Evolutionary history and not phenological cues explain temporal assembly of woody plant communities

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September 25, 2023

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Introduction

1. Plant phenology is changing with climate change:
   (a) Timing of spring bb is changing with anthropogenic climate change
   (b) But changes are not uniform with some regions experiencing greater warming than others.
   (c) Responses are also species specific and highly variable
   (d) Budburst in forest communities is the product of species differences as well as geographic variability in environmental cues.
   (e) Understanding the relative importance of these different drivers of budburst is needed to understand and predict future changes in spring phenology—and their ultimate impacts on growing season length, carbon cycle, species interactions
2. Cues that shape bb
   (a) For woody plants, we do know there are three important environmental cues for bb:
      i. Forcing: spring temperatures
      ii. Photoperiod/daylength
      iii. Chilling: winter length and temperatures
   (b) But these cues interact—forcing can offset low chilling—photoperiod offsets weak forcing (Heide1993, Chuine2000, Caffarra2011, Flynn2018)
   (c) The consistency and strength of these interactions across species and populations remains unclear.
3. Cues can vary geographically and temporally—under future climates—likely to create differences in community dynamics and species composition.
   (a) Increasing winter and spring temperatures = faster accumulation of chilling and forcing (Guy2014)—associated with earlier budburst in many temperate plant species.
   (b) Could create novel niche space early in growing season—facilitating spp invasions or novel community assemblages

   (c) Will also reduce fitness in spp with strong photoperiod cues = limited in their ability to advance (Korner2010) = different competitive landscape later in the growing season
   (d) Differences in species cue responses are likely to shape the diversity and persistence of species across forest communities.

4. Variation in bb phenology across species in a community
   (a) Timing of bb in a forest community can span several weeks—species fill different temporal niche
   (b) e.g. understory shrub spp tend to bb earlier than canopy species, likely reflecting overarching differences in growth strategies.
   (c) But differences in budburst responses are likely to also exist across a species ranges—need to know the relative effects of pop vs sp

5. While climate change may cause climates to shift rapidly, forest communities have assembled over longer timescales, with traits like phenology responding to local conditions.
   (a) Across a species' spatial distribution—we can expect to see differences in both cues and therefore in spp responses in bb that have evolved over time
   (b) Species with large latitudinal distributions experience differences in cues—e.g. photoperiod cues
   (c) But few studies have explored how cue use may differ across spatial gradient for the same forest communities and the role of local environments and biotic communities in shaping budburst across North America.
   (d) To better predict how forest communities will respond and assemble under continued climate change we need to identify the cues that drive budburst in our dominant forest species and functional groups, and how these responses can change across populations.

6. In this study 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.

1 Brainstorming—Main takeaways

1. Population effects were negligible—both across transects and latitudes—weak local adaptation
2. But spp vary a lot—not by functional groups—phylogeny
3. Temporal community assembly—not result of habitat selection—niche partitioning best explained by phylogeny—may be selection on other traits physiological constraints—e.g. competition, water availability, etc selecting for leaf traits
4. Also our observed cue responses were in line with prev obs—chilling strongest, photo weakest, but strong interaction btwn cues

Discussion

Temporal assembly across North America

1. While our western and eastern forest communities differ in both their species composition and local environments—only small differences in budburst phenology or cue responses across populations
   (a) Expected local adaptation = differing selective pressures across populations = leading to differences in cues responses across populations
   (b) But we only observed slightly earlier budburst in our eastern populations when compared to western populations (Fig 1).
   (c) Also found no latitudinal gradients across populations despite differences in local photoperiods (Fig **??**)—contrasts previous work in which poleward populations were later (Lieth1974, Zettlemoyer2021)
   (d) Lack of population level trends suggests the drivers that shape the timing of budburst are not driven by geography alone.

Community composition and interspecific variation in phenology

1. In taking a community approach—able to examine these relationships at the species level—see high variation in species cue responses
   (a) Species varied in the timing of budburst—early to late budbursting spp span a similar period as natural communities (Maycock1961)—suggesting that our experiment captures a realistic breadth in phenology within our forest communities
   (b) Generally—all species showed some cue response—earlier bb with stronger cue
   (c) Cues consistent with previous studies—ie.chilling being strongest, photoperiod weakest, but complex interactions between cues—eg Flynn2018, Heide1993, Caffarra2011
   (d) May be an important adaptation under future warmer winters when chilling might be insufficient and higher forcing needed to offset it
   (e) While spp do differ in cue responses, identifying general trends cue responses across assemblages of species remains challenging.
2. Shrub and tree species differ greatly in their physiology—filling unique ecological niche—but we found little variation in their cue responses on a whole.
   (a) Most tree species budburst later than shrubs species—in line with previous work—earlier bb in shrubs compared to trees (Panchen2014, Yu2015)

(b) But about a quarter of tree species did show earlier budburst dates and a third of shrubs budburst later than expected—suggesting more nuance than previously found—advantage of us having such a large assemblages of species

(c) As trees advance phenologically—with earlier canopy closure and reduced light predicted (Donnelly2019)—some less responsive shrubs will experience reduced fitness—but our finding suggests many have similar cue responses and the capacity to maintain their relative temporal niche space.

(d) Provides novel insights into how species in the understory and canopy layer may respond differently to changes in temperature cues and which species are likely to experience the greatest declines in fitness

Community assembly in responses to cues versus evolutionary history

1. In addition to improving our ecological understanding of budburst phenology at the community level—our results illustrate the critical role of species' evolutionary history in shaping this trait.

   accounting for the effects of species' phylogeny highlighted the critical role evolutionary history plays in shaping this trait.

   (a) In accounting for the effects of species' phylogeny, we found a high level of phylogenetic relatedness amongst clades of species in the timing of budburst.

   (b) This is reflected in the high proportion of variation in bb explained by species' level effects and relatively weak contribution by our three cues (Fig 4)

   (c) Suggests species' budburst is constrainted by their evolutionary history and not as strongly shaped by current environmental conditions as we would expect.

   (d) This phylogenetic niche conservatism is surprising—given phenology is thought of as a highly plastic trait, with local conditions expected to drive variation in the type and magnitude of cue responses

   (e) May be evidence of phenotypic attraction of similar, more closely related species in temperate forests.

   (f) But could also be an indication of limited evolutionary time—some temperate species, like *Nyssa* and *Fagus* have had a shorter geologic time in which to adapt to temperatures

   (g) Concerning—as it could limit species' ability to respond to changing climates and future community dynamics

2. Ecological communities are thought to be shaped by habitat selection—spp that withinstand local abiotic conditions persist—and phenotypic repulsion—limiting niche overlap and competition—but seems not to be the case for species temporal niche (or spring temporal niche?)

   (a) While spp in our forest communities varied in their timing of bb by several weeks—the similarity in temporal niche variation across populations suggests strong phylogenetic niche conservatism and stabilizing selection with little change in phenology in response to local habitats

   (b) This is despite communities having very unique regional spp pools—western community dominated by shrub spp vs eastern communities with more canopy tree spp

   (c) Indicates that cues we think are important for bb may also be selecting for other functional traits—such as traits related to light capture and photosynthesis or nutrient uptake

   (d) Exploring how suites of other triats contribute to species cue response could = greater insights into the mechanisms driving species temporal niche

Predicting budburst phenology under future climates

1. Currently = limited understanding of spp sensitivity to environmental cues and how they interact (Chuine2017, Ettinger2020)
2. Community wide approaches such as ours = critical bc greater diversity of spp and insights into how communities as a whole will respond
3. We address many of the challenges to predicting species responses to further climate change—complexity of regional and increasingly variable seasonality
4. Our findings also highlight the importance of species evolutionary history in shaping budburst—concerning as these ancestral constraints on spring phenology may limit species' ability to respond to climate change
5. to forcast future changes = require further work to know what traits or other cues are contributing to high spp variability