

Aridity and floral architecture drive hysteranthous flowering in the North American cherries (*Prunus* spp.)

December 15, 2021

Introduction

Woody perennials have a unique ability among plants to seasonally begin reproduction prior to vegetative growth (). This flowering-first phenological sequence known as hysteranthly, proteranthly or precocious flowering is particularly common in temperate forests around the globe (). A number of studies suggest that this flower-leaf sequences (FLSs) are under selection, and that flowering first has functional significance ().

The most common, and well-tested explanation for the evolution of hysteranthly is that it is adaptive for wind-pollination as leafless canopies increase wind speeds for pollen transport and reduce the likelihood of pollen interception on vegetation (). However, this hypothesis fails to address the prevalence of hysteranthous taxa that are biotically-pollinated. Approximately 30% of species of Eastern temperate forests of North America flower before leafing out, and of those, approximately 20% are biotically pollinated (). Despite the pervasiveness of this phenological syndrome, direct tests of the function of hysteranthly in biotically pollinated taxa are exceedingly rare.

Yet, based on decades of natural history accounts of hysteranthous species around th globe, we have identified two major hypotheses regarding the function of hysteranthly in biotically-pollinated taxa. Each hypothesis makes logical predictions about how hysteranthous flowering should other plant traits should co-vary, and these hypotheses and their predictions can be used to guide further inquiry into the adaptive significance of hysteranthly.

The **water dynamics hypothesis** suggests that hysteranthly is an adaptation to arid environments, allowing for plant to partition the hydraulic demand of hydrated flowers and transpiring leaves across the growing season (). If this is the case, this hypothesis predicts that hysteranthous species should be more commonly found in dry environments.

The **pollinator visibility hypothesis** suggests that hysteranthly is an adaptation to attract visually-foraging pollinators (). If this is the case, this hypothesis predicts that hysteranthous species may invest less in other floral traits for pollinator attraction such as size of floral display or chemical attraction.

Still others have suggested that hysteranthly is simply the by-product of selection for early flowering (),and that variation in flower-leaf sequences among species is driven by developmental, physical or phylogenetic constraints than adaptive selection (). However, even this null hypothesis make testable predictions. If this is the case, hysteranthly should co-vary with other early-flowering associated traits like long fruit development periods or large fruit sizes () and the phylogenetic signal for hysteranthly should be strong.

With mounting evidence that climate driven shifts in phenological phases are altering the duration and order

of flower-leaf sequences () understanding the functional significance of hysternanthy is vital to forecasting the demography and performance of forest communities in an era of global climate change. However, there are two major methodological challenges to testing these hypotheses:

First, characteristics like aridity tolerance, pollinator attraction, and reproductive investment are the emergent product of a suite of biological traits (). Thus, when analyzing selective drivers of any particular trait at large taxonomic scales, unmeasured trait differences may obscure the estimated effects of the trait of interest, biasing results. This is a common problem in trait-based ecology, and one of the most promising solutions for understanding the functional significance of hysternanthy in woody plants is through character deconstruction (); comparing flower-leaf sequences variation for only a subset of taxa of shared phylogenetic and morphological character.

The second challenge for robust testing of hysternanthy 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 sensitive to observer bias (see, ()).

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 (), but have not be used widely to investigate variability of flower-leaf sequences variation among and within species.

In this study, we combine a large data set of occurrence records with published descriptions of flower-leaf sequences and plant traits for North American species in the genus *Prunus* to test the predicted associations of the major hysternanthy hypotheses at the genus level. We then further deconstruct patterns of flower-leaf sequences

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Methods

0.1 Study system

The genus *Prunus* comprises approximately 200 species distributed across the globe (). Of 40-50 species native to or naturalized in North America, *Prunus* species display the full spectrum of variation in flower-leaf sequences () and show marked inter-specific variation in habitat requirements and functional traits making them an ideal system in which to investigate the inter-relationship between hysternanthy and traits predicted by the two major hysternanthy hypotheses.

Within the genus, The American plums (*Prunus* subsp. *Prunus* sect. *Prunocerasus*) offer potential for an additional, higher resolution investigation of drivers of hysternanthous flowering. Like the genus at large, the 16 species that make up the section are distributed across North America and show pronounced inter-specific variation in flower leaf sequences. While within the larger genus species can be separated into three distinct morphological clades by inflorescence architecture (solitary, corymbose or racemose) all members of the section have solitary inflorescences () allowing for even more refined character deconstruction. Species in this section are well represented in herbaria records, making them a tractable group to measure and assess intra-specific variation in flower-leaf sequences as well as other ecological and morphological characteristics related to the hysternanthy hypotheses described above.

0.2 Genus level analyses

Data source

Methods for analysis

0.3 Section level analyses

Methods for herbaria measurements

Methods for analysis

Results

Drivers of hysteranthly in *Prunus* spp. of North America

Likelihood of hysteranthly was associated increasing aridity, flowering and inflorescence size and their interaction. Fruit size had little effect of the likelihood of hysteranthly and at the genus level, the phylogenetic signal in hysteranthly was X suggesting weak to moderate phylogeny structure.

Drivers of hysteranthly in sect. *Prunocerasus*

Within the section *Prunocerasus*, hysteranthly was associated with smaller fruit (). There was no relationship between flower size, fruit phenology, or mean pdsi and the phylogenetic signal of hysteranthly was virtually non-existent within this sub-clade. When we investigated

Discussion

At the genus level we identified a strong negative relationship between the likelihood a species is hysteranthous and flower size, inflorescence size and aridity (). Fruit size appeared to have little influence on hysteranthly () and the phylogenetic signal for in the evolution of flower-leaf sequences was weak-moderate (). By contrast, with in the section of *Prunocerasus*, fruit size was the only trait significantly associated with increased likelihood relationship, though our estimated effect was relatively weak, and of note the positive relationship between fruit size and FLS category (suggestion that hysteranthly is associated with smaller fruit), is counter to the expectation about the relationship between fruit size and flowering time ().

Floral display in hysteranthly

Two possible explanations. Data type. Taxonomic scale.

There will probably be things about taxonomic scale. Ie attraction showing up at the genus but not section level. Major discussion of why.

Pollinator attraction and drought tolerance are a suite of traits and we only measured one axis of them and even with character deconstruction this could matter

Mechanistic experiments would still be useful, ie does water limitation influence FLS plasticity

Figures

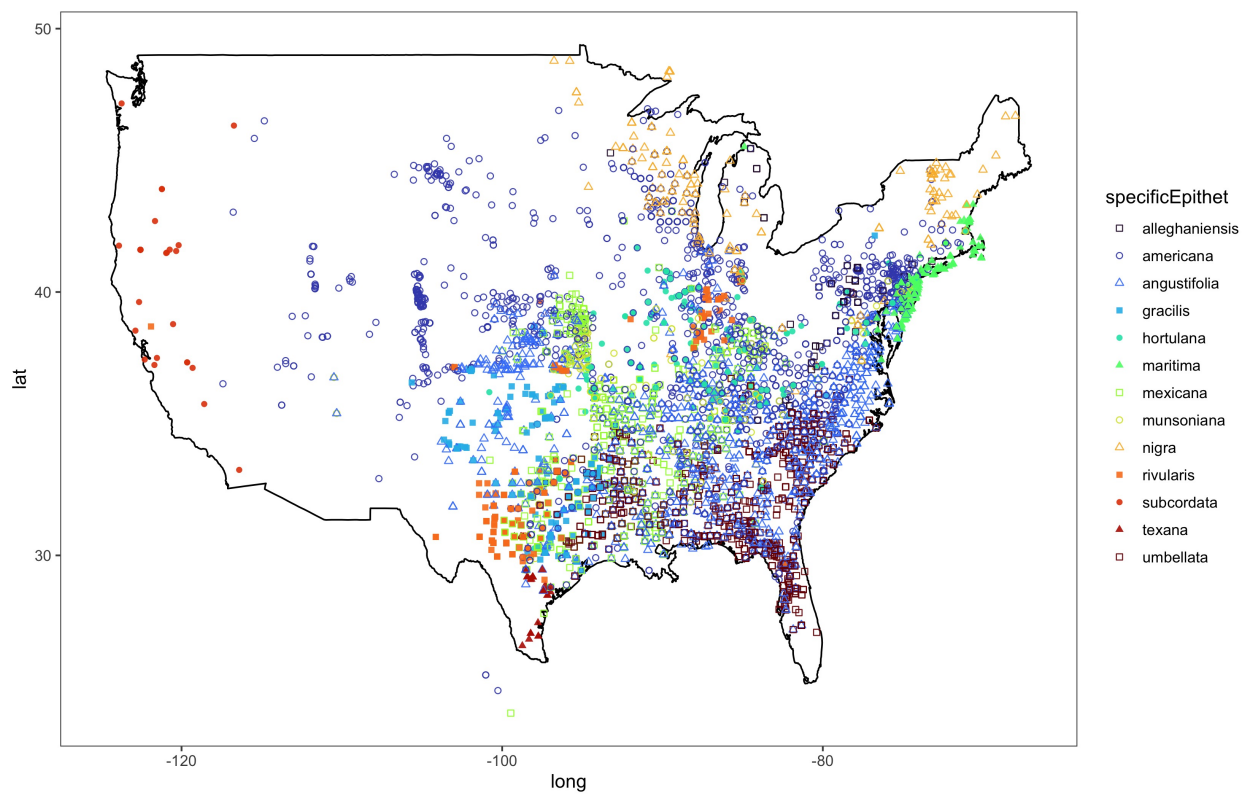


Figure 1: Map to show where data come from and to point out the two never hysternanthy species are highly endemic



Figure 2: place holder for the phylogenies: Ideally will have all N.A. *Prunus* and *Prunocerasus*

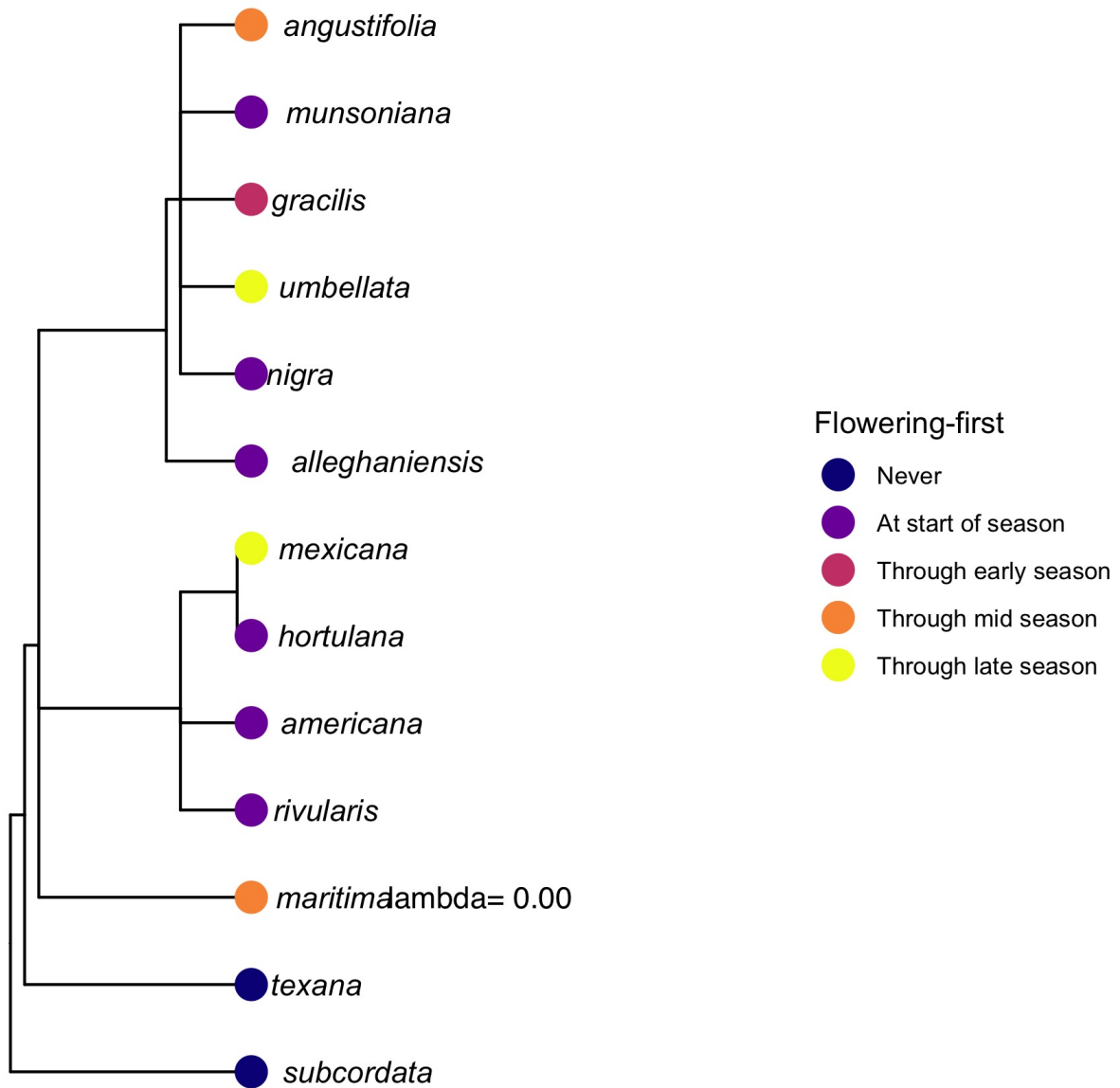


Figure 3: place holder for the phylogenies: Ideally will have all N.A. Prunus and Prunocerasus

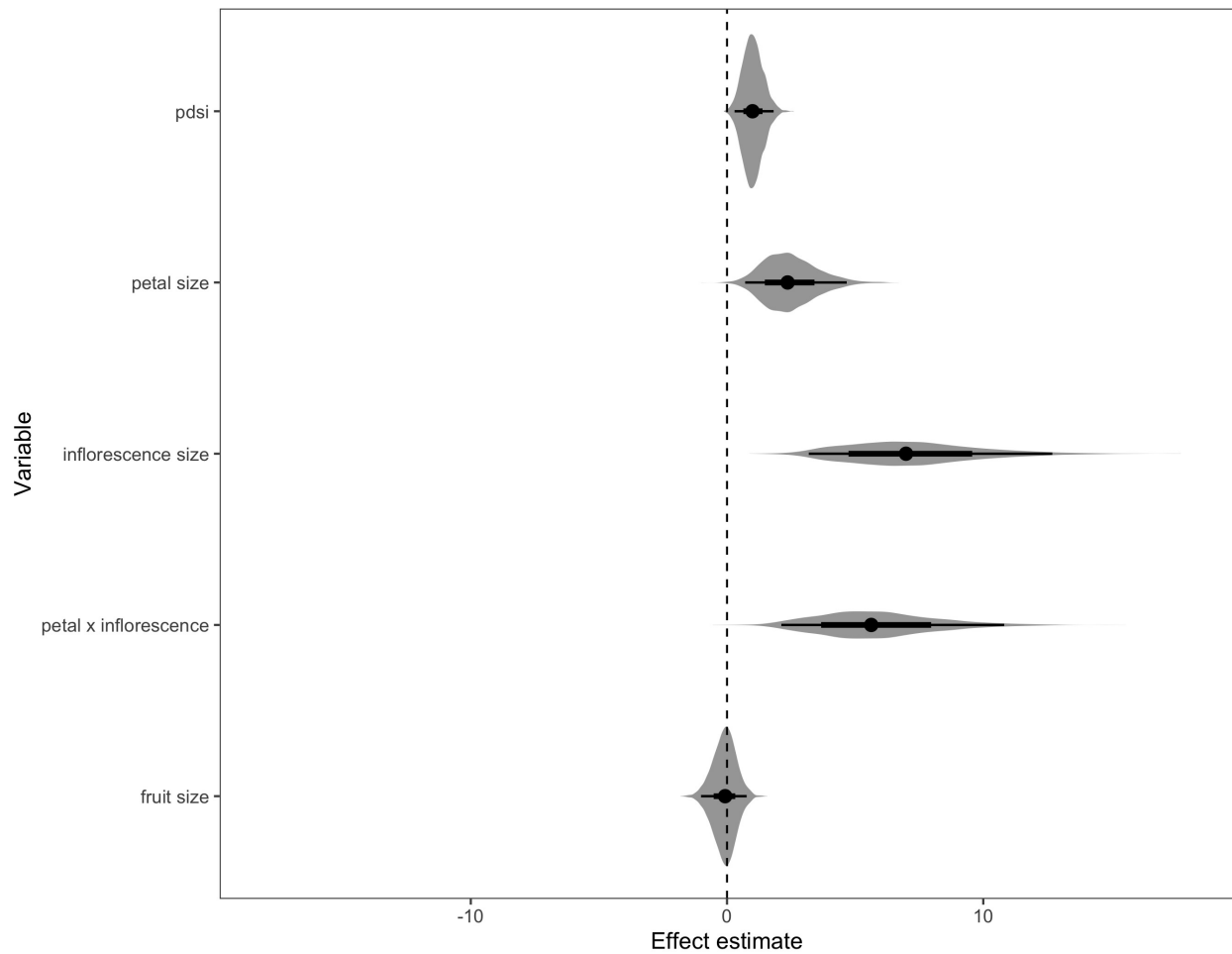


Figure 4: From the full genus analysis: Positive is less hysteranthus so aridity increases ihysteranthus, flower size decreases (ie smaller flowers- more hysteranthous) and no relationship with fruit size

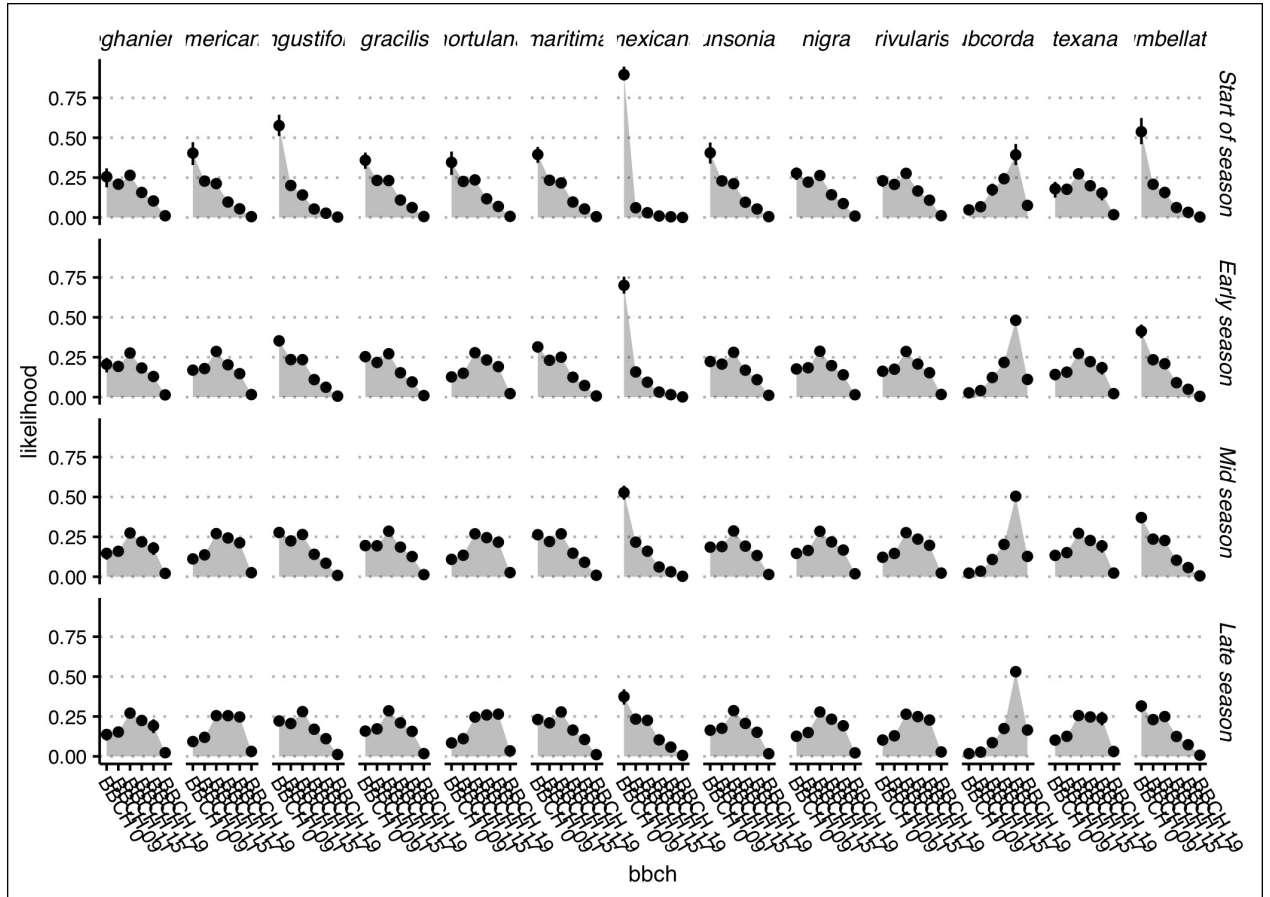


Figure 5: Likelihood of hysteranthly throughout the flowering season for each species in prunocerasus

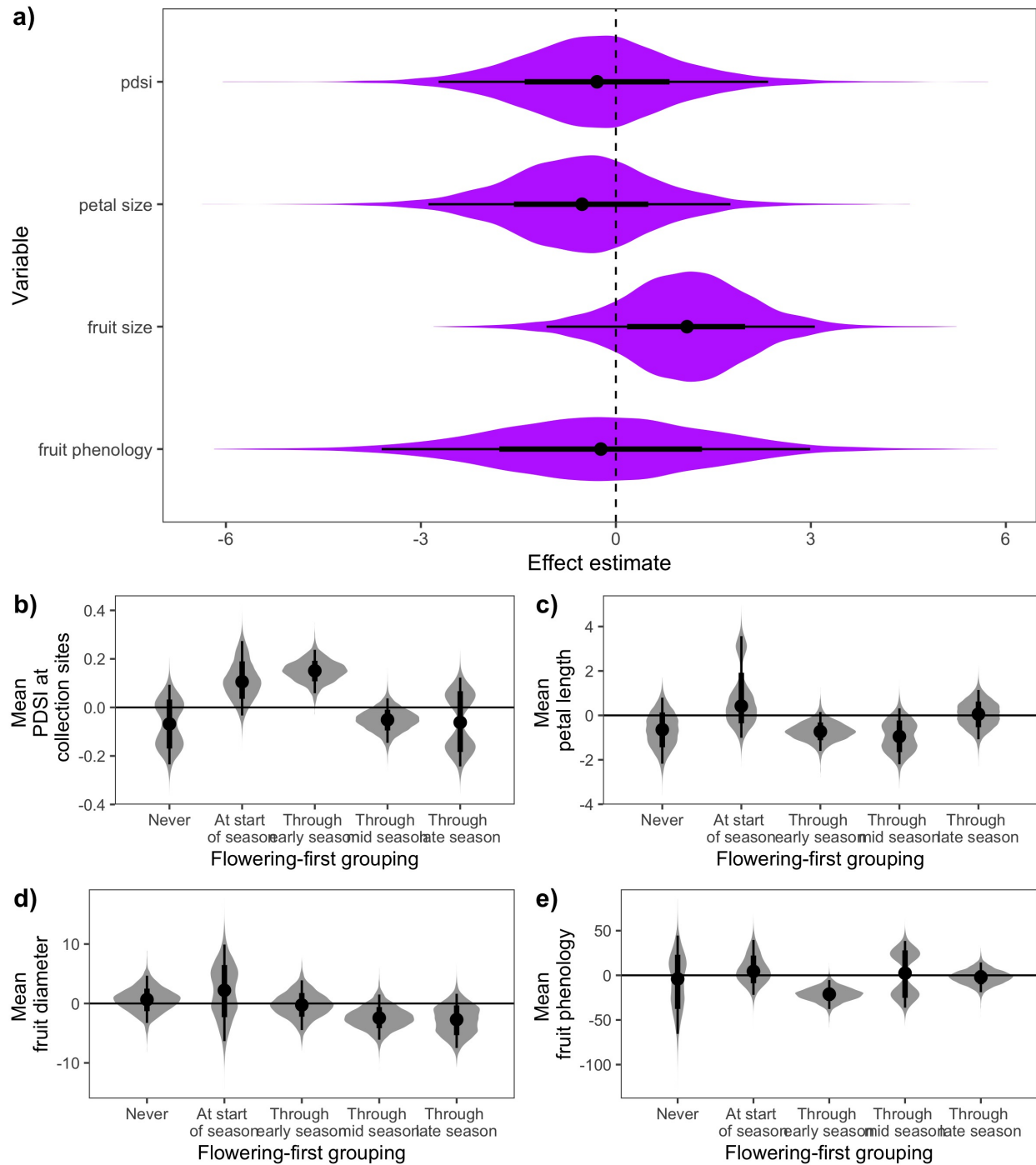


Figure 6: Effect estimates. Why are they so different in *prunocerasus*? 1. measurement error model increases uncertainty. 2. outliers have stronger influence. 3. Maybe too closely related (all flower to some degree while leave are developing)

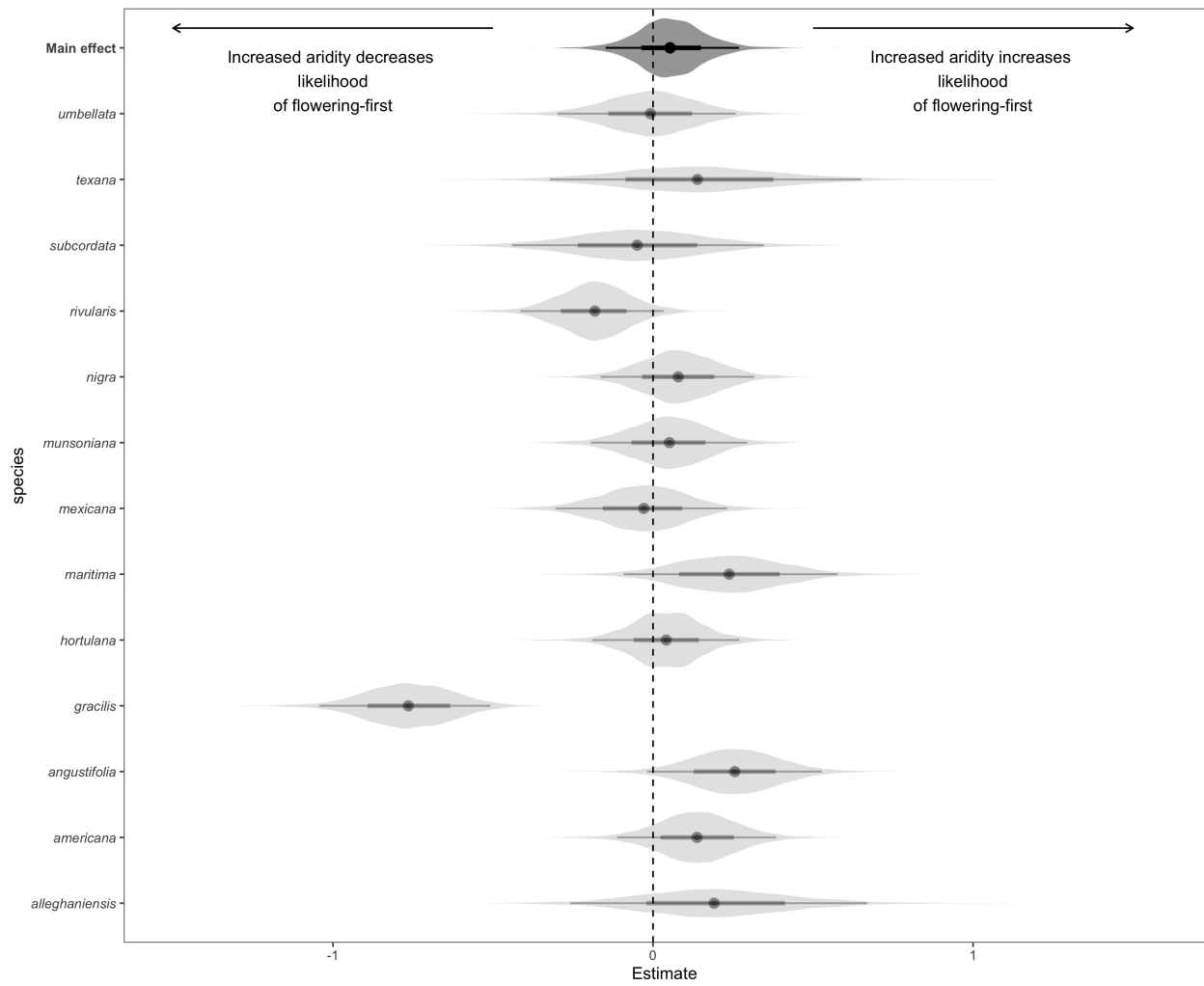


Figure 7: Hysteranthus more likely in drought years.