



Dear Dr. Pinfield-Wells,

Please consider this manuscript “Reconciling competing hypotheses regarding flower-leaf sequences in temperate forests for fundamental and global change biology” as a “Viewpoint” article in *New Phytologist*. We have corresponded with you previously about this piece through a pre-submission enquiry and received approval to submit the manuscript for full consideration.

A century of empirical studies suggests that flowering and leaf phenology are critical fitness components of woody plants (Munguia-Rosas *et al.*, 2011; Forrest & Miller-Rushing, 2010). In recent decades, research has shown that it is not only individual phenophases but also the relationship between them that determines woody plant fitness (Menzel & Fabian, 1999; Ettinger *et al.*, 2018). Many deciduous woody plants flower before leafing, yet sustained research efforts have yet to yield a consistent, well-supported explanation for this. These unresolved hypotheses are important now as climate change is shifting flower-leaf sequences (FLSs)—which may exacerbate fitness differences between species and reshape future ecosystems. Our “Viewpoint” shows how progress in this area has been stalled by the current conceptual framework for FLSs; we detail a new approach that leverages continuous measures of FLSs and intra-specific and within-individual variation to rapidly advance progress.

What hypotheses or questions does this work address?

Research suggests FLSs are under strong selection and critical to fitness. FLS variation may be an adaptation for wind-pollination (Rathcke & Lacey, 1985), reducing water stress (Gougherty & Gougherty, 2018; Reich & Borchert, 1984), or early season flowering (Primack, 1987), but these conflicting hypotheses remain unresolved. A novel approach focusing on intra-specific FLS variation and quantitative comparisons is necessary to accurately evaluate these hypotheses.

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

We show: 1) The current framework fails to capture the inter- and intra-specific FLS variation in nature impeding robust hypothesis testing; 2) Variation provides novel insights about the function of FLSs, revealing complexities critical to advancing the hypotheses; 3) Leveraging intra-specific variation advances our understanding of FLSs.

Why is this work important and timely?

We show that climate change is altering FLSs, but effects vary across species (0.8-4.7 days on average, Fig. 1). Shifts could be beneficial or adverse, and predicting this outcome requires researchers to effectively evaluate the current hypotheses. Our framework is the first that can do this robustly, making it critical to fundamental and applied research.

The main text of this manuscript is 3370 words in length, it contains (4)5 figures. It is co-authored by I. Morales-Castilla, 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

Selected Figures:

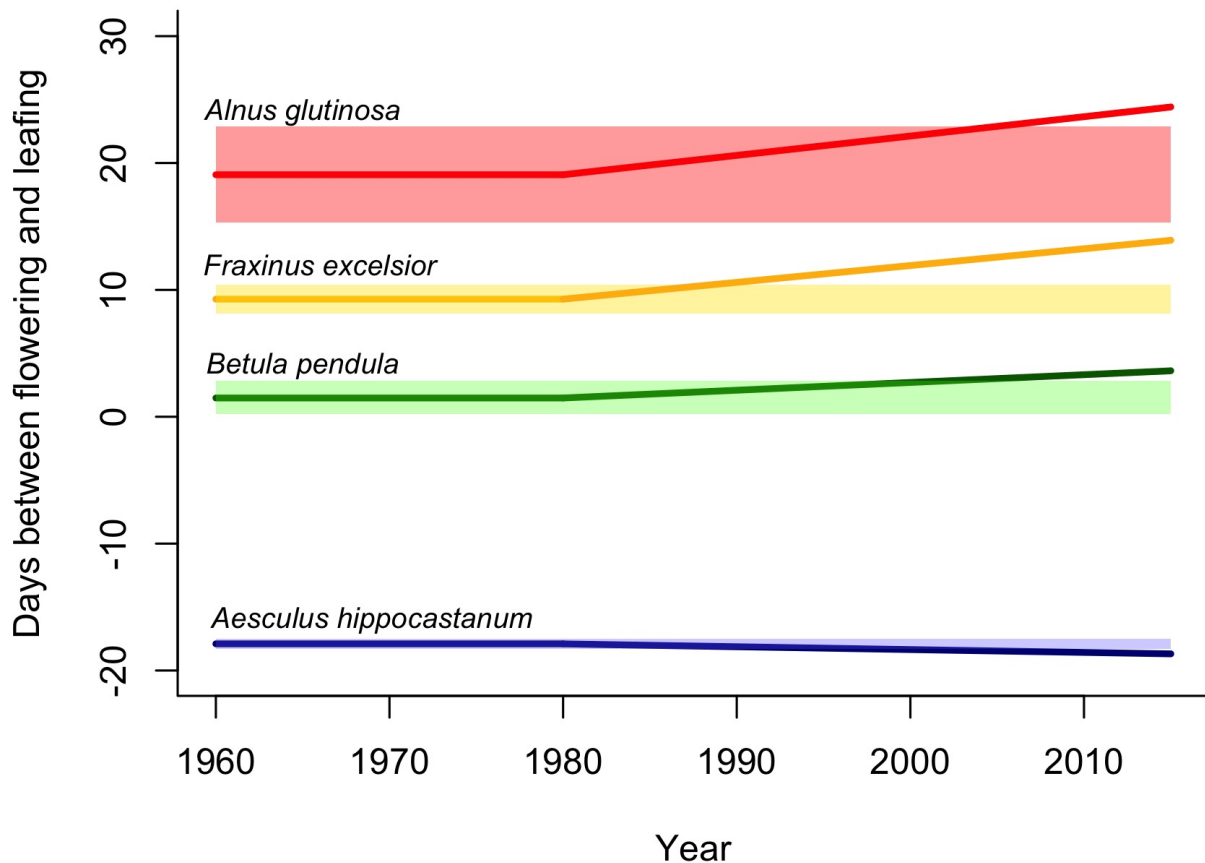


Figure 1: **FLSs across Europe for four tree species from 1960 to 2015 suggests climate change has generally increased the time between flowering and leafing**, but the direction and rate of change differs across species, which may exacerbate fitness differences within forest communities. To detect the effect of climate change on average FLS, we used models that allow for shifts in FLS after 1980. Lines represent the mean trend in FLS per species, and the highlighted regions indicate historic range of FLS variability (95% credible intervals of the pre-1980 average) from the PEP725 database (Templ *et al.*, 2018).

References

- Ettinger, A., Gee, S. & M. Wolkovich, E. (2018) Phenological sequences: how early season events define those that follow. *American Journal of Botany* **105**.
- Forrest, J. & Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3101–3112.
- 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.
- Menzel, A. & Fabian, P. (1999) Growing season extended in Europe. *Nature* **397**, 659.
- Munguia-Rosas, M.A., Ollerton, J., Parra-Tabla, V. & Arturo De-Nova, J. (2011) Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. *Ecology Letters* **14**, 511–521.
- Primack, R.B. (1987) Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* **18**, 409–430.
- Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**, 179–214.
- 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.
- Templ, B., Koch, E., K.Bolmgren, Ungersböck, M., Paul, A., Scheifinger, H. & et al. (2018) Pan european phenological database (pep725): a single point of access for european data. *Int. J. Biome-teorology* .