

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

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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 climate — high interannual variability

4. Cues — phenology

(a) Even day 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 the timing of species life history events—phenology—with average advances of 2.6-2.8 days per decade (Parmesan, 2007; Thackeray et al., 2016; Cohen et al., 2018). Phenological events and their responses to climate change, however, are highly variable. Events, such as leafout, can span a period of weeks in most communities and are shifting in response to rising temperatures at different rates (Parmesan, 2007; Fitter and Fitter, 2002; Menzel et al., 2006; Yu et al., 2010; Fridley, 2012).

Understanding and explaining this variability is an important goal that remains extremely challenging. Some degree of variability is likely due to differences in climate change itself across space—as some areas have warmed faster than others, potentially generating larger phenological shifts (Hoegh-Guldberg et al., 2018). Climate change alone, however, explains a limited amount of the total variation. In contrast, substantial variation is due to species-level differences in phenology (Vitasse et al., 2009; Wolkovich and Cleland, 2014; Zohner and Renner, 2014; Vitasse et al., 2018), but we still have a limited understanding of how these species differences compare to other potential sources of variation, including those at the population-level. Understanding the role and scale of species-level variation, however is necessary to predict future changes in phenology, and ultimately, its 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).

Different species often have unique phenologies—even within the same location and climate conditions. In varying the timing of their phenological events within a community, species can limit the overlap in their resource use and the extent of competition they experience. For example, in forest communities, understory species often budburst earlier than canopy trees, when light and soil nutrients are most available. This niche partitioning allows species to differ in their resource requirements

and responses to environmental conditions as they change across the growing season, ultimately filling different temporal niche (Gotelli and Graves, 1996).

While temporal niche differences allow more species to coexistence in a community, there is considerable evidence that they are also shaped by population differences. Phenology can be highly variable across populations and select for locally optimum trait phenotypes. This has been shown across many ecosystems, including for bird breeding phenology in montane meadows in Sierra Nevada, that differs by 12 days across high and low elevation populations (Saracco et al., 2019). How much of this variability is due to local adaptation or plasticity is still unclear. Across populations, we would expect the presence of strong population-level differences in phenology to indicate that local adaption is an important driver of variation.

While local adaptation can be inferred by comparing populations, teasing apart the effects of plasticity requires knowledge of species cue systems. Both animals and plants often have very similar cue systems, responding to variation in both temperature and photoperiod cues (Renner and Zohner, 2018; Bonamour et al., 2019). Across species distributions, we would expect to find spatial gradients in phenology in response to similar gradients in cues. Both temperatures and photoperiod vary across latitudinal gradients, potentially causing similar gradients in phenology.

To predict how communities will respond to continued climate change requires a holistic approach that accounts for the multiple drivers of phenological variability. For a given community, we must account for differences across species that shape their temporal niche. But this cannot be done in isolation of population-level variation. In conducting experiments in controlled environments, we can remove the relative effects of interannual climate variability and plasticity, allowing us to identify species primary cues. The use of recent phylogenetic methods also provides a means to account for climate variability during the long evolutionary timescales over which communities assembled (Davies et al., 2013).

Spring budburst offers an excellent system to test for species-level and spatial patterns in phenology and cue responses. Budburst of temperate woody plants is known to respond to temperature cues in both the winter and spring, referred to as chilling and forcing respectively, 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 the start of spring growth, with variation in the relative importance of individual cues across species. Phenotypic differences between species — such as functional groups and varying growth strategies — further promotes phenological differences and ultimately optimize species temporal niche within a community.

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. Using a phylogenetic approach allowed us to detect general trends in budburst cue responses in North American deciduous forest communities. We also explored community specific responses to 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.

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