

1 Evolutionary history—more than phenological cues—explain 2 temporal assembly of woody plant communities

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10 Introduction

11 1. Climate change — phenology — variability

12 (a) Paragraph 1

- 13 i. Climate change shifting phenology
- 14 ii. Give example of range of climate change, or the mean etc
- 15 iii. High variability
- 16 iv. Some of the variability — regional warming could explain

17 (b) Paragraph 2

- 18 i. But not enough — species variable
- 19 ii. Why care? — forecasting and ecosystem services

20 2. Why spp may vary

21 (a) Within a community several weeks for diff spp

22 (b) Introduce temporal niche

- 23 i. resource competition
- 24 ii. understory trees

25 3. Does population matter too?

26 (a) Phenology differs in different places

27 (b) Population differ — local adaptation to environment and spp in community — truly different 28 phenology

29 (c) Same underlying phenology but different climate — high interannual variability

30 4. Cues — phenology

31 (a) Even doy varies — animals and plants have identical cue systems — cite Bonamour

32 (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 variation (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 importance across populations. But identifying the drivers of this important life history trait is necessary to predict future changes, and ultimately, 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 competition for limiting resources and persist within a community. 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 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 underlying 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 phenology in response to similar gradients in cues. Both photoperiod and temperatures 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 species distribution and the local adaptation that individual populations may exhibit. By identifying the primary cues for a given phenological event, we can conduct experiments under controlled conditions and remove the relative effects of interannual 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 individual 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.

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