Better title needed: Flower-leaf phenological sequences in the American Plums–unraveling the mystery of hysteranthous flowering in insect-pollinated species

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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 sequences (FLSs) are under selection, and that hysteranthy 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 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). In the dry-deciduous tropics of South and Central America, hysteranthy 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 hysteranthy 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 hysteranthy 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 hysteranthy to included these groups is vital to forecasting the demography and performance of forest communities in an era of global climate change.

Despite the fact that hysteranthous flowering in biotically-pollinated taxa violate (better word), the conventional explanation for this phenological syndrome, several alternative hypotheses to the wind pollination hypothesis have been put forth and may help explain the function of hysteranthy in biotically-pollinated species. Below we review them, and their predictions of trait associations.

Hypotheses of Hysteranthous flowering in biotically pollited taxa

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.

Freeze tolerance hypothesis: There is a demonstrated physiological relationship between drought and freeze tolerance, and it has been suggested that adaptations to drought allowed plants to expand their ranges higher latitudes of the Northern Hemisphere (). It is possible that hysteranthy contributed to this adaptation, though the mechanisms by which hysteranthous flowering may contribute to cold tolerance has not been investigated. One possibility is that for long lived organisms like woody plants, occasional frost damage to flowers has less of an impact on lifetime fitness, than damage to leaves (say better, I think I have old writing that might say this better). With this hypothesis, we would expect hysteranthous species to be found at colder sites than related non-hysteranthous ones. (Drop this if I don’t have readily available data to test it.)

Insect-visibility hypothesis: Hysteranthous flowers are visually conspicuous in the landscape. It is possible that like in wind pollinated taxa, hysteranthy 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) Hysteranthy may be associated with smaller flowers. Since they are easier to see, there is weaker selection on large floral display. 2) Hysteranthy 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 hysteranthy. A second complicating factor is that there is likely to be associates between flower size and hysteranthy 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 dispalys 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 hysteranthy flower is simply a by-product of selection for early flowering. “Recent work from Savage (2019) demonstrated that spring flower phenology is less constrained by prior phenological events than leaf phenology, which would allow selection to drive flowering into the early season, producing the flowering-first FLS. With this hypothesis there is no specific advantage to a species flowering before or after leafing; all that matters is its absolute flowering time.” (quotes indicate self plagiarism and needs to be re-written).

Fruit maturaturion hypothesis: Like the phenological niche hypothesis describe above, there are several aspects of reproductive development that suggest hysteranthy is a by-product for early flowering, driven by development constraints. Hysteranthy 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 reuqire dispersal early in the season. In either case, we should expect fruit size to associate with hysteranthy.

Of course none of the hypotheses are mutually exclusive. One challenge is the same traits correlation could be driven by different mechanisms (ie small flower could be insect-visibility, developmental constraint, aridity tolerance or all of the above). Yet despite this, we should still investigate these associations. Why? because this will help us narrow our study and better understand this trait as a whole. Or because that’s just what science is.

A second 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 be used widely to investigate variability of flower-leaf sequences variation among and within species.

The American plums (*Prunus* subspp. *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. **??**), 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 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 taxonmic 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.

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