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RH: Environmental tracking

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 February 2020)

1. Intro
   (a) Current first paragraph about tracking climate change, seems linked to predicting winners/losers
   (b) Define tracking and link to theory ...
      i. Definition – environmental tracking as the timing of life history events in response to proximate abiotic environmental cues
      ii. Thus tracking is critical to understanding these apparent correlations
      iii. Multiple lines of evidence support the idea that trackers should 'win', at least in broad brush strokes: Plasticity and the temporal niche
      iv. But there has been fundamentally little work to connect tracking and fundamental theory/concepts
      v. As work in this arena grows, both increasing research to estimate tracking and connect it to community assembly we believe more work is needed to integrate this work with fundamental eco concepts and theory
   (c) This disconnect could in part be due to the reality that fundamental theory is for stationary systems, and climate change makes systems nonstationary: Add in what we have already on non-stationarity
   (d) Here we ... **WHAT do we do in this paper?** ... Here, we review current knowledge on temporal environmental tracking both in empirical data and through the lens of basic community ecology theory. ... provide an initial test of how well basic theory supports the current paradigm that climate change should favor species with environmental tracking. ... Finally, we provide a framework using existing ecological theory to understand how tracking in stationary and non-stationary systems may shape communities, and thus help predict the community consequences of climate change.
2. Defining tracking
   (a) While tracking has become a common word in the phenology and climate change literature, there are few, if any, definitions of it.
   (b) At its core – tracking is about an organism matching its event date to the ideal date, measuring the ideal date means measuring fitness: We call this fundamental tracking
   (c) Fundamental tracking results in each species evolving a cue, or suite of cues, that determine event dates across environments (temporal and spatial): this cue model forms the biological basis for how a species tracks, but measuring environmental tracking requies two more parts.
   (d) Environmental variability – how is the environment varying (are aspects that will affect cues varying?) and how much matters.

(e) Then identical genotypes will have different tracking across environments (i.e., different environments in space and time), depending on which cue is dominant.

(f) What aspect of the environment is measured by researchers: if it's the exact model of a species cues then a species will track perfectly (no noise), but if it's only one part then tracking may be far from low.

(g) Under this definition, if the measured environmental variable is not direcly related to the cue(s) that the species actually uses, but one correlated with it (e.g., plant tracks light but researchers measure snowmelt) then it is not tracking per our definition, but potentially may be a proxy or correlation for it.

(h) Accurately measuring tracking requires generally a combination of experiments, models, in-situ data.

(i) Add some examples of where we can do this.

3. Understanding variation across species in tracking: Stationary systems

   (a) How much do species track?

      i. Current estimates mostly come from correlations of long-term data with observational climate: Use the text we have

      ii. Very few estimates link to physiological or experimental studies that show the measured variables are related to the organisms system of cues, thus hard to know which estimates are measures of tracking and which are proxies (correlated environmental variables). But knowing this is key to try to make comparisons across space, time or species.

   (b) Across almost all species-rich studies of phenology-climate relationships, however, there is high variation, including some species that do not track or track poorly (i.e., high noise surrourding observed statistical relationship).

      i. We argue three majors classes of reasons underlie species that do not appear to track climate or are poor trackers: (1) species do not track, (2) lack of firm biological understanding of the cues that underlie tracking, and (3) statistical artifacts that make it difficult to measure tracking robustly (see Box 'Statistical challenges in measuring tracking').

      ii. We make a nod to the stats issues, but keep it in a box. (Maybe we should add measurement error to the box?)

      iii. We make a nod to the issue of firm biological understanding of the cues that underlie tracking and reference Chmura etc.

      iv. Now we turn to the tricky one: why would species track or not?

   (c) There's actually a lot of theory/concepts that relates to this, but it comes from multiple directions and first requires understanding that phenological events are a two-part process. Insert bits of the text after 'The first part of this definition focuses on the timing of life history events (phenology)....'

(d) Insert paragraph: Considering life history events that define part of environmental tracking as a two-part process highlights that tracking is ultimately shaped by resources that species need to grow and reproduce. End with the sentence: These ultimate controllers on tracking are filtered through the abiotic environmental cues species use to time events.

(e) All life history is about when and how much, environmental tracking is focused mostly on when, and generally on all or nothing life-history events.

(f) Predicting tracking thus requires which cue(s) species should have. OCR offers a lot here ... it predicts you should track when

   i. There is a seasonal environment and variability across years

   ii. There is a good cue (good predictor of resources or other critical attributes of the environment)

   iii. Good cost/benefit ratio: expensive cues work given high benefits (like not losing tissue/reproduction to frost), cheap/crappy cues may still reign given low benefits

   iv. Complex, multivariate cues can be predicted in this framework – such cues show up in most in-depth empirical studies of phenological cues – but we don't know enough about why (from an OCR perspective)

   v. Take-home: You should not assume all species will track; instead, OCR says to assume all species track as best for them. And we need more empirical work in this light – costs of cues (very little work here), benefits of cues (some focus here, but need to see it more as cost/benefit ratio)

(g) While OCR assumes there is one general strategy – but in some environments this may not be the case; in such environments theory predicts species should bet-hedge: bet hedging assumes there is no clear optimum and thus multiple strategies should work and is focused more on how much versus when.

4. Understanding variation across species in tracking: Non-stationary systems

(a) Much of the above is fundamentally focused on stationary systems, but most systems are now non-stationary and research is working to make predictions here

(b) Which cues work?

   i. Those tightly coupled to what is changing in the environment

   ii. Multivariate cues may be especially robust a non-stationary environment, assuming they allow better coupling of proximate/ultimate

   iii. But we need to know more on the changing context of cues and whether non-stationarity can make a formerly high-information cue, provide less information by decoupling relationship between proximate/ultimate.

(c) Plasticity theory also provides insights into predictions of a non-stationary environment

   i. Timing is a trait, then tracking is a type of plasticity. A plant may always need a certain thermal sum, but that is the same as plant height responding to nutrients always being the same. (Find notes or remember about environments across time and space.) Cue calendar and resource calendars need to be aligned, and then our julian calendar system. But multiple cues probably really does drive plasticity.

  ii. Often focused on 'novel' environments, but this is one bridge to non-stationary (though perhaps not exact enough)

  iii. Plasticity provides a first opportunity where the multi-species context is clear, the above is often focused on one species, where other species are at best filtered in as an aspect of the environment, but applying plasticty theory to tracking shows how critical the multi-species perspective is

(d) Plasticity theory predicts (trade-offs section)

  i. Theory generally predicts the more plastic species to win, unless there are trade-offs.

  ii. Plasticity thus says tracking is part of trait syndrome

  iii. Insert stuff after 'As tracking often relates to the timing of a resource pulse, traits related to resource acquisition are likely contenders for a trade-off.'

(e) Understanding these trade-offs is clearly critical, but we also argue more theory is needed to understand the short term dynamics of a changing environment and plasticity – most theory predicts the outcome of a new environment, but non-stationarity in the climate today means we need more on the trajectory to that outcome (more eco in the evo needed here).

(f) We know plasticity may potentially lead to a lack of the needed variation (check cites) also.

5. Community ecology theories of tracking in stationary environments

(a) The role of the enviroment in co-existence section

(b) Beyond this, most applicable models fall into two camps: when to go versus how much (when: priority effects – the whole species goes at once; how much – all species go at once but at varying amounts). Both is how many seeds are germinating on what day?

(c) Some models are focused mainly on when ....

  i. When tracking is about timing the main theory is about order of arrival (priority effects is when you get a head start and thus are bigger) and earlier is better. But you probably also need to integrate over how much. No trait predictions from priority effects but you can use traits to predict when you would see priority effetcts (see Fukami Annual Review)

  ii. Competition/colonization (phenology is akin to dispersal) applies when you get in and get to reproduction before the better competitor arrives. Predicts trait syndromes – one species produces more but is weaker competitor.

  iii. Other models—interaction strength depends on timing (e.g., Rudolf, stage-specific models)

iv. Coexistence theory also predicts trade-offs; coexistence models though often invoke how much as well.

(d) When it's also about how much... Some models are focused on how much, but might still be useful ...

   i. Models that fit here are all interannual competition models. Most of classic community ecology fits here where mediating is through density.
   ii. So lots of these models may be useful if you adapt them.
   iii. This is where our model fits! We adapt how much based on match to the environment. (It's about the match to the environment and you can tweak that parameter) ... include here how the environment is modeled – see Box.
   iv. Could also adapt them through priority effects—vary arrival times explicitly.
   v. Mention here that there are not so many models that have when and how much together right now (most of it is bet-hedging).
   vi. No models to our knowledge that do tracking (but see plasticity lit) and see Rudolf as a way you could adapt it (looks much more at species interactions)

6. All this community stuff in non-stationary systems ...

   (a) There is growing stuff on stationary versus non-stationary (Chesson, Rudolf)
   (b) But we need more of this.
   (c) And critically we need more on stationary to non-stationary in community ecology theory.
   (d) Simulations as a useful way to start (see Box)
   (e) Directional change –

7. Future directions

   (a) How is the environment changing? Embrace the joint distribution

      i. Start with first paragraph that we have in this section.
      ii. To measure and predict environmental tracking across species: Full factorial experiments are good, but may need to embrace the joint distribution of reality more.
      iii. OCR as useful framework to understand costs of the cues themselves, as well as benefits, understanding constraints
      iv. This leads to trying to estimate fundamental tracking, which trophic mismatch literature has highlighted is hard. All fields need balance between measures of fundamental tracking, estimating an organism's system of cues and measuring environmental tracking. Clear statements of what is and and is not known and measured will help.
      v. Tread carefully in trying to compare species across space, time or species ...
      vi. Move away from DOY metrics? Try to understand how cues shift with warming, think of other temporal metrics (metabolic ones?)

vii. Embrace multivariate cues, and work to understand how non-stationary today impacts them
viii. Clarify your environment: Progress can come from considering one species in an environment to how the species reshape the ultimate environment, but studies need to be more clear in their assumptions here.

(b) What major traits trade-off with tracking? (Can mostly use this section, just link to plasticity theory and community ecology a little more).

(c) Community models need to add true non-stationarity and combine the when to go and how much

i. Models now basically bifurcate in being about when versus how much, we need to know if these models lead to similar or different conclusions
ii. More non-stationary models

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) SKIPPING: 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) We made the season start earlier by shifting τ_P earlier given communities that had co-occurred for XX runs. We examined outcomes in the τ_i x R* and the α by R* communities.

(c) Changing τ_P shifts the effective τ_i that is favored

(d) Fixed intrinsic start:

i. Earlier τ_i is favored more (R* versus τ_i runs: previously these coexisted via a higher R* and less ideal τ_i) and generally outcompetes formerly co-occurring communities

ii. Almost all 2-spp communities are lost, the only ones that persist are perfectly matched (equalized)

(e) Tracking:

i. Tracking is favored more (α versus R*) .... Tracking can trump R^* ... and generally outcompetes formerly co-occurring communities

ii. you lose a lot of 2-spp communities but not at all as much [explain what happens here ... trade-off space narrows]... equalized 2 spp communities remain

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.

8. *Multivariate nonstationary environments*

(a) Perhaps with changes in two aspects of the environment on which species trade-off, perhaps then trade-off can be maintained?

(b) We additionally examined runs where R0 get smaller as τ_P gets earlier

(c) Generally makes environment more variable and thus drives species losses faster ...

(d) Thus, while there could be special cases where trade-off is maintained, we expect this is rare.

9. **Future research in environmental tracking & non-stationary systems**

(a) Tracking is important, especially now with climate change, lots of growing empirical work highlights this, but they could benefit from closer ties to theory

(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. But they need more work to be most applicable.

(c) So this all leads to major questions in the field ...

(d) *What major traits trade-off with tracking?*

i. Basic theory suggests tracking must trade-off with other traits to exist in multispecies communities, so work should focus more on this.

ii. These traits are most likely on different niche axes, such as:

iii. Traits related to competition....

iv. Predator avoidence or tolerance ...

(e) *How do shifts to non-stationary environments re-shape the relative influence of stabilizing versus equalizing mechanisms?*

i. One obvious finding of our results was that as environments shift from stationary to non-stationary species co-occurring via equalizing mechanisms can persist longer.

ii. While super obvious it suggests climate change may (at least initially) favor species co-occurring simply because they are similar, and thus may make identifying which traits climate change actually promotes more difficult. This works only if communities have species co-occurring via strong equalizing mechanisms; thus understanding the prevalence of these mechanisms more important.

iii. If equalizing mechanisms are rare then climate change should promote species loss by fundamentally re-shaping stabilizing mechanisms.

iv. As species are lost, dispersal may allow communities to adjust to new trade-offs ... or evolution may allow some species to stay in communities they would otherwise have been lost from.

v. But with non-stationarity this axis is constantly shifting, until the environment shifts back to stationarity.

vi. All this suggests we need to better understand transitions from stationary to non-stationary environments more in ecology.

(f) *Which abiotic aspects of the environment are changing? How are they shifting?*

i. Abiotic shifts expected with climate change: single versus synergistic climate shifts

ii. 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 ..

iii. 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 effects of climate change extend well beyond shifts in the mean

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

v. What does this mean in emprical ecology? Researchers should characterizing environmental distributions better: Putting years of study in context.

10. **Stationarity in the future**

(a) Stabilization right now depends on human actions, but we should assume it will happen – CO2 stabilization though does not mean the environment will immediately be stationary. (Some refs in comments).

(b) History of earth is stationary, but interrupted by non-stationary periods so average species experience this often.

(c) Challenge to ecology now is better understand this, given one of the most rapid global changes.

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

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