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.

Conclusions: Our proposed framework provides a path to understand 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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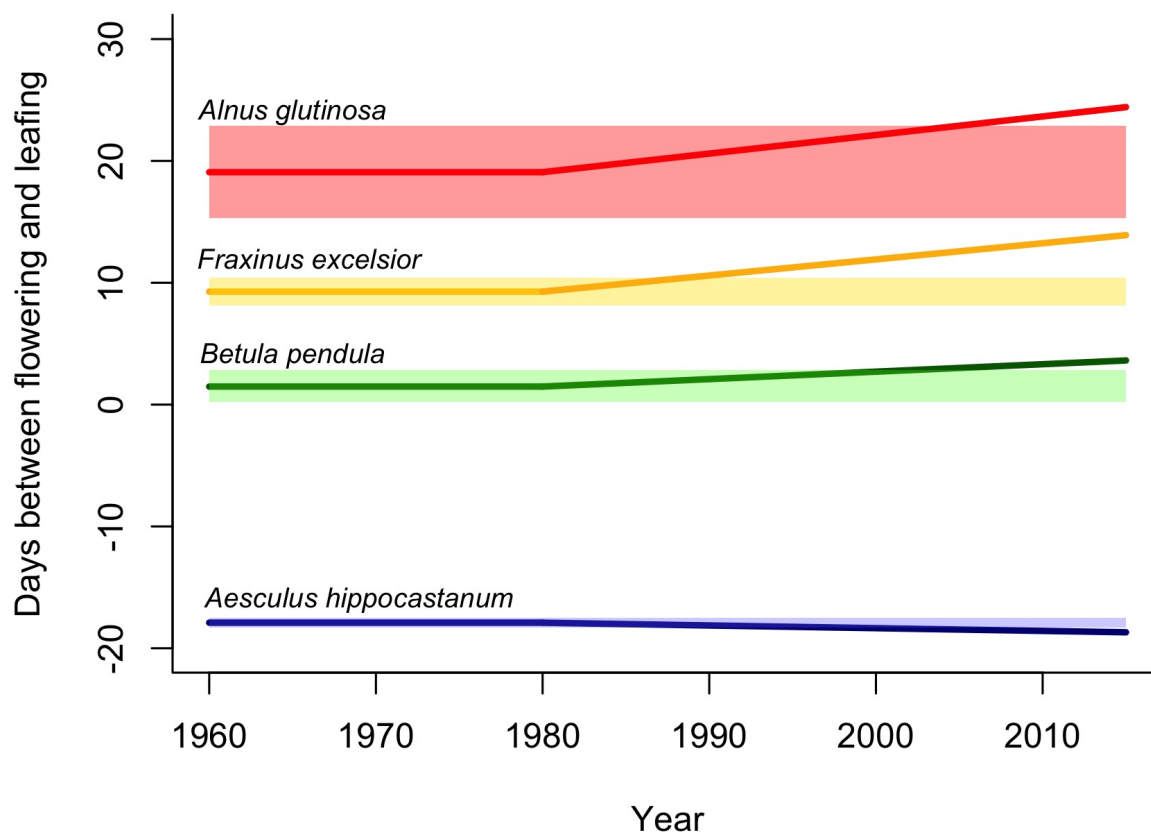[h!]

Figures

Figure 1: **FLSs across Europe for four tree species from 1960 to 2015 suggests climate change has generally increased the time between flowering and leafing**, but the direction and rate of change differs across species, which may exacerbate fitness differences within forest communities. To detect the effect of climate change on average FLS, we used models that allow for shifts in FLS after 1980. Lines represent the mean trend in FLS per species, and the highlighted regions indicate historic range of FLS variability (95% credible intervals of the pre-1980 average) from the PEP725 database (Templ *et al.*, 2018).
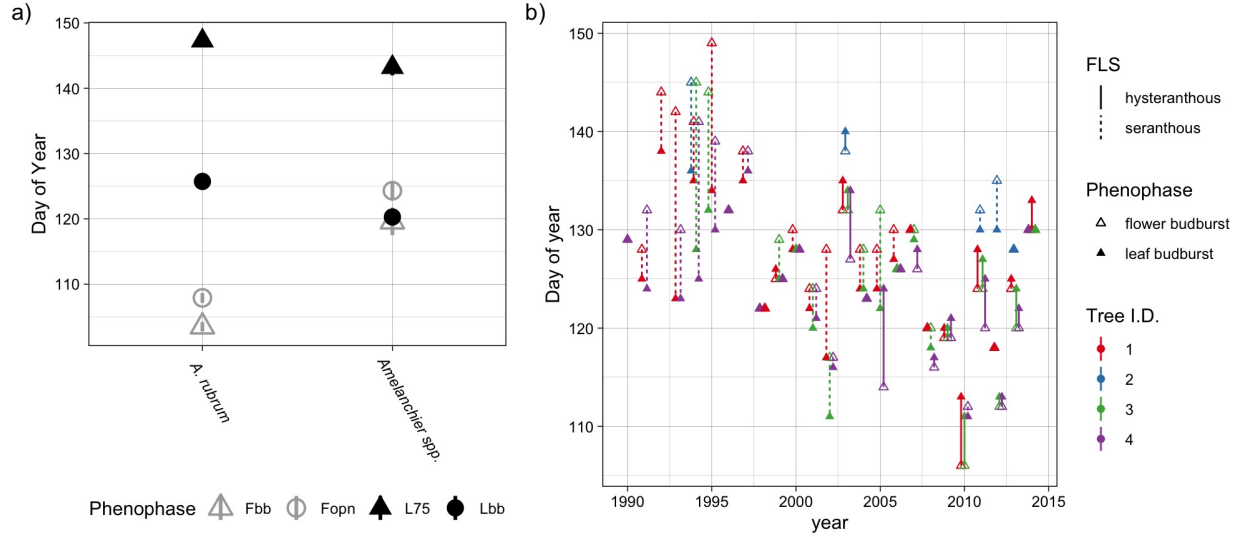
Figure 2: **Categorical descriptions of FLS mask significant variability.** In A), two species, both categorically hysteranthous, show sustantial differences in time between floral and vegetative phenological development. In B) we find that for,*Quercus rubra* a species typically is classified as synanthous, the the order of flower and leaf bud break, and the time between these events varies considerably for each individual over time, and between individuals in any given year. These inter and intra-specific differences can only be assessed with a quantitive, intra-specific measure of FLS, and may be key to understanding the function of hysteranthy in temperate woody plants.
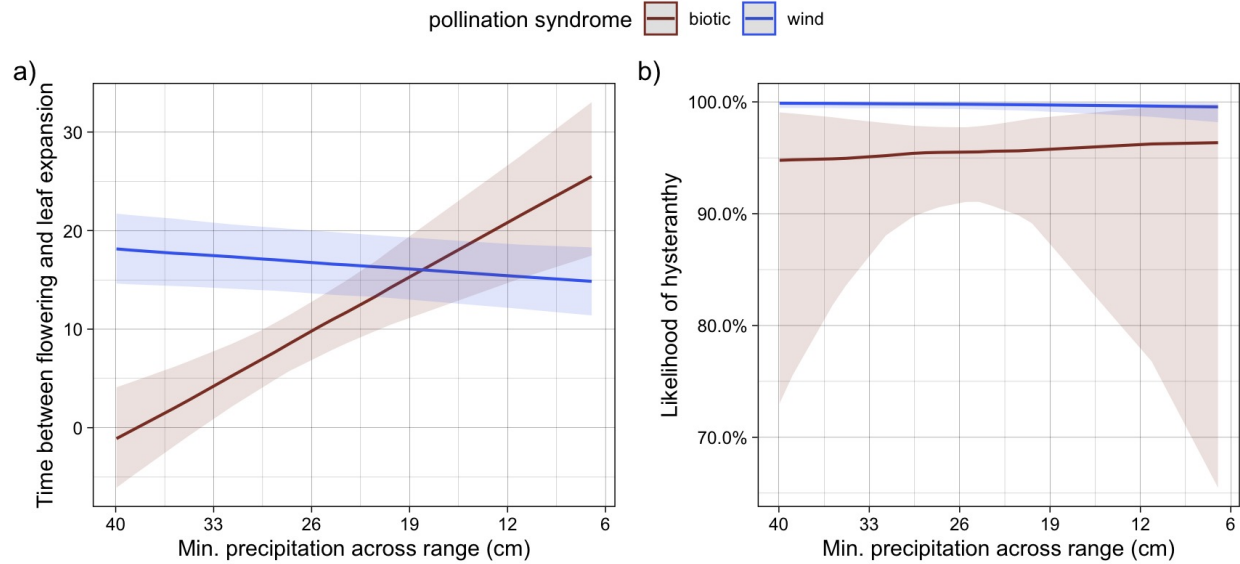

Figure 3: **Average predictive comparisons suggest that water dynamics may be a driver of hysteranthy in biotically-pollinated but not in wind-pollinated taxa.** Given that in the temperate zone abiotic and biotically pollinated taxa evolved in radically different environments, these systematic differences in drivers of FLS may reflect convergent evolution in FLS. Future work on FLS must accommodate overlapping hypotheses.