

RH: Environmental tracking

## **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 Main text

Athropogenic climate change is causing widespread changes in species, with many species shifting in both time and space (CITES). Many species are shifting in time and space in ways predicted by a direct response to track climate—for example, species are shifting up in elevation and poleward as climate warms (CITES), and/or shifting earlier in their recurring life history events (phenology)(CITES). Yet, not all species are shifting as predicted by a simple climate-tracking 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 species and communities to climate shifts is a major aim of current ecology and may be explained by indirect effects. 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 increases in temperature, larger pulses of precipitation, increased drought, and more storms (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 reshaping 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 current 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 affect 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 predictions.

## 1.1 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 that describe the environment and the species within it (CITES). Parameters related to species must always include mechanisms for growth, death, interactions with other species, and generally a bet-hedging 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). How the environ-

ment is defined in most models falls into two broad categories. In some models 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—how 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.

### 1.1.1 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 season (e.g., water from rain or snow-pack). 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 ( $\delta$ ) converted to seeds ( $\phi_i$ ):

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

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  $u_i$ :

$$\frac{dB_i}{dt} = [c_i f_i(R) - m_i] B_i \quad (2)$$

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

With the initial condition:

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

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

$$\frac{dR}{dt} = - \sum_{i=1}^n f_i(R)B_i - \epsilon R \quad (5)$$

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  $\tau_i$ , a species characteristic, and  $\tau_P$ , 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  $\tau_i$  and  $\tau_P$  grows (we refer to this distribution as the 'germination curve').

The model is designed for multiple conceptualizations (Chesson *et al.*, 2004), but given our focus here we consider  $\tau_P$  to represent the environmental (abiotic) start of the growing season each year, and refer to it as the 'environmental start time' while  $\tau_i$  represents the intrinsic biological start time for species  $i$  'intrinsic biological start time,' which we refer to as . How well matched a species is to its environment each year can be measured as  $\tau_i - \tau_P$ , or the distance between *bioSOS<sub>i</sub>* and *env.SOS*

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

Adding phenological tracking to model:  $\tau_i$  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 ( $\alpha$ ) decreases the distance between  $\tau_i$  and  $\tau_P$  such that a species with higher alpha will have a higher germination fraction.

$$\alpha \in 0 \rightarrow 1 \quad (7)$$

$$\hat{\tau}_i = \alpha \tau_P + (1 - \alpha) \tau_i \quad (8)$$

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 biological start time' for species  $i$  (or 'effective  $\tau_i$ '). 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,  $\alpha$ , or a more fixed response,  $\tau_i$ ) or their resource uptake (via  $c_i$ ).

### 1.1.2 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 a germination curve such that their effective biological start time ( $\hat{\tau}_i$ ) is sufficiently close to the environmental start time ( $\tau_P$ ) to allow germination of new seeds before the seedbank is exhausted. In our model this can happen in two ways: species' with fixed environmental start time ( $\tau_i$ ) values close enough to the environmental start time ( $\tau_P$ ) or species with combination of intrinsic biological start time ( $\tau_i$ ) and tracking ( $\alpha$ ) that brings the effective biological start time close enough to the environmental start time ( $\tau_P$ ).

A simple outcome of this model is that in temporally variable environments where all other species characteristics are identical the species with the effective biological start time closest to the average environmental start time will always win—regardless of whether this effective biological start is due to a fixed intrinsic start time or due to tracking. Put another way, in a stationary environment both are equally useful ways to match to the environment, as all that matter is the effective distance between the biological and environmental start of the season.

**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  $\tau_i$  (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!

In a stationary environment both are equally useful ways to match to the environment (what matters in the end is the total  $\tau_{IP}$ ). In a stationary environment you can get the same outcome with either.

So, both can equally trade-off with other niche axes .... (return to outline now)

## 2 Figures

1. Real-world data showing stat/non-stationarity in environment (ideally  $\tau_P$ )
2. Real-world data showing tracking (and less tracking)
3.  $\tau_i$  vs.  $R^*$  trade-off and histogram of persisting  $\tau_i$  under stat/nonstat  $\tau_P$  environment
4. alpha vs.  $\tau_i$  trade-off and histogram of persisting alpha under stat/nonstat  $\tau_P$  environment
5. alpha vs.  $R^*$  trade-off and histogram of persisting alpha under stat/nonstat  $\tau_P$  environment
6. (Scratch this one: we're pretty sure it required a crappy  $\tau_i$  to survive the initial stationary period, then be favored in second time period and we're not so sure crappy  $\tau_i$  species survive the initial stationary period) time-series of one run showing years where  $\tau_i$  of one species is close to  $\tau_P$  and other years where  $\tau_i$  of other species is close to  $\tau_P$  (and show this shift under nonstat)
7. non-stationarity in  $R_0$  and  $\tau_P$

## References

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