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

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 ... overall structure tries to follow this ...

1. Intro (including why you should care about environmental tracking).
2. Environmental change ... Scales (within and between seasons, inter-annual variation versus trends), correlations among variables. (Includes answering How is the environment changing?)
3. What is tracking? (Includes: How variable is tracking? What predicts the variation?)
4. What traits co-vary with tracking (trade-offs and the opposite of trade-offs ... syngergies?)
5. How does tracking affect community coexistence?
6. Major research questions to address now

1 Outline

New outline (as of July 2019)

1. Intro
   (a) Direct effects of climate change are shifting species: especially in space and time
   (b) How well species track is critical to predicting future changes and indirect effects (e.g., shifts in performance, changes in community structure)
   (c) Environmental tracking, in time, has also been implicated in underlying many indirect effects (give a quick nod to spatial tracking here?)
   (d) With climate change, species that can track environmental change best appear to perform well with change also (Lots of work on this)
   (e) Thus tracking is critical. So here we review current knowledge on temporal environmental tracking, highlighting where basic theory predicts complexities and provide a framework to begin to leverage existing ecological theory to understand how tracking in stationary and non-stationay systems may shape communities (link to indirect effects).

2. Environmental change
   (a) Scales of environmental change: Within and between seasons; inter-annual versus trends
   (b) Transitions between stationary and non-stationary ... and what changes (mean, variance)
   (c) The role of the environment in coexistence (contrast some of the model's environmental parameters):
      i. Models of community assembly in ecology build upon coexistence via environmental variability.
      ii. Simple models require a resource pulse.
      iii. To describe that pulse requires a timing and magnitude for it.
      iv. Climate change has caused major shifts in the timing of pulses: changes in τ_P are often observed
      v. Such changes should be most important to impacts on coexistence, thus we focus on how shifts in τ_P impact coexistence.
   (d) Some examples (weave in above or add as a box?)
      i. Temperature records
      ii. Lake Washington
      iii. Snowpack records
      iv. Vernal dams of nutrients

(e) (This could be saved for later, or elaborations of it could come later.) 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?)

3. What is tracking? (Includes: How variable is tracking? What predicts the variation?)

   (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) Focus is on tracking through time; not space here (cite some of that lit; or CUT if covered neatly above)

   (c) How much do species track? How variable is it across (and within) species? (We should have the data to estimate the percentage of species that track, and the min and max tracking.) Some examples ...

      i. plants track abiotic environment

      ii. consumers track biotic environment, aka their prey (plants, or other consumers)

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

4. What predicts variation in tracking?

   (a) Some basic predictions

      i. Predictability of environment – most useful to track when there are predictable cues ... for intra-annual (when does the season start? Investment to avoid tissue-loss) and inter-annual (how good is that year? Investment for getting out lots of offspring)

      ii. And that predictability may vary with generation time ... (Interannual variation in climate versus generation time, and how humans are bad at thinking about this, esp. ecologists)

      iii. Otherwise, some amount of bet-hedging may be best (also, consider cost of static timing (cheap) versus tracking (potentially costly))

      iv. Even in predictable environments, there may be evolutionary limitations (Singer & Parmesan) or gene flow may prevent optimum tracking (see plasticity lit at bottom of file)

      v. Or there may be trade-offs in how well to track ...

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

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

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

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?

(d) BOX maybe: Common and emerging mis-steps in measuring tracking (problem with temperature sensitivity or 'The trouble with tracking')

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

ii. Mish-mash of stuff, some useful I think

A. threshold cues

B. days/degree

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

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

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

F. biotic tracking (competition, predaction etc.)

(e) Transition ... trade-offs as discussed here would have fundamental consequences for community assembly, especially with climate change

5. Coexistence theory

(a) Coexistence models based on variable environments allow us to test whether species that can track environmental change will perform best with change also (as species respond to shifting resources, which are influenced both by abiotic stressors and the use of the resource by other species.

(b) 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

i. Basic storage effect model

A. 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.

B. 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.

ii. Our version of the storage effect model

iii. 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 (Zak *et al.*, 1990) 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.)

iv. 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.

v. Environmental tracking and the storage effect

(c) 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.

i. How τ_i and α matter to coexistence

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

iii. Species that is weakly tracking may be out-competed by a species with a better mean τ_i.

   A. **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!

   B. 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.

   C. So naive assumption that trackers will always win is not the case, even in a simple stationary environment.

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

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

iv. To get coexistence you need other axis of competition for coexistence.

v. Note that this possible trade-off is earlier τ_i could correlate with lower competitive ability, which is mentioned in Chesson *et al.* (2004) 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.

vi. Trade-off between τ_i with R*

vii. Trade-off between tracking with R*

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

(d) *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.

6. 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) If you just vary τ_i across species) then there is no multispecies temporal niche: with you shift from species $min(\tau_i - \tau_{p.old.world})$ to species with $min(\tau_i - \tau_{p.new.world})$ wins... but if you vary more...

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

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

   (d) Tracking is favored more (α versus R*) .... Tracking can trump R^* ... Look at: cases where tracker outcompetes species with lower R^* in nonstationary simulations.

7. 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*

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

8. **Discussion**

   (a) Tracking is important, especially now with climate change

   (b) Current models of coexistence are primed to help understand how a nonstationary environment, such as the one produced by climate change, will alter communities.

   (c) Trackers and non-trackers can coexist in a stationary environment.

   (d) Nonstationarity favors tracking species.

(e) Things get more complicated in multivariate nonstationary environments

(f) So this all leads to major questions in the field:

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

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

    A. 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 ..

    B. 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

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

9. 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 ...

2 Stuff to revisit while/after writing to see if we can include

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?

- 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 Chesson *et al.* (2004). 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 Data we should try to pull...

1. Estimates of 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? Could we use those data?)
4. Lit review of traits and tracking (Do we have data on trade-offs between competition and tracking?)
5. Snowpack and other abiotic shifts

4 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..

5 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)

6 References to cite

Citation for earlier springs

Some key refs we worked with: (Chesson & Huntly, 1993; Chesson, 2000a,b; Chesson *et al.*, 2004). Some papers using storage effect model or Armstong and McGhee with field data: (Angert *et al.*, 2009; Kuang & Chesson, 2008, 2009; Levine & HilleRisLambers, 2009).

7 Figures (not sure when last updated)

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

References

Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 11641–11645.

Chesson, P. (2000a). General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, 58, 211–237.

Chesson, P. (2000b). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.

Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A. & Weltzin, J.F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.

Chesson, P. & Huntly, N. (1993). Temporal hierarchies of variation and the maintenance of diversity. *Plant Species Biology*, 8, 195–206.

Kuang, J.J. & Chesson, P. (2008). Predation-competition interactions for seasonally recruiting species. *American Naturalist*, 171, E119–E133.

Kuang, J.J. & Chesson, P. (2009). Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology*, 90, 170–182.

Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–U130.

Zak, D.R., Groffman, P.M., Pregitzer, K.S., Christensen, S. & Tiedje, J.M. (1990). The vernal dam - plant microbe competition for nitrogen in northern hardwood forests. *Ecology*, 71, 651–656.