Why other studies are weak and available data

1. Direct test of these hypotheses in the literature are rare, and support for them is mixed. Studies tend to test single hypotheses, or present the expectation that hypotheses are mutually exclusive.

   (a) Evidence for wind pollination hypothesis: suggested conceptually in (Robertson, 1895; Rathcke & Lacey, 1985; Whitehead, 1969)

      i. Particle movement through closed and open canopies (Niklas, 1985; Nathan & Katul, 2005; Milleron *et al.*, 2012)

      ii. Quantifying pollen impaction in non-floral structures (Tauber, 1967)

      iii. Janzen (1967) suggests that tropical hysteranthous flowering is a pollinator visability adaptation, but to our knowledge, this hypothesis has never been rigorously developed.

      iv. The possibility that hysteranthous pollination is more effecient regardless of syndrome can be gleaned from comparative anatomy studies. Reduced floral investment has been shown in hysteranthous vs. seranthous dogwoods (Gunatilleke & Gunatilleke, 1984) but we are aware of no other studies that link morphological differences to phenological ones.

   (b) Early flowering

      i. We are aware of no direct test to try and distinguish hysteranthy from selection early flowering.

      ii. Primack (1987) notes that hysteranthous wind pollianted species tend to also have large seed mass, and lack primary seed dormancy for germination. These are traits associated with early flowering in general, making the case that hysteranthy is a part of this.

   (c) Drought hypothesis:

      i. Observations of flowering in dry tropics by Borchert (1983); Reich & Borchert (1984) suggest that flowering happens when plant water status recovers due to leaf drop.

      ii. The work of Franklin (2016)in the Austrailian dry tropics suggests flowering following leaf drop isn't neccisarily mechanistic.

      iii. Feild *et al.* (2009) found that some Basal angiosperm flowers might be hydrated by xylem, suggesting extreme water stress would occur if flowering an leaf overlapping in dry environments, but confirm that most eudicots are hydrated by flower. This hydration by the phloem in may temperate Eastern species was supported by recent work of Savage (2019)

      iv. Only recently has it been suggest that this hypothesis might be relevant in the temperate zone too (Gougherty & Gougherty, 2018) because we

wouldn't expect water status to matter in the spring in the temperate zone. (find citation)

(d) One study by Bolmgren *et al.* (2003) has considered multiple hypotheses, showing that wind pollinated species tend to also be earlier flowering than their biotocially pollinated sister taxa, suggesting an interaction between the early flowering and wind pollination hypotheses.

(e) A recent paper by Gougherty & Gougherty (2018) tested multiple hypotheses by modeling associations trait correlations to FLS pattern in the Great Lakes regions. They found the strongest support for the water dynamics and early flowering (flower timing and seed characteristics) hypotheses, and found strong phylogenetic clustering for FLS. It should be noted that their seed mass findings were contrary to the predictions of (Primack, 1987), with small seeds being associated with hysteranthy. Also, their modeling framework doesn't really allow for direct comparisions (need to say this better).

2. In all of these cases, variability in FLS isn't addressed.

3. Yet, there are datasets widely available that would allow for testing these hypotheses at once and at multiple levels.

4. To address this gap, we supplement our literature review by re-testing some previously-used datasets to examine all hypotheses, and we leverage several widely-available datasets to test how support for these hypotheses varies across the inter- to intraspecific levels.

   (a) Michigan Trees and its companion volume Michigan Shrubs and Vines (Barnes & Wagner, 1981,2004; Burton V. Barnes, Christopher W. Dick, 2016) (MTSV) contains FLS information for 195 Woody plant species. The USFS Silvics mannual volume II (Burns *et al.*, 1990) contains FLS descriptions for 81 woody species. These data can be used to test interspecfic FLS varaiation. Species are categorized as flowers before leaves, flowers before/with leaves and flowers with leaves, and flowering after leaves. As in previous work, we collapsed these categories to binary "hysteranthous" of "seranthous" for modeling.

   (b) But even within this frame work, we built back in variability associated with the hypotheses. We defined 'functional hysteranthy' to accommodate a degree of overlap between flowering and the early stages of leaf out as predicted by the wind pollination hypothesis (including 'flowers before leaves', 'flowers before/with leaves' and 'flowers with leaves') versus 'physiological hysteranthy' (only flowers before leaves) which relates to drought tolerance hypothesis.

   (c) Harvard Forest contains flowering and leaf phenology measurements for individuals 24 woody species over 15 year, allowing for both inter- and intra-specific

comparisons (O'Keefe, 2015). In this dataset we calculated "FLS offset" (flower DOY-leaf DOY), a continuous measure fo FLS, which allows us to better understand the impact of FLS categorization and make comparison even within categories. We approximated "functional" and "physiological" hysteranthy in this data set by calculating 2 offset values (Fopn-L75) and (fbb-lbb).

(d) From the PEP725 (look up citation) database we obtained spatially and temporally explicit flowering and leaf phenology for 3 European hysteranthous species. This allows for test only at the intra-specific level, but unlike the other datasets allow for population level variability to be assessed.

What we know, what we don't know, and what we can do to know more

1. In considering each dataset separately and in tandem, and the previous literature, two clear trend emerge:

2. As presented above, multiple hypotheses are supported by the literature.

3. In our re-analyses, across inter-specific models, multiple hypotheses were too supported. There was generally a strong support for the early flowering and wind pollination hypothesis, poor support for the water dynamics hypothesis, and the phylogenetic signal was variable.

4. This is not a surprise. We wouldn't expect the wind pollination hypothesis to explain hysteranthy in biotically pollinated taxa. Further, with the relative recent community reassmbly of Northeastern forests following the most recent glaciation, it is not surprising our flora consists of species with radically different bio-geographic histories, and hysteranthy could have converged under different selection environments.

5. The relative importance of each the predictors changed significantly depending on how hysteranthy was defined. This effect was minimized when continuous measure of FLS were used over categorical.

Future

1. But perhaps more important that the results of these specific model themselves, is that through considering them together, we are provided a more comprehensive picture of where our understanding of this phenological trait is. and where it needs to go.

2. First, our analysis reveals the clear advantages of continuous data.

(a) As mentioned above, it minimizes the observer bias that comes with categorization.

(b) It reveals important interspecific differences that are masked by categorization. I.e. two hysteranthous species may have dramatically different FLS offsets.

(c) It also reveals that there are large intra-specific difference which, as will be discussed more below, will be instructive to hypothesis testing.

(d) All and all, our work shows categorizing hysteranthy into groups is biased and biologically problematic; future studies about phenological sequences should avoid these categories when possible and treat FLS as continuous traits (whenever possible).

3. A main outgrowth of our model is the realization it is instructive to test questions of hysteranthy at other scales. Because trait modeling in large community level datasets seem to support multiple hypotheses, and are confounded by species' identities and observer bias, the utility of these data can only take us so far. While future large-scale studies must try to study multiple traits across phylo-trees, the evolution of hysteranthy may be better explored through getting into mechanisms, which mean means drilling down in an opposing direction.

   (a) One option is to look within the hypotheses to address sub-grouping of taxa in which overlap between hypotheses could be controlled?

   (b) For example What drives hysteranthy among biotically pollinated taxa? It certain isn't wind pollination efficiency. Or what traits accounts for variability in hysteranthy among wind polliated taxa?

   (c) Further incorperating a phylo-biogeographic approach would probably be instructive at this level, for example: are their phylogeopraphic commonalities between biotocally pollinated hysteranthous species in Eastern flora.

4. But even with sub-groupings, interspecific trait association models can only can take us so far.

   (a) One reality of these kind of studies is that we never know we are picking the right traits. For example we used minimum P across range, one of the only available quantitative drought metrics at the scale of large interspecific models, to represent the water dynamics hypothesis. Is this really a good proxy for drought tolerance?

   (b) Further, species evolve a suit of traits of any function, and unmeasured traits might bias our results (Davies *et al.*, 2019). IE wind pollinated species could compensate for a lack of hysteranthy by over producing pollen or selfing. To really understand this trait across large taxonomic space, you would have to compare species over N-dimensional trait axis.

5. Considering hysteranthy variation at the intraspecific level overcomes many of these limitations and is the the next frontier in understanding FLS.

    (a) As predicted by evolutationary theory the agreement between our intra and interspecific models, suggesting flowering time major driver in FLS variation, suggests that we are in moving the right direction.

    (b) Further, though our datasets were taxonomically and geographically limited, they demonstrate that FLS variability is significant over time and space.

    (c) Looking within species holds most other traits relatively equal, avoids the problem of latent tradeoffs with unmeasured traits.

6. With this equalizing nature of intra-specfic coomparision we can now, move beyond trait associations and actually begin to to look at fitness consequences of FLS variation through experimental manipulations and observations.

    (a) This as a next step is intuative because fitness actually drives trait evoltion, and the hysteranthy hypotheses themselves make fitness predictions. It is tough to tease these appart at the interspecific level beacuse of the N-dimensional trait axis mentioned above, but the hypotheses predict that variability in hysteranthy would lead to varaibility into fitness outcome at the intraspecific level.

        i. For example, the wind pollination hypothesis predicts that years with increased hysteranthy should correlate with more pollination success.

        ii. The water dynamics hypothesis suggests more hysteranthous populations should better tolerate drought.

    (b) These predictions could be directly assessed.

    (c) Working at this level also highlights where local context may matter ... Does community matter ie wind pollination?

7. Looking at fitness consequences will not only help clarify basic scientific hypotheses, but is important for global change, and understanding how changing hysteranthy will impact species fitness.

    (a) For example, if hysteranthy is driven by pollination effciency, increased hysteranthy with climate change might effect demography to favor hysteranthous species. Or if the opposite is true, hysteranthous species may be at greater risk.

    (b) If there really is strong selection on early-flowering what is predicted next (lots of cites you could add here).

0.0.1 Things I didn't sneak in but could considered

- With the strength of flowering time across models should be abandon think of hysteranthy outside of selection for early flowering?
- why we got such different results than gougherty and gougerthy?

References

Barnes, B.V. & Wagner, W.H.J. (1981,2004) *Michigan Trees: A guide to the Trees of the Great Lakes Region*. University of Michigan Press.

Bolmgren, K., Eriksson, O. & Linder, H.P. (2003) Contrasting flowering phenology and species richness in abiotically and biotically pollinated angiosperms. *Evolution* **57**, 2001–2011.

Borchert, R. (1983) PHENOLOGY AND CONTROL OF FLOWERING IN TROPICAL TREES. *BIOTROPICA* **15**, 81–89.

Burns, R.M., Honkala, B.H. & coordinators], T. (1990) Silvics of north america: Volume 2. hardwoods. Tech. rep., United States Department of Agriculture (USDA), Forest Service.

Burton V. Barnes, Christopher W. Dick, M.E.G. (2016) *Michgan Shrubs Vines: A guide to species of the Great Lakes Region*. University of Michigan Press.

Davies, T.J., Regetz, J., Wolkovich, E.M. & McGill, B.J. (2019) Phylogenetically weighted regression: A method for modelling non-stationarity on evolutionary trees. *Global Ecology and Biogeography* **28**, 275–285.

Feild, T.S., Chatelet, D.S. & Brodribb, T.J. (2009) Ancestral xerophobia: a hypothesis on the whole plant ecophysiology of early angiosperms. *GEOBIOLOGY* **7**, 237–264.

Franklin, D.C. (2016) Flowering while lea ess in the seasonal tropics need not be cued by leaf drop: evidence from the woody genus brachychiton (malvaceae). *Plant Ecology and Evolution* **149**, 272–279.

Gougherty, A.V. & Gougherty, S.W. (2018) Sequence of flower and leaf emergence in deciduous trees is linked to ecological traits, phylogenetics, and climate. *New Phytologist* **220**, 121–131.

Gunatilleke, C.V.S. & Gunatilleke, I.A.U.N. (1984) Some observations on the reproductive biology of three species of cornus (cornaceae). *Journal of the Arnold Arboretum* **65**, 419–427.

Janzen, D.H. (1967) Synchronization of sexual reproduction of trees within the dry season in central america **21**, 620–637.

Milleron, M., Lopez de Heredia, U., Lorenzo, Z., Perea, R., Dounavi, A., Alonso, J., Gil, L. & Nanos, N. (2012) Effect of canopy closure on pollen dispersal in a wind-pollinated species (Fagus sylvatica L.). *PLANT ECOLOGY* **213**, 1715–1728.

Nathan, R. & Katul, G. (2005) Foliage shedding in deciduous forests lifts up long-distance seed dispersal by wind. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA* **102**, 8251–8256.

Niklas, K.J. (1985) The aerodynamics of wind pollination **51**, 328–386.

O'Keefe, J. (2015) Phenology of woody species at harvard forest since 1990.

Primack, R.B. (1987) Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* **18**, 409–430.

Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**, 179–214.

Reich, P. & Borchert, R. (1984) WATER-STRESS AND TREE PHENOLOGY IN A TROPICAL DRY FOREST IN THE LOWLANDS OF COSTA-RICA. *JOURNAL OF ECOLOGY* **72**, 61–74.

Robertson, C. (1895) The philosophy of flower seasons, and the phaenological relations of the entomophilous flora and the anthophilous insect fauna **29**, 97–117.

Savage, J.A. (2019) A temporal shift in resource allocation facilitates flowering before leaf out and spring vessel maturation in precocious species. *AMERICAN JOURNAL OF BOTANY* **106**, 113–122.

Tauber, H. (1967) Investigations of the mode of pollen transfer in forested areas. *Review of Palaeobotany and Palynology* **3**, 277–288.

Whitehead, D.R. (1969) Wind pollination in the angiosperms: Evolutionary and environmental considerations **23**, 28–35.