Evolutionary history—more than phenological cues—explain temporal assembly of woody plant communities

Deirdre Loughnan[1] and E M Wolkovich[1]

December 4, 2023

[1] Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, 2424 Main Mall Vancouver, BC, Canada, V6T 1Z4.

Corresponding Author: Deirdre Loughnan, deirdre.loughnan@ubc.ca

Introduction

1. Climate change — phenology — variability
   (a) Paragraph 1
      i. Climate change shifting phenology
      ii. Give example of range of climate change, or the mean etc
      iii. High variability
      iv. Some of the variability — regional warming could explain
   (b) Paragraph 2
      i. But not enough — species variable
      ii. Why care? — forecasting and ecosystem services
2. Why spp may vary
   (a) Within a community several weeks for diff spp
   (b) Introduce temporal niche
      i. resource competition
      ii. understory trees
3. Does population matter too?
   (a) Phenology differs in different places
   (b) Population differ — local adaptation to environment and spp in community — truly different phenology
   (c) Same underlying phenology but different cliamte — high interannual variability
4. Cues — phenology
   (a) Even doy varies — animals and plants have identical cue systems — cite Bonamour
   (b) Universal cues — photo and temp — consistent in controlled environments

   (c) photo by latitude

5. What do we need?
   (a) Spp variability
   (b) Population variability
   (c) Remove interannual variability by identifying cues
   (d) Given that cues/species have evolved over long timescales — consider phylogeny
6. Spring budburst — good study system
   (a) Three primary cues — winter and spring temps and photoperiod
   (b) Temporal niche by cues
   (c) Phenotypic differences — functional groups and growth strategies — spp can vary phenology and optimize their temporal niche.
7. Here we:
   (a) Combined results from two growth chamber studies of woody plant phenological cues
   (b) Data from four populations, from eastern to western North America and a range of 4-6° latitude
   (c) Allows us to detect general trends in how bb of N Am. deciduous forest communities respond to forcing, chilling, photoperiod
   (d) But also community specific responses—detect differences between Western and Eastern forest communities, and at different latitudes
   (e) And trends across different functional groups, exploring differences between the shrubs that dominate the forest understory and tree species.

Climate change is altering species phenology, or the timing of life history events, across the tree of life. Studies synthesizing across diverse species and habitats have found on average phenologies have advanced by 2.6-2.8 days per decade (**???**). Phenology is, however, a highly variable trait, with individual events spanning a period of days in most communities and phenological shifts occurring at different rates (**?**Fitter and Fitter, 2002; **?**; Yu et al., 2010; Fridley, 2012). Some degree of this variability is likely due to regional differences in climate change, as some areas experience greater warming than others, but there remains a considerable amount of unexplained varaition (Hoegh-Guldberg et al., 2018).
While geographic factors could be driving the observed variability in phenology, species-level differences should also be considered (Vitasse et al., 2009; Wolkovich and Cleland, 2014; Zohner and Renner, 2014; **?**). In many communities, we have yet to identify the primary cues of phenology and partition their relative importnace across populations. But identifying the drivers of this important life history trait is necessary to predict future changes, and ultimatley, impacts on community dynamics and ecosystem services, like carbon cycles and pollination (Gotelli and Graves, 1996; Cleland et al., 2007; Richardson, A.D., O'Keefe, 2009).

Across species in a community, the timing of a phenological event can span up to several weeks (Richardson, A.D., O'Keefe, 2009). This phenological variation allows species to fill different temporal niche within a season (Gotelli and Graves, 1996). This allows species to limit the extent of compeition for limiting resources and persist within a community. In forest communtiies, understory species often budburst earlier than canopy trees, when light and soil nutrients are more available. This may further select for differences in species growth strategies and further promote species differences in phenology. While differences in the timing of phenological events across communities can be due to species differences, phenology can also vary within a species (great tit measured in UK vs Netherlands?). Within a population, we would expect traits like phenology to undergo local adaptation to both environmental factors and selection from biotic interactions, like competition. Despite species expressing the same udnerlying phenology, climate cues can be highly variable across years and therefore select for different optimum trait phenotypes across a species distribution.

Despite the high degree of phenological variation within and across species, we often find animals and plants to have very similar cue systems. Most species respond to variation in temperature and photoperiod cues with consistent phenological responses occurring under controlled environments. Across species distributions we would expect to find biogeographic gradients in phenoloy in response to similar gradients in cues. Both photoperiod and temperatues vary across latitudinal gradients, possibly leading to similar gradients in phenology.

To better predict how forest communities will respond and assemble under continued climate change requires a holistic approach to studying the drivers of phenological variability. For a given community, we must account for differences across species to account for the effects of phenotypic variation and biotic interactions. But this cannot be done in isolation of speices distribution and the local adapation that indiviudal populations may exhibit. By indentifying the primay cues for a given phenological event, we can conduct experiments under controlled conditions and remove the relative effects of intannual variability. While for many species, shifts in phenology are relatively recent, we must also account for the longer evolutionary timescales over which communities assembled (Davies et al., 2013).

Spring budburst offers an excellent system to study spatial patterns in phenology and cue responses. The budburst of temperate woody plants responds to temperature cues in both the winter and spring, as well as daylength (Chuine et al., 2010; Polgar and Primack, 2011; Cooke et al., 2012; Basler and Körner, 2014; Laube et al., 2014). These three cues interact to shape species temporal niche, with variation in the relative importance of indiviudal cues across species. Phenotypic differences between species — such as functional groups and varying growth strategies — promote phenological differences and ultimately optimize their temporal niche.

Here we combined results from two growth chamber studies of woody species budburst cues. We used data from four populations, from eastern to western North America, with pairs of populations on each coast spanning 4-6° latitude respectively. Our phylogenetic approach allowed us to detect general trends in budburst cue responses in North American deciduous forest communities. We also explored community specific responses and detect differences between western and eastern forest communities, and across latitudes. By including diverse assemblages of species, we tested for differences between functional groups, comparing the dominant shrub and tree species that characterize our forest understories and canopy.

References

Basler, D., and C. Körner. 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. Tree Physiology 34:377–388.

Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. Science 329:277–278.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. Trends in Ecology and Evolution 22:357–365.

Cooke, J. E., M. E. Eriksson, and O. Junttila. 2012. The dynamic nature of bud dormancy in trees: Environmental control and molecular mechanisms. Plant, Cell and Environment 35:1707–1728.

Davies, T. J., E. M. Wolkovich, N. J. Kraft, N. Salamin, J. M. Allen, T. R. Ault, J. L. Betancourt, K. Bolmgren, E. E. Cleland, B. I. Cook, T. M. Crimmins, S. J. Mazer, G. J. McCabe, S. Pau, J. Regetz, M. D. Schwartz, and S. E. Travers. 2013. Phylogenetic conservatism in plant phenology.

Fitter, A. H., and R. S. Fitter. 2002. Rapid changes in flowering time in British plants. Science 296:1689–1691.

Fridley, J. D. 2012. Extended leaf phenology and the autumn niche in deciduous forest invasions. Nature 485:359–362.

Gotelli, N. J., and G. R. Graves. 1996. The temporal niche. Pages 95–112 *in* Null Models In Ecology. Smithsonian Institution Press, Washington, D. C.

Hoegh-Guldberg, O., D. Jacob, M. Taylor, M. Bindi, S. Brown, I. Camilloni, A. Diedhiou, R. Djalante, K. Ebi, F. Engelbrecht, J. Guiot, Y. Hijioka, S. Mehrotra, A. Payne, S. Seneviratne, A. Thomas, R. Warren, and G. Zhou. 2018. Impacts of 1.5ºC Global Warming on Natural and Human Systems. In: Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of . Tech. rep., Cambridge University Press, Cambridge, UK and New York, NY, USA.

Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. Global Change Biology 20:170–182.

Polgar, C. A., and R. B. Primack. 2011. Leaf-out phenology of temperate woody plants: From trees to ecosystems. New Phytologist 191:926–941.

Richardson, A.D., O'Keefe, J. 2009. Phenological Differences Between Understory and Overstory. Pages 87–117 *in* A. Noormets, ed. Phenology of Ecosystem Processes. Springer US, New York, NY.

Vitasse, Y., S. Delzon, E. Dufrene, J.-Y. Pontailler, J.-M. Louvet, A. Kremer, and R. Michalet. 2009. Leaf phenology sensitivity to temperature in European trees : Do within-species populations exhibit similar responses? Agricultural and Forest Meteorology 149:735–744.

Wolkovich, E. M., and E. E. Cleland. 2014. Phenological niches and the future of invaded ecosystems with climate change. AoB PLANTS 6:1–16.

Yu, H., E. Luedeling, and J. Xu. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. Proceedings of the National Academy of Sciences of the United States of America 107:22151–22156.

Zohner, C. M., and S. S. Renner. 2014. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. Ecology Letters 17:1016–1025.