Concept paper on understanding interactive cues and climate change (with growth chamber studies)

How interactive cues will shape climate change responses

Limiting cues: How spring warming, winter chilling and daylength will shape climate change responses

Spring warming, winter warming or daylength: What cue will be most limiting in future tree phenology?

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Abstract

Climate change has shifted plant phenology globally, with average shifts of 4-6 days/°C and some species shifting several weeks. Globally, such shifts have been some of the most reported and most predictable biological impacts of climate change. This predictability comes from decades of research, which have outlined the major cues that drive most studied plant phenology: temperatures (including spring warming and winter chilling) and daylength. Further simplifying predictions, spring temperatures are often the dominant cue in nature, making linear models of heat sums often excellent at predicting interannual variation in phenology. Yet as climate change has marched on, new research has uncovered failures to predict the current observed changes, with many shifts appearing more muted over certain time periods or in certain locations. Here we argue that such inaccurate predictions are most likely due to simple models that neglect to consider other major cues—especially winter chilling and daylength, which moderate and shape plant phenological responses to spring warming. We highlight how over 60 years of research in controlled environments can improve predictions for when, where and how the interactive effects of other cues will impact simple linear predictions. Finally, we discuss how a new generation of controlled environment experiments could rapidly improve our predictive capacity for woody plant phenology in coming decades.

Main message (and, really, it's important): if you want to project climate change impacts, you need to focus on relevant changes in all three cues. The relevant changes part is about comparing cues, the all three cues is about interactive cues.

Keywords: phenology, climate change, spring warming, forcing, chilling, daylength, photoperiod, non-linear responses, leafout, budburst

Questions, which are in addition to notes in orange throughout and general thoughts/ideas for improvement! Thanks for all your help!

1. Should we finalize that we won't do the PhenoFit figure? As a reminder, the plan was to calculate the current forcing, chilling, photoperiod and the future of each of these. But we don't have the climate data....

2. Can we suggest where cues other than forcing are most critical? Perhaps at least for our focal spp.? If so, where would we add this (1.c)?

   (a) If we know where a non-linearity is in a cue (e.g., from experiments of models), then wherever you're near that on a range, you should expect bigger effects of that cue.

   (b) Maybe where chilling will change to above versus below the threshold that plants can sense.

3. Is the intro too long? If so, please suggest ways to cut and/or re-arrange. (I have moved our PEP725 species outside of the intro, please let me know if you think it works).

4. I wrote this below (it's commented out just now): Unlike budset phenology, research suggests spring phenology is fairly plastic (without high variation in cues across a range); this means species need a set of cues that work across their range ... which got me to wondering: can we explain why cues show so little local adaptation across species ranges?

Outline

1. Introduction

   (a) Shifts in spring phenology are one of the most reported and most predictable changes with climate change

       i. Review the shifts across space and time and how coherent they are

       ii. Outline some studies showing how predictable they are (Schwartz 1997; Ellwood et al. 2013)

       What other citations/examples can we add?

   (b) Recently however predictions have started to fail in certain places or over certain time periods

       i. Yu et al. (2010); Fu et al. (2015)

       Suggest other citations please!

       ii. The main hypothesis for this failure is other cues most observational studies have ignored

(c) There has been a lot of focus on forcing but really it's more complicated

    i. For many species three major cues drive spring phenology: forcing, chilling, daylength

    ii. Research in this has been especially strong for woody species phenology: this is where we understand things best and thus our main focus here, though much of what we say could apply to non-woody species with similar cues (cite *Arabidopsis*).

> What other herbaceous species can we cite here? Should we touch on seed germination?

    iii. These cues may create critical non-linear responses that most current methods cannot predict.

(d) However, measuring these cues and thinking about how they will interactively produce future phenology is hard because:

    i. They are expected to interact; cues may compensate for other cues; meaning they mask one another (e.g., chilling cue not fully being met could look like a photoperiod requirement that has not been met)

    ii. They vary across species (and possibly within species across the range, but see below)

    iii. They are hard to measure.

    iv. To some extent, we haven't really had to measure these other cues to get decent predictions for lots of places and years

(e) But if evidence is rising that these cues are critical, how do we integrate them more into phenological research? Step 1 is clearly to figure out how to robustly measure them.

    i. Methods especially lame at understanding these cues (and thus predicting non-linearities): models from long-term observational data ... somehow mention experiments maybe?

    ii. Comment on the two issues at play here: the data type (e.g., long-term) versus the model type (e.g., linear and sans interactions?)

    iii. The one method designed to look at all these cues is controlled environment (generally growth chamber) studies

(f) Growth chamber studies

    i. Can manipulate all three cues (and even more, humidity etc. nod?)

    ii. Are often focused on interactions (unlike other methods)

    iii. Have been done *forever*. But oddly, never really reviewed.

    iv. ...and are often poorly integrated into current climate change literature. Including debates where they are critical, like about photoperiod.

(g) Our aim is to:

    i. Review how three major phenological cues for woody plant phenology will shift in coming decades with anthropogenic climate change

    ii. Review of the three major phenological cues from growth chamber studies over the past 60 (70?) years

    iii. Compare treatments from controlled environment studies to predicted shifts in cues with climate change.

    iv. Showcase how growth chamber studies can be best designed to better understand these interactive cues (paths forward).

2. To understand cues, it helps to think about the environmental variation a species experiences across its range

    (a) Think about two example tree species: *Fagus sylvatica, Betula pendula*

    (b) Look at their distributions

    (c) In the spring there is selection for species to track the start of resources, and thus they need cues that work across the interannual variation in climate *across a species' range*

    (d) Thus, cues are adapted to high climate variation!

> New term: Cue range limits. What do you think? As in the limits of cues as seen over a species' range, what do you think?

    (e) This is why most temperate species probably have responses to all three cues: forcing, chilling, photoperiod

3. Review how cues will shift with climate change (here we show the figures that Nacho has produced for two PEP725 spp.)

    (a) Forcing: the world will get warmer

        i. Higher altitude and arctic places will warm more

        ii. Give range of warming depending on different scenarios

        iii. Minima (night-time temps) generally warm more than maxima (but not everywhere, see what Yann mentioned)

        iv. Different seasons may warm differently

    (b) Chilling, see forcing but ...

        i. Chilling only occurs between certain temps so some places accumulate more chilling with warming

        ii. And there is so much we don't know about how chilling works and interacts with forcing (sequential model, parallel models etc.)

    (c) Photoperiod: Shifts with phenology

      i. Changes in forcing and chilling will alter the photoperiod that matters so to speak

      ii. Note that although daylengths themselves won't change with cc, the photoperiods experienced by organisms are likely shift as ranges shift and phenology shift (cite our other paper?)

4. Compare treatments from controlled environment studies to predicted shifts in cues with climate change: Part I: Review of the three major phenological cues from growth chamber studies over the last 67 years

  (a) Be sure to note that most studies were *not* done for climate change research, they were done for fundamental science or agricultural purposes

  (b) Quick intro to the data, how long, which cues ....

      i. Fig: Number of studies by year (OSPREE)

      ii. Fig: Map of studies, color coded or such by which of the three cues they manipulated

> Any other reasons for most woody species phenology growth chamber studies?

  (c) For each of the three cues:

      i. X% of studies manipulated that cue

      ii. Variation across latitude (and hemispheres?), continents, and time (and species)?

      iii. Fig: Variation in treatments across space (photo/chill/force)

      iv. Fig: Variation in treatments across time (graph with year on x-axis or divide time in half or such?

      v. Say something about material (seeds/saplings/cuttings)? Can we tie to relevance of predicting future forest communities or such?

  (d) X% of studies manipulated which interacting cues? (i.e., how many studies manipulate 1 cues, 2 cues, 3 cues ... of those manipulating 1 cue, what is the breakdown by cue etc.)

5. Compare treatments from controlled environment studies to predicted shifts in cues with climate change: Part II: What cues will be most limiting with climate change? How do controlled environment studies compare?

  (a) Consider both the range of a species and the climate change projections ...

      i. Take each PEP725 datapoint within our selected species' range and calculate:

        A. Min daily temp for 1-2 months before leafout (Nacho's figures)

        B. Max daily temp for 1-2 months before leafout (Nacho's figures) [1]

      ii. Add potential PhenoFit figure here? 3D of all three cues and how they shifted?

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[1] We used daily min/max, as they're most directly comparable to OSPREE.

6. Paths forward (showcase how growth chamber studies can be best designed to better understand these interactive cues in regards to climate change forecasting)

> I think this section needs the most help! We have a lot of points and I think we need to clarify them and cut some probably.

  (a) If you want work to be most relevant to climate change, then consider the following when designing experiments:

      i. The cues with the current vs. future range of a species (as we did above) to inform experimental range

      ii. If you don't work within the range or projected cue range limits of a species, then consider working on informative extremes...

      iii. Thus you may consider thermal tolerances/limits (and where is the species optimum?) ...These tests could be especially useful for understanding range limits: look at treatments beyond the variation seen within a species' range and see if there is abrupt change or you see continuous change, if no abrupt change then it may suggest that something else must limit range (e.g., biotic cues, minima temperature after which species)

      > I like this but worry it feels too far afield. Can we rein it back in or is it okay or should we slim it down?

      iv. After you carefully select the cues to study, make your reasoning clear

      > Do we need this? AKE says no.

  (b) Manipulating one cue may be less useful, esp. if we want to advance comparisons with long-term data

  (c) Major need to better understand deviations in long-term data are: better non-linear models for more species. How best to do this?

      i. Studies using only long-term observational data must test for and be up front about correlations in predictor variables (e.g., chilling, forcing and daylength often covary) and thus what they can and cannot rule out.

      > Do we need this? And/or are there any ways to untangle cues using long-term data?

      ii. A better option than just long-term data are more efforts to integrate long-term data with growth chamber studies (cite Caffarra, Chuine suggestions, Ford et al. 2015)

          A. Studies that test the extremes are needed to parameterize models (ideally you need to know where the zeros are).

          B. Traditional methods to hold-out data and test how well the model performs

          C. Use growth chamber studies to test model predictions, especially in future climate scenarios where non-linearities are predicted.

D. Improving models means more back-and-forth worth between developing models based on both long-term data and experiments, then testing predictions with new experiments and as newer observational data are generated (i.e., more years and also data from new locations)

(d) Hanging chads in the 'Paths forward' section:

    i. Now that climate change is here, experiments that want to claim climate change relevance must address what the cue impacts of climate change will really be

    ii. Studies not interested in climate change forecasting can still contribute—with little effort—to progress in this area by: Reporting all cues (even the ones you don't measure) so they can be used in modeling efforts.

    iii. Introduce Bayesian hierarchical modeling within this framework? Within PhenoFit?

7. Wrap-up: Climate change: it means all that work on phenology comes due ... now!

(a) If we could better harnass the power of growth chamber studies it could... transform our understanding and forecasting

(b) Rule out or in hypotheses to explain observed discrepancies (move away from trying to tease out cues using only correlated long-term data)

(c) Contribute to more models being developed and improved, which could contribute to global land surface models, community predictions etc.

(d) Need more here! What will doing what we suggest change about the world?

Figures

1. PEP725 spp. 1980 figures

2. PEP725 spp. Future figures

3. Number of studies by year (OSPREE) *Other ideas?!* Such as, number of species studied by year. Show crops or remove or show separately?

4. Map of studies, color coded or such by which of the three cues they manipulated

5. Variation in treatments across space (photo/chill/force)

6. Variation in treatments across time (graph with year on x-axis or divide time in half or such?

7. Not a figure, but analysis-related: X% of studies manipulated which interacting cues? (i.e., how many studies manipulate 1 cues, 2 cues, 3 cues ... of those manipulating 1 cue, what is the breakdown by cue etc.)

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