How environmental tracking shapes communities in stationary & non-stationary systems

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Abstract

Super dry, but better to have something ... I think. Predicting community shifts with climate change requires fundamental appreciation of the mechanisms that govern how communities assemble. Much work to date has focused on how warmer mean temperatures may affect individual species via physiology, generally producing shifts in the species' ranges and phenology and documenting high variation in the magnitude of shifts across different species, which fails to predict the wide diversity of observed shifts. This has led to a growing appreciation that improved understanding will require understanding the direct and indirect consequences of these shifts for species and their communities. Here we review how temporal variability in the environment affects species persistence in stationary environments, extending theory to understand how a species' ability to track the environment may affect their long-term persistence in communities. We then discuss how non-stationary environments may fundamentally alter these conclusions with a focus on how climate change has altered the start of the growing season. Finally we review how the reality that change has and is expected to affect far more than mean temperatures, including widespread affects on growing season length, variability and shifts in extreme events may complicate simple predictions of winners and losers with climate change.

Keywords: phenology, climate change....

1 Main text

Anthropogenic climate change is causing widespread changes in species, with many species shifting in both time and space (IPCC, 2014). Reports often focus on species shifting to higher elevations and poleward (Chen *et al.*, 2011), and/or shifting earlier in their recurring life history events (phenology) as climate warms (Menzel *et al.*, 2006; Wolkovich *et al.*, 2012; Cohen *et al.*, 2018). A large proportion of species, however, are shifting much less (Cook *et al.*, 2012), raising concerns about whether these species may be more vulnerable to population declines with continued warming. Such conclusions come in part from increasing research that links how well species track climate change—especially through temporal shifts—to shifts in biomass, growth and other metrics related to performance (Cleland *et al.*, 2012). Tracking may then be a major component to understanding and predicting indirect effects of climate change—including population declines, with cascading effects on community and ecosystem structure.

How well a species tracks the environment through its phenology has repeatedly been linked to other effects of climate change (Cleland *et al.*, 2012; Ramula *et al.*, 2015). Species that phenologically track warming also appear to perform better in field warming experiments (Cleland *et al.*, 2012), while exotic plant species appear to gain a foothold in warming environments by phenologically tracking climate change (Willis *et al.*, 2010). Simple community ecology theory supports these findings, suggesting that a warming climate should open up new temporal niche space and favor species that can exploit that space (Gotelli & Graves, 1996; Wolkovich & Cleland, 2011; Zettlemoyer *et al.*, 2019). Thus, earlier springs should favor earlier species, especially those that can environmentally track ever-earlier seasons. This hypothesis has gained significant traction in the ecological literature focused on global change (e.g., Cleland *et al.*,

2012), however, there has been comparatively little work examining whether it is supported through coexistence theory and models.

Current or 'modern' coexistence theory is based strongly on understanding how variable environments may promote coexistence—providing one way to study how communities may be shaped by a changing environment, and the importance of tracking. Most theory, however, is based on the assumption of stationarity: though the environment is variable, its underlying distribution is unchanged across time (Barabas *et al.*, 2018). This assumption is common not just to coexistence theory, but to much of the theory that underlies ecology, evolution and myriad other research fields (e.g., Nosenko *et al.*, 2013; Milly *et al.*, 2008).

Climate change upends the assumption of stationarity. By causing increases in temperature, larger pulses of precipitation, increased drought, and more storms (Stocker *et al.*, 2013), climate change has fundamentally shifted major attributes of the environment from stationary to non-stationary regimes. This transition is reshaping ecological systems, and, while new work has aimed to adapt coexistence to non-stationary environments (Chesson, 2017), little work has fundamentally examined what such a transition may mean for communities and the species within them.

Here we review current knowledge on temporal environmental tracking both in empirical data and though the lens of basic community ecology theory, highlighting where simple theory predicts complexities often seen in empirical results. We review current coexistence theory for variable environments, and provide an initial test of how well basic theory supports the current paradigm that climate change should favor species with environmental tracking. Finally, we provide a framework to leverage existing ecological theory to understand how tracking in stationary and non-stationary systems may shape communities, and thus help predict the indirect consequences of climate change.

1.1 Environmental variability & change

Decades of ecological research highlight how variable environments shape species and their communities at multiple scales (Sale, 1977; Chesson & Huntly, 1997). In much of the globe where feasible periods for growth each year are limited (e.g., by temperature or drought) species must manage within-year variability to time when to grow and when to reproduce (Donohue, 2002). This environmental variability compounds into inter-annual variability and critically shapes the start and end of growing seasons. For long stretches of history this variability has been stationary; that is, the underlying probability distribution that produces it does not change even though one year may be dramatically different than the next. The shape of this underlying distribution varies across systems and in how it is measured—the total amount of rainfall in semi-arid systems is often highly skewed compared to the more normal distribution of the thermal sum of many temperate growing seasons.

In other time periods variability is non-stationary in one or multiple dimensions. For example, climate in the northern hemisphere includes long warming and then cooling periods (i.e., increasing then decreasing means of the probability distribution) at the start of the Holocene, when the earth was coming out of the last glacial maximum. Anthropogenic climate change

(henceforth referred to simply as 'climate change') is a similar non-stationary process, with warming seen around the globe and knock-on effects for other climate metrics, such as heat extremes, the size of precipitation events etc.. While only several decades ago, ecology was focused strongly on stochasticity in stationary systems (e.g., Ripa & Lundberg, 1996; Kaitala *et al.*, 1997), climate change has shifted the focus to understanding stochasticity within a non-stationary framework (Cazelles *et al.*, 2008; Ehrlen *et al.*, 2016, e.g.,).

Understanding non-stationarity in ecological systems requires first identifying what has shifted in the underlying distribution that produces variation in the transition from stationary to non-stationary, and what remains constant. For example, with climate change, warming has increased mean temperatures over time, with minimum temperatures generally increasing more than maximum—this results in an underlying distribution for daily temperature where the mean is increasing through time and the variance is decreasing (Stocker *et al.*, 2013; Screen, 2014), despite a growing literature on increasing variance in temperature (e.g., Vasseur *et al.*, 2014). [ADD another example: San Diego or Snowpack or Lake Washington?.]

1.2 Environmental tracking in time

Environmental variability, and the reality that it is often well described by some underlying probability distribution, means most species should benefit from tracking their environment. We focus here on environmental tracking through time (often referred to below as 'tracking') rather than through space because of its well-established links to individual-level physiology, yielding a more robust understanding of what environmental cues determine tracking (Chuine, 2000; Chew *et al.*, 2012), and because it has been repeatedly linked to performance and other fitness-related metrics. Temporal environmental cues, however, are often linked to species' ranges (Morin *et al.*, 2008; Fournier-Level *et al.*, 2011), thus we expect much of this work could extend to environmental tracking through space.

Many species track their environments through time by adjusting their phenologies, but identifying this tracking depends on many factors. Defining—or measuring—environmental tracking depends on the level of the question, and how well researchers understand a species' underlying physiology and ecology. Many, or all species, for example use abiotic cues to trigger major phenological events (e.g., leafout in trees or emergence of insects each spring). Tracking may thus often be defined simply by the relationship between the dates of the phenological event and a simple abiotic metric, such as a relevant mean monthly temperature, with variation in temperature derived from multiple periods of observation or induced through experiments.

Simple environmental metrics are almost always proxies for a more complicated underlying physiology where simple cues—such as those to warm temperatures—can be modified by other cues, such as photoperiod, drought or light spectra (Bagnall, 1993; Stinchcombe *et al.*, 2004). These additional cues almost always appear designed to handle unusual—though not completely uncommon—years when the simple cue alone would fail, that is trigger growth, reproduction or another life history event at a highly suboptimal time. For example, in many temperate forest systems, woody plants cue strongly to warm spring temperatures, but also to cool winter temperatures, which prevents leafout in warm snaps that occur in many climates in the middle of

the winter—long before the last risk of frost damage is past. In some semi-arid systems, species time growth to pulses of rain, but only when those rain events occur with cooler temperatures, that indicate the start of the rainy season, and not a rare summer rainfall event in the middle of months of drought.

The complexities of cues underlying environmental tracking highlight that, at the ultimate level, tracking is shaped by complex resources that species need to grow and reproduce. This is perhaps best recognized in the literature on trophic synchrony where focus is often on how well consumers track their prey resources (Deacy *et al.*, 2018; Kharouba *et al.*, 2018). For example, decades of work has studied how birds (e.g., *Parus major*) time their peak food demands— during their nesting season—to caterpillar (their prey) abundance (e.g., Charmantier *et al.*, 2008). Failure to track prey year-to-year or over time with warming has been well tied to individual-level fitness consequences in some systems (e.g., Charmantier *et al.*, 2008)., but not all (Visser *et al.*, 2006). Tracking of plants and other lower trophic levels is also equally about resources. Alpine plant species that emerge in step with snowmelt are likely responding, at least in part, to light resources for photosynthesis. Light equally appears critical to the sequence of phenology in many temperate forests: with lower-canopy species, and younger (shorter) individuals of higher-canopy species, routinely risking frost damage to leafout before the canopy closes and access to light becomes severely reduced (Vitasse, 2013; Heberling *et al.*, 2019). In both temperate as well as alpine systems, however, access to critical belowground resources also occurs in the spring—both for available water but also for nutrients released at the turnover of the microbial communities (Zak *et al.*, 1990). Thus, plants' spring phenology in many systems is about careful tracking to optimally compete for nitrogen and other soil resources. As in higher trophic level systems, research has linked how well plants track to performance, with species that track warming better tending to grow larger and/or produce more offspring (Cleland *et al.*, 2012).

Variation in metrics of tracking highlights that—despite the clear importance of tracking for resource access—not all species appear to track their environments equally well. Some temperate woody species track spring temperatures strongly (give some examples), but other species do not (NUMBERS) and do not appear linked to other major climate variables (CITES). Variability equally exists when examining consumers tracking their prey (NUMBERS). Such variation in tracking across taxa is driven in part by difficulties in measuring tracking (see BOX). Yet other variation may be real, and suggests perfect environmental tracking may either not be possible or optimal for all species.

Ecological theory predicts variation in tracking across species for multiple reasons. First, how predictable an environment is affects how much species can track. Tracking is only beneficial to species—and possible—when the environment is predictable. Predictability depends on the timescale of interest, which is related to a species' generation time (which itself should be shaped by an environment and its predictability, Davison *et al.*, 2010; Morris *et al.*, 2008). Species with longer generation times may track low frequency climate signals and make investment choices on far longer timescales than species with shorter lifespans (Morris *et al.*, 2008). Perhaps unsurpisingly tracking appears best studied in some of the most predictable environments and at the most predictable timescales; for example much research examines how temperate trees track

the annual start of the temperate growing season, which always corresponds to temperature increasing and daylength lengthening. Inter-annual events such as extremely good or poor years for reproduction may be more difficult in some systems to predict, and thus there is little potential to track. In such cases, species should gain a substantial benefit from bet-hedging or employing other approaches that spread out risk given uncertainty (Venable, 2007; Donaldson-Matasci *et al.*, 2012). Even in highly predictable environments, evolutionary limitations may prevent perfect tracking: species may not be able to closely measure relevant environmental cues (Arnold, 1992; Singer & Parmesan, 2010), gene flow from other other environments may continually push a population away from its local optimum (Lenormand, 2002), or there may be unavoidable trade-offs (Levins, 1968) with tracking.

Within populations, life-history can help predict how much individuals should track while also balancing trade-offs within and across seasons and years. Tracking has been repeatedly linked to fitness benefits (e.g., Farzan & Yang, 2018; Deacy *et al.*, 2018). Such benefits usually break down into avoiding tissue loss or maximizing growth and, relatedly, maximizing reproduction. Species often track the start of growing seasons to avoid substantial tissue loss, for example from frost damage in temperate plants, or start activity only when resources for growth are present, such is the case in animals coming out of hibernation in cold regions. Equally, tracking of resources throughout a season is linked to the timing of reproduction for many species and, for iteroparous species, decisions on how much to invest each season requires estimating how likely a year is to be good for offspring. For species with bounded growing seasons, much literature has reviewed how tracking is a multivariate equation balancing early-season access to resources and its associated risks of tissue loss, with later season tracking of resources for reproduction and time for offspring to mature (Donohue, 2002; Morin & Chuine, 2005; Burghardt *et al.*, 2015). These trade-offs should also scale up to predictions of variation in tracking across species.

Across species, community ecology theory makes predictions for suites of traits that may trade-off with tracking. As tracking fundamentally relates to tracking a resource pulse in most systems, traits related to resource use are likely contenders for a trade-off. Species with traits that make them poor resource competitors may need to track the environment closely, while superior competitors could outcompete trackers, and thus hypothetically track the environment less closely. Examples include under-canopy species leafing out earlier to gain access to light or plants with shallow roots starting growth sooner in semi-arid systems, while species with deeper roots may begin growth later. In such cases, tracking is akin to a competition-colonization trade-off (Amarasekare, 2003), where species that track well gain priority access to resources, and thus may co-exist with superior competitors. [Here we add a short lit review showing that people have found this? Or not ... or not looked.]

Trade-offs with tracking, predicted by basic ecological theory and supported by growing empirical work, would have fundamental consequences for community assembly, especially with climate change. Applying this ecological theory to current environments, however, is difficult because most theory has been developed for stationary systems (as is the case in other sciences also, Milly *et al.*, 2008), which are mathematically more tractable, and can sometimes be extended to non-stationary systems (Chesson, 2017). Almost no community assembly research, however, has examined the consequences of shifting from a stationary to non-stationary en-

vironment. Yet this transition is exactly what anthropogenic climate change has imposed on systems around the globe, making our understanding of how environmental tracking fits within community assembly theory critical.

1.3 Coexistence theory & environmental tracking (or) The role of the environment in coexistence

Recent advances in coexistence models, often heralded under the title modern coexistence theory,' recognize that both mechanisms independent of fluctuations in the environment (e.g., R* and other classical niche differences) and dependent on fluctuations in the environment (relative non-linearity and storage effect) can drive coexistence (Chesson & Huntly, 1997; Chesson, 2000). Models under this new paradigm are thus often composed of parameters the describe the environment and the species within it (Megan–suggest CITES). Parameters related to species must always include mechanisms for growth, death, interactions with other species, and generally a bet-hedging strategy for survival across years (e.g., a seedbank or other long-lived lifestage)— though exactly how these are defined varies across models (e.g., R* and related models focus on resource competition). How the environment is defined in most models falls into two broad categories. In some models the environment is expressed as variation in parameters related to species (e.g., in some lottery models the environment appears, effectively, as variation in birth and death rates). In other models, the environment is more specifically defined. For example, many seed germination models define an environment that begins with a resource pulse each year. Building a changing environment into models thus may require knowing how environmental shifts filter through to species-level parameters (Tuljapurkar *et al.*, 2009) or—perhaps more simply—how the environment is changing. In the aforementioned seed germination models, many systems may be experiencing shifts in the size or variability of the resource pulse.

These models, which underlie much of current community ecology research Mayfield & Levine (2010); Barabas *et al.* (2018); Ellner *et al.* (2019), allow us to test basic predictions of how tracking may shape assembly. While growing empirical research supports that tracking is an important trait—especially in a changing environment—there are few tests of whether models support basic theoretical predictions. Here we examine how tracking may shape communities in stationary and stationary to non-stationary environments.

1.3.1 Model description

We use a simple model that includes dynamics at both the intra-annual and inter-annual scales. As the model is akin to many commonly used seed germination models (Chesson *et al.*, 2004), we follow a similar terminology for ease, however the basic structure of our model could apply to others systems with one dominant pulse of a limiting resource each season (e.g., water from rain or snowpack). This model thus allows within- and between-year dynamics to contribute to coexistence. Between-years the environment is included via variable germination, and within-years the environment is explicitly included as a resource pulse at the start of the season. The model includes a suite of species traits, including some relating to how the species responds to the environment via germination each year and some related to how species may

bet-hedge across years (via a seedbank), as well as traits relating to resource competition each year. Within-season dynamics within the model thus allow for fluctuation-independent coexistence (e.g., trade-offs in resource competition), while interannual variation in the environment provides opportunities for coexistence via fluctuation-dependent mechanisms.

Across years, for a community of n species, the seedbank (N) of species i at time t is determined by the combination of the survival (s_i) of the fraction of seeds that did not germinate that season $(1 - g_i(t))$ plus new biomass (B_i) produced during the length of the growing season (δ) converted to seeds (ϕ_i):

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

The production of new biomass each season follows a basic R* competition model: new biomass production depends on its resource uptake ($f_i(R)$ converted into biomass at rate c_i) less maintenance costs (m_i), with uptake controlled by a_i and u_i:

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

With the initial condition:

$$B(t+0) = N_i(t)g_i(t)b_{0,i} \tag{2}$$

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

$$\frac{\mathrm{d}R}{\mathrm{d}t} = -\sum_{i=1}^{n} f_i(R)B_i - \epsilon R \tag{3}$$

Each year the proportion of seeds that germinate depends on both each species and the environment that year. Each year a species' germination fraction depends on the distance between τ_i, a species characteristic, and τ_P, an attribute of the environment, which varies year to year. We conceptualize this as a variation in the timing and an environmental trigger for germination. Germination fraction declines according to a Gaussian distribution as the distance between τ_i and τ_P grows (we refer to this distribution as the 'germination curve').

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

between $bioSOS_i$ and $env.SOS$

$$g_i = g_{max,i}e^{-h(\tau_p - \tau_i)^2} \tag{4}$$

Adding phenological tracking to model: τ_i can be considered a fixed characteristic of a species or it may respond to the environment dynamically through what we refer to as environmental tracking. Tracking (α) decreases the distance between τ_i and τ_P such that a species with higher alpha will have a higher germination fraction.

$$= \alpha \tau_p + (1 - \alpha)\tau_i$$

Thus:

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

We refer to $\hat{\tau}_i$ as 'effective biological start time' for species i (or 'effective τ_i'). As our interest is primarily in the role of environmental tracking we focus on situations where species vary in their match to the environment (through both tracking, α, or a more fixed response, τ_i) or their resource uptake (via c_i). For simplicity, we focus on two-species communities.

1.3.2 Tracking in stationary environments

Species occurring for long periods of time in any habitat must be sufficiently matched to their environment across years. In our model this means species must have a germination curve such that their effective biological start time ($\hat{\tau}_i$) is sufficiently close to the environmental start time (τ_p) to allow germination of new seeds before the seedbank is exhausted. In our model this can happen in two ways: species' with fixed environmental start time (τ_i) values close enough to the environmental start time (τ_P) or species with combination of intrinsic biological start time (τ_i) and tracking (α) that brings the effective biological start time close enough to the environmental start time (τ_P).

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

temporal niche.

As both a fixed intrinsic start time and tracking represent the same major niche axis species cannot coexist given only variation in these traits—coexistence requires variation in another trait axis. As discussed above, many commonly cited traits for this trade-off revolve around traits related closely to resource competition (Chesson *et al.*, 2004). With this added variation— here we varied species' R^* (via c or what? I forget)—species can persist together (in two species communities) as long as those species with a temporal niche advantage are also the inferior competition (FIGS). That is, species that can draw resources down to a lower level and are thus the superior resource competitors (lower R^*) can persist with species with that are inferior competitors given those species have higher tracking values or fixed intrinsic start times close to the most common timing of the pulse (i.e., species with the superior biological start times). These trade-offs, however, are all environmentally dependent. They hold only so long as the environment is stationary.

1.3.3   Tracking in non-stationary environments

A shifting environment may fundamentally reshape trade-offs that structure communities. Modern coexistence theory is based mainly on variable, but stationary, environments. As systems shift from stationary to non-stationary the trade-offs on which some communities are based may be transformed. Using our simple germination model we shifted the environment of our two-species communities—that otherwise had experienced a variable but stationary environment— to an earlier start of season by shifting the mean XX over XX years (see Supp). By changing a fundamental niche axis—on which these communities were structured—we shifted one major part of the trade-off axis: the new non-stationary environment favored an earlier effective start time than the previous stationary environment. This in turn reshaped communities in both our simulations built on species with fixed intrinsic start times and with start times that vary via tracking.

In communities where species traded off competitive traits (R^*) with a fixed intrinsic start time trait (τ_i), species with earlier start times were clearly favored, generally driving the other species (with a lower R^* and later start time) locally extinct before the end of our XX year time-period. Very few two-species communities persisted through the end of the non-stationary period (X/XX) and those that did were generally persisting via being highly similar—having nearly identical R^* fixed intrinsic start time trait (τ_i) parameters. That is, the species were persisting through equalizing mechanisms—by being almost the same species neither could drive the other extinct, though these species do not coexist (as in longer simulations through drift or related mechanisms one species would be lost). The contrast of equalizing mechanisms— stabilizing mechanisms—include niche differences such as the trade-off in competitive traits (R^*) with a fixed intrinsic start time trait (τ_i). Yet, in this non-stationary system they failed to yield any persistence as the environment shifted away from the previous trade-off axis the communities formed in.

Persistence of two-species communities via both stabilizing and equalizing mechanisms occurred much more often in communities where species traded off competitive traits (R^*) with tracking

10

(α). While again, the non-stationary environment favored higher trackers, who in turn drove the extinction of species with lower tracking values from many two-species communities, some two-species communities persisted (XX/XX). These communities included equalized species, as well as [insert more understanding here.] Taken together, this simple simulations show how non-stationarity can drive local species extinction and reshape the underlying assembly mechanisms of communities. These results however make many assumptions, including how they model non-stationarity in the environment.

Our models impose environmental non-stationarity on an axis fundamental to co-existence. Other results would be expected depending on whether that non-stationary reshapes a fundamental niche axes involved in the trade-off. Non-stationarity in the environment can take on many forms—in what variable it effects and how it reshapes the underlying distribution. Communities that assemble via other axes of the environment than start of season timing may be far less impacted that our simulations suggest. Further, we examined a common trend with climate change—shifts in the mean of the environment. Changes can also occur in the variance or the fundamental shape of the distribution (e.g., shifting from a normal distribution to one that is more similar to a gamma). Additionally, we applied a shift to only one aspect of the environment. In reality climate change may impose multivariate shifts.

Multivariate nonstationary environments

Human modification of climate, the nitrogen cycle and habitat impose complex shifts in the environments of most species. Such myriad shifts could make species more vulnerable to local extirpation (Barnosky *et al.*, 2011; IPCC, 2014). If, however, the environment is altering multiple niche axes—along which species assemble—it may allow trade-offs that structure communities to persist through non-stationary periods. We examined this possibility by again shifting the mean start of season XX earlier over XX years at the same time that we shifted the resource lower (XX over XX years). Thus, our environment favored species with earlier start time and superior competitive abilities (given the lowering resource). We found little evidence of communities persisting via a maintained trade-off—instead the inherent variability of a system shifting in two dimensions drove species extirpations more quickly (XX, XXX). Thus, while theoretically multivariate nonstationary environments could maintain trade-offs, the shifts would need to be so balanced that it seems unlikely.

1.3.4 Future research in environmental tracking & non-stationary systems

Growing empirical research highlights that environmental tracking is linked to species performance, and thus may be critical to understanding the forces that assemble communities—especially as anthropogenic climate change is reshaping the environment of all species. Indeed, research in this area has often been focused on understanding the impacts of climate change, and comparatively less often been guided by testing or developing ecological theory. Current models of coexistence, however, are primed for understanding how the environment can shape the formation and persistence of communities. Yet modeling efforts need more focus on understanding the attributes of an environment shaped strongly by humans, and thus, what advances in theory

may be most useful and applicable in modern ecology. We review several major questions that we believe could most most rapidly unite empirical and theoretical research in environmental tracking to advance the field.

How is the environment changing?

Climate change has shifted the environment of all species, often in myriad ways. Most systems are seeing increases in mean temperatures, which can rapidly impact the metabolism and re-shape of activity periods of many species (Monson *et al.*, 2006; IPCC, 2014). This warming is also altering many other attributes of the climate system, including altered precipitation regimes in many systems (Diffenbaugh *et al.*, 2015), and shifts in cloud cover (Hofer *et al.*, 2017), which can all further influence species. While we focused on one major shift in the climate system (earlier growing seasons), much more research is needed to understand how other singular shifts in the environment impact the assembly dynamics of communities in current models; and to layer on how multivariate environmental shifts may alter these predictions. Empirical ecologists can guide these efforts by identifying environmental shifts that are often linked (e.g., warming temperatures may drive earlier seasons and higher evaporative loss of some resources such as water). They can also aim to more consistently and fully characterize the environmental distributions of their systems that appear to most drive species performance and interactions: the environment of the years of study should be clearly reported and compared against long-term and recent climate for each system.

What major traits trade-off with tracking?

Basic theory suggests environmental tracking must trade-off with other traits to allow multi-species communities. Yet to date empirical work has mainly documented tracking, linked it to performance, or focused on how it varies between native and non-native species (Willis *et al.*, 2010; Wolkovich *et al.*, 2013; Zettlemoyer *et al.*, 2019). Such work lays the groundwork that environmental tracking is important, but advancing empirical research should address how this trait co-occurs with other traits. Research on this has already highlighted some traits, that co-vary with tracking (CITES), but to tie this empirical work to models requires more research on traits that link clearly to theory. Traits that link to resource competition, as we focus on here, may be especially fruitful for greater research, but should not be the only ones considered. For example, traits related to predator tolerance or avoidance may also play a role, but have been effectively unstudied. As empirical research in this area grows models can aid progress in understanding what the outcomes of these trade-offs may be for community assembly.

How do shifts to non-stationary environments re-shape the relative influence of stabilizing versus equalizing mechanisms?

Our simple models showed that as environments shift from stationarity to non-stationarity species co-occurring via equalizing mechanisms can persist longer. While this is a rather obvious outcome—as equalized species will be similarly effected by environmental shifts—it has several important implications. First, it may make identifying which traits climate change promotes through stabilizing mechanisms more difficult. Second, it suggests climate change— or other factors that cause an environment to shift from stationary to non-stationary—may cause a fundamental shift away from assembly via stabilizing mechanisms, but this implication

presumes communities include species co-occurring via strong equalizing mechanisms. Thus understanding the prevalence of stabilizing versus equalizing mechanisms (which ecology has worked on for many decades, CITES) becomes critical for understanding the implications of transitions to non-stationary environments.

If equalizing mechanisms are rare in natural communities then climate change could promote species loss by fundamentally re-shaping stabilizing mechanisms. This finding however assumes a closed community with no evolution. In practice, communities may lose species but also gain new species through dispersal, allowing communities to potentially adjust to new trade-offs as the environment shifts. In addition, evolution may allow some species to stay in communities they would otherwise have been lost from. But with non-stationarity this axis is constantly shifting—so continual community change via species loss, gain and reshaped species via evolution may be the expectation, until the environment shifts back to stationarity.

1.4 Stationarity in the future

While most environments today are climatically non-stationary, and have been for decades, the climate will transition to stationarity in the future. There are many possible pathways to climatic stabilization in the future, but almost all require first the stabilization of greenhouse gases—the subject of much policy and political debate. Once greenhouse gas emissions stabilize climate will not quickly snap back to a new stationary phase. Instead systems will slowly approach a new climatic stationarity depending on how they are effected by the earth's multiple thermal reservoirs, and, in turn, how quickly those reservoirs stabilize. The timescale of this approach is generally expected to be on the scale of centuries, but could be much longer in certain oceanic systems (Collins *et al.*, 2013). Thus, ecologists are—and will remain in—in a research area structured by climatic non-stationarity. As paleobiologists and evolutionary biologists often point out, climatic nonstationarity is a common part of the earth's history (Jansson & Dynesius, 2002)—even if stationary periods of cold or warm (glacial and interglacial periods) are more common. Indeed, much of this work has examined how species survive for millions of years given dramatic climatic change, (Provan & Bennett, 2008)periods that provides the most dramatic community reshuffling—from stationary to non-stationary climate (Vrba, 1980, 1985). Such stories of the past are now fundamentally happening today, and ecology is challenged to understand how transitions between stationary and non-stationary environments reshape species and communities we have today and in our warmer future.

2 Figures

1. Figure for ... The shape of this underlying distribution varies across systems and in how it is measured—the amount of rainfall in semi-arid systems is often highly skewed compared the thermal sum of many temperate growing season

2. With climate change, warming has increased mean temperatures over time, with minimum temperatures generally increasing mre than maximum—this results in an underlying distribution for daily temperature where the mean is both increased through time and the variance is decreasing (Munich garden? Maybe add San Dieg precip example?

3. Real-world data showing stat/non-stationarity in environment (ideally τ_P)

4. Real-world data showing tracking (and less tracking)

5. τ_i vs. R* trade-off and histogram of persisting τ_i under stat/nonstat τ_P environment

6. alpha vs.τ_i trade-off and histogram of persisting alpha under stat/nonstat τ_P environment

7. alpha vs. R* trade-off and histogram of persisting alpha under stat/nonstat τ_P environment

8. (Scratch this one: we're pretty sure it required a crappy τ_i to survive the initial stationary period, then be favored in second time period and we're not so sure crappy τ_i species survive the initial stationary period) time-series of one run showing years where τ_i of one species is close to τ_P and other years where τ_i of other species is close to τ_P (and show this shift under nonstat)

9. non-stationarity in $R0$ and τ_P

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