Ecological drivers of flower-leaf sequences: aridity and pollination success select for flowering-first in insect-pollinated temperate trees

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Summary

- Many trees in temperate forests produce flowers before their leaves emerge. This flower-leaf phenological sequence, known as hysteranthy, is generally described as an adaptation for wind-pollination—which does not explain why it is also common in biotically-pollinated taxa.

- In this study, we quantified flower-leaf sequence variation in the American plums (*Prunus*, subspp. *Prunus* sect. *Prunocerasus*), a clade of insect-pollinated species, using herbaria specimens and Bayesian hierarchical modeling. With these observations, we tested common hypotheses for the evolution of hysteranthy by modeling the associations between hysteranthy and related traits. To better understand how these phenology-trait associations were sensitive to taxonomic scale and flower-leaf sequence classification, we extended these analyses to the more inclusive genus *Prunus*.

- In both groups hysteranthy was associated with aridity and smaller floral displays. These findings indicate that hysteranthy may function to temporally partition hydraulic demand and reduce water stress, or increase pollinator visibility and reduce selective pressure on flower size.

- Our study provides insights into the function of flower-leaf sequences in biotically-pollinated species. Our findings that hysteranthy is linked to aridity tolerance and pollination success highlights the importance of phenological sequences in global change research as climate shifts continue to disrupt pollinator services and impact environmental variability.

Keywords: Deciduous forests, Flower-leaf sequences, Hysteranthy, Phenology, Plant hydraulics, Pollination, Phylogeny

Introduction

Woody perennials have a unique ability among plants to seasonally begin reproduction prior to vegetative growth. This flowering-first phenological sequence, known as hysteranthy, proteranthy 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 sequence is under selection, and that hysteranthy has functional significance (Gougherty & Gougherty, 2018; Buonaiuto *et al.*, 2021; Guo *et al.*, 2014), but the importance of variation in flower-leaf sequences for maintaining fitness may vary across functional types and evolutionary clades within the temperate forest biome. With mounting evidence that anthropogenic climate change is driving shifts in flower-leaf sequences (Ma *et al.*, 2021; Wang *et al.*, 2022), expanding our understanding of the adaptive benefit of hysteranthy may be important to forecasting the demography and performance of forest communities.

The most common, and well-tested explanation for the evolution of hysteranthy 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). However, this explanation does not address the widespread prevalence of hysteranthy in biotically-pollinated taxa found in temperate regions. This number is not trivial; a recent analysis found that approximately 20% of the hysteranthy species in Eastern Temperate Forests of North America are biotically-pollinated (Buonaiuto *et al.*, 2021).

Several alternative hypotheses have been put forward to explain the advantage of hysteranthy in biotically-pollinated species, but they have not been widely evaluated in the literature. Below, we briefly review these hypotheses and their predictions, and then test these predictions using the American plums (*Prunus* subspp. *Prunus* sect. *Prunocerasus*), a widespread clade with high variability in flower-leaf sequences, as a case-study. Our treatment here both clarifies the hypothesized function of flower-leaf sequence variation in biotically-pollinated taxa, and offers insights into how shifting flower-leaf sequences may impact species demography and distributions as climate continues to change.

Hypotheses of hysteranthous flowering in biotically-pollinated taxa

<u>Water limitation hypothesis:</u> In the dry-deciduous tropics of South and Central America, hysteranthy is 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). Under this hypothesis, the function of hysteranthous flowering in temperate regions parallels that in the dry tropics—partitioning hydraulic demand across the season to allow hysteranthous species to tolerate increased aridity. While temperate forests are rarely water-limited in the early season during which flowering and leafing occur (Polgar & Primack, 2011), there is still considerable variation in water availability in space and time within temperate regions of the globe. With this hypothesis, we would expect to find hysteranthous taxa in locations that are, on average,

drier than their non-hysteranthous relatives.

Insect visibility hypothesis: Hysteranthous flowers are visually conspicuous in the landscape. Thus, as in wind-pollinated taxa, hysteranthy in biotically-pollinated taxa may be an adaptation for pollination efficiency as flowering-first species are easier for insect pollinators to locate (Janzen, 1967). This hypothesis predicts that hysteranthy should be associated with smaller floral displays, because flowers are not obscured by leaves, they are easier to see, and there is weaker selection for increasing floral display size.

Fruit maturaturion hypothesis: There are several aspects of reproductive development that suggest hysteranthy is a by-product of developmental constraints related to fruit maturation. Hysteranthy may be common in large fruited species that require lots of time to mature their fruits, or in small, early fruiting species that have evolved dispersal syndromes (wind dispersal, non-dormant seeds) that require dispersal early in the season (Primack, 1987). In either case, we should expect fruit size to associate with hysteranthy, although the sign of the correlation differs.

Alternative to these functional hypotheses is the assertion that hysteranthous flowering is simply a by-product of selection for early flowering. Species that flower before their leaves inherently flower early in the season. Spring flower phenology is less constrained by prior phenological events than leaf phenology (Savage, 2019; Ettinger et al., 2018), which could allow selection to drive flowering into the early season, producing the hysteranthous phenological sequence. Here, there is no specific adaptive advantage to hysteranthy; selection is not operating on the relative timing of flower and leaf emergence, but rather the absolute flowering time alone. Rejection of the above hypotheses might provide support to this null explanation.

A significant challenge for robust testing of hysteranthy 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 been used widely to investigate variability of flower-leaf sequences among and within species.

The American plums offer potential for a high resolution investigation of drivers of hysteranthous flowering in taxa that are not easily explained by the dominant wind-pollination hypothesis. 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-pollinated, yet show pronounced inter-specific variation in flower-leaf sequences. Usefully, species in this section are well represented in herbaria records (Fig. 1a), making them a tractable group to measure and assess variation in flower-leaf sequences.

To interrogate the functional hypotheses for hysteranthous flowering described above, we used herbaria records to to quantify both within- and across- species level variation in flower-leaf sequences of the American plums.

Then we combined environmental attributes, biological traits and phylogenetic data in statistical models to evaluate whether the observed associations between flower-leaf sequence variation and morphological and environmental traits match the predicted associations of the hysteranthy hypotheses. Finally, we compared our findings in this clade to patterns observed in larger genus *Prunus* to better understand whether these phenology-trait associations were sensitive to taxonomic scale and flower-leaf sequence classification.

Materials and Methods

Quantifying flower-leaf sequence variation

We obtained digital herbarium specimens for all members of the section *Prunocerasus* from the Consortium of Midwest Herbaria (CMH) Database (Consortium of Midwest Herbaria, 2023). To quantify flower-leaf sequence variation within and across species we randomly sampled 200 specimens for each species and scored the phenological development of flowers 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 flowers 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). We inferred branch lengths following the method of Grafen & Hamilton (1989) in which node heights are estimated in proportion to number of subtending taxa using the R package "ape" (E. Paradis and K. Schliep, 2019).

To quantify flower-leaf sequence variation, we fit an ordinal, hierarchical, Bayesian phylogenetic mixed model (de Villemeruil P. Nakagawa, 2014) to assess the likelihood an individual would be at any given vegetative BBCH phase while flowering. Our model predicted leaf stage (y_i, ordinal, with six categories) as a function of species and additional phylogenetic effects. Because hysteranthy co-varies with flowering time (i.e., flowering first species will generally flower earlier than other species, on average) we included day of observation as an additional predictor. The model is written below:

$$
y_i = \begin{cases}
1 & if & z_i < 0 \\
2 & if & z_i \in (0, c_2) \\
3 & if & z_i \in (c_2, c_3) \\
4 & if & z_i \in (c_3, c_4) \\
5 & if & z_i \in (c_4, c_5) \\
6 & if & z_i > c_5
\end{cases}
$$

$z_i = \alpha + \alpha_{phylo} + \alpha_{sp} + \beta_{\text{day of year[sp]}} * X_{\text{day of year}} + \epsilon_i$

$\epsilon_i \sim logistic(0, 1)$

where y_i is the ordinal outcome (leaf stage; as 1,2,...6 categories). $c_{2...5}$ are the estimated cutpoints between leaf stages on the logit scale. z_i is the linear component of the underlying latent variable model. α describes an intercept for each category [1,2,...6], while slope ($\beta_{\text{day of year}}$) is constant across cutpoints, but varies among *species*.

The influence of the phylogeny (α_{phylo}) was modeled as:

$\alpha_{phylo} \sim N(0, COR[\sigma^2_{phylo}])$

The α for species effects independent of the phylogeny was modeled as:

$\alpha_{sp} \sim N(0, \sigma^2_{species})$

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 than 50% of their probability distribution occurred at the two earliest stages of vegetative phenology—BBCH 0 ("bud development") and BBCH 09 ("bud break")—and a "0" if not. We summed these values 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) to make sure our result were robust across multiple cutoffs.

Evaluating hysteranthy hypotheses

To test the hypotheses of hysteranthy, we obtained data on petal length and fruit diameter directly from herbarium specimens. To assess aridity tolerance, we computed the average Palmer Modified Drought Index score from 1900-2017, obtained from the National Centers for Environmental Information (2017), for every *Prunocerasus* specimen in the database(n=2305). For any specimens that lacked accurate geo-location information, we extracted PDSI values at the county centroid of the herbaria specimen.

For our morphological measurements, we sampled an additional 321 specimens and 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 then used Bayesian phylogenetic mixed models to test the relationship between flower-leaf sequence index scores and each of the variables. In these models, we modeled species and phylogeny as above.

The model structure is:

$$y_{trait} = \alpha + \alpha_{sp} + \alpha_{phylo} + \beta_{hyst.index} * X_{hyst.index} + \epsilon$$

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

where y_{trait} is observed trait values (PDSI, petal length or fruit diameter), and the slope $\beta_{\text{hyst.index}}$ describes the relationship between extended hysteranthy (higher hysteranthy index value) and the trait of interest. α describes a grand intercept, and α_{sp} and α_{phylo} describe the species and phylogenetic effects respectively.

We also ran each model using our two alternative flower-leaf sequence indexing approaches to make sure our results were robust to choice of index. Though these alternative classification schemes did change the hysteranthy index score for some species (Fig. S1), they 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 *Pruncerasus* scaled to a larger more inclusive group and across coarser taxonomic resolution and flower-leaf sequence classification we also evaluated the relationship between hysteranthous flowering and hypothesis-related traits in all *Prunus* species native to, or established in, North America. For this analysis, we obtained categorical descriptions of flower-leaf sequences and mean estimates of fruit diameter and number of flowers per inflorescence as a proxy for floral investment from the Flora of North America (Rohrer, 1993+). We extracted PDSI values for all herbaria observation of those species in the Consortium of Midwest Herbaria database (n=23,272) as described above.

To account for the influence of evolutionary relationships among species, we reconstructed the phylogenetic relationships in the genus based on the tree topology in Chin *et al.* (2014). As above, we computed branch lengths with the R package "ape" (E. Paradis and K. Schliep, 2019).

We standardized the units of all predictors through z-scoring (Gellman & Hill, 2007) to make their effect size estimates for the following model structure directly comparable to each other:

$$y_i = \begin{cases} 1 & if \quad z_i < 0 \\ 2 & if \quad z_i \in (0, c_2) \\ 3 & if \quad z_i \in (c_2, c_3) \\ 4 & if \quad z_i > c_3 \end{cases}$$

$$z_i = \alpha + \alpha_{phylo} + \beta_{PDSI} * X_{PDSI} + \beta_{\text{fruit diameter}} * X_{\text{fruit diameter}} + \beta_{\text{floral investment}} * X_{flowers/inflorescence} + \epsilon_i$$

$$\epsilon_i \sim logistic(0, 1))$$

7

182 where y_i is the ordinal outcome of flower-leaf sequence category ("flowers before leaves", "flowers before/with

183 leaves", "flowers with leaves" and "flowers after leaves") and $c_{2...3}$ are the estimated cutpoints between cat-

184 egories on the logit scale. As above, z_i is the linear component of the underlying latent variable model. α

185 describes a grand intercept, and we modeled the influence of phylogeny (α_{phylo}) as above.

Model runs

187 We fit models in the R package "brms" (Bürkner, 2018) using weakly informative priors, and four chains. For

188 the "Quantifying flower-leaf sequence variation" and "Evaluating hysteranthy hypotheses" we ran the models

189 with a warm-up of 3000, and 3500 iterations, and 4000, and 4500 sampling iterations respectively, for a total

190 of 4000 sampling iterations across all chains. For the "Hysteranthy in the larger genus *Prunus*" model, we

191 used a warm up of 6,000 iterations and 8,000 sampling iterations for a total of 8,000 sampling iterations to

192 maximize the effective sampling size. Model fits was assessed with $\hat{R}$ <1.01, high effective sample sizes and

193 no divergent transitions. We provide mean estimates and 50% uncertainty intervals in the text with alternate

194 intervals in figures and the Supporting Information.

Results

Quantifying flower leaf sequences in the American plums

197 We found substantial inter-specific differences in flower-leaf sequences within the American plums (Fig. 2,

198 S1). Flower-leaf sequence patterns were strongly dependent on the day of observation, with observations

199 later in the the flowering season of each species decreasing the likelihood of finding flowers open during early

200 vegetative BBCH phases (β_{doy} 0.03, CI_{50} [0.02,0.04]). Based on our flower leaf sequence index, two species

201 (*P. umbellata*, *P. mexicana*) were likely to be hysteranthous regardless of the time of observation and five

202 species (*P. alleghaniensis*, *P. nigra*, *P. rivularis*, *P. subcordata*, and *P. texana*) were always most likely to

203 flower after leaves developed (Fig. 1b). All other species displayed intermediate phenotypes, with four species

204 mostly likely to hysteranthous at the start of the season (*P. americana*, *P. hortulana*, *P. munsoniana* and *P.*

205 *gracilis*), one species through early season (*P. maritima*) and one species through mid season (*P. angustifolia*)

206 (Fig 1b).

Associations between hysteranthy and environmental and morphological traits

208 In the American plums clade, aridity (lower average PDSI) was associated with higher flower-leaf sequence

209 index scores (β: -0.04, CI_{50}[-0.06, -0.03], Fig. 3a), suggesting that species that displayed hysteranthous

210 flowering later into their flowering season are found in drier locations.

Shorter petal and smaller fruit diameters were also associated with higher flower-leaf sequence index scores (β: -.21, CI_{50}[-0.38 -0.05] and β:-1.41, CI_{50}[-2.00 -0.84] respectively, Fig. 3b,c). This suggests that smaller fruits and flowers are associated with increased hysteranthy.

At the genus level, there was a positive association between increasing PDSI and inflorescence size and increasing overlap between flowers and leaves (i.e., decreasing hysteranthy; β: 2.50, CI_{50}[1.17, 3.371] and β 6.41, CI_{50}[3.86, 8.05] per standardized unit, respectively, Fig. 4a), again suggesting that hysteranthy is associated with drier locations and smaller floral displays (Fig. 4b). However, hysteranthy was associated with larger fruits (β: -1.24, CI_{50}[-1.95, -0.21], 4b) though there was high uncertainty around these estimates.

Discussion

Our study provides foundational insights into the evolution of flower-leaf sequences in biotically-pollinated plants. We show that hysteranthous flowering can be linked to both aridity tolerance and pollination success through the predictions of the water limitation and insect visibility hypotheses, highlighting the urgency for advancing our understanding of phenological sequences as human-caused global change continues to disrupt pollinator services and impact environmental variability.

Hysteranthy hypotheses

Using North American *Prunus* species as a case study, our analyses indicate that flower-leaf sequences are under selection by biological and environmental drivers, and that variation in these patterns across species may reflect adaptive tradeoffs. We found that hysteranthous flowering is associated with smaller floral displays and increased aridity in both the American plums, and more broadly across *Prunus* native or established in North America. While we did not find consistent support for the fruit maturation hypothesis, the relationships between hysteranthy and aridity, and hysteranthy and floral display size support the predictions of the water limitation hypothesis and the insect visibility hypothesis, respectively.

Our support for both the water limitation hypothesis and insect visibility hypothesis highlights that these hypotheses are not mutually exclusive, and could be related. Selection on floral size represents a classic evolutionary tradeoff where larger floral displays may generally be more effective for attracting pollinators but demand more resources, including water, to maintain turgor and reproductive function than smaller ones (Galen *et al.*, 1999; Lambrecht & Dawson, 2007). With this trade-off, reproductive displays are often small in harsher environments (Teixido *et al.*, 2016; Lambrecht, 2013), and hysteranthy could represent a compensatory mechanism that both reduces hydraulic demand while increasing pollination efficiency in these environments.

Studies that have compared the transpiration rates among flowers and leaves provide insights to the potential importance of this seasonal partitioning for maintaining water status. Measurements of water movement

(transcription rates, sap flow, hydraulic conductivity) to flowers range from 20%-60% of that of leaves under comparable conditions (Whiley *et al.*, 1988; Roddy & Dawson, 2012; Liu *et al.*, 2017; McMann *et al.*, 2022). This level of additional hydraulic demand can drive loss of stomatal conductance and decrease photosynthetic rates (Galen *et al.*, 1999).

Despite this evidence that hysteranthy can reduced hydraulic demand in dry environments, hysteranthous species in the American plum clade are not found in extremely arid locations (PDSI values typically range from -4 to 4, however our analyses found mean values ranging from -0.5 to 0.2 for species classified as hysteranthous through mid-season or through late season). This contrasts with hysteranthous species in the dry tropics where this phenological syndrome allows them to tolerate more extreme aridity (Franklin, 2016). But the flower-leaf sequences of the hysteranthous species in our study were markedly different from patterns of hysteranthy in these dry-tropics where the water limitation hypothesis was initially proposed. While flowering can precede leafout by as much several weeks for species in the American plums, the process of fruit development, which is also water intensive, occurs when leaves are present. By contrast, in the dry tropics hysteranthous flowering is initiated at the time of leaf drop (Borchert, 1983; Franklin, 2016); thus, the full reproductive cycle occurs in the leafless period. The comparatively small window of leafless reproductive development in our temperate clade, may in part, explain why the association we observed between hysteranthy and aridity in our study was relatively weak with high residual variance. Our results suggest that hysteranthy may allow temperate species to occupy marginally drier environments than non-hysteranthous species, but may not facilitate species' persistence under extreme aridity.

Inter-and intra-specific variation in flower-leaf sequences

We developed a novel approach to assessing flower-leaf sequences that scales from quantitative, individual-level observations to species-level characterizations that were based on empirical likelihood estimates. With this approach, we were able to—for the first time—quantitatively assess intermediate cases of hysteranthy (such as those that are typically described as "flowers before/with leaves"). Previous studies of hysteranthous flowering have either excluded these cases from their analyses (e.g.; Gougherty & Gougherty, 2018) or binned them with the well defined cases (e.g.; Buonaiuto *et al.*, 2021). We found that eight of the thirteen American plum species expressed this intermediate flower-leaf sequence, and our classifications broadly matched previous species-level analyses in this group by Shaw & Small (2004). By estimating the likelihood of hysteranthy across the growing season with Bayesian methods, our approach identified substantial differences in flower-leaf sequences among these intermediate cases (Fig. 2, Fig. S1), which allowed us to assess the trait associations with this phenotype.

Our quantitative analysis of the American plums clade revealed that flower-leaf sequences—often described as a species-level trait—are highly variable within species (Fig. 2, Fig. S1). 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. In many cases there was high likelihood that individuals of a species may

be observed at different vegetative stages during flowering (Fig. 2, S1). This variation could either suggest high levels of local adaptation in flower-leaf sequences or, alternatively, high levels of plasticity through which flower-leaf sequences respond to interannual variation in environmental conditions. For example—in a given population—flower-leaf sequences may respond to interannual variation in precipitation with increased temporal separation between flowers and leaves in drier years. While our data did not have the temporal resolution to address this question, the high levels of within-species variation we observed raise important questions about environmental drivers of flower-leaf sequences operating on both the macro-evolutionary scale we investigated here and on individual physiological responses to environmental change.

Additionally, by scoring these individual, quantitative observations as ordinal response categories with our hysteranthy index, we were able to contrast our findings to those derived from categorical, species-level characterizations based on expert opinion. The coherence between our individual based observational approach for the American plum clade and the top-down, categorical classification across *Prunus* is an encouraging demonstration that the expert opinion-based data can still offer useful insights into the drivers of hysteranthous flowering when higher-resolution data is not available.

Future directions

In this study, we focused on a well-studied, and economically important clade of morphologically similar species, that allowed us to control for unmeasured biological variation. Our case-study provides a road map for evaluating the role of hysteranthy in temperate biotically-pollinated plant taxa (other groups with high interspecific flower-leaf sequence variation include *Magnolia*, *Rhododendron*, *Acer* and *Cornus*), and more broadly across taxa and biomes.

Combining the observational approach with novel experiments could further advance our collective understanding of the adaptive significance of flower-leaf sequences. To test the water-limitation hypothesis, researchers could plant sister-taxa with contrasting flower-leaf sequences in common environments across a gradient of aridity, and evaluate their performance. To test the insect visibility hypothesis, researchers should also consider hysteranthy—and phenology in general—in the more general framework of tradeoffs in pollination biology. The tradeoff between phenology and pollination investment should not only consider flower size, but also the number of flowers, nectar and pollen reward investment, volatiles between related hysteranthous and non-hysteranthous taxa. Findings that hysteranthous species invest fewer resources into these other pollinator attraction traits than non-hysteranthous relatives would support the insect visibility hypothesis. For a simple experiment to test the pollinator visibility hypothesis, researchers could force hysteranthy/non-hysteranthy phenotypes for the same genotype using environmental cues, and systematically release pollinators to observe their preferences, search times and foraging behavior. If pollinators are more readily drawn to the hysteranthous individuals, it would suggest that hysteranthy may be an adaptive trait for pollinator attraction.

With a better mechanistic understanding of the relationship between flower-leaf sequences and ecological

performance in hand, researchers could then use experiments to assess how differences in floral and leaf physiological responses to temperature variation may alter the adaptive benefits of flower-leaf sequences with climate change. The measurement and modeling approaches we developed in our observational study can be readily implemented to analyze data from such experimental settings, presenting an important opportunity to unite observations of broad ecological patterns with targeted experimental manipulations to better understand both the evolutionary past and ecological future of flower-leaf sequences.

Competing Interests:

The authors declare no conflict of interest.

Author contributions

DMB, and EMW conceived of the manuscript; DMB and SC collected the data; DMB led the statistical analyses with TJD and EMW; DMB led the writing of the manuscript. All authors contributed to writing and gave approval for the submission.

Data Availability

The phenology and trait data collected for this study will be made available and archived at KNB: The Knowledge Network for Biocomplexity (https://knb.ecoinformatics.org/) at the time of publication.

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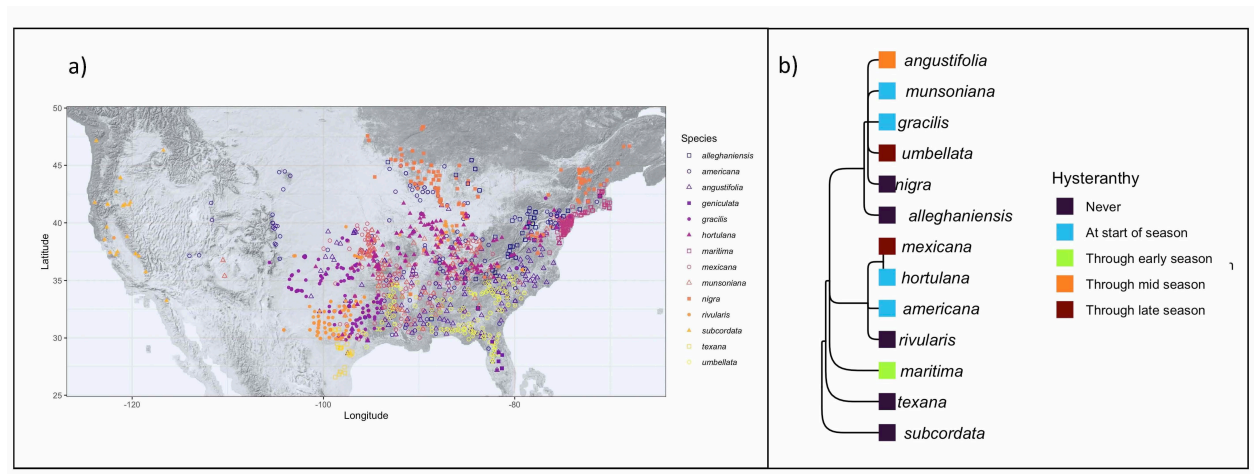402 *Trends in Ecology & Evolution*, **32**: 531–546.

Figures

Figure 1: Geographic distribution and taxonomic relationships among the American plums. a) Maps the localities of all the herbaria records used in this study. b) Depicts phylogenetic relationships among the American plums and the duration of their flowering period they are hysteranthous. These categorizations are based on ordinal phylogenetic mixed models. Tree topology is from Shaw & Small (2004)
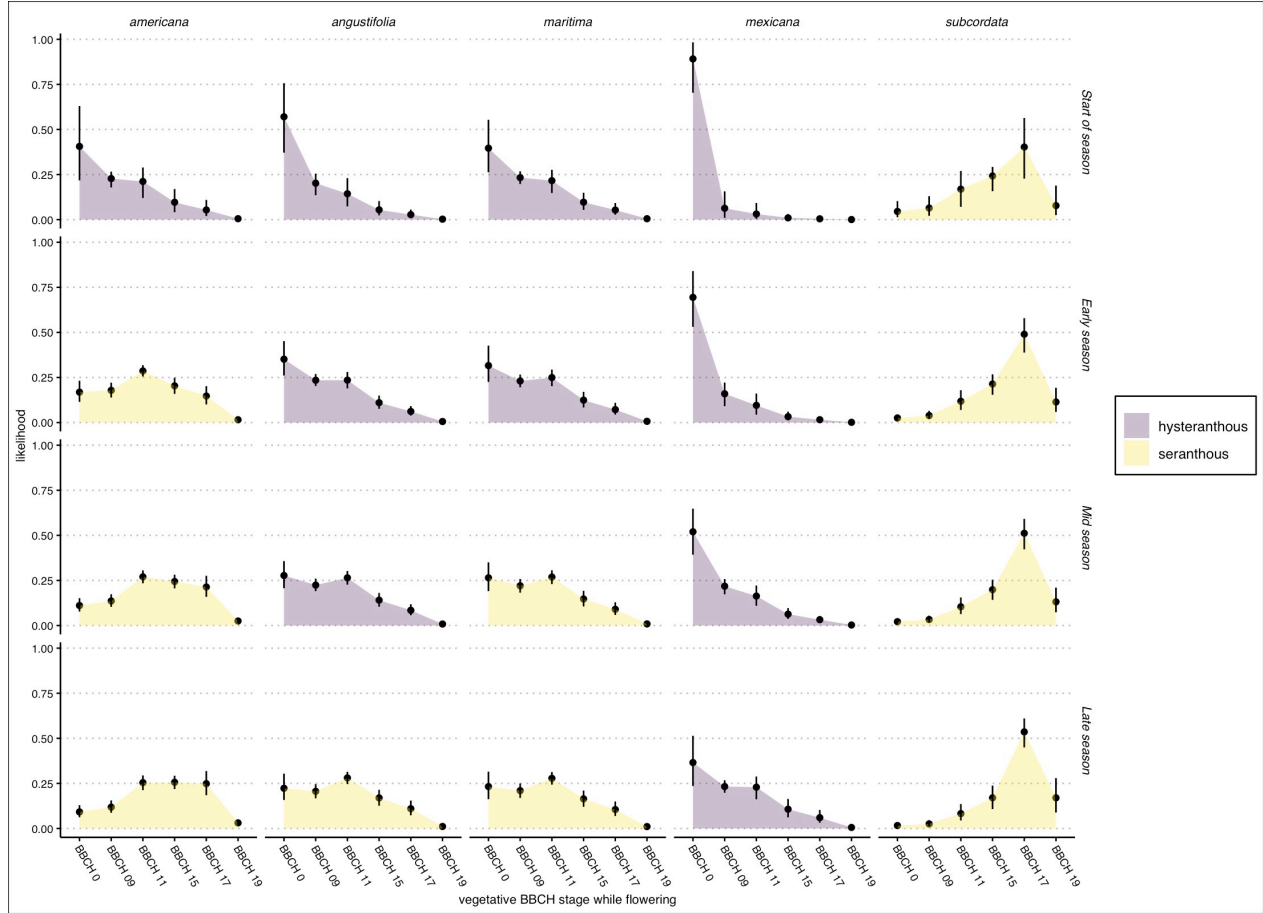
Figure 2: Predicted likelihood that a species would be in flower during each vegetative BBCH phase for five example species in the American plums. Points are the mean likelihood while bars represent 95% uncertainty intervals. Species were classified as hysteranthous if greater than 50% probability flowering occurred in BBCH 0 and BBCH 09 (colors) for each part of the flowering season. See Fig. S1 for all species and alternative hysteranthy classification schemes.
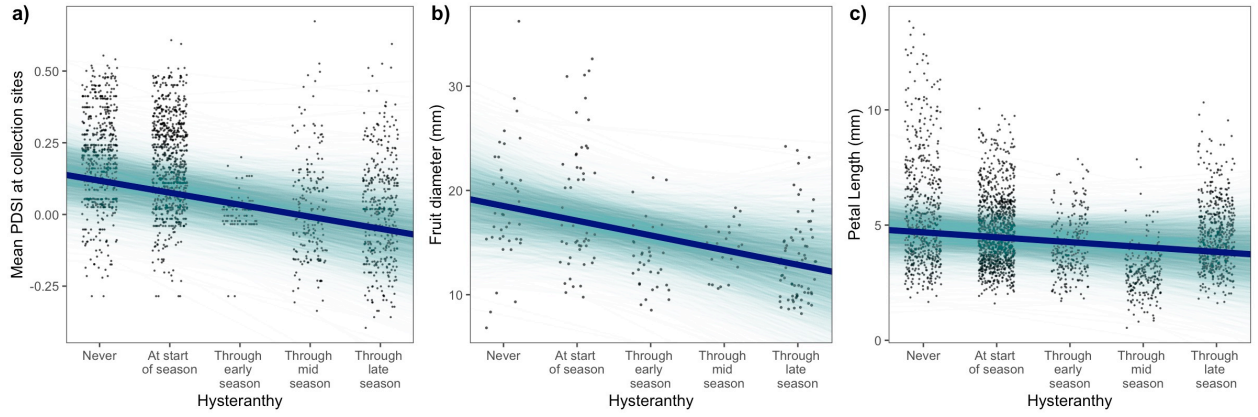
Figure 3: Relationships between the duration of hysteranthy across the flowering period and environmental and biological traits based on Bayesian phylogenetic mixed models. a) b) and c) depict the relationships between the duration of hysteranthy and mean PDSI, fruit diameter, and petal length respectively. Solid lines indicate the mean posterior estimate and shaded areas 4000 draws from the posterior distrubtion as a display of uncertainty. The points are jittered along the x-axis only for visibility.
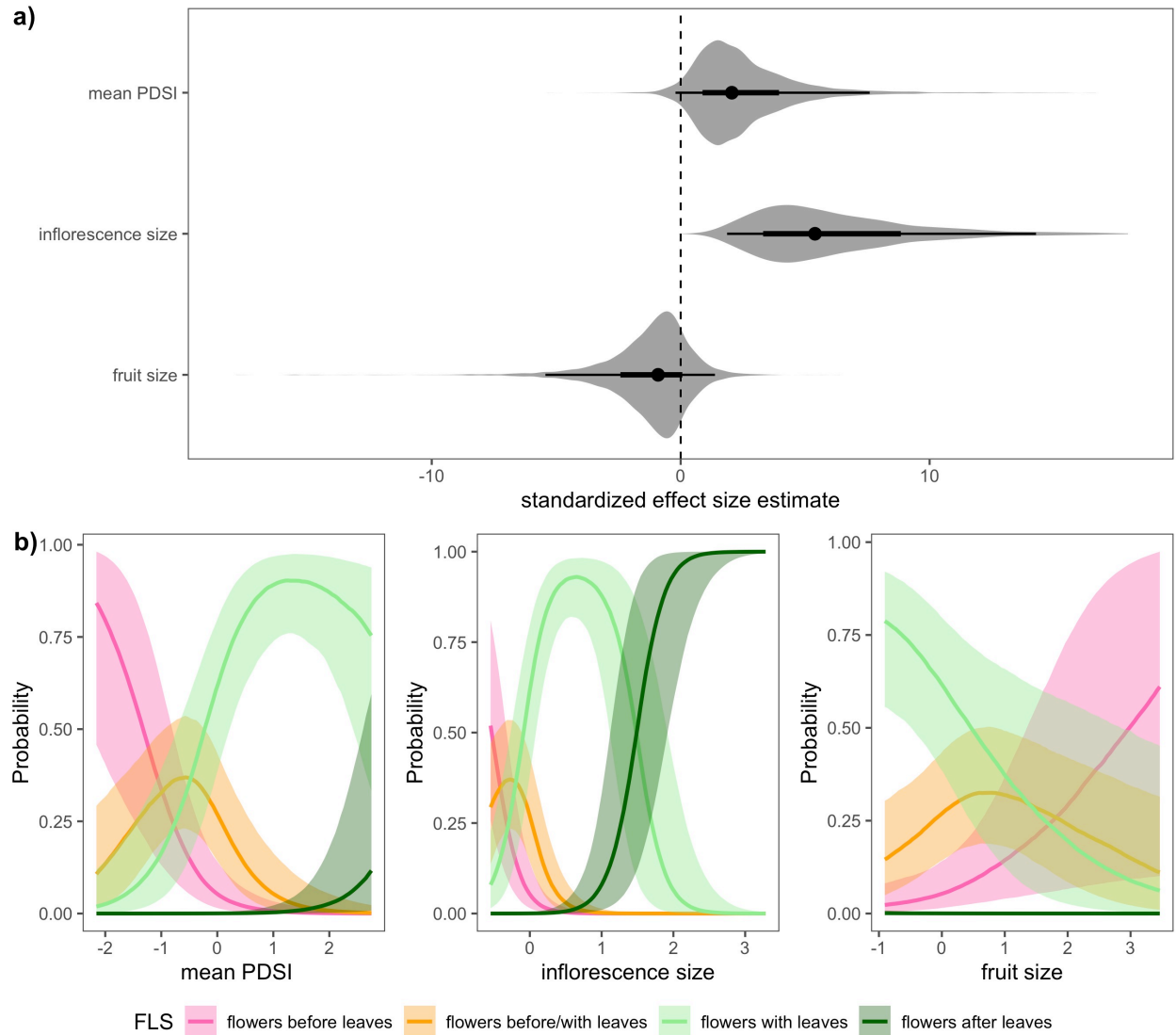
Figure 4: Relationships between the likelihood of hysteranthy and environmental and biological traits in the genus *Prunus* based on Bayesian phylogenetic mixed models. Panel a) shows the estimated effect size of each predictor with negative values indicating an increased likelihood of hysteranthy. Points indicate the mean posterior estimate for each predictor, and thick and thin bars the 50% and 97.5% uncertainty intervals respectively. We also show the full posterior distribution as an additional more of uncertainty, Panel b), c) and d) show the marginal effect of mean PDSI, inflorescence size and fruit size respectively, on the likelihood that of each flower-leaf sequence category. Solid lines indicate the mean likelihood and shaded areas the 50% uncertainty intervals.