

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

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. Reconciling these hypotheses has been impeded by how FLS patterns are described and defined. Here, we advance the existing hypotheses to account for the FLS variation in nature and evaluate them 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, suggesting progress can come from studies addressing overlapping hypotheses. Second, support for FLS hypotheses is sensitive to how FLSs are defined, with quantitative definitions proving most useful. Finally, we identify the limits of trait-based hypothesis testing. We highlight how adopting an intra-specific approach and evaluating fitness consequences of FLS variation could quickly determine the major drivers, with 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 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 is increasing as a result of climate change but the rate of change differs among them. If, as suggested, 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.

Despite recent advances in understanding the physiology and evolution of FLS (Gougherty & Gougherty, 2018; Savage, 2019), a major challenge to predicting how FLS patterns will respond to climate change is that baseline variability in FLS is poorly characterized. 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 hysternanthy, protanthy, proteranthy or precocious flowering describe species that produce flowers before their leaves. Synanthy describes species whose flowering period overlaps their leaf development and seranthy describes species whose flowers open after their leaves emerge (Lamont & Downes, 2011; Heinig, 1899). But applying these conceptual categories to real phenological sequences is not always so straight forward.

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**

Phenological observers could justifiably classify this species as: 1) Hysternanthous because flower budburst proceeds leaf budburst, 2) Synanthous because flowers open during the time between leaf budburst and leafout or 3) Seranthous because peak flowering occurs after leafout. This problem extends beyond this simple example to real datasets, such as the long term phenological records from Harvard Forest in Petersham, MA (O’Keefe, 2015) where the same ambiguities exist (Fig. 2). Different classifications of the same species across different sources 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 dataset in existence come from regional guide books and Flora, it is likely that these categories were originally described to aid with plant identification rather than to describe functional biological processes. The FLS categories imply that a species flowering two days after leaf budburst is more similar to another that flowers two months after leaf budburst than to a third species that flowers two days before budburst. However, biological intuition alone would suggest otherwise. Categorization introduces artificial boundaries between some species while obscuring significant differences between others.

Together, these uncertainties hamper our ability to accurately test the existing FLS hypotheses because any statistical relationship between FLS and other traits predicted by the hypotheses is biased by the subjectivity of the original observer, the modeler, and the possibility that the associations we are testing are biological arbitrary.

102 In order for the traditional inter-specific categorical approach to FLSs to be useful for
103 identify the evolutionary significance of FLS variation, we must consider FLS patterns in
104 the biological context of the various FLS hypotheses. The biological mechanisms underlying
105 each hypothesis make different predictions the degrees of overlap between vegetative
106 and floral phenophases, which is instructive for how to group or divide FLS patterns for
107 hypothesis testing. Below, we review the current FLS hypotheses, identify the underlying
108 biology of each, and clarify how much overlap between flowering and vegetative growth
109 they predict.

110 Wind pollination

111 The most prevalent FLS hypothesis suggests that hysteranthly is an adaptation critical
112 for effective wind pollination, with leafless flowering allowing for more efficient pollen
113 dispersal and transfer (Whitehead, 1969; Stephen H. Spurr, 1980; Friedman & Barrett,
114 2009). This hypothesis hinges on the fact that leaves create a substantial physical disruption
115 to pollen transfer, a premise that we would not necessarily expect to be true
116 for the early stages of leaf expansion when tiny leaf primordia would have little impact
117 on environmental structure. In this framework, we expect that trees that flower during
118 the early stages of leaf expansion would gain similar mechanical advantage to those who
119 complete their flowering before any leaf activity. We see that in Harvard Forest, while
120 wind-pollinated species flower both before and after budburst, they all flower before their
121 leaves reach 75% of their final size (Fig. 2). This hypothesis predicts that wind pollinated
122 species should flower before or with their leaves, while in animal pollinated species, FLS
123 should be random or co-vary with pollinator activities.

124 Water dynamics

125 Another hypothesis, emerging from the dry-deciduous tropics where flowering during
126 the leafless season is also common (Janzen, 1967), suggests that flowering before leaf
127 development is an adaptation to reduce water stress associated with maintaining floral
128 hydration while leaves are transpiring (Franklin, 2016). Because transpiration intensifies
129 as soon as leaves begin to expand in the spring (Breda & Granier, 1996; Wang *et al.*, 2018),
130 this hypothesis asserts there is a significant cost to maintaining floral structures during
131 any stage of leaf activity and only species whose flowering occurs before any leaf expansion
132 would gain a drought advantage. . This hypothesis predicts that species that are drought
133 tolerant should flower before leafing out, with minimal overlap between the floral and
134 vegetative phenophases. Species that are not drought tolerant gain no advantage from
135 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 hysteranthous vs. seranthous, as long as the absolute flowering time is the same. Recent work from Savage (2019) has 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 hysteranthous FLS. This might explain why hysteranthous species tend to be the earliest species to flower (Fig. 2). Here, we expect longer times 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 hysteranthous, we might also expect to see strong associations with other early flowering traits such as seed mass, dispersal season or cold tolerance (Gougherty & Gougherty, 2018), 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 hysteranthous 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.

More biologically-informed determinations of FLS categories should improve the utility of trait association models because they generate expectations as to how the strength of trait associations should vary as FLSs are re-defined. For example, because we asserted that for wind-pollination efficiency both hysteranthous and synanthous species would have similar pollen transfer advantages, we would expect to see a stronger pollination syndrome signal when synanthous species are grouped with hysteranthous ones than when they are combined with seranthous taxa. These kinds of predictions can be explicitly tested in the current FLS framework, adding a second layer of inference to aid our understanding of the biological significance of FLS variation. While this approach is promising, we must address a second problematic assumption of the current 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

175 applied at the species level, and intra-specific variation has never been broadly assessed
176 (Gougherty & Gougherty, 2018). Intra-specific variation is the engine of natural selection,
177 and if it is substantial in FLS patterns, we can infer much about the origins of this trait
178 as well as its trajectory as the climate changes.

179 Variation in FLS

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

189
190 Given the variability of FLSs at the individual and population level, it is clear that
191 considering FLS variability at only higher taxonomic levels obscures important realities
192 about the biology of this phenological trait. Below, we discuss how the observed variation
193 below the species level may alter the existing FLS hypotheses.

194 How FLS variation alters predictions

195 Wind pollination

196 Pollination syndrome is generally treated as a species-level trait, considered to be
197 fairly immutable across ecological time and space. Because of this, we would not ex-
198 pect significant variation in FLS across populations or individuals because we would not
199 expect variation in pollination syndrome. However, as discussed above, a tree with no
200 overlap between flowering and leafing phenology does not necessarily gain a significant
201 pollen transfer advantage over an individual with some overlap. The pollination efficiency
202 advantage from flowering-first should diminish as the canopy fills in, but we do not know
203 at what point during leaf expansion pollination would become significantly encumbered.
204 It is possible that interannual and population-level variation in the timing between flow-
205 ering and leaf out for hysteranthous and synanthous individuals could maintain a wind
206 pollination advantage, as long as the overlap did not cross a certain unknown thresh-
207 old. Therefore, based on the wind pollination efficiency hypothesis, we would not expect
208 high levels of population or individual variation in FLS, but the detection of some FLS
209 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 hysteresis, and wetter years permitting more FLS overlap.

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 hysteresis 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 hysteranthly 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 hysteranthly 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 hysteranthly. 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 hysteranthly 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 234 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. 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. The Harvard Forest data set (HF) contains quantitative flowering and leaf phenology measurements for individuals of 24 woody species over a 15 year period (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. The MTSV and USFS data can be used to test inter-specific FLS variation. The HF data are temporally explicit, allowing for both inter- and intra-specific FLS comparisons. The PEP725 data is species-limited, and allows us to evaluate FLSs only at the intra-specific level, but permits us to address variability in individuals over time and among population.

In considering all data sets together two clear trends 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 ??). The strength of interactions between predictors varied among models with no systematic patterns. For several case studies, we detected a positive interaction between pollination syndrome and water dynamics and negative interactions between early flowering and water dynamics. The presence of interactions further suggests that multiple drivers may be structuring FLS patterns. For example, when we performed average predictive comparisons on the HF models, we found that the hysteresis did indeed increase significantly with lower minimum precipitation across their range for insect-pollinated species but not for wind-pollinated taxa (figure 5).

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 hysteresis in the dataset. As predicted, the signals for each trait effect were stronger when the degree of flower-leaf temporal overlap built into the FLS definition used matched the underlying biological assumptions of the hypothesis. We also found that using continuous measures of FLS 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. 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 (Fig. 4, PEP725 estimates). This suggest that FLS variation at this scale is still primarily driven by flowering time rather than water availability.

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

Each of our case studies provided its own insights into the nature of the relationship between FLS variation and the FLS hypotheses for woody species. For MTSV and USFS, we found that the strength of each predictor’s effect varied depending on how the FLSs were defined. From the HF study, we found that re-defining continuous FLS as binary masked important species level variation in trait associations and from PEP725, we identified a new hypothesis for the physiology behind FLS; that FLS variation is generally driven by variation in the first phenophase of the sequence. However, it is in considering the results of the cased studies together, that 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 tax-

onomic 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; if 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.

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 but we have no way of knowing for certain that this is 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, detailed below.

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 hysteresis 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.

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.

References

(2019) Dwd climate data center (cdc): Multi-annual grids of soil moisture in 5cm depth under grass and sandy loam, version 0.x,. digital.

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.

Breda, N. & Granier, A. (1996) Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*). *Annales des Sciences Forestieres* **53**, 521–536, International Symposium on Oaks in a Changing Environment - Ecological and Physiological Aspects, VELAINE-EN-HAYE, FRANCE, SEP, 1994.

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**.

Finn, G.A., Straszewski, A.E. & Peterson, V. (2007) A general growth stage key for describing trees and woody plants. *Annals of Applied Biology* **151**, 127–131.

- 463 Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phe-
 464 nology across all species in a temperate forest community. *New Phytologist* **219**, 1353–
 465 1362.
- 466 Forrest, J. & Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of
 467 phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B:*
 468 *Biological Sciences* **365**, 3101–3112.
- 469 Franklin, D.C. (2016) Flowering while leafless in the seasonal tropics need not be cued by
 470 leaf drop: evidence from the woody genus brachychiton (malvaceae). *Plant Ecology and*
 471 *Evolution* **149**, 272–279.
- 472 Friedman, J. & Barrett, S.C.H. (2009) Wind of change: new insights on the ecology and
 473 evolution of pollination and mating in wind-pollinated plants. *Annals of Botany* **103**,
 474 1515–1527.
- 475 Gougherty, A.V. & Gougherty, S.W. (2018) Sequence of flower and leaf emergence in
 476 deciduous trees is linked to ecological traits, phylogenetics, and climate. *New Phytologist*
 477 **220**, 121–131.
- 478 Heinig, R. (1899) Glossary of the botanic terms used in describing flowering plants. Cal-
 479 cutta, India.
- 480 Janzen, D.H. (1967) Synchronization of sexual reproduction of trees within the dry season
 481 in central america. *Evolution* **21**, 620–637.
- 482 Lamont, B.B. & Downes, K.S. (2011) Fire-stimulated flowering among resprouters and
 483 geophytes in australia and south africa. *Plant Ecology* **212**, 2111–2125.
- 484 Lechowicz, M.J. (1995) Seasonality of flowering and fruiting in temperate forest trees.
 485 *Canadian Journal of Botany* **73**, 175–182.
- 486 Milleron, M., Lopez de Heredia, U., Lorenzo, Z., Perea, R., Dounavi, A., Alonso, J., Gil,
 487 L. & Nanos, N. (2012) Effect of canopy closure on pollen dispersal in a wind-pollinated
 488 species (*Fagus sylvatica* L.). *PLANT ECOLOGY* **213**, 1715–1728.
- 489 Nathan, R. & Katul, G. (2005) Foliage shedding in deciduous forests lifts up long-distance
 490 seed dispersal by wind. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCI-*
 491 *ENCES OF THE UNITED STATES OF AMERICA* **102**, 8251–8256.
- 492 Niklas, K.J. (1985) The aerodynamics of wind pollination **51**, 328–386.
- 493 O’Keefe, J. (2015) Phenology of woody species at harvard forest since 1990.

- 494 Piao, S., Friedlingstein, P., Ciais, P., Viovy, N. & Demarty, J. (2007) Growing season
495 extension and its impact on terrestrial carbon cycle in the northern hemisphere over
496 the past 2 decades. *Global Biogeochemical Cycles* **21**.
- 497 Primack, R.B. (1987) Relationships among flowers, fruits, and seeds. *Annual Review of*
498 *Ecology and Systematics* **18**, 409–430.
- 499 Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual*
500 *Review of Ecology and Systematics* **16**, 179–214.
- 501 Reich, P. & Borchert, R. (1984) Water-stress and tree phenology in a tropical dry forest
502 in the lowlands of costa-rica. *Journal of Ecology* **72**, 61–74.
- 503 Robertson, C. (1895) The philosophy of flower seasons, and the phaenological relations of
504 the entomophilous flora and the anthophilous insect fauna **29**, 97–117.
- 505 Savage, J.A. (2019) A temporal shift in resource allocation facilitates flowering before leaf
506 out and spring vessel maturation in precocious species. *American Journal of Botany*
507 **106**, 113–122.
- 508 Stephen H. Spurr, B.V.B. (1980) *Forest Ecology*. John Wiley Sons, 3rd edn.
- 509 Templ, B., Koch, E., K.Bolmgren, Ungersböck, M., Paul, A., Scheifinger, H. & et al.
510 (2018) Pan european phenological database (pep725): a single point of access for euro-
511 pean data. *Int. J. Biometeorology* .
- 512 Wang, Y., Li, G., Di, N., Clothier, B., Duan, J., Li, D., Jia, L., Xi, B. & Ma, F. (2018) Leaf
513 Phenology Variation within the Canopy and Its Relationship with the Transpiration of
514 *Populus tomentosa* under Plantation Conditions. *Forests* **9**.
- 515 Whitehead, D.R. (1969) Wind pollination in the angiosperms: Evolutionary and environ-
516 mental considerations. *Evolution* **23**, 28–35.
- 517 Wilczek, A.M., Burghardt, L.T., Cobb, A.R., Cooper, M.D., Welch, S.M. & Schmitt,
518 J. (2010) Genetic and physiological bases for phenological responses to current and
519 predicted climates. *Philosophical transactions of the Royal Society of London. Series*
520 *B, Biological sciences* **365**, 3129–3147.

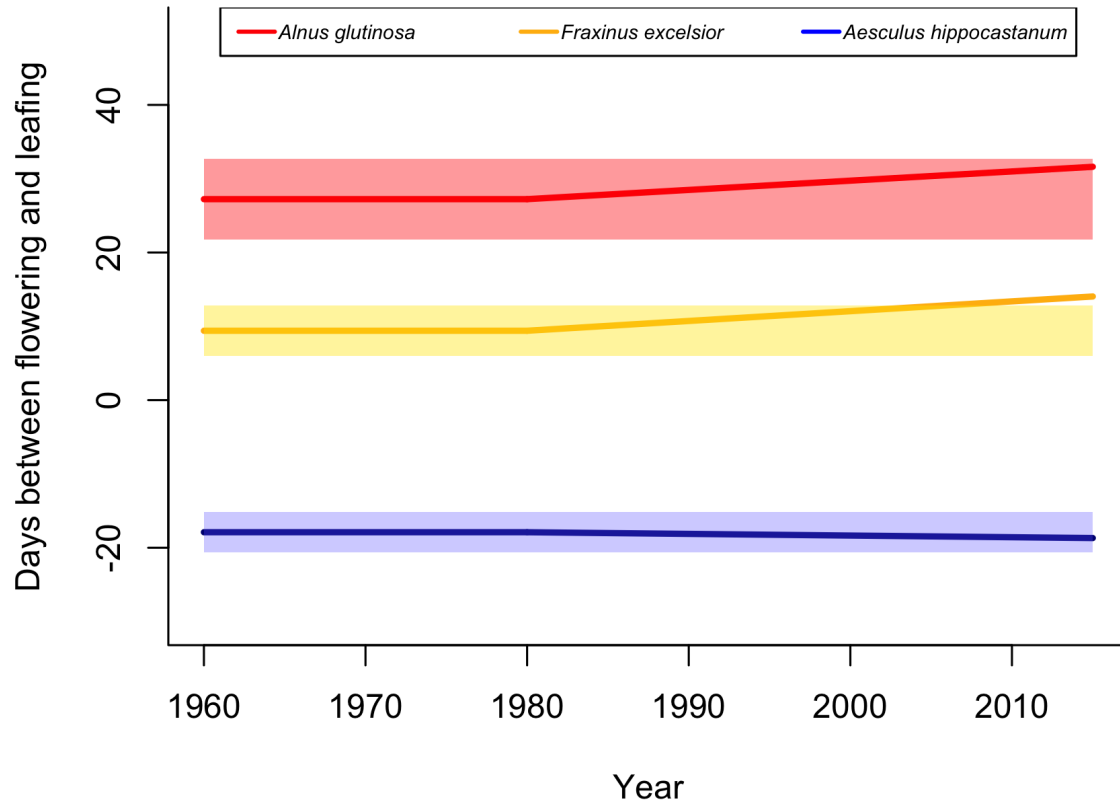


Figure 1: **Modeled FLS response to climate change across Europe for three tree species from 1960 to 2015.** To detect the effect of climate change on average FLS, the models allows for shifts in FLS after 1980. Each line represents a population from the PEP725 database and the highlighted regions indicate historic range of FLS variability (upper and lower 95% credible intervals of the pre-1980 average). There is significant intra-specific variation in average FLS and the FLS response to climate change. For all species, the time between flowering and leafing is generally increasing but the direction and rate of change differs across species and sites.

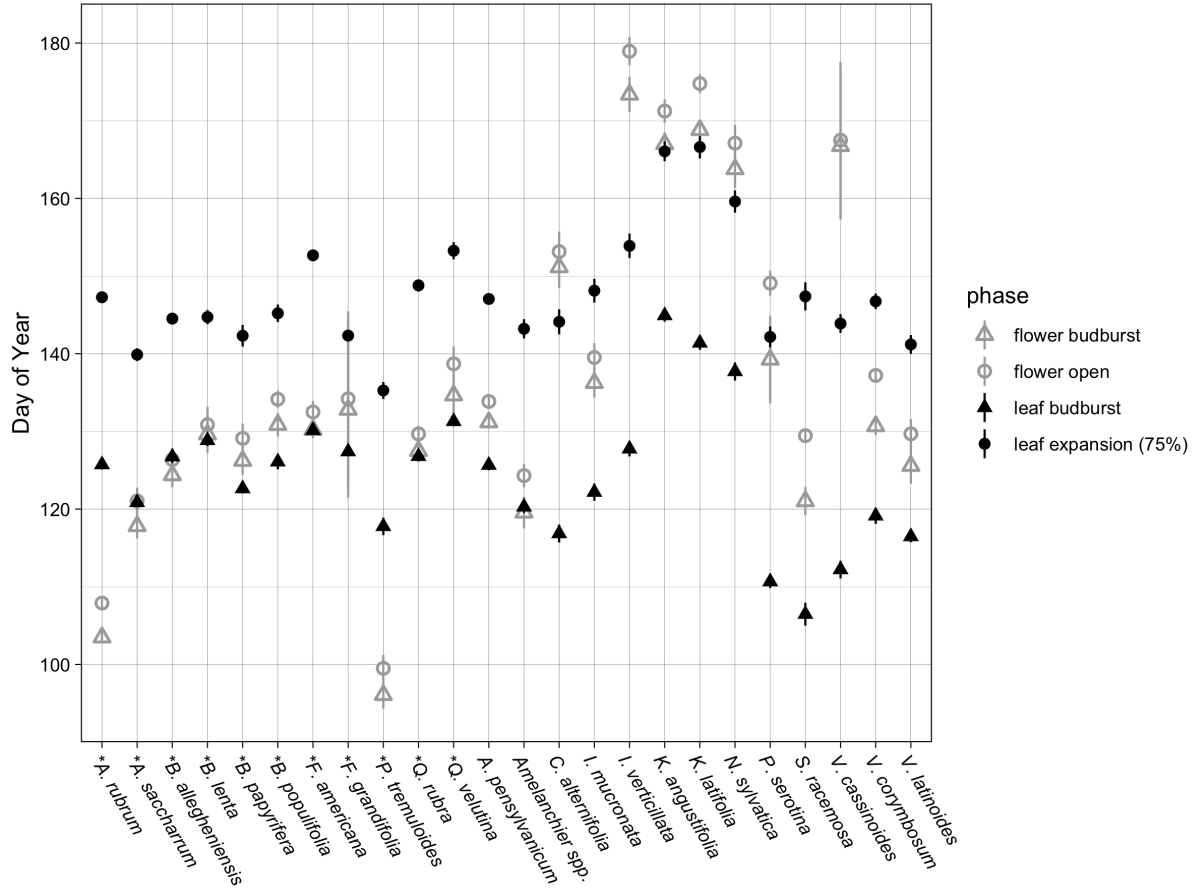


Figure 2: **Average inter-specific FLS variation at Harvard Forest, MA from 1990-2015.** This community displays all major FLS patterns, but because of overlapping floral and vegetative sub-phases and interannual variability in phenology (lines indicate standard error for each phenophase mean), it is difficult to neatly assign all species to a FLS category. Other notable patterns relevant to the FLS hypotheses can be seen. 1) As predicted by the early flowering hypothesis, the earliest species to initiate spring phenology are hysteranthous. 2) 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%.

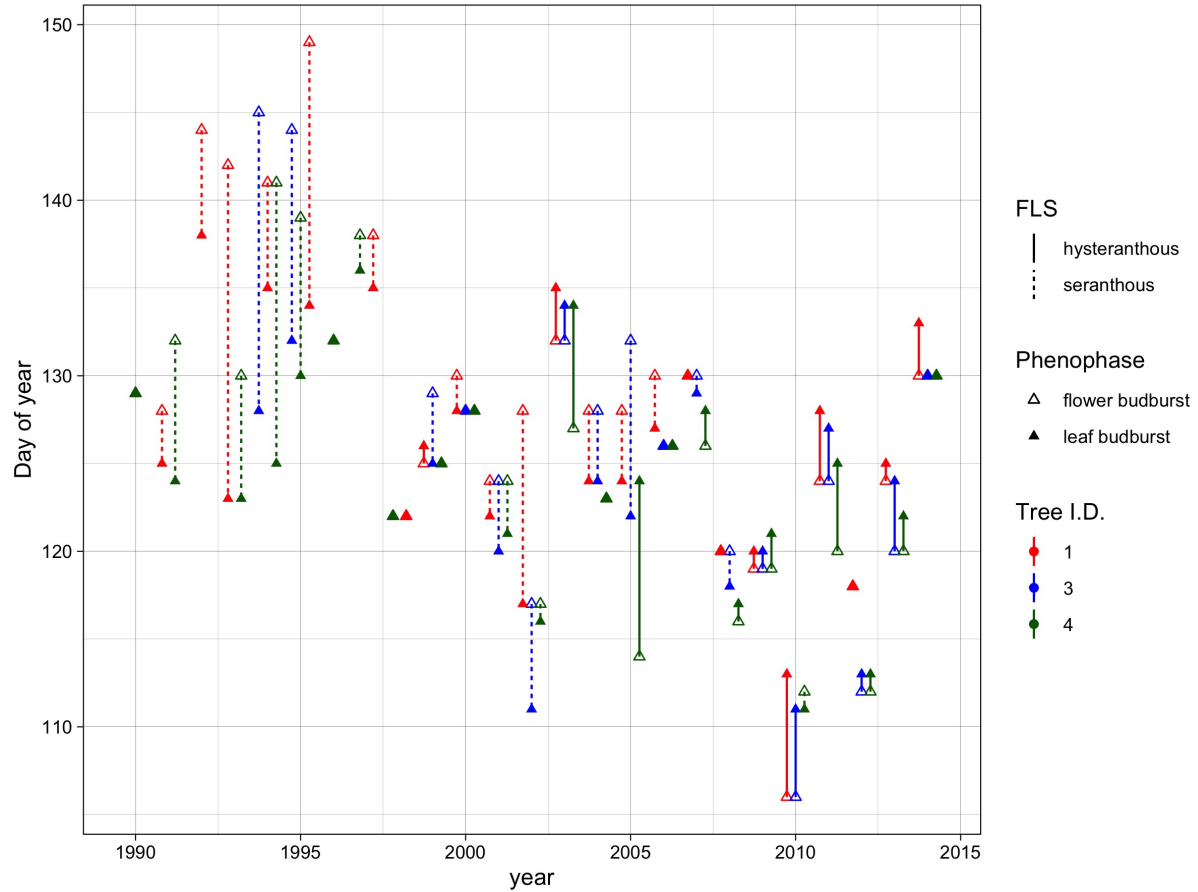


Figure 3: **Individual FLS variability over time for *Quercus rubra* at Harvard Forest.** While this species is typically is classified as synanthous, we see here that the the order of flower and leaf bud break, and the time between these events varies considerably for each individual over time, and between individuals in any given year. None of this variation can be accounted for in a categorical FLS classification system.

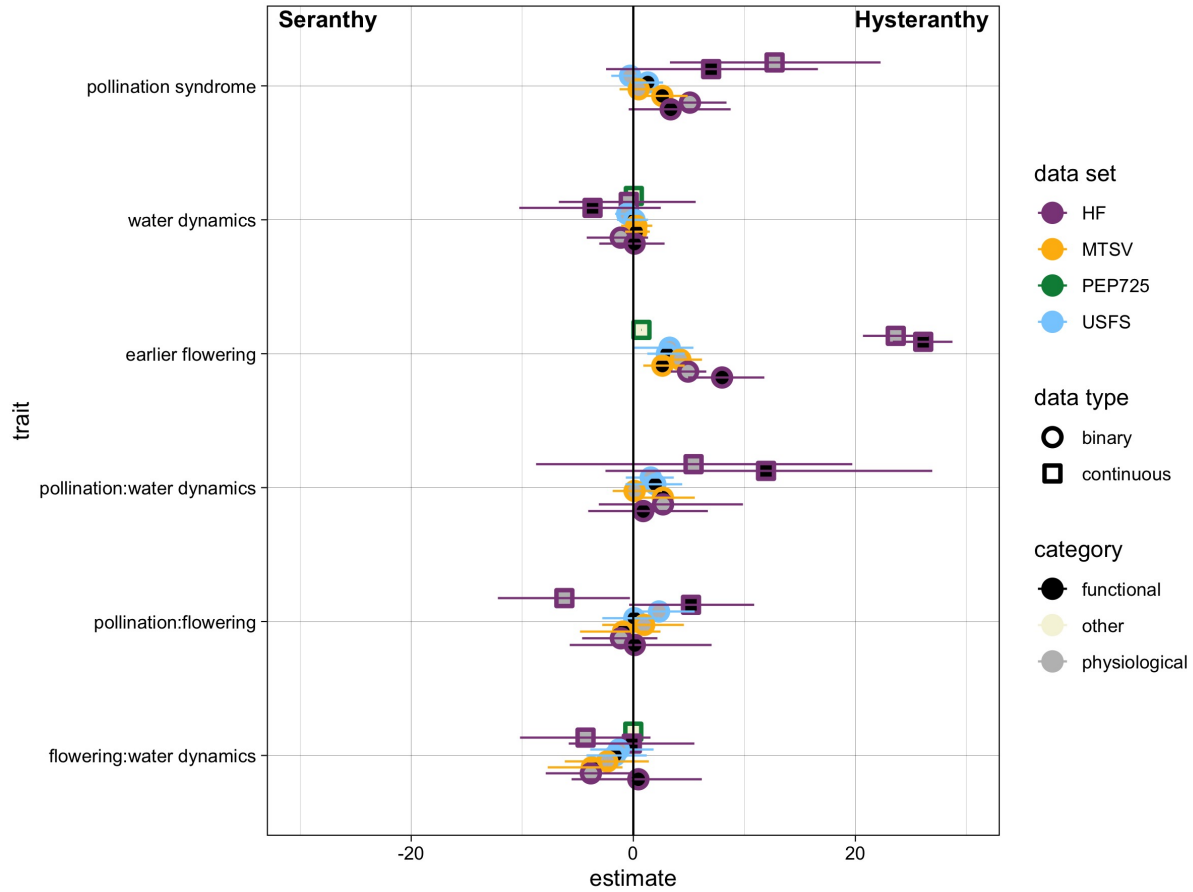


Figure 4: Estimated effects of water dynamics (minimum precipitation across species range or average soil moisture), pollination syndrome, and earlier flowering time on FLS patterns across four case studies. We used phylogenetic adjustments and standardized units to make a basic comparison of four datasets 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. Interactions between predictors varied across studies with no clear trends but suggest that it would be instructive to investigate FLS variation in sub-grouping of taxa in which overlap between hypotheses is minimal. Lines represent 95% bootstrap or credible intervals depending on the modeling framework.

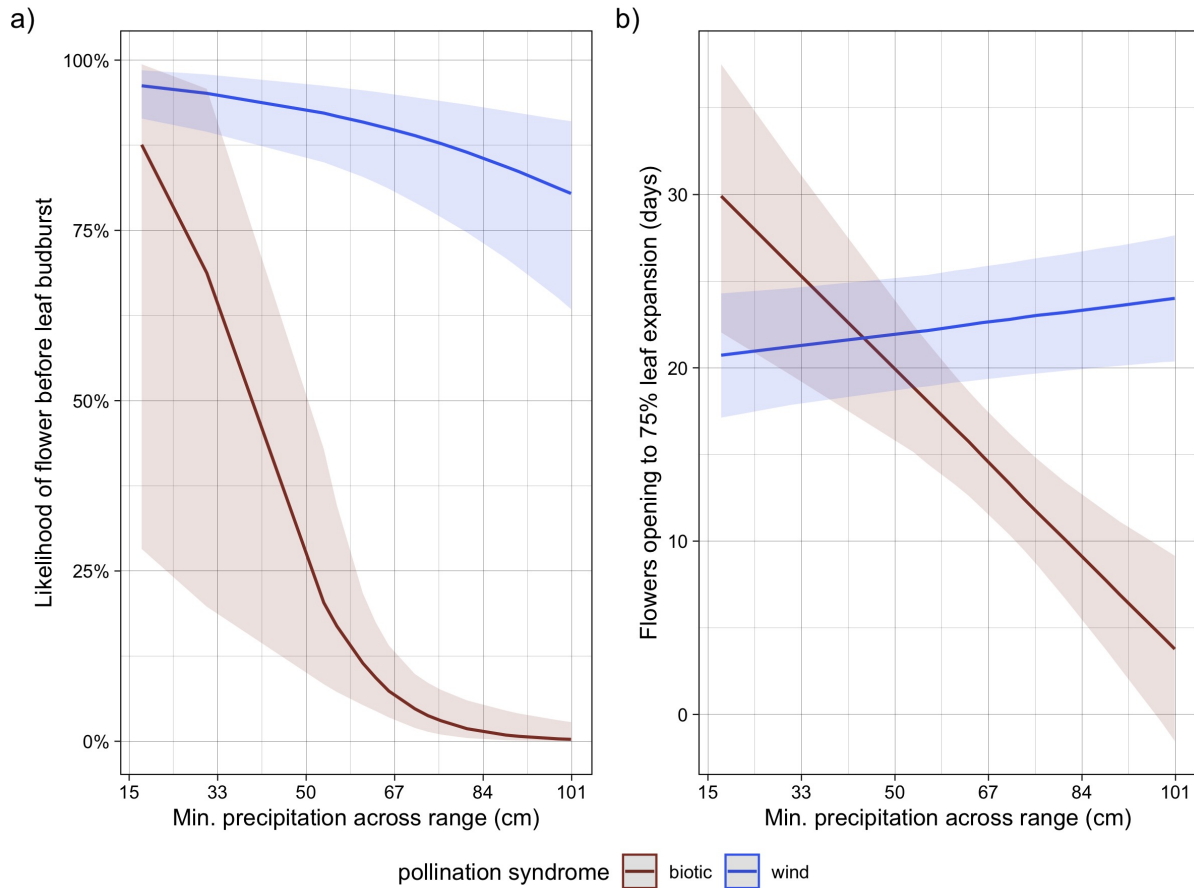


Figure 5: **Average predictive comparisons reveal that drought tolerance may be a driver of hysteranthry in biotically-pollinated but not in wind-pollinated taxa, suggesting future work on FLS must accommodate overlapping hypotheses.** The figure depicts the predicted values and 50% credible intervals for a) the likelihood a species is hysteranthous and b) the time between flowering and leafing. Predictions are function of drought tolerance and pollination syndrome for species flowering in mid-May at Harvard Forest in Petersham, MA. Figure a) is based on the physiological-binary model of FLS and figure b) is based on the functional-continuous model (See supplement for details of model formulation).