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The long and the short of it: Mechanisms of synchronous and compensatory dynamics across temporal scales

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Abstract

Synchronous dynamics (fluctuations that occur in unison) are universal phenomena with widespread implications for ecological stability. Synchronous dynamics can amplify the destabilizing effect of environmental variability on ecosystem functions such as productivity, whereas the inverse, compensatory dynamics, can stabilize function. Here we combine simulation and empirical

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analyses to elucidate mechanisms that underlie patterns of synchronous versus compensatory dynamics. In both simulated and empirical communities, we show that synchronous and compensatory dynamics are not mutually exclusive but instead can vary by timescale. Our simulations identify multiple mechanisms that can generate timescale-specific patterns, including different environmental drivers, diverse life histories, dispersal, and non-stationary dynamics. We find that traditional metrics for quantifying synchronous dynamics are often biased toward long-term drivers and may miss the importance of short-term drivers. Our findings indicate key mechanisms to consider when assessing synchronous versus compensatory dynamics and our approach provides a pathway for disentangling these dynamics in natural systems.

KEYWORDS

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

INTRODUCTION

The extent to which communities of interspecific competitors exhibit synchronous versus compensatory temporal fluctuations and the underlying mechanisms driving these fluctuations have been of fundamental interest in ecology for decades (MacArthur, 1955). Community synchrony and its alternative pattern, compensatory dynamics, describe how the dynamics of species aggregate to influence community stability through time. Synchronous fluctuations of species' abundances reduce stability and often arise when species respond similarly to environmental fluctuations (Ives, 1995; Loreau & de Mazancourt, 2013), or through facilitative interactions between species. In contrast, compensatory dynamics stabilize overall community properties, as species fluctuate in a negatively correlated manner (Peterson, 1975) often due to competitive interactions or opposing responses to environmental drivers (Gonzalez & Loreau, 2009; Ives, 1995; Loreau & de Mazancourt, 2013). Quantifying the degree of synchronous versus compensatory dynamics has emerged as a key component of several recent advances in community ecology, such as how functional diversity influences resilience and how environmental change may impact coexistence (Hallett et al., 2019; Lindegren et al., 2016).

Synchronous and compensatory dynamics have often been considered mutually exclusive, as they reflect opposite correlations among abundances (e.g., Houlahan et al., 2007); however, there is a growing recognition that synchronous and compensatory dynamics can instead be timescale and spatial scale dependent (Downing et al., 2008; Lasky et al., 2016; Vasseur et al., 2014). 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). A wide range of processes can influence species dynamics and correlations in species fluctuations, including environmental variation (Allstadt et al., 2015; Tredennick et al., 2017), biotic interactions (Pedersen et al., 2016), variability in species demographic rates (Jucker et al., 2014), and dispersal (Wang et al., 2019). While all of these processes may affect synchronous versus compensatory dynamics, many have not been explored in a timescale-specific manner.

Linking patterns of timescale-specificity to mechanisms is essential for predicting stability patterns under global change. For example, multiple environmental drivers operating at different timescales are one potential mechanism explaining timescale-specificity (Frost et al., 1995; Sheppard et al., 2016). If this is a primary mechanism, then shifts in the timescale of dynamics would reflect shifts in the timescale of each driver. Alternatively, different life history strategies, in which some species respond quickly to the environment while others exhibit a lagged response, are another mechanism that could drive timescale-specific dynamics (Loreau & de Mazancourt, 2013). If this is the primary mechanism, then shifts in the timescale of environmental drivers may have a nonlinear effect on synchronous versus compensatory dynamics, depending on whether lagged species have sufficient time to recover (Benton et al., 2001). These primary effects may be further mediated by species interactions, causing emergent fluctuations to depend not only on underlying environmental drivers or species demographic rates, but also on the abundances of other species in the community (Gonzalez & Loreau, 2009; Loreau & de Mazancourt, 2013).

While there is a long history in population ecology of assessing the timescale of oscillations for single-species abundance patterns (Sheppard et al., 2016), and even how species interactions may modulate these oscillations (Ives, 1995; Ripa et al., 1998), at the community level many fundamental studies of synchronous versus compensatory dynamics have used simple covariance and correlation methods that aggregate across timescale (e.g., de Mazancourt et al., 2013; Grman et al., 2010; Gross et al., 2014; Hallett et al., 2014; Houlahan et al., 2007). However, when 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). Advances in scale-specific metrics allow us to gain a new understanding of synchronous versus compensatory dynamics (Brown et al., 2016; Downing et al., 2008; Keitt & Fischer, 2006; Vasseur et al., 2014; Vasseur & Gaedke, 2007), and new and less data-intensive methodologies are opening up our ability to empirically characterize timescale-specificity in terrestrial and aquatic systems (Zhao et al., 2020). These methodologies, coupled with growing open-access and long-term monitoring data, have the potential to expand our understanding of temporal fluctuations and their drivers across a wide range of ecosystems, with implications for connecting patterns of synchrony and stability to underlying mechanisms.

Here we use simulations and empirical analyses to examine four mechanisms that can underlie timescale-specificity of synchronous and compensatory dynamics. We first examine timescale-specific dynamics with multiple underlying environmental drivers of species' abundances, where environmental fluctuations occur at different timescales. Second, we assess a biotic mechanism in which species share a response to drivers but differ in their demographic rates. Third, we assess a spatial mechanism in which different timescale dynamics occur in local patches connected via dispersal, and we examine how they aggregate to affect larger-scale metacommunity dynamics. Finally, we consider a nonstationarity mechanism in which global change may alter the timescale-specific signature of synchronous and compensatory dynamics coupled with species-specific threshold responses. We focus our analyses on pairwise interactions to mechanistically and directly examine how differences in species' environmental responses and demography manifest across timescales. Our approach identifies key ecological factors that may cause synchronous and compensatory dynamics to operate at different timescales, while providing a path forward to parsing these dynamics and understanding their importance for stability in natural systems.

A TIMESCALE-SPECIFIC VARIANCE RATIO

Studies of synchronous and compensatory dynamics in community ecology have classically focused on their implications for ecosystem stability (Gonzalez & Loreau, 2009), with many studies approaching synchronous and compensatory dynamics phenomenologically, using covariance methods such as the variance ratio and related metrics (Klug et al., 2000; Loreau & de Mazancourt, 2008; Peterson, 1975; Schluter, 1984). 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) and is defined for a timeseries $x_i(t)$ of species abundances $i = 1\ldots,S$ as

$$\varphi = \frac{\sum_{i,j}\mathrm{cov}\left(x_i(t),x_j(t)\right)}{\sum_i \mathrm{var}\left(x_i(t)\right)}. \tag{1}$$

A variance ratio >1 reflects synchrony, whereas a variance ratio <1 describes compensatory dynamics. While applications of the variance ratio have advanced our understanding of drivers of synchrony, this summary metric cannot distinguish timescale-specificity in synchronous versus compensatory dynamics.

Timescale-specific metrics make it possible to parse the timescales of dynamics (Downing et al., 2008; Lindström et al., 2012). We use a newly developed approach that extends the classic variance ratio (see Zhao et al. [2020] and the R package *tsvr* [Reuman et al., 2019]). Paralleling the notation for the variance ratio (Equation 1), the timescale-specific variance ratio is denoted for a given timescale σ as $\varphi_{\mathrm{ts}}(\sigma)$. The variances and covariances are now replaced by power spectra and co-spectra. We denote the power spectrum of $x_i(t)$ as $s_{ii}(\sigma)$ and the co-spectrum of $x_i(t)$ and $x_j(t)$ as $s_{ij}(\sigma)$. We then can define the timescale-specific variance ratio as

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

This provides a variance ratio value across multiple timescales. As with the classic variance ratio, values $\varphi_{\mathrm{ts}}(\sigma) > 1$ correspond to synchrony at a given timescale σ, whereas values $\varphi_{\mathrm{ts}}(\sigma) < 1$ 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, $w(\sigma) = \sum_i s_{ii}(\sigma) / \sum_i \mathrm{var}(x_i(t))$, which allows for a mapping between variance ratios such that $\sum_\sigma w(\sigma)\varphi_{\mathrm{ts}}(\sigma) = \varphi$ (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 have adopted the practice of computing weighted averages of the $\varphi_{\mathrm{ts}}(\sigma)$ over "short" ($\sigma < 4$ years) and "long" ($\sigma \geq 4$ years) timescale bands (Sheppard et al., 2016; Zhao et al., 2020). We follow this convention for all of our analyses below for ease of interpretation, but note that dynamics on individual timescales can be studied instead. The threshold of $\sigma = 4$ time steps (sampling intervals) for differentiating short and long timescales was chosen because $\sigma = 4$ corresponds to a frequency that 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 and de Mazancourt (2013), adapted for multiple environmental drivers:

$$N_i(t+1) = N_i(t)\exp$$
$$\times \left[\overbrace{r_i}^{\text{intrinsic growth}} \left(1 - \underbrace{\frac{N_i(t)}{K_i} - \frac{\beta_{i,j}N_j(t)}{K_j}}_{\text{competition}} \right) + \overbrace{\epsilon_{1,i}\mu_1(t)}^{\text{env.1 effect}} + \underbrace{\epsilon_{2,i}\mu_2(t)}_{\text{env. 2 effect}} \right]. \tag{3}$$

$N_i(t)$ 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 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 baseline model and its parameters to examine each of our four mechanisms. For each, we run the model for 100 time steps, with the first 50 discarded to remove any potential effects of initial conditions, and the last 50 time steps included in our synchrony analyses. We set species' initial abundances to their carrying capacities, K_1 and K_2. All analyses have complete code provided online (see *Data Availability*).

EMPIRICAL CASE STUDY

To test mechanisms 1 and 2 in an empirical case study, we applied the timescale-specific variance ratio to long-term data from a California serpentine grassland (Appendix S1: Figure 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 (Hallett et al., 2018; Hobbs et al., 2007). Within the site, gopher activity creates disturbances that remove all of the vegetation in small patches across the landscape (Hobbs et al., 2007; Hobbs & Mooney, 1985; Appendix S1: Figure S1d). We (R. J. Hobbes and L. M. Hallett) have collected plant species composition data and gopher disturbance data in 216 0.5 × 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 specificity via abiotic and biotic mechanisms.

MECHANISM 1: MULTIPLE ENVIRONMENTAL DRIVERS

Theoretical test

Environmental variability is a key driver of abundance fluctuations, and different environmental drivers may affect species in similar or opposing manners (Downing et al., 2008; Ives, 1995; Keitt & Fischer, 2006; Zhao et al., 2020). The combination of different environmental drivers operating a different timescales may generate a timescale-specific pattern of synchronous versus compensatory dynamics (Frost et al., 1995). To assess this mechanism we 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 Figure 1a–c, individual species responses in Figure 1d,e; model parameters in Appendix S1: Section S1).

Empirical test

To test the empirical implications of different environmental drivers on timescale-specific synchronous and compensatory dynamics, we focused on two species of annual forbs that exhibit highly variable abundances over time at Jasper Ridge, California: *Plantago erecta* and *Microseris douglasii* (Appendix S1: Figure 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; Hallett et al., 2018; Hobbs et al., 2007). To test this, we filtered the full data set to include only years and quadrats in which both species were initially present at moderate to high abundances ($>3\%$ 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

Our simulated community exhibited highly synchronous dynamics at short timescale and highly compensatory dynamics at long timescales, and this expected pattern was easily discernable using the timescale-specific variance ratio (Figure 1f,g). In comparison, the effect of the short-timescale driver was largely masked with the classic variance ratio (Figure 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. Further, the classic variance ratio primarily captured the longer timescale dynamics (Figure 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

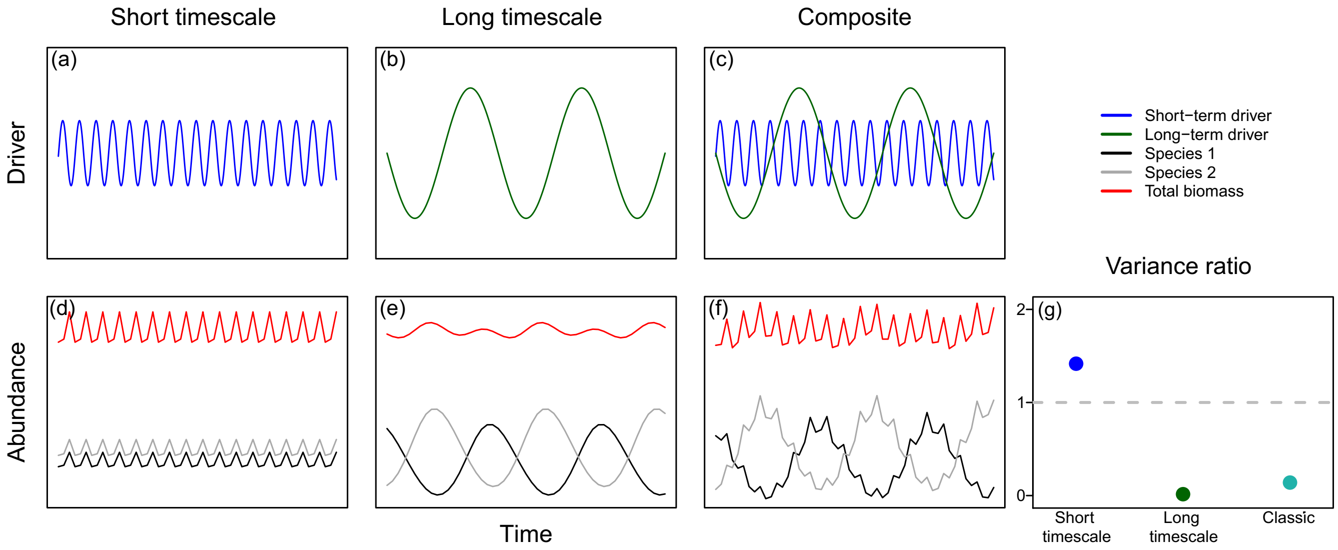

FIGURE 1 Environmental drivers operating on different timescales can create timescale-specific synchronous and compensatory dynamics. Environmental drivers may operate over (a) short timescales, (b) long timescales, and (c) in combination. (d) Shared species responses to a single, high-frequency driver result in high species synchrony and unstable total biomass, whereas (e) opposite responses to a single, low-frequency driver result in compensatory dynamics and stable total biomass. The combination of these responses results in (f) synchrony at short timescales and compensatory dynamics 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

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), 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 (Chiba et al., 2012; Downing et al., 2008). Long-term climate drivers like the Pacific Decadal Oscillation may underlie the pattern of long-timescale compensatory dynamics we observed at Jasper Ridge (Figure 2a,b), where annual species often rebound quickly from frequent disturbance (such as gophers), leaving only a fleeting signature on patterns of community synchrony (Figure 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

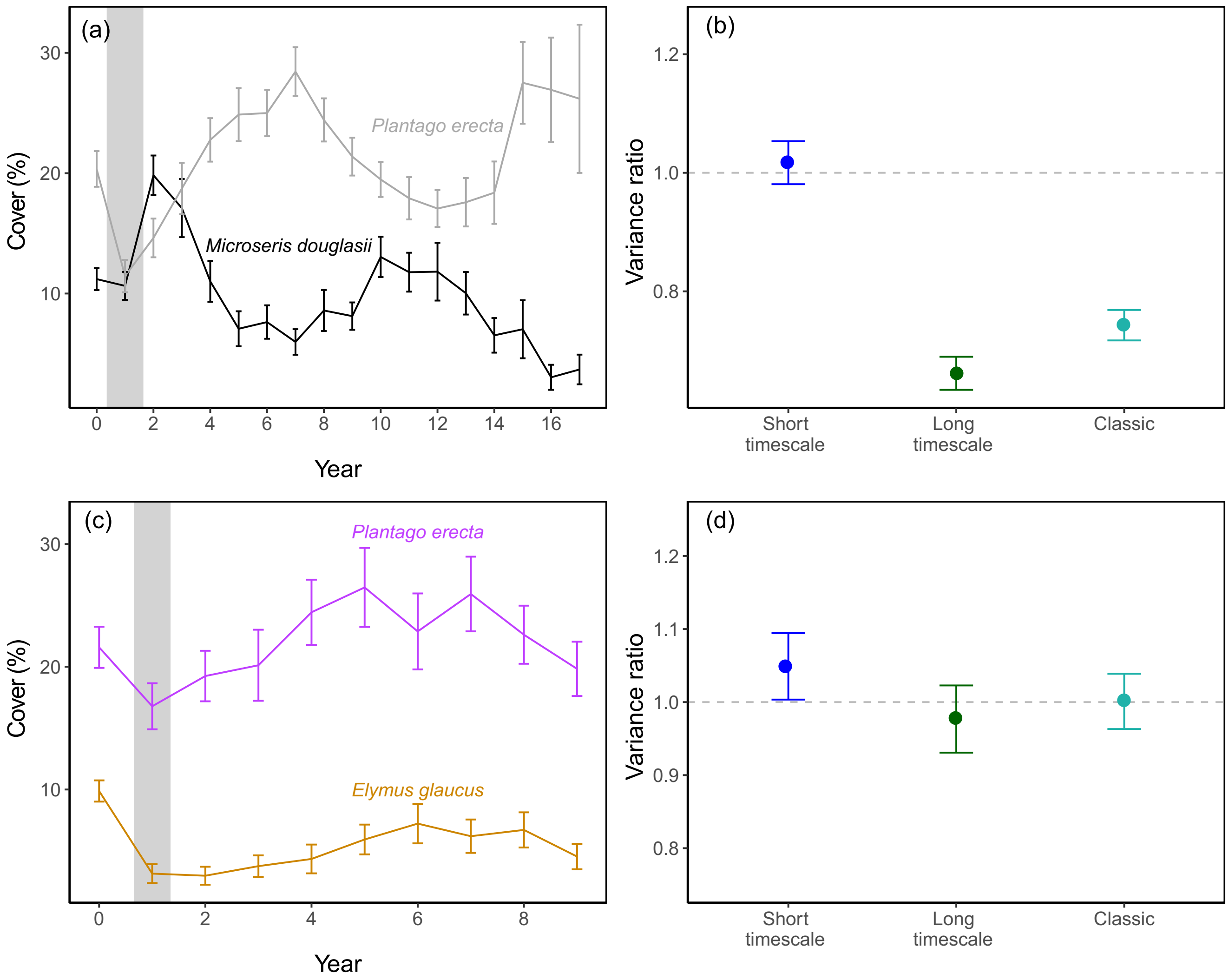

FIGURE 2 Applying the timescale-specific synchrony metric to a case study at Jasper Ridge, California, USA. (a) Averaged timeseries (± SE) of two native annual forbs *Plantago erecta* and *Microseris douglasii* before and after gopher disturbance (disturbance occurred during the gray bar at time 1). (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 ± SE). (c) Averaged timeseries (± SE) of a native annual forb *P. erecta* and native perennial grass *Elymus glaucus* before and after gopher disturbance (gray band). (d) Short timescale, long timescale, and classic variance ratio for *P. erecta* and *E. glaucus* communities (± SE)

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 compenasatory dynamics in communities (Till et al., 2019).

MECHANISM 2: DIFFERENCES IN SPECIES DEMOGRAPHIC RATES

Theoretical test

Species differ in their intrinsic growth rates, which can manifest in differences in the timescale of their response to an environmental driver (Grime, 1977). For example, a species that exhibits a lagged response to the environment may appear compensatory with respect to one that rapidly tracks the environment, even when both species share the same directional response to environmental conditions (Ives, 1995; Loreau & de Mazancourt, 2008). To explore this mechanism, 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; Figure 3a). We compared three different examples. In the first, both species' growth rates track environmental fluctuations (Figure 3b; $r_1 = r_2 = 1.00$). In the second, one species tracks the environment and the other exhibits a lagged response due to its slow intrinsic growth rate (Figure 3c; $r_1 = 1.00$, $r_2 = 0.15$). In the last, one species tracks the environment while the other exhibits dampening oscillatory responses to environmental fluctuations (Figure 3d; $r_1 = 1.00$, $r_2 = 1.8$).

Empirical test

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* (Appendix S1: Figure 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 subsetted the data following the protocol described for mechanism 1, analyzing 41 timeseries ranging from 10–35 years in length with 13 different starting years.

Results and discussion

The presence of species with different environmental response rates can reduce synchrony and even generate

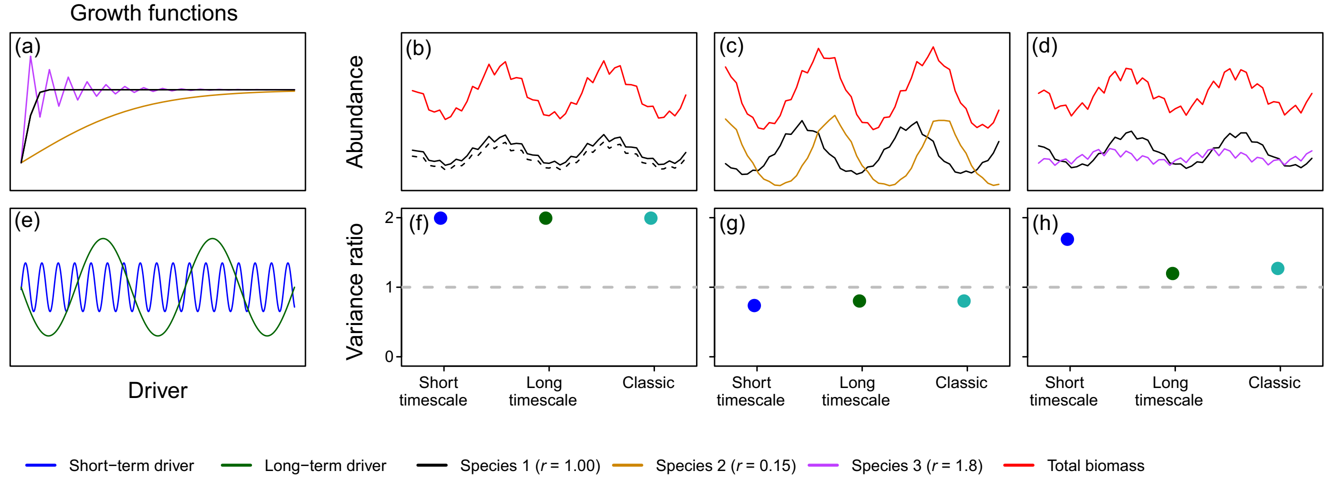

FIGURE 3 Differences in the growth rates of species can alter the timescale of synchrony, even when species share the same directional response to the environment. (a) Growth curves of species with different density-independent growth rates, r. The black species tracks the environment, the tan species 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

compensatory dynamics, even when all species share the same directional response to the environmental driver, as shown in our simulations (Figure 3b–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 compensatory dynamics across all timescales (Figure 3c,g). Across systems, differences in the timescale of species responses versus recovery times in poor environmental conditions may drive timescale-dependent patterns. We observed this at Jasper Ridge, in which both the annual and perennial species shared an initial, negative response to disturbance that enhanced short-timescale synchrony (Figure 2c,d). However, the perennial species had a slower recovery rate (i.e., a lagged response) that promoted compensatory dynamics at longer timescales by delaying its recovery relative to the annual species (Figure 2c,d). These difference in recovery rate caused timescale-specific dynamics, even when species responded similarly to underlying abiotic drivers, such as disturbance.

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 (Figure 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 (Figure 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 (Figure 3d,h). Consequently, internal dynamics generated by fast growth rates may also promote increased compensatory dynamics, particularly in communities structured by long-timescale drivers.

MECHANISM 3: DISPERSAL AND SPATIAL PROCESSES

Theoretical test

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. As such, we explore if the timescale of a driver affecting a single patch may still generate timescale specificity in other patches and at the landscape-scale via dispersal. To examine this mechanism, 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; Figure 4a,d). We quantified 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

$$N_{i,x}(t+1)= \overbrace{N_{i,x}(t)\exp\left[r_i\left(1-\frac{N_{i,x}(t)}{K_i}-\frac{\beta_{i,j}N_{j,x}(t)}{K_j}\right)+\varepsilon_{x,i}\mu_x(t)\right]}^{\text{local dynamics}} + \underbrace{dN_{i,y}(t)}_{\text{immigration}} - \overbrace{dN_{i,x}(t)}^{\text{emmigration}} \tag{4}$$

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

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 (Figure 4a,d). For example, in the absence of dispersal, synchrony in abundances was driven solely by within-patch dynamics, as expected (Figure 4b,e). Here, the timescale-specific variance ratios recover the classic variance ratio. However, at the larger landscape scale (Figure 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 toward the long-term drivers occurring in patch 2 (Figure 4i).

Dispersal between patches was detectable in a heterogeneous landscape using the timescale-specific metric, highlighting how spatial processes can impact our interpretation of temporal synchrony (Figure 4c,f,h). In this case, synchronous dynamics from short-term drivers

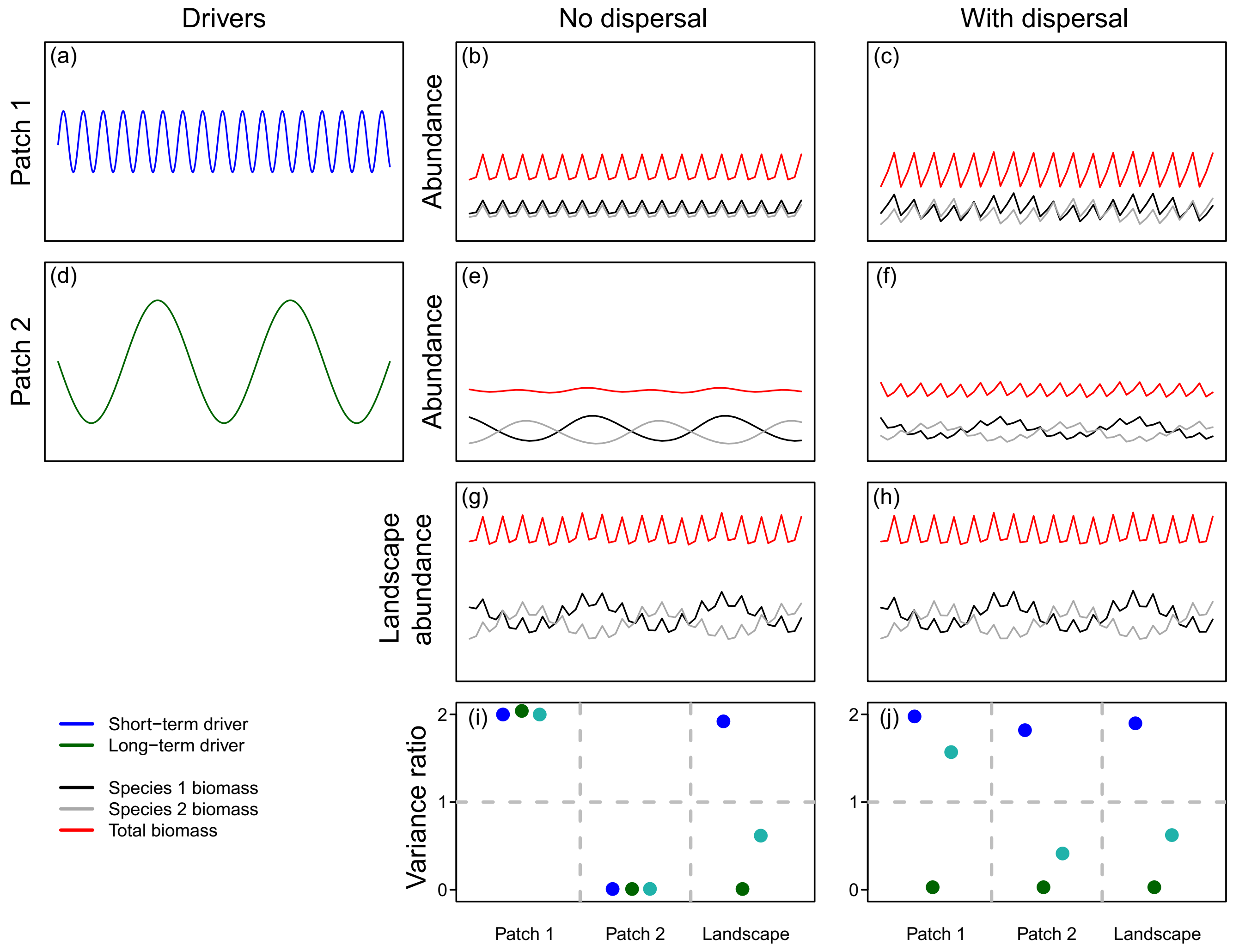

FIGURE 4 Spatial connectivity can alter local and landscape patterns of synchrony. (a) A short timescale driver operates in Patch 1 and (b, c) species dynamics in Patch 1 without (b) and with (c) dispersal from neighboring patch 2. Species 1 (black) and species 2 (gray) both respond to the local driver 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 (short in blue and long in green) and classic variance ratios (teal) 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

(in patch 1) and compensatory dynamics from long-term drivers (in patch 2) were evident in both patches (Figure 4i vs. j). Within patches, comparing the timescale-specific variance ratio with the classic ratio elucidated the focal patch; the classic variance ratio was synchronous in patch 1 but compensatory in patch 2 (Figure 4j). This shows how a temporally-focused method can detect spatial heterogeneity and dispersal effects when applied at different levels of spatial aggregation. In more complex scenarios, we expect these spatiotemporal 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 kernals and propagule density, yielding complex spatiotemporal dynamics (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 compensatory dynamics of species within patches, but also on trade-offs among patches (Wang et al., 2019; Wilcox et al., 2017). These among patch trade-offs can create compensatory flucutuations among patches, stabilizing overall landscape fluctuations. Our results provide additional insight into the role of dispersal and how connectivity between plots manifest as different synchrony and stability patterns depending on the scale of spatial aggregation.

MECHANISM 4: GLOBAL CHANGE AND NONSTATIONARITY

Theoretical test

Changes in synchronous and compensatory dynamics, and their timescale-specificity, 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; Radeloff et al., 2015). For example, a rise in climate extremes may increase synchronous dynamics if temperatures periodically surpass the physiological limits of all species in a community; while these thresholds may be present under stationary conditions, they are predicted to be increasingly important under global change (Somero, 2012). To examine these potential global change and threshold effects, for our final mechanism, we modeled an individual driver that oscillated on both short-term and long-term timescale (Figure 5a). To do so, we summed the effects of short- and long-term fluctuations of a single driver (Figure 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 (Figure 5c), and (3) under a new environmental steady state (e_{new}, where $e_{\text{new}} = e_{\text{historic}} + 0.5$. Figure 5d; 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

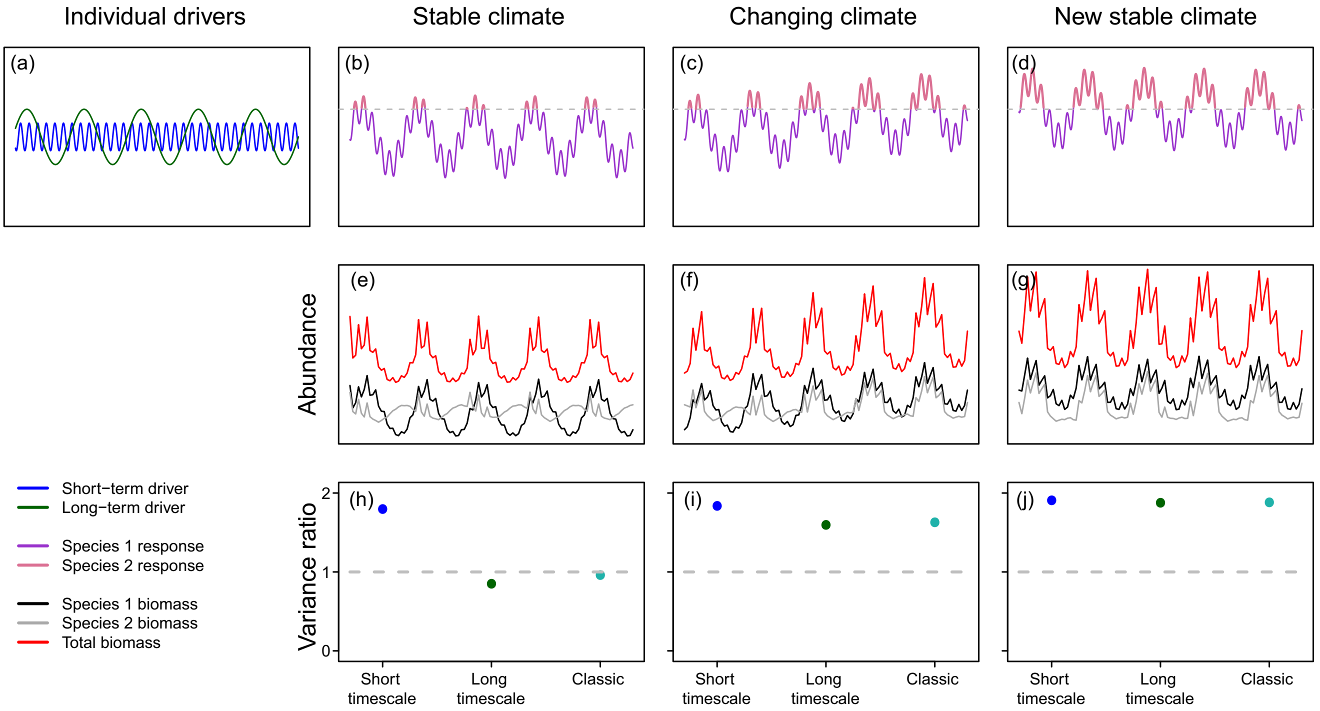

FIGURE 5 Climate change has the potential to alter the strength and timescale of synchrony. (a) A climate driver such as temperature may vary over different timescales, often with both a low frequency (green) and high frequency component (blue). (b–d) The overall environmental driver and species' sensitivities 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 gray line. (e–g) The abundance of species 1 (black), species 2 (gray), and their aggregate abundance (red) in response to the above environmental driver. (h–j) Variance ratios for the above communities. With stable climate (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)

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, 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 strong compensatory dynamics on long timescales and weaker compensatory dynamics with the classic variance ratio (Figure 5b,e,h). This occurred even though species responded in the same manner to environmental fluctuations. Compensatory dynamics driven by competition overshadowed synchronizing effects of a shared environmental driver, as species 2 responded to the environment only relatively rarely. In contrast, global change increased synchrony at all timescales, with dynamics intermediate between those observed under the historic versus new environment (Figure 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 (Figure 5d,g,j).

Our model results hint 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 & Liebhold, 2016), and Greenland caribou (Post & Forchhammer, 2004). In contrast, however, climate-induced shifts in phenology can disrupt synchrony in plant–herbivore (Hunter & Elkinton, 2000; Tikkanen & Julkunen-Tiitto, 2003), predator–prey (Logan et al., 2006; Sanford, 1999), and host–parasitoid interactions (Hance et al., 2007; Klapwijk et al., 2010; Visser & Holleman, 2001), causing increased extinction risk for codependent species. Our model suggests that, as for single-species populations, synchrony within communities may increase with climate change. The application of timescale-specific methods in empirical communities, including Fourier transformations as employed here, and wavelet analyses when longer timeseries are available, provides a pathway for assessing whether natural communities match theoretical expectations.

FUTURE DIRECTIONS

Our findings suggest promising next steps for both theoretical studies as well as challenges for empirical research. A promising avenue for future theoretical work is to investigate the interaction between different mechanisms. For example, resource fluctuations may directly alter the timescale of synchrony, but resource availability may also alter the growth rate of different species, creating a scenario in which mechanisms 1 and 2 vary interactively (Benton et al., 2001). In addition, analyses of species fluctuations commonly focus on either phenological, population, or community dynamics, yet phenological and population synchrony can impact community dynamics and vice versa (Ripa et al., 1998). Linking these different forms of synchrony could increase theoretical understanding of synchronous and compensatory dynamics across spatial as well as temporal scales. Finally, demographic and environmental stochasticity may also alter the signature of synchronous versus compensatory dynamics (Loreau & de Mazancourt, 2008, 2013), which could inform both future theoretical and empirical studies (Shoemaker et al., 2020). A key challenge for empirical studies will be to extend a timescale-specific approach to mechanistically understand dynamics in diverse as well as pairwise communities. A second key empirical challenge will be to design experiments that can disentangle mechanisms that operate on long versus short timescales, as our analyses indicate that long-term drivers consistently had a stronger effect on overall dynamics.

CONCLUSIONS

Understanding patterns of synchronous versus compensatory dynamics remains an ongoing challenge in community ecology. Our results demonstrate how multiple mechanisms, including environmental drivers, species demography, and dispersal can shape the timescale of synchronous versus compensatory dynamics. To date, most empirical assessments of community synchrony, particularly in terrestrial systems, have not accounted for timescale specificity. Building from recent methodological advances that allow timescale specificity to be determined with shorter timeseries of abundances (Zhao et al., 2020), our work points to specific mechanisms of community dynamics that, if characterized, can help us better understand synchrony and stability patterns across timescales.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Lauren M. Hallett and Lauren G. Shoemaker contributed equally. Lauren G. Shoemaker, Lauren M. Hallett, and Katharine N. Suding developed the manuscript framing, Lauren G. Shoemaker, Lauren M. Hallett, Lei Zhao, Daniel C. Reuman, Shaopeng Wang, and Katharine N. Suding helped with model construction, Lauren G. Shoemaker coded the models, Lauren M. Hallett, and Richard J. Hobbs collected Jasper Ridge data, Lauren G. Shoemaker, Lauren M. Hallett, Daniel C. Reuman, Kathryn L. Cottingham, and Katharine N. Suding structured the manuscript, and Lauren G. Shoemaker and Lauren M. Hallett wrote the manuscript. The manuscript was developed through conversations with the entire author list and all authors contributed to manuscript edits.

DATA AVAILABILITY STATEMENT

All data and code is provided at https://doi.org/10.5281/zenodo.5676439.

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