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

| 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 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 towards 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.

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Running Head: Synchrony across timescales

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1 Abstract

2 Synchronous dynamics (fluctuations that occur in unison) are universal phenomena with
3 widespread implications for ecological stability. Synchronous dynamics can amplify the
4 destabilizing effect of environmental variability on ecosystem functions such as productivity,
5 whereas the inverse, compensatory dynamics, can stabilize function. Here we combine simu-
6 lation and empirical analyses to elucidate mechanisms that underlie patterns of synchronous
7 versus compensatory dynamics. In both simulated and empirical communities we show that
8 synchronous and compensatory dynamics are not mutually exclusive but instead can vary
9 by timescale. Our simulations identify multiple mechanisms that can generate timescale-
10 specific patterns, including different environmental drivers, diverse life histories, dispersal,
11 and non-stationary dynamics. We find that traditional metrics for quantifying synchronous
12 dynamics are often biased towards long-term drivers and may miss the importance of short-
13 term drivers. Our findings indicate key mechanisms to consider when assessing synchronous
14 versus compensatory dynamics and our approach provides a pathway for disentangling these
15 dynamics in natural systems.

16 *Keywords:* community dynamics, compensatory dynamics, disturbance, environmental fluc-
17 tuations, life history, metacommunity, stability, variance ratio

18 Introduction

19 The extent to which communities of interspecific competitors exhibit synchronous versus
20 compensatory temporal fluctuations and the underlying mechanisms driving fluctuations
21 have been of fundamental interest in ecology for decades (MacArthur, 1955). Community
22 synchrony and its alternative pattern, compensatory dynamics, describe how the dynamics
23 of species aggregate to influence community stability through time. Synchronous fluctua-
24 tions of species' abundances reduce stability and often arise when species respond similarly

25 to environmental fluctuations (Ives, 1995; Loreau and de Mazancourt, 2013), or through

26 facilitative interactions between species. In contrast, compensatory dynamics stabilize over-

27 all community properties, as species fluctuate in a negatively correlated manner (Peterson,

28 1975) often due to competitive interactions or opposing responses to environmental drivers

29 (Ives, 1995; Gonzalez and Loreau, 2009; Loreau and de Mazancourt, 2013). Quantifying the

30 degree of synchronous versus compensatory dynamics has emerged as a key component of

31 several recent advances in community ecology, such as how functional diversity influences

32 resilience and how environmental change may impact coexistence (Lindegren et al., 2016;

33 Hallett et al., 2019).

34   Synchronous and compensatory dynamics have often been considered mutually exclusive,

35 as they reflect opposite correlations among abundances (e.g. Houlahan et al. 2007); however,

36 there is a growing recognition that synchronous and compensatory dynamics can instead be

37 timescale and spatial scale dependent (Downing et al., 2008; Vasseur et al., 2014; Lasky

38 et al., 2016). For instance, species may be synchronous at one timescale and compensatory

39 at other timescales (Downing et al., 2008; Vasseur et al., 2014), they may be synchronous

40 in certain life history stages but asynchronous in others (Lasky et al., 2016), and they

41 may be synchronous under some environmental conditions and asynchronous in others (Xu

42 et al., 2015). A wide range of processes can influence species dynamics and correlations

43 in species fluctuations, including environmental variation (Allstadt et al., 2015; Tredennick

44 et al., 2017), biotic interactions (Pedersen et al., 2016), variability in species demographic

45 rates (Jucker et al., 2014), and dispersal (Wang et al., 2019). While all of these processes

46 may affect synchronous versus compensatory dynamics, many have not been explored in a

47 timescale-specific manner.

48   Linking patterns of timescale-specificity to mechanisms is essential for predicting stability

49 patterns under global change. For example, multiple environmental drivers operating at dif-

50 ferent timescales are one potential mechanism explaining timescale-specificity (Frost et al.,

51 1995; Sheppard et al., 2016). If this is a primary mechanism, then shifts in the timescale

52 of dynamics would reflect shifts in the timescale of each driver. Alternatively, different life

53 history strategies, in which some species respond quickly to the environment while others

54 exhibit a lagged response, are another mechanism that could drive timescale-specific dy-

55 namics (Loreau and de Mazancourt, 2013). If this the primary mechanism, then shifts in

56 the timescale of environmental drivers may have a nonlinear effect on synchronous versus

57 compensatory dynamics, depending on whether lagged species have sufficient time to recover

58 (Benton et al., 2001). These primary effects may be further mediated by species interac-

59 tions, causing emergent fluctuations to depend not only on underlying environmental drivers

60 or species demographic rates, but also on the abundances of other species in the community

61 (Gonzalez and Loreau, 2009; Loreau and de Mazancourt, 2013).

62 While there is a long history in population ecology of assessing the timescale of oscillations

63 for single-species abundance patterns (Sheppard et al., 2016), and even how species inter-

64 actions may modulate these oscillations (Ives, 1995; Ripa et al., 1998), at the community

65 level many fundamental studies of synchronous versus compensatory dynamics have used

66 simple covariance and correlation methods that aggregate across timescale (e.g., Houlahan

67 et al. 2007; de Mazancourt et al. 2013; Grman et al. 2010; Gross et al. 2014; Hallett et al.

68 2014). However, when examining community dynamics using a timescale-specific methodol-

69 ogy, multiple signals of differing periodicity can be identified in a single timeseries (Downing

70 et al., 2008; Vasseur et al., 2014). Advances in scale-specific metrics allow us to gain a new

71 understanding of synchronous versus compensatory dynamics (Vasseur et al., 2014; Vasseur

72 and Gaedke, 2007; Downing et al., 2008; Keitt and Fischer, 2006; Brown et al., 2016), and

73 new and less data-intensive methodologies are opening up our ability to empirically char-

74 acterize timescale-specificity in terrestrial and aquatic systems (Zhao et al., 2020). These

75 methodologies, coupled with growing open-access and long-term monitoring data, have the

76 potential to expand our understanding of temporal fluctuations and their drivers across a

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77 wide range of ecosystems, with implications for connecting patterns of synchrony and sta-
78 bility to underlying mechanisms.

79 Here we use simulations and empirical analyses to examine four mechanisms that can
80 underlie timescale-specificity of synchronous and compensatory dynamics. We first examine
81 timescale-specific dynamics with multiple underlying environmental drivers of species' abun-
82 dances, where environmental fluctuations occur at different timescales. Second, we assess
83 a biotic mechanism in which species share a response to drivers but differ in their demo-
84 graphic rates. Third, we assess a spatial mechanism in which different timescale dynamics
85 occur in local patches connected via dispersal, and we examine how they aggregate to affect
86 larger-scale metacommunity dynamics. Finally, we consider a nonstationarity mechanism in
87 which global change may alter the timescale-specific signature of synchronous and compen-
88 satory dynamics coupled with species-specific threshold responses. We focus our analyses on
89 pairwise interactions to mechanistically and directly examine how differences in species' en-
90 vironmental responses and demography manifest across timescales. Our approach identifies
91 key ecological factors that may cause synchronous and compensatory dynamics to oper-
92 ate at different timescales, while providing a path forward to parsing these dynamics and
93 understanding their importance for stability in natural systems.

94 A timescale-specific variance ratio

95 Studies of synchronous and compensatory dynamics in community ecology have classically
96 focused on their implications for ecosystem stability (Gonzalez and Loreau, 2009), with
97 many studies approaching synchronous and compensatory dynamics phenomenologically,
98 using covariance methods such as the variance ratio and related metrics (Peterson, 1975;
99 Schluter, 1984; Klug et al., 2000; Loreau and de Mazancourt, 2008). For instance, the classic
100 variance ratio, denoted by φ, compares covariances (cov) among species over time to the
101 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:

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

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 (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:

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

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

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123 that $\sum_\sigma w(\sigma)\varphi_{\text{ts}}(\sigma) = \varphi$ (Zhao et al., 2020). The different timescales that can be assessed

124 depend on the overall time series length, T, ranging from a lower bound of $\sigma = T/(T-1)$ to

125 an upper bound of $\sigma = T$. For annually sampled data, previous authors have adopted the

126 practice of computing weighted averages of the $\varphi_{\text{ts}}(\sigma)$ over "short" ($\sigma < 4$ years) and "long"

127 ($\sigma \geq 4$ years) timescale bands (Sheppard et al., 2016; Zhao et al., 2020). We follow this

128 convention for all of our analyses below for ease of interpretation, but note that dynamics

129 on individual timescales can alternatively be studied. The threshold of $\sigma = 4$ time-steps

130 (sampling intervals) for differentiating short and long timescales was chosen because $\sigma = 4$

131 corresponds to a frequency which is half the maximum frequency that can be assessed (one

132 cycle every two time points). Additionally, $\sigma = 4$ is the boundary between persistent and

133 anti-persistent dynamics for sinusoidal oscillations, as measured with a lag-1 autocorrelation

134 (Sheppard et al., 2016; Zhao et al., 2020).

Theoretical model overview

136 We applied the timescale-specific variance ratio to output from theoretical models and an

137 empirical case study. All theoretical scenarios are based upon a model of population and

138 community dynamics that uses a modified version of the model of Loreau & de Mazancourt

139 (2013), adapted for multiple environmental drivers:

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

140 $N_i(t)$ is the abundance of species i at time t, r is the intrinsic (density-independent) growth

141 rate, K is the carrying capacity, and $\beta_{i,j}$ is the competition coefficient of species j on i.

142 We incorporate two environmental drivers, creating environmental fluctuations of varying

143 timescales and amplitudes where $\mu_e(t) = a_e\sin(b_e t + c_e)$ for environmental conditions $e = 1, 2$.

144 Environmental fluctuations vary based on a sinusoidal function (sin), where a_e denotes the

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145 amplitude, b_e controls the period, and c_e denotes the phase shift. Species' sensitivities to

146 environmental fluctuations are defined via $\epsilon_{e,i}$. We modify the above base-line model and

147 its parameters to examine each of our four mechanisms. For each, we run the model for 100

148 timesteps, with the first 50 discarded to remove any potential effects of initial conditions, and

149 the last 50 timesteps included in our synchrony analyses. We set species' initial abundances

150 to their carrying capacities, K_1 and K_2. All analyses have complete code provided at `https:`

151 `//github.com/lash1937/synchrony_timescales`.

Empirical case study

153 To test mechanisms 1 and 2 in an empirical case study, we applied the timescale-specific vari-

154 ance ratio to long-term data from a California serpentine grassland (Fig. S1a-c). California

155 serpentine grasslands are dominated by annual forbs and support native perennial grasses.

156 They are characterized by a highly variable climate; at our site, Jasper Ridge in San Mateo

157 County, California, USA, annual rainfall ranges from 200 to 1200 mm (Hallett et al., 2018).

158 Climate patterns are influenced by long-term cycles, including the El Niño Southern Oscilla-

159 tion and the Pacific Decadal Oscillation, and species exhibit differential responses to wet and

160 dry years (Hobbs et al., 2007; Hallett et al., 2018). Within the site, gopher activity creates

161 disturbances that remove all of the vegetation in small patches across the landscape (Hobbs

162 and Mooney, 1985; Hobbs et al., 2007) (Fig. S1d). We (RJH and LMH) have collected plant

163 species composition data and gopher disturbance data in 216 0.5 m x 0.5 m quadrats annu-

164 ally for 37 years (1983-2019) (see Hobbs et al. 2007 for sampling details). Using these data,

165 we focused on species contrasts that we hypothesized would exhibit timescale-specificity via

166 abiotic and biotic mechanisms.

Mechanism 1: Multiple environmental drivers

168 **Theoretical Test:** Environmental variability is a key driver of abundance fluctuations,

169 and different environmental drivers may affect species in similar or opposing manners (Ives,

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170 1995; Downing et al., 2008; Keitt and Fischer, 2006; Zhao et al., 2020). The combination

171 of different environmental drivers operating a different timescales may generate a timescale-

172 specific pattern of synchronous versus compensatory dynamics (Frost et al., 1995). To assess

173 this mechanism we applied the timescale-specific variance ratio to the simulated two-species

174 community influenced by two drivers: a short-timescale driver to which species had a shared

175 response, and a long-timescale driver to which species had opposing responses (drivers repre-

176 sented in Fig. 1a-c, individual species responses in Fig. 1d, e; model parameters in Appendix

177 S1).

178 **Empirical Test:** To test the empirical implications of different environmental drivers on

179 timescale-specific synchronous and compensatory dynamics, we focused on two species of

180 annual forbs that exhibit highly variable abundances over time at Jasper Ridge, California:

181 *Plantago erecta* and *Microseris douglasii* (Fig. S1e, f). We hypothesized that these species

182 would share a similar, short-timescale response to gopher disturbance (initially negative

183 but rebounding quickly) but contrasting long-timescale responses to climate (*P. erecta* does

184 better in dry years and *M. douglasii* has no discernible response) (Hobbs et al., 2007; Hallett

185 et al., 2018). To test this, we filtered the full dataset to include only years and quadrats in

186 which both species were initially present at moderate to high abundances (> 3 percent cover

187 in year 0), the quadrat was disturbed in year 1, and was undisturbed through at least year

188 9. We set this minimum length to ensure timeseries of at least 10 years (as recommended by

189 Zhao et al. 2020), although all retained timeseries were longer (ranging from 17 to 35 years).

190 This process resulted in 85 timeseries with 19 different starting years. We then applied the

191 timescale-specific variance ratio to each timeseries.

192 **Results and discussion:** Our simulated community exhibited highly synchronous dy-

193 namics at short timescale and highly compensatory dynamics at long timescales, and this

194 expected pattern was easily discernable using the timescale-specific variance ratio (Fig. 1f,

195 g). In comparison, the effect of the short-timescale driver was largely masked with the classic

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196 variance ratio (Fig. 1g). Our empirical case study at Jasper Ridge mirrored our theoret-

197 ical results, such that species were synchronous on short timescales and compensatory on

198 long timescales. Further, the classic variance ratio primarily captured the longer timescale

199 dynamics (Fig. 2).

200   There are both statistical and ecological explanations for the striking importance of long-

201 timescale dynamics for the classic variance ratio. Statistically, the relationship between the

202 classic variance ratio and the timescale-specific decomposition depends on the length of the

203 timeseries and on differences in the amplitude of short-term versus long-term environmental

204 fluctuations (a_e) and species' sensitivities (ϵ). As such, the contribution of long-term dynam-

205 ics to the variance ratio increases with both timeseries length and the amplitude of long-term

206 drivers. As all timeseries here are relatively long (i.e. 17 years or greater), the classic vari-

207 ance ratio mirrors the long timescale signal. Ecologically, long-timescale drivers may most

208 strongly influence patterns of community synchrony for several reason. First, long-timescale

209 climate drivers, such as the Pacific Decadal Oscillation and the North Atlantic Oscillation,

210 are more regular than short interannual variation in weather patterns, and may therefore

211 be more detectable in their effect on community structure (Downing et al., 2008; Chiba

212 et al., 2012). Long-term climate drivers like the Pacific Decadal Oscillation may underlie

213 the pattern of long-timescale compensatory dynamics we observed at Jasper Ridge (Fig. 2a,

214 b), where annual species often rebound quickly from frequent disturbance (such as gophers),

215 leaving only a fleeting signature on patterns of community synchrony (Fig. 2a, b). Second,

216 long-timescale fluctuations may reflect the differing role that rare versus common events

217 have on populations. Daily temperature fluctuations and summer heat waves, for example,

218 can both influence population dynamics. The effect of daily temperature fluctuations on

219 populations are typically felt over short timescales, whereas high mortality due to a rare

220 and extreme heat wave may have a long-lasting signal on population dynamics (Lindström

221 et al., 2012). While the effects of the timescales of environmental fluctuation and disturbance

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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 and 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) (Fig. 3a). We compared three different examples. In the first, both species' growth rates track environmental fluctuations (Fig. 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 (Fig. 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 (Fig. 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* (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 subsetted the data following the protocol described for mechanism

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248 1, analyzing 41 timeseries ranging from 10-35 years in length with 13 different starting years.

249 **Results and discussion:** The presence of species with different environmental response

250 rates can reduce synchrony and even generate compensatory dynamics, even when all species

251 share the same directional response to the environmental driver, as shown in our simulations

252 (Fig. 3b, c, d). The compensatory effect of lagged responses was strongest when the timescale

253 of the lag matched the timescale of the environmental driver. For example, the presence of a

254 species with a slow growth rate generated compensatory dynamics across all timescales (Fig.

255 3c, g). Across systems, differences in the timescale of species responses versus recovery times

256 to poor environmental conditions may drive timescale-dependent patterns. We observed this

257 at Jasper Ridge, in which both the annual and perennial species shared an initial, negative

258 response to disturbance that enhanced short-timescale synchrony (Fig. 2c, d). However,

259 the perennial species had a slower recovery rate (i.e., a lagged response) that promoted

260 compensatory dynamics at longer timescales by delaying its recovery relative to the annual

261 species (Fig. 2c, d). These difference in recovery rate caused timescale-specific dynamics,

262 even when species responded similarly to underlying abiotic drivers, such as disturbance.

263   Endogenous population cycles, often induced by fast growth rates, may decouple some

264 species' fluctuations from the environment (Haynes et al., 2019). As such, species cycling

265 at different rates will be less synchronous than predicted based solely on environmental

266 response, although this effect is timescale-dependent (Fig. 3d, h). In our simulation, a

267 species with a fast growth rate more closely tracked short-timescale environment fluctuations,

268 reflecting the fact that environmental conditions changed before the species internal dynamics

269 dominated its population cycles. As a result, the fast-growing species was synchronous with

270 a species whose growth tracked the environment at short timescales (Fig. 3d, h). At long

271 timescales, however, the population cycles of the fast-growing species became increasingly

272 decoupled from the environmental driver, and correspondingly, the other species (Fig. 3d, h).

273 Consequently, internal dynamics generated by fast growth rates may also promote increased

274 compensatory dynamics, particularly in communities structured by long-timescale drivers.

Mechanism 3: Dispersal and spatial processes

276 **Theoretical Test:** Species interactions and responses to environmental fluctuations do not
277 occur in isolation, but rather local-scale dynamics are embedded in a larger spatial context,
278 where communities are connected via dispersal. As such, we explore if the timescale of a
279 driver affecting a single patch may still generate timescale-specificity in other patches and
280 at the landscape-scale via dispersal. To examine this mechanism, we modified our general
281 model of species' abundances through time (Eqn. 3) to create a two-patch metacommunity,
282 where patches exhibited different underlying timescales of environmental fluctuations. In
283 our model, species responded similarly to short-term fluctuations that occurred in patch 1
284 (denoted by the subscript x), but in opposing manners to long-term fluctuations in patch 2
285 (subscript y) (Fig. 4a, d). We quantified the timescale-dependent signature of dispersal (d)
286 by comparing cases without ($d = 0.0$) versus with ($d = 0.4$) strong dispersal between patches
287 (parameters in Appendix S1). Abundances of species i within patches x and y followed:

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

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

288 **Results and discussion:** Applying the timescale-specific variance ratio at multiple spatial
289 scales elucidated the interplay between local and regional processes in landscapes with spatial
290 heterogeneity (Fig. 4a, d). For example, in the absence of dispersal, synchrony in abundances
291 was driven solely by within-patch dynamics, as expected (Fig. 4b, e). Here, the timescale-
292 specific variance ratios recover the classic variance ratio. However, at the larger landscape
293 scale (Fig. 4g), the signatures of each patch's environmental fluctuations were detected with
294 the timescale-specific variance ratio, while the classic variance ratio was again biased towards

295   the long-term drivers occurring in patch 2 (Fig. 4i).

296   Dispersal between patches was detectable in heterogeneous landscape using the timescale-

297   specific metric, highlighting how spatial processes can impact our interpretation of temporal

298   synchrony (Fig. 4c, f, h). In this case, synchronous dynamics from short-term drivers (in

299   patch 1) and compensatory dynamics from long-term drivers (in patch 2) were evident in

300   both patches (Fig. 4i vs. j). Within patches, comparing the timescale-specific variance ratio

301   with the classic ratio elucidated the focal patch; the classic variance ratio was synchronous

302   in patch 1 but compensatory in patch 2 (Fig. 4j). This shows how a temporally-focused

303   method can detect spatial heterogeneity and dispersal effects when applied at different levels

304   of spatial aggregation. In more complex scenarios, we expect these spatio-temporal patterns

305   to also yield signatures in the timescale-specific variance ratio. For example, the order in

306   which species arrive can alter long-term community composition and patterns in synchrony

307   (Fukami et al., 2016). Furthermore, arrival itself can depend on fluctuations in underlying

308   environmental conditions that alter species' dispersal kernals and propagule density, yielding

309   complex spatio-temporal dynamics (Sullivan et al., 2018).

310   At larger spatial scales, spatial patterning and interdependence between patches plays

311   a key role in determining stability. Here we compare patches with different underlying

312   environmental drivers. However, previous work highlights how overall landscape stability

313   depends not only on trade-offs and compensatory dynamics of species within patches, but

314   also on trade-offs among patches (Wilcox et al., 2017; Wang et al., 2019). These among

315   patch trade-offs can create compensatory flucutuations among patches, stabilizing overall

316   landscape fluctuations. Our results provide additional insight into the role of dispersal

317   and how connectivity between plots manifest as different synchrony and stability patterns

318   depending on the scale of spatial aggregation.

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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 (Fig. 5a). To do so, we summed the effects of short- and long-term fluctuations of 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) (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, 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 competi-

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tion and species-specific environmental thresholds yielded strong compensatory dynamics on long timescales and weaker compensatory dynamics with the classic variance ratio (Fig. 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 (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 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 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 timescale-specific methods in empirical communities—including

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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 pheno- logical, 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 dy- namics across spatial as well as temporal scales. Finally, demographic and environmental stochasticity may also alter the signature of synchronous versus compensatory dynamics (Loreau and 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 ex- periments 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 community ecology. Our results demonstrate how multiple mechanisms, including

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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.

Acknowledgements

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567 **_Figure 1:_** Environmental drivers operating on different timescales can create timescale-
568 specific synchronous and compensatory dynamics. Environmental drivers may operate over
569 (a) short timescales, (b) long timescales and (c) in combination. (d) Shared species re-
570 sponses to a single, high-frequency driver results in high species synchrony and unstable
571 total biomass, whereas (e) opposite responses to a single, low-frequency driver results in
572 compensatory dynamics and stable total biomass. The combination of these responses re-
573 sults in (f) synchrony at short timescales and compensatory dynamics at long timescales.
574 As a result, (g) a timescale-specific variance ratio differentiates these dynamics, whereas the
575 classic variance ratio does not reflect short timescale synchrony.

576 **_Figure 2:_** Applying the timescale-specific synchrony metric to a case study at Jasper Ridge,
577 California, USA (a) Averaged timeseries ($\pm$ SE) of two native annual forbs _Plantago erecta_
578 and _Microseris douglasii_ before and after gopher disturbance (disturbance occurred during
579 the grey bar at time 1). (b) Short timescale, long timescale, and classic variance ratio for
580 _P. erecta_ and _M. douglasii_ communities (average value of the metric after it was calculated
581 on individual timeseries $\pm$ SE). (c) Averaged timeseries ($\pm$ SE) of a native annual forb _P._
582 _erecta_ and native perennial grass _Elymus glaucus_ before and after gopher disturbance (grey
583 band). (d) Short timescale, long timescale, and classic variance ratio for _P. erecta_ and _E._
584 _glaucus_ communities ($\pm$ SE).

585 **_Figure 3:_** Differences in the growth rates of species can alter the timescale of synchrony,
586 even when species share the same directional response to the environment. (a) Growth
587 curves of species with different density-independent growth rates. The black species tracks
588 the environment, the tan species exhibits a lagged response, and the pink species responds
589 rapidly enough to create dampened internal oscillations. (b-d) Population dynamics among
590 species that share directional responses to (e) two timescale-specific environmental drivers.
591 (f-h) The resulting timescale-specific and classic variance ratios.

592 **_Figure 4:_** Spatial connectivity can alter local and landscape patterns in synchrony. (a) A

25

593 short time scale driver operates in Patch 1 and (b,c) species dynamics in Patch 1 without (b)

594 and with (c) dispersal from neighboring patch 2. Species 1 (black) and species 2 (grey) both

595 respond to the local driver in similar ways. (d) A long timescale driver operates in Patch 2 and

596 (e,f) species dynamics in Patch 2 without (e) and with (f) dispersal. (g, h) Aggregate species

597 and total biomass dynamics at the landscape scale without (g) and with (h) dispersal. (i-j)

598 Timescale-specific (short in blue and long in green) and classic variance ratios (teal) for the

599 above communities. (i) Without dispersal, local drivers dominate, leading to synchronous

600 dynamics in patch 1 and compensatory dynamics in patch 2. Within patches the classic

601 variance ratio tracks these dynamics, and at the landscape scale it reflects an aggregate of

602 the two patches. (j) With reciprocal dispersal, landscape level synchrony remains the same

603 but patch level dynamics vary, with the classic variance ratio representative of the dynamics

604 of the focal patch.

605 *Figure 5:* Climate change has the potential to alter the strength and timescale of synchrony.

606 (a) A climate driver such as temperature may vary over different timescales, often with both a

607 low frequency (green) and high frequency component (blue). (b-d) The overall environmental

608 driver and species' sensitivities under a stable, changing, and altered climate. Species 1

609 responds to all variability (red and purple), whereas species 2 only responds to the driver

610 above a threshold level (red). The environmental threshold is depicted by the dashed grey

611 line. (e-g) The abundance of species 1 (black), species 2 (grey) and their aggregate abundance

612 (red) in response to the above environmental driver. (h-j) Variance ratios for the above

613 communities. With stable climate (b, h), species have different threshold responses, yielding

614 compensatory dynamics on long timescales. Species becomes increasingly synchronized as

615 climate means increase (c, i), causing species 2 to respond to the driver more frequently.

616 Finally, under a stable climate with an elevated mean, both species become synchronized by
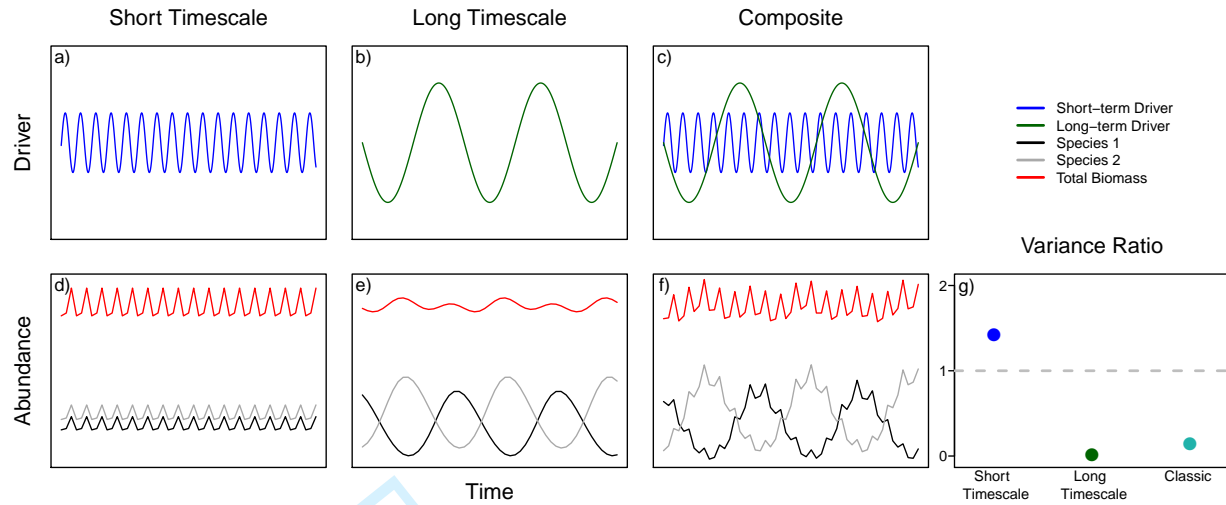
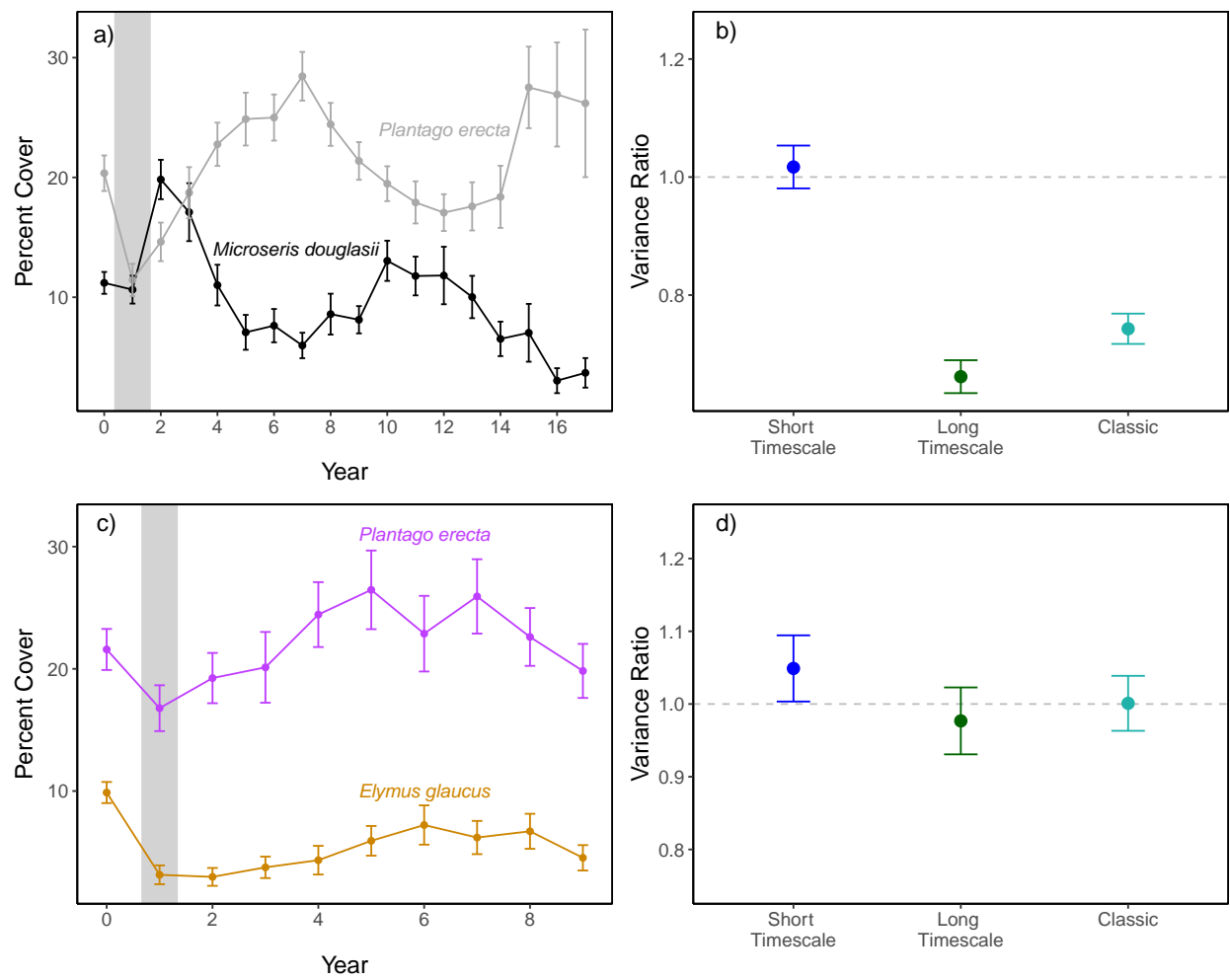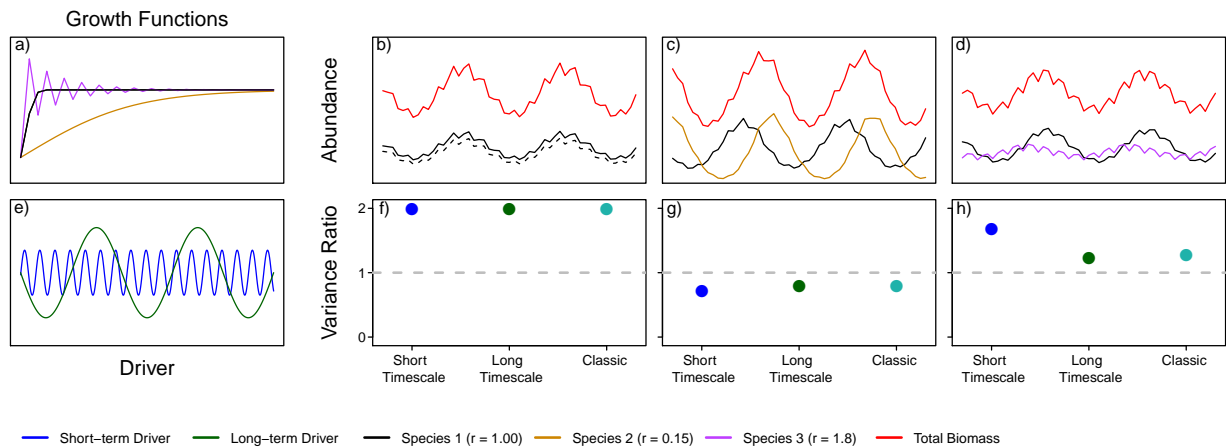617 environmental variability across timescales (d, j).
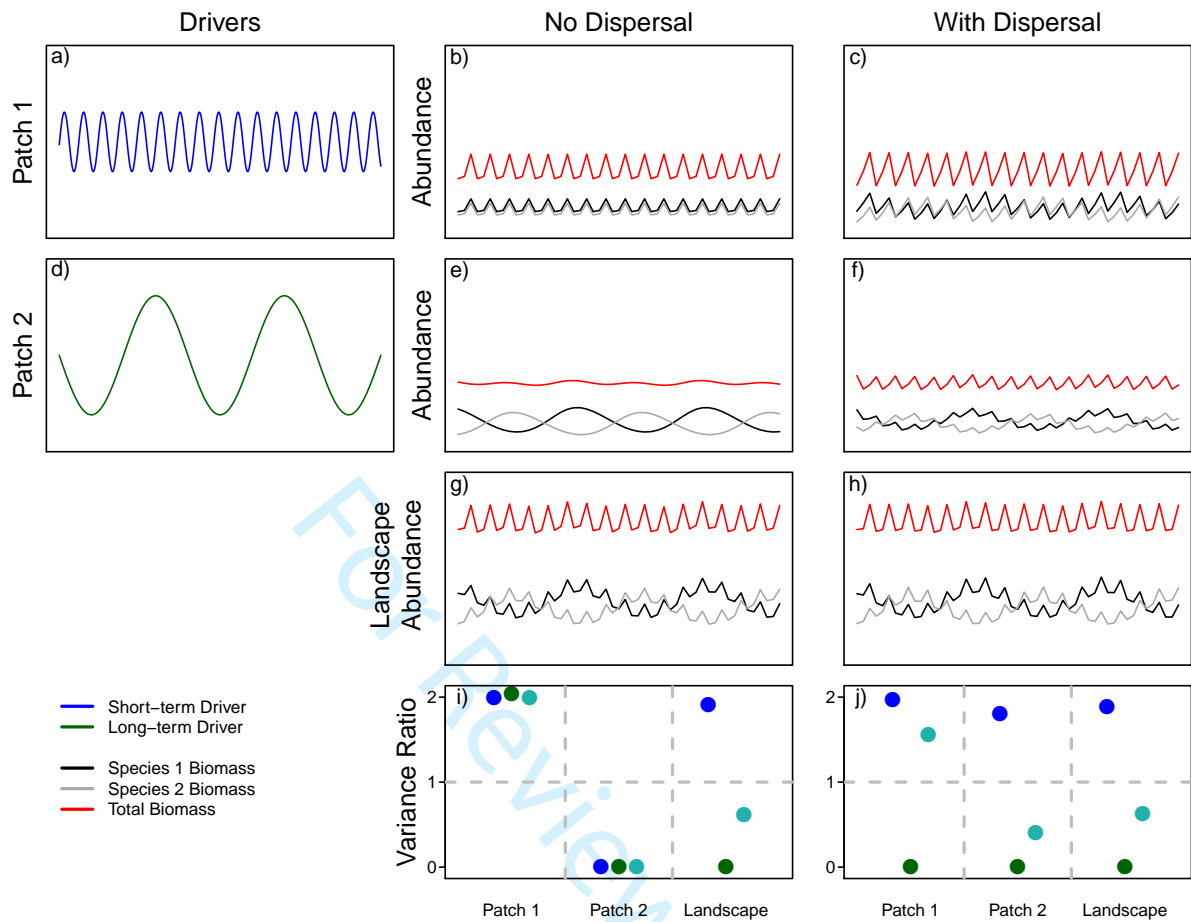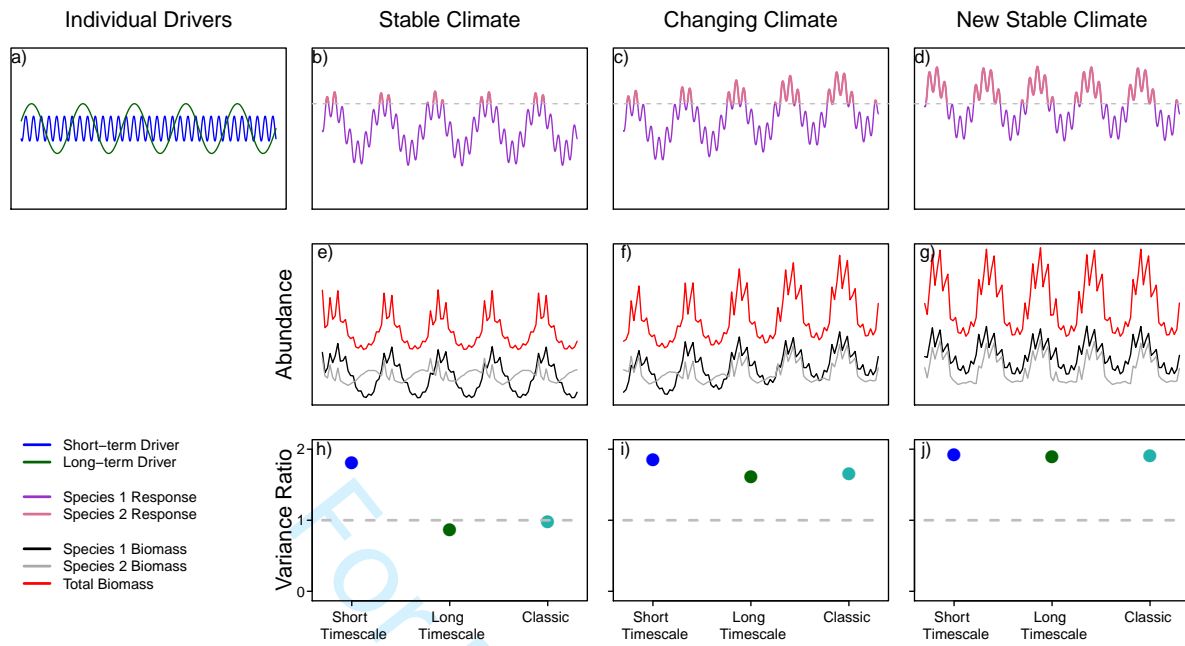
Figure 1:

Figure 2:

Figure 3:

Figure 4:

Figure 5:

Response to reviewers: Manuscript ECY21-0029

Dear Dr. Joseph Yavitt,

Thank you very much for the opportunity to revise and resubmit our manuscript ECY21-0029 for consideration in *Ecology*. After careful consideration, we believe that the reviewers came to two different recommendations based on what each saw as the thesis of our manuscript. Our manuscript focuses on uncovering the *mechanisms* (both abiotic and biotic) that can lead to timescale specificity in community synchrony. We fully agree that the methods for detecting timescale specificity are not novel to our manuscript, but think that Reviewer 1 saw this as our primary aim. Rather, as Reviewer 2 noted, our goal is to apply newly developed methods to investigate the different abiotic and biotic mechanisms that can create timescale specificity in synchronous and compensatory dynamics. As a *Concepts and Synthesis* piece, our goal is to show the breadth of mechanisms that may be at play, ideally inspiring further in-depth investigations of these mechanisms in the future.

We have substantially revised the Introduction and Abstract to clarify our thesis and justify its importance, and we have edited the entire manuscript to emphasize the concepts rather than the methods. Additionally, we have added a "Future Directions" section (as suggested by Reviewer 2) and have modified our model presentation to emphasize the key mechanisms we mathematically incorporate into the model.

These changes have increased the length of the manuscript by only one page. Following this letter, we include a point-by-point reply to all of the comments. The original reviewers' comments are included below with our responses immediately following in blue. We appreciate your close reading of the manuscript and the comments and suggestions provided. We hope you find this revised manuscript suitable for publication.

Sincerely, and on behalf of my coauthors,

Lauren Shoemaker

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Handling Editor

Dear Dr. Shoemaker:

Thank you very much for submitting your manuscript "The long and the short of it: Decomposing synchrony and compensation across temporal scales" ECY21-0029 to Ecology. The reviewers and I appreciate the work you have accomplished. Based on the reviews, we will not be able to accept this manuscript for publication at this time.

I must admit in the many, many years that I have been a subject-matter editor, this is the first time that two ad hoc reviewers came to opposite recommendations: Reject, not publishable versus Accept. I read the paper but am torn trying to make a decision one-way or the other. Rather than seek a third ad hoc reviewer, I am going to recommend reject, but leave open the 'possibility' to reconsider. I ask that you consider the critical comments very, very carefully.

Should you decide to revise the manuscript for further consideration, your revisions should address the specific points made by each reviewer. Please include a cover letter indicating your responses to the review comments and the changes you have made in the manuscript. If you disagree with a reviewer's point, explain why.

I must stress that the revised manuscript will go to two new ad hoc reviewers, so do write specifically to these reviewers.

If you wish to resubmit, once you have revised your manuscript, go to
https://mc.manuscriptcentral.com/ecology and login to your Author Center. Click on "Manuscripts with Decisions," and then click on "Create a Resubmission" located next to the manuscript number. Then, follow the steps for resubmitting your manuscript.

The resubmission would be assigned a new manuscript number and likely be sent out for additional review.

Sincerely,

Dr. Joseph Yavitt

Subject Matter Editor, Ecology

jby1@cornell.edu

Thank you for the synthesis of the reviewer recommendations and the opportunity to revise and resubmit. With the rewrite of the Abstract and Introduction and edits throughout that emphasize our focus on *mechanisms* of timescale specificity (rather than the statistical method), we aimed to address Reviewer 1's concerns while maintaining the positives Reviewer 2 emphasizes.

Reviewer 1

This manuscript illustrates how a time-scale specific variance ratio can be used to characterize synchrony and compensatory dynamics in ecological time series. The study includes simulations of a discrete-time two-species model under four different simulation scenarios, and an analysis of two different pairs of plant species from long-term studies at Jasper Ridge.

The paper is well written, and the scale-dependent variance ratio is a nice idea that may useful. However, this particular paper does not make enough of a new advance to merit publication Ecology. To be clear, the method on which this paper is based has already been published by many

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of these same authors (Zhao et al., 2020). Thus, the method is not new. What advance does this manuscript provide, then? The new material consists of simulations and an application to real data from Jasper Ridge. With regard to the simulations, it wasn't clear to me what the reader was meant to learn from the simulations, or what could be learned. The four scenarios are idiosyncratic, and the piecemeal approach doesn't cohere into any deeper understanding of the ecological causes or consequences of synchrony.

We disagree that the scenarios are idiosyncratic; they address in turn abiotic drivers, biotic drivers, spatial scale, and temporal change—four key considerations in any ecological study. We have clarified this by explicitly naming these aspects when each mechanism is introduced. We additionally have rephrased these four scenarios as mechanisms, better reflecting the aim of our manuscript: exploring how key mechanisms of community dynamics, both in isolation and through interactions with one another, can yield timescale specific patterns of synchrony and compensation. By applying the timescale approach that we recently developed (i.e. Zhao et al. 2020) to these various scenarios, our study contributed to resolving how ecological processes shape the timescale patterns of synchrony.

Moreover, the treatment of each scenario is (I am sorry to be harsh) somewhat superficial. Perhaps this is a matter of style, but it seems to me that a simulation context allows for a much deeper and more satisfying exploration of synchrony than these limited simulations provide. There are several possible directions one could pursue to provide a more thorough treatment. First, because the data-generating model is known, it should be possible to linearize these models and approximate the spectra analytically, instead of relying on simulation. It may even be possible to calculate spectra without linearizing first — author Reuman is the expert here.

We think this comment reflects a misinterpretation of our thesis with this paper. Our intent was to outline the key mechanisms that would generate time-scale specific patterns of synchronous versus compensatory dyanmics, and to provide readers with a pathway toward application. As a "Concepts and Synthesis" submission, our goal is to discuss a breadth of mechanisms, as going into depth on any single one could be its own contribution. We have substantially rewritten the Abstract, Introduction, and framing of the paper to clarify our aims and engage a wider readership.

Second, even if one does want to use simulation, it isn't clear why one should coarsen the timescale specific variance ratio into "short" and "long" timescale bands, given that the simulation can always be run longer to obtain more precise information for any time scale. Short simulation runs might be interesting if the focus were on the sampling properties of the ratio with short time series, but that does not seem to be the focus here. Alternatively, perhaps one could study the effect of coarsening into short and long timescale bands, but if that were the intent, the simulation would have to be structured much differently.

Dividing into short and long timescale bands is common practice in the population synchrony literature, and in our case it helps to emphasize our key thesis in a readily interpretable way for a general audience. For example, a discrete break point between short and long timescales works to differentiate short-term disturbance from long-term climate cycles and simplifies interpretation compared to a continuous approach. We have included these references and a justification of the short versus long timescale breakpoint in the section "A timescale-specific variance ratio on Ln 125-134. All our code is provided on GitHub (and will be archived on Zenodo if accepted) for readers wishing to examine multiple timescales rather than binning into "short" versus "long" timescales.

Finally, considering only two competing species whose dynamics obey the simple Ricker model and its variants unnecessarily constrains the scope. Does the behavior of the variance ratio revealed here extend to more complex communities with more than two species, and/or to species whose dynamics require more complex descriptions than the Ricker model? Unfortunately, the limited results in this manuscript provide no insights along these lines.

We focused on pairwise species interactions to aid with interpretation of each mechanism. Given the complexity even with two species, we argue this is a necessary first step for understanding underlying drivers of timescale specificity before interpreting results from more diverse communities. We have included a discussion of how these dynamics could relate in diverse communities and pointed to these questions in a new future direction section (Ln 374-391).

If the theoretical advance is small, then this leaves us with the two applications to the Jasper Ridge data shown in Figure 2. While these results are interesting — both with respect to illustrating now the new method performs, and with respect to providing some insights about these particular pairs of species — it is again not clear what we can learn from the analysis. Placing the real data side-by-side with various simulation scenarios does not allow for strong inference about the mechanisms that may be driving the observed degree of synchrony.

Altogether, then, I'm afraid the results do not make enough of an advance in our understanding to merit publication in a competitive journal such as Ecology.

Our revision now better emphasizes the knowledge gaps our manuscript fills and that further work is necessary that examines mechanisms of timescale specificity in communities. We clarify that our aim is not to present a new statistical method, but to apply a recently developed method to connect community assembly mechanisms to timescale specific patterns of synchronous and compensatory dynamics.

Finally, as an aside, I'm sorry to say that I was taken aback by the length of the author string. Perhaps I'm wrong, but I can't imagine that all 18 authors made meaningful intellectual contributions to this paper. I realize that the prevailing norm in the discipline is to extend authorship to every member of a working group, which is how I suspect this author string came to be. However, this practice has a cost, too, in that it dilutes authorship as a meaningful signifier of scholarly input, which ultimately disservices the authors who have made a meaningful scholarly contribution to this work. To make a suggestion, perhaps one alternative to consider might be to retain individual authorship for those who have made a meaningful scholarly contribution to the work, and then to list the LTER Synchrony Synthesis Group as an author to recognize the collective contributions of the larger group. In any case, I realize that re-examining authorship practices in the field is a large discussion that will not be settled here, but this author string suggests that perhaps it is time to initiate that discussion.

We have added an author contribution section to clarify roles and contributions (Ln 404-408.

Reviewer 2

First I want to say this is a really exciting topic. I found the paper approachable. I am hoping it will introduce a wider readership into the contextual nature of synchrony and compensation. In

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summary, the authors provide a series of empirical and theoretical case studies and analyze them using frequency based approach versus correlation approaches. The authors sound a needed call for more research on the context of compensatory dynamics and synchrony.

The authors thesis statements read super clear. The science from my perspective is sound. I have questions about certain modeling decisions but those are readily remedied. I also have included some questions that are more there to address my own curiosity and are beyond the scope of the paper. Overall, I enjoyed the paper and the authors are tackling an important question that will push the field forward.

Thank you very much. In the revision, we endeavor to keep the paper approachable to a wide readership while further strengthening our thesis as discussed above.

Below is my list of specific minor comments.

I think a simple schematic of the model would be useful for explaining your results.

Thanks for this suggestion. We played around with this idea, but in the end our ideas were fairly redundant with Figure 1 panels a-f; additionally, space concerns necessitate that this figure would be in a supplement. As such, we decided to modify how we present the equations to make the model clearer and more intuitive to a broad readership. We have added brackets to our model (equations 3 and 4) to more thoroughly highlight the key components of the model and increase readability for a general audience who may not wish to dive into the model details.

The authors use compensation and compensatory dynamics interchangeably. Gonzales and Loreau (2008) differentiate between the two.

We now use "compensatory dynamics" throughout the manuscript, matching Gonzalez' and Loreau's differentiation between density compensation (referring to individual species' growth rates) and compensatory dynamics between species.

The authors cite Tony Ives work but I think Ripa, Lundberg, and Kaitala's (1998) paper on noise shows the time scale dependence of species interactions in terms of power spectra. They derive the power spectra for both discrete and continuous. I think could be an exciting new path for your work to provide analytical solutions and could provide some context for why compensatory dynamics are changing across time scales.

We now refer to the excellent work by Ripa, Lundbergy, and Kaitala in the Introduction, "WWhile 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., Houlahan et al. 2007; de Mazancourt et al. 2013; Grman et al. 2010; Gross et al. 2014; Hallett et al. 2014)" (Ln 62-68). We additionally briefly mention the connections between Ripa, Lundbergy, and Kaitala's work and community synchrony in our Future Directions section. Ln 379-381.

27 I think the authors should differentiate asynchrony and compensatory dynamics. The methods the authors propose differentiate the two. Thus maybe change the sentence to: In contrast, species exhibit asynchronous dynamics due to opposing responses to environmental drivers or competitive

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interactions (Ives, 1995; Gonzalez and Loreau, 2009; Loreau and de Mazancourt, 2013). Asynchronous dynamics can stabilize community properties overall through compensatory dynamics (Peterson, 1975),

We have decided to avoid referring to 'asynchronous dynamics' throughout the manuscript due to the different definitions present in the literature. While asynchrony can refer to negatively correlated dynamics, it also is used to refer to independent species fluctuations—especially in the population synchrony literature. Due to these two opposing definitions, we have decided to use compensatory dynamics to refer to negatively correlated fluctuations. We define this on Ln 26-28: "In contrast, compensatory dynamics stabilize overall community properties as species fluctuate in a negatively correlated manner (Peterson, 1975)".

45 The topic of this concluding sentence does not match with the preceding paragraph. As the authors go from explaining mechanistic reasons for differences for synchrony across scales to talking about methodological limits. I would suggest finishing this paragraph by citing and summarizing some of the time scale dependent mechanisms they discussed and then next paragraph can be segued to by stating that new methods have alleviated the need for using only very long time series allowing for new opportunities.

We have largely rewritten the Introduction to better emphasize the novelty and thesis of our manuscript. This paragraph (now Ln 34-47) now focuses on mechanisms of synchrony and timescale specificity. We wait until the paragraph on Ln 62-78 to now discuss methods.

49 Maybe rewrite as: Advances in scale-specific metrics allow us to gain a new understanding of synchrony versus compensation.

Changed as suggested.

58 this sentence is repetitive as written but if you rewrite 45 you should keep this as is.

We deleted this sentence.

65 A very clear thesis statement however I feel like sometimes more attention is giving to the statistical method than the new insights to how compensatory dynamics operate across time scales.

We agree and think this led to many of reviewer 1's concerns about novelty. We have modified the manuscript accordingly, with particular attention to the framing in the Abstract, Introduction, and Conclusion. In our revision, we aim to emphasise how ecological dynamics alter time scales of synchronous versus compensatory dynamics rather than the statistical method.

81 This is a really clear thesis statement and outlines the paper really well.

Thank you.

143 thanks for sharing!!!

Thanks.

198 an interesting comparison for future research would be to see how different methods perform in detecting synchrony with external or demographic noise. An added piece might be to consider how the wavelet approaches use by Keitts and Vasseur work here as they are data hungrier so does this approach allow us to measure something we wouldn't otherwise be able too with wavelet? Also

6

dealing with problems such as spectral mimicry to reshuffle the time series to maintain the same power spectra but different levels of autocorrelation.

We suggest future models incorporate demographic and environmental stochasticity in our added Future Directions section (Ln 381-386). We now emphasize in the Introduction our choice to use a timescale specific variation ratio due, in large part, to its ability to use shorter timeseries of data (Ln 73). Furthermore, the classic variance ratio is common in community ecology studies, so using a timescale-specific variance ratio allows for connections to previous literature, whereas wavelet approaches are more commonly employed in studies of population synchrony. Given that three of our four mechanisms focus on scenarios with stationary, applying wavelets as opposed to Fourier analyses will yield the same conclusions.

Finally, we aren't clear what the reviewer is suggesting in the last point. You cannot change the autocorrelation of a timeseries while keeping the same spectrum. As such, we have not incorporated this last part of this comment in our revision.

223 maybe clarify that this is because of the differences in intrinsic rate of increase. I know it is in the supplement but I had to double check that you didn't introduce time delays into the model.

Throughout this section, we have clarified that these differences are due to changes in species' intrinsic growth rates. This paragraph now reads, " In the second, one species tracks the environment and the other exhibits a lagged response due to its slow intrinsic growth rate (Fig. 3c; $r_1 = 1.00$, $r_2 = 0.15$)" (Ln 238-239). We similarly define growth rates of all examples throughout this section (Ln 236-241).

260 Shouldn't the fast species intrinsic oscillations be occurring on faster time scales than the long time scales. I don't understand how these two are interacting. Can you please clarify.

We have deleted this sentence, as its original placement implied intrinsic oscillations in our empirical example. We now only discuss our empirical case study in the proceeding paragraph, where we compare species who track environmental change to one that responds more slowly (Ln 249-262).

306 Delete counterintuitively.

Deleted.

322 Do you think that thresholds like this explain the Vasseur et al 2008 result about synchrony being limited to particular seasons?

We think this comment refers to Vasseur et. al. (2005), as there are no first-authored Vasseur et al. manuscripts from 2008. Please let us know if this is in reference to a different manuscript.

Yes, threshold behavior, such as we model in combination with mechanism 4 (non-stationarity and global change) can also explain seasonal differences, if one season has conditions below a species' detection threshold versus another season has conditions above the threshold. Vasseur et. al. suggest this for nutrients in particular, where winter and spring are below the nutrient threshold that would yield high competition. In comparison, summer and fall have higher nutrient competition, yielding compensatory dynamics due to increased competition given the nutrient threshold between summer/fall versus winter/spring seasons.

323 Using a threshold is biologically relevant and fourier based approaches are robust to discontinuous variation. However, it just seems like a departure from the previous analysis so creates hard

to comparison. Why did you perform this analysis without the threshold? Also does the long term trend itself get picked up or because of the windowed nature of the fourier it is excluded as too long?

We incorporated a threshold with the exploration of the global change/nonstationarity mechanism, as global change may cause species to cross performance thresholds (e.g. thermal performance or other stress thresholds). Thresholds may be present in systems even without global change (as we mention in response to the above comment), but are especially interesting to consider along with nonstationarity in environmental conditions. We now motivate this when first presenting Mechanism 4: "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..." (Ln 320-328).

342 Mostly for my own curiosity and is too complicated for the intended audience. A threshold will create a box wave right? This could be modeled using the convolution of a box and sine waves. I think this could be combined with Ripa, Lundberg, and Kaitala 1998 to place into a single analytical framework.

Yes, an alternative approach could use a box wave to create a similar threshold behavior. This is a great suggestion for future work. We now discuss the connections to the Ripa, Lundberg, and Kaitala 1998 paper in both the Introduction and Future Directions.

322 this section is dealing with nonstationarity thus a comparison with wavelet approaches could be useful? Fourier based approaches assume stationarity to cut the difference maybe break the time series up into early or late sections.

We have decided to maintain the Fourier approach for consistency throughout the manuscript, though we now reference the use of wavelets when longer timeseries are available. (Ln 369-372). Breaking up the "changing climate" (Fig. 5 c, f, i) timeseries, as suggested, yields more fine-scale intermediate dynamics between those observed under the "stable climate" (Fig. 5 h) and "New stable climate" (Fig. 5j), as shown below (Fig. 1 in the response letter). We have clarified that these transitory dynamics yield the patterns observed in the main text, Fig. 5i on Ln 349-351.

358 I think it would be could to propose how to translate this model to phenological changes. As while they appear closely related they are very different and phenological mismatches can produce new behaviour such as subharmonic resonance which may confound some of these results.

Thanks for this exciting suggestion. Several of the authors have discussed connecting phenological synchrony to community synchrony as an interesting future direction and possible future grant application. Tying to phenology is beyond our scope here, as we've decided to focus on key mechanisms of community assembly, mirroring those outlined in HilleRisLambers et. al. (2012): environment, biotic interactions, and disperal. We additionally include nonstationarity and global change, given the significance for future ecological communities. Including these four mechanisms puts us slightly over the page limit for *Ecology*. However, we hint at this tie to phenology in our section on Global
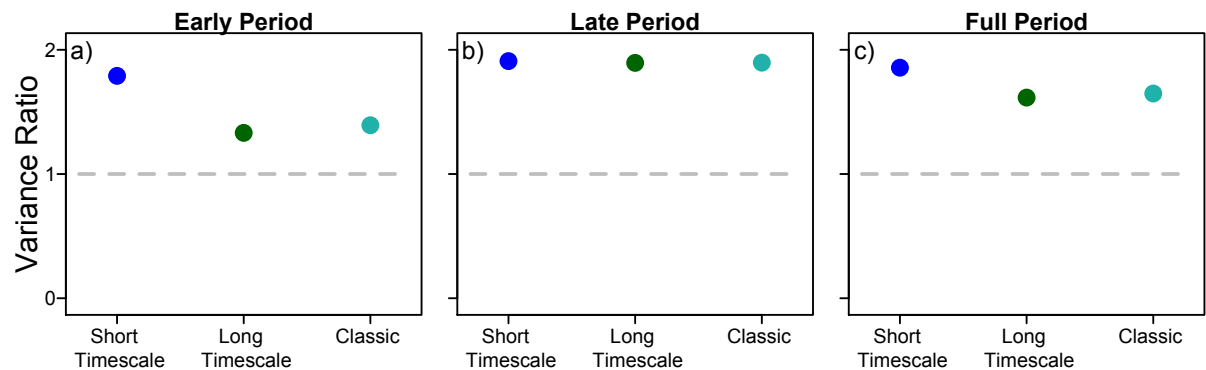
Fig. 1: Variance ratios with the nonstationary timeseries broken into early (a) and late (b) sections compared to analyzing the entire nonstationary period (c).

Change and Nonstationarity (Ln 363-367).

368 How does this compare if you didn't include the threshold? Also is this being driven by transient behaviour or the ramp creating variation at longer time scales?

This is driven by transient behavior where the dynamics are intermediate between the two stationary environments ($e_{historic}$ and e_{new}). We now state this on Ln 349-351: "In contrast, global change increased synchrony at all timescales, as synchrony was intermediate between the dynamics observed under the historic versus new environment."

387 I think putting a dedicated future directions section at the end of the paper would be useful. This paper could outline future directions of the field and which would benefit with a laundry list of future research directions.

We now include a Future Directions section (Ln 373-391).

Figure 4 caption: In previous figures you mark the blue, light blue, and green dots but here you do not because of size. I think just add the description to the figure for this case. I had to refer to other figures to remember what the colours meant.

Thanks for pointing this out. We have altered the legend to read "(i-j) Timescale-specific (short in blue and long in green) and classic variance ratios (teal) for the above communities."

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Appendix 1 for:

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

Authors: Lauren G. Shoemaker, Lauren M. Hallett, Lei Zhao, Daniel C. Reuman, Shaopeng Wang, Kathryn L. Cottingham, Richard J. Hobbs, Max C.N. Castorani, Amy L. Downing, Joan C. Dudney, Samuel B. Fey, Laureano A. Gherardi, Nina Lany, Cristina P. Reyes, Andrew L. Rypel, Lawrence W. Sheppard, Jonathan A. Walter, and Katharine N. Suding

Model Parameterization

Mechanism 1: Multiple environmental drivers

To investigate mechanism 1 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 $a_1 = 0.5$, $b_1 = \dfrac{2\pi}{3}$, and $c_1 = 2$ while long-term environmental fluctuations are defined by $a_2 = 1$, $b_1 = \dfrac{2\pi}{20}$, 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.

Mechanism 2: Differences in species demographic rates

To assess mechanism 2, we define short- and long-term drivers as above: $a_1 = 0.5$, $b_1 = \dfrac{2\pi}{3}$, $c_1 = 2$ and $a_2 = 1$, $b_1 = \dfrac{2\pi}{20}$, and $c_2 = 0$. In contrast to mechanism 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.

Mechanism 3: Dispersal and spatial processes

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

Following similar parameterizations to the previous mechanisms, we parameterize 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.

Mechanism 4: Global change and nonstationarity

To assess mechanism 4, we define the short-term fluctuations (e_1) by $a_1 = 0.25$, $b_1 = \dfrac{2\pi}{3}$, and $c_1 = 2$ while long-term environmental fluctuations (e_2) are defined by $a_2 = 0.5$, $b_1 = \dfrac{2\pi}{20}$, and $c_2 = 0$. The total fluctuations of the stationary environment are 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 this model, demographic parameters are $r_i = 0.65$ 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.

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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.

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