

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

Wolkovich, Donahue . . .

Last updated: 21 September 2012

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. 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 then examine how coexistence outcomes under shifting climate regimes vary with the ability of species to track the timing of major climate events. *We (might) find out that synergistic effects of multiple shifting abiotic variables reduce coexistence greater than single variables. 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, fall 2012 goals!

Was September-October 2011 goals, ohbother

Be sure to check out *Notes from August 2012* section below.

We have Matlab and R code running the model as a 2 species (we decided to start here, and then debate whether and how to extend to a more diverse community, but the code is in matrix format so the mechanics, if not the concepts and results, will be easy to extend) but we need to:

1. Check that it's running well and time-scales issues (intra- to inter-annual variability) are handled well. **Megan** needs to do this, including deciding 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.'
2. **Soon!:** Megan needs to update this with new equation for phenological tracking.

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

After the July 2011 meeting there are a couple major angles to this paper. I am not sure one has been picked yet, but one needs to pick up center stage someday and the others fall behind.

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

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.

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).

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_θ)
 - ii. Timing of resource pulse (τ_p)
 - iii. Abiotic loss rate of resource (ϵ)
- (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)
- (a) Section 1: Shifting abiotic variables, single versus co-varying shifts
 - (b) Section 2: Species traits: Phenological tracking and shifting abiotic variables
4. Discussion

5 Variables of interest

We consider 2 primary traits of the environment (ϵ , R , which code to evaporative stress and inter-annual variability for our approach basically) and 1 species response trait (phenology, specifically flexibility in phenology as modeled by a species' ability to shift τ_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 μ and *var* of R , which can lead to:
 - (a) Changes to relative non-linearity (shifts on the X axis due to new extremes etc.)
 - (b) Changes in inter-annual covar(E, C)
 - (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 ϵ* : Shifts in climate means that lead to greater abiotic stress on environments, as modeled by changes to ϵ . For example, warmer growing seasons may produce greater evapotranspiration, shifting competition for the remaining resource. (By the way, we have notes about treating ϵ as a function itself.) This should affect:
 - (a) Changes to relative non-linearity
 - (b) Changes in inter-annual covar(E, C)
3. *Changes to τ* : Longer growing seasons, with several scenarios:

- (a) Season is longer (earlier τ_p but community of species do not shift their timing (e.g., no change to $\tau_{i...n}$)
 - (b) Season is longer (earlier τ_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_θ increasing inter-annual variance with some giant years (extreme events), for snowpack systems it's decreasing generally
 - (b) τ_p getting earlier, also for snowpack systems earlier years probably also have higher evaporative stress (ϵ , 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.

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* $\rightarrow m_i$.)

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).

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.)

The 3 ingredients of the storage effect are:

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

6 Little things done and to do:

1. Done:

- (a) 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:
 - i. Species can have fixed flowering/leafing (not track).
 - ii. Species can phenological track pulse.
 - iii. 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).

- (b) 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.

- (c) Have looked twice now at 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.
 - (d) 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 balanced by inputs.
2. To do (Lizzie):
- (a) 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).
 - (b) Does evaporative stress increase with climate change (absolute, versus relative, oceans burn off while temperatures increase etc.)
 - (c) When seasons start earlier does evaporative stress increase (I suspect so, but need to pull together refs)
 - (d) Does lower snowpack mean earlier seasons?

7 Notes from August 2012

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 τ_i corresponds well to τ_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?

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

1. Use peak biomass instead of biomass at δ (when the growth rate goes below 0).
2. Set different δ for each species (δ_i)

Worries over growing season continue! 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.'

New response variables, perhaps? What are the traits of species that persist?

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.

8 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

δ 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

θ_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

τ_p time of pulse

τ_i time of max germination of species i

ϵ abiotic loss of resource

ϕ_i conversion of biomass of species i to seedbank

b_i seedling biomass of species i

α 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:

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

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

Adding phenological tracking to the model:

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

thus, when:

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

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

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 δ .

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

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
δ	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	days^{-1}
a_i	uptake increase as R increases for species i	days^{-1}
d_i	max uptake for species i	$\frac{(\text{days})(\text{biomass})}{\text{resource}}$
ϕ_i	conversion of biomass to seedbank for species i	biomass^{-1} , but conceptually $\frac{\text{seeds}}{(\text{biomass})(\text{seeds})}$
ϵ	abiotic loss of R	days^{-1}
G_i	max germination of species i	unitless
h_i	max germination of species i following R pulse	days^{-2}
g_i	germination fraction	unitless
τ_p	timing of pulse	days
τ_i	timing of max germination of species i	days
α_i	phenological tracking of species i	unitless
θ_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 (γ) 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:

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

References

- Chesson, P. (2000a). General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, 58, 211–237.
- Chesson, P. (2000b). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A. & Weltzin, J.F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.
- Chesson, P. & Huntly, N. (1993). Temporal hierarchies of variation and the maintenance of diversity. *Plant Species Biology*, 8, 195–206.
- Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, 331, 324–327.
- Kuang, J.J. & Chesson, P. (2008). Predation-competition interactions for seasonally recruiting species. *American Naturalist*, 171, E119–E133.
- Kuang, J.J. & Chesson, P. (2009). Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology*, 90, 170–182.
- Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–U130.
- Yu, H., Luedeling, E. & Xu, J. (2010). Winter and spring warming result in delayed spring phenology on the tibetan plateau. *Proceedings of the National Academy of Sciences of the United States of America*, p. doi: 10.1073/pnas.1012490107.
- Zak, D.R., Groffman, P.M., Pregitzer, K.S., Christensen, S. & Tiedje, J.M. (1990). The vernal dam - plant microbe competition for nitrogen in northern hardwood forests. *Ecology*, 71, 651–656.

Resource pulse: plant-free case

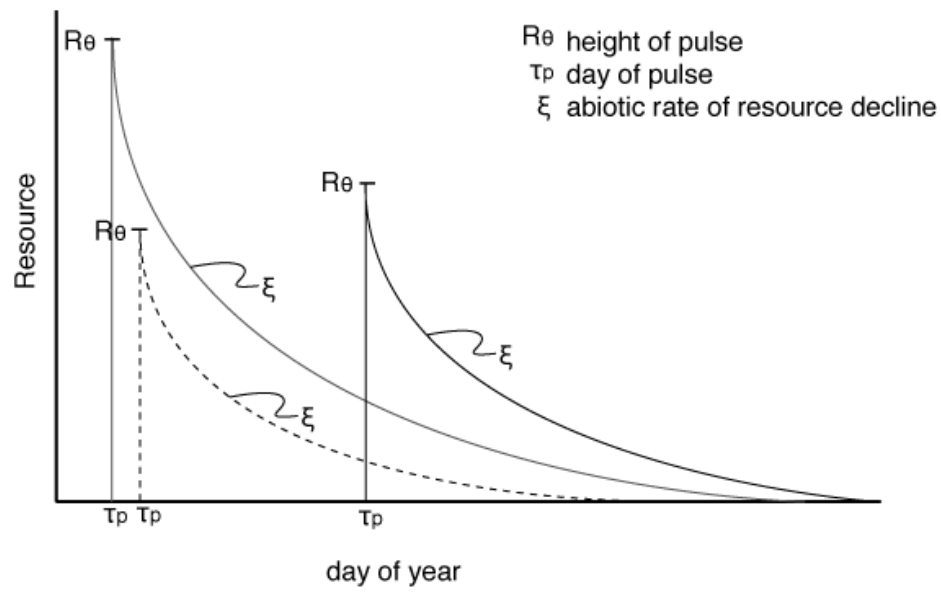


Figure 1: **Major coexistence variables directly affected by climate change** We focus on three major coexistence variables that have been (or will be) influenced by climate change—a couple examples of how varying them changes the resource pulse (without plants).

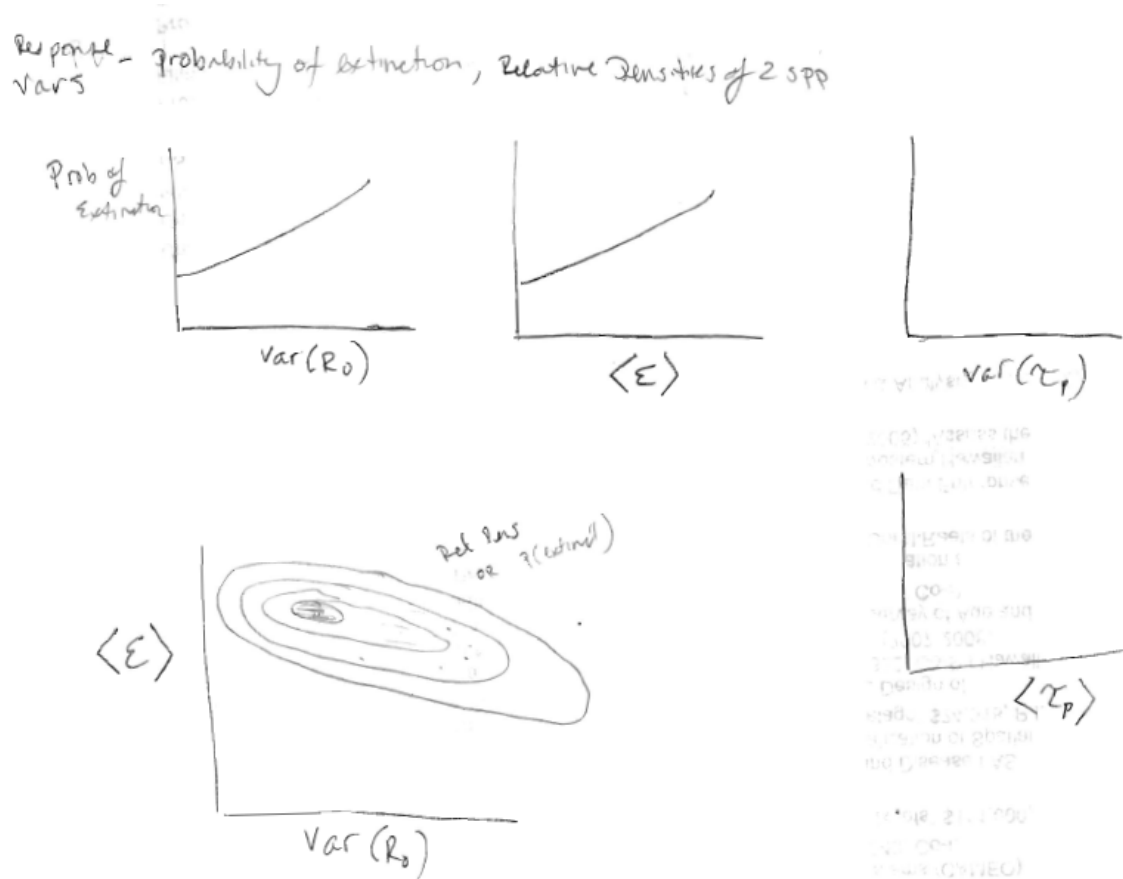


Figure 2: **Synergistic environmental effects.** Figure aspirations for part 1 of the paper, which covers how varying environmental variables (τ_p , R_0 , ϵ) alone and in concert (as predicted by climate change) alters coexistence. Single variables will be simple graphs, while contour plots will come 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.

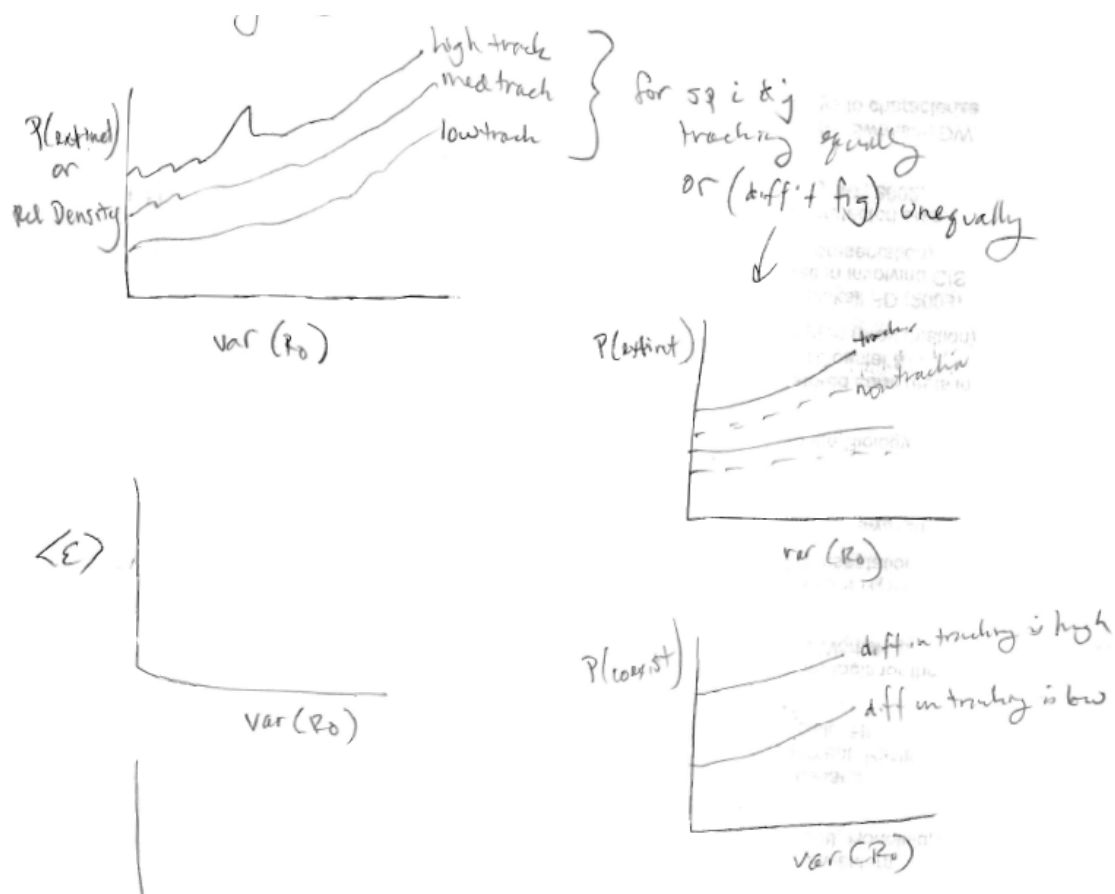


Figure 3: **Phenological tracking and coexistence under climate change.** We didn't quite nail these down: do we vary both species so they both track or look at one tracking and one not tracking? Hoping this will become clear as we get the model up and running. From July 2011 meeting.