

# Floral size and aridity drive hysteranthous flowering in the

January 25, 2023

## Introduction

Woody perennials have a unique ability among plants to seasonally begin reproduction prior to vegetative growth. This flowering-first phenological sequence known as hysteranth, proteranth or precocious flowering is particularly common in temperate, deciduous forests around the globe (Rathcke & Lacey, 1985). A number of studies suggest that this flower-leaf sequences (FLSs) are under selection, and that hysteranth has functional significance (Gougherty & Gougherty, 2018; Buonaiuto *et al.*, 2021; Guo *et al.*, 2014).

The most common, and well-tested explanation for the evolution of hysteranth in temperate forests is that it is adaptive for wind-pollination, as leafless canopies increase wind speeds for pollen transport and reduce the likelihood of pollen interception by vegetation (Whitehead, 1969; Niklas, 1985). In the dry-deciduous tropics of South and Central America, hysteranth is also common (Rathcke & Lacey, 1985; Franklin, 2016), and is regarded as an important adaptation to alleviate water stress by partitioning the hydraulic demand of flowers and leaves across the season (Gougherty & Gougherty, 2018; Franklin, 2016; Borchert, 1983; Reich & Borchert, 1984).

However, these explanations do not address the widespread prevalence of hysteranth in biotically-pollinated taxa found in temperate regions that are rarely water-limited in the early season during which flowering and leafing occur (Polgar & Primack, 2011). This number is not trivial; a recent analysis found that approximately 20% of the hysteranth species in the moist, Eastern Temperate Forests of North America are biotically pollinated (Buonaiuto *et al.*, 2021). With mounting evidence anthropogenic climate change is driving shifts in flower-leaf sequences (Ma *et al.*, 2020), expanding our understanding of the functional significance of hysteranth to included these groups is vital to forecasting the demography and performance of forest communities in an era of global climate change.

## Hypotheses of Hysteranthous flowering in biotically pollited taxa

Several alternative hypotheses to the wind pollination hypothesis have been put forth and may help explain the function of hysteranth in biotically-pollinated species.

Water limitation hypothesis: Despite being considered a “wet” biome, there is still considerable variation in water availability in space and time within temperate regions of the globe. It is possible that the function of hysteranthous flowering in thes regions parallels that in the dry tropics—partitioning hydraulic demand across the season to allow hysteranthous species to tolerate increased aridity. If this is the case, we would expect to find hysteranthous taxa in locations that are, on average, drier than their non-hysteranthous kin.

Insect-visibility hypothesis: Hysteranthous flowers are visually conspicuous in the landscape. It is possible

that like in wind pollinated taxa, hysteranthly in biotically pollinated taxa is an adaptation for pollination efficiency as a flowering-first species are easier for insects pollinators to locate (). This hypothesis predicts that flower displays will differ in size between flowering- first and leafing-first species. Though the direction is unclear. 1) Hysteranthly may be associated with smaller flowers. Since they are easier to see, there is weaker selection on large floral display. 2) Hysteranthly may be associated with bigger flowers. Because these species are going all in on visual displays, big flower might be additive to the benefits of hysteranthly. A second complicating factor is that there is likely to be associates between flower size and hysteranthly even if pollinator visibility doesn't matter due to developmental constraints. For example it requires more time and energy to produce big displays, so non-hysteranthous species that flower later in the season, after leaves emerge to gather energy are can produce bigger displays than early flowering hysteranthous species. (Could also move some of these nuances and contradictions for the discussion)

Phenological niche extension: Species that flower before their leaves inheirantly flower early in the season. It is possible that hysteranthly flower is simply a by-product of selection for early flowering. Spring flower phenology is less constrained by prior phenological events than leaf phenology (Savage, 2019), which could allow selection to drive flowering into the early season, producing the hysteranthous phenological sequence. With this hypothesis there is no specific adaptive advantage to hysteranthly; selection is not opperating on the relative timing of flower and leaf emergence, but rather the absolute flowering time alone.

Fruit maturaturion hypothesis: Like the phenological niche hypothesis describe above, there are several aspects of reproductive development that suggest hysteranthly is a by-product for early flowering, driven by development constraints. Hysteranthly may be common in large fruited species that require lots of time to mature their fruits. Alternatively, its may be common in small, early fruiting species that have evolved dispersal syndromes (wind dispersal, non-dormant seeds) that reuquire dispersal early in the season. In either case, we should expect fruit size to associate with hysteranthly.

Of course none of the hypotheses are mutually exclusive. One challenge is the same traits correlation could be driven by different mechanisms (i.e., small flower could be insect-visibility, developmental constraint, aridity tolerance or all of the above). Yet, a detailed investigation of the association between hysteranthly and the representative traits of each of these hypotheses would pinpoint those with the strongest theoretical underpinning and empirical evidence, as well as identify clear directions for future work to better understand the role that flower-leaf sequences play in woody plant fitness.

A second challenge for robust testing of hysteranthly hypotheses is that most characterizations of flower-leaf phenological sequences are based on expert-opinion verbal descriptions (e.g. "flowers before leaves" or "flower before/with leaves"), which make comparisons across taxa, time and space difficult and sensitive to observer bias (see; Buonaiuto *et al.*, 2021). This problem can be overcome by adopting standardized quantitative measures of plant phenology for observational studies and applying them to historic data records. Herbarium records are an excellent source of data that can be leveraged for quantitative phenological measurements (Willis *et al.*, 2017), but have not be used widely to investigate variability of flower-leaf sequences variation among and within species.

The American plums (*Prunus* subssp. *prunus* sect. *prunocerasus*) offer potential for a higher resolution investigation of drivers of hysteranthous flowering in taxa that don't fit the bill. (Better topic sentence needed.) The 16 species that make up the section are distributed across the temperate zone of North America and, like the genus *Prunus* at large, are all insect-polliated, yet show pronounced inter-specific variation in flower-leaf sequences. Species in this section are well represented in herbaria records (Fig. 1), making them a tractable group to measure and assess variation in flower-leaf sequences as well as other ecological and morphological characteristics that may explain the evolution of this variation (eww this paragraph needs help).

In this study, we used herbaria records to quantify flower-leaf sequence patterns in the American plums, (subspecies *Prunus*, sect. *prunocerasus*). We then evaluated the association between hysteranthy and several ecological and morphological traits to interrogate the functional hypotheses for hysteranthous flowering described above. We then compare our findings in this clade to associations between hysteranthy and traits in the larger genus obtained from published accounts in flora to better understand how these dynamics vary over taxonomic scales. Our findings both clarify the hypothesized function of flower-leaf sequence variation in biotically-pollinated taxa, and offer insights into how shifting flower-leaf sequences may impact species demography and distributions as climate continues to change.

## Methods

### 0.1 Quantifying flower-leaf sequence variation

We obtained digital herbarium specimens for all member of the section *Prunocerasus* from the Consortium of Midwest Herbaria (CMH) Database. To quantify the flower-leaf sequence variation within and across species we randomly sample 200 specimens for each species and scored the phenological development of flower and leaves using a modified BBCH scale for woody plants (Finn *et al.*, 2007). In total, we evaluated the phenology of 2521 specimens, but only specimens with visible flower were included in this analysis (n=1009). We reconstructed the phylogenetic relationships among species in this group based on the tree topology in Shaw & Small (2004). Following the methods of Grafen & Hamilton (1989) we computed branch lengths for this phylogeny by assigning each node a height and computing the distance between upper and lower nodes using the R package “ape” ().

To quantify FLS variation, we fit an ordinal, hierarchical, Bayesian, phylogenetic mixed model (de Villemereuil P. Nakagawa, 2014) to assess the likelihood an individual would be at any given vegetative BBCH phase while flowering. Because we expect that hysteranthy is more likely to occur earlier in the flowering period and species differ in their flowering periods, we included the day of the observation as a varying slope, main effect in the model and species and phylogeny as random effects. The model is written below:

$$\text{logit}(P(Y \leq j)) = \beta_{[j]phylo[i]} + \beta_{[j]sp[i]} + \beta_{dayofyear[sp[i]]} * X_1 + \epsilon_i$$

$$\epsilon_i \sim N(0, \sigma_y^2)$$

where Y is the ordinal outcome (leaf stage) and j is the number of categories (1,2,...6).  $P(Y \leq j)$  is the probability of Y less than or equal to a category j=1,...j-1. In this varying slope and intercept model,  $\beta_{[j]}$  describes an intercept for each category [1,2,...6], while slope  $\beta_{dayofyear[sp[i]]}$  is constant across categories.

The influence of the phylogeny  $\alpha_{phylo}$  was modeled as follows:

$$\alpha_{sp} \sim N(\mu_\alpha, COR[\sigma_{phylo}^2])$$

The  $\alpha$  for species effects independent of the phylogeny was modeled as follows:

$$\alpha_{sp} \sim N(\mu_\alpha, \sigma_{species}^2)$$

We fit the model in the R package “brms” (Bürkner, 2018) using weakly informative priors, and ran the

model on four chains with a warmup of 3,000 iterations and 4,000 sampling iterations for a total of 4,000 sampling iterations. Model fit was assessed with Rhats <1.01 and high effective sample sizes and no divergent transitions.

Because the day of observation strongly influenced the BBCH stage likelihood, quantifying flower-leaf sequences among species was intractable without accounting for this temporal trend. To address this issues, we used our model to predict the likelihood each species would be observed at a given vegetative BBCH stage during flowering at the 0%, 25% 50% and 75% quantiles of their flowering period. We then developed a flower-leaf sequence index, by assigning a numerical score to each species per seasonal quantile, and summing over the full flowering season. In each seasonal quantile, species received a 1 if more that 50% of their probability distribution occurred at BBCH 0 and BBCH 09 and a 0 if not. These values were summed across the season generating an index from 0 (never hysteranthous) to 4 (hysteranthous through late season (Q75)), where 1= hysteranthous at start of season, 2= hysteranthous through early season (Q25) and 3 = hysteranthous through mid season (Q50). We also used two alternative indexing schemes (>25% of the probability distribution occurred at BBCH 0 and >40% of the probability distribution occurred at BBCH 0 and BBCH 09).

## 0.2 Evaluating hysteranthly hypotheses

To test the predictions of the hypotheses of hysteranthly we obtained data on petal length, fruit diameter and directly from herbarium specimens and characterized the aridity of the sites specimens were collected from using the Palmer Modified Drought Index (PDSI) ().

For our morphological measurements, we sampled an additional 321 specimens measured the petal length of up to 10 randomly selected petals per specimen (n=2757) using ImageJ image processing software. We also used ImageJ to measure the diameter of fruits on an additional 316 specimens, measuring up to 5 fruit per specimen (n=224). We computed the average Palmer Modified Drought Index score from 1900-2017 for every *Prunocerasus* specimen in the database (n=2305) from the North America Drought Atlas (Cook & Krusic, 2004). For any specimens that lacked accurate geo-location information, we extracted PDSI values at the county centroid

We than used Bayesian phylogenetic mixed models to test the relationship between flower-leaf sequence index scores and each of the variables. In these models, we included species and phylogeny as the random effect.

The model structure is written below:

$$y_i = \alpha_{ind/sp[i]} + \alpha_{phylo[i]} + \beta_{hyst.index} * X_{hyst.index} + \epsilon_i$$

$$\epsilon_i \sim N(0, \sigma_y^2)$$

The effect of the phylogeny was model as above.

Like above, we fit these models in the R package “brms” (Bürkner, 2018) using weakly informative priors, and ran the model on four chains with a warmup of 3,500 iterations and 4,500 sampling iterations for a total of 4,000 sampling iterations. Model fit was assessed with Rhats <1.01 and high effective sample sizes and no divergent transitions. We also ran each model using our two alternative FLS indexing approaches to make sure our particular indexing approach was not influencing our results. Though these alternative classification scheme did change the hysteranthly index score for some species (Fig. S1), they changes did not substantially impact the inference from our models (see Tab. S1 for comparisons).

## Hysteranthy in the larger genus *Prunus*

To better understand how the patterns we identified in our in depth study of the sect. *Pruncerasus* scale across coarser taxonomic resolution we also evaluated the relationship between hysteranthous flowering and hypothesis-related traits in the all the *Prunus* species that are native or naturalized in North America. For this analyses, we obtained categorical descriptions of flower-leaf sequences and mean estimates of fruit diameter and number of flowers/inflorescence as a proxy for floral investment from the Flora of North America () for 32 species in the genus. As above, we evaluated the average aridity tolerance of each species by extracting average PDSI values from all herbaria records of those species in the CMH database (n=x).

To account for the influence of evolutionary relationships among species, we reconstructed the phylogenetic relationships in the genus based on the tree topology in . As as above, we computed branch lengths with the R package “ape” ().

We standardized the units of all predictors to make the directly comparable in the following model structure:

$$\text{logit}(P(Y \leq j)) = \beta_{[j]phylo[i]} + \beta_{pdsi[sp[i]]} * X_1 + \beta_{fruitdiamter} * X_2 + \beta_{floralinvestment} * X_3 + \epsilon_i$$

$$\epsilon_i \sim N(0, \sigma_y^2)$$

where Y is the ordinal outcome of flower-leaf sequence category (“flowers before leaves”, “flowers before/with leaves”, “flowers with leaves” and “flowers after leaves”) and j is the number of categories (1,2,...4).  $P(Y \leq j)$  is the probability of Y less than or equal to a category j=1,...,j-1.

As above, the influence of the phylogeny  $\alpha_{phylo}$  was modeled as follows:

$$\alpha_{sp} \sim N(\mu_{\alpha}, COR[\sigma_{phylo}^2])$$

We fit these models in the R package “brms” (Bürkner, 2018) using weakly informative priors, and ran the model on four chains with a warmup of 6,000 iterations and 8,000 sampling iterations for a total of 8,000 sampling iterations to maximize the effective sampling size. Model fit was assessed with Rhats <1.01 and high effective sample sizes and no divergent transitions.

## Results

### Quantifying flower leaf sequences in the American plums

We found substantial inter-specific differences in flower-leaf sequences within the American plums (Fig. 2, S1). Flower-leaf sequence patterns were strongly dependent on the day of observations, with observations later in the the flowering season of each species decreasing the likely hood of finding flowers open during early vegetative BBCH phases ( $\beta_{day}$  0.03,  $CI_{50}$  [0.02,0.03] ). Based on our flower leaf sequence index, two species (*P. umbellata*, *P. mexicana*) were likely to be hysteranthous regardless of the time of observation and three species (*P. rivularis*, *P. subcordata*, and *P. texana*) were always most likely to flower after level expansion began (Fig. 3). All other species displayed intermediate phenotypes with five species mostly likely to hysteranthous at the start of the season (*P. alleghaniensis*, *P. americana*, *P. hortulana*, *P. munsoniana* and *P. nigra*), one species through early season (*P. gracilis*) and two species through mid season (*P. angustifolia*, *P. maritima*) (Fig 3).

## Associations between hysteranthy and environmental and morphological traits

In the American plums clad we found a negative association between flower-leaf sequence index and mean pdsi ( $\beta$ : -0.03,  $CI_{50}$ [-0.05, 0.02], Fig. 4a.), suggesting that species that displayed hysteranthous flowering later into their flowering season are found in dryer locations.

We found a negative association between flower-leaf sequence index and both petal length and fruit diameter (-.21,  $CI_{50}$ [-0.38 -0.04], -1.40,  $CI_{50}$ [-1.97 -0.82] respectively), though the relationship between FLS index and fruit size was much stronger (Fig. 4b.,c.). This suggests that smaller fruits and flowers are associated with species that displayed hysteranthous flowering later into their flowering season.

At the genus level, there was a positive association between increasing pdsi and inflorescence size and increasing overlap between flowers and leaves ( $\beta$ : 2.50,  $CI_{50}$ [1.17, 3.371] and  $\beta$  6.41,  $CI_{50}$ [3.86, 8.05] respectively, Fig. 5a), suggesting that hysteranthy is associated with drier locations and smaller floral displays (Fig. 5b). The estimated effect of fruit size in the model was negative ( $\beta$ : -1.24,  $CI_{50}$ [-1.95,-0.21], 5a)]. Small fruits were mostly likely to be associated with species that flower with their leaves, and large fruits with species that flower before leaves, though there was high uncertainty around these estimates in our model (Fig. 5b).

## Discussion

Our analyses of hysteranthous flowering in North American *Prunus* species offer several critical insights into the evolution and function of this phenological syndrome in this genus, that can be extended to make inference on the role of hysteranthy in biotically-pollinated species at large.

Our high-resolution analysis of the American plums clade revealed that even within species flower-leaf sequences are highly labile. For all members of the clade the day of phenological observation was a strong predictor of the likelihood that flowers would be visible before the emergence of leaves, and at any observation time over the course of the flowering season, for many there was high likelihood that individual of a species may be observed at different vegetative stages during flowering (Fig. 4, S1). The intra-specific variability we detected in our study furthers a growing call to adopt a bottom-up, observational approach to the study of flower-leaf sequences by quantifying flower-leaf sequences at the individual level and modeling these patterns are coarser taxonomic scales rather than treating them as immutable categorical patterns at the species level ().

Despite this, the coherence of inference between our bottom-up, observational approach for the American plum clade and the top-down, categorical approach we took for the larger genus *Prunus* is an encouraging demonstration that the categorical species level based on expert opinion approach can still offer useful insights into the drivers of hysteranthous flowering when higher-resolution data is not available. Our modeled flower-leaf sequences patterns of the American plums qualitatively with previous characterizations of the species-level variation in this group (). Across taxonomic scales and data approaches, our analyses agree that within the North American species of the genus *Prunus*, hysteranthous taxa occurred in more arid environments, and tended to have smaller floral displays. In the American plums clade, smaller fruits were associated with less overlap between flowering and leaf development while at the genus level, smaller fruits were weakly associated with more flower-leaf overlap. Comparing the direction and strength of these associations across taxonomic scales helps to hone the hypotheses of hysteranthy and identifies important realms of further inquiry.

## Relationships to the hypotheses

### Hydraulic demand

The direction associations between pdsi and flower-leaf sequences follow the expectations the hydraulic demand hypothesis, with hysteranthous species occupying generally drier area.

Studies that have compared the transpiration rates among flowers and leaves that occur simultaneously provide insights to the potential importance of this seasonal partitioning for maintaining water status. These studies report floral transpiration rates of flowers can range from 20%-60% of that of leaves under comparable conditions (Whiley *et al.*, 1988; Roddy & Dawson, 2012). This additional hydraulic demand can drive loss of stomatal conductance and decrease photosynthetic rates (Galen *et al.*, 1999). A recent study Liu *et al.* (2017) comparing hydraulic properties of flowers and leaves in two hysteranthous tree species (*Magnolia spp*), found that sap flow to flowers (a measure of water movement) was 22-55% that of leaves. When considering species in or study specifically, the xylem conductivity of spring floral branches of *Prunus americana* is reported to be 20% of summer foliage branches (McMann *et al.*, 2022). Taken together, magnitude of water loss through floral organs in these physiological measurements demonstrate an underlying mechanism for the macro-ecological patterns we observed in our data.

However, when considering the likelihood that aridity is an evolutionary driver of hysteranthous flowering in biotically-pollinated species, its is important to consider the strength of the relationship as well as the direction. In the American plums, the mean PDSI at which all species were found ranged between -0.40 and 0.67, and at the larger genus PDSI values ranged from -.39 to .28 . The slope we estimate for PDSI on shifts between FLS categories was weak with high residual variance, indicating that while hysteranth species may, on average, occupy marginally drier environments, hysteranth may not accomidate extreme aridity (say better).

To better understand this, we must consider the flower-leaf sequences in the context of the full season phenological cycle of the clades we studied in comparison to the taxa that display this habit in the dry deciduous forest of neotropics (do we still say this word or is it colonialist?).

In all temperate *Prunus* species, there is significant overlap between vegetative and reproductive phenological phases, even in hysteranth species. While flowering may precede leafout by as much several weeks, the process of fruit development, which is also water intensive, occurs when leaves are present for all species. This basically undoes the hydralic demand partitioning.

By contrast, hysteranth in the dry tropics follows a different pattern. In these regions, flowering is initiated at the time of leaf drop, meaning that the full reproductive cycle occurs in the leafless period.

Yet, the relationship we observed suggest wwe shoudl study this moore This field of inquiry would benefit from more mechanistic experiments. Do species with contrasting FLS behave differently in drought (physiological measurements, fruit abortion, flower production, etc?) Given we saw so much lability, can aridiy induce increased hysterhanthy?

The same caveat about the strength of relationships must be raised regarding the relationship between floral display size and hysteranth in the context.

The negative relationship between flower size and hysteranth at both scales reflects several hypotheses. It is compatable with the insect visibility hypothesis. Though far from convince. Mechanistic studies would be helpful here.

It is also reflective of the developmental constraint hypothesis.

Again the full range of flower size in *Prunocerasus* was (Xmm- Ymm). How important is that. By contrast the larger genus includes species with large inflorescences. This is probably why the signal is so strong at the genus level.

The contrasting result for fruit size is interesting. The small fruits, petals and aridity fit nicely into a resource constraint, hypotheses. Larger fruits are at the genus level development time hypotheses. We highlight that this trait was the poorest sampled in both of our data, with small observation numbers in the herbaria data and high uncertainty in the genus model.

Taking a bird's eye view this is like OE evolution. It certainly matters at the extremes, but in the middle drifts dominate, or general selective forces on flowers and leaves create incidences of patterns. In this study we intentionally chose to analyze a small, and morphologically restricted taxonomic clade in order to reduce the impact of unmeasured biological variation on our traits of interest.

It would be useful to look at other temperate groups with high FLS variation including *Magnolia*, *Rhododendron*, *Acer*, *Cornus*.

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## Figures

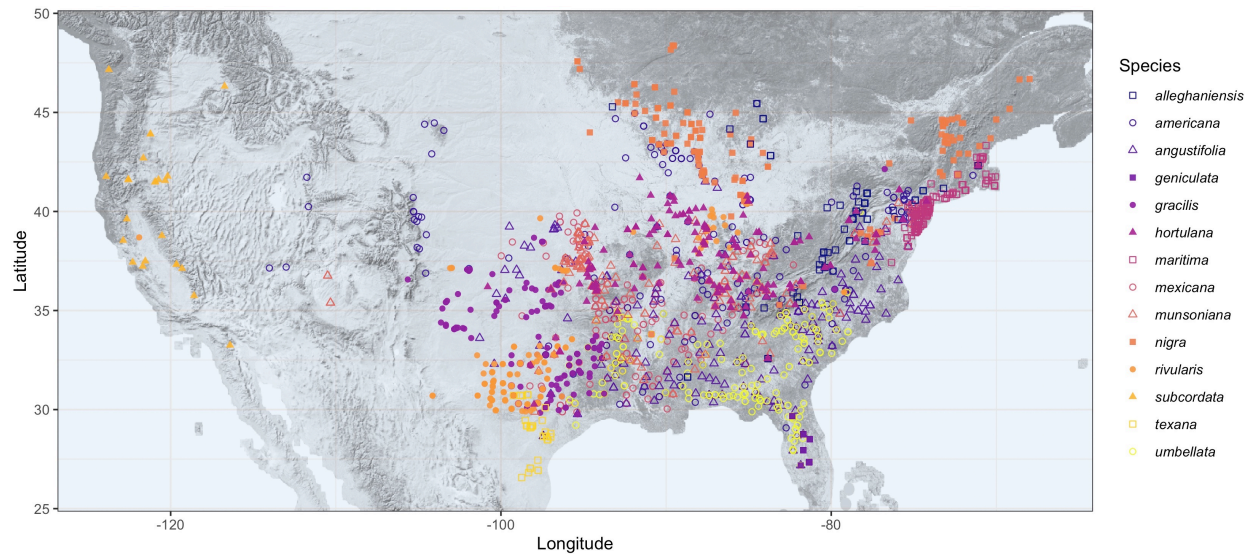


Figure 1: This is a map of all the herbaria records of our focal clade. Maybe better in the supplement

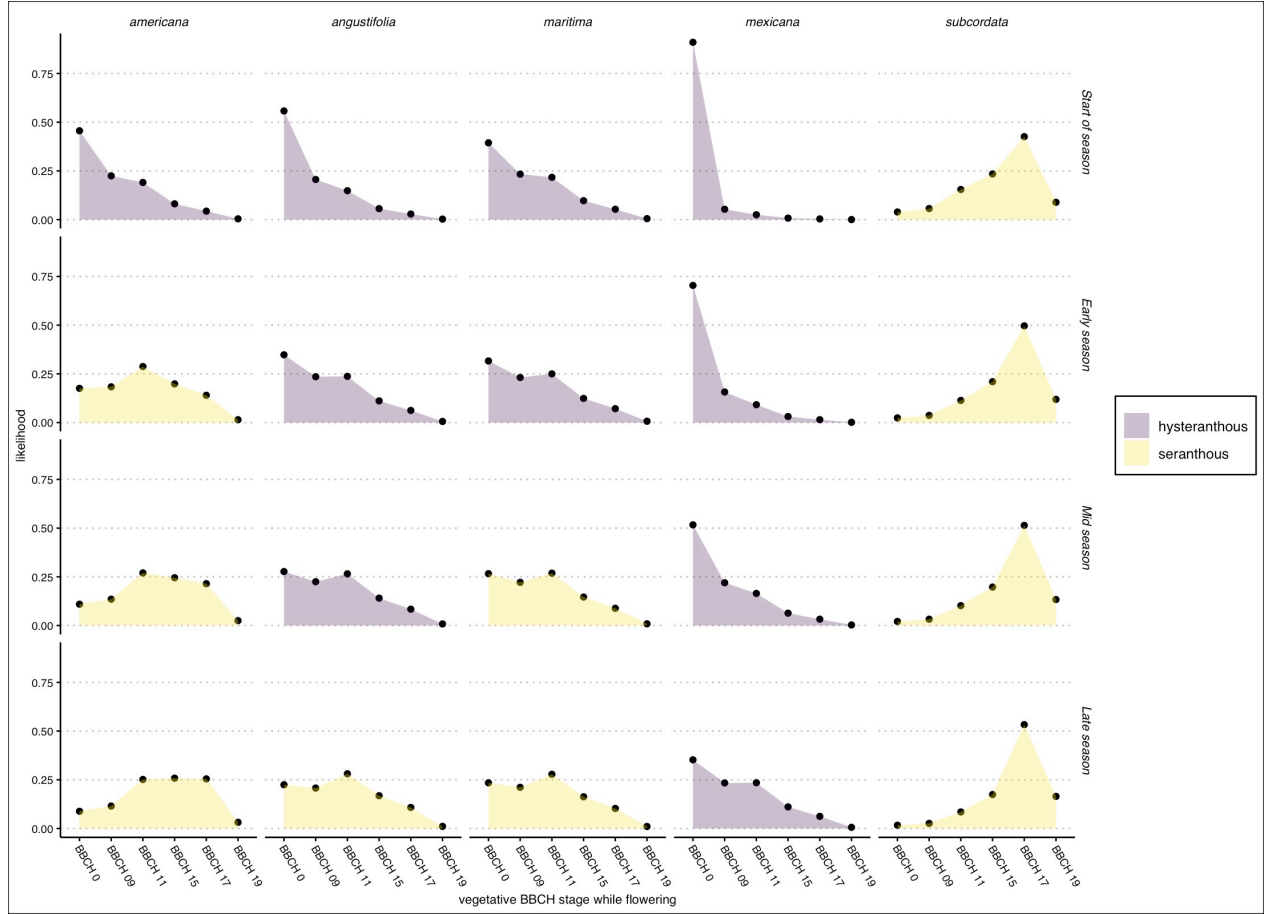


Figure 2: Predicted likelihood that a species would be in flower during each vegetative BBCH phase for five example species in the American plums. Points are the mean likelihood and bar the 95% uncertainty intervals. Species were classified as hysternthous if greater than 50% probability flowering occurred in BBCH 0 and BBCH 09 (colors) for each part of the flowering seasion. See Fig. S1 for all species and alternative hysternthous classification schemes.

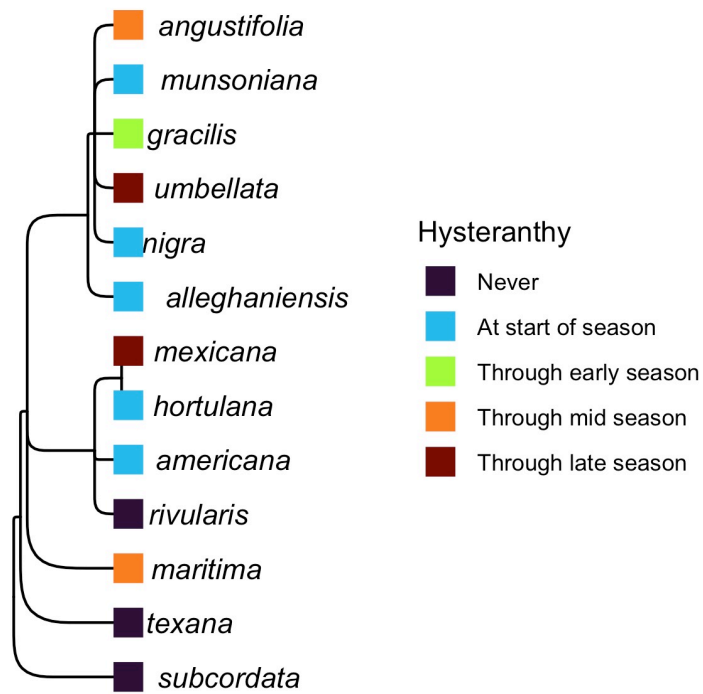


Figure 3: Phylogenetic relationships among the American plums and the duration of their flowering period they are hysteranthous. These categorizations are based on ordinal phylogenetics mixed models. Tree topology is from Shaw.

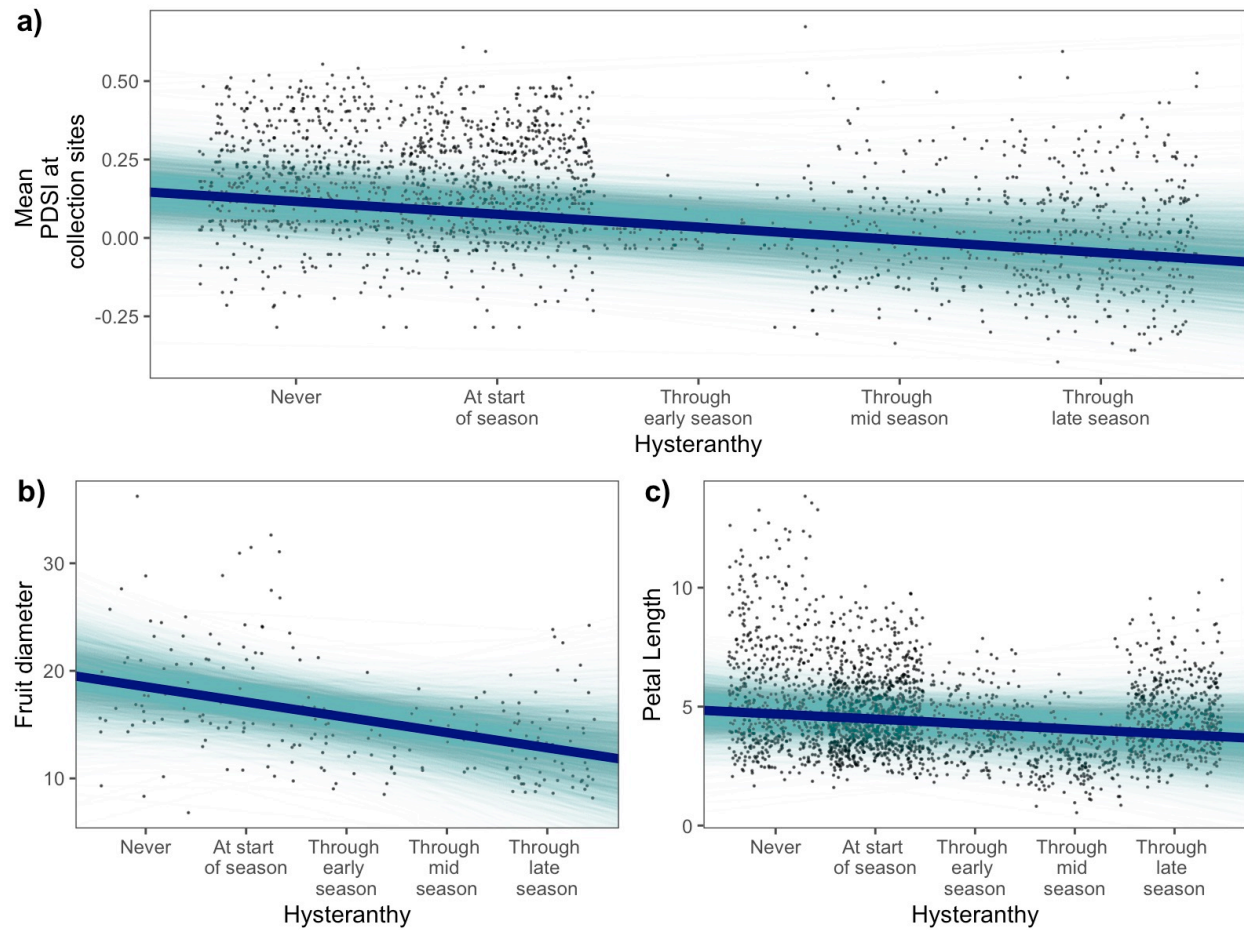


Figure 4: Relationships between the duration of hysteresis across the flowering period and environmental and biological traits based on Bayesian phylogenetic mixed models.

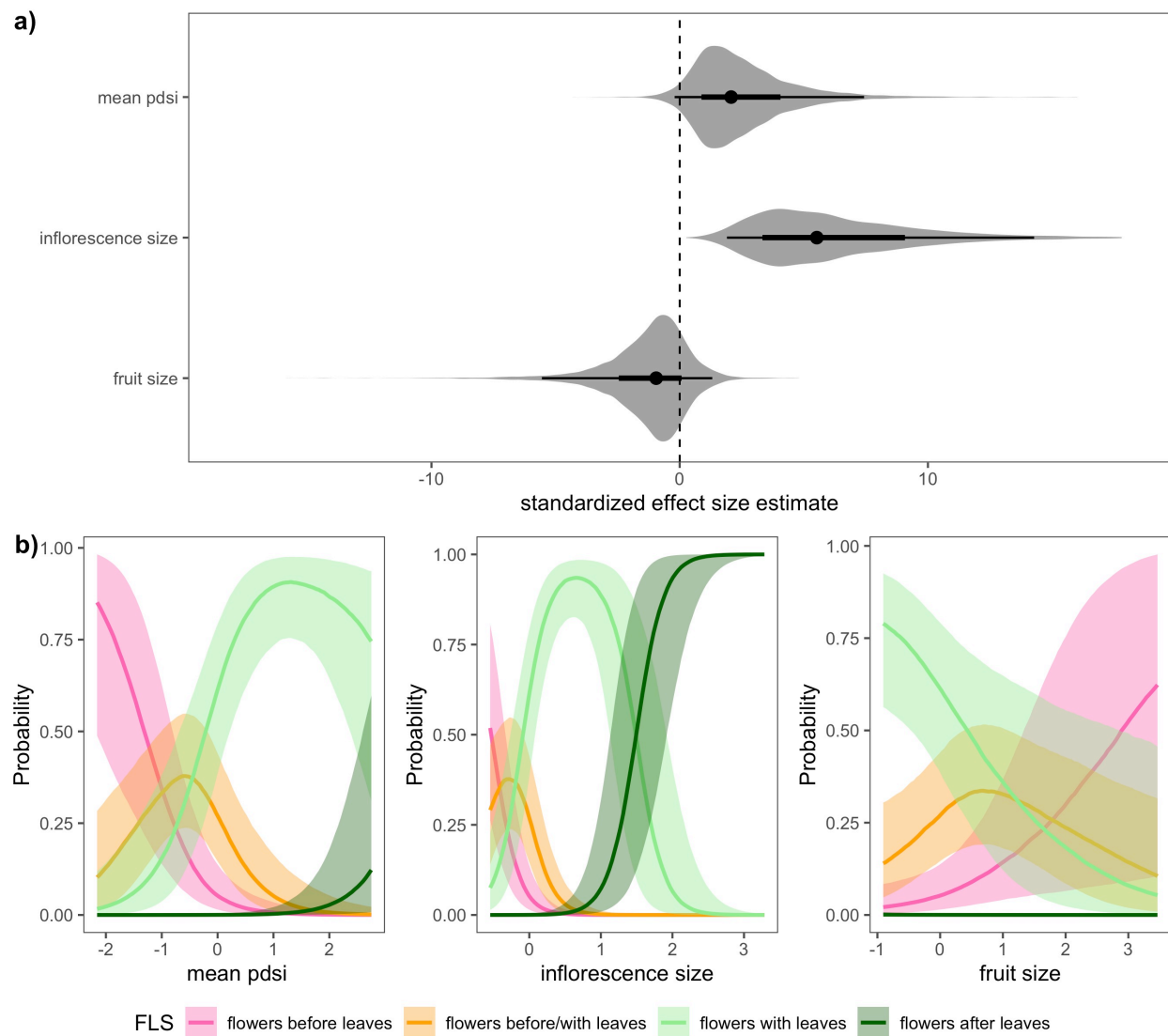


Figure 5: