

Daniel Buonaiuto

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Green is the color of spring, but any keen observer walking the temperate, deciduous forest of the Eastern United States early in the season would readily witness that it is often the subtle whites, reds and yellows of emerging tree flowers that are the first harbingers of spring in temperate forest communities. In some deciduous tree species, seasonal flowering proceeds leaf development, while in others, it is leaf expansion that occurs first. The study of phenology, the timing of annual life cycle events, has a long history, and even in the late 1800's, naturalists speculated that such contrasting floral-foliate sequences were not merely incidental, but that these patterns, in and of themselves, may be adaptive (). However, despite increasing scientific interest in the study of phenology over the past several decades, the phenology of reproductive (flowering, fruiting) and productive (budburst, leafout and drop) stages have long been treated separately, and both the mechanisms and effects of floral-foliate phenological patterns remain poorly studied empirically (?).

Even finding suitable language to describe floral-foliate patterns in the existing literature is an difficult endeavour. Early botanical dictionaries define flowering followed by leaves as both "proterany" and "hysteranthly" (which grammatically should be antonyms). Others describe flowering before leafing as "precocious" flower, but that term can also refer to flowering early in ontogeny and have nothing to do with seasonality. To the aim of maintaining a consistency of usage, I will adopt the terminology used by Auth in which proteranthly refers to flowering before leafing, synanthly refers to flowering and leafing simultaneously and seranthly refers to flowering after leafing.

As global climate is predicted to change dramatically in the coming decades it is imperative that we, as scientists, better understand these phenological patterns. The effects of climate change have already appeared in phenology (??) and the degree to which these phenological shifts are altering floral foliate sequences is virtually unknown. If the sequences themselves are indeed adaptive, conferring a significant fitness benefit to individuals under historical conditions, disruptions and alterations to these patterns caused by changing climate conditions could have negative demographic consequences for many forest trees. To better

understand the importance of these sequences and the ability for species to maintain them in a changing world, researchers should focus their attention on gaining a more complete picture of mechanisms and effects of this. To this end, in section one of this paper, I will first present the dominant hypothesis for proteranthly in the context of life history theory, and then evaluate the empirical and theoretical evidence for its support. In section two, I will discuss some of the biological mechanisms producing the phenological patterns we see today and discuss how they may enable or constrain plastic responses to changing climate in forest trees.

## 1 Proteranthly and Life History Theory

Life history theory seeks to explain how organisms achieve reproductive success. The classical theory is based on an optimization model- life history traits of organisms (for example: age of reproduction, seed size ) are determined by tradeoffs in both extrinsic (environmental, community) and intrinsic (genetics, physiology) factors, which result in a lineage specific optimum for life history characters (?). Typically, life history theory is applied to the full lifespan of an organism, but in the context of tree phenology, I will consider its optimization model in the context of seasonal optimization.

For flowering alone, optimization in a seasonal environment depends on several factors. For flower tissues and ultimately reproductive output, there is likely tradeoff between flowering minimizing risk for early season frost damage and maintaining enough time for fruit development and dispersal. The timing is further selection by the vectors of pollination. There is also an observed tradeoff where there is increased pollinator abundance for midseason flowers, but also increased competition to attract them (). There is likely a tradeoff between pollination efficiency and investment which I will discuss further below. Now, considering leaf phenology alone, optimization is thought to maximize the growing season and minimizing the risk of damage from late season frost ().

But with spring conditions varying greatly interannual how do deciduous trees

But now we must consider the timing of leaves and flowers together. Might the presence of leaves change the behaviors of pollen vectors? Might the presences of flowers with out leaves change the resource allocation dynamics? The sequencing of leaves and flowers, in and of itself, produces its own set of tradeoffs, which I

will now discuss as we review the main hypothesis about proteranthly.

Proteranthly is thought to be an adaptation for pollination efficiency. Theorists explain that this trait is common in wind pollinated species, because producing flowers in the leafless state allows for maximum wind flow through the canopy and significantly reduces the potential for pollen interception by non floral parts (). While usually assumed associated in the literature with wind pollination, similiary theory could be applied to insect pollinated species in that tree flowers are easier for pollinators to located when there are no leaves as barriers or obstacles. Presumably, more effecient pollination would allow for species to reduce their overall investment in reproduction. However, their would still be costs associated with this life history trait. Proteranthous flowering would only be effective if it occured before the community as a whole leafed out, which would push such flowering early into the season to a time when risk of frost damage is high. Additionally, proteranthous flowering probably has an energetic cost, taking place at a time of the year when stored carbohydrates are at their lowest, with out the assistance of supplimental carbon from foliar photosynthesis(). To my knowledge, there have been no empircal studies testing this hypothesis, but several studies seem to support it though indirect evidence. Independence vs. constraits. Phenophases are not optimized in a vaccum, but timing is based on that leaf and flower physiology and the functional relationship between them.

evidence: Wind pollination arose at same time of deciduousness, modeling wind flow through canopy, interception in that bog paper. dogwoods

We understand that phenophases are not optimized in a vaccum, but timing is based on that leaf and flower physiology and the functional relationship between them. Climate change is already having dramatic impact on phenology. cite lizzie. Will flowering and leafing phenophase shift relative to each other, maintaining their optimized temporal relationship? To what degree is their timing constrained Lechowicz respond to same cues same genetic pathways?

same cues ( cherry paper) my work