Available evidence for FLS hypotheses in temperate woody species

Despite a strong conceptual basis, direct tests of these hypotheses of hysteranthy in the literature are relatively rare, and support for them is mixed. Many studies only test a singal hypothesis at once, making comparision between them difficult. For example, the primary evidence supporting the wind pollination hypotheses comes from pollen diffusion studies, e.g., particle movement through closed and open canopies (**???**), which provide no framework for comparatively evaluating the other hysteranthy hypotheses. We are aware of no direct test to try and distinguish hysteranthy from selection early flowering, but **?** 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 may simply be one component of a larger suit of early flowering traits. We are also aware of no studies that have mechanistically evaluated the water dynamics hypothesis, though observations of flowering in the dry tropics by **??** suggest that the timing of flowering in hysteranthous taxa is associated with a plant water status recovery due to leaf drop. Only recently has it even been suggested that this hypothesis might be relevant in the temperate zone as well, as it is not expected that water status would limit biological activity in the wet spring months of the temperate zone (**?**).

In contrast, studies testing multiple hypotheses have generally found support for more than one evolutionary driver of hysteranthy. One study by **?** showed 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. A recent study by **?** tested multiple hypotheses by modeling associations bwtween species' trait and FLS patterns in the Great Lakes regions. They found strong support for both the water dynamics and early flowering (flower timing and seed characteristics) hypotheses, and found strong phylogenetic clustering for FLS.

In all of these cases, variability in FLS below the species level isn't addressed. Yet, there are datasets widely available that would allow for concurrently testing these several hysteranthy hypotheses concurrently, and at multiple taxonomic levels. 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.

We evaluated hysteranthy in four phenological datasets. Michigan Trees and its companion volume Michigan Shrubs and Vines (**??**) (MTSV) contains catagorical FLS information for 195 Woody plant species. The USFS Silvics mannual volume II (**?**) contains catagorical FLS descriptions for 81 woody species. These data can be used to test interspecfic FLS variation. Within these datasets, we applied 2 alternative FLS classification schemes; physiological hysteranthy, which allowed for no overlap between floral and leaf phenophases, and functional hysteranthy, which allowed for a degree of overlap as predicted by the wind pollination hypotheses. The Harvard Forest dataset (HF) contains quantatitive flowering and leaf phenology measurements for individuals of 24 woody species over a 15 year period, allowing for both inter- and intra-specific comparisons

Future

Our analysis reveals the clear advantages of treating hysteranthy as a continuous trait. As mentioned above, continous data minimizes the observer bias that comes with categorization. It also reveals important inter-specific differences that are masked by categorization. For example, two catagorically hysteranthous species may have dramatically different FLS offsets. Through working with continous measures of hysteranthy, substantial intra-specific differences in FLS emerge, and as will be discussed more below, these will be valuable for hypothesis testing. 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.

Another main outgrowth of our analysis is the realization that it is instructive to test questions of hysteranthy at many 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 there is certainly value to broad taxonmic studies, and future large-scale analyses should continue,it is possible the evolutionary dynamics of hysteranthy may be better explored with a more mechanistic approach, which may mean utalizing a more taxonomically restricted focus.

One option is to look within the hypotheses to address sub-grouping of taxa in which overlap between hypotheses could be controlled. For example, what drives hysteranthy among biotically pollinated taxa? It certain isn't wind pollination efficiency. Or, what factors accounts for variability in hysteranthy among wind polliated taxa? Incorperating a more explicit phylo-biogeographic approach would probably be instructive at this level, for example: are their phylogeopraphic commonalities between biotocally pollinated hysteranthous species in Eastern flora?

But even with drilling down to sub-groupings, interspecific trait association models can only can take us so far. One reality of these kind of studies is that we never know we are picking the right traits. For example we used minimum precipitation across a species' 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? Further, species evolve a suit of traits for any function, and unmeasured traits might bias our results (**?**). For example, wind pollinated species could compensate for a lack of hysteranthy by over producing pollen or through self-pollination. To really understand this trait across large taxonomic space, you would have to compare species across an unfeasibly large, N-dimensional trait space.

Considering hysteranthy variation at the intraspecific level overcomes many of these limitations, and is the the next frontier in testing the evolutionary and ecological significance of FLS. Evolutationary theory predicts that intraspecific variation should follow the same trends as interspecific varaition. The agreement between our intra- and interspecific models supports this, and may suggests that we are narrowing in on certain hypotheses. Further, though our datasets were taxonomically and geographically limited, they demonstrate that FLS variability is significant over time and space. Looking within species holds most other traits relatively equal, avoiding the problem of latent tradeoffs with unmeasured traits.

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. This 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. For example, the wind pollination hypothesis predicts that years with increased hysteranthy should correlate with more pollination success. The water dynamics hypothesis suggests more hysteranthous populations should better tolerate drought. These predictions could be directly assessed through well designed experiments.

Looking at fitness consequences will not only help clarify basic scientific hypotheses, but is essential for understanding how global change induced alterations to hysteranthy will impact species demographics. For example, if hysteranthy is driven by pollination effciency, increased hysteranthy with climate change might favor hysteranthous species. Or, if climate changes reduces FLS offset, hysteranthous species may be at greater risk for reproductive failure. If there really is strong selection on early-flowering what is predicted next (lots of cites you could add here). A better understanding of consequences of variation in hysteranthy is essential both for understanding the evolutionary origins of this trait, and for predicting the fate of species with this phenologic syndrome as global climate continues to change.

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.

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.

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.

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

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.