/Users/danielbuonaiuto/Desktop/arb_logo.png

Dear Dr. Hetherington,

We propose a "Viewpoint" about the drivers of flower-leaf phenological sequences (FLSs), with implications for future plant communities. 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 (**??**). In recent decades, this work has been extended to predict that it is not only individual phenophases but also the relationship between them that determines woody plant fitness (**??**). 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 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 (**?**), for reducing water stress (**?**), or to facilitate extreme early season flowering (**?**). Studies that directly compare these hypotheses, however, are rare; those that do, tend to find support for more than one (**??**). 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?

Long term data shows that climate change is altering FLS patterns, but these effects vary across species and populations (Fig. 1). If FLSs are an important component of woody plant fitness, differential sensitivity to climate change will exacerbate fitness differences among species, individuals and populations, influencing both how and where species will persist under altered climate conditions. The effects of FLS shifts depend on the functional significance of FLSs, and predicting outcomes will require researchers to effectively evaluate the current FLS hypotheses. Our framework provides the ability to do just this, paving the way for 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 an organism's fitness. While individual phenological events affect fitness, growing evidence suggests that the relationship between events may be equally or more important. This may explain why 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, with several competing hypotheses to explain their function. Reconciling these hypotheses has been impeded by our conceptual orientation towards them. Here, we advance 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, suggesting progress can come from studies addressing overlapping hypotheses. Second, support for FLS hypotheses is sensitive to how FLSs are defined, with quantitative definitions proving most useful. 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:

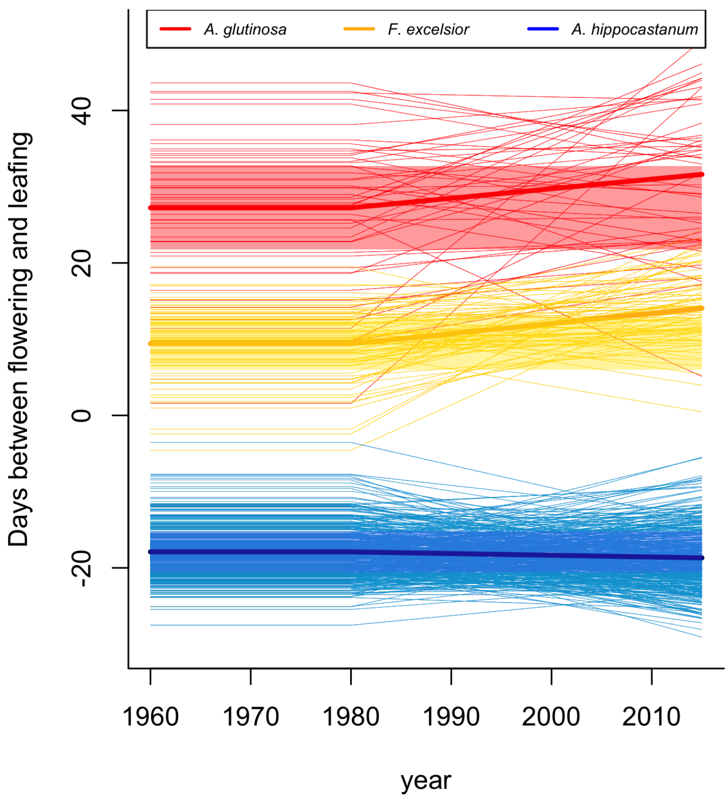

Figure 1: **FLS across Europe for three tree species from 1960 to 2015 suggests climate change has generally increased the time between flowering and leafing**, but the direction and rate of change differs across species and sites which may exacerbate fitness differences between species and communities. To detect the effect of climate change on average FLS, we used models that allow for shifts in FLS after 1980. Each small line represents a population from the PEP725 database while thicker lines represent the mean trend per species 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.