RH: Environmental tracking

How environmental tracking shapes communities in stationary & non-stationary systems

1 Notes from November 2018 meeting

- Take home messages of paper:

  - 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?

  - For coexistence of species tracking must trade off with something else, in a stationary environment

  - τ_i and α are both useful ways to deal with stochasticity in a stationary envrionment ... show via stationary co-existing runs of τ_i x R* and α x R*

  - Stabilizing mechanisms, like a trade-off with tracking, do not survive (univariate) non-stationarity ... just equalizing mechanisms (and thus slow drift), instead trackers generally win. **Latter point: How to show?**.

  - Maybe say something about additional nonstationarity in other environmental factors

- Next steps ...

  - Megan makes runs with slope of bfin estimated for each species, so we can better identify equalizing versus stabilizing mechanisms. **This may work, but species that are super similar may drift slowly**

  - Lizzie should really start writing as there is no need to wait on non-stationary τ_p and R_0 runs. She also should consider whether we need the three traits varying runs (R*, τ_i, α) and whether we need the τ_i x α varying runs ... we may not! Main message to Lizzie: try to get stuck less often, or unstick more quickly

  - Megan does non-stationary τ_p and R_0 runs.

  - **Lizzie!** Analyze the megaD runs! (Just an aside)

- Where to submit? Maybe plan on ELE and do postulates etc..

2   Smaller to do items (less critical)

- 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).

- My current plot of three different season resource pulse is too correlated (change if we decide to use it)

3   Outline

Thinking on submitting as a R & S to *Ecology Letters*
"For this section of the journal, we are specifically interested in authoritative syntheses of important (and fast moving) areas of ecology. These can be quite flexible in terms of content, but typically include a strong quantitative component in the form of theory (simulation or analytical) and/or data synthesis (e.g., meta-analysis), and typically are somewhat broader in scope than a typical analysis for a standard paper."

And I said we would offer: "The complexity of phenological 'tracking' (how well species track environmental change), including the complexity in measuring it and how it may structure communities in stationary and non-stationary systems. We've been working on a version of the storage effect model that gives us some interesting insights via simulations and I think a Review Synthesis where we marry these results with some of the long-term and experimental data available now could help advance the field."

So ... new structure might follow this ...

1. Intro (including why you should care about environmental tracking).

2. What is tracking?

3. How variable is tracking? What predicts the variation?

4. How is the environment changing (not sure where this goes or how critical)?

5. What traits co-vary with tracking (trade-offs and the opposite of trade-offs ... syngergies?)

6. How does tracking affect community coexistence?

7. Major research questions to address now

New outline (as of June 2019)

1. Intro

2. What is tracking? (Including how much do species track?)

(a) Environmental tracking ... could be on abiotic or biotic cues. Ecology once focused on tracking mainly via stochastic interannual and intra-annual variation, but now much greater focus on it due to trends with climate change.

(b) How much do species track? How variable is it across (and within) species? Some examples ...

    i. plants on environment tracking

    ii. consumers on plants

    iii. consumers on consumers

    iv. mention hypotheses re: synchrony (if linked spp do track, then how do we have differences overall across trophic levels?)

3. What predicts variation in tracking?

(a) How does it work across cues and environments? (We're good at simple temperature, we're bad at drought/precip).

(b) Basic predictions about tracking ...

    i. Generation time (Perennials have greater sensitivities in our 2012 meta-analysis....)

    ii. Interannual variation in climate versus generation time

    iii. Gene flow? (See plasticity lit at bottom of file)

(c) Common and emerging mis-steps in measuring tracking (problem with temperature sensitivity or 'The trouble with tracking')

    i. threshold cues

    ii. days/degree

    iii. plots of plants, insects, birds on climate, and then the same insects/birds as trackers of their lower level

    iv. complexity in multicue species: multicue species may appear as single cue initially with warming ... snowmelt date versus temp and similar correlations

    v. space for time substitions (maybe check out: Critique of the Space-for-Time Substitution Practice in Community Ecolocy by Damgaard, downloaded)

    vi. biotic tracking (competition, predaction etc.)

(d) What traits co-vary with tracking (trade-offs and the opposite of trade-offs ... syn-gergies?)

    i. Meta-analysis of traits that co-vary with tracking (small, quick one)

    ii. Links to trait literature? Not enough study of traits that include tracking components (because that's hard)

        A. how much do people look at trade-offs?

        B. phenology can impact traits themselves, so how to analyse (competition experiments?

4. How does tracking affect community coexistence?

(a) Blah ...

5. Major research questions to address now

   (a) What does this mean for basic ecology? (1) Characterizing environmental distributions better (and fitness?): Putting years of study in context.

   (a) Blah ...

6. How is the environment changing (not sure where this goes or how critical)?

   (a) Transitions between stationary and non-stationary ... and what changes (mean, variance)

   (b) Contrast R0, epsilon and tauP?

   (c) Some examples

      i. Temperature records
      ii. Lake Washington
      iii. Snowpack records

   (d) Discuss how correlations between environmental variables may shift (i.e., shifting snowpacks from snow to rain control could cause shifts in correlations between timing and evaporation). ... Conceptual figure on snowpack and temp and what they mean for modeling (use synch data for temp? Could we do a quick search of ecological studies that look at snowpack?)

Stuff to fit in

1. Nonstationarity versus transient dynamics.

2. Nonstationarity now versus earlier in history.

3. Performance x tracking? Can we add in more data?

So, here's the 'pretty basic structure to what we want to walk through' from early 2019 (keeping for now):

1. Introduction

   (a) Climate change impacts

      i. Direct effects of climate change are shifting species: especially in space and time
      ii. But also many other effects of climate change, including possibly indirect effects – e.g., shifts in performance, changes in community structure

   (b) Environmental tracking and species interactions

      i. Environmental tracking has been implicated in underlying many indirect effects
      ii. The theory goes that as seasons get earlier, earlier species win out over later species

iii. With climate change, species that can track environmental change best appear to perform well with change also ...

iv. Lots of work on this....

v. Yet no one to date has ever examined whether this hypothesis is supported through community coexistence theory and models

(c) Coexistence theory

i. Coexistence models based on variable environments allow us to do this

ii. As species respond to shifting resources, which are influenced both by abiotic stressors and the use of the resource by other species.

(d) **Here we ....**

i. Review how current coexistence theory handles variable environments and...

ii. What predictions it makes for tracking in stationary environments

iii. In particular, 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.)

iv. Using a simple example, show how current models can be extended to non-stationary environments (similar to those due to climate change) to examine how changing environments alter predictons.

2. The role of the environment in coexistence:

(a) Models of community assembly in ecology build upon coexistence via environmental variability.

(b) Simple models require a resource pulse.

(c) To describe that pulse requires a timing and magnitude for it.

(d) Climate change has caused major shifts in the timing of pulses: changes in τ_P are often observed

(e) Such changes should be most important to impacts on coexistence, thus we focus on how shifts in τ_P impact coexistence.

3. The role of species traits in coexistence:

(a) Traits relate to optimum of timing of pulse τ_i and to resource use

(b) Species traits and climate change: environmental 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)?

4. Model description: We consider the effects of climate variation with a model that considers dynamics at both the intra-annual and inter-annual scale. So, our model explicitly considers how within and between year dynamics can drive coexistence

   (a) Basic storage effect model

      i. All species 'go' each year, at least a little; that is, we're not looking at communities where some species have true supra-annual strategies.

      ii. There is one dominant pulse of the limiting resource (e.g., light or water) at the start of each growing season; thus we model a single pulse per season.

   (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.

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

      ii. 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)

      iii. 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.)

   (d) 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.

   (e) Environmental tracking and the storage effect

5. In *stationary environments* ... Moving onto interannual variation: in temporally variable environments species with tauI closer to average tauP should always win... Competition/colonization trade-off.

   (a) How τ_i and α matter to coexistence

   (b) Somewhere say (perhaps): in temporally variable environments species with τ_i closer to averae τ_P should always win ... and same for tracking....

      i. **Are these effectively the same trait (so no trade-off possible)?** Right, NO trade-off possible, but it's not so much that they are the same trait, but they are trading off on the same species-response to the environment. ... things that we conceptualize as two different traits in a biological sense are the same mathematically (biologically you can imagine a trade-off between tracking and

fixed tauI (and in a broader fitness model, you could put energy in either place), but in this environmental space they both get you to the same space). It's the same niche axis!

    ii. In a stationary environment both are equally useful ways to match to the environment (what matters in the end is the total tauIP). In a stationary environment you can get the same outcome with either.

    iii. Having a $\tau_i = \tau_P$ is the same as having tracking=1

    iv. So, both can equally trade-off with other niche axes ....

(c) To get coexistence you need other axis of competition for coexistence.

(d) 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.

(e) Trade-off between τ_i with R*

(f) Trade-off between tracking with R*

(g) Here we expect the figures (alpha x R* and tau x R*) to look more similar ... **why don't they?**

6. *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.

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?

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

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

3. Tracking is favored more (α versus R*)

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. *Multivariate nonstationary environments*

1. Show what happens when R0 get smallers as τ_P gets earlier

Discussion

1. Quick review: Current models of coexistence are primed to help understand how a nonstationary environment, such as the one produced by climate change, will alter communities.

2. Trackers and non-trackers can coexist in a stationary environment.

3. Nonstationarity favors tracking species.

4. Things get more complicated in multivariate nonstationary environments

5. So this all leads to major questions in the field:

   (a) Critical question: What major traits does tracking trade-off with? Traits related to competition.... predator avoidence or tolerance ...

   (b) Critical question: How many abiotic aspects of the environment are changing? Abiotic shifts expected with climate change: single versus synergistic climate shifts

      i. We focused on τ_P getting earlier (i.e., start of season gets earlier), but there are other aspects of the environment, even in the simplest models ..

      ii. Magnitude of and interannual variance in resource pulse ($R_\theta \downarrow$, e.g., in systems started by a pulse of water from snowpack) ... note that sffects of climate change extend well beyond shifts in the mean

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

Random notes on real data we have and could add:

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

2. Some estimates of shifts in growing season length....

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

4. Do we have data on trade-offs between competition and tracking?

3.1   References to cite

Citation for earlier springs

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

3.2   Stuff to revisit at end of February 2019 meeting

- 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?

This tracking angle matches to the 'Generalists, specialists and plasticity' section of **?**. You could imagine by removing the benefit of trade-offs associated with not being plastic, then nonstationarity could favour generalists (plastic species, that is). Here's the most relevant bit (according to Lizzie):

> However, plasticity, or any generalist resource consumption behaviors, including those involving drought resistance, may come at a cost .... In such circumstances, there is no contradiction that a generalist can coexist with specialists so long as the specialists are in fact superior performers during the times or conditions that favor them, and there are some times when no specialists are favored so that the generalist is then superior.

3.3 Semi-outline to guide runs/plots 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.

4 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_i 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. (Scratch this one: we're pretty sure it required a crappy τ_i to survive the initial stationary period, then be favored in second time period and we're not so sure crappy τ_i species survive the initial stationary period) 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