



The long and the short of it: Decomposing synchrony and compensation across temporal scales

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	<p>Synchrony can amplify the destabilizing effect of environmental variability on ecosystem functions such as productivity, whereas the inverse dynamic, compensation, can stabilize function. Describing and explaining these phenomena remains an ongoing challenge, in part because synchrony is an emergent property shaped by multiple environmental drivers and species interactions operating across scales. Here, we employ a newly developed timescale-specific metric to examine the interplay of environmental and biotic variables on synchrony across timescales. Using both modeled and empirical data, we first highlight that synchrony and compensation are not mutually exclusive but instead can vary by timescale. Second, we demonstrate multiple mechanisms that may generate timescale-specific patterns, including different environmental drivers, diverse life histories, dispersal, and non-stationary dynamics. We find that traditional metrics for quantifying synchrony are often biased towards long-term drivers and may miss the importance of short-term drivers of synchrony or compensation. Our results highlight the importance of partitioning drivers of synchrony and compensation across timescales and that timescale-specific patterns arise via the interplay of both abiotic and biotic mechanisms.</p>

The long and the short of it: Decomposing synchrony and compensation across temporal scales

Running Head: Synchrony across timescales

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Abstract

Synchronous dynamics (fluctuations that occur in unison) are universal phenomena with widespread implications for ecological stability. Synchrony can amplify the destabilizing effect of environmental variability on ecosystem functions such as productivity, whereas the inverse dynamic, compensation, can stabilize function. Describing and explaining these phenomena remains an ongoing challenge, in part because synchrony is an emergent property shaped by multiple environmental drivers and species interactions operating across scales. Here, we employ a newly developed timescale-specific metric to examine the interplay of environmental and biotic variables on synchrony across timescales. Using both modeled and empirical data, we first highlight that synchrony and compensation are not mutually exclusive but instead can vary by timescale. Second, we demonstrate multiple mechanisms that may generate timescale-specific patterns, including different environmental drivers, diverse life histories, dispersal, and non-stationary dynamics. We find that traditional metrics for quantifying synchrony are often biased towards long-term drivers and may miss the importance of short-term drivers of synchrony or compensation. Our results highlight the importance of partitioning drivers of synchrony and compensation across timescales and that timescale-specific patterns arise via the interplay of both abiotic and biotic mechanisms.

Keywords: community dynamics, compensatory dynamics, disturbance, environmental fluctuations, life history, metacommunity, stability, wavelet, variance ratio

Introduction

The extent to which communities of interspecific competitors exhibit synchronous temporal fluctuations has been of fundamental interest in ecology for decades (McNaughton, 1977). In communities, synchrony and its alternative pattern, compensation, describe how the dynamics of populations aggregate to influence community stability through time. Synchronous

dynamics amplify community variability and often arise when species respond similarly to environmental fluctuations (Ives, 1995; Loreau and de Mazancourt, 2013), or through facilitative interactions between species. In contrast, compensatory dynamics stabilize overall community properties because species fluctuate in a negatively correlated manner (Peterson, 1975), often due to opposing responses to environmental drivers or competitive interactions (Ives, 1995; Gonzalez and Loreau, 2009; Loreau and de Mazancourt, 2013). These concepts have emerged as key elements in several recent advances in community ecology, such as how functional diversity influences resilience and how environmental change may impact coexistence (Lindgren et al., 2016; Hallett et al., 2019).

Synchrony and compensation have often been considered mutually exclusive as they reflect opposite correlations among abundances (e.g. Houlahan et al. 2007). However, recent work indicates that synchrony and compensation may instead be timescale and spatial scale dependent (Downing et al., 2008; Vasseur et al., 2014; Lasky et al., 2016). For instance, species may be synchronous at one timescale and compensatory at other timescales (Downing et al., 2008; Vasseur et al., 2014), they may be synchronous in certain life history stages but asynchronous in others (Lasky et al., 2016), and they may be synchronous under some environmental conditions and asynchronous in others (Xu et al., 2015). Indeed, a wide range of processes operating at differing temporal and spatial scales can influence population dynamics, including environmental variation (Allstadt et al., 2015; Tredennick et al., 2017), interactions with other species (Pedersen et al., 2016), variability in species demographic rates (Jucker et al., 2014), and dispersal. While we expect these processes to alter the timescales of synchrony versus compensation, our ability to detect scale-specific patterns and their underlying mechanisms has largely been limited to theoretical models or empirical analyses of very long timeseries.

A strong understanding of synchrony versus compensation in ecological communities requires scale-specific metrics that can be appropriately applied across a wide range of datasets.

By examining community dynamics using a timescale-specific methodology, multiple signals of differing periodicity can be identified in a single timeseries (Downing et al., 2008; Vasseur et al., 2014). For example, wavelet analyses applied to long aquatic timeseries have consistently highlighted differential drivers and consequences of synchrony versus compensation across timescales (Vasseur et al., 2014; Vasseur and Gaedke, 2007; Downing et al., 2008; Keitt and Fischer, 2006; Keitt, 2008; Brown et al., 2016). Analyses across space allow additional comparison of how spatial variation may affect timescale-specific signals of synchrony (Sheppard et al., 2016; Anderson et al., 2018). New and less data-intensive methodologies are opening up our ability to empirically characterize the timescale of synchrony versus compensation in terrestrial and aquatic systems (Zhao et al., 2020). These advances, coupled with growing open-access and long-term monitoring data, have the potential to expand our understanding of temporal fluctuations and their underlying drivers across a wide range of ecosystems, with implications for connecting patterns of synchrony and stability to underlying drivers.

Here, our goal is to consider synchrony and compensation as processes that can operate simultaneously at different temporal scales and to examine the drivers that underlie timescale-specific dynamics. We overview and apply a recently derived timescale-specific variance ratio (Zhao et al., 2020) to disentangle patterns of synchrony and compensation in both a novel theoretical model and a temperate grassland community case study. We expand our current understanding of the timescale of synchrony and explore the effect of multiple abiotic and biotic drivers, including dispersal and directional (i.e. nonstationary) environmental drivers. We focus our analyses on pairwise interactions to mechanistically and directly examine how differences in species' environmental responses and demography manifest across timescales. Our methods and models are, however, easily extended to diverse systems (Zhao et al., 2020). Specifically, we consider a baseline scenario with multiple underlying environmental drivers to which we add additional ecological complexity, including (Scenario 1:)

differential species responses to multiple drivers, (Scenario 2:) shared species' responses to drivers but varying demographic rates, and (Scenario 3:) spatial scaling from local patches, connected via dispersal, to larger-scale, metacommunity dynamics. Finally, we extend our framework to consider how (Scenario 4:) climate change (or other directional changes in environmental drivers) may alter timescale-specific signatures of species' fluctuations. Our approach identifies key ecological reasons that may cause synchrony and compensation to operate at different timescales, while highlighting a recent statistical tool that aids in parsing these dynamics and understanding their importance for ecological stability.

A timescale-specific variance ratio

Studies of synchrony and compensation in community ecology have classically focused on their implications for ecosystem stability (Gonzalez and Loreau, 2009), with many studies approaching synchrony and compensation phenomenologically, using covariance methods such as the variance ratio and related metrics (Peterson, 1975; Schluter, 1984; Klug et al., 2000; Houlahan et al., 2007; Loreau and de Mazancourt, 2008). For instance, the classic variance ratio, denoted by φ , compares covariances (cov) among species over time to the variances (var) of the individual, component species (Peterson, 1975; Schluter, 1984). The classic variance ratio is defined for a timeseries $x_i(t)$ of species abundances $i = 1 \dots, S$ as:

$$\varphi = \frac{\sum_{i,j} \text{cov}(x_i(t), x_j(t))}{\sum_i \text{var}(x_i(t))}. \quad (1)$$

A variance ratio greater than one reflects synchrony, whereas a variance ratio less than one describes compensatory dynamics. While applications of the variance ratio have advanced our understanding of drivers of synchrony, this summary metric cannot distinguish whether community synchrony varies depending on the timescale of interest.

Timescale-specific metrics make it possible to parse the timescales of synchrony versus compensation (Downing et al., 2008; Lindström et al., 2012). We utilize a newly developed

approach that extends the classic variance ratio (see Zhao et al. 2020 and the R package “tsvr” (Reuman et al., 2019) for full derivations of the metric and extensions to additional synchrony and stability calculations). Paralleling the notation for the variance ratio (Eqn. 1), the timescale-specific variance ratio is denoted for a given timescale σ as $\varphi_{\text{ts}}(\sigma)$. The variances and covariances are now replaced by power spectra and cospectra. We denote the power spectrum of $x_i(t)$ as $s_{ii}(\sigma)$ and the cospectrum of $x_i(t)$ and $x_j(t)$ as $s_{ij}(\sigma)$. We then can define the timescale-specific variance ratio as:

$$\varphi_{\text{ts}}(\sigma) = \frac{\sum_{i,j} s_{ij}(\sigma)}{\sum_i s_{ii}(\sigma)}. \quad (2)$$

This provides a variance ratio value across multiple timescales. As with the classic variance ratio, values $\varphi_{\text{ts}}(\sigma) > 1$ correspond to synchrony at a given timescale σ , whereas values $\varphi_{\text{ts}}(\sigma) < 1$ correspond to compensatory dynamics.

The timescale-specific variance ratio allows for a direct comparison to the classic, non-timescale-specific approach, facilitating a comparison between studies that implement either approach. To average the timescale-specific variance ratio such that the classic variance ratio is recovered, we define a normalized timescale-specific measure of population variability, $w(\sigma) = \sum_i s_{ii}(\sigma) / \sum_i \text{var}(x_i(t))$, which allows for a mapping between variance ratios such that $\sum_{\sigma} w(\sigma) \varphi_{\text{ts}}(\sigma) = \varphi$ (Zhao et al., 2020). The different timescales that can be assessed depend on the overall time series length, T , ranging from a lower bound of $\sigma = T/(T - 1)$ to an upper bound of $\sigma = T$. For annually sampled data, previous authors (Sheppard et al., 2016; Zhao et al., 2020) have adopted the practice of computing weighted averages of the $\varphi_{\text{ts}}(\sigma)$ over “short” ($\sigma < 4$ years) and “long” ($\sigma \geq 4$ years) timescale bands. We follow this convention for all of our analyses below. The threshold of $\sigma = 4$ time-steps (sampling intervals) for differentiating short and long timescales was chosen because $\sigma = 4$ corresponds to a frequency which is half the maximum frequency that can be assessed (one

cycle every two time points). Additionally, $\sigma = 4$ is the boundary between persistent and anti-persistent dynamics for sinusoidal oscillations, as measured with a lag-1 autocorrelation (Sheppard et al., 2016; Zhao et al., 2020).

Theoretical model overview

We applied the timescale-specific variance ratio to output from theoretical models and an empirical case study. All theoretical scenarios are based upon a model of population and community dynamics that uses a modified version of the model of Loreau & de Mazancourt (2013), adapted for multiple environmental drivers:

$$N_i(t+1) = N_i(t) \exp\left[r_i \left(1 - \frac{N_i(t)}{K_i} - \frac{\beta_{i,j} N_j(t)}{K_j}\right) + \epsilon_{1,i} \mu_1(t) + \epsilon_{2,i} \mu_2(t)\right]. \quad (3)$$

Here, $N_i(t)$ is the abundance of species i at time t , r is the intrinsic (density-independent) growth rate, K is the carrying capacity, and $\beta_{i,j}$ is the competition coefficient of species j on species i .

We incorporate two environmental drivers, creating environmental fluctuations of varying timescales and amplitudes where $\mu_e(t) = a_e \sin(b_e t + c_e)$ for environmental conditions $e = 1, 2$. Environmental fluctuations vary based on a sinusoidal function (sin), where a_e denotes the amplitude, b_e controls the period, and c_e denotes the phase shift. Species' sensitivities to environmental fluctuations are defined via $\epsilon_{e,i}$. We modify the above base-line model and its parameters to examine each of our four scenarios described above. For each scenario, we run the model for 100 timesteps, with the first 50 discarded to remove any potential effects of initial conditions, and the last 50 timesteps included in our synchrony analyses. We set species' initial abundances to their carrying capacities, K_1 and K_2 . All analyses, both theoretical and empirical, have complete code provided at https://github.com/lash1937/synchrony_timescales.

Empirical case study

To test scenarios 1 and 2 in a case study, we applied the timescale-specific variance ratio to long-term data from a California serpentine grassland (Fig. S1a-c). California serpentine grasslands are dominated by annual forbs and support native perennial grasses. They are characterized by a highly variable climate; at our site, Jasper Ridge in San Mateo County, California, USA, annual rainfall ranges from 200 to 1200 mm (Hallett et al., 2018). Climate patterns are influenced by long-term cycles, including the El Niño Southern Oscillation and the Pacific Decadal Oscillation, and species exhibit differential responses to wet and dry years (Hobbs et al., 2007; Hallett et al., 2018). Within the site, gopher activity creates disturbances that remove all of the vegetation in small patches across the landscape (Hobbs and Mooney, 1985; Hobbs et al., 2007) (Fig. S1d). We (RJH and LMH) have collected plant species composition data and gopher disturbance data in 216 0.5 m x 0.5 m quadrats annually for 37 years (1983-2019) (see Hobbs et al. 2007 for sampling details). Using these data, we focused on species contrasts that we hypothesized would exhibit timescale-specific synchrony dynamics through different mechanisms.

Scenario 1: Timescale of environmental drivers

Theoretical Methods: Environmental variability is a key driver of fitness and different environmental drivers may affect species in similar or opposing manners (Ives, 1995; Downing et al., 2008; Keitt and Fischer, 2006; Zhao et al., 2020). As such, the timescale-specific variance ratio must parse environmentally driven patterns of synchrony versus compensation by timescale. To test the metric and highlight its utility, we first applied the timescale-specific variance ratio to the simulated two-species community influenced by two drivers: a short-timescale driver to which species had a shared response, and a long-timescale driver to which species had opposing responses (drivers represented in Fig. 1a-c, individual species responses in Fig. 1d, e; model parameters in Appendix S1).

Empirical Methods: To test the empirical implications of different environmental drivers on timescale-specific synchrony and compensation, we focused on two species of annual forbs that exhibit highly variable abundances over time at Jasper Ridge, California: *Plantago erecta* and *Microseris douglasii* (Fig. S1e, f). We hypothesized that these species would share a similar, short-timescale response to gopher disturbance (initially negative but rebounding quickly) but contrasting long-timescale responses to climate (*P. erecta* does better in dry years and *M. douglasii* has no discernible response) (Hobbs et al., 2007; Hallett et al., 2018). To test this, we filtered the full dataset to include only years and quadrats in which both species were initially present at moderate to high abundances (> 3 percent cover in year 0), the quadrat was disturbed in year 1, and was undisturbed through at least year 9. We set this minimum length to ensure timeseries of at least 10 years (as recommended by Zhao et al. 2020), although all retained timeseries were longer (ranging from 17 to 35 years). This process resulted in 85 timeseries with 19 different starting years. We then applied the timescale-specific variance ratio to each timeseries.

Results and discussion: The timescale-specific variance ratio effectively allowed us to disentangle the effects of individual drivers on synchrony versus compensation, as expected (Fig. 1f, g). In comparison, the effect of the short-timescale driver was largely masked in the classic variance ratio (Fig. 1g). Our empirical case study at Jasper Ridge mirrored our theoretical results, such that species were synchronous on short timescales and compensatory on long timescales, and the classic variance ratio primarily captured the longer timescale dynamics (Fig. 2). There are both statistical and ecological explanations for the striking importance of long-timescale dynamics for the classic variance ratio. Statistically, the relationship between the classic variance ratio and the timescale-specific decomposition depends on the length of the timeseries and on differences in the amplitude of short-term versus long-term environmental fluctuations (a_e) and species' sensitivities (ϵ). As such, the contribution of long-term dynamics to the variance ratio increases with both timeseries length and the

amplitude of long-term drivers. As all timeseries here are relatively long (i.e. 17 years or greater), the classic variance ratio mirrors the long timescale signal.

Ecologically, long-timescale drivers may most strongly influence patterns of community synchrony for several reason. First, long-timescale climate drivers, such as the Pacific Decadal Oscillation and the North Atlantic Oscillation, are more regular than short interannual variation in weather patterns, and may therefore be more detectable in their effect on community structure (Downing et al., 2008; Chiba et al., 2012). Long-term climate drivers like the Pacific Decadal Oscillation may underlie the pattern of long-timescale compensation we observed at Jasper Ridge (Fig. 2a, b), where annual species often rebound quickly from frequent disturbance (such as gopher disturbance), leaving only a fleeting signature on patterns of community synchrony (Fig. 2a, b). Second, long-timescale fluctuations may reflect the differing role that rare versus common events have on populations. Daily temperature fluctuations and summer heat waves, for example, can both influence population dynamics. The effect of daily temperature fluctuations on populations are typically felt over short timescales, whereas high mortality due to a rare and extreme heat wave may have a long-lasting signal on population dynamics (Lindström et al., 2012). While the effects of the timescales of environmental fluctuation and disturbance have been explored in the context of population synchrony and extinction risk (Heino, 1998; Schwager et al., 2006), if some species can tolerate extreme events while others cannot, extreme events may leave a long-lasting signature of compensation on the community (Till et al., 2019).

Scenario 2: Timescale of species responses

Theoretical Methods: Species differ in their intrinsic growth rates, which can manifest in differences in the timescale of their response to an environmental driver (Grime, 1977). Consequently, the degree of community synchrony versus compensation may depend jointly on species response times and the timescale of the environmental driver (Ives, 1995; Loreau and de Mazancourt, 2008). To explore this scenario, we modified our model such that

species shared the same directional response to two environmental drivers but differed in their response times (parameters in Appendix S1). Species either tracked the environment, exhibited a lagged response, or exhibited a rapid response (initially overshooting their carrying capacity and then exhibiting dampening oscillations) (Fig. 3a). We compared three different examples. In the first, both species' growth rates track environmental fluctuations (Fig. 3b). In the second, one species tracks the environment and the other exhibits a lagged response (Fig. 3c). In the last, one species tracks the environment while the other exhibits dampening oscillatory responses to environmental fluctuations (Fig. 3d).

Empirical Methods: To explore whether differences in the timescale of species responses to the environment are reflected in the timescale of synchrony, we focused on *P. erecta* and a perennial grass, *Elymus glaucus* (Fig. S1e, g). We hypothesized that they would share similar, negative short-timescale responses to gopher disturbance, but that their recovery times would differ, with the annual *P. erecta* rebounding quickly but the perennial *E. glaucus* recovering more slowly. We subsetting the data following the protocol described in Scenario 1, analyzing 41 timeseries ranging from 10-35 years in length with 13 different starting years.

Results and discussion: Our simulations highlighted that the presence of species with different environmental response rates can reduce synchrony and even generate compensatory dynamics, even when all species share the same directional response to the environmental driver (Fig. 3b, c, d). The compensatory effect of lagged responses was strongest when the timescale of the lag matched the timescale of the environmental driver. For example, the presence of a species with a slow growth rate generated compensation across all timescales (Fig. 3c, g). Across systems, differences in the timescale of species responses versus recovery times to poor environmental conditions may drive timescale-dependent patterns. We observed this dynamic at Jasper Ridge, in which both the annual and perennial species shared an initial, negative response to disturbance that enhanced short-timescale synchrony (Fig. 2c, d). However, the perennial species had a slower recovery rate (i.e., a lagged response)

that promoted compensation at longer timescales by delaying its recovery relative to the annual species (Fig. 2c, d).

Endogenous population cycles, often induced by fast growth rates, may decouple some species' fluctuations from the environment (Haynes et al., 2019). As such, species cycling at different rates will be less synchronous than predicted based solely on environmental response, although this effect is timescale-dependent (Fig. 3d, h). In our simulation, a species with a fast growth rate more closely tracked short-timescale environment fluctuations, reflecting the fact that environmental conditions changed before the species internal dynamics dominated its population cycles. As a result, the fast-growing species was synchronous with a species whose growth tracked the environment at short timescales (Fig. 3d, h). At long timescales, however, the population cycles of the fast-growing species became increasingly decoupled from the environmental driver, and correspondingly, the other species (Fig. 3d, h). Consequently, internal dynamics generated by fast growth rates may also promote increased compensation, particularly in communities structured by long-timescale drivers. This pattern was hinted at in the Jasper Ridge empirical data, in which the annual species recovered quickly from a short-timescale disturbance and then oscillated independently, while the perennial species continued to slowly recover from the disturbance (Fig. 2c, d).

Species' internal dynamics can interact with environmental variation in complex ways. For example, population growth rates are often affected by the environment, causing potential co-variance between environmental variability and species growth rates. A favorable environment can cause rapid population growth and potentially generate subsequent endogenous cycling, making it hard to tease apart the drivers of synchrony even within a single species. For example, the generation time of mites can vary four-fold (between 9 and 40 days) depending on resource availability and density (Benton et al., 2001). Adult fecundity is strongly linked to resources, such that egg production tracks the environment. However, under low resource conditions, juveniles stop growing and their growth rates no longer track

the environment (Benton et al., 2001). Given the myriad of ways that timescales of environmental fluctuations and species rates of responses can manifest in multi-species communities, it is perhaps not surprising that compensatory dynamics and their drivers have been hard to isolate in natural communities (Houlahan et al., 2007). Disentangling timescale-specific dynamics therefore provides an exciting avenue for further exploration.

Scenario 3: Spatial scale of response

Methods: Species interactions and responses to environmental fluctuations do not occur in isolation, but rather local-scale dynamics are embedded in a larger spatial context, where communities are connected via dispersal through the landscape. To examine how dispersal may alter timescale-specific synchrony across spatial scales, we modified our general model of species' abundances through time (equation 3) to create a two-patch metacommunity, where patches exhibited different underlying timescales of environmental fluctuations. In our model, species responded similarly to short-term fluctuations that occurred in patch 1 (denoted by the subscript x), but in opposing manners to long-term fluctuations in patch 2 (subscript y) (Fig. 4a, d). We examined the timescale-dependent signature of dispersal (d) by comparing cases without ($d = 0.0$) versus with ($d = 0.4$) strong dispersal between patches (parameters in Appendix S1). Abundances of species i within patches x and y followed:

$$N_{i,x}(t+1) = N_{i,x}(t) \exp\left[r_i\left(1 - \frac{N_{i,x}(t)}{K_i} - \frac{\beta_{i,j}N_{j,x}(t)}{K_j}\right) + \epsilon_{x,i}\mu_x(t)\right] + dN_{i,y}(t) - dN_{i,x}(t) \quad (4)$$

$$N_{i,y}(t+1) = N_{i,y}(t) \exp\left[r_i\left(1 - \frac{N_{i,y}(t)}{K_i} - \frac{\beta_{i,j}N_{j,y}(t)}{K_j}\right) + \epsilon_{y,i}\mu_y(t)\right] + dN_{i,x}(t) - dN_{i,y}(t). \quad (5)$$

Results and discussion: Applying the timescale-specific variance ratio at multiple spatial scales elucidated the interplay between local and regional processes in landscapes with spatial heterogeneity (Fig. 4a, d). For example, in the absence of dispersal, synchrony in abundances was driven solely by within-patch dynamics, as expected (Fig. 4b, e). Here, the timescale-

specific variance ratios recover the classic variance ratio. However, at the larger landscape scale (Fig. 4g), the signatures of each patch’s environmental fluctuations were detected with the timescale-specific variance ratio, while the classic variance ratio was again biased towards the long-term drivers occurring in patch 2 (Fig. 4i).

Dispersal between patches was detectable in heterogeneous landscape using the timescale-specific metric, highlighting how spatial processes can impact our interpretation of temporal synchrony (Fig. 4c, f, h). In this case, synchrony from short-term drivers in patch 1 and compensation from long-term drivers (in patch 2) were evident in both patches (comparing 4i to j). Within patches, comparing the timescale-specific variance ratio with the classic ratio elucidates the focal patch; the classic variance ratio was synchronous in patch 1 but compensatory in patch 2 (Fig. 4j). This highlights how applying a temporally-focused method can, counter-intuitively, detect spatial heterogeneity and dispersal effects when applied at different levels of spatial aggregation. In more complex scenarios, we expect these spatio-temporal patterns to also yield signatures in the timescale-specific variance ratio. For example, the order in which species arrive can alter long-term community composition and patterns in synchrony (Fukami et al., 2016). Furthermore, arrival itself can depend on fluctuations in underlying environmental conditions that alter species’ dispersal kernels and propagule density, yielding complex spatio-temporal dynamics (Grainger et al., 2018; Sullivan et al., 2018).

At larger spatial scales, spatial patterning and interdependence between patches plays a key role in determining stability. Here we compare patches with different underlying environmental drivers. However, previous work highlights how overall landscape stability depends not only on trade-offs and compensation of species within patches, but also on trade-offs among patches (Wilcox et al., 2017; Wang et al., 2019). These among patch trade-offs can create compensatory fluctuations among patches, stabilizing overall landscape fluctuations. Our results provide additional insight into the role of dispersal, highlighting how connectivity and dispersal between plots manifest as different synchrony and stability patterns depending

on the scale of spatial aggregation.

Scenario 4: Climate change applications

Methods: Changes in community synchrony and its underlying timescales will likely also be impacted by global change and non-stationary environmental fluctuations, especially as species cross thresholds where their responses to environmental conditions shift (Ives, 1995; Ruel and Ayres, 1999; Radeloff et al., 2015). To examine these potential effects, in our final scenario, we modeled an individual driver that oscillated on both short-term and long-term timescale (Fig. 5a). To do so, we summed the effects of short- and long-term fluctuations in a single driver (Fig. 5b); this could, for example, represent temperature oscillating over seasons with a multi-year effect from drivers such as the North Atlantic Oscillation. We examined the timescale of synchrony: (1) in the original stable environment ($e_{historic}$), (2) under directional environmental change (Fig. 5c), and (3) under a new environmental steady state (e_{new} , where $e_{new} = e_{historic} + 0.5$. Fig. 5d) (model parameters in Appendix S1).

We considered a community where both species responded with the same strength to environmental fluctuations ($\epsilon_e = 0.5$), but the second species responded to the environment only above a certain threshold, e.g. when $e > 0.5$. As such, e_{new} was more often above the threshold for species two's response than under $e_{historic}$ conditions. This case represents commonly observed demographic responses across species and ecosystems. For example, tree establishment has been shown to only occur in years with rainfall above a given threshold (López et al., 2008), rainfall and moisture thresholds are common for breaking impermeable seed coat dormancy (Jaganathan et al., 2019), and phytoplankton species often have different threshold responses to pH (Klug et al., 2000).

Results and discussion: Under baseline historic conditions, the combination of competition and species-specific environmental thresholds yielded compensatory dynamics on long timescales and slight compensation with the classic variance ratio (Fig. 5b, e, h). This occurred even though species responded in the same manner to environmental fluctuations,

as competition between the two species tended to drive compensatory dynamics. Compensation driven by competition overshadowed synchronizing effects of a shared environmental driver, as species 2 responded to the environment only relatively rarely.

In contrast, directional environmental change increased synchrony at all timescales, as the transitory environmental drivers dominated dynamics (Fig. 5c, f, i). Once the environment settled on a new equilibrium, our model yielded increased synchrony. This increase in synchrony occurred because the environment was more often above the threshold where both species responded to the driver. Environmental fluctuations therefore were more important under e_{new} , while competition dominated dynamics under $e_{historic}$ conditions (Fig. 5d, g, j).

Our model results highlight that increased environmental forcing from more extreme climate conditions in the future may overshadow competitive effects, yielding an increase in community synchrony and a loss of compensatory dynamics. To date, the effects of climate change on synchrony have been examined primarily in a single-species context or in relation to phenological synchrony between pairs of species. For example, increased spatial synchrony between populations has been observed among populations of damselfish in the Great Barrier Reef (Cheal et al., 2007), North American wintering birds (Koenig and Liebhold, 2016), and Greenland caribou (Post and Forchhammer, 2004). In contrast, however, climate-induced shifts in phenology can disrupt synchrony in plant-herbivore (Hunter and Elkinton, 2000; Tikkanen and Julkunen-Tiitto, 2003), predator-prey (Sanford, 1999; Logan et al., 2006), and host-parasitoid interactions (Visser and Holleman, 2001; Hance et al., 2007; Klapwijk et al., 2010), causing increased extinction risk for co-dependent species. Our model suggests that, as for single-species populations, synchrony within communities may increase with climate change. The application of the timescale-specific variance ratio to empirical communities provides a pathway to assessing whether natural communities match theoretical expectations.

371 Conclusions

372 Understanding patterns of synchrony versus compensation remains an ongoing challenge in
373 ecology. Our results highlight the myriad ways that timescale specific processes—both exoge-
374 neous and endogenous—can result in synchrony versus compensation dominating at different
375 timescales. Yet to date, most assessments of synchrony and compensation, particularly in
376 terrestrial systems, have calculated a single metric for a given time series. Recently, the
377 timescale-specific variance ratio revealed how the balance of synchronous versus compen-
378 satory dynamics can differ across timescales in empirical communities (Zhao et al., 2020).
379 Here, we demonstrate its utility for linking timescale-specific patterns to process. Our work
380 points to specific aspects of communities that if characterized can help us better understand
381 synchrony and stability patterns at different timescales such as the timescale of environmental
382 variability, species responses to environmental variability, life-history traits such as growth
383 rates, and the degree of dispersal. Finally, our analyses highlight potential mismatches
384 between experimental tests of synchrony and compensation in natural systems: most exper-
385 imental tests explore short-term drivers, whereas the influence of long-timescale drivers on
386 community synchrony suggests that short experiments may fail to capture key structuring
387 dynamics. We argue that further experimental and theoretical analyses of timescale-specific
388 fluctuations are critical for characterizing synchrony versus compensation and identifying
389 their underlying mechanisms.

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Figure Legends

Figure 1: Environmental drivers operating on different timescales can create timescale-specific synchrony and compensation. Environmental drivers may operate over (a) short timescales, (b) long timescales and (c) in combination. (d) Shared species responses to a single, high-frequency driver results in high species synchrony and unstable total biomass, whereas (e) opposite responses to a single, low-frequency driver results in compensatory dynamics and stable total biomass. The combination of these responses results in (f) synchrony at short timescales and compensation at long timescales. As a result, (g) a timescale-specific variance ratio differentiates these dynamics, whereas the classic variance ratio does not reflect short timescale synchrony.

Figure 2: Applying the timescale-specific synchrony metric to a case study at Jasper Ridge, California, USA (a) Averaged timeseries (\pm SE) of two native annual forbs *Plantago erecta* and *Microseris douglasii* before and after gopher disturbance (disturbance occurred during the grey bar at time 1). (b) Short timescale, long timescale, and classic variance ratio for *P. erecta* and *M. douglasii* communities (average value of the metric after it was calculated on individual timeseries \pm SE). (c) Averaged timeseries (\pm SE) of a native annual forb *P. erecta* and native perennial grass *Elymus glaucus* before and after gopher disturbance (grey band). (d) Short timescale, long timescale, and classic variance ratio for *P. erecta* and *E. glaucus* communities (\pm SE).

Figure 3: Differences in the growth rates of species can alter the timescale of synchrony, even when species share the same directional response to the environment. (a) Growth curves of species with different density-independent growth rates. The black species tracks the environment, the tan species exhibits a lagged response, and the pink species responds rapidly enough to create dampened internal oscillations. (b-d) Population dynamics among species that share directional responses to (e) two timescale-specific environmental drivers.

(f-h) The resulting timescale-specific and classic variance ratios.

Figure 4: Spatial connectivity can alter local and landscape patterns in synchrony. (a) A short time scale driver operates in Patch 1 and (b,c) species dynamics in Patch 1 without (b) and with (c) dispersal from neighboring patch 2. Species 1 (black) and species 2 (grey) both respond to the local driver in similar ways. (d) A long timescale driver operates in Patch 2 and (e,f) species dynamics in Patch 2 without (e) and with (f) dispersal. (g, h) Aggregate species and total biomass dynamics at the landscape scale without (g) and with (h) dispersal. (i-j) Timescale-specific and classic variance ratios for the above communities. (i) Without dispersal, local drivers dominate, leading to synchronous dynamics in patch 1 and compensatory dynamics in patch 2. Within patches the classic variance ratio tracks these dynamics, and at the landscape scale it reflects an aggregate of the two patches. (j) With reciprocal dispersal, landscape level synchrony remains the same but patch level dynamics vary, with the classic variance ratio representative of the dynamics of the focal patch.

Figure 5: Climate change has the potential to alter the strength and timescale of synchrony. (a) A climate driver such as temperature may vary over different timescales, often with both a low frequency (green) and high frequency component (blue). (b-d) The overall environmental driver and species' sensitivities under a stable, changing, and altered climate. Species 1 responds to all variability (red and purple), whereas species 2 only responds to the driver above a threshold level (red). The environmental threshold is depicted by the dashed grey line. (e-g) The abundance of species 1 (black), species 2 (grey) and their aggregate abundance (red) in response to the above environmental driver. (h-j) Variance ratios for the above communities. Under the stable climate scenario (b, h), species have different threshold responses, yielding compensatory dynamics on long timescales. Species becomes increasingly synchronized as climate means increase (c, i), causing species 2 to respond to the driver more frequently. Finally, under a stable climate with an elevated mean, both species become synchronized by environmental variability across timescales (d, j).

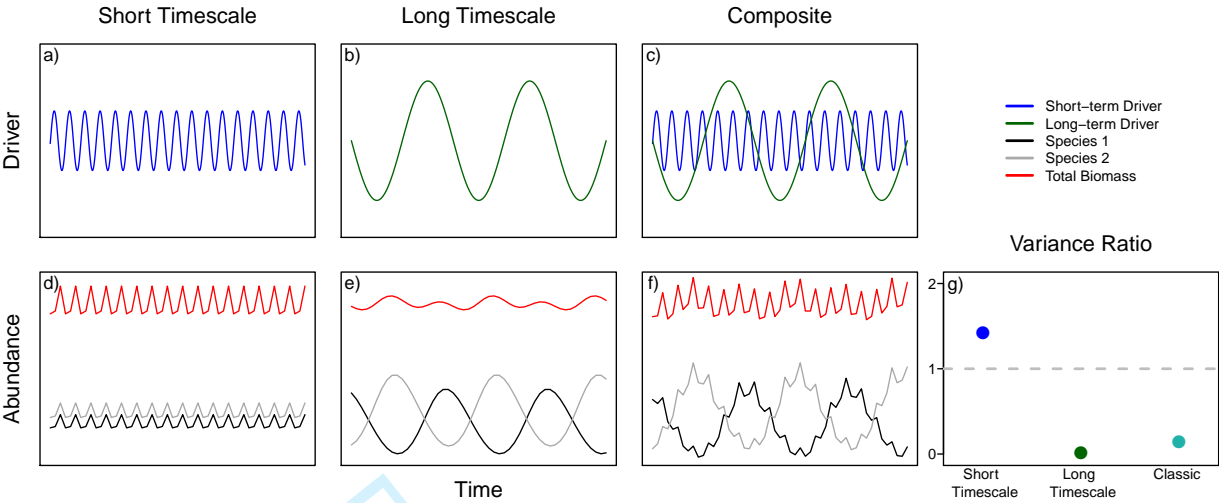


Figure 1:

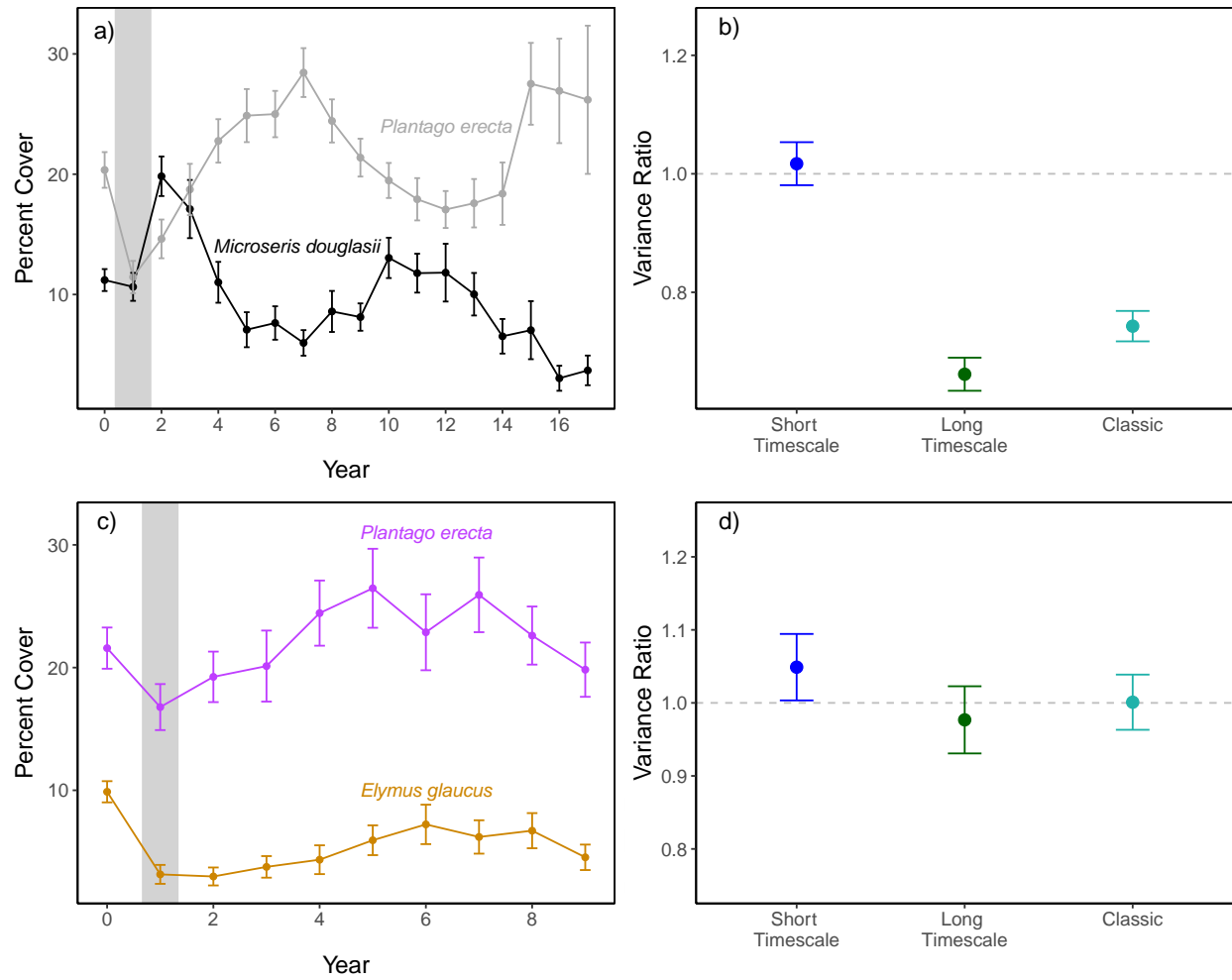


Figure 2:

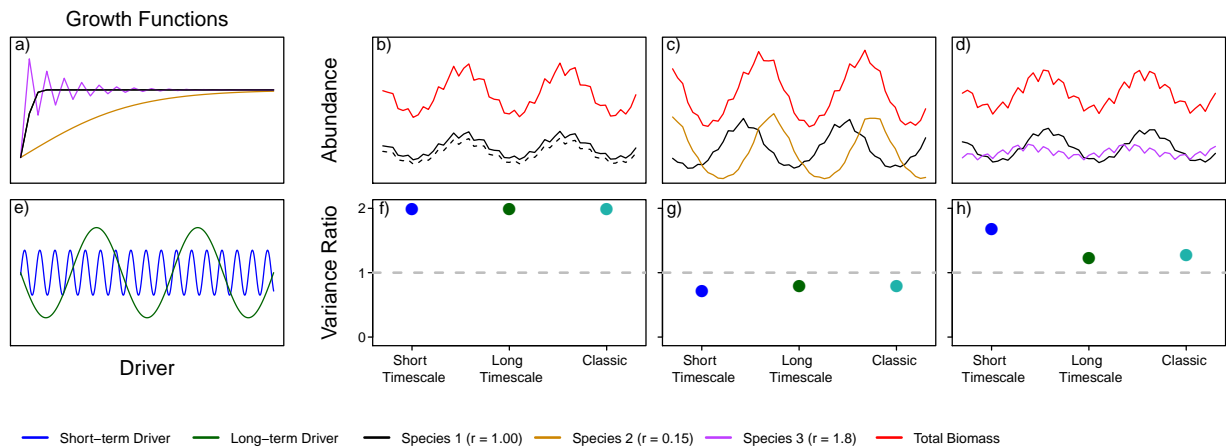


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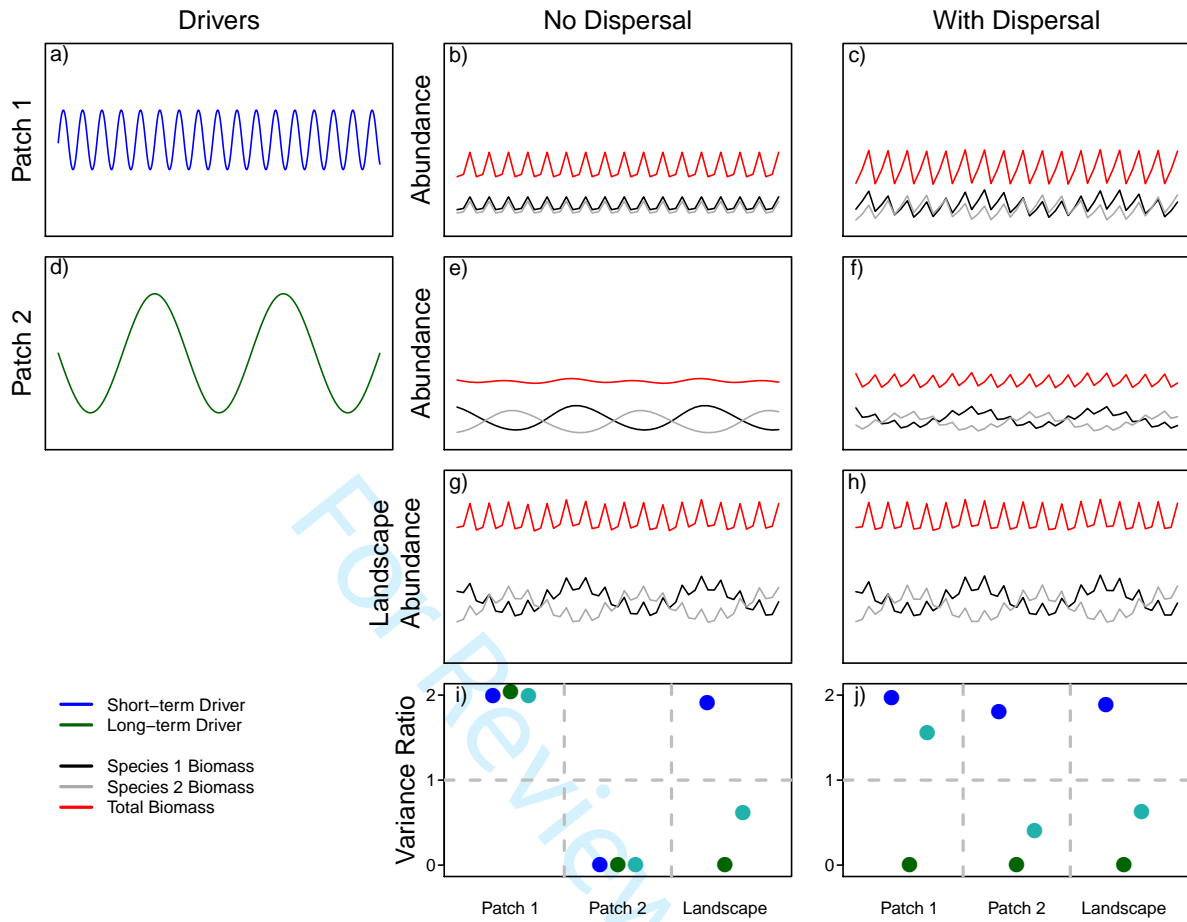


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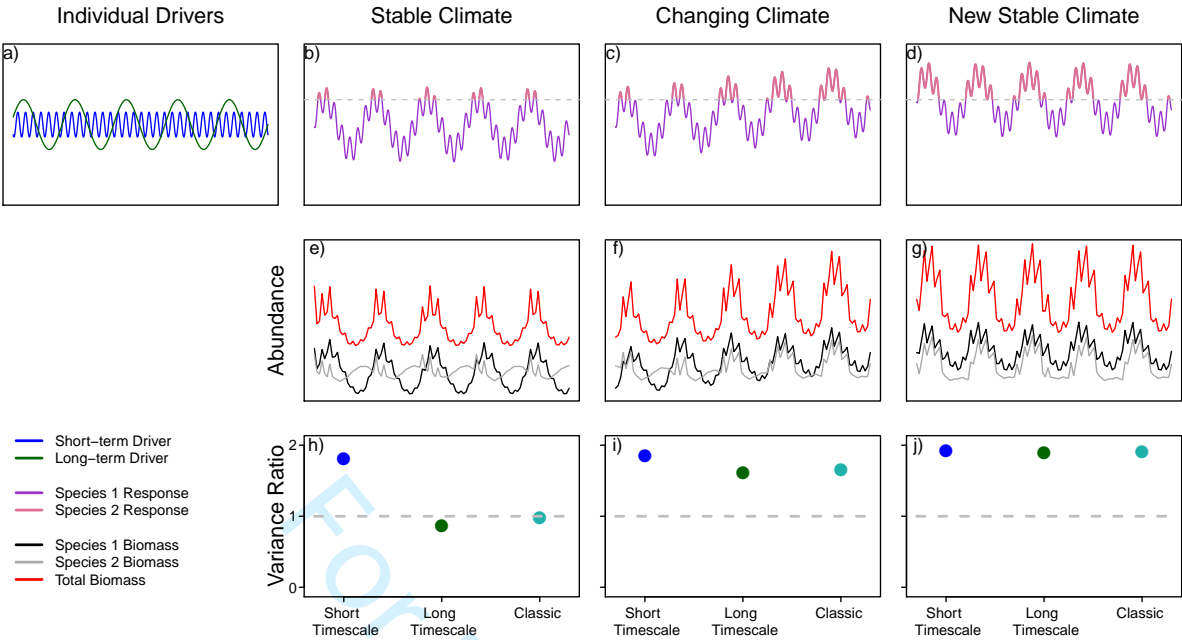


Figure 5:

Appendix 1 for: The long and the short of it: Decomposing synchrony and compensation across temporal scales

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Model Parameterization

Scenario 1: Timescale of environmental drivers:

We parameterize scenario 1 such that we include two environmental drivers: short-timescale driver to which species had a shared response ($\epsilon_{1,1} = \epsilon_{1,2} = 0.2$), and a long-timescale driver to which species had opposing responses ($\epsilon_{2,1} = 0.1$ while $\epsilon_{2,2} = -0.1$). Here, short-term drivers are defined by $a_1 = 0.5$, $b_1 = \frac{2\pi}{3}$, and $c_1 = 2$ while long-term environmental fluctuations are defined by $a_2 = 1$, $b_1 = \frac{2\pi}{20}$, and $c_2 = 0$. The net effect of each driver on community dynamics is equal, as species are twice as sensitive to the short-timescale driver (ϵ), but the amplitude of the long-timescale driver is twice that of the short-term driver (a).

To isolate the effect of multiple environmental fluctuations, species have identical growth rates ($r = 0.5$), interspecific competitive coefficients ($\beta_{1,2} = \beta_{2,1} = 0.5$), and similar carrying capacities ($K_1 = 1000$ while $K_2 = 1100$), which are set to be slightly offset for ease of visualization.

Scenario 2: Timescale of species responses:

In this scenario, we define short- and long-term drivers as above: $a_1 = 0.5$, $b_1 = \frac{2\pi}{3}$, $c_1 = 2$ and $a_2 = 1$, $b_1 = \frac{2\pi}{20}$, and $c_2 = 0$. In contrast to scenario 1, we set species to have identical directional responses to environmental drivers with $\epsilon_{1,1} = \epsilon_{1,2} = 0.1$ and $\epsilon_{2,1} = \epsilon_{2,2} = 0.2$. We set $K_1 = 1100$ and $K_2 = 1000$, $\beta_{1,2} = \beta_{2,1} = 0.5$. We compared three examples with different pair-wise species intrinsic growth rates. In the first, both species' growth rates track environmental fluctuations ($r_1 = r_2 = 1.00$). In the second, one species tracks the environment ($r_1 = 1.00$) while the second exhibits a lagged response ($r_2 = 0.15$). In the last, one species tracks the environment ($r_1 = 1.00$) while the other exhibits dampening oscillatory responses to environmental fluctuations ($r_2 = 1.8$). These examples are chosen as they produced different desired outcomes with respect to how populations responded to and tracked the environment.

Scenario 3: Spatial scale of response:

Modifying from the previous scenarios, in the spatial model, we parameterize patch one so that it has a short-term driver ($a_1 = 0.5$, $b_1 = \frac{2\pi}{3}$, $c_1 = 2$, denoted by the subscript x). Patch two has a long-term environmental driver that species respond in opposing manners to ($a_2 = 1$, $b_1 = \frac{2\pi}{20}$, $c_2 = 0$, denoted by the subscript y).

Following similar parameterizations as previous scenarios, we parameterized the model where $r_i = 0.5$ for both species, $\beta_{1,2} = \beta_{2,1} = 0.5$, $K_1 = 1100$, $K_2 = 1000$, $\epsilon_{x,1} = \epsilon_{x,2} = 0.5$, and $\epsilon_{y,1} = 0.1$ while $\epsilon_{y,2} = -0.1$. We examined the timescale-dependent signature of dispersal, comparing cases without ($d = 0.0$) versus with ($d = 0.4$) strong dispersal between patches.

Scenario 4: Climate change applications:

In scenario 4, we defined the short-term fluctuations (e_1) by $a_1 = 0.25$, $b_1 = \frac{2\pi}{3}$, and $c_1 = 2$ while long-term environmental fluctuations (e_2) were defined by $a_2 = 0.5$, $b_1 = \frac{2\pi}{20}$, and $c_2 = 0$. The total fluctuations of the stationary environment were given by $e_{historic} = e_1 + e_2$. As stated in the main text, we examined the timescale of synchrony: (1) in the original stable environment ($e_{historic}$), (2) under directional environmental change, and (3) under a new environmental steady state (e_{new}). We define e_{new} such that $e_{new} = e_{historic} + 0.5$.

In the fourth scenario, demographic parameters were $r_i = 0.65$ for both species, $\beta_{1,2} = \beta_{2,1} = 0.5$, and $K_1 = 1100$, $K_2 = 1000$. Here, we include the full 100 timesteps in our variance ratio calculations so that we incorporate initial transient dynamics with the changing climate (Fig. 5b), and all analyses have an equal number of timesteps.

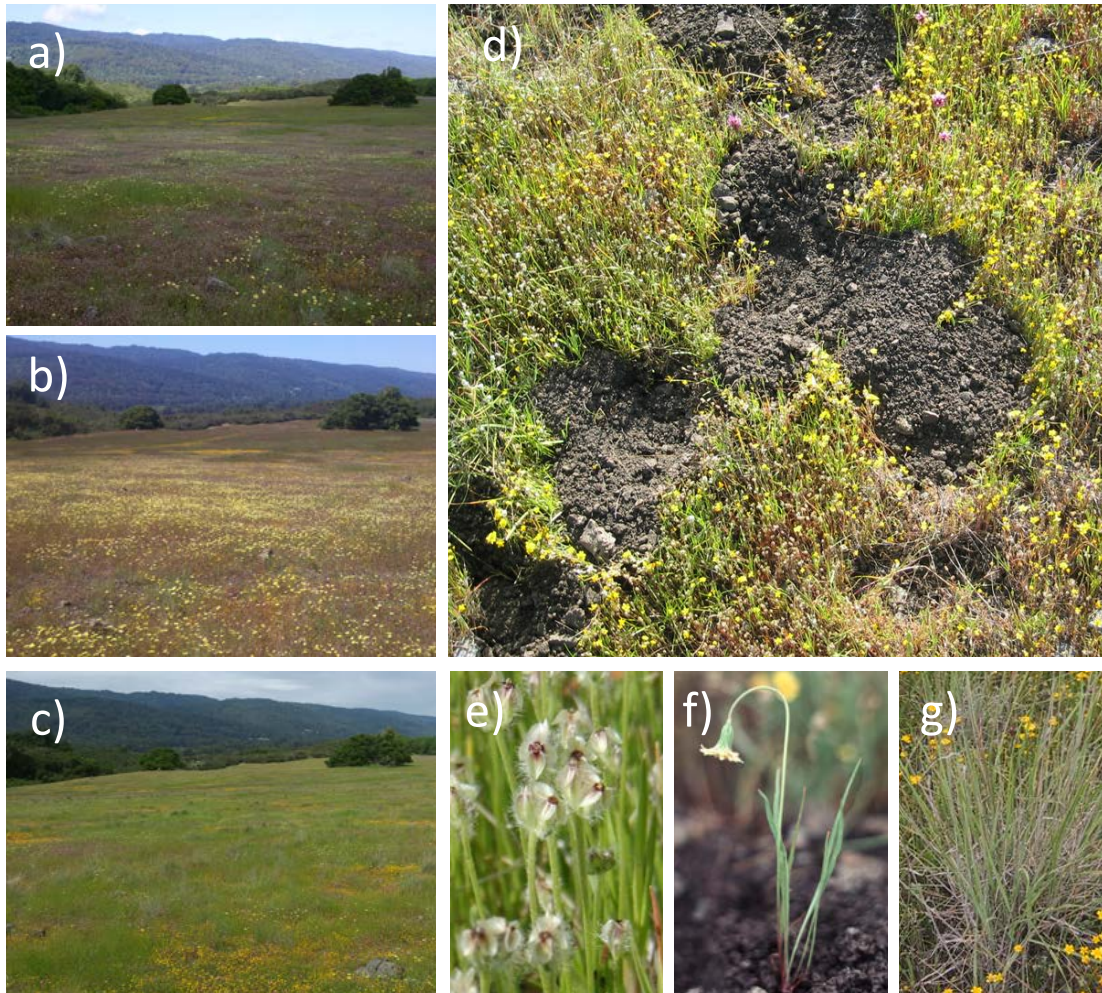


Figure S1: Jasper Ridge, a serpentine grassland in San Mateo, California, USA and the focal site for our empirical analyses. (a-c) The site across three different years. The site is dominated by native annual forbs and a few native perennial grasses but composition over space and time is highly variable. (d) Gopher disturbance frequently creates small patches without vegetation. (e) *Plantago erecta*, the dominant annual forb at the site. (f) *Microseris douglasii*, a common annual forb at the site. (g) *Elymus glaucus*, the dominant perennial grass at the site. Photo credit: Richard Hobbs.