

RH: Environmental tracking

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

Lizzie<sup>1</sup> & Megan<sup>2</sup>

<sup>1</sup> *Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main  
Mall, Vancouver, BC V6T 1Z4*

<sup>2</sup> *Hawaii Institute of Marine Biology*

**Corresponding author:** XX, see <sup>1,2</sup> above ; E-mail:.

## Abstract

*Super quick draft for now, I will work on it ....* Predicting community shifts with climate change requires fundamental appreciation of the mechanisms that govern how communities assemble. Growing evidence that phenological shifts with warming are associated with performance responses to warming—where species that track warming better often also perform better—has led to suggestions that phenological tracking may be a structuring force in communities, and an important element to predicting future communities. Here we review how phenological tracking where tracking fits within community ecology theory. 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 effects 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 causes 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 through 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—for example, the total amount of rainfall across years 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 and the size of precipitation events. 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 (e.g., Cazelles *et al.*, 2008; Ehrlén *et al.*, 2016).

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).

## 1.2 Environmental tracking in time

Environmental variability, and the reality that it is often well described by some underlying probability distribution (Fig. 1), 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 (Chaine, 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 (see Box). 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, would 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 (Wainwright *et al.*, 2012; Wainwright & Cleland, 2013).

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 maximal prey (caterpillar) 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 (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 with the turnover of seasonal 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 more tending to grow larger and/or produce more offspring (Cleland *et al.*, 2012).

### 1.3 Interspecific variation in tracking

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 (?). Many plant species track spring temperatures strongly (multiple meta-analysis now show plants’ spring phenology on average track spring or annual temperatures 4-6 days/°C Richardson *et al.*, 2006; Wolkovich *et al.*, 2012; ?, and simple temperature models can often explain over 90% of interannual variation in phenology), but other species do not (Cook *et al.*, 2012) and do not appear linked to other major climate variables (?). Variability equally exists when examining consumers tracking their prey (across diverse species tracking over time is 6.1 days/decade but ranges from zero to 15 days/decade, see Kharouba *et al.*, 2018). 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 unsurprisingly 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 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 (Zhu *et al.*, 2016). 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.

Research on phenological tracking and traits has increased greatly in recent years, with a major

uptick in studies after 2010 (see Supp Fig. S1). Of 176 papers we found using terms related phenological tracking and traits 82% were published in 2011 or later. Despite increasing interest in this topic, very few papers actually evaluated relationships between tracking and traits (13 papers, see Supp for more details), with most lacking data on one aspect of the relationship or the other (102 papers), some focusing on intraspecific variation (32 papers), and others discussing links and having relevant data, but providing no robust statistical tests (X studies). Of the few studies that did link tracking and traits, most were on plants (9 papers), with three on butterflies and one on birds. By far the most studied trait was how early or late a phenophase occurred (e.g., date of flowering or start of migration for a species, termed ‘earlyness’ by some authors), with earlier species tending to track more. While this is an important link it is vulnerable to statistical challenges (see Box). Few studies examined whether tracking correlates with resource acquisition traits, though those that did examine such traits generally found species with higher tracking also had traits associated with lower competitive abilities under low resources (e.g., shallower rooted). The link between tracking and ‘earlyness,’ if robust, may provide a further link to resource acquisition traits as previous work has documented that species with earlier phenophases tend to have traits associated with lower competitive abilities (e.g., they tend to be of lower height, have shallower roots, narrower diameter vessels, thinner leaves, and grow faster, Wolkovich & Cleland, 2014).

These trade-offs with tracking, predicted by basic ecological theory and tentatively 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, 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 environment. 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.

## 1.4 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 paradigm are thus often composed of parameters that 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 for example, 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 tests of basic predictions of how tracking may shape communities. While growing empirical research supports that tracking is an important trait—especially in a changing environment—there are few tests of whether models support these basic theoretical predictions. Below we examine how tracking may shape communities in stationary environments and environments transitioning from stationary to non-stationary.

#### 1.4.1 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 species respond 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 ( $\delta$ ) converted to seeds ( $\phi_i$ ):

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

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 main-



tenance costs ( $m_i$ ), with uptake controlled by  $a_i$  and  $u_i$ :

$$\frac{\partial B_i}{\partial t} = [c_i f_i(R) - m_i] B_i \quad (2)$$

$$f_i(R) = \frac{a_i R^{\theta_i}}{1 + a_i u_i R^{\theta_i}} \quad (3)$$

With the initial condition:

$$B(t + 0) = N_i(t) g_i(t) b_{0,i} \quad (4)$$

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

$$\frac{dR}{dt} = - \sum_{i=1}^n f_i(R) B_i - \epsilon R \quad (5)$$

Each year the proportion of seeds that germinate depends on both each species and the environment that year. The fraction of seeds germinating each year for a species is determined by the distance between  $\tau_i$ , a species characteristic, and  $\tau_P$ , an attribute of the environment, which varies year to year. Germination fraction declines according to a Gaussian distribution as the distance between  $\tau_i$  and  $\tau_P$  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  $\tau_P$  to represent the environmental (abiotic) start of the growing season each year, and refer to it as the ‘environmental start time’ while  $\tau_i$  represents the ‘intrinsic biological start time’ for species  $i$ . How well matched a species is to its environment each year can be measured as  $\tau_i - \tau_P$ , or the distance between the intrinsic (biological) start time and the environmental start time.

$$g_i = g_{max,i} e^{-h(\tau_P - \tau_i)^2} \quad (6)$$

*Adding phenological tracking to model:*

$\tau_i$  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 ( $\alpha$ , which can vary between 0 to 1) decreases the distance between  $\tau_i$  and  $\tau_P$  such that a species with higher tracking will have a higher germination fraction.

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

$$\hat{\tau}_i = \alpha \tau_P + (1 - \alpha) \tau_i \quad (7)$$

Thus:

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

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

We refer to  $\hat{\tau}_i$  as ‘effective biological start time’ for species  $i$  (or ‘effective  $\tau_i$ ’).

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,  $\alpha$ , or a more fixed response,  $\tau_i$ ) or their resource uptake (via  $c_i$ ). For simplicity, we focus on two-species communities.

#### 1.4.2 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 ( $\tau_P$ ) to allow germination of new seeds before the seedbank is exhausted. In our model this can happen in two ways: species with fixed intrinsic biological start time ( $\tau_i$ ) values close enough to the environmental start time ( $\tau_P$ ) or species with a combination of intrinsic biological start time ( $\tau_i$ ) and tracking ( $\alpha$ ) that brings the effective biological start time ( $\hat{\tau}_i$ ) close enough to the environmental start time ( $\tau_P$ , see Fig. 2).

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, theory and empirical work suggest this trade-off may involve traits related closely to resource competition (Chesson *et al.*, 2004). With this added variation—here we varied species’  $R^*$  (via  $c_i$ )—species can persist together as long as those species with a temporal niche advantage are also the inferior competitors (Fig. 3-4). 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 resource 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.

#### 1.4.3 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 500 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 biological 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 varied via tracking.

In communities where species traded off competitive traits ( $R^*$ ) with a fixed intrinsic biological start time trait ( $\tau_i$ ), 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 500 year time-period (Fig. 3). Very few two-species communities persisted through the end of the non-stationary period (2 out of 547 two-species communities persisting after end of stationary, or 0.04%) and those that did were generally persisting via being highly similar—having nearly identical  $R^*$  and fixed intrinsic biological start time traits ( $\tau_i$ ). These species were persisting through equalizing mechanisms—by being almost the same neither species could drive the other extinct, though these species do not coexist (as in longer simulations one species would be lost through drift or related mechanisms). The contrast of equalizing mechanisms—stabilizing mechanisms—include niche differences, such as the trade-off in competitive traits ( $R^*$ ) with a fixed intrinsic biological start time trait ( $\tau_i$ ). Yet, in this non-stationary system stabilizing mechanisms failed to yield any persistence of two-species communities 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 more often in communities where species traded off competitive traits ( $R^*$ ) with tracking ( $\alpha$ ). 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 (257 out of 1698 two-species communities persisting after end of stationary, or 15.1%, Fig. 4). These communities included equalized species, as well as [insert more understanding here PLEASE HELP MEGAN!]. Taken together, these 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 coexistence. Other results would be expected depending on whether the imposed 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 than 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. If 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 size of the resource pulse lower (XX over XX years). Thus, our environment favored species with earlier start time and superior competitive abilities (given the decreasing resource). We found little evidence, however, of communities persisting via a maintained trade-off—instead the inherent variability of a system shifting in two dimensions drove species extirpations slightly more (14.8% of two-species communities remaining after non-stationary). Thus, while theoretically multivariate nonstationary environments could maintain trade-offs, the shifts would need to be so balanced that it seems unlikely. More likely appears the possibility that myriad shifts in the environment make species more vulnerable to local extirpation (Barnosky *et al.*, 2011; IPCC, 2014).

#### 1.4.4 Future research in environmental tracking & non-stationary systems

As we have reviewed, 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 clearly 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. To this aim, we review several major questions that we believe could 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 multivariate ways (Fig. 1). Most systems are seeing increases in mean temperatures, which can rapidly impact the metabolism and reshape 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; Zettlemyer *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 (e.g., Kharouba *et al.*, 2014; Lasky *et al.*, 2016; Zhu *et al.*, 2016), 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, Caswell, 1976; Gravel *et al.*, 2006; Chesson, 2000) 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 evolu-

tion may be the expectation, until the environment shifts back to stationarity.

## 1.5 Stationarity in the future

While most environments today are climatically non-stationary, and have been for decades, the climate will return 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, while much of this work has examined how species survive for millions of years given dramatic climatic change (Provan & Bennett, 2008), the periods that provide 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 is reshaping the species and communities we have today and will in our warmer future.

## 2 Box: The trouble with tracking

*In development....* Much recent research in phenological tracking has focused on variability in tracking across species (e.g., Willis *et al.*, 2008; Cook *et al.*, 2012; Bolmgren *et al.*, 2013; CaraDonna *et al.*, 2014; Zettlemoyer *et al.*, 2019), with growing work highlighting how some species do not appear to track climate change closely. Progress in understanding how tracking may structure current and future communities requires identifying variation in tracking across species, but this task is difficult in most systems.

We argue three major classes of reasons can underlie species that do not appear to track climate change: (1) species do actually not track, (2) lack of biological understanding of the cues that underlie tracking, and (3) statistical artifacts that make it difficult to measure tracking robustly. As we reviewed in the main text, species in highly variable environments or which otherwise face high uncertainty in when to time investment decisions may be best served to not attempt to track the environment. Growing evidence suggests a potential fundamental trade-off where early species track, and possess a suite of traits related to faster growth and shorter lifespans, while later species appear to track less, possess traits related to slower growth and longer lifespans, which may bet-hedge more given their longer investment window (CITES).

This, however, could equally be an artifact where early species use simpler cues and thus their tracking is measured more accurately given current methods.

Multiple studies have shown how simple correlations between phenological events and environmental variables may mask complicated relationships (Cook *et al.*, 2012)(ADDCITES). Most well-studied species have multiple cues to time critical biological events (Chuine & Regnier, 2017), but modelling them well is inherently difficult (Chuine *et al.*, 2016), especially since one cue may dominate in many conditions. Perhaps the best example of this is endodormancy and the related phase of vernalization in plants (Chuine *et al.*, 2016; Burghardt *et al.*, 2015). While much work focuses on how spring warming triggers leafout or seed germination, fall and winter cool temperatures also shape timing—however this effect may often be masked by sufficiently cold conditions. With warming, however, this additional trigger—which appears to vary by site, species and even inter-annual conditions (Burghardt *et al.*, 2015)—may become critical. Despite decades of work how this process works is still not fully understood; thus, despite the apparent efficacy of many current phenological models, they may fail spectacularly in the future as additional cues come into play (Chuine *et al.*, 2016).

Perhaps the most widespread reason currently for widespread observations of species that do not track is statistical artifacts, including non-stationarity in units and unrecognized low power. All of these can be addressed given improved statistical approaches, though such approaches may (uncomfortably) highlight how uncertain many current estimates are (Brown *et al.*, 2016). Non-stationarity in units comes in many forms—estimates of days/decade depend strongly on the climate of the decade(s) studied. Estimates based on a relevant climate variable can sometimes ameliorate this problem, but may be equally vulnerable to non-stationarity in units. For example, processes that depend on thermal sums reported as days/°C will generally appear to decline with warming, as the thermal sum of each day increases. Relatedly, estimates of long-term change using simple linear regression are influenced by the climate at the start of the time-series (with greater changes seen from time-series that started in unusually cold decades, such as the 1950s for much of North America). Impacts of start-years for long-term time-series can be muted by applying change-point or hinge models (e.g., Kharouba *et al.*, 2018). Finally, low power is widespread in ecology, where even ‘long’ time-series may be far too short for robust analyses (Bolmgren *et al.*, 2013; Kharouba *et al.*, 2018). Authors should be especially cautious if they find only large effects appear significant (e.g., CaraDonna *et al.*, 2014), which is a well-known statistical bias associated with p-values. Mixed models can help better leverage understanding by pooling information across species, and often better capture uncertainty (CITEPEARSE), but they require more effort to properly fit and test. We suggest they should be much more widely used alongside simulation models to better estimate and communicate uncertainty and power in studies. A related low-power issue comes from climate variation across seasons—in temperate habitats for example, temperature is highly variable in the spring and summer, meaning it is statistically easier to detect tracking in these seasons (because variation in the predictor variable is higher).

## References

- Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters*, 6.
- Arnold, S.J. (1992). Constraints on phenotypic evolution. *American Naturalist*, 140, S85–S107.
- Bagnall, D.J. (1993). Light quality and vernalization interact in controlling late flowering *Arabidopsis* ecotypes and mutants. *Annals of Botany*, 71, 75–83.
- Barabas, G., D’Andrea, R. & Stump, S.M. (2018). Chesson’s coexistence theory. *Ecological Monographs*, 88, 277–303.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011). Has the earth’s sixth mass extinction already arrived? *Nature*, 471, 51–57.
- Bolmgren, K., Vanhoenacker, D. & Miller-Rushing, A.J. (2013). One man, 73 years, and 25 species. evaluating phenological responses using a lifelong study of first flowering dates. *International Journal of Biometeorology*, 57, 367–375.
- Brown, C.J., O’Connor, M.I., Poloczanska, E.S., Schoeman, D.S., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Pandolfi, J.M., Parmesan, C. & Richardson, A.J. (2016). Ecological and methodological drivers of species’ distribution and phenology responses to climate change. *Global Change Biology*, 22, 1548–1560.
- Burghardt, L.T., Metcalf, C.J.E., Wilczek, A.M., Schmitt, J. & Donohue, K. (2015). Modeling the influence of genetic and environmental variation on the expression of plant life cycles across landscapes. *American Naturalist*, 185, 212–227.
- CaraDonna, P.J., Iler, A.M. & Inouye, D.W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences*, 111, 4916–4921.
- Caswell, H. (1976). Community structure - neutral model analysis. *Ecological Monographs*, 46, 327–354.
- Cazelles, B., Chavez, M., Berteaux, D., Menard, F., Vik, J.O., Jenouvrier, S. & Stenseth, N.C. (2008). Wavelet analysis of ecological time series. *Oecologia*, 156, 287–304.
- Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. & Sheldon, B.C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, 320, 800–803.
- Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.



- Chesson, P. (2017). Aedt: A new concept for ecological dynamics in the ever-changing world. *Plos Biology*, 15.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A. & Weltzin, J.F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.
- Chesson, P. & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist*, 150, 519–553.
- Chew, Y.H., Wilczek, A.M., Williams, M., Welch, S.M., Schmitt, J. & Halliday, K.J. (2012). An augmented Arabidopsis phenology model reveals seasonal temperature control of flowering time. *New Phytologist*, 194, 654–665.
- Chuine, I. (2000). A unified model for budburst of trees. *Journal of Theoretical Biology*, 207, 337–347.
- Chuine, I., Bonhomme, M., Legave, J.M., de Cortazar-Atauri, I.G., Charrier, G., Lacointe, A. & Ameglio, T. (2016). Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global Change Biology*, 22, 3444–3460.
- Chuine, I. & Regniere, J. (2017). Process-based models of phenology for plants and animals. *Annual Review of Ecology, Evolution, and Systematics*, 48, 159–182.
- Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S. & Wolkovich, E.M. (2012). Phenological tracking enables positive species responses to climate change. *Ecology*, 93, 1765–1771.
- Cohen, J.M., Lajeunesse, M.J. & Rohr, J.R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, 8, 224–+.
- Collins, M., Knutti, R., Arblaster, J.L., Dufresne, T., Fichefet, P., Friedlingstein, X., Gao, W., Gutowski, T., Johns, G., Krinner, M., Shongwe, C., Tebaldi, A., Weaver & Wehner, M. (2013). *Climate Change 2013: The Physical Science Basis – Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, chap. Long-term Climate Change: Projections, Commitments and Irreversibility, pp. 1029–1119.
- Cook, B.I., Wolkovich, E.M. & Parmesan, C. (2012). Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 9000–9005.
- Davison, R., Jacquemyn, H., Adriaens, D., Honnay, O., de Kroon, H. & Tuljapurkar, S. (2010). Demographic effects of extreme weather events on a short-lived calcareous grassland species: stochastic life table response experiments. *Journal of Ecology*, 98, 255–267.
- Deacy, W.W., Erlenbach, J.A., Leacock, W.B., Stanford, J.A., Robbins, C.T. & Armstrong, J.B. (2018). Phenological tracking associated with increased salmon consumption by brown bears. *Scientific Reports*, 8.

- Diffenbaugh, N.S., Swain, D.L. & Touma, D. (2015). Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 3931–3936.
- Donaldson-Matasci, M.C., Bergstrom, C.T. & Lachmann, M. (2012). When unreliable cues are good enough. *American Naturalist*, 182, 313–327.
- Donohue, K. (2002). Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*. *Ecology*, 83, 1006–1016.
- Ehrlén, J., Morris, W.F., von Euler, T. & Dahlgren, J.P. (2016). Advancing environmentally explicit structured population models of plants. *Journal of Ecology*, 104, 292–305.
- Ellner, S.P., Snyder, R.E., Adler, P.B. & Hooker, G. (2019). An expanded modern coexistence theory for empirical applications. *Ecology Letters*, 22, 3–18.
- Farzan, S. & Yang, L.H. (2018). Experimental shifts in phenology affect fitness, foraging, and parasitism in a native solitary bee. *Ecology*, 99, 2187–2195.
- Fournier-Level, A., Korte, A., Cooper, M.D., Nordborg, M., Schmitt, J. & Wilczek, A.M. (2011). A map of local adaptation in *Arabidopsis thaliana*. *Science*, 333, 86–89.
- Gotelli, N.J. & Graves, G.R. (1996). The temporal niche. In: *Null Models in Ecology* (eds. Gotelli, N.J. & Graves, G.R.). Smithsonian Institution, Washington, DC, pp. 95–111.
- Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006). Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters*, 9, 399–409.
- Heberling, J.M., Cassidy, S.T., Fridley, J.D. & Kalisz, S. (2019). Carbon gain phenologies of spring-flowering perennials in a deciduous forest indicate a novel niche for a widespread invader. *New Phytologist*, 221, 778–788.
- Hofer, S., Tedstone, A.J., Fettweis, X. & Bamber, J.L. (2017). Decreasing cloud cover drives the recent mass loss on the Greenland ice sheet. *Science Advances*, 3.
- IPCC (2014). *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jansson, R. & Dynesius, M. (2002). The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. *Annual Review of Ecology and Systematics*, 33, 741–777.
- Kaitala, V., Ylikarjula, J., Ranta, E. & Lundberg, P. (1997). Population dynamics and the colour of environmental noise. *Proceedings of the Royal Society B-Biological Sciences*, 264, 943–948.
- Kharouba, H.M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E. & Wolkovich, E.M. (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 5211–5216.

- Kharouba, H.M., Paquette, S.R., Kerr, J.T. & Vellend, M. (2014). Predicting the sensitivity of butterfly phenology to temperature over the past century. *Global Change Biology*, 20, 504–514.
- Lasky, J.R., Uriarte, M. & Muscarella, R. (2016). Synchrony, compensatory dynamics, and the functional trait basis of phenological diversity in a tropical dry forest tree community: effects of rainfall seasonality. *Environmental Research Letters*, 11, 15.
- Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends in Ecology Evolution*, 17, 183–189.
- Levins, R. (1968). *Evolution in changing environments: some theoretical explorations*. Princeton University Press, Princeton, NJ.
- Mayfield, M.M. & Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatcza, K., Mage, F., Mestre, A., Nordli, O., Penuelas, J., Piri-nen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S. & Züst, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12, 1969–1976.
- Milly, P.C.D., Betancourt, J., Falkenmark, M., Hirsch, R.M., Kundzewicz, Z.W., Lettenmaier, D.P. & Stouffer, R.J. (2008). Climate change - stationarity is dead: Whither water management? *Science*, 319, 573–574.
- Monson, R.K., Lipson, D.L., Burns, S.P., Turnipseed, A.A., Delany, A.C., Williams, M.W. & Schmidt, S.K. (2006). Winter forest soil respiration controlled by climate and microbial community composition. *Nature*, 439, 711–714.
- Morin, X. & Chuine, I. (2005). Sensitivity analysis of the tree distribution model phenofit to climatic input characteristics: implications for climate impact assessment. *Global Change Biology*, 11, 1493–1503.
- Morin, X., Viner, D. & Chuine, I. (2008). Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology*, 96, 784–794.
- Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C.V., Boggs, C.L., Boyce, M.S., Bruna, E.M., Church, D.R., Coulson, T., Doak, D.F., Forsyth, S., Gaillard, J.M., Horvitz, C.C., Kalisz, S., Kendall, B.E., Knight, T.M., Lee, C.T. & Menges, E.S. (2008). Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, 89, 19–25.
- Nosenko, T., Schreiber, F., Adamska, M., Adamski, M., Eitel, M., Hammel, J., Maldonado, M., Mueller, W.E.G., Nickel, M., Schierwater, B., Vacelet, J., Wiens, M. & Woerheide, G. (2013). Deep metazoan phylogeny: When different genes tell different stories. *Molecular Phylogenetics and Evolution*, 67, 223–233.

- Provan, J. & Bennett, K.D. (2008). Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology & Evolution*, 23, 564–571.
- Ramula, S., Johansson, J., Linden, A. & Jonzen, N. (2015). Linking phenological shifts to demographic change. *Climate Research*, 63, 135–144.
- Richardson, A.D., Bailey, A.S., Denny, E.G., Martin, C.W. & O’Keefe, J. (2006). Phenology of a northern hardwood forest canopy. *Global Change Biology*, 12, 1174–1188.
- Ripa, J. & Lundberg, P. (1996). Noise colour and the risk of population extinctions. *Proceedings of the Royal Society B-Biological Sciences*, 263, 1751–1753.
- Sale, P.F. (1977). Maintenance of high diversity in coral reef fish communities. *American Naturalist*, 111, 337–359.
- Screen, J.A. (2014). Arctic amplification decreases temperature variance in northern mid- to high-latitudes. *Nature Climate Change*, 4, 577–582.
- Singer, M.C. & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3161–3176.
- Stinchcombe, J.R., Weinig, C., Ungerer, M., Olsen, K.M., Mays, C., Halldorsdottir, S.S., Purugganan, M.D. & Schmitt, J. (2004). A latitudinal cline in flowering time in *Arabidopsis thaliana* modulated by the flowering time gene FRIGIDA. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 4712–4717.
- Stocker, T., Qin, D. & Plattner, G. (2013). Climate change 2013: The physical science basis. *Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Summary for Policymakers (IPCC, 2013)*.
- Tuljapurkar, S., Gaillard, J.M. & Coulson, T. (2009). From stochastic environments to life histories and back. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 364, 1499–1509.
- Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D.G., McCann, K.S., Savage, V., Tunney, T.D. & O’Connor, M.I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B-Biological Sciences*, 281.
- Venable, D.L. (2007). Bet hedging in a guild of desert annuals. *Ecology*, 88, 1086–1090.
- Visser, M.E., Holleman, L.J.M. & Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, 147, 164–172.
- Vitasse, Y. (2013). Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist*, 198, 149–155.

- Vrba, E.S. (1980). Evolution, species and fossils - how does life evolve. *South African Journal of Science*, 76, 61–84.
- Vrba, E.S. (1985). Environment and evolution - alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science*, 81, 229–236.
- Wainwright, C.E. & Cleland, E.E. (2013). Exotic species display greater germination plasticity and higher germination rates than native species across multiple cues. *Biological Invasions*, 15, 2253–2264.
- Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2012). Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *Journal of Applied Ecology*, 49, 234–241.
- Willis, C.G., Ruhfel, B., Primack, R.B., Miller-Rushing, A.J. & Davis, C.C. (2008). Phylogenetic patterns of species loss in Thoreau’s woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 17029–17033.
- Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J., Losos, J.B. & Davis, C.C. (2010). Favorable climate change response explains non-native species’ success in Thoreau’s woods. *PLoS ONE*, 5, e8878.
- Wolkovich, E.M. & Cleland, E.E. (2011). The phenology of plant invasions: A community ecology perspective. *Frontiers in Ecology and the Environment*, 9, 287–294.
- Wolkovich, E.M. & Cleland, E.E. (2014). Phenological niches and the future of invaded ecosystems with climate change. *AoB Plants*, 6, plu013.
- Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E., Pau, S., Regetz, J., Davies, T.J., Kraft, N.J.B., Ault, T.R., Bolmgren, K., Mazer, S.J., McCabe, G.J., McGill, B.J., Parmesan, C., Salamin, N., Schwartz, M.D. & Cleland, E.E. (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature*, 485, 494–497.
- Wolkovich, E.M., Davies, T.J., Schaefer, H., Cleland, E.E., Cook, B.I., Travers, S.E., Willis, C.G. & Davis, C. (2013). Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany*, 100, 1407–1421.
- Zak, D.R., Groffman, P.M., Pregitzer, K.S., Christensen, S. & Tiedje, J.M. (1990). The vernal dam - plant microbe competition for nitrogen in northern hardwood forests. *Ecology*, 71, 651–656.
- Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019). Phenology in a warming world: differences between native and nonnative plant species. *Ecology Letters*.
- Zhu, J.T., Zhang, Y.J. & Wang, W.F. (2016). Interactions between warming and soil moisture increase overlap in reproductive phenology among species in an alpine meadow. *Biology Letters*, 12, 4.

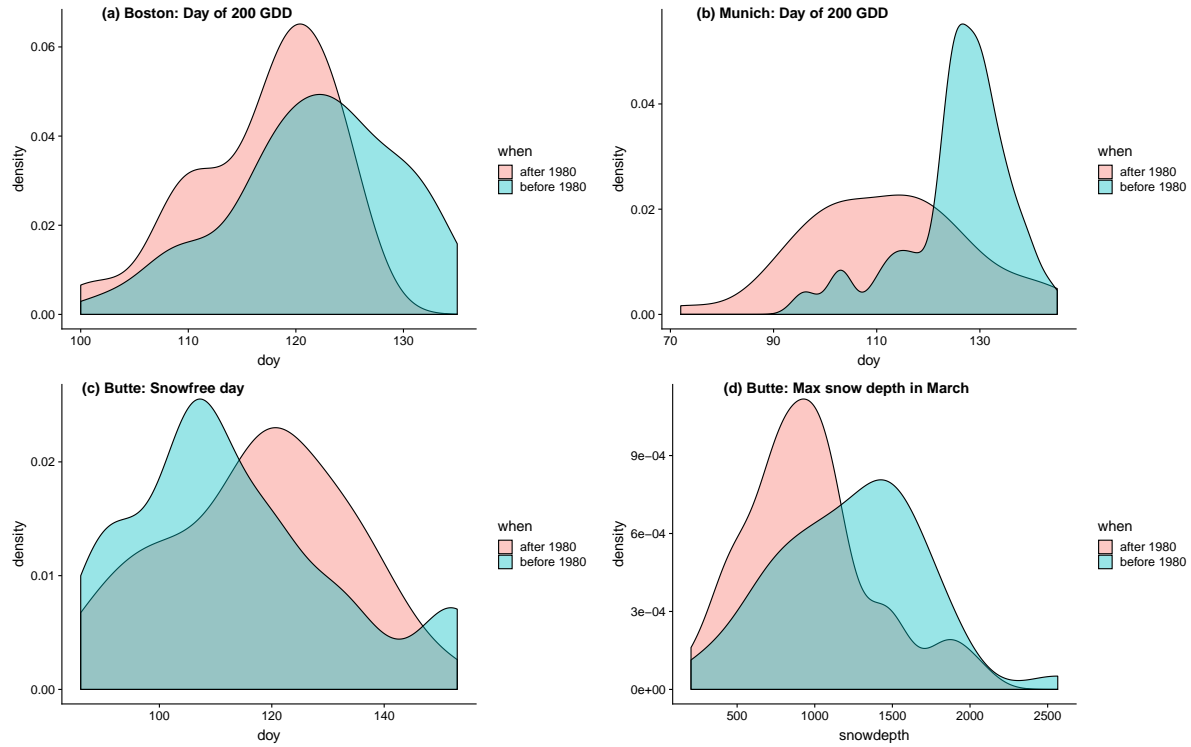


Figure 1: Examples of shifts before and after 1980 (a major changepoint in climate for many areas) in some abiotic metrics related to start of growing seasons (a-c) or resource pulse connected to growing season (d). Density plots of day of 200 growing degree day units (based on 0 degree base temperature using daily minima in  $^{\circ}\text{C}$ ) in Boston, MA, USA (a), and Munich, Germany (b), first snowfree day (followed by at least 9 snowfree days) in Crested Butte, CO, USA (c) and maximum snowdepth (mm) in March (often the month before the first snowfree day) in Crested Butte, CO, USA (d). We selected sites that have been studied for plant phenological data and included at least 80 years of daily climate data from a Global Historical Climatology Network site (downloaded from <https://climexp.knmi.nl/>); we subsetting data so that there was 40 years before and after 1980 for all sites.

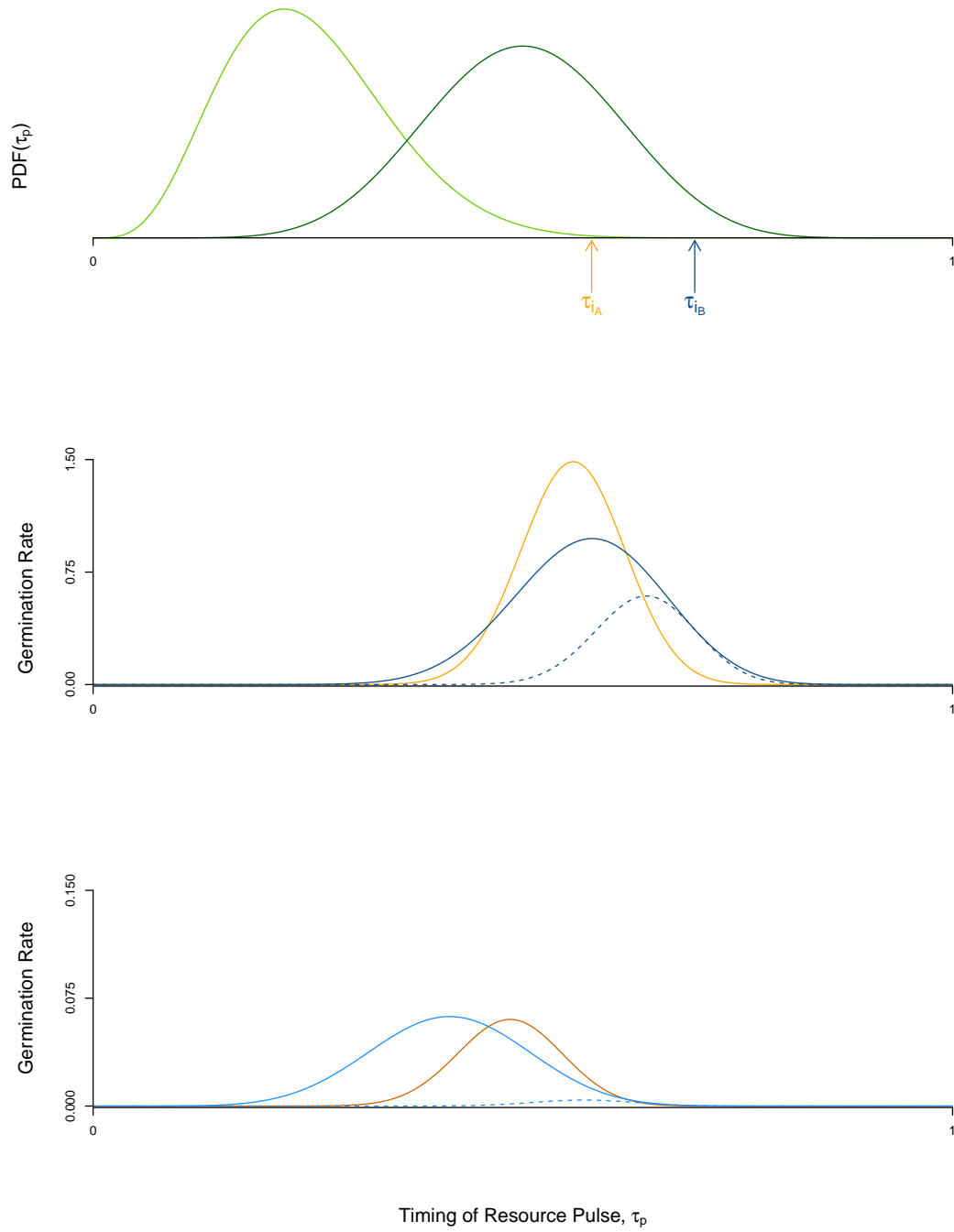


Figure 2: A) The timing of the resource pulse ( $\tau_p$ ) is  $\beta$ -distributed with parameters  $\beta(10, 10)$  during the stationary period (dark green) shifting to  $\beta(5, 15)$  through the nonstationary period. (B) Realized germination rate as a function of  $\tau_p$  for two species during the stationary period: the orange line is a non-tracking species A with preferred germination time,  $\tau_{iA}$  close to the mean of the stationary period; the blue lines show the germination of a tracking species with a preferred germination time  $\tau_{iB}$  further from the mean of the stationary period both with (solid) and without (dashed) the effect of tracking. (C) Realized germination rate of sp A and sp B at the end of the nonstationary period. Note the change in axes from (B) to (C) shows the decline in overall germination rate as the environment moves away from the preferred germination time of both species.

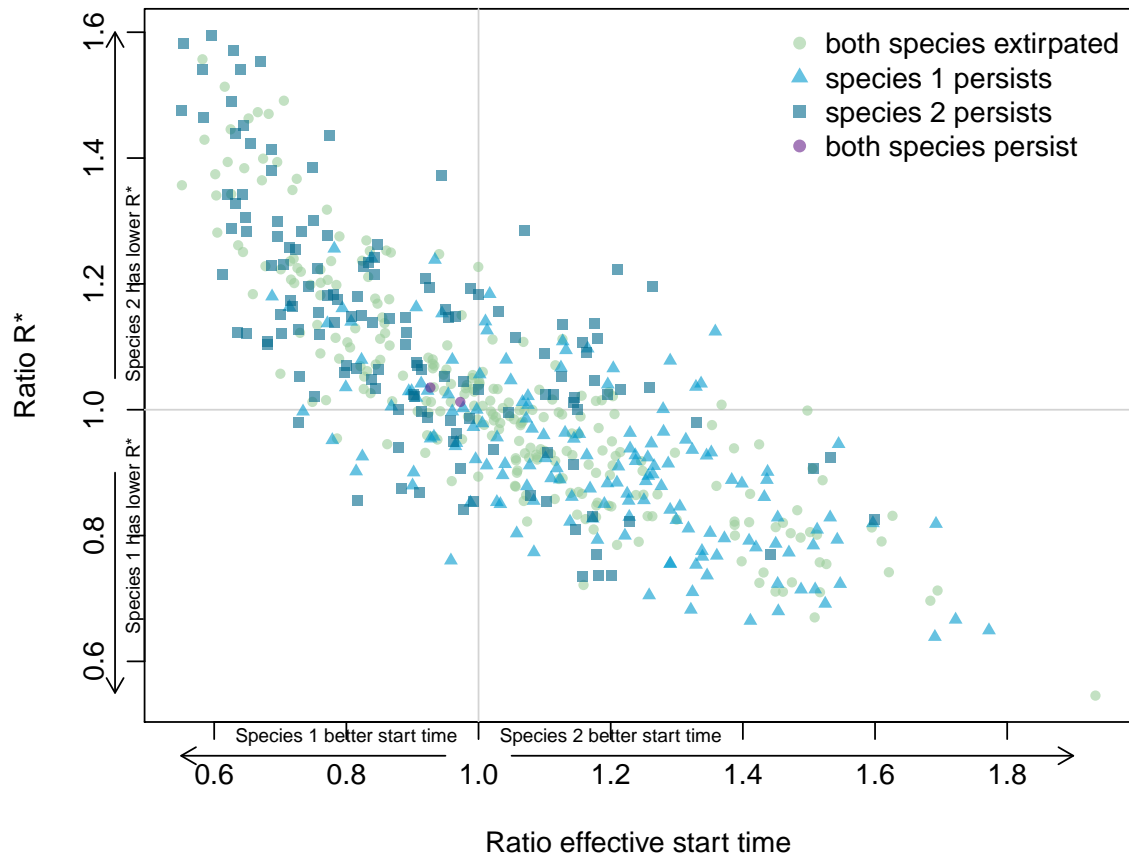


Figure 3: How non-stationarity reshapes two-species communities in a simple model where effective start time (X axis: species 1/species 2) trades off with  $R^*$  (Y axis: species 1/species 2): each point represents one two-species community that persisted through 500 years of stationary dynamics while the shape and color represent the outcome for that two-species community of 500 years of non-stationarity, where the abiotic start of the season shifts earlier.



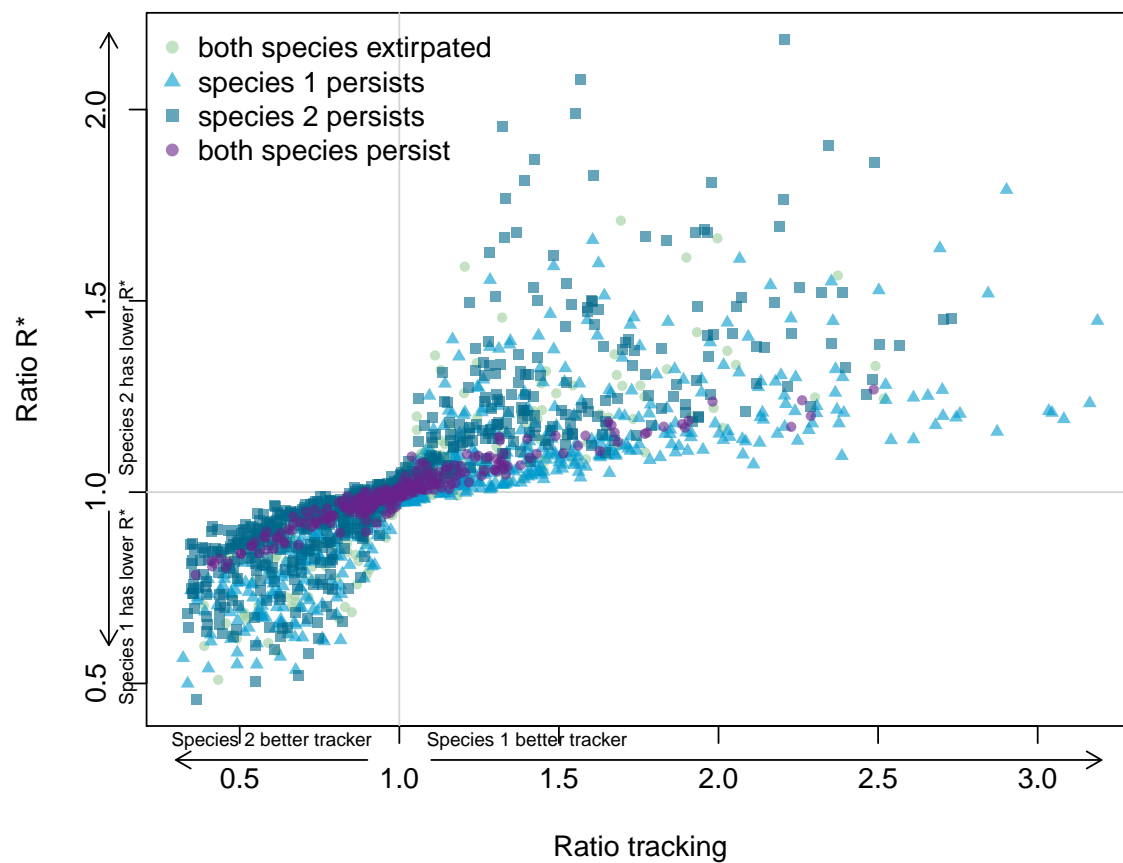


Figure 4: How non-stationarity reshapes two-species communities in a simple model where tracking (X axis: species 1/species 2) trades off with  $R^*$  (Y axis: species 1/species 2): each point represents one two-species community that persisted through 500 years of stationary dynamics while the shape and color represent the outcome for that two-species community of 500 years of non-stationarity, where the abiotic start of the season shifts earlier.