Running title: Tracking & climate change

How temporal tracking shapes species and communities in stationary and non-stationary environments

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Abstract

Climate change reshapes the environments of all species. Predicting species responses requires understanding how well species can track environmental change, and how such tracking shapes communities. Growing empirical evidence suggests that environmental temporal tracking—how an organism shifts the timing of major biological events in response to proximate environmental cues—is linked to species performance and is a structuring force of species and communities today. Here, we review the concept of tracking in empirical studies and through the lens of community ecology theory. We argue that much current theory for tracking ignores the importance of a multi-species context beyond trophic interactions. Yet community assembly theory predicts competition should drive variation in tracking and trade-offs with other traits. Existing community assembly theory can help us understand tracking in stationary and non-stationary systems and, thus, predict the species- and community-level consequences of climate change. But it will require greater efforts to integrate priority effects into modern coexistence theory and improved empirical estimates of tracking and the underlying environmental cues.

1 Main text

Anthropogenic climate change is causing widespread changes in species distributions, with many species shifting in both time and space (IPCC, 2014; Hoegh-Guldberg *et al.*, 2018). Species are moving to higher elevations and poleward (Chen *et al.*, 2011), shifting their recurring life history events (phenology) earlier (Wolkovich *et al.*, 2012; Cohen *et al.*, 2018), or both as climate warms (Amano *et al.*, 2014; Socolar *et al.*, 2017). These general trends, however, hide high variability across species. A large proportion of species are not shifting (Cook *et al.*, 2012; Amano *et al.*, 2014), 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 changes in biomass, growth and other metrics related to performance (Cleland *et al.*, 2012). Tracking—a form of phenotypic flexibility—may then be a major component to understanding and predicting the fitness consequences of climate change, including population declines, with cascading effects on community and ecosystem structure (Menzel *et al.*, 2006; Parmesan, 2006).

The hypothesis that tracking improves fitness outcomes with climate change has gained significant traction in the ecological literature (e.g., Cleland *et al.*, 2012) and several areas of theory support it. Evolutionary models predict species that track will be favored in novel environmental conditions (Chevin *et al.*, 2010). Niche models of community assembly suggest 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). However, empirical data on the costs (and benefits) of tracking are mixed (e.g., Block *et al.*, 2019). Further, there has been comparatively little work connecting tracking to community assembly theory, which shows temporal sequencing and environmental variability can alter the relative fitness and niche differences between species that determine coexistence, suggesting important ecological constraints to tracking..

This disconnect could be because most ecological theory was constructed for stationary systems (e.g., Chesson & Huntly, 1997). While major arenas of research such as 'modern coexistence theory' or population ecology now embrace environmental stochasticity, they generally still assume stationarity, where the underlying distribution of the environment is unchanged across time (i.e., constant mean and variance, Barabas *et al.*, 2018).

Climate change upends the assumption of stationarity. By causing increases in temperature, larger pulses of precipitation, shifts in snowpack, 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 (see Fig. 1 and Box: Environmental variability & change). This transition is reshaping ecological systems. New work has aimed to adapt coexistence theory to non-stationary environments (Chesson, 2017; Rudolf, 2019). Yet there is still little theoretical work on what such a transition may mean for communities and the species within them, including how community-level processes might feedback to modify species responses.

Here, we review the concept of tracking as commonly used in the empirical climate change impacts literature and in related ecological theory. We provide definitions that distinguish between fundamental and environmental tracking, highlighting the distinction between measuring

tracking and its fitness outcomes in empirical systems. Then, after briefly reviewing evolutionary theory that predicts variation in tracking across species and environments, we examine how well community assembly theory—especially priority effects and modern coexistence theory—can be extended to test the current paradigm that climate change should favor species that track.

1.1 Defining & measuring tracking

Defining tracking

Tracking is a commonly used word in the climate change literature, especially relating to phenology (e.g., Menzel *et al.*, 2006; Parmesan, 2006; Cleland *et al.*, 2012; Deacy *et al.*, 2018). Yet there are few, if any, definitions of it. Conceptual and theoretical treatments of tracking often relate how well an organism matches the timing of a life history event to the ideal timing for that event, what we refer to as 'fundamental tracking'. In contrast, empirical studies of tracking often focus on estimating a change in the timing of an event relative to a measured environmental variable, with the aim of measuring what we refer to as 'environmental tracking' (Fig. 2)—the change in timing of a major biological event due to an organism's cue system given change in the environment (though most studies lack the required knowledge of the underlying cue system, Chmura *et al.*, 2019). Both these definitions are readily applied to phenology—the timing of recurring life history events—though they can also apply to non-recurring life history events (e.g., seed germination), or events not normally defined as part of life history.

Fundamental tracking rests on an assumption that there is a timing (an 'ideal timing') that yields maximum fitness, and event timings moving away from this ideal result in reduced fitness. This is a foundational concept of the trophic mis-match literature (Visser & Gienapp, 2019), which often assumes the peak timing of a resource defines the ideal timing for phenological events dependent on that resource (e.g. egg laying dates dependent on caterpillar abundance, Visser & Both, 2005). For most events, however, fitness outcomes are likely dependent on a suite of interacting forces (e.g., Reed *et al.*, 2013)—for example, egg laying dates for migratory birds may depend both on the timing of peak prey abundance and the need to leave nesting grounds before winter. Additionally, the timing of events is often connected to the investment process of an event (e.g., number of eggs in a clutch, Inouye *et al.*, 2019) in current, and sometimes past and future, years. Whatever their full underlying causes, fitness consequences of suboptimal timing should drive the evolution of organismal cues to predict and match the optimal timing (the degree of this match defines cue reliability, Fig. 2). Environmental tracking combines the outcome (timing) of these cues with environmental variation.

Environmental tracking depends on the intersection of the environment's variability—which aspects of the environment vary, how (e.g., temporally each year, spatially at x scale) and how much—and an organism's response to the environment via its proximate cues. If the varying components of the environment are not in the organism's set of cues, then the organism does not 'track' per this definition (although covariation with other environmental components might give the appearance of tracking). Environmental tracking at the individual-level is a purely plastic response to environmental variation (in line with current findings on most climate change

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97 responses, Bonamour *et al.*, 2019), with the plasticity itself an outcome of selection (Chevin
98 *et al.*, 2010) through its connection to fundamental tracking (Fig. 2). At the population-level,
99 tracking may also incorporate evolutionary change—change in genotype frequencies—depending
100 on both the timescales of study and the species' generation time (this evolutionary response
101 can be predicted as the difference between the environmental sensitivity of phenotypic selection
102 and an organism's plasticity, $|B - b|$ in Chevin *et al.*, 2010).

103 *Measuring tracking*

104 Measuring 'tracking' and comparing variation in it across species, space and time is a rapidly
105 growing area of ecological research (e.g., Cook *et al.*, 2012; Fu *et al.*, 2015; Thackeray *et al.*,
106 2016; Cohen *et al.*, 2018). Studies that directly quantify fundamental tracking are uncommon
107 (but see Visser *et al.*, 2006; Charmantier *et al.*, 2008), given in part the difficulty of estimating
108 fitness, though many studies in the synchrony literature attempt to link consumer change to
109 resource change, with an assumption that the measured resource is the dominant determinant
110 of ideal timing for the consumer (though this may rarely be true, see Singer & Parmesan,
111 2010; Johansson & Jonzen, 2012; Reed *et al.*, 2013). Instead, most studies focus on estimates
112 closer to environmental tracking. Some studies estimate simply change in days over time (e.g.,
113 Parmesan, 2007; Kharouba *et al.*, 2018), though most studies now estimate shifts as responses
114 per unit temperature (for example, multiple meta-analyses show plants' spring phenology shifts
115 with spring or annual temperatures 4-6 days/°C on average across species, Richardson *et al.*,
116 2006; Wolkovich *et al.*, 2012; Thackeray *et al.*, 2016) or precipitation (Inouye *et al.*, 2002; Craine
117 *et al.*, 2012).

118 All species-rich studies of phenology-climate relationships find high variation (Cook *et al.*,
119 2012; Thackeray *et al.*, 2016), including some species that do not track or track poorly (i.e.,
120 high noise surrounding observed statistical relationships). Researchers have worked to link such
121 variation to the underlying cues (e.g., Cook *et al.*, 2012), species traits (e.g., Cohen *et al.*, 2018)
122 and trophic level (e.g., Thackeray *et al.*, 2016). These approaches hint at the three majors
123 explanations for why some species do not appear to track climate or appear to track poorly:
124 (1) environmental tracking is either not possible or optimal for all species or in all environments
125 (Simons, 2011), (2) researchers have measured the wrong environmental variable (i.e., a variable
126 species do not track, Chmura *et al.*, 2019), and (3) statistical artifacts that make it difficult to
127 measure tracking robustly (see Box 'Challenges & opportunities in measuring tracking').

128 These confounding factors may make many current estimates of interspecific variation in track-
129 ing less reliable than they appear. This in turn makes robust quantitative analyses across
130 species difficult (Brown *et al.*, 2016; Kharouba *et al.*, 2018), yielding a muddy picture of which
131 species, when, and where, do and do not track. Given this difficulty, we believe clear testable
132 predictions from ecological theory are especially critical to guide the field forward (Smaldino &
133 McElreath, 2016).

1.2 Tracking in single-species environments

135 *Predicting variation in environmental tracking in stationary systems*
136 Evolutionary models predict strong selection for tracking in heterogeneous environments where

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there are predictable cues for the ideal timing of events and the underlying genetics to develop a heritable cue system (Piersma & Drent, 2003; Reed *et al.*, 2010). Tracking is likely strongly heritable, given that many cue systems are themselves heritable (e.g., van Asch *et al.*, 2007; Wilczek *et al.*, 2010). The strength of selection is determined by the costs and benefits of cues (Donahue *et al.*, 2015). The costs include the machinery an organism uses to monitor its environment (e.g., accumulated temperature or daylength), while the benefits are the increases in fitness gained from better timing (e.g., how much tissue is saved by avoiding a coldsnap). Selection, however, can be lower than expected from reaction norms predicted by simple evolutionary models for many reasons, including trade-offs with tracking (Singer & Parmesan, 2010; Johansson & Jonzen, 2012), gene flow from other environments that may continually push a population away from its local optimum (Lenormand, 2002), limits due to standing genetic variation (Franks *et al.*, 2007; Ghalambor *et al.*, 2015), or deeper evolutionary history that may produce co-evolved traits making it difficult for selection to act solely on tracking (Ackerly, 2009).

Apparently poor cues may occur for organisms in environments where there is both a low cost and low benefit to the cue(s). Whereas expensive cues, such as complex multivariate systems, are possible given a high pay-off. Most in-depth studies of species' phenological cues find evidence for complex multivariate systems that appear adapted to handle unusual—though not completely uncommon—years (Chuine & Regniere, 2017). This suggests that multivariate cues may better couple environmental tracking to fundamental tracking, while simple cues are more likely to trigger growth or reproduction at a suboptimal time.

Tracking should generally not be favored in unpredictable environments (e.g. when early season climate cannot be used to predict later season climate), or environments where species otherwise face high uncertainty in the timing of investment decisions. Instead theory suggests the optimal strategy may often be to bet-hedge (Venable, 2007; Donaldson-Matasci *et al.*, 2012; de Casas *et al.*, 2015) via a high diversity of timings or a conservative timing. Because bet-hedging, by definition, maximizes geometric-mean fitness in the long-run, its short-term outcomes can appear maladaptive. How often observed 'maladaptations,' which may easily include species that do not track or appear to track poorly, are actually the outcome of bet-hedging is difficult to estimate, as robustly assessing bet-hedging requires studies of fitness over longer timescales than many current field experiments (Simons, 2011). Environmental variation often includes both predictable and less predictable aspects. In such cases theory predicts organisms may evolve tracking that is a mixed strategy between bet-hedging and plasticity (Wong & Ackerly, 2005).

Evolutionary theory, which integrates over the sometimes hidden costs and benefits of particular cue systems and considers environmental predictability, thus provide multiple reasons species may not track or track weakly. This suggests that—at least in stationary systems—we should expect a number of species that do not track.

Predicting variation in environmental tracking in non-stationary systems

A major open area of research is adapting life history theory to the non-stationary environments introduced by climate change. Critical to predictions is whether cue systems maintain

their reliability with change; i.e., whether they continue to yield high fundamental tracking (Bonamour *et al.*, 2019). Consider a simple case in which an organism's cues evolved based on a correlation between peak prey abundance and daylength: in a stationary environment the daylength cue may be fairly reliable (generally predicting peak prey abundance based on daylength, with some interannual variation), but would become unreliable, and lead to fitness declines, if warming continually advances peak prey abundance. Multivariate cues are often argued to be more reliable because they can capture multiple attributes of the environment (Dore *et al.*, 2018; Bonamour *et al.*, 2019), but they may be equally vulnerable to failure if non-stationarity decouples the cues from fundamental tracking (Bonamour *et al.*, 2019) and thus optimal fitness is no longer associated with the cue system. Predicting the outcome of non-stationarity from the stationary environment requires that researchers know: (1) the full cue system of an organism, (2) how it relates to fundamental tracking, and (3) how both that cue system and the underlying fundamental model shift with non-stationarity.

In recent years, plasticity theory has developed to provide insights on non-stationarity (or 'sustained environmental change,' see Chevin *et al.*, 2010). 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. At the individual level, environmental tracking is a plastic response, and thus we might predict greater individual tracking in non-stationary environments. This outcome, however, assumes there are no costs related to plasticity (Ghalambor *et al.*, 2007; Tufto, 2015). If there are costs associated with tracking, as discussed above in stationary systems, then species may evolve lower tracking (Auld *et al.*, 2010).

1.3 Tracking in multi-species environments

Life history theory often ignores other (non-focal) species or abstracts them as an aspect of the environment. While the trophic mis-match literature has addressed this gap for trophic interactions (Visser & Both, 2005; Visser & Gienapp, 2019), these is little consideration of competitive coexistence, yet this perspective is critical to understanding environmental tracking (Metcalf *et al.*, 2015). Considering selection in multi-species environments structured by competition highlights that tracking cannot be considered as a singular trait, but must be evaluated as part of a trait syndrome (or mosaic of traits, Ghalambor *et al.*, 2007) and should ultimately produce communities of species where tracking trades-off with other traits.

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) and thus may need to be more stress tolerant. 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 (Heberling *et al.*, 2019) or species with shallow roots starting growth sooner in an

alpine meadow system, while species with deeper roots 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 to date supports this, with several studies linking higher tracking to traits associated with being poor competitors (Dorji *et al.*, 2013; Lasky *et al.*, 2016; Zhu *et al.*, 2016). Further, many studies have found a correlation between higher tracking and 'early-ness' each season, which has been linked to resource acquisition traits associated with lower competitive abilities (Wolkovich & Cleland, 2014, see Box 'Trait trade-offs with tracking').

Understanding these trade-offs is clearly critical, but the short-term dynamics of a changing environment with plastic species is additionally important and highlights how little ecological theory we have for tracking. While evolutionary theory sometimes predicts the fitness out-comes of a new environment, non-stationarity in the climate today means understanding the trajectory may be most relevant—and bridges across evolutionary and ecological timescales. Evolutionary models show how plasticity may limit standing variation and thus reduce fitness in novel environments (Ghalambor *et al.*, 2007; Fournier-Level *et al.*, 2016; Fox *et al.*, 2019). But such findings may not hold if ecological dynamics reshape the environment as systems transition from stationary to non-stationary.

Including tracking in multi-species community assembly models

Predicting how tracking may determine which species are effectively winners and losers with climate change requires integrating non-stationary environments into models of 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 lead to coexistence (Chesson & Huntly, 1997; Chesson, 2000). These models, which underlie much of current community ecology research (Mayfield & Levine, 2010; Barabas *et al.*, 2018; Ellner *et al.*, 2019), provide a framework to begin to integrate tracking and non-stationarity into community ecology theory.

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 many lottery models the environment appears, effectively, as variation in birth and death rates; in storage effect models the environment appears as filtered through species low density per capita growth rates (E_i). Building a changing environment into such models thus requires knowing how environmental shifts filter through to species-level parameters (Tuljapurkar *et al.*, 2009) to impact fundamental tracking. For example, storage effect models predict shifts in communities when environmental change impacts low density per capita growth rates in such a way that the environmental change decreases the covariance between the E_i and competition (i.e., changing $cov(E_i, C_i)$ that leads to a decrease in the storage effect as a means of competitive coexistence). In another example, Rudolf (2019) added the temporal environment to competition models by defining interaction strength as dependent on the temporal distance between species. This is somewhat similar to models that include the environment effectively through different levels of asynchrony (e.g., Nakazawa & Doi, 2012; Revilla *et al.*, 2014).

In other models the environment is more specifically defined as a resource (e.g., many seed

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germination models that begin with a resource pulse each year), and thus again generally model something close to fundamental tracking. Models that explicitly include the environment provide a major opportunity to predict how tracking and non-stationarity determine future communities. As an example, we modeled a shift to earlier growing seasons using a common coexistence model where the environment is defined as a limiting resource that determines the start of growth each year. The timing of the resource also determines the offspring species produce each year, allowing us to include fundamental tracking. The shift to earlier seasons favored species that could track (making them, effectively, better colonizers), increasing their prevalence by shifting a modelled trade-off between tracking and competitive ability (via R^*, see Fig. 3 and Box: 'Adding tracking and non-stationarity to a common coexistence model'). Like all models, it rests on a number of assumptions, including that species' cues remain as reliable in the non-stationary environment, but shows how non-stationarity could benefit trackers.

Most current models (including the previous example) examine the environment from only one of two relevant perspectives: they represent the environment as directly affecting fitness (e.g., the storage effect model), or they represent the environment as used for species' cues (e.g., many models of plasticity). Combining these two perspectives, which connect to fundamental and environmental tracking (respectively), may be especially critical to understanding the costs, benefits and community outcomes of tracking in non-stationary environments.

Layered onto these different views of the environment is how species responses are defined. In general, species responses to the environment can be broadly grouped into models that explicitly define when species start an event (e.g., spawning or germination) versus those that model the magnitude of response (e.g., the number of propagules or seeds). Models that explicitly include when a species starts an event are often focused on situations where order of arrival is critical. For example, models of priority effects through niche pre-emption highlight the advantage tracking may provide when it allows species to be early: 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 (Fukami, 2015). Such models predict early-arriving species to out-compete other species, unless there is a cost to being too early or there are trade-offs with other species' traits (see Fig. 4).

Other models canalize species' responses to the environment into production and investment. Most models of inter-annual competition (most explicit examples of 'modern coexistence theory,' e.g., Chesson *et al.*, 2004; Angert *et al.*, 2009) fall into this camp. Species produce (via investment in offspring, tissue etc.) differentially depending on the environment each year and outcomes are mediated through density. While these models superficially may seem disconnected from timing, they highlight how event timing often relates to production and, thus, investment across years. Further, they almost always model the environment as a distribution (see Fig. 4), which provides the opportunity for the environment to alter the competitive environment each year and, thus, structure coexistence.

A model where species vary both when they start an event and how much they invest would capture the important attributes of fundamental tracking—combining head-start advantages from being early with production variation based on the fitness of the environment. To our knowledge, however, most models approach these questions separately, though models of bet-

hedging come closest (Gourbiere & Menu, 2009; Tufto, 2015). A model that explicitly includes the linked decisions of when to time an event and how much offspring/tissue to produce during the event could provide insights on the relative importance of each aspect of this process. Such a model could be adapted to address multiple questions of tracking, including how these decisions ('when' and 'how much') may trade-off and which other traits may be most strongly linked to tracking, as well as explicitly modeling the costs and benefits of tracking in stationary systems—a critical precursor to extending it to non-stationary systems.

Extending models to non-stationary systems is crucial to testing how environmental tracking relates to fundamental tracking and species persistence with climate change, and research has already begun to tackle this non-trivial challenge (Chesson, 2017; Legault & Melbourne, 2019; Rudolf, 2019). Most work to date, however, focuses on conclusions from systems that are initialized as non-stationary, ignoring the transition between stationary and non-stationary environments. Yet we expect this transition may be critical because communities formed in stationary environments (or periods with lower non-stationarity) are effectively filtered and assembled by that environmental regime and thus produce the baseline of variation and assembly dynamics for a shifting environment. While analytical solutions for systems transitioning from stationary to non-stationary may take time to develop (Chesson, 2017), simulation work can provide an immediate intuition and framework to address this challenge (for an example, see Box: Adding tracking and non-stationarity to a common coexistence model).

Outcomes for such community assembly models also depend on how effectively closed communities are (i.e., without dispersal or evolution). Dispersal of species or individuals with traits that make them better matched to the non-stationary environment would lead to new communities that may persist 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 (Willis *et al.*, 2010; Wolkovich & Cleland, 2011). Evolutionary responses could also rescue species with low plasticity. Long-term population (e.g., Colautti *et al.*, 2017) and resurrection studies (Wilczek *et al.*, 2014; Yousey *et al.*, 2018), as well as field experiments (Colautti *et al.*, 2017; Exposito-Alonso *et al.*, 2019), 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., Wilczek *et al.*, 2014), associated with reduced population viability (e.g., Colautti *et al.*, 2017), and that other factors may constrain adaptive responses.

1.4   Future directions

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. We have outlined above how current community ecology theory could make advances through models that combine effects of variation in timing and production amounts and models that include environment as impacting species' cues, as well as species' fitness. Such models

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would explicitly allow the potential costs and benefits of tracking depending on how closely environmental tracking matches fundamental tracking. But to best test and develop such models we need a greater understanding of how the environment is changing, more robust estimates of environmental tracking and how it fits within a mosaic of other correlated traits that determine individual fitness.

How is an organism's environment changing?

Currently, much research has focused on one major shift in the climate system (earlier growing seasons), but research on multivariate environmental shifts is growing and will be critical to understanding how climate change affects an organism's whole environment. We can help guide these efforts by identifying environmental shifts that are often linked. For example, warming temperatures may drive earlier seasons and higher evaporative water loss. Researchers can also aim to more consistently and fully characterize the environmental distributions of their systems that appear to 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.

More interdisciplinary research with climate science could also speed a fuller understanding of what shifts are and are not expected with climate change, and what climate variables are inherently correlated. Such correlations make estimating cues and other biological parameters from long-term data especially precarious (Tansey *et al.*, 2017). But these correlations are equally critical in considering how species may view their environment and whether environmental change will couple or uncouple links between proximate cues and fundamental tracking (Bonamour *et al.*, 2019).

Understanding and measuring 'tracking'

Understanding how the environment is changing represents just one step towards robust measures of environmental tracking. Shifting environmental regimes must then be filtered through species cues, and impacts on growth and survival. Studies should clarify their definition of tracking, how the environment is defined, how an event relates to fitness, and how well—or not—the underlying cue system is understood (see Box: 'Challenges & opportunities in measuring tracking'). Currently, many studies examine fundamental and environmental tracking simultaneously(e.g., Visser *et al.*, 2006; Charmantier *et al.*, 2008; Cleland *et al.*, 2012; Yang & Cenzer, 2020), which is clearly helpful in advancing the field. However, the more researchers can clarify when and how they are addressing fundamental tracking versus environmental tracking, the more easily we can compare results across studies. We expect progress will come from a balance between measures of fundamental tracking (measuring both event date variation and fitness), estimating an organism's system of cues (generally through controlled experiments followed by tests in the field), and measuring the change in an event date relative to environmental variation that is due to cues (environmental tracking). Clear statements of what is known, not known and what is measured will help.

What major traits trade-off with tracking?

Basic theory of plasticity and competition suggest 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 (Willis *et al.*, 2010; Wolkovich *et al.*, 2013; Zettlemoyer *et al.*, 2019). Research has 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 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 Rudolf, 2019), 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.

1.5 Stationarity in the future

While most environments today are climatically non-stationary and have been for decades, the climate will return to a more stationarity form 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 (Collins *et al.*, 2013). 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 (Jansson & Dynesius, 2002)—even if stationary periods— be they cold or warm (glacial and interglacial periods), or dry or wet (e.g., megadroughts or pluvials)—are more common. Indeed, while much of this work has examined how species survive for millions of years given large oscillations in climate (Provan & Bennett, 2008), the periods that provide the most dramatic community reshuffling are periods shifting from stationary to non-stationary climate regimes (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 are reshaping the species and communities we have today and will in the altered climates of our future.

2 Acknowledgments

3 Boxes

3.1 Box: Environmental variability & change

Decades of ecological research highlight how temporally variable environments shape species and their communities at multiple scales (Sale, 1977; Chesson & Huntly, 1997). In seasonal landscapes, the environment limits periods for growth each year (e.g., by temperature or drought); within-year variability in the environment (e.g., daily, hourly or finer resolution temperatures or rainfall amounts) compounds into inter-annual variability that shapes the distribution of the start and end of growing seasons. For long stretches of history this variability has been effectively stationary; that is, the underlying probability distribution that describes the start (or end) of the season (e.g., the date of the last major frost) does not change, even though the date may be dramatically different from one year to the next.

In other time periods, variability has been 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 is a similar non-stationary process, with warming evident around the globe and knock-on effects for other climate metrics, such as heat extremes and the size of precipitation events.

Understanding non-stationarity in ecological systems requires first identifying which aspects of the environment have shifted—and how they have shifted with respect to one another—as the underlying distributions transition from stationary to non-stationary (Fig. 1). 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 while the within-day variance is decreasing (Stocker *et al.*, 2013; Screen, 2014). Understanding the impacts of climate change further requires recognizing that most systems can be considered stationary or non-stationary depending on the timescale and period of study. Thus, predicting the consequences of current non-stationarity in ecological systems benefits from identifying the type and scale of non-stationarity, relative to long-term trends.

3.2 Box: Challenges & opportunities in measuring tracking

Increasingly, research has outlined statistical difficulties in measuring tracking, which may underlie many observations of species that do not track. These issues mostly relate to the challenges of observing phenological distributions (Steer *et al.*, 2019; Carter *et al.*, 2018) using discrete (calendar) time, low power, and the complexity of climate data.

Our units of observation may be non-stationary—estimates of mean days shifted per decade depend on the climate of the decade(s) studied, which is not consistent in many systems (McCabe *et al.*, 2012). Estimates based on a relevant climate variable can sometimes ameliorate this problem, but may be equally vulnerable to non-stationarity in units (e.g., Sagarin, 2001). 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 depend on 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).

Even 'long' time-series may be too short for robust analyses of trends (Bolmgren *et al.*, 2013). 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 (Loken & Gelman, 2017). 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.

Many statistical issues can be addressed by improved statistical approaches (e.g., Gienapp *et al.*, 2005; Pearse *et al.*, 2017), though such approaches may uncomfortably highlight how uncertain many current estimates are (Brown *et al.*, 2016) or reveal lower effect sizes. 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). We suggest mixed models should be used more widely alongside randomization and/or data-simulation approaches (e.g., Bolmgren *et al.*, 2013), and we need models that can discriminate among confounding factors. For example, growing evidence suggests a potential fundamental trade-off where early species track grow fast and die young, while later species track less, grow slowly and live longer—this might suggest later species bet-hedge more given their longer investment window. Or it could be an artifact where early species use simpler cues, and, thus, their tracking is measured more accurately given current methods.

Even without statistical issues, translating phenological and climate data into estimates of tracking requires a firm biological understanding of an organism's cues that we rarely have (Chmura *et al.*, 2019). Currently, 'tracking' is often measured as the relationship between the dates of the phenological event and a simple abiotic metric. Such measures, however, are almost always proxies for a more complicated underlying physiology where simple cues—such as warm temperatures or snowpack—can be modified by other cues, such as photoperiod, drought or light spectra (Bagnall, 1993; Stinchcombe *et al.*, 2004). Teasing out these other cues requires nuanced approaches to observational data with explicit assumptions (Tansey *et al.*, 2017) or controlled experiments (Wilczek *et al.*, 2009; Caffarra *et al.*, 2011).

Modeling multivariate cues is inherently difficult (Chuine *et al.*, 2016), especially since one cue may dominate in many conditions. For example, woody plant leafout responds to warm spring temperatures, but also to cool winter temperatures to prevent leafout in mid-winter warm snaps. Often this cool-temperature effect may be masked by sufficiently cool conditions. With warming from climate change, however, this additional trigger may become critical (and potentially lead many phenological models to fail spectacularly in the future, see Chuine *et al.*, 2016). 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 (Morris *et al.*, 2008). In some semi-arid systems, species time growth to pulses of rain that occur with cooler temperatures, indicating the start of the rainy season, and not a rare summer rainfall event in the middle of months of drought (Wainwright & Cleland, 2013).

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Addressing these issues is possible if we embrace our inner physiologists, or collaborate with one, to develop models that explicitly include species' cues, and consider the framework under which we expect cue systems have evolved (e.g., bet-hedging). We then must interrogate these models to understand when they work and where they fail (see Johansson & Bolmgren, 2019, for an example). This approach can help embrace the contradictory pulls of conducting experiments to identify mechanistic cues and understanding how they are filtered through the multivariate climate of the real world (see Wilczek *et al.*, 2010, 2009).

3.3   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 of start of migration for a species, termed 'earlyness' by some authors), with earlier species tending to track more (studies included both birds and Lepidotera, Diamond *et al.*, 2011; Ishioka *et al.*, 2013; Kharouba *et al.*, 2014; Jing *et al.*, 2016; Du *et al.*, 2017). 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 Dorji *et al.*, 2013; Lasky *et al.*, 2016; Zhu *et al.*, 2016). These species were often also early (e.g., Dorji *et al.*, 2013; Zhu *et al.*, 2016), 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 Wolkovich & Cleland, 2014).

3.4   Box: Adding tracking and non-stationarity to a common coexistence model

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 (Chesson *et al.*, 2004), we follow a similar terminology for ease; however the basic structure of our model could apply to other systems with one dominant (non-renewing) 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. We adjust the biological start time of species (τ_i for species i) 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 (making it effectively a superior colonizer, see SI for complete description and equations).

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 theory and empirical work suggest this trade-off may involve traits related closely to resource competition, we varied species' R^*. With variation in tracking and in R^* species can persist together as long as those species with a temporal niche advantage are also the inferior competitors (Fig. 3). 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 (earlier timing of the resource pulse, τ_p, Fig. 3; 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 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. 3). 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. 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 (Diamond *et al.*, 2011; Dorji *et al.*, 2013; Ishioka *et al.*, 2013; Kharouba *et al.*, 2014; Du *et al.*, 2017), but may be part of a larger trait syndrome. Indeed, this model trivially shows 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 (Lasky *et al.*, 2016; Zhu *et al.*, 2016)—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. As environments shifted from stationarity to non-stationarity, species that co-occurred via equalizing mechanisms persisted longer. While the outcome that equalized species will be more similarly affected by environmental shifts is rather obvious, it has several important implications. First, it may make identifying which traits climate change promotes

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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.
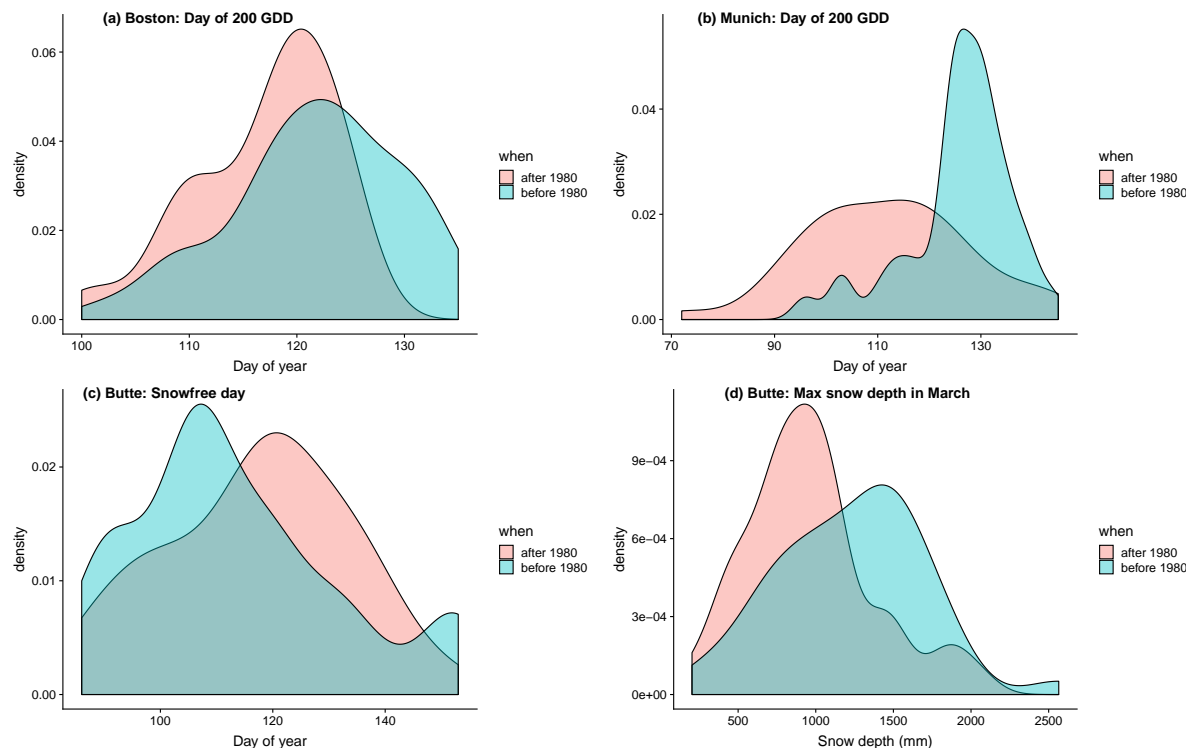
4 Figures

Figure 1: 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 °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 subsetted data so that there were 40 years before and after 1980 for all sites.
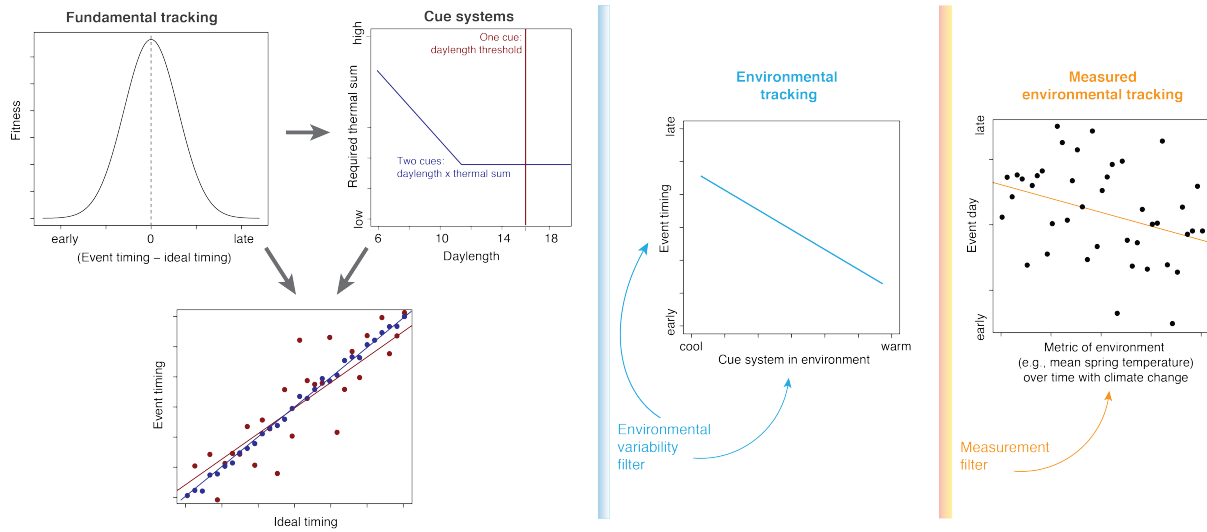
Figure 2: Defining tracking: Fundamental tracking (top left) represents how an organism matches the actual timing of a life history event to the timing that maximizes its fitness (i.e., ideal timing). Here, we show one conceptualization, where fitness declines as event timing moves away from the ideal timing, though realizations in nature may take diverse forms. The cue system is the physiological machinery that an organism uses to predict the ideal timing; we show one dependent only on daylength (red line: the event occurs when the organism's environment exceeds a certain daylength) and one that depends on a combination of daylength and thermal sums (navy line: the event occurs when the organism accumulates enough temperature for the current daylength). The skill of a cue system in predicting the ideal timing represents cue quality (bottom left). The combination of environmental variability and an organism's cue system results in different event timings depending on the environment, what we define as environmental tracking (middle). Measured environmental tracking (right) depends both on environmental tracking and the metric(s) of the environment that researchers measure. MAKE SURE WE GET ACROSS: Why we have such a picky definition of environmental tracking (versus measured environmental tracking)—because covariation between timing and the measured environment is not so useful to model and could lead to wildly incorrect predictions!
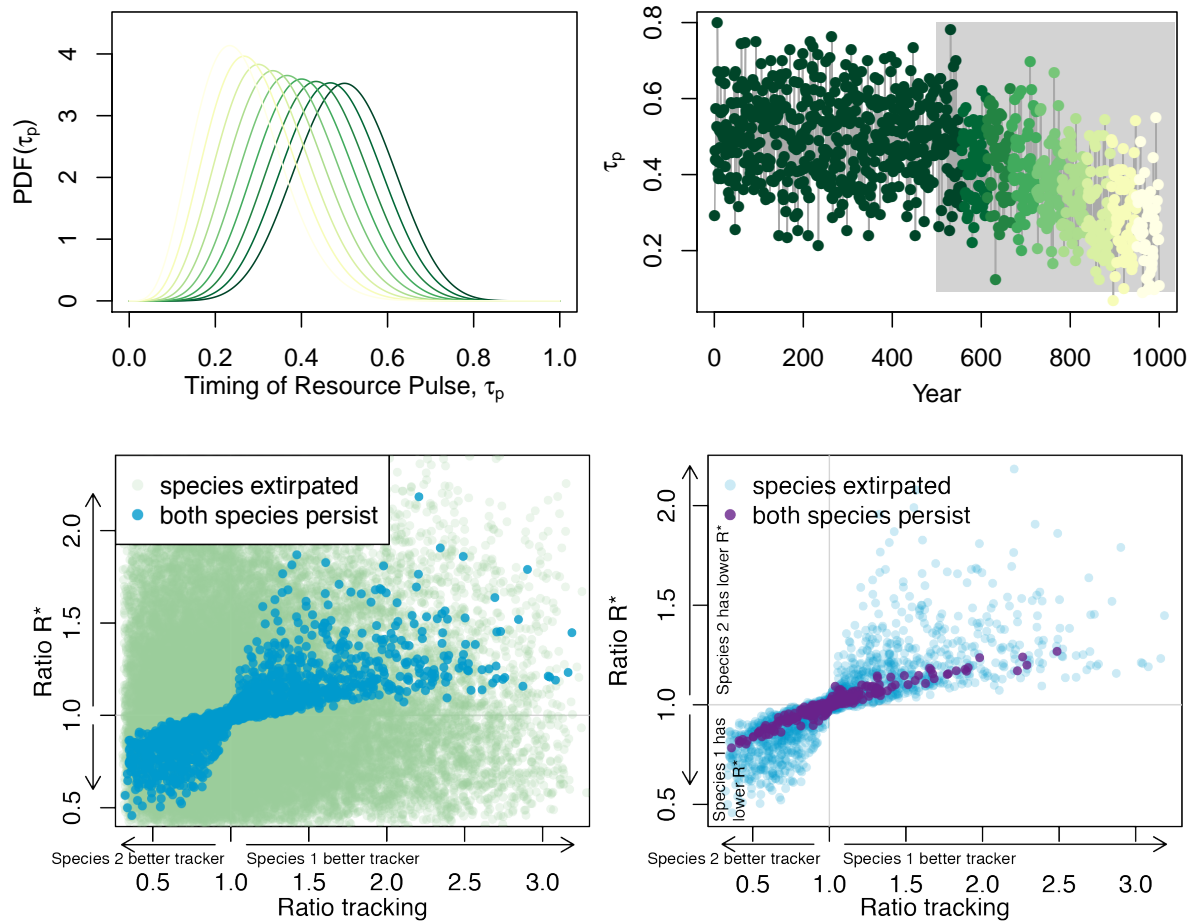
Figure 3: Example of how non-stationarity can reshape communities in a simple model. We shifted the environment (top panels) by changing the timing of the resource pulse from a stationary period ($\tau_p \sim \beta(10, 10)$ for the 500 years) to a nonstationary period ($\tau_p \sim \beta(5, 15)$ over the 500 years), then examined outcomes for two-species communities (bottom panels) 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 (bottom-left), followed by an additional 500 years of non-stationary environment (bottom-right, only two-species communities that persisted through the stationary period are shown).
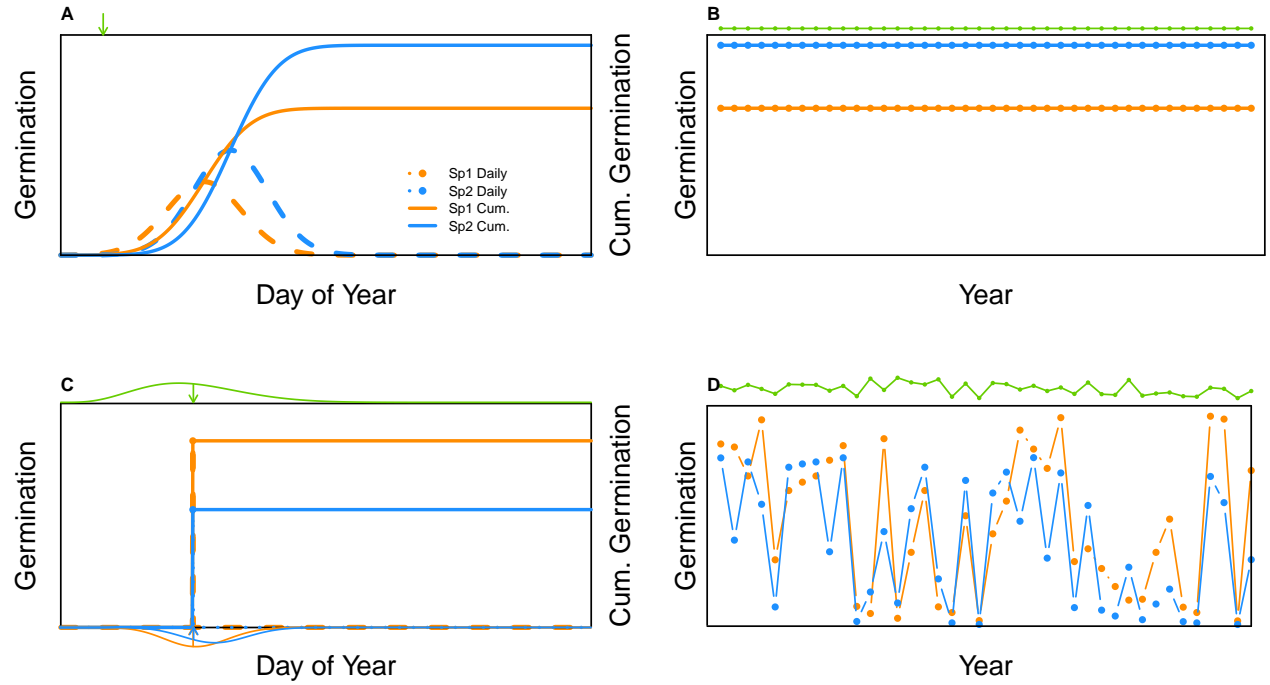
Figure 4: Tracking can be conceptualized as changes in priority effects or changes in storage effects. In a priority effect model (A,B), the coexistence mechanism is a within-year tradeoff between, an early-germinating species that pre-empts resources (sp 1) and late-germinating species that is a superior resource competitor (sp 2) (A, where green arrow indicates the start of season); no between-year variation is required to maintain coexistence. In a storage effect model (C,D), variation in the timing of the start of season (indicated by the distribution in green, top of C) results results in differential species-response to the environment (illustrated by species-specific germination curves, bottom of C); this interannual variation in species-response to the environment (D)—along with a seedbank or other interannual storage mechanism—can maintain coexistence through reduced interspecific competition.

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