

# Coexistence and climate change: The role of temporal-variability in structuring future communities

Wolkovich & Donahue

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## Abstract

Predicting community shifts with climate change requires fundamental appreciation of the mechanisms that govern how communities assemble. Most work to date has focused on how warmer mean temperatures may affect individual species via physiology, generally producing range shifts towards the poles and uphill, which fails to predict the wide diversity of observed shifts. Climate 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. Additionally, cascading effects on species and communities are qualitatively predicted but there have been no efforts, to our knowledge, to predict shifts based on coexistence theory. Here we extend the two possible mechanisms for species coexistence based on variable environments—relative nonlinearity and the storage effect—to predict how communities will respond to climate change. We focus on both (1) shifts in climate variability and extreme events that link to stabilizing coexistence mechanisms and (2) traits that may make species the most vulnerable to climate change. We examine how coexistence via the storage effect shifts under non-stationary climate regimes, and how outcomes vary with the ability of species to phenologically track the timing of major climate events. *Findings go here. Such as: Species that can track variability are least vulnerable to climate change (perhaps). Also, we add an emphasis on integrating intra and inter-annual scales here, if we manage to make that happen well.*

# 1 Next steps, goals!

World of possibilities goes here soon.

## 2 Introduction

*Need to write more someday*

Understanding how plant communities will respond to climate change requires synthesizing information on both direct effects of climate on species and indirect effects driven by responses to other species' shifts. (Coexistence models based on variable environments allow us to do this, as species respond to shifting resources, which are influenced both by abiotic stressors and the use of the resource by other species.)

## 3 Overview of project and directions

1. We consider the effects of climate variation at both the intra-annual and inter-annual scale and scale up responses to short-term (1-10 yr?) and long-term (>100 yr) dynamics.
2. We focus (for now) only on the storage effect. We leave out relative non-linearity.
3. We also look at how species traits related to their responses to climate variability effect coexistence and long-term diversity maintenance. (This is the tracking part of the project.)

We also note that one possible way to make this project more interesting, useful and forward-thinking than others is to make scenarios most realistic—link to real climate scenarios or use existing data to rule out and in shifts in abiotic variables (and possibly species traits—we should have the data to estimate the percentage of species that track, maximum tracking and if only early-season species track, we could add that in, and of course we have a lot of climate data on hand). The new *Physical Sciences Basis* of the IPCC came out in September 2013 so we have good recent estimates of how climate has and will shift (and Lizzie can slog through this).

## 4 Current outline

1. Introduction
  - (a) Direct and indirect effects of climate change
  - (b) Links to ecological coexistence theory
  - (c) Abiotic shifts expected with climate change: single versus synergistic climate shifts
  - (d) Things that will shift with climate change, related to coexistence models
    - i. Magnitude of and interannual variance in resource pulse ( $R_\theta$ )

- ii. Timing of resource pulse ( $\tau_p$ )
    - iii. Abiotic loss rate of resource ( $\epsilon$ )
  - (e) Species traits and climate change: phenological tracking
  - (f) Goals of paper
2. Model description (a whole section on this below)
- (a) Basic storage effect model
  - (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.
    - 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 (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.)
  - (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) Phenological tracking and the storage effect
  - (f) Our implementation of tracking
  - (g) Derivation of aspects of the storage effect and relative non-linearity in our model (this is a big *to do*).
3. Results: Response variables are (1) probability of extinction, (2) relative densities in 2 spp models, and as of 2012-2013, what are the traits of species that persist? How much of a trade-off is needed to offset shifts in coexistence favouring early or tracking species with non-stationary climate change?
- (a) Section 1: Shifting abiotic variables
  - (b) Section 2: Species traits: Phenological tracking and shifting abiotic variables
4. Discussion

## 5 Variables of interest

We consider 3 primary traits of the environment ( $\epsilon, R, \tau_p$ , which code to evaporative stress, inter-annual variability, and start of season pulse for our approach basically) and 1 species response trait (phenology, specifically flexibility in phenology as modeled by a species' ability to shift  $\tau_i$ ) to model the dominant expectations of current and future climate change:

1. *Changes to R*: Shifts in climate means and variability (greater var  $\approx$  extreme events) as modeled by changes to  $\mu$  and *var* of R, which can lead to:
  - (a) Changes in inter-annual covar(E, C)
  - (b) We ignore, for now, possible changes related to this in relative non-linearity
  - (c) For variability: changes related to buffered population growth: for example, when the periodicity of certain extreme events declines such that species with certain buffering times no longer get their 'good' years enough (e.g., periodicity of rainy years every 5 years, switches to 10 and the species seedbank is 7 years). This means for simulations changing  $var(R)$  must be consider in concert with the scale of  $s_{i...n}$ .
2. *Changes to  $\epsilon$* : Shifts in climate means that lead to greater abiotic stress on environments, as modeled by changes to  $\epsilon$ . For example, warmer growing seasons may produce greater evapotranspiration, shifting competition for the remaining resource. (By the way, we have notes about treating  $\epsilon$  as a function itself.) This should affect:
  - (a) Changes in inter-annual covar(E, C)
  - (b) We ignore, for now, possible changes related to this in relative non-linearity
3. *Changes to  $\tau$* : Longer growing seasons, with several scenarios:
  - (a) Season is longer (earlier  $\tau_p$  but community of species do not shift their timing (e.g., no change to  $\tau_{i...n}$ )
  - (b) Season is longer (earlier  $\tau_p$  and some species ('climate-trackers') change their timing (community shift in temporal (phenological) synchrony), that is (e.g., certain species change to  $\tau_{i...n}$ ) such that the distance  $\tau_p - \tau_i$  is constant across years.
  - (c) Could also look at complementarity (histogram of variation in  $\tau_{i...n}$ ; could pull  $\tau_{i...n}$  from a beta distribution. (Note: I also wonder if we shouldn't just use variation due to above to look at this, versus a whole new approach.)
4. How do these variables shift with climate change and co-vary?
  - (a)  $R_\theta$  increasing inter-annual variance with some giant years (extreme events), for snowpack systems it's decreasing generally
  - (b)  $\tau_p$  getting earlier, also for snowpack systems earlier years probably also have higher evaporative stress ( $\epsilon$ , due to warmer year)

We assume that:

1. All species ‘go’ each year, at least a little; that is, we’re not looking at a communities where some species have true supra-annual strategies.
2. 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.
3. While interactions between the above-considered ‘traits’ may be important, first understanding how each of these forces act alone is critical enough to let alone interactions for this manuscript.

## 5.1 Tracking thoughts & fun

In August 2012 Megan came up with a new way to model phenological tracking, it’s linear and better than the one presented here. We also discussed three key ways to think of tracking:

1. Species can have fixed flowering/leafing (not track).
2. Species can phenologically track pulse.
3. Species can phenological track something at least at one time in history correlated with the pulse.

We agreed that while (3) is interesting—would allow you to look at mismatch ideas etc.—(1) and (2) have more biological support for plants and are interesting enough in and of themselves, so we will focus on and mode (1) and (2) and not (3).

In August 2013 an issue we worried about: Will tracker always win? Answers: No, not if it’s a poor competitor, that is, if it responds quickly to resource pulse but then does poorly at low resource levels. I also think it’s important to remember that not all tracking species will track perfectly so some species should grow before trackers some years, when their fixed  $\tau_i$  corresponds well to  $\tau_p$ . Also, we have a note high intraspecific competition could dampen trackers, especially when greater than interspecific competition.

New things we came up with that we want to look at in regards to **phenological tracking**:

How big do trade-offs have to be for tracking to be non-advantageous (to allow coexistence with other species)?

Has climate change made tracking more advantageous? That is, is tracking the dominant strategy with a shifting environment (distribution) vs. stationary environment distribution?

Follow up from October: How much does climate have to shift (non-stationarity in system) given some level of fitness differences trading off with tracking for tracking to become the optimal strategy *or, given that we know something about climate projections* how big do the trade-offs have to be with climate change to make non-tracking

a feasible strategy (that is, to make tracking not the optimal strategy with climate change)?

New notes as of October 2013:

*How will we adjust the equations for simulations about shifts in the environment?*<sup>1</sup>

We do **not** have relative nonlinearity: So we set all species  $f(R)$  the same.

We have to create some species differences for the storage effect to ‘ameliorate’ (EMW phrasing here, probably not ideal), so how do we want to do that?

- mean species differences in  $c_i$  and storage effect through  $g_i$
- mean species differences in  $G_i$  and make them totally equivalent within season and temporal storage effect through  $\tau_p - \tau_i$

Note:  $h$  yields different bet hedging strategies (you could think of it as ‘germination plasticity’)

Question: do we need to make sure that for all  $i$ ,  $\int g_i$  are equal, or is it that  $\int g_i(t)\tau_p(t)dt$  should be constant (the latter being the average of  $g_i$  weighted by the distribution of  $\tau_p$  through time).

## 5.2 How the world changes with climate change

In July 2011, I looked at whether the start of spring has gotten more variable (using some key datasets from NECTAR) and it hasn’t, at all. No change.

Old list of tasks on this I should make sure are thought through:

Get on top of climate change lit: which variables will shift? Which ones are coupled and how will their coupling shift with climate change (go from uncoupled to coupled, or vice-versa, or just the coupling itself changes).

Does evaporative stress increase with climate change (absolute, versus relative, oceans burn off while temperatures increase etc.)

When seasons start earlier does evaporative stress increase (I suspect so, but need to pull together refs)

Does lower snowpack mean earlier seasons?

*Environmental shifts with climate change, from October 2013 meeting:*

Systems we’re thinking about (see above) but, effectively, alpine where snowpack meltout is start of season (SOS), nutrient turnover SOS and some precip controlled systems with just one pulse.

1.  $\tau_p$  will get earlier in many systems (alpine and nutrient), not sure on precip—there it might just get more variable

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<sup>1</sup>Not phenological tracking, which are other simulations.

2.  $\epsilon$  increase in mean and increase in extreme events (this seems pretty possible across a lot of systems—good one)
3.  $R_0$  increase or decrease in mean maybe (who knows what happens in precip system), increase in variance (for precip systems), increase in extreme events
4. Correlations in  $\tau_p$  and  $\epsilon$  - this basically says ‘does the first day of the growing season correlate with the average temperature of the growing season?’ which, yeah, is weird. Lizzie thinks there’s probably a weak positive covariance here (just because there’s a lot of noise in annual weather but wet soils hold cold, and dry soils hold heat so *all other things being equal* you could see this correlation. From an email from Ben Cook from 30 May 2013:

So, both Europe and the Northeast US have had super crappy springs in March and April (so annoying!). Mostly it was due to an almost unprecedented negative swing of the NAO, which just funneled lots of cold arctic air in the region. As for the summer? Harder to tell. If an area gets lots of rain in the spring, it can mean really wet soil which can keep things cooler in the summer. But other than that, we don’t really have much skill in predicting summer time climate.

Otherwise, not sure anyone has looked at this at all in precip systems and for snowpack there may be something here since Pederson et al. 2011 says that snowpack control has basically shifted from precipitation control to temperature control so with climate change you could start seeing a correlation in alpine systems between  $\tau_p$  and  $\epsilon$  (which is kind of cool, but sort of something that is not low-hanging, obvious fruit – or maybe it’s low hanging fruit and only obvious to us).

5. Correlations in  $\epsilon$  and  $R_0$  maybe for alpine you could see, with climate change, increases in  $R_0$  and decreases in  $\epsilon$ , but we’re still bickering on this and what  $\epsilon$  really is (incident irradiance vs. relative humidity?)
6. Correlations in  $R_0$  and  $\tau$  nothing to date or in future? Maybe in alpine systems?

So, where did we arrive at after all this? Even though we used to be interested in correlated shifts in these we’re no so much anymore. Instead the *best place to start* seems to be: earlier  $\tau_p$  and increases in  $\epsilon$  and  $\epsilon$  extreme events. Then maybe move on to  $R_0$  (mean and extreme events). And again, just skip correlations.

Note that increased extreme events for  $\epsilon$  will effectively reduce biomass (you could also consider modeling this so it ties to  $m_i$  or modify  $g_i$  to lead to total loss, perhaps).

While here, though, I will mention that we discussed *which* correlations will shift with climate change and the big one seems to be the North American alpine story: where the relationship between how  $\tau_p$  affects mortality has shifted with species’  $\tau_i$  such that there is now higher mortality imposed on species with earlier  $\tau_i$ . We did briefly discuss how to

model this and think maybe the best way is to add in, external to the within-year integral, a fraction that germinated and died as a  $f(x)$  of  $\tau u_i$  and frost event time.

## 6 Random things to remember, worry over, generally absorb

**Key question:** Should we add asymmetry in  $g_i$  such that  $\tau_i$  earlier than  $\tau_p$  is worse than  $\tau_i$  later than  $\tau_p$ ?

**Key stuff:** We will build in trade-offs (versus running a bunch of random parameter space models where—in order to get stability—we end up with related trade-offs) such that we’re effectively saying ‘the world works this way now, we add climate change and see what happens. . . .’ We think these trade-offs should be:

decrease  $\phi_i$  correlated with  $\tau_i$  close to  $\tau_p$

(for phenological tracking questions) decrease  $\phi_i$  correlated with higher tracking<sup>2</sup>

Remember to worry a little about how biomass is converted to seed: It happens for all species at  $\delta$ —so, early species may have peaked and have lower-than-their-peak biomass at  $\delta$  while later season species may be at peak. Ways around this?

Use peak biomass instead of biomass at  $\delta$  (when the growth rate goes below 0).

Set different  $\delta$  for each species ( $\delta_i$ )

*The way the growing season ends in the equations is interesting.* First, as brilliantly stated: the growing seasons ends [in these equations] when plants stop growing. And related, the equations do not deal with setting the end of the growing season. In my head (Lizzie), abiotic forces can stop a growing season, but in reality with plant phenology data, the start and end of the growing season are fundamentally different: at the start species are most sensitive to abiotic cues and climate change effects are large and often consistent. For the end of the season effects have been more muted and variable—suggesting plants in some way do seem to set the end of the growing season more than abiotic cues do, at least when compared to the start of season. (And the model follows this.)

Worries over growing season continue (from August 2012 notes)! Worries over very short growing seasons (agree to stay with what we have for now, but keep in mind this possible issue and idea of continuous  $R$  dripping in (or cyclically) for ‘growing season.’

The intra-annual model does not have a useful closed solution (I have some Maxima code that shows only the trivial solution gives an equilibrium). This actually makes sense since the model is not a chemostat (a la Tilman  $R^*$ ), we have a pulse that drains out and is not

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<sup>2</sup>though we could also alter  $c_i$  or  $d_i$ , or might work better to adjust  $a_i$  so you can make earlier faster growers (or adjust  $a_i/d_i$  so when you’re faster you’re a higher  $R^*$ , but we need to check through all this thinking more.



balanced by inputs.

**Key question:** Can we simplify within-year dynamics to focus on a better model for timing (see photo of October 2013 whiteboard that Megan has)? To rephrase this: Our internal equation is basically  $R^*$  rankings could we create a ‘deterministic look up table’ for the within-year dynamic so we can make think more carefully about the timing part of this. (Related note from 2012 meeting: Decide if we need to ODE solve the intra-annual dynamics, then use the discretized version only inter-annually. Note from Lizzie: best ODE solver is now in package ‘desolve.’)

The 3 ingredients of the storage effect are:

1. differential response to the environment (subadditivity)
2.  $\text{covar}(E, C)$
3. buffered population growth

Ingredients for the storage effect *in our model*:

buffered population growth:  $s_i$

variable response to the environment:  $\tau_i$ , which generates:

$\text{covar}(E, C)$

$\tau_p$  is conceptualized as a photoperiod cue, it’s a species going on the same day every year—for our phenological tracking we adjust it so it can vary year-to-year for some species.

We keep an eye on who has cited Chesson et al. 2004 and for actual modeling work it’s just Chesson, and for that it’s all his seed predation work.

More random notes: Chesson (2000b) (pg. 354)  $r$  holds temporal variation in  $\delta I$  and  $\delta N$  so effectively:

- species can coexist via intra-annual temporal mechanisms (for example, maybe this is what most mid-season species in the mesic temperate zone do), and/or
- species can coexist via inter-annual temporal mechanisms (maybe early-season species in most mesic temperate environments)

### Some notes for writing

1. Understanding the variable responses of communities and species due to climate shifts is a major aim of current ecology.
  - (a) Varied responses
    - i. reversed phenology (Yu *et al.*, 2010)
    - ii. downhill shifts (Crimmins *et al.*, 2011)

- (b) Effects of climate change extend well beyond shifts in the mean
- 2. Models of community assembly in ecology build upon coexistence via environmental variability.
- 3. Launch into set-up.

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

## 7 Equations and related notes

For a species  $i$  let:

$N_i$  seedbank of species  $i$

$s_i$  survival of seedbank of species  $i$ , buffered pop'ln growth occurs via this constant

$\delta$  total time of growing season

$B_i$  biomass of species  $i$

$R$  resource

$f_i(R)$  resource uptake rate of species  $i$  of  $R$

$c_i$  conversion of uptake to biomass of species  $i$

$m_i$  partial mortality of species  $i$

$a_i$  uptake increase for species  $i$  as  $R$  increases

$\theta_i$  shape of uptake of species  $i$

$d_i^{-1}$  max uptake of species  $i$

$G_i$  max germination of species  $i$

$h_i$  max rate of germination decrease of species  $i$  following a pulse

$\tau_p$  time of pulse

$\tau_i$  time of max germination of species  $i$

$\epsilon$  abiotic loss of resource

$\phi_i$  conversion of biomass of species  $i$  to seedbank

$b_i$  seedling biomass of species  $i$

$\alpha$  phenological tracking of species  $i$

System of equations, for a community of  $n$  species based on resource competition:

$$N_i(t+1) = N_i(t+\delta)s_i$$

where

$$N_i(t+\delta) = N_i(t)[\text{germination fraction}][\text{seeds produced per germinant}]$$

so then:

$$N_i(t+1) = s_i(N_i(t)(1 - g_i) + N_i(t)g_i\phi_i \int_t^{t+\delta} [c_i f_i(R(t)) - m_i] B_i(t) dt)$$

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

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

where:

$$g_i = G_i e^{-h(\tau_p - \tau_i)^2}$$

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

Adding phenological tracking to model (October 2013 version):

$$\alpha \in 0 \rightarrow 1$$

$$\hat{\tau}_i = \alpha \tau_p + (1 - \alpha) \tau_i$$

thus:

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

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

Getting this into simulation-landia means:

$$B_i(0) = [\text{number of seeds}][\text{germination fraction}][\text{seedling biomass}]$$

which also looks like:

$$B_i(0) = N_i(t)g_ib_i$$

$$B_i(t + dt) = B_i(t) + [c_if_iR(t) - m_i]B_i(t)dt$$

Also note that I made one change from the February 2011 board: I think we used  $h$  accidentally twice for different meanings: one was in the equation for  $g_i$  which we stole from Chesson *et al.* (2004) (appendix, see next note), and then one was for the total length of time for the growing season. Thus I changed this ‘season-length’  $h$  to  $\delta$ .

Finally, equations for  $\frac{dB_i}{dt}$ ,  $f_i(R)$ ,  $g_i$ ,  $\frac{dR}{dt}$  were taken from the appendix of Chesson *et al.* (2004) (*Oecologia*).

Old (pre 2012) version of adding phenological tracking to the model:

$$\hat{\tau}_i = \tau_p - (\tau_p - \tau_i)e^{-\alpha}$$

thus, when:

$$\alpha = 0, \hat{\tau}_i = \tau_i$$

$$\alpha = \infty, \hat{\tau}_i = \tau_p$$

## Dimensional analysis

*Exciting new product as of August 2012, oh la la!*

Table 1: Table of parameter values, their definitions and lightweight version of their dimensions (i.e., not yet deemed ‘grams’ or such).

Parameter	Definition	Unit
$N_i$	seedbank of species $i$	seeds
$s_i$	survival of species $i$	unitless
$\delta$	total length of growing season	days
$B_i$	biomass of species $i$	biomass
$R$	resource	resource
$f_i$	resource uptake rate	$\frac{\text{resource}}{(\text{days})(\text{biomass})}$
$c_i$	conversion of $R$ uptake to biomass of species $i$	$\frac{\text{biomass}}{\text{resource}}$
$m_i$	maintenance costs of species $i$	$\text{days}^{-1}$
$a_i$	uptake increase as $R$ increases for species $i$	$\text{days}^{-1}$
$d_i$	max uptake for species $i$	$\frac{(\text{days})(\text{biomass})}{\text{resource}}$
$\phi_i$	conversion of biomass to seedbank for species $i$	$\text{biomass}^{-1}$ , but conceptually $\frac{\text{seeds}}{(\text{biomass})(\text{seeds})}$
$\epsilon$	abiotic loss of $R$	$\text{days}^{-1}$
$G_i$	max germination of species $i$	unitless
$h_i$	max germination of species $i$ following $R$ pulse	$\text{days}^{-2}$
$g_i$	germination fraction	unitless
$\tau_p$	timing of pulse	days
$\tau_i$	timing of max germination of species $i$	days
$\alpha_i$	phenological tracking of species $i$	unitless
$\theta_i$	shape of uptake for species $i$	unitless
$b_i$	seedling biomass of species $i$	$\frac{\text{biomass}}{\text{seeds}}$
$f_i(R)$	$R$ uptake $f(x)$ for species $i$	$\frac{\text{resource}}{(\text{days})(\text{biomass})}$

**Some random notes from the whiteboard:**

Relative nonlinearity is:

$$\left( \frac{d^2}{dR^2} \right) (var(R))$$

Non-additivity ( $\gamma$ ) is (in general, still working on what it is for our equations) when considering population growth ( $r_i$ ):

$$r_i = \omega_i(E_i, C)$$

$$\gamma = \frac{\partial \omega}{\partial E \partial C}$$

but, what is  $E$  and  $C$  in our system?

$$C = - \sum_{i=1}^n f_i(R) B_i \rightarrow f_i R$$

is this (above) the response to competition? An alternative note we had with many question marks was:

$$covar(E, C) \approx covar \left( R_i, \sum_{i=1}^n B_i \right)$$

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## 8 Small, somewhat random but fascinating questions

So what does it mean if species co-exist in the same community via mechanisms operating on totally different timescales?

New random query: Is there humidity without plants?

Also, someday, you could wonder if earlier  $\tau_p$  allows for more niche space for species at the end of the season that have a really low  $R^*$  (but for this we have to vary  $R^*$  among species, which we don't plan on doing now).

*Also, totally random note for Lizzie:* Trees use previous year's resources to flush leaves/flowers in current year.

Temporal redness, Mayan megadroughts and Californian invaders  
or  
Red noise and the sunset of Mayans and European invaders

Can we use this model to test if certain strategies (say, high tracking) can increase over shorter timescales but be completely excluded from this system given rarer, long-term (red) periods of environmental ‘harshness’?

To expand: My theory works as such: If a closed population of a species has a relatively short length for its buffered population growth—for example, imagine an annual grass with a 3 year seedbank—and enters a new system where the climate has long term fluctuations, could that population possibly do well during certain environmental phases, but be completely excluded (local extinction) during others. For example, the scenario is California annual invasive grasses: they do great now, but less well in drought years and large very long droughts (Mayan megadroughts are part of the ENSO cycle, possibly, and are decade or multi-decadal) could possibly throw them entirely out of the system. Thus the answer to the question I always get: If European annual grasses do so well in coastal sage scrub why weren’t there any native annual grasses? would be—wait a while and then you’ll see.

There is also an evolutionary angle to this: short lifespans and short seedbanks with these sorts of long-term cycles could lead to evolving quickly, during one climate phase, towards a damn stupid strategy when the next climate phase kicks in. But I don’t want to go there, just to point it out.

Opportunity to coin new term (from one term I hate and one that I like): **invasion extinction debt**, the number of invaders that would go extinct if you wait a very long time.

## 9 Old ideas

### 9.1 Mortality & phenology

We also discussed mucking with  $m_i$  (the partial mortality of species) to play around with shifts in extreme events such as more frost dates following spring warmth. But the above is more well-demonstrated or expected as climate-related issues so we're not going there. (Note from Lizzie in July 2011: I think this topic will be cool someday as it might be a real issue in subalpine communities, but for now it's not for sure. And given the equations we're using, it's not as crisp as the above to get from *environment*  $\rightarrow m_i$ . Note from Lizzie in October 2013: there is more on this now and it's been demonstrated for multiple communities. I have a literature review of this in the Appendix to my *New Phytologist* Tansley paper if we ever want to look at this. But I continue to think it is still a touch ahead of its time (which, really, just means that everyone is already excited about it and thus working on it without good data, so once I go running after truly just hot topics, this would be the one to do! But, luckily, I am not there yet).)

### 9.2 Correlated climate change variables

*From an old version of the abstract:* Specifically we examine how synergistic effects of climate on multiple abiotic variables—for example, earlier precipitation pulses and higher evapotranspiration associated with earlier snowpack melting in the Sierras—alter coexistence compared to single, unlinked variables ... We (might) find out that synergistic effects of multiple shifting abiotic variables reduce coexistence greater than single variables.

This was our big plan in July 2011, notes include:

We compare the compounding effect of climate change: examining how shifts in single versus multiple environmental variables affect coexistence.

As of July 2011 I would say that the greatest interest in setting up the paper lied in focusing on single vs. multiple variables, then putting in tracking as subordinate.

### 9.3 Do drivers of coexistence change with climate change? Scwing!

We decided not to work on this (for now) as of October 2013 meeting.

**Note:** Before our topic of interest was pretty damn significant: Do drivers of coexistence change with climate change (*schwing! Sexy!*)? So we should work this up, if not right away then soon after!

We decided on *no analytical solutions* to storage effect versus relative nonlinearity (which are the main coexistence mechanisms), but we could do some of this conceptually post-simulations. We noted in October 2013 that even if we come up with these analytical

solutions we'll still need an example, that is we would have to start with a community of  $n$  species that coexists via  $z\%$  relative non-linearity,  $x\%$  storage effect etc. and then we would impose climate change and see how  $z\%$  etc. change.

Again in October 2013: We again discussed the use to partition out relative non-linearity and storage effect and how they will shift with climate change (fluctuation independent mechanisms seem less important here) but again we felt this was tricky and still depends on the simulations we run so we focused on how we will alter the equations to focus on shifts in the storage effect with climate change.

## Resource pulse: plant-free case

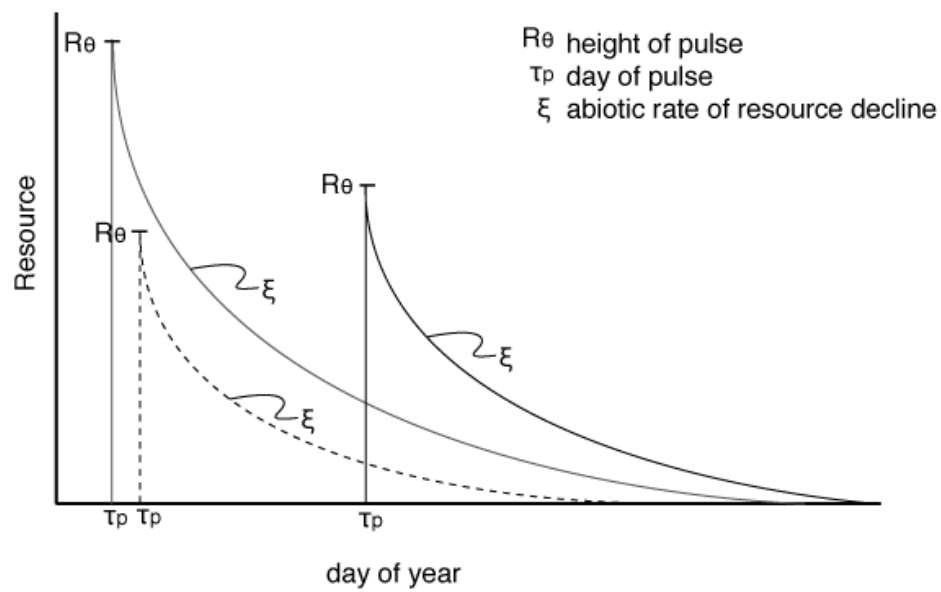


Figure 1: **Major coexistence variables directly affected by climate change** We focus on three major coexistence variables that have been (or will be) influenced by climate change—a couple examples of how varying them changes the resource pulse (without plants).

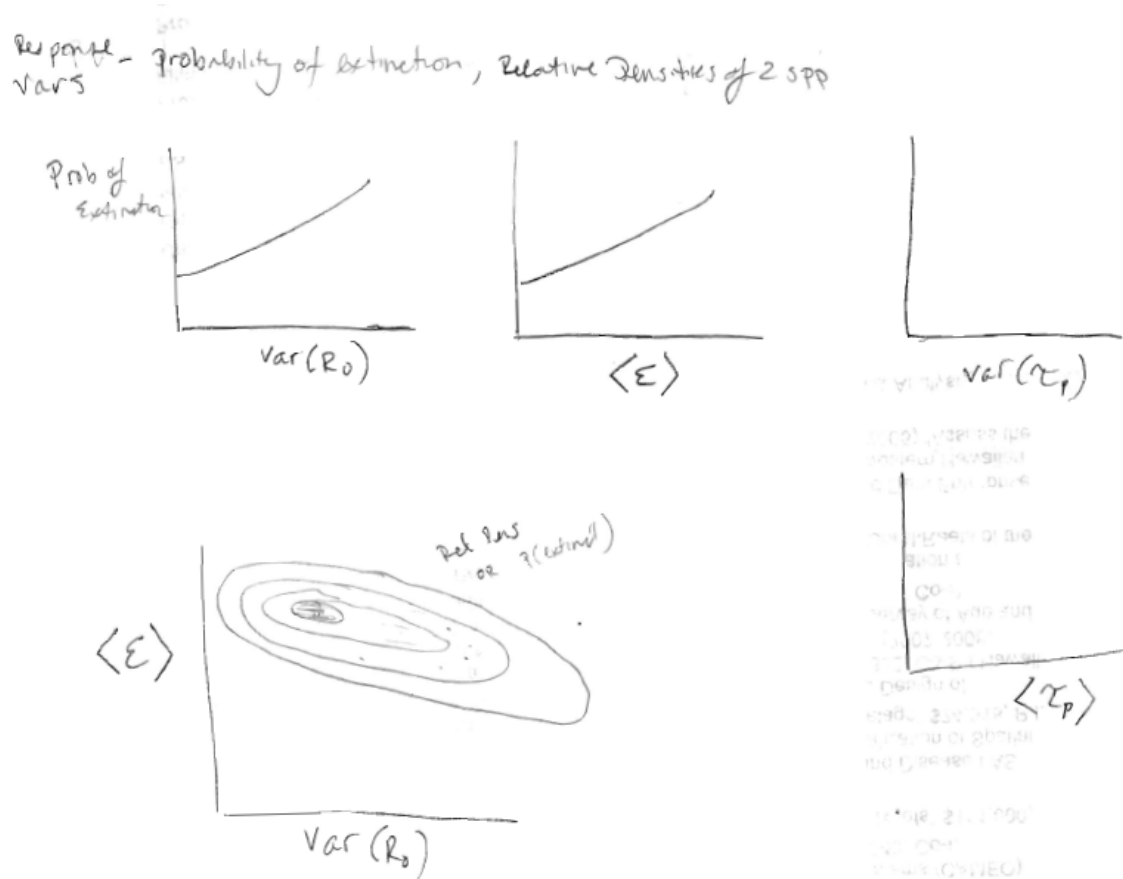


Figure 2: **Synergistic environmental effects.** Figure aspirations for part 1 of the paper, which covers how varying environmental variables ( $\tau_p$ ,  $R_0$ ,  $\epsilon$ ) alone and in concert (as predicted by climate change) alters coexistence. Single variables will be simple graphs, while contour plots will come in for varying more than one variable together. (There is no phenological tracking by species in this section of the paper.) From July 2011 meeting.

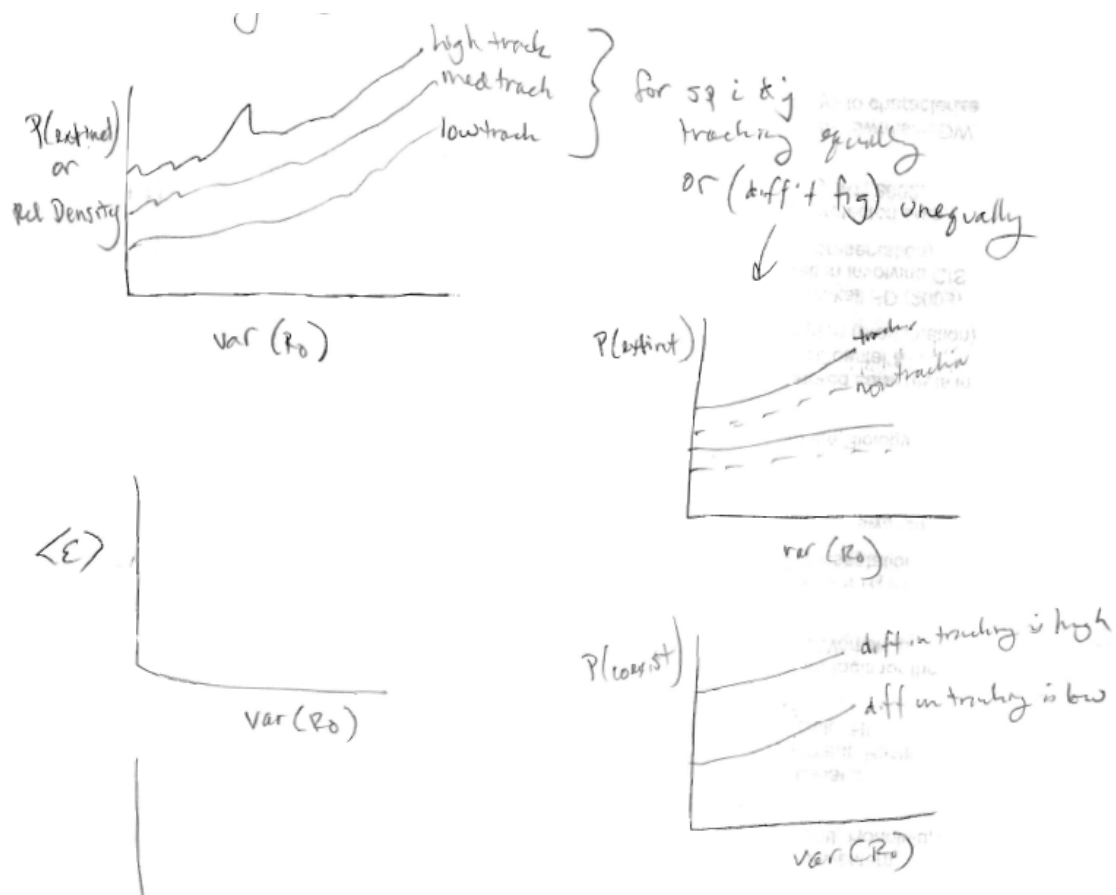


Figure 3: **Phenological tracking and coexistence under climate change.** We didn't quite nail these down: do we vary both species so they both track or look at one tracking and one not tracking? Hoping this will become clear as we get the model up and running. From July 2011 meeting.

## 10 Notes from meeting with various people

*Meeting with Jenn Williams*

15 October 2013

There are two big areas in modeling flowering reproduction stuff in plants:

1. When (which year) to reproduce
2. Bet-hedging across years (how much to reproduce)

There is not much (anything of which she is aware) of when within a year to reproduce. She pointed out that this is probably because it's easy to measure how fitness varies year to year but there not very good estimates of how fitness varies with weather a species' phenology is early or late.

Once she said this I though 'right!' and this jives with my reading of the literature (especially late 1970s and early 1980s, culminating a little with Ollerton & Lack's TREE paper). But, interestingly, climate change seems to be making this issue of how fitness correlates with phenology a critical topic (and something I realized I sort of work on, ugh). Also, Jeff Diez (new prof at Riverside) is doing some of this with a snowpack study he has started in the Alps (Levine lab).

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Most of the models include multiple decisions. And almost models to date work on death as the cost of reproduction (her and Tom Miller are actually pioneering how to model non-lethal costs such as 'if I reproduce I grow less').

How do models handle competition? They generally include density dependence in the seedling stage. Some sort of DD is necessary for any of the ESS (evolutionary stable strategy) models and everyone just tosses it in at the seedling stage.

Costs vs. trade-offs: costs manifest as trade-offs in many models. She thinks we should totally just toss in a trade-off and go for it. She does this a lot, she is just sure to apply the cost at several different doses (levels) although sometimes she only presents one level.

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She doesn't know the plasticity literature, Pigliucci (looks like he's in UT-Knoxville, I think) does some very general theory and plasticity stuff.



*Meeting with Sally Otto*

22 October 2013

Okay, so she didn't really answer my costs versus trade-offs question directly. She just dove in and suggested a new formulation with costs. She felt like a model that incurred mortality when germination occurred before the pulse would be better. You could then treat  $g_i$  possibly as a constant or such. I pointed out that  $g_i$  often creates  $covar(E, C)$  but I think her model may as well, but through the intra-annual part of the equation. I think there are probably other issues with her conceptualization as well (like how we would make tracking happen) but I haven't got there yet.

Let:

$D$  = normal distribution representing time of germination of species  $i$

$T$  = intra-annual time

Then, how about this (with a less funky equation for  $g_i$ ):

$$N_i(t+1) = s_i(N_i(t)(1 - g_i) + N_i(t)g_i\phi_i \int_{D=\tau_p}^{\infty} norm(\mu_p, \sigma_p)_D [\int_{T=D}^{t+\delta} B_i(T)dT]dD)$$