

# 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, or phenology, across the tree of life. In synthesizing across diverse species and habitats, we find on average species phenologies have advanced by 2.6-2.8 days per decade (Parmesan, 2007; Thackeray et al., 2016; Cohen et al., 2018). Phenology is, however, a highly variable trait, with individual events often spanning a period of weeks in most communities and phenological shifts occurring at different rates (Parmesan, 2007; Fitter and Fitter, 2002; Menzel et al., 2006; Yu et al., 2010; Fridley, 2012). Some degree of this variability is likely due to regional differences in climate change, as some areas warm faster than others. But there remains a considerable amount of variation we have yet to explain (Hoegh-Guldberg et al., 2018).

In addition to considering the contribution of geographic factors to phenological variability, species-level differences are also important (Vitasse et al., 2009; Wolkovich and Cleland, 2014; Zohner and Renner, 2014; Vitasse et al., 2018). For many species, we have a limited understanding of their phenological cues and their relative importance across populations. But identifying the drivers of this important life history trait 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).

In varying the timing of their phenological events within a community, species can fill different temporal niche within a season (Gotelli and Graves, 1996). This can limit the overlap in species resource use and the extent of competition, promoting species coexistence and diversity. For example, in forest communities, 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 promote species differences in traits, like phenology.

Differences in species temporal niche can also arise from varying environmental conditions. Within a population, we expect traits like phenology to undergo local adaptation to both environmental factors, in addition to selection from biotic interactions, like competition. Despite species expressing the same underlying phenology, climate cues can be highly variable across years and therefore select for locally 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 phenology in response to similar gradients in cues. Both photoperiod and temperatures vary across latitudinal gradients, possibly leading to similar gradients in phenology.

To predict how forest 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 as shaped by their phenotypic variation and local biotic interactions. But this cannot be done in isolation of species distribution and biogeography. In conducting experiments in controlled environments, we can remove the relative effects of interannual climate variability and 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, 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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