



Dear Dr. Hetherington,

We propose a “Viewpoint” about the drivers of flower-leaf phenological sequences (FLSs) in deciduous woody plants. Evolutionary theory predicts that both flowering and leaf phenology are critical fitness components of woody plants, and a century of empirical research supports this assertion (1; 2). In recent decades, this body of theory has been extended to suggest that it is not only individual phenophases but also the relationship between them that determines woody plant fitness (3; 4). Many deciduous woody plants flower before leafing, yet sustained research efforts have yet to yield a well-supported explanation for this. These unresolved hypotheses are critically important now as climate change is shifting FLSs—which may exacerbate fitness differences between species and reshape eco-systems of the future. Our “Viewpoint” shows how progress in this area has been stalled by our conceptual framework for FLSs; we detail a new approach built on continuous measures of FLS and intra-specific and within-individual-level variation to rapidly advance progress.

What hypotheses or questions does this work address?

Studies have variously suggested that flowering before leafing may be an adaptation for wind-pollination (5), for reducing water stress (6), or to facilitate extreme early season flowering (7). Studies that directly compare these hypotheses, however, are rare, and those that do, tend to find support for more than one (8; 9). While FLS patterns are usually treated as qualitative descriptors at the species level, for example, “*flowers emerge before leaves*”, we demonstrate that a novel approach focusing on intra-specific FLS variation and quantitative inter-specific comparisons is necessary to accurately evaluate these hypotheses.

How does this work advance our current understanding of plant science?

In our “Viewpoint”, we would: 1) Review the hypotheses of woody plant FLSs. 2) Comprehensively evaluate FLS variation across and within species, and explore how this variation alters the predictions of the hypotheses. 3) Test the FLS hypotheses using several case studies from temperate forests. 4) Make recommendations for future study of FLSs to improve our ability to accurately test FLS hypotheses and better predict how changing FLS will impact species in an era of climate change.

Through this novel approach, we show that: 1) There are high levels of both inter- and intra- specific variation in FLS that cannot be accommodated in the current FLS framework, and, that it the current framework itself that obscures our ability to effectively test and differentiate between hypotheses. 2) FLS variation provides novel insights about the function of FLSs and reveals consistencies and anomalies in support for FLS hypotheses. 3) Leveraging this intra-specific variation in phenological research provides an avenue forward to advance our understanding of FLS.

Why is this work important and timely?

From analyzing long term data it is clear that climate change is altering FLS patterns, but that these effects vary across species and populations (Fig. 1). If, as suggested, FLSs are indeed an important component of woody plant fitness, differential sensitivity to climate change will exacerbate fitness differences among species, individuals and population, influencing both how and where species will persist under altered climate conditions. The implications of FLS shifts for plants could be beneficial, benign, or disastrous. The effects of FLS shifts depend on the functional significance of FLSs, and predicting these outcome will require researchers to effectively evaluate the currently FLS hypotheses. Our framework provides the ability to do just this, paving the way meaningful fundamental and global change research in this area.

We expect this manuscript will be titled “Reconciling competing hypotheses regarding flower-leaf sequences in temperate forests for fundamental and global change biology”. It will be co-authored by I. Morales-Castilla, and E.M. Wolkovich. This proposed manuscript is not under consideration anywhere else. Thank you for your consideration.

Sincerely,

Daniel Buonaiuto

Abstract:

Phenology is a major component of organism fitness. It is not only individual phenological events that affect fitness, but also the relationship between events. Deciduous woody plants exhibit considerable variation in the order of reproductive and vegetative events, or flower-leaf sequences (FLSs). Research suggests that FLSs are adaptive, and several competing hypotheses may explain their function. Reconciling these hypotheses has been impeded by our conceptual orientation towards them. Classically, FLSs are treated categorically at the species level, obscuring substantial inter- and intra-specific variation. We develop the existing hypotheses to account for the FLS variation in nature and evaluate them with four case studies. Our inquiry provides major insights towards a new framework for understanding FLSs. First, we find concurrent support for multiple hypotheses. Future research should allow for overlapping hypotheses and test them in smaller sub-groupings. Second, support for FLS hypotheses is sensitive to how FLSs are defined. Researchers should switch from categorical to continuous measures of FLS. Finally, we highlight the limits of inter-specific trait-association models for hypothesis testing. Researchers should adopt an intra-specific approach and evaluate fitness consequences of FLS variation to test the FLS hypotheses and to predict how climate-related alterations to FLSs will affect plant communities.

Selected Figures:

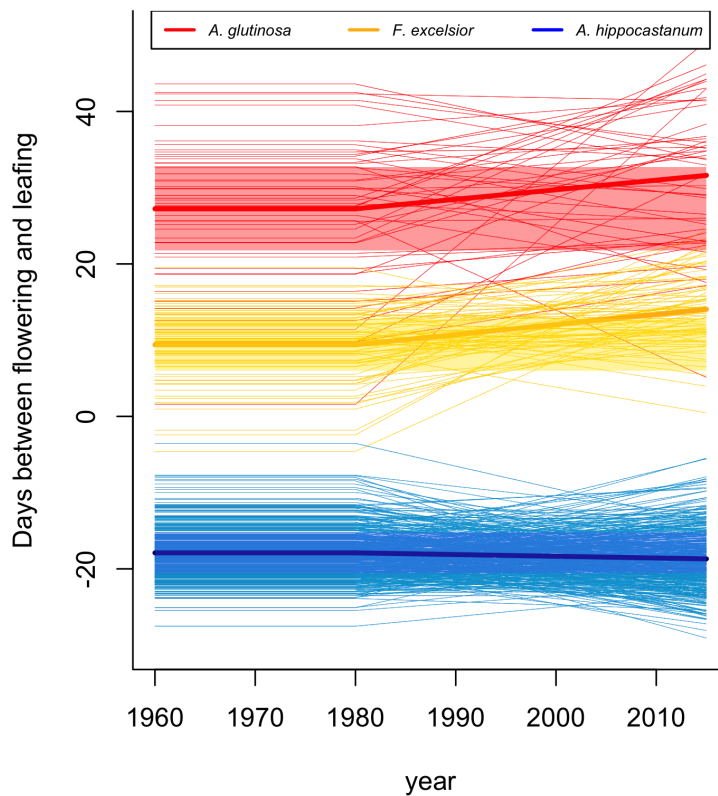


Figure 1: **Modeled FLS response to climate change across Europe for three tree species from 1960 to 2015.** To detect the effect of climate change on average FLS, the models allows for shifts in FLS after 1980. Each line represents a population from the PEP725 database and the highlighted regions indicate historic range of FLS variability (upper and lower 95% credible intervals of the pre-1980 average). There is significant intra-specific variation in average FLS and the FLS response to climate change. For all species, the time between flowering and leafing is generally increasing but the direction and rate of change differs across species and sites.

References

- [1] Munguia-Rosas, M. A., Ollerton, J., Parra-Tabla, V., and Arturo De-Nova, J. Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. *Ecology letters* **14**(5), 511–521, May (2011).
- [2] Forrest, J. and Miller-Rushing, A. J. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**(1555), 3101–3112, Sep (2010).
- [3] Menzel, A. and Fabian, P. Growing season extended in Europe. *Nature* **397**(6721), 659, Feb 25 (1999).
- [4] Ettinger, A., Gee, S., and M. Wolkovich, E. Phenological sequences: how earlyseason events define those that follow. *American Journal of Botany* **105**, 10 (2018).
- [5] Rathcke, B. and Lacey, E. P. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**(1), 179–214 (1985).
- [6] Reich, P. and Borchert, R. Water-stress and tree phenology in a tropical dry forest in the lowlands of costa-rica. *Journal of Ecology* **72**(1), 61–74 (1984).
- [7] Primack, R. B. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* **18**(1), 409–430, 2018/01/17 (1987).
- [8] Gougherty, A. V. and Gougherty, S. W. Sequence of flower and leaf emergence in deciduous trees is linked to ecological traits, phylogenetics, and climate. *New Phytologist* **220**, 121–131, Jun (2018).
- [9] Bolmgren, K., Eriksson, O., and Linder, H. P. Contrasting flowering phenology and species richness in abiotically and biotically pollinated angiosperms. *Evolution* **57**(9), 2001–2011 (2003).