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

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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.

Keywords: phenology, climate change....

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

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

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* ...

(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.

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) 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*)

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) 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.

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

(c) Nonstationarity favors tracking species.

(d) Things get more complicated in multivariate nonstationary environments

(e) 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 avoidance 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)

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 Main text

Athropogenic climate change is causing widespread changes in species, with many species shifting in both time and space (CITES). Species are shifting up in elevation and poleward as climate warms (CITES), and many species are shifting their recurring life history events (phenology) earlier (CITES). Yet, not all species are shifting in a way predicted by a simple direct physiological response; species in the same community can include some that do not shift or even shift in an apparently opposing direction (e.g., delayed spring phenology with warming). Understanding these variable responses of communities and species due to climate shifts is a major aim of current ecology and may be explained by indirect effects. For example, research has already documented changes in a species performance (CITES) and community composition that appear to be—at least in part—indirect effects (CITES). Understanding ecological responses to climate change will thus require synthesizing information on both direct effects of climate on species and indirect effects driven by responses to other species' shifts.

How well a species tracks the environment has been repeatedly implicated in underlying indirect effects of climate change (CITES). Species that phenologically track warming also appear to perform better in field warming experiments (CITES), while exotic plant species appear to also gain a foothold in warming environments by phenologically tracking climate change

(CITES). Simple community ecology theory supports these findings, suggesting that a warming climate should open up new temporal niche space and favor species that can exploit that space (CITES). Thus, earlier springs should favor earlier species, especially those that can environmentally track the ever-earlier seasons. While this hypothesis has gained significant traction in the ecological literature (CITES), there is little work examining whether this hypothesis is supported through coexistence theory and models.

Current or 'modern' coexistence theory is based strongly on understanding how variable environments may promote coexistence—providing one way to study how communities may be shaped by a changing environment. Importantly, models based on the theory can help highlight which species 'traits,' including those related to how species are matched to and respond to the environment, are favored under different environmental regimes.

Most theory, however, is based on the assumption of stationarity: though the environment is variable, its underlying distribution is unchanged across time (**?**). This assumption is common not just to coexistence theory, but to much of the theory that underlies ecology, evolution and myriad other research fields (CITES). Climate change upends the assumption of stationarity. By causing increasing in temperature, larger pulses of precipitation, increased drought, and more (CITES), climate change has fundamentally shifted major attributes of the environment from stationary to non-stationary regimes. This transition—from stationary to non-stationary environments—is rehaping ecological systems, and while new work has aimed to adapt coexistence to non-stationary environments (**?**), little work has fundamentally examined what such a transition may mean for communities.

Here we review current coexistence theory for variable environments, and provide an initial test of how well basic theory supports the curent paradigm that climate change should favor species with environmental tracking. We begin with an overview of coexistence theory for variable environments and what predictions models from this theory make for stationary environments. In particular, we look at how species traits related to their responses to environmental variability effect coexistence and long-term persistence in community maintenance. Using a simple example, we 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.

4.1   The role of the environment in coexistence

Recent advances in coexistence theory, often heralded under the title 'modern coexistence theory,' recognize that both mechanisms independent of fluctuations in the environment (e.g., R* and other classical niche differences) and dependent on fluctuations in the environment (relative non-linearity and storage effect) can drive coexistence (CITES). Models under this paradigm are thus often composed of parameters the describe the environment and the species within it (CITES). In some cases the environment is expressed as variation in parameters related to species (e.g., in some lottery models the environment appears, effectively, as variation in birth

and death rates). In other models, the environment is more specifically defined. For example, many seed germination models define an environment that begins with a resource pulse each year. Building a changing environment into models thus may require knowing how environmental shifts filter through to species-level parameters (CITES) or, perhaps more simply, the environment is changing. In the aforementioned seed germination models, many systems may be experiencing shifts in the size or variability of the resource pulse. Parameters related to species must always include mechanisms for growth, death, interactions with other species, and generally a bet-heding strategy for survival across years (e.g., a seedbank or other long-lived lifestage)—though exactly how these are defined varies across models (e.g., R* and related models focus on resource competition).

4.1.1 Model description

To understand the role of environmental tracking by species in variable environments we use a simple model that includes dynamics at both the intra-annual and inter-annual scales. As the model is akin to many commonly used seed germination models (CITES), we follow a similar terminology for ease, however the basic structure of our model could apply to others systems with one dominant pulse of a limiting resource each resource (e.g., water from rain or snowpack). This model thus allows within- and between-year dynamics to contribute to coexistence. Between-years the environment is included via variable germination, and within-years the environment is explicitly included as a resource pulse at the start of the season. The model includes a suite of species traits, including some relating to how the species responds to the environment via germination each year and some related to how species may bethedge across years (via a seedbank), as well as traits relating to resource competition each year. Within-season dynamics within the model thus allow for fluctuation-independent coexistence (e.g., trade-offs in resource competition), while interannual variation in the environment provides opportunities for coexistence via fluctuation-dependent mechanisms.

Across years, for a community of n species, the seedbank (N) of species i at time t is determined by the combination of the survival (s_i) of the fraction of seeds that did not germinate that season $(1-g_i(t))$ plus new biomass (B_i) produced during the length of the growing season (δ) converted to seeds (ϕ_i):

$$N_i(t+1) = s_i(N_i(t)(1-g_i(t)) + \phi_i B(t+\delta)$$ (1)

The production of new biomass each season follows a basic R* competition model: new biomass production depends on its resource uptake ($f_i(R)$ converted into biomass at rate c_i) less maintenance costs (m_i), with uptake controlled by a_i and u_i:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = [c_i f_i(R) - m_i]B_i$$ (2)

$$f_i(R) = \frac{a_i R^{\theta_i}}{1 + a_i u_i R^{\theta_i}}$$ (3)

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With the initial condition:

$$B(t + 0) = N_i(t)g_i(t)b_{0,i} \tag{4}$$

The resource (R) itself declines across a growing season due to uptake by all species and abiotic loss (ϵ):

$$\frac{\mathrm{d}R}{\mathrm{d}t} = -\sum_{i=1}^{n} f_i(R)B_i - \epsilon R \tag{5}$$

Each year the proportion of seeds that germinate depends on both each species and the environment each year. Each year a species' germination fraction depends on the distance between τ_i, a species characteristic, and τ_P, an attribute of the environment, which varies year to year. We conceptualize this as a variation in the timing and an environmental trigger for germination. Germination fraction declines according to a Gaussian distribution as the distance between τ_i and τ_P grows.

$$g_i = g_{max,i} e^{-h(\tau_p - \tau_i)^2} \tag{6}$$

Adding phenological tracking to model: τ_i can be considered a fixed characteristic of a species or it may respond to the environment dynamically through what we refer to as environmental tracking. Tracking (α) decreases the distance between τ_i and τ_P such that a species with higher alpha will have a higher germination fraction.

$$\alpha \in 0 \to 1 \tag{7}$$
$$\hat{\tau}_i = \alpha \tau_p + (1 - \alpha)\tau_i \tag{8}$$

Thus:

$$\text{when } \alpha = 0 : \hat{\tau}_i = \tau_i$$
$$\text{when } \alpha = 1 : \hat{\tau}_i = \tau_p$$

We refer to $\hat{\tau}_i$ as 'effective τ_i.' As our interest is primarily in the role of environmental tracking we focus on situations where species vary in their match to the environment (through both tracking, α, or a more fixed response, τ_i) or their resource uptake (via c_i).

4.1.2   Tracking in stationary environments

Species occurring for long periods of time in any habitat must be sufficiently matched to their environment across years—in our model this means species must have germination curves [define above?] such that their $\hat{tau}_i$ is sufficiently close to τ_p to allow germination of new seeds before the seedbank is exhausted. In our model this can happen in two ways: species' with fixed τ_i values close enough to τ_p or species with combination of τ_i and tracking (α) that brings the $\hat{\tau}_i$ close enough to τ_P.

Moving onto interannual variation: in temporally variable environments species with tauI closer to average tauP should always win... To get coexistence you need a trade-off. tauI versus R* alpha versus R* Alpha versus tauI ... Competition/colonization trade-off. Figures: alpha vs Rstar, tauIP.t1 versus alpha???

5 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