

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

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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. (**Check!** As of December 2013 it seems all options are back on the table!)
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).

3.1 Do drivers of coexistence change with climate change? Schwing!

We decided not to work on this (for now) as of October 2013 meeting. But then we did an about face and were all over it by the December 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 urge 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.

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, 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 (ϵ , R , τ_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 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 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 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 in inter-annual covar(E, C)
 - (b) We ignore, for now, possible changes related to this in relative non-linearity
 - (c) Note that one basic prediction could be a decline in the storage effect with declines in ϵ . From Chesson *et al.* (2004):

... large evaporational [sic] water losses decrease the contribution of shallow-rooted plants to soil moisture depletion ... therefore decreasing the link between uptake and resource shortage As a result, the effectiveness of temporal resource partitioning by the storage effect would be lower in shallow-rooted species, because covariance between environment and competition would be less pronounced. Conversely, the storage effect should be stronger for plants rooted in soil layers where plant use of water is the dominant mode of depletion
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.

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 phenologically 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 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**. First off, we have a lot of versions of similar questions.

- 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?
- Follow up from October 2013: 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 dominant strategy?

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 perspectives. 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 (this ‘feasible’ and ‘dominant’ terminology is a little wobbly; I admit that))?

This tracking angle matches to the ‘Generalists, specialists and plasticity’ section of Chesson *et al.* (2004). You could imagine by removing the benefit of trade-offs associated with not being plastic, then nonstationarity could favour generalists (plastic species, that is). Here’s the most relevant bit (according to Lizzie):

However, plasticity, or any generalist resource consumption behaviors, including those involving drought resistance, may come at a cost In such circumstances, there is no contradiction that a generalist can coexist with specialists so long as the specialists are in fact superior performers during the times or conditions that favor them, and there are some times when no specialists are favored so that the generalist is then superior.

New notes as of October 2013:

How will we adjust the equations for simulations about shifts in the environment?¹

- We do **not** have relative nonlinearity: So we set all species $f(R)$ the same. (**Check!** As of December 2013 it seems all options are back on the table!)
- 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 $g_{max,i}$ and make them totally equivalent within season and temporal storage effect through $\tau_p - \tau_i$
 - As of 9 Dec 2013 Megan says: ϕ, c, m should be constant across species, while a, u, ψ could vary between species (but we did not discuss this much, it was just proclaimed quietly in passing).
- Note that one possible trade-off is earlier τ_i could correlate with lower competitive ability, which is mentioned in Chesson *et al.* (2004) on page 245: Coexistence would be promoted only when this temporal pattern entails tradeoffs, e.g., when later pulse users are able to draw down soil moisture to lower levels than are early users.
- 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 τ_p through time).

¹Not phenological tracking, which are other simulations.

New notes on trade-offs from 12 November 2013:

In nature early species have quicker-return-investments on growth and early is often high tracking, so it's hard to tell whether early *or* high-tracking trades off with this quicker-return angle. So what we plan on doing:

For now, for coexistence: we'll trade off c_i and τ_i , when we add in alpha we'll leave this above trade-off and maybe:

- get some coexisting species and add high tracking randomly to all and see what happens
- get some coexisting species and add high tracking to the early ones and see what happens

Megan's thoughts from the plane home: Can think of trade-off as competition-colonization one: rapid response to resource availability (colonization) versus special case of competition.

Megan! We would all benefit if you fix my hack of the following: Without tracking we may predict benefits to early-colonizers decline with earlier seasons. As start-date moves earlier, early folks lose benefit and you get more late folks. Late species may be less different than one another—and less responsive to environment. Early folks, effectively, become more similar to environment.

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.

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. τ_p will get earlier in many systems (alpine and nutrient), not sure on precip—there it might just get more variable
2. ϵ 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 τ_p and ϵ - 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 τ_p and ϵ (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 ϵ and R_0 maybe for alpine you could see, with climate change, increases in R_0 and decreases in ϵ , but we're still bickering on this and what ϵ really is (incident irradiance vs. relative humidity?)
6. Correlations in R_0 and τ 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 not so much anymore. Instead the *best place to start* seems to be: earlier τ_p and increases in ϵ and ϵ extreme events. Then maybe move on to R_0 (mean and extreme events). And again, just skip correlations.

Note that increased extreme events for ϵ 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 τ_p affects mortality has shifted with species' τ_i such that there is now higher mortality imposed on species with earlier τ_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 τ_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 τ_i earlier than τ_p is worse than τ_i later than τ_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 ϕ_i correlated with τ_i close to τ_p
- (for phenological tracking questions) decrease ϕ_i correlated with higher tracking²

(**Note:** As of December 2013 I think code has been adjusted to deal with this.) 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?

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

Set different δ for each species (δ_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 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

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

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: τ_i , which generates:
- $\text{covar}(E, C)$

τ_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 δI and δN 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: (Angert *et al.*, 2009; 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

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

u_i^{-1} max uptake of species i

$g_{max,i}$ 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, includes overwintering of seeds (as of December 2013)

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:

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

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

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 δ .

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:

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

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

Conceptualization of our germination equations:

A long debate with much thought in October 2013 (see also notes on meeting with Sally Otto, which offers an equation with a clearer cost, but also effectively assumes plants are dumber. Or to say that last bit more positively, ‘Peter’s model assumes plants are smarter,’ says Megan). Below are mainly Lizzie’s thoughts in December 2013.

I think you can compare our formulation to the basically 2-cue system discussed in Chesson *et al.* (2004). From pg. 238 he describes how each species basically has a temperature-dependent germination and how far from the pulse is from that optimum determines how much a species germinates each year. Importantly, he notes ‘The phenological difference in germination discussed above involves timing that is independent of water availability, in the sense that rain at the wrong time of the year or wrong temperature would not bring on germination or physiological activity.’ I can think of two examples you could conceptualize that are similar to this and relevant to the systems we have been thinking about.

- Snow meltout date in alpine communities as the pulse and temperature requirements (the sum of chilling and spring warming) as the other cue (this maybe works also for some other meadow communities).
- Nutrient flush date (due to microbial biomass turnover) in temperate systems as the pulse and temperature requirements (again, winter chilling and spring warming together) as the other cues.

These are a little sloppy in that the pulse is supposed to be separate from the cue I think (according to Chesson *et al.* (2004), see page 244); but this is sloppy in almost all systems in reality because climate is correlated and evolution means that species probably use that to their benefit.

So, basically I am happy with either the Chesson *et al.* (2004) formulation or the Otto formulation (which is Table 6.1, model 2 in Chesson (2008), ours is actually also in Table 6.1; it's model 3 but with variable adult biomass). The Chesson *et al.* (2004) seems one step ahead of Otto: costs in Otto's model would eventually remove most species with τ_i before the pulse while Chesson says species never germinate before the pulse, they just germinate to varying amounts depending on τ_p . One benefit of Sally's model though is that it may be better for climate change scenarios because it allows species to make 'bad decisions' (if you will) and get hammered for them; as many species have in recent years (e.g., Inouye, 2008).

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
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}
u_i	max uptake for species i	$\frac{(\text{days})(\text{biomass})}{\text{resource}}$
ϕ_i	conversion of biomass to seedbank for species, includes overwintering of seeds i	biomass^{-1} , but conceptually $\frac{\text{seeds}}{(\text{biomass})(\text{seeds})}$
ϵ	abiotic loss of R	days^{-1}
$g_{\max,i}$	max germination of species i	unitless
h_i	controls the the rate at which germination declines as τ_p deviates from optimum for species i	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	$\frac{\text{resource}}{(\text{days})(\text{biomass})}$
d_i	death rate of species i , used in calculations of lifespan	unitless
T	between year time	years
τ	within season time	days

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:

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

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8 Almighty figure aspirations

Figure 2 and 3 are ideas from Lizzie as of 11 December 2013, see also some older figure ideas at end of the paper (from 2011).

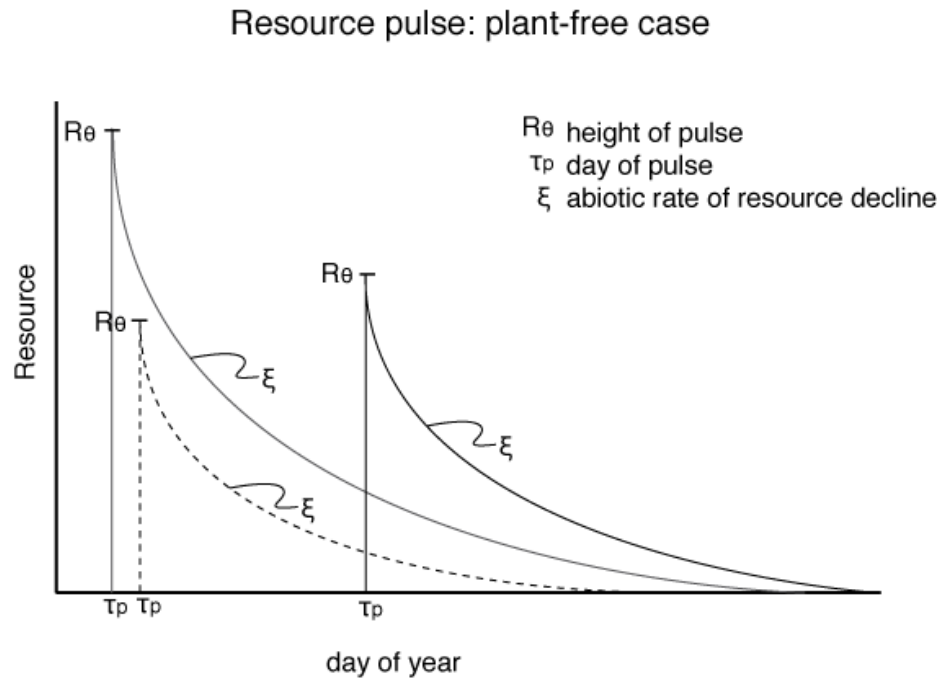


Figure 1: **Major coexistence variables directly affected by climate change** We focus on three major coexistence variables that have been (or will be) influenced by climate change—a couple examples of how varying them changes the resource pulse (without plants).

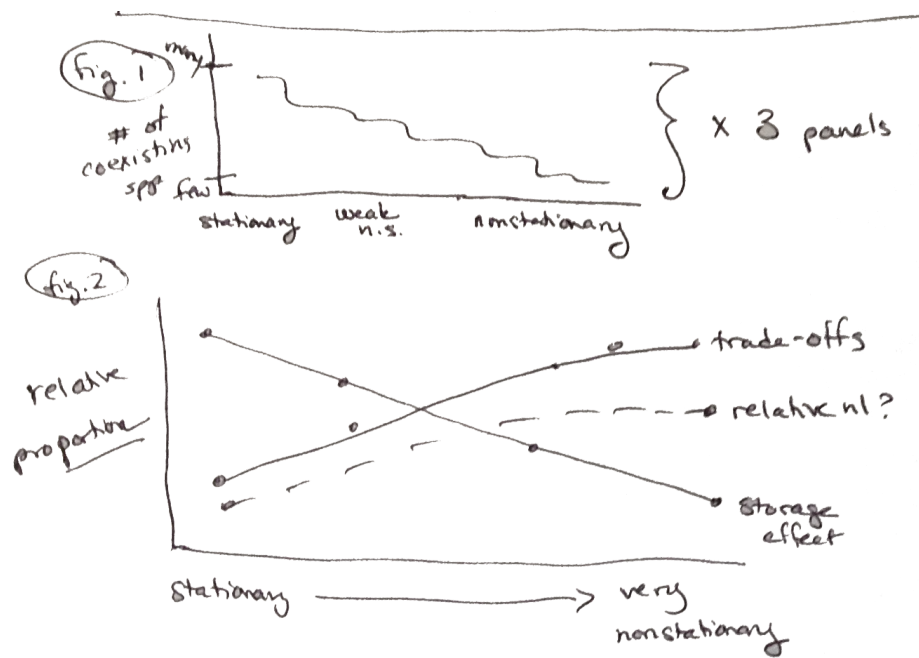


Figure 2: **How does climate change affect mechanisms of coexistence?** Two figures: the first is simple it's just the number (or percent of total possible) of species coexisting; the second figure is to look at how mechanisms shift with scenarios that are stationary, weakly nonstationary or strongly nonstationary. Each of these figures should be one panel for each variable manipulated (ϵ , τ_p and maybe R_0).

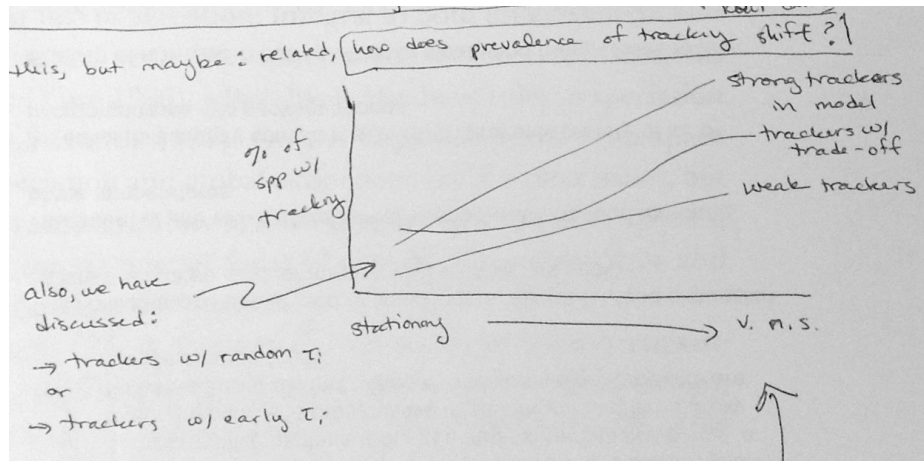


Figure 3: **How does the prevalence of tracking shift with nonstationarity?** See the section on tracking questions above for the full plethora of questions related to this (e.g., this is also the realm of how strong does the negative correlation between tracking and competitive ability have to be to make tracking non-advantageous). But, basically we want to look at how tracking shifts in stationary versus nonstationary systems. So we could do something like this (we also discussed looking at trackers with random τ_i versus trackers with early τ_i as you usually see in nature) and/or we could re-do the mechanisms of coexistence figures above with trackers in the mix.

9 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 τ_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.

We could bring Ben Cook on this project to give us some info on how frequencies of droughts have shifted over the past 2K years or so in North America. Or, maybe we could look at some shifts in drought periodicities globally just to press home the message that these can vary a lot across time.

10 Old ideas

10.1 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).)

10.2 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.

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?

11 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):

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

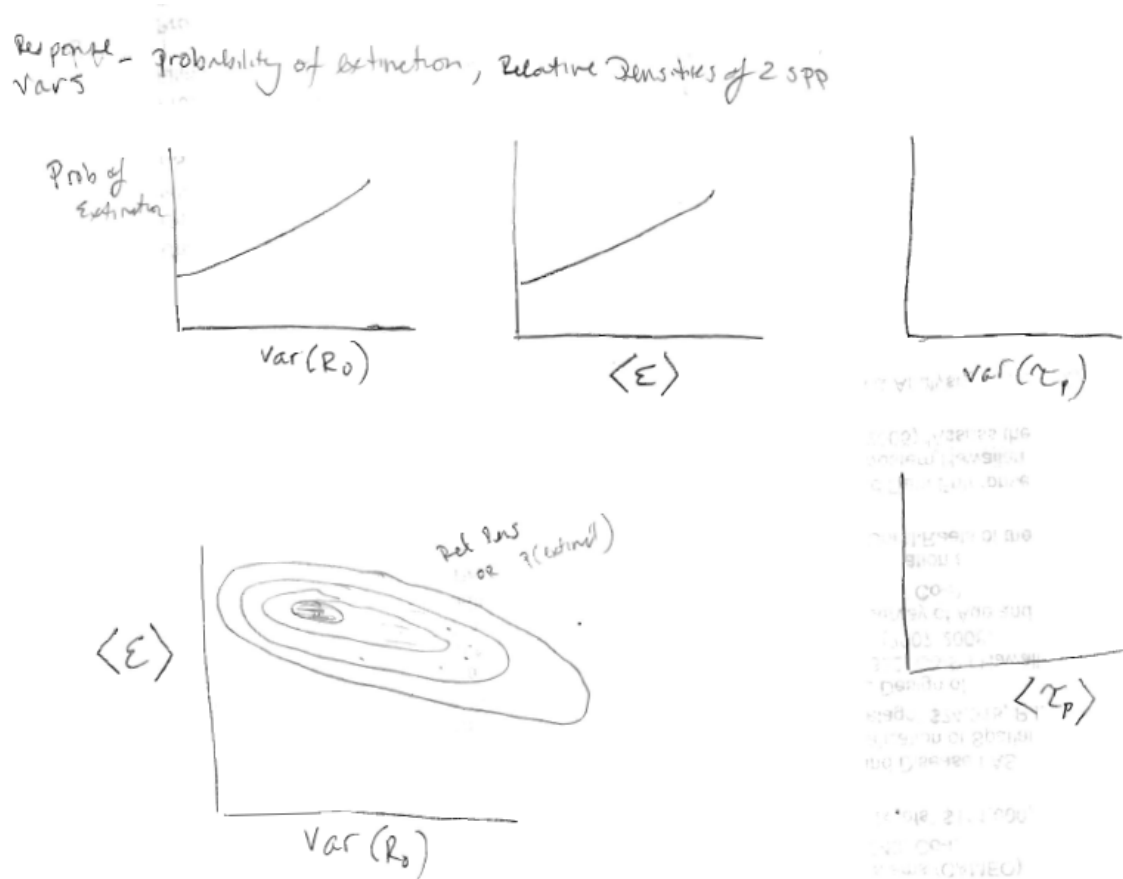


Figure 4: **Synergistic environmental effects (from 2011).** Figure aspirations for part 1 of the paper, which covers how varying environmental variables (τ_p , R_0 , ϵ) alone and in concert (as predicted by climate change) alters coexistence. Single variables will be simple graphs, while contour plots 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.

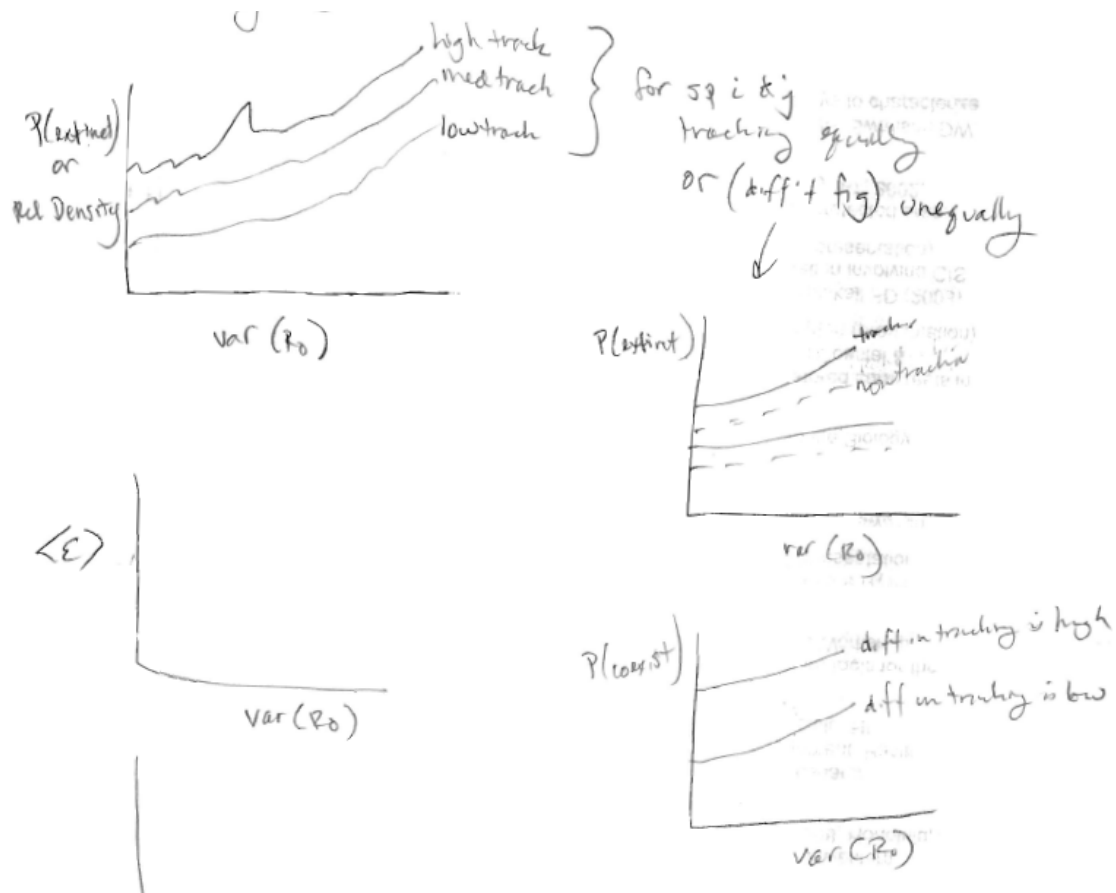


Figure 5: **Phenological tracking and coexistence under climate change (from 2011).** We didn't quite nail these down: do we vary both species so they both track or look at one tracking and one not tracking? Hoping this will become clear as we get the model up and running. From July 2011 meeting.