

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

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10 Discussion

11 Quick overview

- 12 1. In our study of woody plant budburst phenology across North America, we found the assembly
13 of species' temporal niche to only be partially explained by environmental cues and population
14 level variation.
- 15 2. Within a community, there was considerable species level variation.
- 16 3. Evidence of a strong phylogenetic structure to the timing of species bb

17 Temporal assembly across North America

- 18 1. While our western and eastern forest communities differ in both their species composition and
19 local environments—only small differences in budburst phenology or cue responses across popu-
20 lations
 - 21 (a) Expected local habitat selection = differing selective pressures across populations = leading
22 to differences in cues responses across populations
 - 23 (b) But we only observed slightly earlier budburst in our eastern populations when compared
24 to western populations (Fig ??)—such negligible differences could be due to differences in
25 the methodologies used—eg differences in timing of sample collection or the slightly greater
26 levels of chilling eastern spp experienced as a result
 - 27 (c) Also found no latitudinal gradients across populations despite differences in local photoperi-
28 ods (Fig ??)—contrasts previous work in which poleward populations were later (Lieth1974,
29 Zettlemoyer2021)
 - 30 (d) Lack of population-level trends suggests the drivers that determine the timing of budburst
31 are not shaped by current geography, at least at our continental scale

Community composition and interspecific variation in phenology

1. We found 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
 - (c) Cues responses were consistent with previous studies—ie.chilling being strongest, photoperiod weakest, but complex interactions between cues that are advantageous under warming climates (???)
 - (d) While spp do differ in cue responses, we did not find the clear, generalizable trends we expected across species with similar growth strategies.
2. Shrub and tree species differ greatly in their physiology—filling different 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 = earlier budburst dates, more similar to the timing of shrub species, and a third of shrubs budburst at similar times as trees —suggesting more nuance to this 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 are likely to also advance with warming with the potential to maintain their relative temporal niche space.
3. Given the number of shrub and tree species exhibiting uncharacteristic budburst phenologies—suggests cues we think are important for bb may also be selecting for other functional traits
 - (a) Selection for earlier budburst may correlate with traits related to light capture and photosynthesis in understory shrub species or nutrient uptake in trees associated with early successional stages or disturbance.
 - (b) The fitness of species across different temporal niche = determined by species overall suite of traits— but currently we lack a sufficient understanding of the the underlying mechanisms
 - (c) By incorporating phenology into a broader trait framework = greater insight into the considerable variation observed within species functional groups.

Community assembly in responses to cues versus evolutionary history

1. With continued warming, our ability to predict the timing of spring growth will depend on our understanding of cue responses at the species and community level.
 - (a) Within a community, species varied in their timing of bb by several weeks— but the similarity across populations suggests strong niche conservatism and stabilizing selection with little change in response to local habitats
 - (b) While the effects of population level variation on cue responses appears be negligible, individual species within community assemblages do differ in their responses to cue (Fig 5).
 - (c) Species' budburst responses were dependent on the magnitude of cues—populations that are warming at a faster rate = strongest bb advances and changes in spp bb order (Fig 5 & S4)—altering community dynamics and species interactions.

- (d) But we can't simply focus on current cues—species current phenotypes are the result of multiple interacting and complex environmental cues that have shaped species over evolutionary time scales (Ackerly2009).
2. The high degree of phylogenetic relatedness among species suggests that species with shared ancestry, and presumably more similar phenotypes and growth strategies, exhibit similar timing in budburst.
- (a) A high proportion of variation in budburst is explained by species' level effects, with cues only explaining about two-thirds of variation in budburst (Fig ??)
- (b) Our study applied extreme differences in cues to test for responses—useful for longer-term predictions/parameterizing process based models—but variation due to phylogenetic structure likely underestimated
- (c) Surprising evolutionary history has such a large effect—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
- (d) But it indicates we are not accounting for other key drivers of spring phenology—additional cues or functional traits—limiting our predictive abilities.
3. The evolutionary history and ancestral phenotype of a species has the potential to effect their ability to adapt to future climates.
- (a) Could prevent adaptation to new environmental conditions, if spp are physiologically constrained by their ancestral, optimum phenotype
- (b) Potential for processes occurring across different time scales to be strongly interdependent—the evolution of traits shaped over 'deep' timescales is influencing species' abilities to respond to several decades of climate change.
- (c) Constraints could skew species assemblages, favouring spp with traits adapted for warmer climates—lower chilling and photoperiod requirements—better able to track and benefit from future climate conditions
- (d) But could also indicate limited evolutionary time—some temperate species, like *Nyssa* and *Fagus* have had a shorter geologic time in which to adapt to temperatures—especially in populations at northern range limits.
- (e) Identifying how and to what extent latent traits contribute to the phylogenetic structuring of temperate forest communities = unknown, but important if we are to predict how communities will respond to continued changes in climate.

Predicting budburst phenology under future climates

1. Our results provide new insights into the key factors and ecological processes that are critical to forecasting future phenoloiges under climate change.
- (a) Provides evidence that changes in budburst cues will produce consistent trends across populations—allowing us to forecast across populations for which we have limited local phenological data but similar species assemblages.
- (b) The high phylogenetic structure in budburst timing also allows us to use our existing knowledge of species' phenological cue responses to forecasts trends in phylogenetically related species.
- (c) But must also be cautious in our assumptions—as we did not find strong general trends at coarser taxonomic groupings (shrubs vs trees)—the number of exceptions within tree and shrub functional group suggests still selective pressures shaping bb we do not understand.

- 119 2. Our ability to predict changes in spring phenology and mitigate the cascading effects on forest
120 communities is increasingly urgent in light of anthropogenic climate change.
- 121 (a) Requires community wide approaches such as ours—one of the first to include these three
122 types of drivers at a large geographic scale and across forest communities.
- 123 (b) Critical bc provides greater diversity of spp and insights into how communities as a whole
124 will respond
- 125 (c) to forecast future changes = we need to identify the key underlying ancestral traits that
126 link species' evolutionary histories and are driving the high spp variability observed within
127 temperate forest communities.