

Running title: Environmental tracking

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

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Abstract

[NEED TO FIX ABSTRACT...] Climate change is reshaping the environments of all species. Predicting how communities will shift in response requires understanding the mechanisms that govern how communities assemble, and how these mechanisms will shift with warming. Growing empirical evidence suggests that environmental tracking—how much an organism can shift the timing of key life history events in response to the environment—is linked to species performance and is a structuring force in communities today. Here, we review current knowledge on temporal environmental tracking both in empirical data and through the lens of community ecology theory. We focus on how climate change has altered the start of the growing season, examine the available evidence that tracking may trade-off with other traits, and provide an initial test of how well basic theory supports the paradigm that climate change should favor environmental tracking. We show how trade-offs that promote coexistence in stationary environments break down in non-stationary environments and may shift the fundamental mechanisms that structure ecological communities. Finally, we consider how the reality that climate change has widespread effects beyond mean temperature, including shifts in growing season length, variability, and in extreme events, may complicate simple predictions of winners and losers.

1 Main text

Anthropogenic climate change is causing widespread changes in species distributions, with many species shifting in both time and space (?). Reports often focus on species shifting to higher elevations and poleward (?) and/or shifting their recurring life history events (phenology) earlier as climate warms (??). Across species, however, there is high variability. A large proportion of species are not shifting at all (?), which has raised concerns about whether these species may be more vulnerable to population declines with continued warming. Such concerns 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 (?). Tracking climate change may then be a major component to understanding and predicting the indirect effects of climate change, including population declines, with cascading effects on community and ecosystem structure.

Multiple areas of ecological theory suggest that trackers should ‘win’ with climate change. For example, if tracking is considered a form of plasticity, then models predict species that track will be favored in novel environmental conditions. Similarly, models of community assembly suggest that a warming climate should open up new temporal niche space and favor species that can exploit that space (???). Thus, a shift toward earlier spring should favor earlier species, especially those that can environmentally track ever-earlier seasons. The hypothesis that tracking may predict fitness outcomes with climate change has gained significant traction in the ecological literature focused on global change (e.g., ?); however, there has been comparatively little work to formally connect tracking to foundational ecological theory.

This disconnect could in part be due to the reality that most ecological theory today is for stationary systems. While major arenas of research such as ‘modern coexistence theory’ or population ecology are now built on assumptions of a stochastic environment, they generally still assume stationarity, where the underlying distribution of the environment is unchanged across time (i.e., constant mean and variance, ?). 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., ??).

Climate change upends the assumption of stationarity. By causing increases in temperature, larger pulses of precipitation, increased drought, and more storms (?), 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 theory to non-stationary environments (?), little work has examined what such a transition may mean for communities and the species within them.

Here, we review current knowledge on tracking both in empirical data from the climate change impacts literature and through its related ecological theory. We provide a definition of environmental tracking that highlights both why it must be fundamentally related to fitness, and also the complexity of defining it in empirical systems. We then show how life history theory—specifically drawing on optimal control, bet-hedging and plasticity—make predictions for variation in tracking across species and environments in stationary and non-stationary systems. Moving from life-history theory, which often abstracts other species, we examine how well basic community

ecology theory can be extended to test the current paradigm that climate change should favor species with environmental tracking. Our aim is provide a framework using existing ecological theory to understand how tracking in stationary and non-stationary systems may shape communities, and thus help predict the species-level and community consequences of climate change.

1.1 Defining environmental tracking

While tracking has become a common word in the phenology and climate change literature (CITES), there are few, if any, definitions of it. Yet, most interpretations of tracking come from a model of what we call fundamental tracking: how well an organism matches the timing of a life history event to the ideal timing for that event. Fundamental tracking thus rests on an assumption that there is a timing (an ‘ideal timing’) that yields maximum fitness, and event timings moving away from this timing result in reduced fitness, a foundational concept of the trophic mismatch literature (CITES). Yet this ideal timing is generally only clear in simplified models or in retrospect, thus species must use environmental cues to attempt to predict and match their event timing to the ideal timing across environments in both space and time. Each organism’s set of cues forms the biological basis for how a species tracks, but measuring environmental tracking requires two more parts.

First, environmental variability in part determines measured environmental tracking, specifically which aspects of the environment vary, and how much. If the varying components of the environment do not relate directly or indirectly to the organism’s cues, then the species does not track this variability. Under this definition, identical genotypes will have different tracking across environments, depending on the interaction of the cues and environmental variability.

Second, what aspect(s) of the environment researchers measure will further determine measured environmental tracking. If researchers know the exact cue (e.g., a thermal threshold) or suite of cues (e.g., a interaction of thermal sums and daylength) and can perfectly measure these in an environment where the cue(s) varies then an organism will track the environment perfectly. If researchers measure some related attribute (e.g., mean spring temperature in place of thermal sums) or only some of the organism’s cues, then tracking will be estimated to be lower (i.e., a noisier statistical relationship). If the measured environmental variable is not directly related to the cue(s) that the species actually uses, but one correlated with it (e.g., plant tracks light but researchers measure snowmelt) then it is not tracking per our definition, but potentially may be a proxy or correlation for it.

Accurately measuring environmental tracking thus requires a complete knowledge of the organism’s cue(s), the environment’s variability and the relationship between the actual cues and measured environmental metrics. Knowing an organism’s cues is inherently difficult, generally requiring a suite of experiments, process-based models and in-situ data to show that the model of cues is accurate. Not surprisingly then we lack this for almost all species on earth, coming closest for some model species (CITE Shcmitt work as example), other economically important plants and insects (CITES) and have some basic information for many other species (give coral and/or bird example CITES).

1.2 Understanding variation in environmental tracking

Attempting to measure environmental tracking and compare variation in it across species, space and time is a rapidly growing area of ecological research (????, e.g.,). Multiple meta-analyses now show plants' spring phenology tracks spring or annual temperatures 4-6 days/°C on average across species (???), but also highlight high variation across species (?), even after examining multiple major climate variables (?). Variability across species 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 ?).

All species-rich studies of phenology-climate relationships find high variation, including some species that do not track or track poorly (i.e., high noise surrounding observed statistical relationship). Researchers have worked to link such variation at times to the underlying cues (e.g., ?), species traits (e.g., ?) or trophic level (e.g., ?). These approaches hint at the three major classes of reasons that underlie species that do not appear to track climate (or appear to be poor trackers): (1) species do not track, (2) lack of firm biological understanding of the cues that underlie tracking, and (3) statistical artifacts that make it difficult to measure tracking robustly. Increasing research has outlined the statistical difficulties in measuring tracking, which often relate to the complexity of climate data and the use calendar dates in a non-stationary system (see Box 'Statistical challenges in measuring tracking'). Increasingly, research has highlighted how rarely metrics of tracking are linked to a firm biological understanding of an organism's cues CITES, which will generally lead to lower estimates of tracking for species with usual or under-studied cues. Further, it means that many estimates of 'tracking' may be proxies (i.e., environmental variables correlated with one or more actual cue that a species uses) for an organism's true tracking. [COULD ADD here something on how ecologists are bad at multivariate environments/joint distributions etc.] Yet other variation may be real and suggests perfect environmental tracking may either not be possible or optimal for all species.

A number of research areas in ecology predict variation across species in how well they track the environment, but applying these areas of research to environmental tracking first requires understanding phenological events and the two organism-level decisions that lead to them. While we may view some phenological events as simple on/off switches (e.g., a bird lays eggs or seeds germinate), they are almost always defined by investment decisions that are part of a continuous developmental process (CITEINOUE). Thus, we argue these events are best considered as the outcome of a two-part sequential decision process that is repeatedly evaluated over time. At each temporal unit, an event can either happen or not (step 1) and, if it happens, there is a secondary decision regarding the size of the event (step 2). This decision process is generally applied at the level of the individual (but it could potentially apply at lower levels, for example buds on a branch, or potentially higher levels, such as all the offspring from a parent). Across time, it produces an event's distribution. After starting, many events are entrained to continue based on the underlying physiological process: for example, laying eggs within one clutch (in this example, the decision is whether to lay eggs or not and then how many to lay at each temporal unit, such as per day or hour) or flowering each growing season (in this example, the decision is whether to flower or not and then how many flowers to burst during each temporal unit, such as per day or hour). In such cases, first events at the individual-level

are somewhat unique from the rest of the event’s distribution. [MEGAN: Can we cite Mangel dynamic state variable models here?]. In all cases, these individual-distributions scale up to the population (or pseudo-population) level estimates of these events generally used by researchers (CITEINOUE for an excellent discussion of the outcomes of this scaling).

Considering the life history events that define part of environmental tracking as a two-part process highlights that tracking is ultimately shaped by resources that species need to grow and reproduce, and circles back to an organism’s fundamental tracking. This is perhaps best recognized in the literature on trophic synchrony where there is often focus on how well consumers’ environmental tracking matches to the seasonal distributions of their prey (??). For example, decades of work has studied how birds (e.g., *Parus major*) time their peak food demands—during their nesting season—to maximum prey (caterpillar) abundance (e.g., ?). Failure of environmental tracking to match prey year-to-year or over time with long-term warming has been well tied to individual-level fitness consequences in some systems (?), but not all (?). Environmental tracking in plants and other lower trophic levels is also about resources. Alpine plant species that emerge in step with snowmelt or temperature 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 leaf out before the canopy closes and access to light becomes severely reduced (??). In both temperate as well as alpine systems, however, access to critical belowground resources also occurs in the spring—both for available water and for nutrients released with the turnover of seasonal microbial communities (??). Thus, plants’ spring phenology in many systems is about careful tracking of 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 tending to grow larger and/or produce more offspring (?). These ultimate controllers on tracking—which determine fundamental tracking—are then filtered through the abiotic environmental cues species use to time events. From here, predicting tracking relates to predicting which cue(s) an organism should have.

Predicting variation in environmental tracking in stationary systems

Optimal control rules predict which cues an organism should have based on a consideration of the costs, benefits and constraints, in any one organism by environment system. First, it requires there is an optimal time that varies, thus it requires a seasonal environment with variability (across time or space). Next, there must be a useful cue—some aspect of the environment that predicts resources or otherwise links to back to the ultimate factors that shape environmental tracking. Some environments may inherently lack useful predictors, such as desert systems where few early-season variables seem to predict high or consistent rainfall years. From here, the exact cue or suite of cue(s) that an organism should have depends on: the cost of those cues (i.e., how much energy or other resource(s) an organisms expends to maintain a cue), and the benefits derived from the cue(s). For example, cues which prevent leafout before the last frost or arriving at breeding grounds well before prey populations are abundant have high benefits. Ultimately the balance of the costs of cue(s) and their benefits should determine exactly what cue(s) a species uses: apparently poor cues may occur for organisms in environments where there is both a low cost and low benefit to the cue(s). Similarly, expensive cues such as complex multivariate ones are possible given a high pay-off. Most in-depth studies of species’

phenological cues find evidence for complex multivariate ones, which may provide large benefit in best coupling the timing of cues to the ultimate controls (i.e., cues that couple environmental tracking strongly to fundamental tracking). For example, woody plant leafout responds strongly to warm spring temperatures, but also to cool winter temperatures and/daylength to prevent leafout in mid-winter warm snaps that occur long before the last frost. Finally, constraints also shape cues—these may arise from standing genetic variation that limits phenotypic variation and thus can slow the evolution of optimal cues (CITES rapid evolution stuff), or deeper evolutionary history that may produce co-evolved traits making it difficult for selection to act on a single trait axis (CITES ‘a Felsen’ etc.), and other fundamental evolutionary limits to the rates of trait change and what traits are possible (CITES spandrels).

Optimal control highlights that not all species should track, but instead that tracking based on an optimization of costs, benefits and constraints. Importantly, it generally assumes there is an optimal strategy. In environments where this is not the case, life-history theory predicts species should bet-hedge: bet hedging assumes there is no clear optimum and thus multiple strategies should work and is focused more on how much versus when.

Predicting variation in environmental tracking in non-stationary systems

Much of life-history theory, including optimal control and bet-hedging, rests on assumptions of stationarity, thus a major open area of research is adapting life history theory to non-stationary environments. Multivariate cues may be especially robust to a non-stationary environment if they provide a tight coupling of cues to fundamental tracking, and that coupling is maintained in the non-stationary environment. But multivariate cues may equally be most vulnerable to failure, if the exact form of non-stationary decouples the cues from fundamental tracking. For example, consider an organism’s whose cues evolved based on a correlation between peak prey abundance and daylength—these cues may work well in a stationary environment but fail if warming advances peak prey abundance. Predicting the outcome of non-stationarity thus relies critically on knowing both the full cue system of an organism, how it relates to fundamental tracking and how both that cue system and the underlying fundamental model shift with non-stationarity.

Another area of life-history theory, that focused on plasticity, may be more primed to provide insights on non-stationarity. Considering phenology as a trait (as we and others do, CITES), environmental tracking is thus one type of plasticity. Researchers could thus more broadly understand environmental tracking through modeling an organism’s reaction norms (CITE CHMURA) and understanding how cues and suites of cues—across environments—determine how fundamentally plastic an organism may be in its tracking. For example, multivariate cues should yield higher plasticity in this framework. From here, models of the role of plasticity in novel environments provide an important bridge to understanding the outcomes of non-stationarity, generally predicting non-stationarity should favor highly plastic species. This outcome, however, assumes there are no costs related to plasticity (CITES).

If there are costs associated with plasticity, akin here directly to costs associated with tracking, then species may evolve lower tracking, because it should trade-off with other traits. Plasticity theory—in contrast to much of the life-history theory discussed above (where other species are, at best, filtered into models as an aspect of the environment)—shows how critical a multi-

species perspective is to understanding environmental tracking. In this light, tracking cannot be considered as a singular trait, but must be evaluated as part of a trait syndrome.

As tracking often relates to the timing of a resource pulse, traits related to resource acquisition are likely contenders for a trade-off. Species with traits that make them poor resource competitors may need to track the environment closely to take advantage of transient periods of available resources, but will risk tissue loss to harsh environmental conditions more prevalent early in the season (e.g., frost or snow). In contrast, species with traits that make them superior resource competitors may perform well even if they track environments less closely, because their resource acquisition is not strongly constrained by competitors. Examples include under-canopy species leafing out earlier to gain access to light (?) or species with shallow roots starting growth sooner in an alpine meadow system, while species with deeper roots begin growth later (?). In such cases, tracking is akin to a competition-colonization trade-off (?), where species that track well gain priority access to resources and, thus, may co-exist with superior competitors. Research to date supports this, with several studies linking higher tracking to traits associated with being poor competitors (???). Further, many studies have found a correlation between higher tracking and ‘earlyness’ each season, which has been linked to resource acquisition traits associated with lower competitive abilities (?, see Box ‘Trait trade-offs with tracking’).

Understanding these trade-offs is clearly critical, but we also argue more theory is needed to understand the short term dynamics of a changing environment and plasticity—most theory predicts the outcome of a new environment, but non-stationarity in the climate today means we need more on the trajectory to that outcome (more eco in the evo needed here). For example, models show how plasticity may limit standing variation and thus reduce fitness in novel environments (CITES). Whether such findings extend to systems transitioning from stationary to non-stationary will likely depend on how non-stationarity affects the rate of adaptation (CITES).

1.3 Including tracking in multi-species models

Predicting how tracking may determine which species are effectively winners and losers with climate change requires integrating non-stationary environments into models of plasticity and also community assembly. Recent advances in coexistence models, sometimes called ‘modern coexistence theory,’ recognize that both mechanisms independent of fluctuations in the environment (e.g., R^* and other classical niche differences) and mechanisms dependent on fluctuations in the environment (relative non-linearity and storage effect) can drive coexistence (??). These models, which underlie much of current community ecology research (???), provide a framework to begin to model environmental tracking and non-stationarity.

How the environment is defined in most community models falls into two broad categories. In some models the environment is expressed as variation in parameters related to species. For example, in some lottery models the environment appears, effectively, as variation in birth and death rates. In a more recent, CITERUDOLF added the temporal environment to competition models by making interaction strength dependent on the temporal distance between species.

Building a changing environment into such models thus requires knowing how environmental shifts filter through to species-level parameters (?). 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 these models requires knowing how the environment is changing, and we suggest may provide the greatest opportunity to understanding how environmental tracking and non-stationarity determine future communities. These models generally define the environment as a resource and thus generally model something close to fundamental tracking.

Species responses to the (resource) environment are also be broadly grouped into two modeling camps: those that explicitly model when species start an event (e.g., spawning or germination) in response to the environment versus those that model the magnitude (e.g., the number of propagules or seeds) of response to the environment. Models that explicitly model when a species starts an event are often focused on situations where order of arrival is critical to predicting coexistence outcomes. Models of priority effects through niche pre-emption make up much of the recent literature in this area: early arrivals receive a head-start advantage, by gaining priority access to resources (the environment) they can draw down the resources available to later arrivals. Species that track in this model could be considered those that arrive earliest, however, priority effects generally require species that are highly similar to one another and thus models of priority effects do not predict variation in tracking across species, and further would not predict trade-offs between tracking and other traits. Trade-offs, however, are predicted from competition/colonization models: if species that track well are akin to species with high-dispersal, trackers may coexist by gaining early access to resources and reproducing before the later arrival of superior competitors.

Other models canalize species' responses to the environment into investment decisions. For example most models of inter-annual competition (much of 'modern coexistence theory') fall into this framework. Species invest (via offspring, tissue etc.) differentially depending on the environment each year and outcomes of this are mediating through density. While these models superficially may seem disconnected from timing, they critically highlight how phenology relates to investment decisions (in contrast, priority effect models explicitly model timing, but do not allow investment to vary as a function of the environment). They also may provide a simple way to begin to abstract tracking into such coexistence models, and test the outcomes of non-stationarity (see box).

A model where species can vary both when they start an event and how much they invest on dependent on the environment seems to capture the major attributes required for tracking. To our knowledge, however, most models approach the questions of when to go, and how much to invest separately. Models of bet-hedging perhaps come closest (ADDCITES AND MORE HERE). A model that explicitly models the linked decisions of when to time an event and how much to invest in the event could provide fundamental insights on the relative importance of each aspect of this decision process. Such a model could be adapted to address multiple questions of environmental tracking, including how these decisions may trade-off and which other traits tracking may be most strongly linked to, as well as explicitly modeling the costs and benefits of tracking in stationary systems, a precursor to extending it to non-stationary

systems.

Extending models to non-stationary systems is crucial to fully testing how environmental tracking relates to species persistence with climate change, and research has already begun to tackle this non-trivial challenge (??) ADDRUDOLF. Most work to date, however, focuses on conclusions from stationary or non-stationary systems. Thus, the transition between stationary and non-stationary is often ignored, yet we expect it may be most critical. Communities formed in stationary environment periods (or periods with environments lower non-stationarity) are effectively filtered and assembled by that environmental regime and thus produce the base variation and assembly dynamics for a shifting environment. While analytical solutions for systems transitioning from stationary to non-stationary may take time to develop, simulation work can provide an immediate intuition and framework to address this challenge.

1.4 Future directions

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 and determine species persistence—especially as anthropogenic climate change is reshaping the environment of all species. Current models of coexistence are clearly primed for understanding how a variable environment can shape the formation and persistence of communities. Moving forward, we need more focus on understanding the attributes of an environment shaped strongly by humans, and, thus, what advances in theory may be most useful for making predictions in the Anthropocene. 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. 3). Most systems are seeing increases in mean temperatures, which can rapidly impact the metabolism and activity periods of many species (??). This warming is also altering many other attributes of the climate system, including precipitation regimes (?), and cloud cover (?), which can all further influence species via altering environmental cues.

While we focused on one major shift in the climate system (earlier growing seasons), much more research is needed to understand how multivariate environmental shifts may alter these predictions. 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). Researchers 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.

1. How is the environment changing? Embrace the joint distribution
 - (a) Start with first paragraph that we have in this section.
 - (b) To measure and predict environmental tracking across species: Full factorial experiments are good, but may need to embrace the joint distribution of reality more.
 - (c) OCR as useful framework to understand costs of the cues themselves, as well as benefits, understanding constraints
 - (d) This leads to trying to estimate fundamental tracking, which trophic mismatch literature has highlighted is hard. All fields need balance between measures of fundamental tracking, estimating an organism's system of cues and measuring environmental tracking. Clear statements of what is and and is not known and measured will help.
 - (e) Tread carefully in trying to compare species across space, time or species ...
 - (f) Move away from DOY metrics? Try to understand how cues shift with warming, think of other temporal metrics (metabolic ones?)
 - (g) Embrace multivariate cues, and work to understand how non-stationary today impacts them
 - (h) Clarify your environment: Progress can come from considering one species in an environment to how the species reshape the ultimate environment, but studies need to be more clear in their assumptions here.
2. What major traits trade-off with tracking? (Can mostly use this section, just link to plasticity theory and community ecology a little more).
3. Community models need to add true non-stationarity and combine the when to go and how much
 - (a) Models now basically bifurcate in being about when versus how much, we need to know if these models lead to similar or different conclusions
 - (b) More non-stationary models

What major traits trade-off with tracking?

Basic theory requires that 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 (???). Such work lays the groundwork that environmental tracking is important, but future empirical research should address how this trait co-occurs with other traits. Research has highlighted some traits that co-vary with tracking (e.g., ???), but to tie this empirical work to models requires more research on traits that link clearly to theory, and a fuller understanding of how tracking and other traits jointly contribute to performance under varying environments. Traits that link to resource competition, as we focus on here (as others have as well, see ?), 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 the outcomes of these trade-offs 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 that co-occur via equalizing mechanisms can persist longer. While this is a rather obvious outcome—as equalized species will be more similarly affected 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. Thus understanding the prevalence of stabilizing versus equalizing mechanisms (which ecology has worked on for many decades, ??) 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, comes from our modeling approach here, which assumed a closed community without dispersal or evolution. In practice, dispersal of species or individuals with traits that make them better matched to the non-stationary environment (e.g., fixed intrinsic start times that are earlier or with a suite of traits that match to the transformed trade-off axis) would lead to new communities that may persist longer or be continually re-assembled as long as the environment remains non-stationary. Indeed, this logic underlies the argument that invasive species may be superior trackers benefiting from how climate change has altered growing seasons (??). Evolution equally could alter our findings by allowing species traits to evolve in step with environmental change. Long-term population (e.g., ?) and resurrection studies (??), as well as field experiments (??), have repeatedly shown species can shift to earlier flowering times, higher thermal tolerances or related genetically-controlled traits that confer higher fitness in warmer climates. Yet these studies also highlight that responses can be lagged (e.g., ?), associated with reduced population viability (e.g., ?), or other factors that may constrain adaptive responses

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, 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 (?). Thus, ecologists are—and will remain for the foreseeable future—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 (?—even if stationary periods—be they 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 large oscillations in climate (?), the periods that provide the most dramatic community reshuffling are periods shifting from stationary to non-stationary climate regimes (??). Such stories of the past are now fundamentally happening today, and ecology is challenged to understand how transitions between stationary and non-stationary environments are reshaping the species and communities we have today and will in our warmer future.

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Many (or potentially all) species use abiotic cues to trigger major phenological events. These cues in turn result in different rates of tracking. At one extreme, some cues yield a fixed timing, resulting in no tracking over time. A common example of a fixed cue is photoperiod, which results in event timing that is constant across years (but variable across space, allowing—for example, later timings poleward for spring events) and appears widespread for some insect emergence and for fall senescence of many trees (??). Fixed timings are perhaps the simplest option and may be efficient for events where there is low predictability, low variability, or low costs to being too late or early. In cases where there is a high cost to mis-timing an event across a variable environment, cues that yield more variability in timing are far more prevalent and usually rely on climate. Temperature is a widespread cue for start of season events with many organisms needing a certain thermal sum to start visible growth. Such a cue has the benefit of shifting the date of an event early or late, depending on climatic conditions, each year, but may be a poor cue in years with aberrant events (e.g., a late frost). In most systems, species must use environmental cues such as temperature to forecast the ideal date for an event—a date which is only obvious in retrospect. ... Measuring tracking depends on many factors (see Box ‘What underlies variability in species tracking?’).

2.1 Interspecific variation in tracking

Despite the clear importance of tracking for resource access,

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., ??). Such benefits usually break down into avoiding tissue loss or maximizing growth and, relatedly, maximizing reproduction. 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 (???). 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 often relates to the timing of a resource pulse, traits related to resource acquisition are likely contenders for a trade-off. Species with traits that make them poor resource competitors may need to track the environment closely to take advantage of transient periods of available resources, but will risk tissue loss to harsh environmental conditions more prevalent early in the season (e.g., frost or snow). In contrast, species with traits that make them superior resource competitors may perform well even if they track environments less closely, because their resource acquisition is not strongly constrained by competitors. Examples include under-canopy species leafing out earlier to gain access to light (?) or species with shallow roots starting growth sooner in an alpine meadow system, while species with deeper roots begin growth later (?). In such cases, tracking is akin to a competition-colonization trade-off (?), where species that track well gain priority access to resources and, thus, may co-exist with superior competitors. Research to date supports this, with several studies linking higher tracking to traits associated with being poor competitors (???). Further, many studies have found

a correlation between higher tracking and ‘earliness’ each season, which has been linked to resource acquisition traits associated with lower competitive abilities (see Box ‘Trait trade-offs with tracking’).

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 ecological theory to current environments, however, is difficult because most theory has been developed for stationary systems, which are mathematically more tractable, but can sometimes be extended to non-stationary systems (?). Almost no community assembly research, however, has examined the consequences of shifting from a stationary to non-stationary environment.

These include the costs to the organism of having a cue (or system of cues) to the environment (e.g., the machinery of monitoring temperature or daylength), the benefits of a cue (for example, how much tissue is saved by avoiding a coldsnap) and any constraints, such as cues that cannot be developed or evolutionary history making some cues more likely.

2.2 Environmental variability & change

2.2.1 Future research in environmental tracking & non-stationary systems

3 Box: What underlies variability in species tracking?

Much recent research in phenological tracking has focused on variability across species (e.g., ???), with growing work highlighting that some species do not appear to track climate closely. Indeed, theory predicts some species, for some events, should not track the environment, but identifying non-trackers is difficult in most systems.

We argue three major classes of reasons underlie species that do not appear to track climate: (1) species do not track, (2) lack of firm biological understanding of the cues that underlie tracking, and (3) statistical artifacts that make it difficult to measure tracking robustly (see Box ‘Statistical challenges in measuring tracking’). In some cases, species may be best served to not track; this includes species in highly variable environments or which otherwise face high uncertainty in when to time investment decisions. In such cases, species should gain a substantial benefit from bet-hedging or employing other approaches that spread out risk given uncertainty (?). Additionally, evolutionary limitations may prevent tracking: species may not be able to closely measure relevant environmental cues (?), gene flow from other environments may continually push a population away from its local optimum (?), or there may be unavoidable trade-offs (?) with tracking. 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 track less and possess traits related to slower growth and longer lifespans—these later species may bet-hedge more given their longer investment window. This, however, could equally be an artifact where early species use simpler cues, and, thus, their tracking is measured more accurately given current methods.

Accurately measuring environmental tracking depends on the temporal scale of the question

(e.g., intra-annual versus inter-annual versus decadal), and how well researchers understand a species' underlying physiology and ecology. Tracking is often measured simply by the relationship between the dates of the phenological event and a simple abiotic metric, such as mean monthly temperature (with variation in temperature derived from multiple periods of observation or induced through experiments). Simple environmental metrics, however, are almost always proxies for a more complicated underlying physiology where simple cues—such as warm temperatures—can be modified by other cues, such as photoperiod, drought or light spectra (??). Indeed, multiple studies have shown how simple correlations between phenological events and environmental variables can mask complicated relationships (??). Most well-studied species have multiple cues to time critical biological events (?). These additional cues almost always appear adapted 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 suboptimal time).

Modeling this multi-cue complexity well is inherently difficult (?), especially since one cue may dominate in many conditions. For example, woody plant leafout responds strongly to warm spring temperatures, but also to cool winter temperatures to prevent leafout in mid-winter warm snaps that occur long before the last frost. Often this cool-temperature effect may be masked by sufficiently cold conditions. With warming, however, this additional trigger—which appears to vary by site, species and even inter-annual conditions (?—may become critical. 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 (??). Thus, despite the apparent efficacy of many current phenological models, many models may fail spectacularly in the future as additional cues come into play (?). Tracking in species with longer generation times may be especially complicated, as species may track low frequency climate signals and make investment choices on far longer timescales than species with shorter lifespans (?).

4 Box: Statistical challenges in measuring tracking

Perhaps the most widespread reason for 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 (?). Non-stationarity in units comes in many forms—estimates of mean days shifted per decade (i.e., days/decade, a common metric summarizing observed shifts in phenology over time in long-term datasets) depend strongly on the climate of the decade(s) studied, which is not consistent in many systems (??). 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 an average day has increased in most regions with climate change. 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., ?).

Low power is widespread in ecology, where even ‘long’ time-series may be far too short for robust analyses (??). Authors should be especially cautious if they find only large effects appear significant (e.g., ?), which is a well-known statistical bias associated with p-values (?). Additionally, effect sizes that are higher when climate variability is higher (for example, in temperate habitats temperature is highly variable in the spring and autumn compared to summer) may be more related to variation in statistical power than to biology (periods with higher variation yield greater variation in the predictor variable, and thus higher power). Mixed models can help better leverage understanding by pooling information across species, and often better capture uncertainty (?). We suggest mixed models should be used more widely alongside randomization and/or data-simulation approaches (e.g., ??) to better estimate and communicate uncertainty in studies.

5 Box: Trait trade-offs with tracking

Research on phenological tracking and traits has increased greatly in recent years, with a major uptick in studies after 2010 (see SI Fig. ??). Most papers examining tracking and other traits across species have focused on plants (20/30), followed by birds and Lepidoptera (both 4/30), plankton and aphids (both 1/30). 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 (studies included both birds and Lepidoptera, ?????). While this is an important link, it is vulnerable to statistical challenges (see Box ‘Statistical challenges in measuring tracking’). Few studies examined whether tracking correlates with resource acquisition traits; those that did generally found species with higher tracking also had traits associated with lower competitive abilities under low resources (e.g., being shallower or lacking a taproot rooted ???). These species were often also early (e.g., ??), suggesting tracking may relate to a syndrome of traits that allow species to be rapid colonizers each season, but poor competitors for resources. Indeed, previous work has documented that species with earlier phenophases tend to have resource acquisition 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, reviewed in ?).

6 Model box

To understand the role of environmental tracking by species in variable environments we use a simple model that allows within- and between-year dynamics to contribute to coexistence. As the model is akin to many commonly used seed germination models (?), we follow a similar terminology for ease; however the basic structure of our model could apply to other systems with one dominant pulse of a limiting resource each season (e.g., water from rain or snowpack), or a multivariate resource pulse that acts effectively as one resource (e.g., nitrogen and light

drawn down together over the season). In this model the environment is included between-years via variable germination, and within-years the environment is explicitly included as a resource pulse at the start of the season.

In this model, biological start time, can be considered a fixed characteristic of a species, but we adjust it to also allow species to respond to the environment dynamically through what we refer to as tracking. Here, tracking effectively moves a species intrinsic start time closer to the environmental start time in that year, resulting in a higher germination fraction (see SUPP).

In this model, species can co-occur via equalizing mechanisms, but they require stabilizing mechanisms to coexist. Species that is, cannot coexist given only variation in tracking—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. With this added variation—here we varied species’ R^* —species can persist together as long as those species with a temporal niche advantage are also the inferior competitors (Fig. 2). That is, species that can draw resources down to a lower level and are thus the superior within-season resource competitors (lower R^*) can persist with species with that are inferior competitors but have realized biological start times closer to the environmental start time—a finding inline with currently observed empirical trade-offs (see Box ‘Trait trade-offs with tracking’). These trade-offs, however, are all environmentally dependent. They hold only so long as the environment is stationary.

We examined how trade-offs may be transformed by a non-stationary environment, by transitioning a stationary environment—in which two-species communities had persisted for 500 years—to non-stationary, via an earlier start of season (Fig. ??a; see SI for more details). By changing a fundamental niche axis (the distribution of the environment, an axis along which these communities were structured), we shifted one major part of the trade-off: the new non-stationary environment favored an earlier effective biological start time than the previous stationary environment. This, in turn, reshaped our two-species communities, which depended on this trade-off for persistence.

While 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. 2). These two-species communities persisted because the same fundamental trade-off between biological start time and within-season competitive ability, while narrowed, was not fully lost (Fig. 2). Taken together, these simple simulations show how non-stationarity can drive local species extinction and reshape the underlying assembly mechanisms of communities.

Our simulations support growing work that tracking should not be considered alone (?????), but may be part of a larger trait syndrome. Indeed, this model trivially show that multi-species communities cannot form given only variation in the temporal niche—a trade-off is required. Our results thus support empirical work showing a trade-off where trackers are also inferior resource competitors (??)—we show this must be the case for multi-species persistence; otherwise, the species best matched to the environment would drive the other extinct. Finally, our results highlight that non-stationarity may reshape the balance of equalizing versus stabilizing mechanisms (discussed further below).

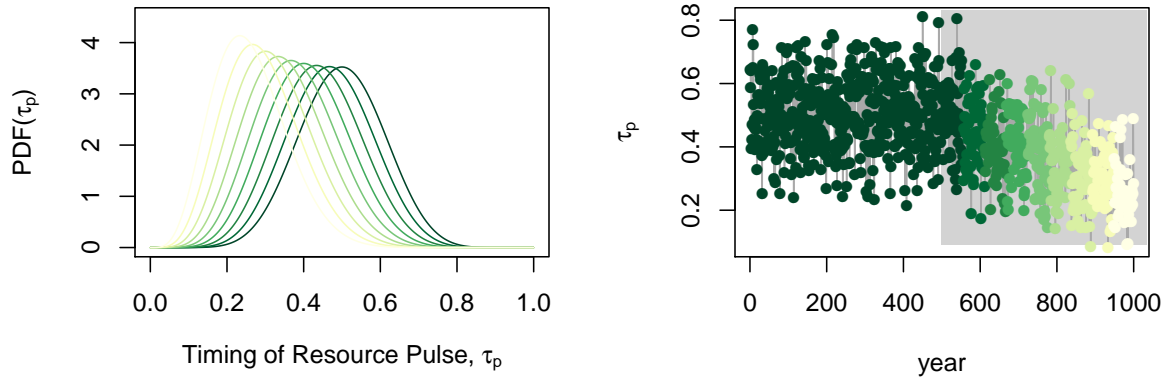


Figure 1: How the environment shifts from the stationary period to the nonstationary period. The timing of the resource pulse shifts from $\tau_p \sim \beta(10,10)$ for the 500 year stationary period to $\tau_p \sim \beta(5,15)$ over the 500 year nonstationary period.

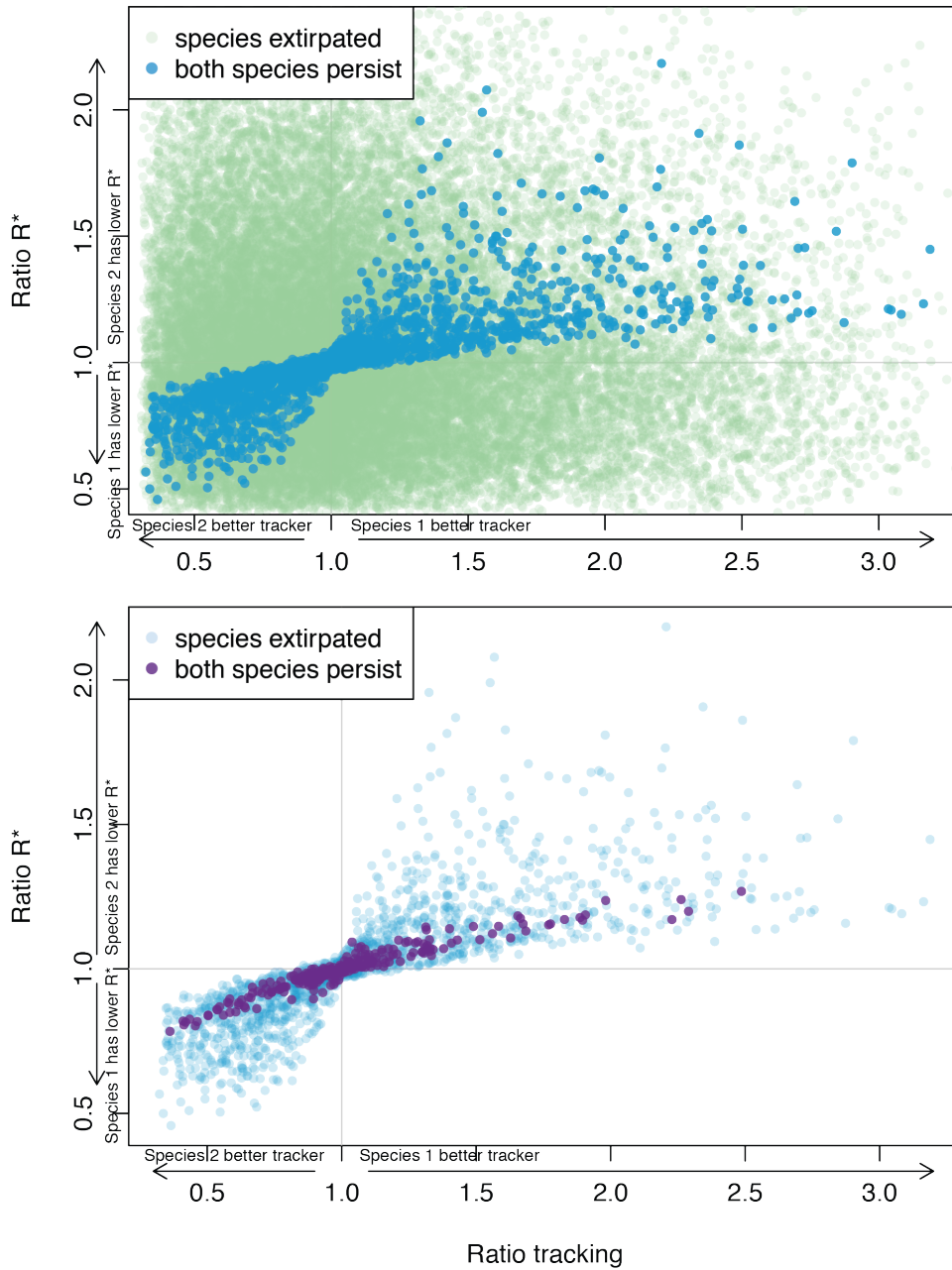


Figure 2: How non-stationarity reshapes two-species communities in a simple model where tracking (X axis: species 1/species 2) trades off with R^* (Y axis: species 1/species 2): each point represents one two-species community color-coded by whether both species persisted or one or more species was extirpated through 500 years of a stationary environment (top), followed by an additional 500 years of non-stationary environment (bottom), where the abiotic start of the season shifts earlier. Only two-species communities that persisted through the stationary period are shown in the bottom panel. See Fig. ?? for an alternative version of this figure detailing one-species outcomes.

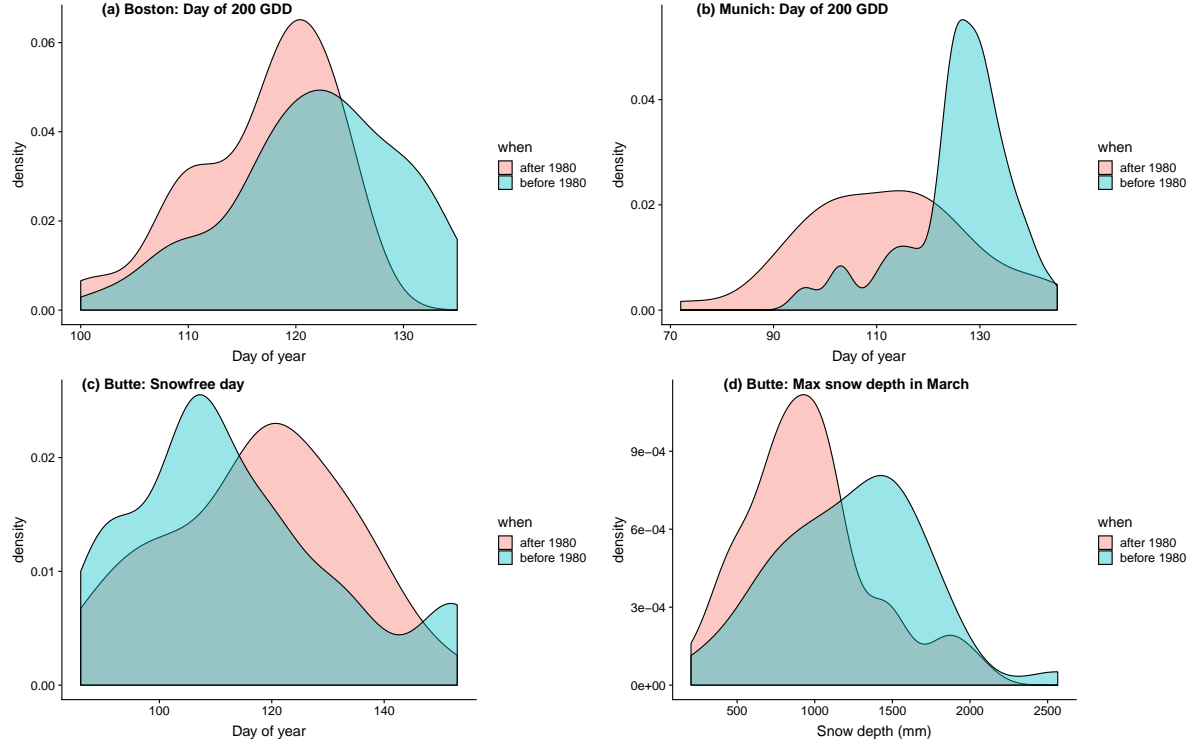


Figure 3: Examples of non-stationarity in climate variables linked to environmental tracking: shifts before and after 1980 (a major change-point in climate for many regions) in several metrics related to the start of growing seasons (a-c) or resource pulse connected to growing season length (d). Density plots of day of 200 growing degree day units (a metric of thermal sum, here 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). Note that (c) and (d) are likely related, with lower snowpacks leading to an earlier first snowfree day. 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; we subsetting data so that there were 40 years before and after 1980 for all sites.