

Dear Dr. Hetherington,

Please consider this manuscript “Ecological drivers of flower-leaf sequences: aridity and pollination success select for flowering-first in insect-pollinated temperate trees” as a “Full paper” in *New Phytologist*.

Many tree and shrub species in temperate forests produce flowers before their leaves emerge each season. This flower-leaf sequence, known as hysteranthly, proteranthly or precocious flowering is generally described as an adaptation to facilitate wind-pollination (Rathcke & Lacey, 1985). However, this explanation does not address the widespread prevalence of hysteranthly in biotically-pollinated taxa, which comprise a substantial portion of the hysteranthous species in some temperate forests (Buonaiuto *et al.*, 2021).

What hypotheses or questions does this work address?

In biotically-pollinated species, flower-first may be an adaptation for reducing water stress (**Water limitation hypothesis**; Gougherty & Gougherty, 2018; Buonaiuto *et al.*, 2021), or pollinator attraction (**Insect visibility hypothesis**; Janzen, 1967). We quantified flower-leaf sequence variation in a clade of insect-pollinated trees, using herbaria specimens and Bayesian hierarchical modeling to test these hypotheses by modeling the associations between hysteranthly and environmental or biological traits.

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

We show that flowering-first is associated with aridity and reduced flower size as predicted by the water limitation and insect visibility hypotheses. We present a novel modeling approach to quantify phenological variation that can be implemented in both experimental and observational studies to better integrate observations of broad ecological patterns with targeted experiments in the future.

Why is this work important and timely?

Climate change is already altering the flower-leaf sequences of woody plants (Ma *et al.*, 2021; Wang *et al.*, 2022). Our finding that flower-leaf sequences may be important adaptations for environmental tolerance and pollination success suggest that they are critical to forecasting the demography and performance of forest communities in an era of global climate change.

The main text of this manuscript is 3829 words in length, it contains 4 figures. It is co-authored by T.J. Davies, S. Collins and E.M. Wolkovich and is not under consideration elsewhere. We hope that you will find it suitable for publication in *New Phytologist*, and look forward to hearing from you.

Sincerely,



Daniel Buonaiuto

References

- Buonaiuto DM, Morales-Castilla I , Wolkovich EM. 2021.** Reconciling competing hypotheses regarding flower–leaf sequences in temperate forests for fundamental and global change biology. *New Phytologist*, **229**: 1206–1214.
- Gougherty AV , Gougherty SW. 2018.** Sequence of flower and leaf emergence in deciduous trees is linked to ecological traits, phylogenetics, and climate. *New Phytologist*, **220**: 121–131.
- Janzen DH. 1967.** Synchronization of sexual reproduction of trees within the dry season in central america. *Evolution*, **21**: 620–637.
- Ma Q, Huang JG, Hämmnen H, Li X , Berninger F. 2021.** Climate warming prolongs the time interval between leaf-out and flowering in temperate trees: Effects of chilling, forcing and photoperiod. *Journal of Ecology*, **109**: 1319–1330.
- Rathcke B , Lacey EP. 1985.** Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, **16**: 179–214.
- Wang S, Wu Z, Gong Y, Wang S, Zhang W, Zhang S, De Boeck HJ , Fu YH. 2022.** Climate warming shifts the time interval between flowering and leaf unfolding depending on the warming period. *Science China Life Sciences*, **65**: 2316–2324.