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Content

<b>220</b>	Replacements
<b>32</b>	Insertions
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Styling and Annotations

<b>0</b>	Styling
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[Go to First Change \(page 1\)](#)

<sup>1</sup> Ecological drivers of flower-leaf sequences: aridity and **proxies for**  
<sup>2</sup> pollinator attraction select for flowering-first in the American Plums

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<sup>13</sup>

<sup>14</sup> Word Count: Introduction **945**, Materials and Methods: **1735**, Results: **503**, Discussion:**1647**, **Total: 4830**

<sup>15</sup> Figures: 4

<sup>16</sup>

<sub>17</sub> **Summary**

- <sub>18</sub> • Across temperate forests many tree species produce flowers before their leaves emerge. This flower-  
<sub>19</sub> leaf phenological sequence, known as hysteranthy, is generally described as an adaptation for wind-  
<sub>20</sub> pollination. However, this explanation does not address why hysteranthy is also common in biotically-  
<sub>21</sub> pollinated taxa.
- <sub>22</sub> • We quantified flower-leaf sequence variation in the American plums (*Prunus*, subspp. *Prunus* sect.  
<sub>23</sub> *Prunocerasus*), a clade of insect-pollinated trees, using herbaria specimens and Bayesian hierarchical  
<sub>24</sub> modeling. We tested two common, but rarely interrogated hypotheses—that hysteranthy confers aridity  
<sub>25</sub> tolerance and/or pollinator visibility—by modeling the associations between hysteranthy and related  
<sub>26</sub> traits. To understand how these phenology-trait associations were sensitive to taxonomic scale and  
<sub>27</sub> flower-leaf sequence classification, we then extended these analyses to all *Prunus* species in North  
<sub>28</sub> America.
- <sub>29</sub> • Our findings across two taxonomic levels support the hypotheses that hysteranthy may help temporally  
<sub>30</sub> partition hydraulic demand to reduce water stress, and increase pollinator **visibility**—thereby reducing  
<sub>31</sub> selective pressure on inflorescence size.
- <sub>32</sub> • Our results provide foundational insights into the evolution of flower-leaf sequences in the genus *Prunus*,  
<sub>33</sub> with implications for understanding these patterns in biotically-pollinated plants in general. Our ap-  
<sub>34</sub> proach suggests a path to advance these hypotheses to other clades, but teasing out drivers fully will  
<sub>35</sub> require new experiments.

<sub>36</sub> Keywords: Deciduous forests, Flower-leaf sequences, Hysteranthy, Phenology, Plant hydraulics, Pollination,  
<sub>37</sub> Phylogeny

## <sup>38</sup> Introduction

<sup>39</sup> Woody perennials are among a subset of plant types with the unique ability to seasonally begin reproduction  
<sup>40</sup> prior to vegetative growth. This flowering-first phenological sequence, known as hysteranthy, proteranthy or  
<sup>41</sup> precocious flowering, is apparent in temperate deciduous forests around the globe (Rathcke & Lacey, 1985).  
<sup>42</sup> A number of studies suggest that this flower-leaf sequence is under selection, and that hysteranthy can confer  
<sup>43</sup> performance advantages (Guo *et al.*, 2014; Gougherty & Gougherty, 2018; Buonaiuto *et al.*, 2021), but the  
<sup>44</sup> importance of variation in flower-leaf sequences for maintaining fitness may vary across functional types, taxa  
<sup>45</sup> and biomes.

<sup>46</sup> The most common, and well-tested explanation for the evolution of hysteranthy in temperate forests is that it  
<sup>47</sup> is adaptive for wind-pollination, as leafless canopies increase wind speeds for pollen transport and reduce the  
<sup>48</sup> likelihood of pollen interception by vegetation (Whitehead, 1969; Niklas, 1985). However, this explanation  
<sup>49</sup> does not address the widespread prevalence of hysteranthy in biotically-pollinated taxa found in temperate  
<sup>50</sup> regions. This number is not trivial; a recent analysis found that approximately 20% of the hysteranthy species  
<sup>51</sup> in Eastern Temperate Forests of North America are biotically-pollinated (Buonaiuto *et al.*, 2021).

<sup>52</sup> Alternative hypotheses have been put forward to explain the advantage of hysteranthy in biotically-pollinated  
<sup>53</sup> species, but they have not been widely evaluated in the literature. Below, we briefly review these hypotheses  
<sup>54</sup> and their predictions, then test their predictions using the American plums (*Prunus* subspp. *Prunus* sect.  
<sup>55</sup> *Prunocerasus*)—a widespread clade with high variability in flower-leaf sequences—as a case-study. Our study  
<sup>56</sup> both clarifies the hypothesized function of flower-leaf sequence variation in the genus *Prunus* and lays the  
<sup>57</sup> groundwork for understanding the origins of flower-leaf sequence variation in biotically-pollinated taxa more  
<sup>58</sup> generally.

## <sup>59</sup> Hypotheses of hysteranthous flowering in biotically-pollinated taxa

<sup>60</sup> Water limitation hypothesis: In the dry-deciduous tropics of South and Central America, hysteranthy is  
<sup>61</sup> common (Rathcke & Lacey, 1985; Franklin, 2016), and is regarded as an important adaptation to alleviate  
<sup>62</sup> water stress by partitioning the hydraulic demand of flowers and leaves across the season (Borchert, 1983;  
<sup>63</sup> Reich & Borchert, 1984; Franklin, 2016; Gougherty & Gougherty, 2018). Under this hypothesis, the function  
<sup>64</sup> of hysteranthous flowering in temperate regions parallels that in the dry tropics. While temperate forests are  
<sup>65</sup> rarely water-limited in the early season during which flowering and leafing occur (Polgar & Primack, 2011),  
<sup>66</sup> there is still considerable variation in water availability in space and time within temperate regions of the  
<sup>67</sup> globe. With this hypothesis, we would expect to find hysteranthous taxa in locations that are, on average,  
<sup>68</sup> drier than their non-hysteranthous relatives.

<sup>69</sup> Insect visibility hypothesis: Hysteranthous flowers are visually conspicuous in the landscape. Thus, as in  
<sup>70</sup> wind-pollinated taxa, hysteranthy in biotically-pollinated taxa may be an adaptation for pollination efficiency  
<sup>71</sup> as flowering-first species are easier for insect pollinators to locate (Janzen, 1967). A challenge to evaluating this

72 hypothesis is that correlated selection between flower-leaf sequences and pollinator visibility could have either  
73 a positive or negative relationship depending on the pollination environment. In one scenario, hysteranthy  
74 may be associated with smaller floral displays: because flowers are not obscured by leaves, they are easier  
75 to see and there is weaker selection for increasing floral display size. In an alternative scenario, hysteranthy  
76 could be associated with larger floral displays, especially in environments where plants are more often pollen-  
77 limited and selection may favor both hysteranthy and increased floral display size to augment floral attraction  
78 to visual pollinators.

79 In contrast to these functional hypotheses, hysteranthous flowering could simply be a by-product of selection  
80 for early flowering. Species that flower before their leaves inherently flower early in the season. For example,  
81 fruit development or dispersal constraints may drive early flowering (Primack, 1987), and because spring  
82 flower phenology is less constrained by prior phenological events than leaf phenology (Ettlinger *et al.*, 2018;  
83 Savage, 2019), this selection for early flowering could incidentally produce the hysteranthous phenological  
84 sequence. Here, there is no specific adaptive advantage to hysteranthy; selection is not operating on the  
85 relative timing of flower and leaf emergence, but rather the absolute flowering time alone. Rejection of the  
86 above functional hypotheses might provide support to this null explanation.

87 A significant challenge for robust testing of hysteranthy hypotheses is that most characterizations of flower-  
88 leaf phenological sequences are based on expert-opinion verbal descriptions (e.g. “flowers before leaves” or  
89 “flower before/with leaves”), which make comparisons across taxa, time and space difficult and sensitive  
90 to observer bias (see Buonaiuto *et al.*, 2021). This problem can be overcome by adopting standardized  
91 quantitative measures of plant phenology for observational studies and applying them to historical data  
92 records. Herbarium records are an excellent source of data that can be leveraged for quantitative phenological  
93 measurements (Willis *et al.*, 2017), but have not been widely used to investigate variability of flower-leaf  
94 sequences.

95 The American plums are a useful model clade to investigate drivers of hysteranthous flowering in biotically-  
96 pollinated species. The species that make up this group are distributed across the temperate zone of North  
97 America and, like the genus *Prunus*, generally show pronounced inter-specific variation in flower-leaf se-  
98 quences. Usefully, species in this clade are well represented in herbaria records (Fig. 1a), making them a  
99 tractable group to measure and assess variation in flower-leaf sequences.

100 To interrogate the functional hypotheses for hysteranthous flowering described above, we used herbaria records  
101 to quantify variation in flower-leaf sequences of the American plums. Then we combined environmental  
102 attributes, biological traits and phylogenetic data in statistical models designed to evaluate whether the  
103 observed associations between flower-leaf sequences and morphological and environmental traits match the  
104 predicted associations of the hysteranthy hypotheses. Finally, we compared our findings in this clade to  
105 patterns observed in larger genus *Prunus* to test whether these phenology-trait associations were sensitive to  
106 taxonomic scale and flower-leaf sequence classification.

<sup>107</sup> **Materials and Methods**

<sup>108</sup> **Quantifying flower-leaf sequence variation**

<sup>109</sup> We obtained digital herbarium specimens of the American plums from the Consortium of Midwest Herbaria  
<sup>110</sup> (CMH) Database (of Midwest Herbaria, 2023). Specimen collection dates ranged from 1844-2020,<sup>x</sup> with the  
<sup>111</sup> majority collected between 1950-2000. To quantify flower-leaf sequence variation in this group we randomly  
<sup>112</sup> sampled 200 specimens for each species and scored the phenological development of flowers and leaves; we  
<sup>113</sup> used a modified BBCH scale for woody plants designed to evaluate vegetative and reproductive phenological  
<sup>114</sup> progress through a standardized quantitative index (Finn *et al.*, 2007). For species with less than 200  
<sup>115</sup> specimens in the collection, we included all available specimens. In total, we evaluated the phenology<sup>x</sup> of 2521  
<sup>116</sup> specimens, but only specimens with visible flowers were included in this analysis. We also removed specimens  
<sup>117</sup> with flowering dates that were major outliers from the observed flowering period of each species.<sup>x</sup> We removed  
<sup>118</sup> outliers visually, and by excluding observations that were beyond three standard deviations<sup>x</sup> of the median  
<sup>119</sup> flowering time for each species ( $n=9$ ). Our final analyses included 1000 specimens (see Tab. S1<sup>x</sup> for number  
<sup>120</sup> of observations/species).

<sup>121</sup> We reconstructed the phylogenetic relationships among species in this group based on the tree topology in  
<sup>122</sup> Shaw & Small (2004). We inferred branch lengths following the method of Grafen & Hamilton (1989) in  
<sup>123</sup> which node heights are estimated in proportion to number of subtending taxa using the R package “ape” (E.  
<sup>124</sup> Paradis and K. Schliep, 2019).

<sup>125</sup> To quantify flower-leaf sequence variation, we fit an ordinal, hierarchical, Bayesian phylogenetic mixed model  
<sup>126</sup> (de Villemur & Nakagawa, 2014) designed to assess the likelihood an individual would be at any given  
<sup>127</sup> vegetative BBCH phase while flowering. Our model predicted leaf stage ( $y_i$ , ordinal, with six categories  
<sup>128</sup> representing stage from 1 for “buds closed” and 6 for “leaf expansion complete”) as a function of species and  
<sup>129</sup> additional phylogenetic effects. Because hysteronathy co-varies with flowering time (i.e., flowering first species  
<sup>130</sup> will generally flower earlier than other species, on average), and collection dates were not evenly distributed  
<sup>131</sup> across the flowering season (see Fig. S1), we included day of year of observation as an additional predictor.  
<sup>132</sup> Additionally, because climate change could affect the interval between flowering and leafout over the course  
<sup>133</sup> of our time series, we included the year of collection of each specimen as a covariate. Following previous  
<sup>134</sup> conventions for modeling the possible effects of climate change on spring phenology, we parameterized *year*  
<sup>135</sup> as a hinge variable, using 1980 as a break point (Stocker *et al.*, 2013; Buonaiuto *et al.*, 2021).

<sup>136</sup> The model is written below:

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

<sup>138</sup>  $z_i = \alpha + \alpha_{phylo} + \alpha_{sp} + \beta_{\text{day of year[sp]}} * X_{\text{day of year}} + \beta_{\text{year}} * X_{\text{year}} + \epsilon_i$

<sup>139</sup>

<sup>140</sup>  $\epsilon_i \sim \text{logistic}(0, 1)$

<sup>141</sup>

<sup>142</sup> where  $y_i$  is the ordinal outcome (leaf stage; as 1,2,...6 categories).  $c_{2...5}$  are the estimated cutpoints between  
<sup>143</sup> leaf stages on the logit scale and  $X_{\text{year}}$  is the year the specimen was collected – 1980.  $z_i$  is the linear  
<sup>144</sup> component of the underlying latent variable model.

<sup>145</sup>  $\alpha$  describes an intercept for each category [1,2,...6] and slopes ( $\beta_{\text{day of year}}$  and  $\beta_{\text{year}}$ ) are constant across  
<sup>146</sup> cutpoints.  $\beta_{\text{day of year}}$  also varies among *species* while  $\beta_{\text{year}}$  is a pooled estimate across species.

<sup>147</sup> The influence of the phylogeny ( $\alpha_{phylo}$ ) was modeled as:

<sup>148</sup>

$$\alpha_{phylo} \sim \text{normal}(0, COR[\sigma_{phylo}^2])$$

<sup>149</sup> The  $\alpha$  for species effects independent of the phylogeny was modeled as:

<sup>150</sup>

$$\alpha_{sp} \sim \text{normal}(0, \sigma_{species}^2)$$

<sup>151</sup> We used our model to predict the probability that each species would be observed at a given vegetative  
<sup>152</sup> BBCH stage during flowering for each day of the flowering period of each species by extracting 1000 ran-  
<sup>153</sup> dom draws from the posterior distribution. Next, for each day of the flowering season, we summed the  
<sup>154</sup> predicted likelihood that species would be at BBCH 0 (“bud closed”), BBCH 07/09 (“bud break”) or BBCH  
<sup>155</sup> 11 (“start of leaf unfolding”) vs. BBCH 15 (“leaf unfolding”), BBCH 17 (“most leaves unfolded”), BBCH 19  
<sup>156</sup> (“leaf expansion complete”)—this allowed us to quantify the likelihood that a species would be hysteranthous  
<sup>157</sup> or non-hysteranthous respectively for each day of the season. We chose the BBCH 11/BBCH 15 boundary to  
<sup>158</sup> define hysteranthous flowering because this is the earliest point in development when most leaves are unfurled  
<sup>159</sup> enough to visually obscure flowers and transpire. Finally, we used these estimates to develop a flower-leaf  
<sup>160</sup> sequence index: for this, we summed the likelihood of hysteranthous vs. non-hysteranthous across the full flower-  
<sup>161</sup> ing period of each species, with 0 being never hysteranthous and 1 being always hysteranthous. To evaluate  
<sup>162</sup> the sensitivity of our model to choice of cutoff, we also calculated a hysteranthous index using an alternative

<sup>163</sup> cutoff at the BBCH 09/BBCH 11, which did not alter the species' ranks on the index (see Tab. S2).

<sup>164</sup> To better understand how within-season dynamics affected our inference, we also refit our model excluding  
<sup>165</sup> *day of year* as a predictor. This version of the model did not substantially alter the species' ranks on the index  
<sup>166</sup> or our inference about the relationships between flower-leaf sequence variation and the trait representing the  
<sup>167</sup> main hysteranthy hypotheses (Tab. S2, Tab. S3).

## <sup>168</sup> Evaluating hysteranthy hypotheses

<sup>169</sup> To test the hypotheses of hysteranthy, we first recorded petal length measurements directly from herbarium  
<sup>170</sup> specimens. For these morphological measurements, we sampled 321 specimens and measured the petal length  
<sup>171</sup> of up to 10 randomly selected petals per specimen ( $n=2757$ ) using ImageJ image processing software (see  
<sup>172</sup> Tab. S2, for  $n$  per species).

<sup>173</sup> To assess aridity tolerance, we computed the average Palmer Modified Drought Index score from June-August  
<sup>174</sup> (hereafter: PDSI), obtained from Gille *et al.* (2017) for every *Prunocerasus* specimen in the database ( $n=2305$ ,  
<sup>175</sup> see Tab. S2, for  $n$  per species). PDSI is a unitless, standardized drought index that integrates temperature  
<sup>176</sup> and precipitation data to estimate relative dryness in time and space (Heim, 2002). Negative PDSI values  
<sup>177</sup> indicate more arid conditions and positive values wetter conditions. For any specimens that lacked accurate  
<sup>178</sup> geo-location information, we extracted PDSI values at the county centroid of the herbaria specimen.

<sup>179</sup> Because all of our measurements were made on different individuals—with different sample sizes—we used  
<sup>180</sup> two different modeling approaches to test the relationship between flower-leaf sequence index scores, aridity  
<sup>181</sup> tolerance and floral displays.

<sup>182</sup> First we computed species-level means of PDSI and petal length and used a beta regression to evaluate the  
<sup>183</sup> relationship between flower-leaf sequences, PDSI, petal length and their interaction. We standardized the  
<sup>184</sup> units of all predictors through *z*-scoring (Gelman & Hill, 2007) to make their effect size estimates directly  
<sup>185</sup> comparable within the following model structure:

<sup>186</sup>

$$\text{187 } y_i = (\mu, \mu(1 - \mu)/(1 + \phi))$$

<sup>188</sup>

<sup>189</sup> where  $\mu$  and  $\phi$  are the two shape parameters of the beta regression. Due to the limited sample size of this  
<sup>190</sup> analysis (13 species), we only modeled the effect of our predictors on the mean parameter,  $\mu$ , and fit a grand  
<sup>191</sup> intercept for the precision parameter,  $\phi$ . We modeled the  $\mu$  parameter as:

<sup>192</sup>

$$\text{193 } \mu = \alpha + \beta_{PDSI} * \overline{X_{PDSI}} + \beta_{\text{petal length}} * \overline{X_{\text{petal length}}} + \beta_{PDSI \times \text{petal length}} * (\overline{X_{PDSI}})(\overline{X_{\text{petal length}}})$$

<sup>194</sup>

<sup>195</sup> We chose this model structure because it allowed us to assess the additive and interactive effects of PDSI

196 and petal size on flower-leaf sequences. However, by using mean trait values as predictors, we could not  
 197 incorporate within-species variation in these trait/environmental predictors or account for their phylogenetic  
 198 structure. To understand how these factors affected our inferences about the relationship between flower-leaf  
 199 sequences and traits, we fit two additional models to estimate relationship between flower-leaf sequences index  
 200 values and PDSI, and between flower-leaf sequences index values and petal size separately which included  
 201 the intra-specific variation and phylogenetic structure of each of these traits (see Supporting Information:  
 202 Extended Methods for details). This alternative modeling approach produced similar results for phenology-  
 203 trait relationships to our main model.

## 204 Hysteranthry in the larger genus *Prunus*

205 To better understand how the patterns we identified in the American Plums clade scaled across a coarser  
 206 taxonomic resolution, we also evaluated the relationship between hysteranthous flowering and hypothesis-  
 207 related traits for additional *Prunus* species native to, or established in, North America ( $n=32$ ). For this  
 208 analysis, we obtained categorical descriptions of flower-leaf sequences and mean estimates of the number of  
 209 flowers per inflorescence as a proxy for floral investment from the [Flora of North America](#) (Rohrer, 1993+).  
 210 We extracted PDSI values for all herbaria observations of those species in the Consortium of Midwest Herbaria  
 211 database ( $n=23,272$ ) as described above.

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

215 As above, we standardized the units of all predictors through  $z$ -scoring (Gelman & Hill, 2007). The model  
 216 structure is:

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

217  $z_i = \alpha + \alpha_{phylo} + \beta_{PDSI} * X_{PDSI} + \beta_{\text{floral investment}} * X_{\text{flowers/inflorescence}} + \beta_{PDSI_x \text{floral investment}} (X_{PDSI})(X_{\text{flowers/inflorescence}}) + \epsilon_i$   
 218  $\epsilon_i$

219

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

220 where  $y_i$  is the ordinal outcome of flower-leaf sequence category (“flowers after leaves”=1, “flowers with  
 221 leaves”=2, “flowers before/with leaves”=3 and “flowers before leaves”=4) and  $c_{2..3}$  are the estimated cutpoints  
 222 between categories on the logit scale.  $z_i$  is the linear component of the underlying latent variable model.  $\alpha$

223 describes a grand intercept, and we modeled the influence of phylogeny ( $\alpha_{phylo}$ ) as above. Note that this  
224 model includes four ordinal categories, while our model of the American Plums clade included six, due to the  
225 different underlying structures of the two datasets.

## 226 Model runs

227 We fit all models in the R package “brms” (Bürkner, 2018) using weakly informative priors, and four chains.  
228 For the models aimed at “Quantifying flower-leaf sequence variation” and “Evaluating hysteranthy hypotheses”  
229 in the American plums, we ran the models with a warm-up of 3000 iterations, and 4000, and 5000 sampling  
230 iterations respectively, for a total of 4000 and 8000 sampling iterations across all chains. For the “Hysteranthy”  
231 in the larger genus *Prunus* model, we used a warm up of 6,000 iterations and 8,000 sampling iterations for  
232 a total of 8000 sampling iterations to maximize the effective sampling size. Model fits were assessed with  $\hat{R}$   
233 <1.01, high effective sample sizes, and no divergent transitions. We provide mean estimates with uncertainty  
234 intervals in-text, and 50% and 89% intervals for all figures and tables.

## 235 Results

### 236 Quantifying flower leaf sequences in the American plums

237 We found substantial inter-specific differences in flower-leaf sequences within the American plums (Fig. 1b,  
238 Fig. 2a). Several species (*P. mexicana*, *P. umbellata*, *P. angustifolia*, *P. maritima* and *P. gracilis*) were  
239 most likely to be hysteranthous for all—or most—of their flower period, while for others, (*P. americana*, *P.*  
240 *munsoniana*, *P. alleghaniensis*, *P. nigra*, *P. hortulana*, *P. texana* and *P. rivularis*), hysteranthous flowering  
241 was only likely in the early part of their flowering session. One species, *P. subcordata*, was unlikely to be  
242 hysteranthous at any point in its flowering period (Fig. 2a). These relative ranking of species’ hysteranthy  
243 likelihoods were consistent with our alternative method for constructing the hysteranthy index (Tab. S2, Fig.  
244 S2).

245 Across all species of American Plums, day of year increased the likelihood of flowering during a later vegetative  
246 phenological stage (Fig. 2b). Year of observation did not substantially impact the likelihood of hysteranthy  
247 for this taxonomic group (Fig. 2b).

### 248 Associations between hysteranthy and environmental and morphological traits

249 In the American plums, predominately hysteranthous species had marginally smaller flowers and occurred in  
250 historically drier localities than species with more overlap between flowers and leaves (i.e., increased likelihood  
251 of hysteranthy  $\text{was negatively associated with PDSI and petal length without a substantial interaction between}$   
252 them, Fig. 3a; parameter estimates from this model were  $\beta_{PDSI} : -0.47, UI_{89}[-0.96, 0.01]$ ,  $\beta_{\text{petal length}} :$

253  $-0.14, UI_{89}[-0.54, 0.24]$   $\beta_{PDSI_x}$  petal length :  $-0.14, UI_{89}[-0.91, 0.65]$ ). These estimates were comparable to  
254 estimates from models where we treated each predictor separately and accounted for phylogeny (Fig. S3), and  
255 where we used the hysteranthy index derived from models that did not include day of year as a predictor (Tab.  
256 S3). The direction and magnitude of the estimated effects support the predictions of the water-limitation  
257 hypothesis and marginally support the predictions of the insect-visibility hypothesis.

258 In the larger genus *Prunus*, hysteranthous species had smaller inflorescences and were found in drier locations  
259 (Fig. 4a, b; i.e., there was a negative association between hysteranthy and PDSI and number of flowers  
260 per inflorescence, as well as a substantial negative interaction between them, parameter estimates from  
261 this model were  $\beta_{PDSI} : -8.0, UI_{89}[-16.6, -2.44]$ ,  $\beta_{flowers/inflorescence} : -15.5, UI_{89}[-31.46, -5.56]$  and  
262  $\beta_{PDSIx flowers/inflorescence} : -13.06, UI_{89}[-28.53, -2.93]$ ). The direction and magnitude of the estimated  
263 effects support the predictions of both the water-limitation hypothesis and the insect-visibility hypothesis.

264 The estimated effects of floral traits and their interactions with PDSI were stronger in the larger genus *Prunus*  
265 than in the American plums clade. This is not surprising given that all species in the American plums clade  
266 have solitary flowers, making the variation in floral display size highly constrained. By contrast, *Prunus*  
267 species included in our secondary analysis include those with solitary flowers and species with as many as 100  
268 flowers per inflorescence—substantially more variation in both floral investment and in hydraulic demand.  
269 This suggests that the correlated selection between flower-leaf sequences and these floral traits may be more  
270 pronounced at coarser taxonomic resolutions, where underlying trait variation is greater.

## 271 Discussion

272 Using North American *Prunus* species as a case study, our results indicate that flower-leaf sequences are likely  
273 under selection. We show that variation in flower-leaf sequences across species may reflect adaptive tradeoffs  
274 between a) the timing of investment in reproduction relative to the timing of resumption of carbon acquisition  
275 through leafout, and b) other aspects of plant performance, such as environmental tolerance and pollinator  
276 attraction strategies that we investigated in this study. We show that hysteranthous flowering is associated  
277 with historic aridity (PDSI) and smaller flower displays in both the American plums, and more broadly  
278 across *Prunus* species native to, or established in, North America. The relationships between hysteranthy  
279 and aridity, and hysteranthy and floral display size support the predictions of the water limitation hypothesis  
280 and the insect visibility hypothesis.

281 Our models estimated a strong relationship between aridity (PDSI) and flower-leaf sequences at both taxo-  
282 nomic scales we studied, but the relationship between floral display size and flower-leaf sequences predicted  
283 by the insect visibility was better supported at the coarser taxonomic scale of the full genus *Prunus* than  
284 in the American plums clade. While species in the American plum clade have solitary flowers, they are  
285 still clustered on branches, so it is unlikely the unit of attraction that pollinators are responding to is the  
286 individual flower, which may explain why the relationships between hysteranthy and petal size we observed

were weak (Fig. 3b). The inflorescences of the larger genus *Prunus*, are probably a better proxy for differences in units of attraction, which may explain their stronger association with flower-leaf sequences variation among species (Fig 4). This contrast may suggest that associated selection between flower-leaf sequences and pollinator traits has more strongly influenced inflorescence architecture than the morphology of individual flowers though our estimates at both scales agreed in directionality (i.e., hysteranthry associated with smaller floral displays).

Under the insect visibility hypothesis, floral display size could either be positively or negatively associated with hysteranthry depending on the pollination environment. The association between hysteranthry and smaller flower displays that we found supports the prediction that increased visibility of hysteranthous flowers reduces selection pressure on flower display size. These results fit with other comparative anatomy studies in plants that report hysteranthous species typically have smaller inflorescences than non-hysteranthous relatives (Gunatilleke & Gunatilleke, 1984), and studies on pollinator foraging behavior that suggest the presence of leaves substantially alters the visual perception of pollinators (Rivest *et al.*, 2017; Forrest & Thomson, 2009).

Our support for both the water limitation hypothesis and insect visibility hypothesis (especially in the larger genus *Prunus*), and the strong positive interactions between PDSI and floral investment that we observed in the larger genus *Prunus*, highlight 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 (Lambrecht, 2013; Teixido *et al.*, 2016), and hysteranthry 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 hysteranthry for maintaining water status. Measurements of water movement (transpiration 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).

The PDSI records that we incorporated in this study—spanning over two millennia—offer additional insights into why the water limitation hypothesis may still be relevant to temperate forest regions that are typically well saturated in the spring. These records reveal that the southeastern United States (the region in which much of our data originates) was once much drier than it has been in contemporary times (Cook *et al.*, 2010, Fig S4), suggesting that the spatial patterns of hysteranthry we see in the American plums may represent a lagged-correlation with historical climate conditions.

Despite this evidence that hysteranthry can reduce hydraulic demand in dry environments, hysteranthous species in the American plum clade are not found—even historically—in extremely arid locations (PDSI values typically range from -4 to 4, although the values that we observed in our analyses were more restricted,

323 ranging from -0.5 to 0.2). This contrasts with hysteranthous species in the dry tropics where this phenological  
324 pattern appears to allow them to tolerate more extreme aridity (Franklin, 2016). But the flower-leaf sequences  
325 of the hysteranthous species in our study were markedly different from patterns of hysteranthy in these dry-  
326 tropics where the water limitation hypothesis was initially proposed. While flowering can precede leafout  
327 by as much several weeks for species in the American plums, the process of fruit development, which is also  
328 water intensive, occurs when leaves are present. By contrast, in the dry tropics hysteranthous flowering is  
329 initiated at the time of leaf drop (Borchert, 1983; Franklin, 2016); thus, the full reproductive cycle occurs in  
330 the leafless period. The comparatively small window of leafless reproductive development in our temperate  
331 clade suggests that hysteranthy may allow temperate species to occupy marginally drier environments than  
332 non-hysteranthous species, but may not facilitate species' persistence under extreme aridity.

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

334 We developed a novel approach to assessing flower-leaf sequences that scales from quantitative, individual-  
335 level observations to species-level characterizations. With this approach, we were able to—for the first  
336 time—quantitatively assess intermediate cases of hysteranthy (such as those that are typically described as  
337 “flowers before/with leaves”). Previous studies of hysteranthous flowering have either excluded these cases  
338 from their analyses (e.g.; Gougherty & Gougherty, 2018) or binned them with the well defined cases (e.g.;  
339 Buonaiuto *et al.*, 2021). We found that many American plum species expressed this intermediate flower-leaf  
340 sequence. Further, while our classifications broadly matched previous species-level analyses in this group by  
341 Shaw & Small (2004), our approach identified substantial differences in flower-leaf sequences among these  
342 intermediate cases (Fig. 1b), which allowed us to assess the trait associations with this phenotype.

343 Our quantitative analysis of the American plums clade revealed that flower-leaf sequences—often described  
344 as a species-level trait—are highly variable within species (Fig. 2a). For almost all members of the clade,  
345 hysteranthy was strongly predicted by the day of the observation (“day of year” in our model, Fig. 2b). In  
346 many cases there was a high likelihood that individuals of a species may be observed at different vegetative  
347 stages during flowering (Fig. 2a, Fig. S2). The variation we observed here could either suggest high levels of  
348 local adaptation in flower-leaf sequences or, alternatively, high levels of plasticity through which flower-leaf  
349 sequences respond to interannual variation in environmental conditions. Because our study was based on  
350 herbaria records collected on different individuals across space and time without repeat sampling, we could  
351 not robustly estimate how much flower-leaf sequences vary within vs. among species. However, this would be  
352 an important next step for understanding how the environment and species interactions have shaped these  
353 phenological patterns.

354 Interestingly, while there is substantial evidence that both flowering and leaf phenology have advanced over  
355 the last several decades in response to anthropogenic climate change (Menzel *et al.*, 2006; Cleland *et al.*,  
356 2007; Augspurger & Zaya, 2020), we did not observe changes in flower-leaf sequences over that time scale  
357 in our dataset (Fig. 2b). This supports a recent finding that despite changes in both flowering and leafout,

<sup>358</sup> the time interval between them has remained relatively stable (Guo *et al.*, 2023), but does not preclude that  
<sup>359</sup> possibility that these the sequences will eventually be disrupted as climate change continues to become more  
<sup>360</sup> extreme in the future (Buonaiuto & Wolkovich, 2021).

## <sup>361</sup> Future directions

<sup>362</sup> We focused on a well-studied, and economically important clade of morphologically similar species. Our  
<sup>363</sup> case-study provides a road map for evaluating the role of hysteranthy more generally in temperate biotically-  
<sup>364</sup> pollinated plant taxa (other groups with high interspecific flower-leaf sequence variation include *Magnolia*,  
<sup>365</sup> *Rhododendron*, *Acer* and *Cornus*), and more broadly across taxa and biomes.

<sup>366</sup> Combining the observational approach with novel experiments could further advance our collective under-  
<sup>367</sup> standing of the adaptive significance of flower-leaf sequences. To test the water-limitation hypothesis, re-  
<sup>368</sup> searchers could plant sister-taxa with contrasting flower-leaf sequences in common environments across a  
<sup>369</sup> gradient of aridity, and evaluate their performance. To test the insect visibility hypothesis, researchers  
<sup>370</sup> should consider hysteranthy—and phenology in general—in the broader framework of tradeoffs in pollination  
<sup>371</sup> biology. The tradeoff between phenology and pollination investment could not only consider flower size, but  
<sup>372</sup> also the number of flowers, nectar and pollen reward investment, volatiles between related hysteranthous and  
<sup>373</sup> non-hysteranthous taxa. Findings that hysteranthous species invest fewer resources into these other pollinator  
<sup>374</sup> attraction traits than non-hysteranthous relatives would support the insect visibility hypothesis. For a simple  
<sup>375</sup> experiment to test the pollinator visibility hypothesis, researchers could force hysteranthy/non-hysteranthy  
<sup>376</sup> phenotypes for the same genotype using environmental cues and systematically release pollinators to ob-  
<sup>377</sup> serve their preferences, search times and foraging behavior. If pollinators are more readily drawn to the  
<sup>378</sup> hysteranthous individuals, it would support hysteranthy as an adaptive trait for pollinator attraction.

<sup>379</sup> With a better mechanistic understanding of the relationship between flower-leaf sequences and ecological  
<sup>380</sup> performance, researchers could then use experiments to assess how differences in floral and leaf physiological  
<sup>381</sup> responses to temperature variation shape flower-leaf sequences. The measurement and modeling approaches  
<sup>382</sup> we developed in our observational study can be readily implemented to analyze data from such experimental  
<sup>383</sup> settings, presenting an important opportunity to unite observations of broad ecological patterns with targeted  
<sup>384</sup> experimental manipulations to better understand both the evolutionary past and ecological future of flower-  
<sup>385</sup> leaf sequences.

## <sup>386</sup> Competing Interests:

<sup>387</sup> The authors declare no conflict of interest.

## <sup>388</sup> Author contributions

<sup>389</sup> DMB, and EMW conceived of the manuscript; DMB and SC collected the data; DMB led the statistical  
<sup>390</sup> analyses with TJD and EMW; DMB led the writing of the manuscript. All authors contributed to writing  
<sup>391</sup> and gave approval for the submission.

## <sup>392</sup> Data Availability

<sup>393</sup> The phenology and trait data collected for this study will be made available and archived at KNB: The  
<sup>394</sup> Knowledge Network for Biocomplexity (<https://knb.ecoinformatics.org/>) at the time of publication.

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## 492 Figures

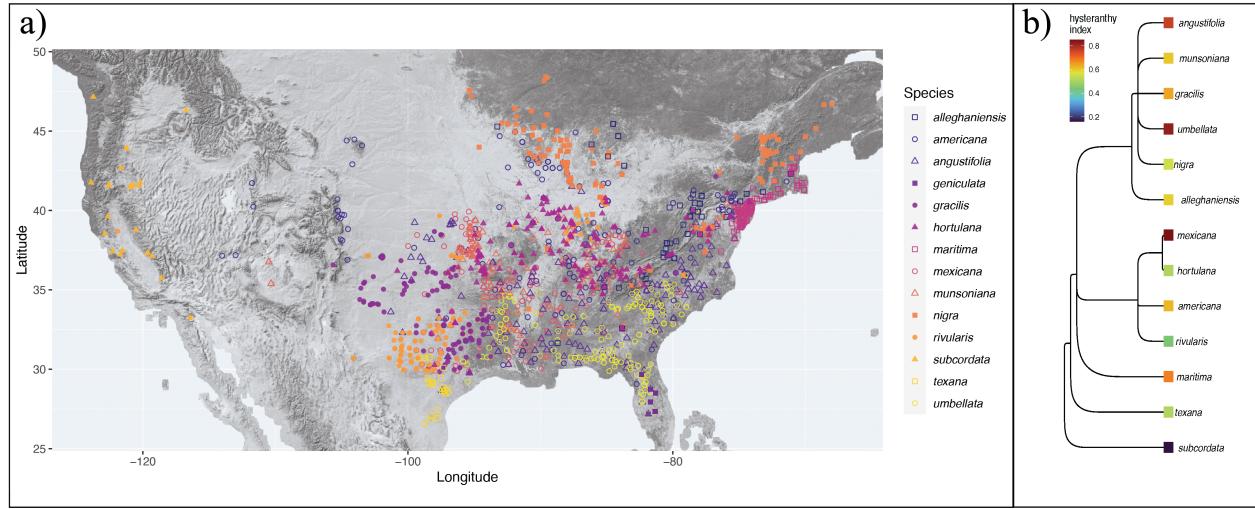


Figure 1: Geographic distribution and taxonomic relationships among the American plums. a) Maps the localities of all the herbaria records used in this study. b) Depicts phylogenetic relationships among the American plums and the likelihood they each species is hysteranthous across its full flowering period, represented by a hysteranthous index where 0 is never hysteranthous and 1 is always hysteranthous. These designations are based on ordinal phylogenetic mixed models. Tree topology is from Shaw & Small (2004)

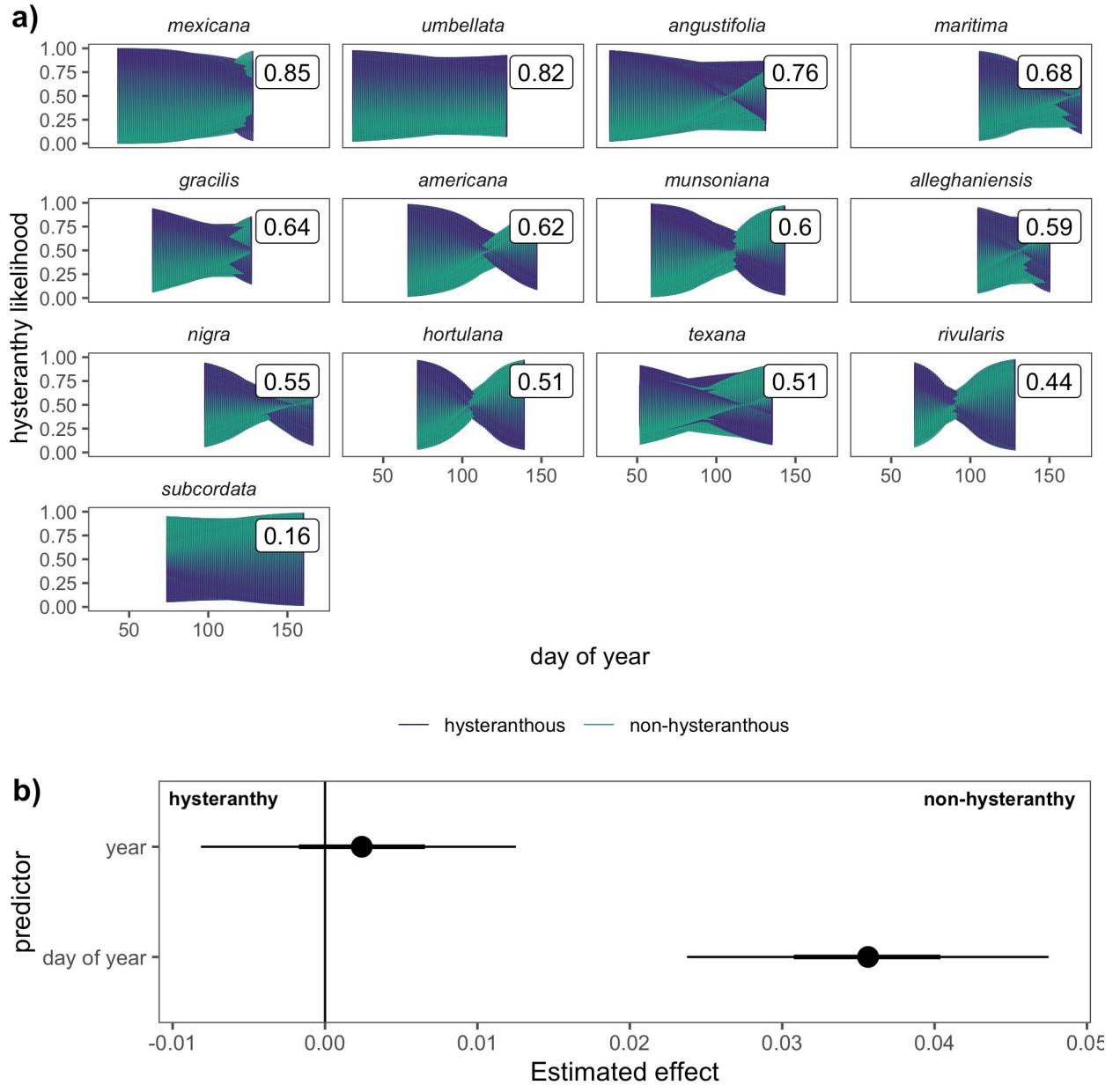


Figure 2: Predicted likelihood of hysteranthy across the flowering period of 13 American plum species and the temporal predictors that drive these patterns. Panel a) depicts the predicted likelihood that each species would express hysteranthy on each day of their flowering season based on 1000 draws from the posterior distribution of Bayesian hierarchical models. The colored shapes represent how the likelihood changes over time and the boxed numerical values represent the average likelihood a species would express hysteranthy, summed across the full flowering period. Panel b) depicts the influence of among season (year of sample) and within season (day of year of sample) trends on the likelihood species would express hysteranthy. Points are the mean effect size estimates, while thick and thin bars represent the 50% and 89% uncertainty intervals respectively.

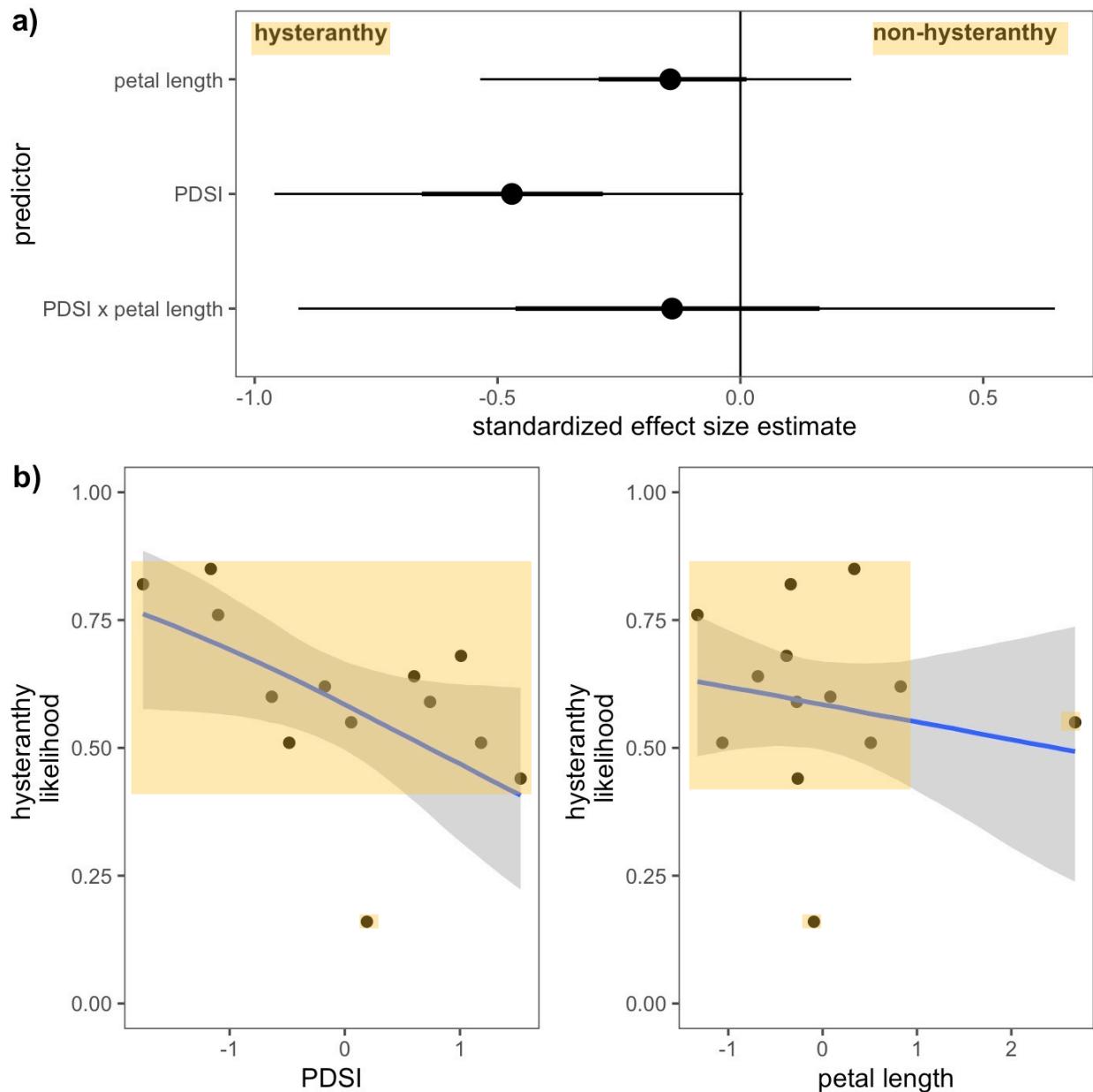


Figure 3: Relationships between hysteranity and environmental and biological traits for the 13 species of the American Plums. Panel a) shows the estimated effects of each predictor and their interaction on the likelihood hysteranity. Points indicate the mean effects and the thick and thin bars represent the 50% and 89% uncertainty intervals, respectively. Panel b) depicts the conditional effects of each predictor on hysteranity likelihood. Blue lines indicate the mean estimate and grey fill the 89% uncertainty intervals. Predictor values ( $x$ -axis) have been  $z$ -scored to allow direct comparisons between predictors.

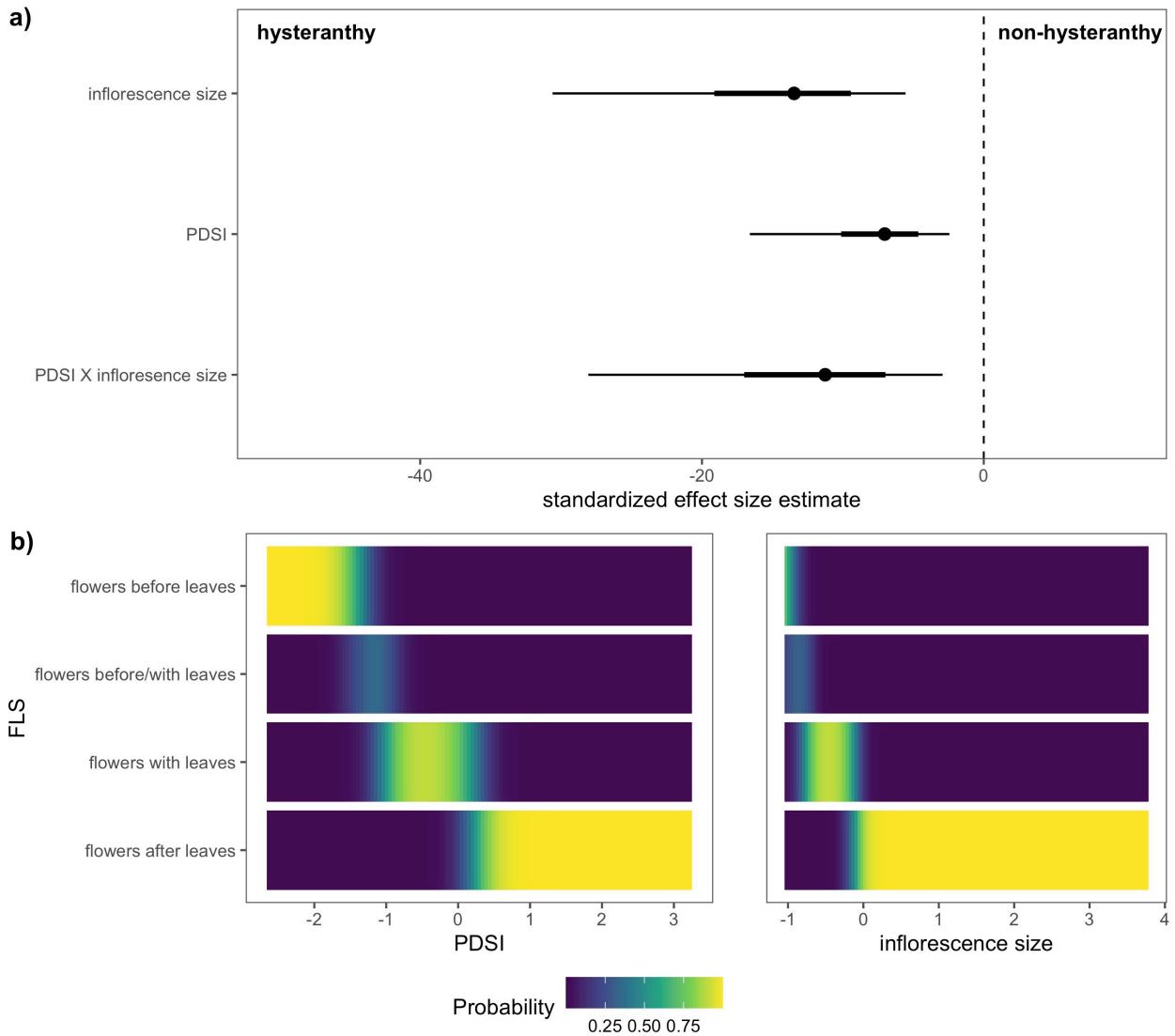


Figure 4: Relationships between the likelihood of hysteranthry and environmental and biological traits for 32 species of the genus *Prunus* native to, or established in North America. Panel a) shows the estimated effect size of each predictor. Points indicate the mean estimate for each predictor, and thick and thin bars the 50% and 89% uncertainty intervals, respectively. Panel b) depicts the likelihood for each flower-leaf sequence stage (*y*-axis) at any given values of PDSI or number of flowers/inflorescence (predictor values (*x*-axis) have been *z*-scored to allow direct comparisons between predictors.