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RH: Phenological tracking

Phenological tracking in communities in stationary & non-stationary environments

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Abstract

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Abstract

Super dry, but better to have something ... I think. Predicting community shifts with climate change requires fundamental appreciation of the mechanisms that govern how communities assemble. Much work to date has focused on how warmer mean temperatures may affect individual species via physiology, generally producing shifts in the species' ranges and phenology and documenting high variation in the magnitude of shifts across different species, which fails to predict the wide diversity of observed shifts. This has led to a growing appreciation that improved understanding will require understanding the direct and indirect consequences of these shifts for species and their communities. Here we review how temporal variability in the environment affects species persistence in stationary environments, extending theory to understand how a species ability to track the environment may affect their long-term persistence in communities. We then discuss how non-stationary environments may fundamentally alter these conclusions with a focus on how climate change has altered the start of the growing season. Finally we review how the reality that change has and is expected to affect far more than mean temperatures, including widespread affects on growing season length, variability and shifts in extreme events may complicate simple predictions of winners and losers with climate change.

Note from meeting, lab meeting etc.

- Check out trade-off figures are intuitive (for example: the trade-off of tracking and R* is intuitively negative but it's positive because a lower R* is better and a higher α is better).
- what would happen if we increase variance (leave mean unchanged): trackers would win
- My current plot of three different season resource pulse is too correlated (change if we decide to use it)
- Question: how important is tracking the environment vs pure resource competitive ability in determining coexistence?
- What is the trade-off of tracking is that youre too sensitive tracking covaries with mortality. Is this where variability would be bad?
- Framing: people think of tracking as a trump card but really its part of coexistence theory already, and can be outmatched by other species attributes, but with climate change, will it become more important?

- Has climate change made tracking more advantageous? Or, how prevalent is tracking in a stationary versus nonstationary system? Basically, one hoped-for outcome (by Lizzie) is to show that with stationary climate tracking strategies and non-tracking strategies may coexist happily, but when you add nonstationarity the world shifts that tracking is so strongly favoured as to make non-tracking rare or to require a very huge trade-off etc.. So we have a bunch of related questions to this:
  - How big do trade-offs have to be for tracking to be non-advantageous (to allow coexistence with other species)?
  - Another angle, is tracking the dominant strategy with a shifting environment (distribution) vs. stationary environment distribution?

Outline

Possible titles: 'Phenological tracking: It's more complicated than you think' (we hope) or 'Phenological tracking: Is it naive?'

So, there's a pretty basic structure to what we want to walk through:

1. Direct and indirect effects of climate change are shifting species (and communities)
2. Understanding these variable responses of communities and species due to climate shifts is a major aim of current ecology.
3. Phenology has been implicated in driving this
4. The theory goes that as seasons get earlier, earlier species win out over later species (don't get into tracking yet)
5. Yet no one to date has ever examined whether this hypothesis is supported through community coexistence theory and models
6. Understanding how plant communities will respond to climate change requires synthesizing information on both direct effects of climate on species and indirect effects driven by responses to other species' shifts.
7. Coexistence models based on variable environments allow us to do this
8. Models of community assembly in ecology build upon coexistence via environmental variability.
9. As species respond to shifting resources, which are influenced both by abiotic stressors and the use of the resource by other species.

10. More intro

    (a) Things that will shift with climate change, related to coexistence models

        i. Magnitude of and interannual variance in resource pulse ($R_\theta \downarrow$, e.g., in systems started by a pulse of water from snowpack)

        ii. Timing of resource pulse... τ_P gets earlier (i.e., start of season gets earlier)

        iii. Abiotic loss rate of resource ($\epsilon \uparrow$, i.e., it gets hotter and resources like water evaporate quicker)

        iv. Of these, changes in τ_P are aguably the most observed and should be most important to impacts on coexistence via phenology thus we focus on how shifts in τ_P impact coexistence.

    (b) Species traits and climate change: phenological tracking

    (c) **It would be great to add real data here!** Some options: First, Lizzie may be able to track down information about negative correlations between tracking and competitive abilities (for nutrient resources). This would put some of the trade-off questions in perspective. Next, we could also see *what we know about climate projections* and from there see how big do the trade-offs have to be with climate change to make non-tracking a feasible strategy strategy (this 'feasible' and 'dominant' terminology is a little wobbly; I admit that)?

    (d) Goals of paper

11. Model description: note that our model explicitly considers how within and between year dynamics can drive coexistence

    (a) Basic storage effect model

    (b) Our version of the storage effect model

    (c) Systems for which model is applicable: This is effectively a system with a single large pulse of resource, that, in a plant-free scenario, is lost exponentially each year: alpine where snowpack meltout is start of season (SOS), nutrient turnover SOS and some precip controlled systems with just one pulse.

    (a) Alpine systems (resource is water): initial large pulse of precipitation from snowpack that gradually is used up throughout season

    (b) Arid systems? (resource is water): Major pulse of rains (okay, spread out some, but really they often concentrate for a couple months and then season continues for 3-4 more months)

    (c) Temperate systems (resource is nutrients): Work with me here, I think this is cool. Early in the season turnover of microbes leads to a huge flush of nutrients (**?**) that microbes (and plants) draw down all season. There's no other pulse really—am I crazy here or doesn't this work well? (And so microbes draw it down in the plant-free case which could easily be affected by climate change, e.g., increased temperatures lead to increased microbial activity and more rapid draw-down.)

12. Systems it probably doesn't work for: Light-limited systems (there is not a single, plant-free decreasing pulse of resource), Great Plains or others with multiple pulses.

13. Phenological tracking and the storage effect

14. Our implementation of tracking

15. In *stationary environments* ...

    (a) Describe R* and how species with lower R* always wins (intra-annual dynamics generally) ... need other axis of competition for coexistence

    (b) Moving onto interannual variation: in temporally variable environments species with τ_i closer to averae τ_P should always win

    (c) For variation in τ_i to exist, need other axis of coexistence (such as R*)

    (d) But what if τ_i is not a fixed species attribute? Introduce tracking...

    (e) Then speices with higher α should win

    (f) Unless you have another axis of coexistence (such as R* or τ_i)

    (g) Note that this possible trade-off is earlier τ_i could correlate with lower competitive ability, which is mentioned in **?** on page 245: Coexistence would be promoted only when this temporal pattern entails tradeoffs, e.g., when later pulse users are able to draw down soil moisture to lower levels than are early users.

    (h) *Comparisons with competition/colonization trade-offs:* Can think of trade-off as competition-colonization one: rapid response to resource availability (colonization) versus special case of competition.

16. In *nonstationary environments* ... (need some help with phrasing) Under a non-stationary environment of earlier τ_P how: (1) does this trade-off change and (2) do communities change?

    (a) Earlier τ_i is favored more (R* versus τ_i runs: previously these coexisted via a higher R* and less ideal τ_i)

    (b) Tracking is favored more ... or effective τ_i is really favored more (τ_i vs. α runs)

    (c) Tracking is favored more (α versus R*)

17. But this all assumes that nonstationarity happens on only one dimension of the environment; just like species niches, the environment is multidimensional and nonstationarity in it may be multidimensional also.

(a) Show what happens when R0 get smallers as τ_P gets earlier

18. And, we conclude.

19. A little on how we do this:

    (a) We consider the effects of climate variation with a model that considers dynamics at both the intra-annual and inter-annual scale.

    (b) We look at how species traits related to their responses to climate variability effect coexistence and long-term persistence in the community maintenance. (This is the tracking part of the project.)

20. Random notes on real data we have and could add:

    (a) We should have the data to estimate the percentage of species that track, and the min and max tracking.

    (b) Some estimates of shifts in growing season length....

    (c) Data showing correlations between tracking and abudance given non-stationary climate (Question: how to think about experiments and non-stationarity)

    (d) Do we have data on trade-offs between competition and tracking?

Semi-outline from May 2017

Naive assumption: Trackers will always win; but not always the case in a stationary or non-stationary world.

1. In a stationary world (SW):

    (a) In a stationary world (SW) with no multispecies temporal niche: species with $min(\tau_i - \tau_{P.one.wold})$ wins.

    (b) Simple temporal niche: R^* trades off with τ_i (species with τ_i further from τ_P must have lower R^*.

    (c) Dynamic temporal niche scenario 1: with no difference in R^* among species, then the best tracker (α) often wins, with some nuance about τ_i ... i.e., $\tau_i - \tau_p$ versus $\hat{\tau}_i - \tau_p$ ... something that is weakly tracking may be out-competed by a species with a better mean τ_i. So we need to find cases where tracking does not beat out non-tracker.

    (d) Dynamic temporal niche scenario 2: R^* trades off with α ... and the more complex version where R^* trades off with α and τ_i combo: main point here is that what matter is $\hat{\tau}_i - \tau_P$

2. In a non-stationary world (NSW):

   (a) No multispecies temporal niche (just vary τ_i across species): with you shift from species $min(\tau_i - \tau_{p.old.world})$ to species with $min(\tau_i - \tau_{p.new.world})$ wins.

   (b) With dynamic temporal niche: consider just varying α, then species with $max(\alpha)$ wins.

   (c) What happens to communities that were coexisting via $R* - \alpha$ trade-off?

      i. Perhaps tracking can trump R^* ... Look at: cases where tracker outcompetes species with lower R^* in nonstationary simulations.

      ii. Maybe do runs with stationarity, then non-stationarity: this could tell you things like 'these species will stop coexisting or X% of runs now go extinct or this part of parameter space that was coexisting goes away first' ... we could also do runs with same params started non-stationary period and see if combinations become possible.

Some key refs we worked with: (**????**). Some papers using storage effect model or Armstong and McGhee with field data: (**????**).

Figures

1. Real-world data showing stat/non-stationarity in environment (ideally τ_P)
2. Real-world data showing tracking (and less tracking)
3. τ_P vs. R* trade-off and histogram of persisting τ_i under stat/nonstat τ_P environment
4. alpha vs.τ_i trade-off and histogram of persisting alpha under stat/nonstat τ_P environment
5. alpha vs. R* trade-off and histogram of persisting alpha under stat/nonstat τ_P environment
6. time-series of one run showing years where τ_i of one species is close to τ_P and other years where τ_i of other species is close to τ_P (and show this shift under nonstat)
7. non-stationarity in $R0$ and τ_P