

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. Much 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.*

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1 Next steps, goals!

1.1 Write-up current state of progress for mechanisms of coexistence

Megan will write up where she arrived at as of 8 August 2015 working off Chesson 1994 (TPB) and Chesson 2003 (TPB also I think). See file `VarEnv_CoexistEqns.tex`.

1.2 Get R^* model running by 7 September 2015

So, Megan needs to (1) confirm issue we left last were working on with model and (2) help solve it (note, we think the problem was how to get ODE solver to end a season for each species when it reaches its R^* value).

1.3 Get parameter simulations running by 7 September 2015

So, Lizzie needs to get the code to run through sweeps of parameters running, including figuring out how to get it up on Research Computing.

1.4 Figure out rankings of species?

This should come be R^* (fluctuation independent) plus the equalizing bits (fluctuation dependent). Once we have this, it will be good to look at: (1) if the cut-off in coexistence shifts with nonstationarity and (2) how the spread between species shifts with nonstationarity.

1.5 Get phenological tracking up and running

Old note, does this still apply? First, to make life easy I (Lizzie) will swap the hats when coding. So what we call $\hat{\tau}_i$ I will call τ_i and vice versa.

1.6 Writing tasks for Lizzie

(1) Write out clear questions to address in each paper and (2) add references for Chesson citations above and below. Also, maybe (3) remove equations from Feb-Jan 2015 below. And add in any references to other files that Megan works up. *And then read all these notes over for clarity etc..*

1.7 Schedule when to next meet

Right-o.

2 Introduction

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 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 aim to make this project more interesting, useful and forward-thinking than others by making 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, trade-offs between competition and early flowering, 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).

Predictions: Even though we are not shifting $var(R_0), var(\tau_p), var(\epsilon)$ we are shifting E (species' responses to environment) and thus $var(E)$ may increase. That could be cool.

Products: We currently envision two papers:

1. *Shifting drivers of coexistence with climate change*, which includes all the work to date (December 2013), plus phenological tracking
2. *Mayan megadroughts and climate change*

See below for outlines and info on each.

4 Notes from 8 August 2015

In May 2014 we wrote, ‘To review, the goal really is the Mayan invaders project. Once we’re there we’re in good shape.’ And that’s basically back where we ended up after a week of work in August 2015, skipping for now all the mechanisms of coexistence.

The longer story behind this outcome is that we spent about a week working through Chesson 1994 (TPB, section 5.5) and Chesson 2003 (TPB also I think) trying to figure out how to fully sort out the mechanisms of coexistence using a simple Lotka-Volterra model we started working on in January-February 2015 (though I think we started re-working on mechanisms of coexistence as of December 2013 at least). We decided for now to table this work and switch back to the R^* with a focus on the phenological tracking questions.

5 Notes on coexistence mechanisms

We spent a substantial amount of time carefully working through Chesson 1994. A few notes on how this might apply to nonstationarity

- In the General Model, growth rate is divided into E and C components. To examine the effects of fluctuations using a Taylor approximation, r is examined around E^* , C^* , where growth rate is 0.
- The model is reparameterized in terms of curly-E, curly-C, which is the complete growth function, reparameterized around C^* and E^* , respectively. To make the Taylor approximation, it is limited to variability around E^* , C^* of order O_2
- the approximation is also limited to the behavior of the function around the point E^*, C^* , such that if the curvature of the function changed at a point far from E^*, C^* , this nonlinearity would not be captured.
- the approximations are made with the assumption of a stationary process, without temporal autocorrelation and drawn from the same distribution through time. This approximation is the one that makes studying nonstationarity with these approximations difficult.
- we came up with a couple ideas about how coexistence mechanism partitioning might still be useful, even without stationarity. For example, you could compare coexistence and coexistence mechanisms present at the beginning and end of a period of change. The likely outcome is that species will continue to persist after they should have gone extinct because of lags. It is hard to think of a case when the converse would be true, at least under the case of mean change. If the variance is changing, then the outcomes are less obvious and might include increased coexistence

I worked through Section 4: Analysis of the General Model, however, actually doing those calculations with any particular model is tricky, particularly making an assumption for E^*, C^* . Using Section 5.5 as an example, I tried to work through the calculations for our

simple model. Equation 95 is largely equivalent to our simple model. The only difference is that we originally parameterized competition as $(1 + \sum j(g_{j,t} * X_{j,t} * \alpha_{ij}))$ (CHECK this equation, where does j belong?), but equation 96 has competition as a simple sum, with no additional $+1$.

Section 5.5 is the same as our simplified model. Understanding through Equation 99 is clear. Table II lists the parameters of the seedbank model, and the definition of these terms is clear. To understand the terms in Table III, we still need to define rho and sigma and to make the correct assumption about the value of E^* and C^* . The assumptions around E^* , C^* are a sticking point and where I got stuck. Looking back at the notes now, however, it seems like there may still be some room forward here. We are proceeding on the simulations, but Megan will spend a little more time to see if we can actually make the calculations in Table III.

5.1 Overview

After thought, discussion, up and downs we have decided to move ahead on... **the R^* model of 2014 and before and phenological tracking.** This has several benefits:

- It focuses the work on a biologically-meaningful topic Lizzie can write easily about.
- It makes the work hinge less strongly on how we model nonstationarity.
- It does not require calculating the mechanisms of coexistence, which really would be handy to make sense out of any project where we focused more broadly on answering ‘What happens to communities when the environment becomes nonstationary?’
- The R^* is complicated enough to have interesting dynamics and make it less obvious why we do not calculate mechanisms of coexistence.
- It still lets us get to the Mayan megadrought question (which requires a pulse size to have droughts occur). Yay!

5.2 Three-part approach to project

Possible titles: ‘Phenological tracking: It’s more complicated than you think’ (we hope) or ‘Phenological tracking: Is it naive?’

1. Under a stationary environment what trade-off is required with tracking to allow coexistence?

(a) Two species (i, j) case

- i. Vary τ_P by drawing from a stationary distribution and let R^* and α also vary by being drawn from each of their own (non-joint) distributions, run a bunch of models of 2 species communities and extract co-existing ones.
- ii. Plot $\frac{\alpha_i}{\alpha_j}$ (or, perhaps better: realized proximity to τ_P) by $\frac{R_i^*}{R_j^*}$ for coexisting pairs of species (PhenTrackFig. 1, not currently shown here, see paper notes)
 - we expect a cloud of space where coexistence is possible.

(b) Multi-species case

- i. (Similar to above) Vary τ_P by drawing from a stationary distribution and let R^* and α also vary by being drawn from each of their own (non-joint) distributions for a $n > 2$ set of species, and pull out coexisting species from each run.
 - ii. Plot α (or realized proximity to τ_P) against R^* for each community of coexisting species (PhenTrackFig. 2, not currently shown here, see paper notes), measure the correlation and the noise around it.
 - iii. Examine the distribution of correlations (and maybe noise) for all communities (PhenTrackFig. 3, not currently shown here, see paper notes).
2. Under a non-stationary environment of earlier τ_P how: (1) does this trade-off change and (2) do communities change?¹
 - (a) Two species case: take the coexisting 2-species communities from part I and add nonstationarity in τ_P and ...
 - i. see how long it takes to lose one species.
 - ii. see which ones persist longest and mark on PhenTrackFig. 1 (e.g., re-do PhenTrackFig. 1 with bubble plots or such for how long the two species persist together).
 - (b) Multi-species case: take the coexisting multi-species communities from part I and add nonstationarity in τ_P and ...
 - i. stop at X timepoint and re-do PhenTrackFig. 2 and 3 to see how they have shifted (e.g., you may lose the middle species — those that are not the best competitors nor the best trackers ...).
 - ii. extract timepoints when 10% and/or 50% of species are lost.
 - iii. extract when each species is lost in a community and order the species loss of PhenTrackFig. 2.
3. Are there environmental conditions under which tracking won't work as a strategy?
 - (a) Thinking about environmental correlations (e.g., spring gets earlier and drier or such), are there some where tracking will not be favored?
 - (b) Answer: Yes, probably whenever you shift the environment in another way (in addition to earlier τ_P) that does not impact the competitive dominant but does negatively impact the competitive inferior/tracker (See also Figure 1 below).
 - (c) So, for example if τ_P gets earlier *and* R_0 gets smaller then the trackers may decline.

A few things:

- We may also need to think about how τ_i works in these simulations to better understand how α_i works.
- Measuring coexistence, a couple options

¹Megan may have better notes on this section

- Long-term persistence
- Run the model to persistent-looking conditions and show each species can increase from low-density using long-term mean densities of other species.

5.3 Connections to Mayan Megadroughts project

We broke down this trade-off to: Wider (probably shorter) germination curves trade off with shorter seedbank life such that ...

- Exotics have wider (probably shorter) germination curves – so they go basically whenever a pulse is, no matter what size it is.
- Natives have narrower (probably taller) germination curves – so they go only when a pulse happens at a certain time.
- Exotics have short-life seedbanks, natives have longer-life seedbanks.
- Thus, if you add in mega-droughts (repetitive low-pulse size years) the exotic species will continue to germinate a high fraction of seeds each year, but get little biomass and new seeds out of the germinating seeds, leading to a negative growth rate that does not rebound before the whole seedbank is wiped out. Natives don't do this. (See also Figure 1 below).

This is similar to the tracking in that both have to do with how *responsive to the environment* species are.

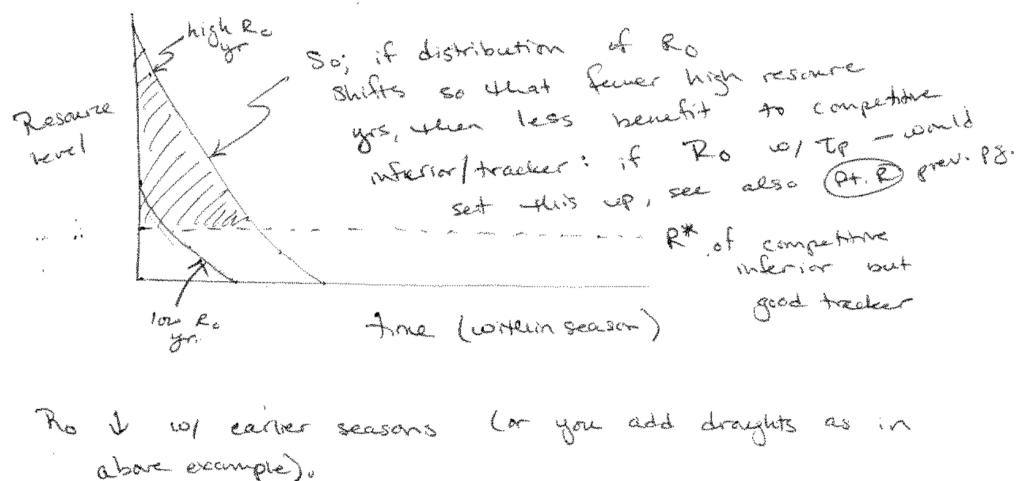


Figure 1: **How drought could negatively impact phenological trackers:** Two curves for the same species—a competitively-inferior phenological tracking species—one showing how it responds to a drought (low resource pulse, R_0) and another to how it responds in a high drought year (high resource pulse).

6 Equations and related notes: January-February 2015

Megan's notes from 27 January 2015, following Chesson (2003) and Godoy & Levine (2014). Note that j is the species index (focal species), i is the invader and l is the supplementary index (that is, all the other species):

$$N_j(t+1) = (1 - d_j)N_j(t) + R_j(t)N_j(t) \quad (1)$$

$$g_j F_j = \frac{\lambda_j}{1 + \sum_l \alpha_{jl} g_{l,t} N_{l,t}} \quad (2)$$

Breaking down equation 1 and following how Godoy & Levine (2014) treats d we can separate E and C in the following way:

$$(1 - d_j) = \text{survival in seedbank} = s_j(1 - g_j) \quad (3)$$

$$R_j(t) = \text{germination \& death in seedbank} = 0(1 - g_j)(1 - s_j) + g_j F_j = g_j F_j \quad (4)$$

$$g_j F_j = \frac{g_j \lambda_j}{1 + \sum_l \alpha_{jl} g_{l,t} N_{l,t}} \quad (5)$$

$$= \underbrace{\ln(g_j \lambda_j)}_{E_j(t)} - \underbrace{\ln(1 + \sum_l \alpha_{jl} g_{l,t} N_{l,t})}_{-C_j(t)} \quad (6)$$

However, this definition of E and C results in d that varies with time because d includes $g_j(t)$. How do we avoid this?

Currently:

$$N_j(t+1) = (1 - d_j)N_j(t) + R_j(t)N_j(t) \quad (7)$$

$$= \underbrace{s_j}_{\text{surv. did not germ.}} \underbrace{(1 - g_j(t))}_{\text{surv. did not germ.}} N_j(t) + g_j(t) F_j(t) N_j(t) \quad (8)$$

$$= s_j N_j(t) + g_j(t) F_j(t) N_j(t) \quad (9)$$

Alternatively, we can rearrange the equation so that sN is a distinct term (i.e., d does not vary with time). If we continue to assume a pre-season count, then rearrange:

$$\begin{aligned} N_g F + N(1 - g)s * 1 + N(1 - g)(1 - s) * 0 \\ gFN + s(1 - g)N \\ sN - sgN + gFN \\ sN + g(F - s)H \end{aligned}$$

Reorganizing the survival and germination terms in this way gives equation:

$$N_j(t+1) = (1 - d_j)N_j(t) + R_j(t)N_j(t) \quad (10)$$

$$= s_j N_{j,t} + g_{j,t}(F_{j,t} - s_j)N_{j,t} \quad (11)$$

$$\ln R_{j,t} = \ln(g_{j,t}(\frac{\lambda_j}{1 + \sum_l \alpha_{jl} g_{l,t} N_{l,t}} - s_j)) \quad (12)$$

$$= \underbrace{\ln g_{j,t}}_{E_{j,t}} + \underbrace{\ln(\frac{\lambda_j}{1 + \sum_l \alpha_{jl} g_{l,t} N_{l,t}} - s_j)}_{-C_{j,t}} \quad (13)$$

Now that we have defined the general form of the equation, we can calculate the long-term low density growth rate for each species as invader (i.e., invasibility criterion for coexistence). The long-term low-density growth rate (including temporal but not spatial variability) has three components (Table 1 in Chesson (2003): **mean fitness**, **storage effect**, and **relative nonlinearity**.

Evaluate the growth rate of each species as invader. Note that i is for invader, j is any species, and l is a counter to go through all species, with or without invader.

Mean Fitness

$$\begin{aligned} \frac{\bar{r}_i'}{d_i} &= \delta\mu_i + \delta V_i \\ \delta\mu_i &= \mu_i - \bar{\mu}_l^{(l \neq i)} \\ &= \mu_i - \frac{1}{n-1} \sum_{l \neq i}^n \mu_l \\ \mu_j &= \langle E_j \rangle - \ln d_j \\ &= \langle E_j \rangle - \ln(1 - s_j) \\ \sigma_j^2 &= \text{var}(E_j) \\ \delta V_i &= \frac{1}{2}(1 - d_i)\sigma_i^2 - \frac{1}{2}(1 - d_j)\sigma_j^2 \quad (j \neq i) \\ &= \frac{1}{2}(s_i\sigma_i^2 - \frac{1}{2} \sum_{l \neq i}^n s_l \text{var}(E_l)) \end{aligned}$$

$$\langle E_j \rangle = \langle \ln g_{j,t} \rangle \quad (14)$$

$$\mu_j = \langle \ln g_{j,t} \rangle - \ln(1 - s_j) \quad (15)$$

$$(16)$$

$$\text{var}(E_j) = \text{var}(\ln(g_{j,t})) \quad (17)$$

$$\delta V_i = \frac{1}{2} s_i \text{var}(\ln(g_{i,t})) - \frac{1}{2} s_j \text{var}(\ln(g_{j,t}))^{(j \neq i)} \quad (18)$$

$$\text{var}(\ln g_{j,t}) = h^2 \text{var}(\tau_{p,t}^2 - 2\tau_{p,t}\tau_i) \quad (19)$$

$$(20)$$

$$g_{j,t} = G_{\max} e^{-h(\tau_{p,t} - \tau_i)^2} \quad (21)$$

$$\ln g_{j,t} = \ln G_{\max} - h(\tau_{p,t} - \tau_i)^2 \quad (22)$$

$$\langle \ln g_{j,t} \rangle = \ln G_{\max} - h \langle (\tau_{p,t} - \tau_i)^2 \rangle \quad (23)$$

$$\dots \text{skipping some intervening equation work...} \quad (24)$$

$$= \ln G_{\max} - h(\sigma_{\tau_{p,t}}^2 + (\mu_{\tau_{p,t}} - \tau_i)^2) \quad (25)$$

For the case where $\tau_p \sim \beta(p, q)$

we can calculate the expected value and variance of $\tau_{p,t}$ explicitly :

$$\text{var}(\tau_p) = E\langle \tau_p^2 \rangle - \langle E\langle \tau_p \rangle \rangle^2$$

$$\text{var}(\tau_p) + E\langle \tau_p \rangle^2 \text{ Megan, is this extra from above or ...?}$$

$$E\langle \tau_p \rangle = \frac{p}{p+q}$$

$$\text{var}(\tau_p) = \frac{pq}{(p+q)^2(p+q+1)}$$

Storage Effect

$$\begin{aligned} \frac{\Delta I_i}{d_i} &= \overline{(1-d_j)\chi_j^{(-i)}}^{(j \neq i)} - (1-d_i)\chi_i^{(-i)} \\ &= \sum_{j \neq i} s_j \chi_j^{(-i)} - s_i \chi_i^{(-i)} \end{aligned}$$

$$\chi_j^{(-i)} = \text{cov}(E_j, C^{(-i)}) \text{ where } C_{(-i)} \text{ is competition when sp } i \text{ is invader}$$

$$\chi_j^{(-i)} = \text{cov}(\ln g_{j,t}, \ln(\frac{\lambda_j}{1 + \sum_{l \neq i} \alpha_{jl} g_{l,t} N_{l,t}} - s_j))$$

$$\chi_i^{(-i)} = \text{cov}(\ln g_{i,t}, \ln(\frac{\lambda_i}{1 + \sum_{l \neq i} \alpha_{il} g_{l,t} N_{l,t}} - s_i))$$

Relative Nonlinearity

$$\frac{\Delta N_i}{d_i} = \frac{1}{2} \text{var}(C^{(-i)})(d_i - \bar{d}_j^{(j \neq i)})$$

$$\text{var}(C^{(-i)}) = \text{var}\left(\ln \frac{\lambda_j}{1 + \sum_l \alpha_{il} g_{l,t} N_{l,t}} - s_j\right)$$

$$\bar{d}_s^{(s \neq i)} = \frac{1}{n-1} \sum_{l=i} (1 - s_l)$$

Calculation of C_t In Chesson 2003, the calculations in Table 1 are for $C_t^{(-i)}$, i.e., the community competition with the invader absent. In principle this makes sense: if we consider competition experienced by the invader to reflect the level of resource remaining after consumption by all resident species, then $C_t^{(-i)}$ depends only on the identity of the invader. For calculate the storage effect, we must calculate the covariance between environment and competition: $Cov(C_{j,t}, E_{j,t})$. In this case, we can calculate species-specific $C_{j,t}$ and $E_{j,t}$, with $C_{j,t}$ as the annual competition experienced by species j , i.e., $C_{j,t} = \ln\left(\frac{\lambda_j}{1 + \sum_{l \neq i} \alpha_{jl} g_{l,t} N_{l,t}} - s_j\right)$. However, when we calculate relative nonlinearity using the equation in Chesson (2003) Table 1, we need to calculate $\text{var}(C_t^{(-i)})$, which should be the same for all species. It is not clear how the annual community competitive effect should be calculated. The denominator in the equation for C is easy to calculate for all but the invader. But this is multiplied by a species-specific term (λ_j) and a species-specific term is subtracted s_j . Therefore, I wonder if the simple equations in Table 1 are not appropriate for this case. Even if the competitive effects were proportional by species (not the case because of the subtraction of s_j) then the terms in Table 1 would need to be scaled by λ_j .

7 Equations and related notes: R^* model

For a species i let (note: see dimensional analysis for full list of current terms, I need to update this here someday):

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

7.1 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 (peak biomass)	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 (formerly T)	years
$0 \rightarrow \delta$	within season time (formerly τ)	days
b_0	initial biomass per germinant (seed)	biomass
ξ	$\frac{\text{final biomass}}{\text{initial biomass}}$	unitless

Note for δ : $B(t+0)$ is start of season biomass while $B(t+\delta)$ is the end of season biomass. Also note: that s applies to seeds *in* seedbank, while ϕ thus includes some death for current season seeds (see red/blue diagram from 12 May 2014 whiteboard photos).

7.2 System of equations

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:

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

where:

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

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

and the initial condition is:

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

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:

$$B_i(0) = N_i(t) g_i b_i$$

$$B_i(t + dt) = B_i(t) + [c_i f_i R(t) - m_i] B_i(t) dt$$

7.3 Notes related to equations

Also note that I (Lizzie) 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*).

R^* does not change with nonstationarity because it is based solely on species-specific characteristics not related to the environment (says Megan, December 2013).

7.4 Definitions of coexistence

In December 2013, we discussed how we will define coexistence. There are a couple options, the second one is better:

1. Persistence of species in simulations: This is not ideal since you would have to run things a long time and still not know what would truly coexist. But if we do have to do this it is not all bad: if we run stationary then nonstationary environments (one after another, not separate) we can think of it as ‘here are the species co-occurring.

Sure, some may be on Hubbellian random walk to extinction, but that is probably how the real world works anyway.’

2. Recovery from low-density: For this we need to calculate long-term low density growth rate from either (1) simulations or (2) equations. Equations would be better and would allow us to run stationary and nonstationary simulations separately. This equation should come out of final storage effect equations.

7.5 How biomass is converted to seed and growing seasons end

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 climate change 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.)

So what we do about it... It used to happen 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. Instead now we let resources go to the lowest R^* and then we take peak biomass (for each species) instead of biomass at δ (when the growth rate goes below 0), to convert to seeds.

7.6 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).

Note: h yields different bet hedging strategies.

7.7 A few assumptions spelled out

We assume that:

1. All species 'go' each year, at least a little; that is, we're not looking at communities where some species have true supra-annual strategies.
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.

7.8 Simplifying within-year dynamics thoughts

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, so could we create a 'deterministic look up table' for the within-year dynamics so we can 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'.)

7.9 Tiny notes about the storage effect to help Lizzie

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

8 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 model (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 that 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 perspective. Next, we could also see *what we know about climate projections* and from there see how big do the trade-offs have to be with climate change to make non-tracking a feasible strategy (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.

As of August 2015 we decided **against doing tracking with joint distributions**, but here are the old notes on it:

Next up, I need to work on how to make joint distributions in R (all different types, not just multivariate normal ones) so we can link α_i with c_i . For this I need to look into copulas and the R package `copula`. See also these pages:

<http://www.r-bloggers.com/copulas-made-easy/>

<https://sites.google.com/a/wisc.edu/jed-frees/multivariate-regression-using-copulas>

9 Coexistence with climate change: Notes related to implementing and writing

9.1 Current outline for paper

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) 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) number of species coexisting, (2) relative shifts in coexistence via storage effect, relative nonlinearity and other factors and (3) the traits of species that persist? Additionally, response variables (probably α, τ_i, c_i) related to 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

9.2 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) 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) 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)

9.3 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.

9.4 Species differences: How to thoughts

New notes as of October-December 2013: *Models without tracking*:

How will we adjust the equations for simulations about shifts in the environment? For now we plan to let parameters vary some and see if we can pick out patterns. If this gets tricky we can switch to trade-offs between τ_i and c_i .

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.

(Old question from October 2013, maybe should cut): 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).

Models with tracking:

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
- add weak versus strong tracking

Comparisons with competition/colonization trade-offs: Can think of trade-off as competition-colonization one: rapid response to resource availability (colonization) versus special case of competition.

Without tracking we may predict benefits to early-colonizers decline with earlier seasons. As start-date moves earlier, early folks lose benefit (assuming they tend to often go at optimum time) 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.

10 Notes on megadroughts paper

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 of 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.

11 Miscellaneous notes

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)

11.1 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).

11.2 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:

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

11.3 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^* .

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

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13 Almighty figure aspirations

Figure 3 and 4 are ideas from Lizzie as of 11 December 2013, see also some older figure ideas at end of the paper (from 2011).

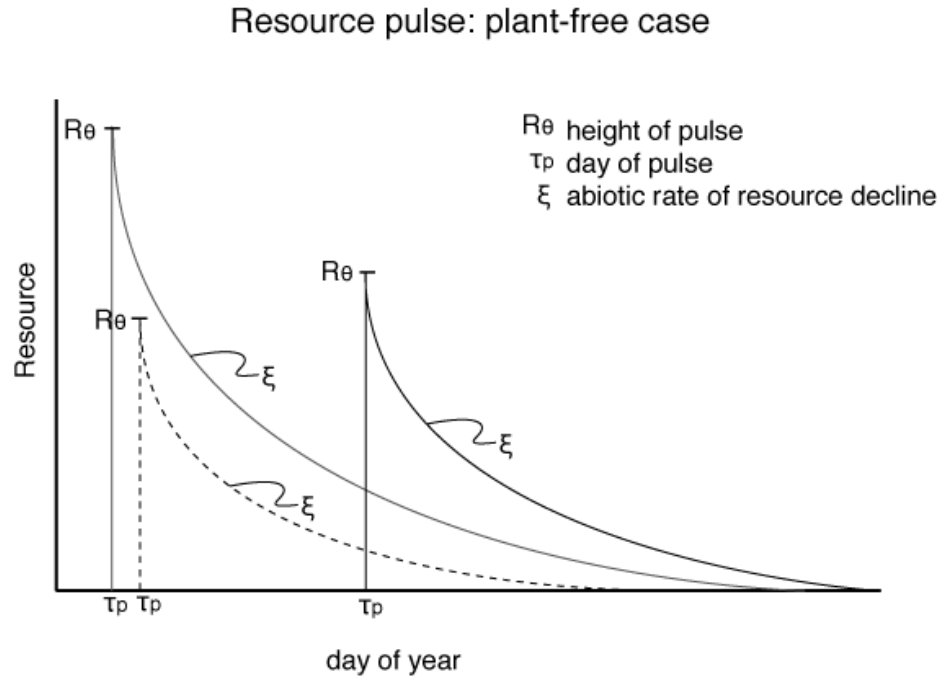


Figure 2: **Major coexistence variables directly affected by climate change** We focus on three major coexistence variables that have been (or will be) influenced by climate change—a couple examples of how varying them changes the resource pulse (without plants).

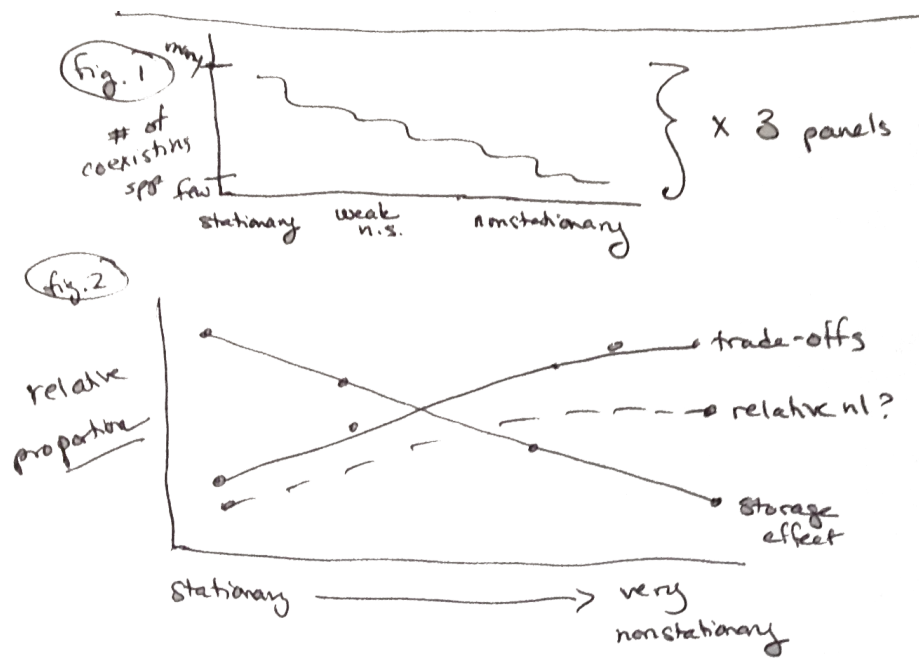


Figure 3: **How does climate change affect mechanisms of coexistence?** Two figures: the first is simple it's just the number (or percent of total possible) of species coexisting; the second figure is to look at how mechanisms shift with scenarios that are stationary, weakly nonstationary or strongly nonstationary. Each of these figures should be one panel for each variable manipulated (ϵ , τ_p and maybe R_0).

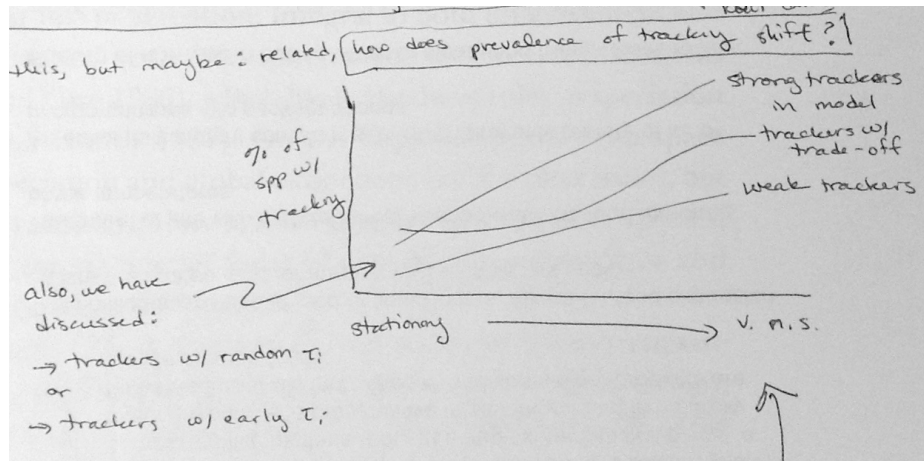


Figure 4: **How does the prevalence of tracking shift with nonstationarity?** See the section on tracking questions above for the full plethora of questions related to this (e.g., this is also the realm of how strong does the negative correlation between tracking and competitive ability have to be to 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.