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Short time series obscure compensatory dynamics in ecological communities

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The degree of synchronous versus compensatory dynamics among species is crucial for determining the stability of ecological communities. Although robust quantification of species synchrony requires long-term observations, empirical studies are often based on short time series. Here we explore the effects of time series length on species synchrony by combining spectral analysis, dynamical community models and empirical plant community data. Our theoretical analyses show that competition contributes to decreasing species synchrony over long timescales but causes increases in synchrony over short timescales. As a result, species synchrony tends to decrease with time series length. In model communities, species synchrony calculated from long time series decreases with species diversity and competition, whereas that calculated from short time series increases with diversity and competition. Empirical analyses of >2,000 time series of plant communities support these theoretical predictions. Our analyses demonstrate that both species synchrony itself and its relationship with species richness can exhibit opposite patterns, depending on the length of time series, challenging the implicit assumption in ecological studies that observational length should not qualitatively alter patterns of interest. Our findings help reconcile results from theoretical and empirical studies on synchrony and have implications for sampling design.

Natural ecosystems undergo a variety of perturbations and stochasticity[1,2]. Species diversity is a key characteristic that can help ecosystems resist perturbations by providing biological insurance, whereby decreases in population sizes of some species can be compensated by increases in population sizes of other species[3,4]. Such compensatory or asynchronous dynamics have been regarded as a major mechanism underlying the stability of ecosystems[5–7]. Within ecological communities, compensatory dynamics arise from either species' opposing responses to environmental fluctuations[8–10] or species interactions such as interspecific competition[11–14].

The relationship between species diversity and the degree of synchronous versus compensatory dynamics, however, is a source of debate. Theoretical models predict that species richness can decrease synchrony (for example, average pairwise correlation) among competing species[12,15]. However, empirical studies showed that species synchrony could either increase or decrease with species richness[7,16]. Attempts to reconcile theoretical and empirical findings often focus on differentiating the mechanism underlying species synchrony versus compensation. For example, if competing species share similar environmental responses, species synchrony induced by environmental fluctuations may override the insurance effect of biodiversity[17]. However, disentangling these mechanisms empirically has been difficult, as the covariance analyses traditionally used to describe synchrony inform emergent temporal patterns, but obscure underlying mechanisms[14].

More recent studies have highlighted that synchrony from shared environmental responses versus competition-induced compensation

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may depend on the timescale of observation[18,19]. For example, across US grasslands, ref. 18 found that plant species exhibited more synchronous dynamics over short time periods but more compensatory dynamics over long ones. Timescale-specific patterns of synchrony can arise if species respond to multiple environmental drivers operating at different timescales (for example, annual weather patterns and larger scale multidecadal climate oscillations), or if species exhibit differential response times to the drivers[19]. These studies suggest that differentiating synchrony by timescale may help elucidate its underlying drivers. At a more fundamental level, they suggest that time series length alone may contribute to the differences between theoretical and empirical studies. Specifically, empirical analyses using short time series tend to detect synchronous dynamics[20], while theoretical analyses generally consider much longer timescales and often predict a large region of parameter space where compensatory dynamics arise[15,21]. This issue is particularly relevant in ecological studies where empirical analyses often rely on short time series, sometimes as brief as 3 years (refs. 22–24).

Here we combine theoretical analyses and empirical data to investigate how time series length may influence empirical analyses of species synchrony. Our study measures species synchrony by the ratio of total community variance to the sum of species variance, referred to as the variance ratio[25,26] (ϕ). We first develop a theory of the variance ratio in finite time series based on the spectral analysis of stationary time series. In light of this theory, we show how studies using short time series may introduce bias in the inference of synchrony versus compensation. In particular, by applying spectral analysis to a competition model, we show that competing species can exhibit contrasting patterns of temporal correlation on short and long timescales (that is, at high and low spectral frequencies). Consequently, time series length can qualitatively change the observed patterns of species synchrony and its relationships with species richness and competition strength. We then confirm these theoretical predictions using empirical data of >2,000 observational and experimental plant communities. Our work helps to reconcile theoretical and empirical results and aids in designing sampling protocols for future experiments.

A spectral theory of species synchrony in finite time series

To illustrate the measure of species synchrony and extend the classic measure to a frequency-specific version, we consider a community consisting of n species exhibiting stationary dynamics over time, denoted by $\{x_i(t); t = 1, 2, \ldots\}_{i=1}^{n}$, where $x_i(t)$ represents the abundance of species i at time t. The classic variance ratio (ϕ) is then defined as[25,26]: $\phi \triangleq \frac{\sum_i \sum_j v_{ij}}{\sum_i v_{ii}}$, where v_{ii} denotes the temporal variance of species i and v_{ij} is the covariance between species i and j. A larger value of ϕ indicates more positive or less negative covariance in temporal fluctuations between species. In particular, $\phi > 1$ means that the community exhibits overall more synchronous dynamics than a collection of independently fluctuating species; $\phi < 1$ indicates overall more compensatory dynamics[7,20].

On the basis of the spectral analysis of time series, we denote the co-spectrum $I_{i,j}(f)$ as the frequency-specific covariance between species i and j at the frequency f (ref. 27; Methods). The frequency-specific variance ratio (frequency-specific synchrony) can be defined as[18]:

$$\phi(f) \triangleq \frac{I_C(f)}{I_S(f)} = \frac{\sum_{i,j} I_{ij}(f)}{\sum_i I_{ii}(f)} \tag{1}$$

where $I_C(f) = \sum_{i,j} I_{ij}(f)$ represents the frequency-specific total community variance at the frequency f and $I_S(f) = \sum_i I_{ii}(f)$ represents the sum of frequency-specific species variance. Like the classic variance ratio, a larger value of $\phi(f)$ indicates more synchronous dynamics among species at the frequency f, whereas a smaller $\phi(f)$ indicates more compensatory dynamics. Here, the frequency f takes values between 0 and 0.5 cycles per time step (with respect to infinite time series), where $1/f$ indicates the period or timescale of fluctuations[18,28].

In ecological research, species synchrony (ϕ) can only be estimated using finite time series (Fig. 1b). Under the assumption that the observed time series represents a random sample from a stationary stochastic process, we can derive the expected species synchrony ($\hat{\phi}$). For samples collected every L time steps for a total of K times, ($\{x_i(t); t = 1, 1+L, 1+2L, \ldots, 1+(K-1)L\}$), the expected species synchrony is approximately (Supplementary Note 1):

$$\hat{\phi} \approx \int_0^{\frac{1}{2}} W_{K,L}(f)\,\phi(f)\,\mathrm{d}f \tag{2}$$

where $W_{K,L}(f) = \frac{g_{K,L}(f) I_S(f)}{\int_0^{\frac{1}{2}} g_{K,L}(\lambda) I_S(\lambda)\,\mathrm{d}\lambda}$ and $g_{K,L}(f) = \frac{2}{K-1}\left(K - \sum_{h=-K}^{K} \frac{K-|h|}{K}\cos(2\pi h L f)\right)$ are weighting functions (their integrals over [0, 0.5] are both 1). Equation (2) illustrates how species synchrony is expected to depend on the sampling interval (L) and sampling intensity (K). In empirical studies, a common sampling regime involves collecting samples at every time step over a period T ($\{x_i(t); t = 1, 2, \ldots, T\}_{i=1}^{n}$), which represents a special case of equation (2) when $L = 1$ and $K = T$. Below we examine the effect of time series length (T) under this sampling regime ($L = 1$) unless otherwise specified.

Equation (2) establishes a link between the expected values of species synchrony ($\hat{\phi}$) and its underlying frequency distribution ($\phi(f)$). Species synchrony calculated from finite time series represents a weighted average of frequency-specific synchrony, with weights (across frequencies) depending not only on the power spectra of species dynamics ($I_s(f)$), but also on the sampling regime. Importantly, given a community with stationary dynamics, the expected species synchrony ($\hat{\phi}$) from finite time series can substantially differ from its theoretical counterparts based on infinite time series. Below we use a competition model and empirical data to illustrate how short time series can often lead to overestimation of species synchrony in competitive communities and can bias relationships between synchrony and species diversity or competition strength.

Species synchrony and diversity–synchrony relationships in competition models

To understand the effects of species diversity and competition on species synchrony, we consider a discrete-time Lotka–Volterra competition model with environmental stochasticity[15]:

$$x_i(t+1) = x_i(t) \times \exp\left(r_i\left(1 - \frac{x_i(t) + \sum_{j \neq i} a_{ij} x_j(t)}{k_i}\right) + \epsilon_i(t)\right) \tag{3}$$

Here, r_i and k_i represent the intrinsic growth rate and carrying capacity of species i, respectively; $\alpha_{i,j}$ denotes the competitive strength of species j on species i; and $\varepsilon_i(t)$ is a Gaussian white noise representing the response of the growth rate of species i to environmental fluctuations. The environmental responses of different species can be correlated: $\rho_{ij} = \mathrm{corr}(\varepsilon_i, \varepsilon_j)$. We assume $r_i < 1$ for all species according to empirical observations[29,30].

We first investigate a special case of the model with symmetric dynamics ($r_i \equiv r$, $k_i \equiv k$, $a_{ij} \equiv a$ and $\rho_{ij} \equiv \rho$). Under this assumption, we can derive an approximate analytical solution for the frequency-specific synchrony (Supplementary Note 2):

$$\phi(f) = \frac{1 + (n-1)\rho}{1 - (1-\rho)\theta} \tag{4}$$

where θ is a function of frequency (f), the number of species (n) and model parameters (r, k, a and ρ) (Methods). Equation (4) illustrates how patterns of species synchrony vary across frequencies (f) and

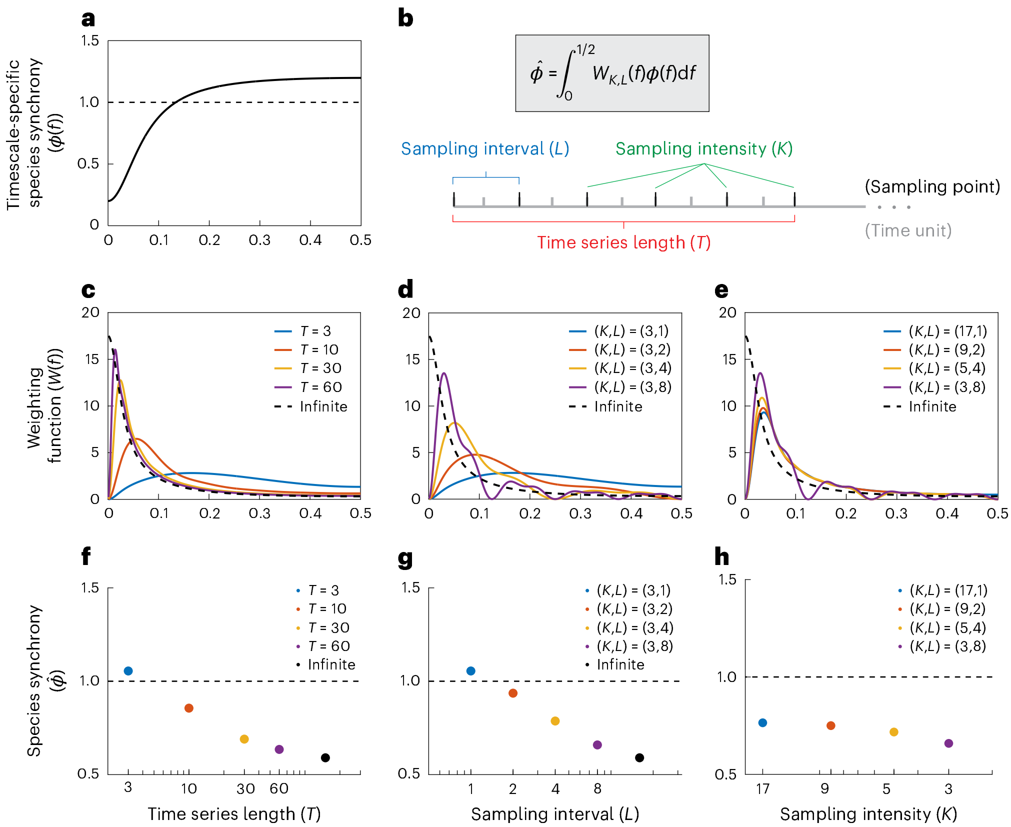

Fig. 1 | Patterns of species synchrony in competition models. a, Species synchrony ϕ(f) as a function of frequency (f). **b**, Illustrations of sampling regimes and the master formula for converting frequency-specific synchrony (ϕ(f)) to the expected synchrony ($\hat{\phi}$) in finite time series. The grey bold horizontal line indicates time, with the grey vertical bars indicating the unit of time step. Sampling events are indicated by black bars, which are conducted every L units of time (sampling interval) for K times (sampling intensity). Time series length (T) corresponds to the overall time span of the sampling. These sampling regimes determine the weights ($W(f)$) that scales from frequency-specific synchrony (ϕ(f)) to the expected synchrony ($\hat{\phi}$). **c**–**e**, Weighting functions corresponding to different time series lengths T (with fixed sampling interval $L = 1$) (**c**), different sampling intervals L (with fixed sampling intensity $K = 3$) (**d**) and different sampling intensity K (with fixed study period of 17) (**e**). The dashed lines correspond to infinitely long time series with $L = 1$. **f**–**h**, Theoretical expectations for species synchrony (the coloured points) under different sampling strategies corresponding to those in **c**–**e**, which are obtained by calculating the weighted average of frequency-specific variance ratio following the formula in **b**. Parameters: $n = 2$, $\alpha_{12} = \alpha_{21} = 0.5$, $r_1 = r_2 = 0.5$, $k_1 = k_2 = 10$, $\rho = 10$, $\mathrm{var}(\varepsilon_1) = \mathrm{var}(\varepsilon_2) = 0.01$.

along gradients of species richness (n) and competition strength (a). Numerical analyses indicate that $\phi(f)$ increases with f, regardless of the degree of correlation in species environmental responses (ρ). Under the special case of independent environmental responses ($\rho = 0$), the community exhibits more compensatory dynamics than expected in a collection of independently fluctuating species ($\phi(f) < 1$) at low frequencies or long timescales, but more synchronous dynamics ($\phi(f) > 1$) at high frequencies or short timescales (Fig. 1a).

By substituting equation (4) into equation (2), we can obtain the expected species synchrony for competitive communities in finite time series ($\hat{\phi}$) under different sampling regimes. Our analyses show that, even when the underlying model is identical, species may exhibit contrasting patterns of species synchrony in short and long time series. In particular, under the scenario of $\rho = 0$, species exhibit more synchronous dynamics than expected in a collection of independently fluctuating species ($\hat{\phi} > 1$) in short time series, but more compensatory dynamics ($\hat{\phi} < 1$) in long time series (Fig. 1f). This can be understood from equation (2): $W_{T,1}(f)$ gives relatively more weights to high frequencies in short time series (small T), but substantially greater weights to low frequencies in long time series (large T) (Fig. 1c). In addition, we investigate the effects of sampling interval (L) and intensity (K) on expected species synchrony (Fig. 1d,e,g,h). Under an extremely low sampling intensity ($K = 3$), we find that expected synchrony decreases as L increases (Fig. 1g). In comparison, given the overall time span ($1 + (K - 1) \times L$), increasing the sampling intensity K (implying a decrease in the sampling interval L) has little effect on species synchrony (Fig. 1h). Critically, this suggests that the overall time span, rather than the sampling intensity, is a key factor influencing species synchrony.

We further investigate how time series length can influence the relationships of species synchrony with species richness and competition strength. Our analyses show that species synchrony decreases with both species richness and competition strength in long time series, but opposite patterns are observed in short time series (Fig. 2a,d). These results can also be understood from the frequency dependency of synchrony and the dependence of weights on the length of time series. Both species richness and competition strength decrease frequency-specific synchrony and generate more compensatory dynamics at low frequencies, whereas they have contrasting effects at high frequencies (Supplementary Fig. 2a,b). Because the length of time series changes the weights ($W_{T,1}(f)$) at different frequencies in equation (2), it alters the relationships between species synchrony and species richness or competition strength, leading to opposing patterns in short versus long time series. Similarly, given the sampling intensity, increasing the sampling interval can qualitatively alter the relationships between species synchrony and richness or competition strength (Fig. 2b,e). Again, given the overall time span, increasing the sampling intensity has little effect on those relationships (Fig. 2c,f).

Overall, our analyses of the symmetric competition model reveal two effects of time series length: (1) species synchrony is expected to generally decrease with time series length, such that shorter time series

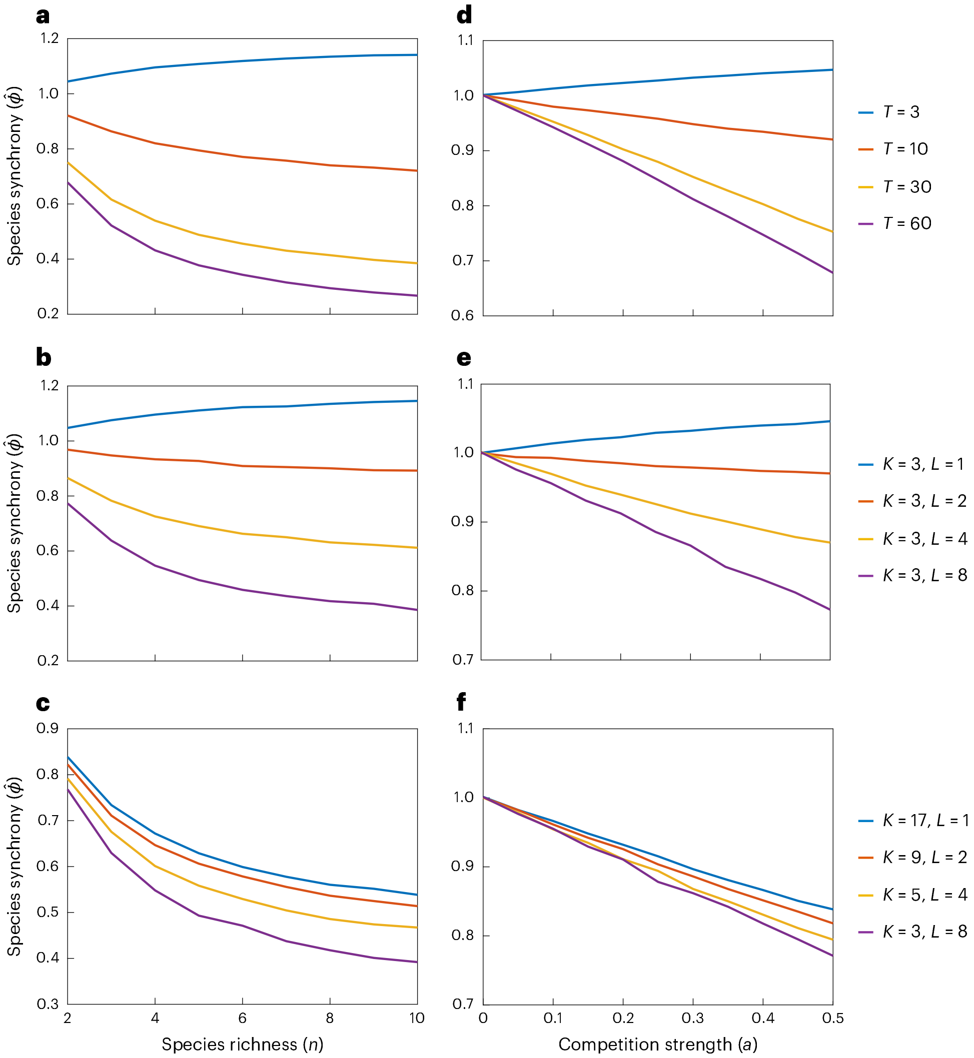

Fig. 2 | Relationships between species synchrony with species richness and competition strength. a–**f**, Relationships between species synchrony with species richness (**a**–**c**) and competition strength (**d**–**f**) in competitive models under different sampling strategies. **a**,**d**, Different time series lengths (T), with fixed sampling interval ($L = 1$). **b**,**e**, Different sampling intervals (L), with fixed sampling intensity ($K = 3$). **c**,**f**, Different sampling intensities (K), with fixed study period ($T = 17$). Parameters: $r_1 = 0.5$, $k_1 = 10$, $\mathrm{var}(\varepsilon_1) = 0.01$ for every i, $\rho_{i,j} = 0$ for every $i \neq j$. In **a**–**c**, competition strengths $\alpha_{i,j} = 0.5$; in **d**–**f**, species richness $n = 2$.

tend to exhibit more synchronous dynamics and longer time series tend to exhibit more compensatory dynamics; (2) while species richness and competition strength both decrease species synchrony in long time series, they contribute to increasing species synchrony in short time series. As these results are derived under restricted scenarios of symmetric competition and environmental noise, we also test the robustness of our results to asymmetric competition, strong positive or negative correlations in environmental responses and temporally autocorrelated environmental responses (Supplementary Note 3). Our analyses demonstrate that prediction (1) holds consistently across a broad range of scenarios, while prediction (2) generally holds except under very high temporal autocorrelation and/or between-species correlations in environmental responses (Extended Data Figs. 1–3 and Supplementary Fig. 1). The robustness of these theoretical findings is critical for their relevance to reality, as natural communities typically exhibit asymmetric species interactions and correlated environmental responses[15,19].

Empirical tests of theory

We used observational and experimental data on plant communities through time to test the effects of time series length on species synchrony and its relationship with species diversity. Our dataset included temporal observations of species abundance or biomass in 1,906 plant communities surveyed across 18 distinct sites over 15–40 years (extracted from ref. 7), along with two grassland biodiversity experiments from Cedar Creek LTER, Minnesota, United States (Methods). Specifically, the two experiments consist of time series of 119 plots lasting for 17 years (BigBio from the Cedar Creek dataset e120) and 46 plots lasting for 20 years (BioCON from the Cedar Creek dataset e141). Using these data, we examined how species synchrony changes as the time series length decreases (by artificially eliminating data to simulate shorter time series) and how time series length influences the relationship between synchrony and species diversity.

Our analyses revealed patterns broadly consistent with theoretical predictions. As the time series length increased, species synchrony decreased on average in both natural and experimentally manipulated communities (Fig. 3 and Supplementary Fig. 3). Across the 1,906 natural communities, 55.2% exhibited significant declining trends in species synchrony as the observational length increased, 27.3% exhibited no significant change and 17.5% exhibited significant increasing trends. The number of communities with declining trends was 1,342, which is highly significant ($P < 0.001$) compared to a null binomial distribution with number of trials 1,906 and probability 0.5. On average, species synchrony decreased from 1.25 in 5-yr time series to 0.89 in 25-yr time series, indicating a shift from more synchronous dynamics in short time

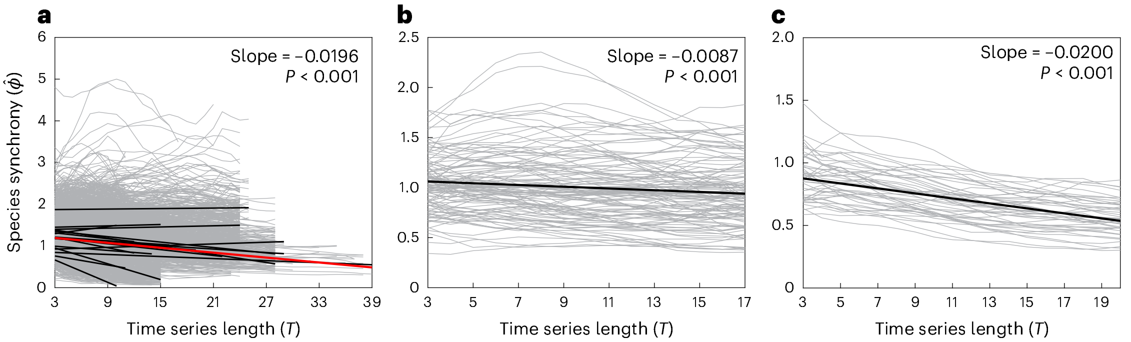

Fig. 3 | Relationships between species synchrony and time series length in observational and experimental data. a, The observational dataset consists of 1,906 local communities (grey curves) extracted from 18 studies. The red line represents the overall relationship fitted by a linear mixed-effects model with random intercepts and slopes across studies and black lines are predicted slopes for each of the 18 studies. **b**,**c**, The experimental datasets include the BigBio (datasets e120; **b**) and BioCON (dataset e141; **c**) experiments in Cedar Creek. The black lines represent the overall relationship fitted by linear mixed-effects models with random intercepts across plots (grey curves) within each experiment. Likelihood ratio tests (one-sided) are performed by comparing the linear mixed-effects models with null models where the time series length has no effect on synchrony.

series to more compensatory dynamics in long time series. Across the 165 experimental communities, 64.7% exhibited significant declining trends in species synchrony as the observational length increased, 14.1% exhibited no significant change and 21.2% exhibited significant increasing trends (Fig. 3; 126 exhibited declining trends, $P < 0.001$ according to a binomial test). On average, species synchrony decreased from 1.04 in 5-yr time series to 0.94 in 17-yr time series for the BigBio experiment and from 0.88 in 5-yr time series to 0.63 in 20-yr time series for the BioCON experiment.

Using the two datasets from Cedar Creek LTER that experimentally manipulated biodiversity and local species pools, we further tested whether the relationship between synchrony and species diversity (measured by the inverse of Simpson's index) may change with the length of time series. Our results showed that, whereas species synchrony exhibited a negative relationship with species diversity over the whole experimental period (17 or 20 years) in both experiments, non-significant relationships would be concluded if short time series were used (Fig. 4a,d). Importantly, these non-significant relationships in shorter time series were not explained by greater uncertainties (that is, larger confidence interval of the regression slope) due to their smaller sample sizes, but instead by smaller effect sizes (a decrease in the estimated mean of slope) as the time series length decreased (Fig. 4). In addition, we tested the effects of sampling interval L by resampling three observations ($K = 3$; the minimum used in the literature, for example, refs. 22,23) from the experimental period with varying sampling interval (for example, years 1–3–5, 1–5–9, ...). We found that, given the number of samples ($K = 3$), the relationship between species synchrony and species diversity switched from being non-significant to negative as the sampling interval increased (Fig. 4b,e). In comparison, given the time span (that is, fixing the start and end years), increasing the sampling intensity had little effect on the qualitative outcome (Fig. 4c,f). These patterns generally agree with our competition model (Fig. 2).

Discussion

Our analyses demonstrate that species synchrony and its relationships with species richness and competition strength are influenced by time series length and sampling intervals. Specifically, competing species exhibit more compensatory dynamics in longer time series but appears to exhibit more synchronous dynamics in shorter ones. Moreover, species synchrony decreases with increasing species richness and competition strength in long time series but appears to increase with increasing richness and competition in short time series. Early studies have showed that the temporal variability of population dynamics tends to increase with time series length[31,32]. Our results further highlights the role of time series length in ecological studies of between-population dynamics, suggesting caution when analysing species synchrony from short-term studies and when comparing studies with different time series lengths.

The effects of time series length on species synchrony can be understood through the lens of spectral analysis. Spectral analysis shows that competition tends to generate more compensatory dynamics than expected in a collection of independently fluctuating species ($\phi < 1$) at low frequencies (or long timescales) but more synchronous dynamics ($\phi > 1$) at high frequencies (or short timescales), even when species respond to environmental fluctuations independently. These findings corroborate theoretical results[14] showing that competition tends to increase species synchrony in population growth rates (representing short-term dynamics) but decrease species synchrony in population sizes (representing long-term dynamics) (see also Extended Data Fig. 4). While the desynchronizing effects of competition over long timescales has been well acknowledged in the literature[11,12,15], its synchronizing effect over short timescales has largely been overlooked. To understand these timescale-dependent effects, consider how a two-species community responds to a pulse perturbation over short and long terms. Starting from equilibrium, assume a perturbation that decreases the abundance of one species (the perturbed species) while leaving the other (the unperturbed species) unchanged. Following this perturbation, the abundance of both species would increase due to reduced intraspecific and interspecific competition, leading to positive correlations in the short term. These synchronous dynamics are followed by compensatory dynamics in the long term, in which the unperturbed species begins to decrease once the abundance of the perturbed species has reached a certain level (Extended Data Fig. 4a,b). For communities experiencing continuous perturbations, the observed species dynamics reflect the combined influences of the short-term synchronizing and long-term desynchronizing effects of competition (Extended Data Fig. 4c).

The synchronizing effect of competition over short timescales not only influences the quantification of species synchrony, but also leads to a counterintuitive, positive diversity–synchrony relationship in short time series. This contradicts theoretical predictions, implicitly based on long time series, that species synchrony should decrease with species richness and competition strength[11,15]. However, while the diversity–synchrony relationship can vary qualitatively with time series length, our theoretical and empirical analyses demonstrate consistently positive relationships between species diversity and community stability (the inverse of temporal variability), regardless of time series length (Supplementary Figs. 5 and 6). This arises because competition has opposite effects on species synchrony and species-level

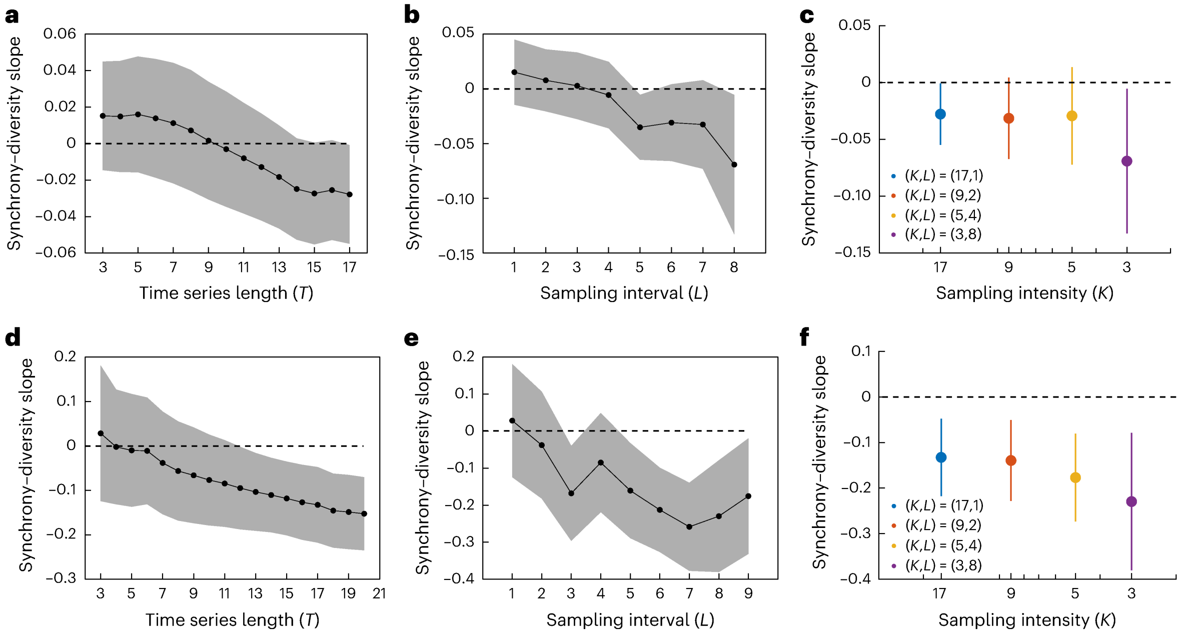

Fig. 4 | Relationships between species synchrony and species diversity under different resampling strategies in Cedar Creek biodiversity experiments. **a**–**f**, The BigBio (datasets e120) (**a**–**c**) and BioCON (dataset e141) (**d**–**f**) experiments. On the basis of the original experimental data, linear regression slopes and 95% confidence intervals of slopes between species synchrony and species diversity (Simpson diversity) are shown under different resampling approaches: different time series lengths (by fixing sampling interval $L = 1$) (**a**,**d**); sampling intervals (by fixing sampling intensity $K = 3$) (**b**,**e**). **c**,**f**, Different sampling intensities. The mean and 95% confidence intervals of regression slopes are represented by points and shade in **a**,**b**,**d**,**e** and by points and bars in **c**,**f**. The BigBio and BioCON experiments contain $n = 119$ and $n = 46$ mixture plots, respectively.

fluctuations at all frequencies, which tend to cancel out and result in weak net effect on community stability[11,15]. Overall, our results suggest that time series length will not affect the sign of the diversity–stability relationship, but it can influence inference on the mechanisms underlying that relationship by altering the diversity–synchrony relationship.

While our analyses used the variance ratio to quantify synchrony, our results apply, at least partially, to other measures of species synchrony proposed in the literature[33]. One commonly used measure is pairwise correlation[13]. For this measure, our results generally hold, namely that pairwise correlation decreases with time series length and its relationships with species richness and competition shift from positive in short time series to negative in long time series (Extended Data Fig. 5a–c). Another commonly used measure is the community-wide synchrony metric[14], which compares the observed community variance to that of a hypothetical community with perfectly correlated species. This synchrony metric also decreases with time series length and its relationship with competition strength exhibits a similar shift between short and long time series (Extended Data Fig. 5d,f). That said, since this metric depends on both the correlation between species and the number of species itself, it tends to always decrease with species richness, regardless of time series length (Extended Data Fig. 5e).

Our results shed light on the interpretation of empirical patterns of species synchrony reported in recent studies. For instance, previous work found that plant communities exhibit more synchronous dynamics over short periods but more compensatory dynamics over long periods[18,19]. In the original papers, these patterns were interpreted as differential responses of species to environmental fluctuations over short versus long periods. Our theoretical results provide an (non-mutually exclusive) alternative explanation: even without changes in external environmental forcing, species interactions themselves are sufficient to reshape species dynamics and synchrony across timescales and cause contrasting patterns between short and long time series. In addition, our findings provide a potential explanation for why species dynamics that are more synchronous than expected in a collection of independently fluctuating species (for example, $\phi > 1$) are commonly found in studies of natural communities using relatively short time series[20] and suggest caution in comparing studies of species synchrony that use different time series lengths. We note, however, that in addition to time series length, several other factors may also bias the inference of species synchrony from observations of natural communities, including non-equilibrium dynamics and directional trends[34] (Supplementary Note 3 and Supplementary Fig. 4), periodic environmental forcing (for example, seasonality) and species longevity.

Our results also have important implications for experimental or sampling designs. Our theoretical and empirical analyses show that increasing the sampling interval (for a fixed number of samples) has similar effects to increasing the study duration with a fixed sampling interval; however, increasing the sampling intensity within a fixed study duration has little effect on the measured species synchrony (Figs. 1, 2 and 4). Thus, if the practical constraint (for example, financial cost) is mainly sampling rather than running the experiment, we recommend maintaining the experiment for a long time while sampling with a relatively longer interval to capture long-term dynamics. This has been the strategy adopted by some large-scale surveys on natural ecosystems, such as the Forest Inventory and Analysis programme in the United States[35] and the Forest Global Earth Observatory[36], which resample forest plots every 5–10 years. However, if constraints primarily derive from running the experiment for a given period of time, but not from sampling, we caution that studies may reach biased conclusions by overlooking long-term dynamics. In such cases, increasing the sampling intensity will not necessarily help elucidate patterns of synchrony. To determine the minimum necessary period for an experiment, a simulation-based power analysis could be conducted by simulating the dynamics of the focal ecosystems based on prior knowledge[28], for example following a similar workflow to what we present for the Lotka–Volterra model in Supplementary Note 4. This analysis shows that the critical time series length depends on the parameters of species dynamics and the number of replicates (Extended Data Fig. 6 and Supplementary Fig. 7).

Conclusion

Despite repeated calls for long-term ecological research, most time series are still relatively short[37,38]. Short time series have been frequently used in ecological studies with the implicit assumption that the length of time series should not alter the patterns of interest and the capacity to infer underlying relationships[24,39]. Our results show that this assumption does not necessarily hold for studies investigating important topics in community ecology. Previous studies have shown that short-term observations may lead to biased conclusions because of time-dependent ecological processes, for example, transient dynamics[40], cyclical reversing responses[41] or succession[42]. Here, our results show another type of bias which can emerge from short time series: short time series reflect mainly the immediate responses of population dynamics to environmental variation and species interactions; as such, short time series can obscure competition-driven compensatory dynamics that operate over long timescales. In comparison, long time series contain information on both immediate and long-term species responses, including the desynchronizing effect of interspecific competition. Therefore, long-term data are important not only for reliable estimation of ecological variables[32], but also for inference on the relationships between factors and phenomena which are of widespread importance in community ecology. Our findings contribute interpretations of empirical patterns of species synchrony from observational data and reconcile the contrasting patterns between theoretical and empirical studies. Future experiments will be needed to unravel the drivers of species synchrony, for example by quantifying the relative importance of external and internal ecological processes. Although our analyses are grounded in ecology, the principles revealed here should apply more broadly to studies of synchrony in other disciplines[43] (for example, epidemics and economics). Understanding the temporal dependence of synchrony in these systems could provide useful insights for reconciling short- and long-term observations.

Methods

Derivation of the expected species synchrony in finite time series

Given an ergodic multivariate stationary stochastic process $\{X_i(t); t = 1, 2, \dots\}_{i=1}^{n}$, we assume that the observed time series represents a random sample from this process. On the basis of the spectral theory of stationary time series, we can derive the expected species synchrony ($\hat{\phi}$).

First, we sample the first two variables (for example, two species) of length T, that is, $\{x_1(t)\}_{t=1}^{T}$ and $\{x_2(t)\}_{t=1}^{T}$. The expected synchrony can be approximated by the weighted mean of frequency-specific synchrony (Supplementary Note 1): $\hat{\phi} \approx \int_0^{\frac{1}{2}} W_T(f)\,\phi(f)\mathrm{d}f$, where $\phi(f)$ represents the frequency-specific synchrony and $W_T(f) = \frac{g_T(f) I_s(f)}{\int_0^{\frac{1}{2}} g_T(\lambda) I_s(\lambda)\mathrm{d}\lambda}$, with $g_T(f) = \frac{2}{T-1}\left(T - \sum_{h=-T}^{T} \frac{T-|h|}{T}\cos(2\pi h f)\right)$. Both $W_r(f)$ and $g_r(f)$ are weighting functions (that is, their integrals over [0, 0.5] are both 1). While $g_r(f)$ depends only on T and f and is thus system independent, $W_r(f)$ depends on the spectral patterns of population dynamics and is thus system specific. In addition, $I(f) = \sum_i I_{ii}(f)$ is the summed power spectrum across all component species. Because $I(f)$ is model or system specific, the weighted function W also depends on the study system.

Second, we consider more general scenarios of sampling where K observations are made in every L time steps, that is, data are collected at time $\{1, 1+L, 1+2L, \dots, 1+(K-1)L\}$. Similarly, the expectation of species synchrony can be approximated by: $\hat{\phi} \approx \int_0^{\frac{1}{2}} W_{K,L}(f)\,\phi(f)\mathrm{d}f$, where $W_{K,L}(f)$ is a weighted function as described in the main text.

Analyses of the competition model

Under the symmetric assumptions that $r_i = r$, $k_i = k$, $\mathrm{var}(\varepsilon_i) = \sigma^2$, $\alpha_{i,j} = \alpha$ and $\mathrm{cor}(\varepsilon_i, \varepsilon_j) = \rho$, we can obtain the equilibrium species abundance: $x_i^* = \frac{k}{1+(n-1)a}$, which is locally stable when $r < 2$ and $\alpha < 1$. Let $c = 1 - r$, $d = \frac{r}{1-r} \times \frac{-a}{1+(n-1)a}$ and $u = \cos(2\pi f)$, we define: $\theta = \frac{(n-1)cd(-2c+ncd+2u)}{1+(-c+ncd)^2+2(-c+ncd)u}$. The diagonal and off-diagonal elements of the spectral matrix of population dynamics are $\sigma^2\left(x_i^*\right)^2 \frac{(1-\alpha)+\alpha\rho}{1+c^2-2cu}$ and $\sigma^2\left(x_i^*\right)^2 \frac{\alpha+(n-1-\alpha)\rho}{(1+c^2-2cu)(n-1)}$, respectively. Thus the timescale-specific synchrony can be solved asymptotically as (see Supplementary Note 2 for derivation): $\phi(f) = \frac{1+(n-1)\rho}{1-(1-\rho)\theta}$.

To test the robustness of our results, we conducted different sets of simulations by relaxing the assumption of symmetric competition, incorporating temporal autocorrelation and/or high species correlation in environmental responses, involving successional dynamics and so on (Supplementary Note 3).

Empirical analyses

We compiled a dataset of time series of natural plant communities, by extracting community data with at least 15 years of observations from ref. 7. This resulted in 1,906 plant communities (grassland, forest, savanna or shrubland communities) with temporal observations of species cover, biomass or frequency from 18 study sites, corresponding to the studies no. 2, 3, 5, 7, 17, 18, 21, 25, 26, 30, 31, 53, 57, 63, 64, 66, 67 and 76 in ref. 7 (see Supplementary Information in ref. 7 for detailed descriptions for the datasets). For any community i with the time series length T, we calculated species synchrony for different time series length $T_1(<T)$, taking the mean value of the variance ratio across all sub-time series with length T_1 (number of trials $T - T_1 + 1$). The effects of time series length on synchrony were then evaluated by linear mixed-effects models (function lme in R), where the random effects of both the intercept and slope are represented by the community nested within study.

For the two biodiversity experiments (Cedar Creek datasets e120 (BigBio) and e141 (BioCON)), we use 119 and 46 multispecies communities, respectively, with time series length (T) of 17 (from 2001 to 2018, without 2009) and 20 (from 2001 to 2020). For the BigBio dataset, we used all experimental plots, with species richness ranging from 2 to 14. For the BioCON dataset, we used only control plots without any environmental treatment, with richness from 9 to 14. Similarly, we evaluate the effects on the variance ratio of time series length ($T_1 < T$), sampling interval ($L = 1, 2, \dots, 8$ under fixed sampling intensity $K = 3$), sampling intensity ($K = 3, 5, 7, 9$ under fixed total period T). We calculate the effective species diversity in each plot using the Simpson diversity $(\sum_{i=1}^{n} p_i^2)^{-1}$, where p_i is the temporally averaged proportion of species i in the community in the subsetted time series. Using linear regressions, we test the relationships between species diversity and synchrony in sub-time series with different lengths, sampling interval and sampling intensities.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The analysed data and the codes to generate simulated data are available via figshare at https://figshare.com/s/52cd8c1a35f7cb8d801c (ref. 44).

Code availability

Numerical simulations were performed on Matlab2024b. Data analyses were performed on R (v.4.4.0) and linear mixed-effects models are analysed using R package lme4. Codes are available via figshare at https://figshare.com/s/52cd8c1a35f7cb8d801c (ref. 44).

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Author contributions

S.W. designed the research. M. Luo and S.W. performed the research. M. Luo derived analytic solutions and analysed the model and data. M. Luo, L.M.H., D.C.R., L.G.S., L.Z. and S.W. contributed new reagents/analytic tools. P.B.R. and D.T. curated the field data. M. Luo and S.W. wrote the first draft of the paper. L.M.H., D.C.R., L.G.S., L.Z., L.J., M. Loreau, P.B.R. and D.T. contributed substantially to revision.

Competing interests

The authors declare no competing interests.

Additional information

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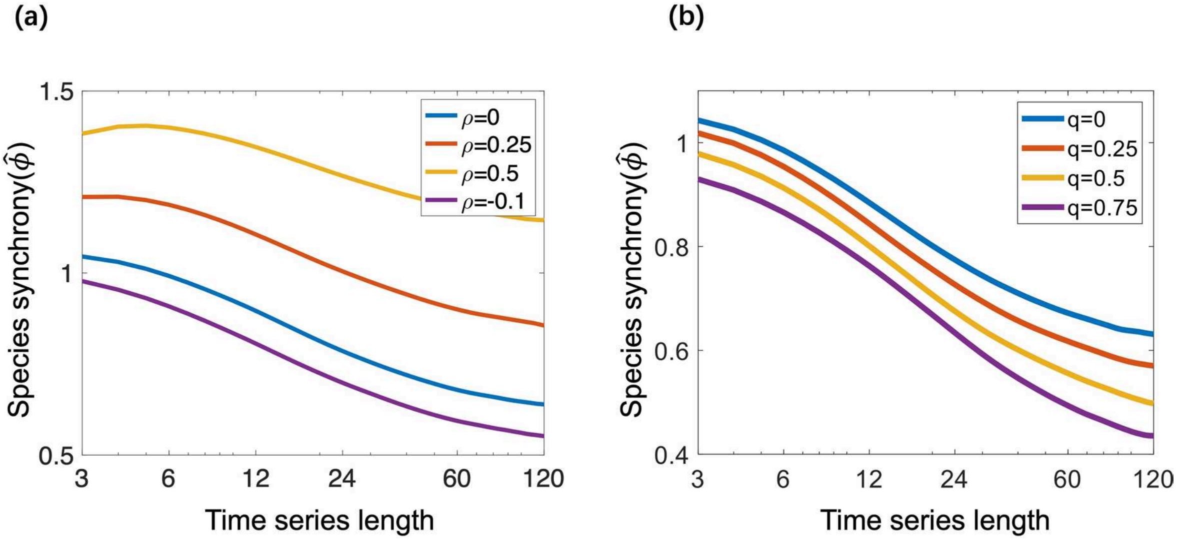
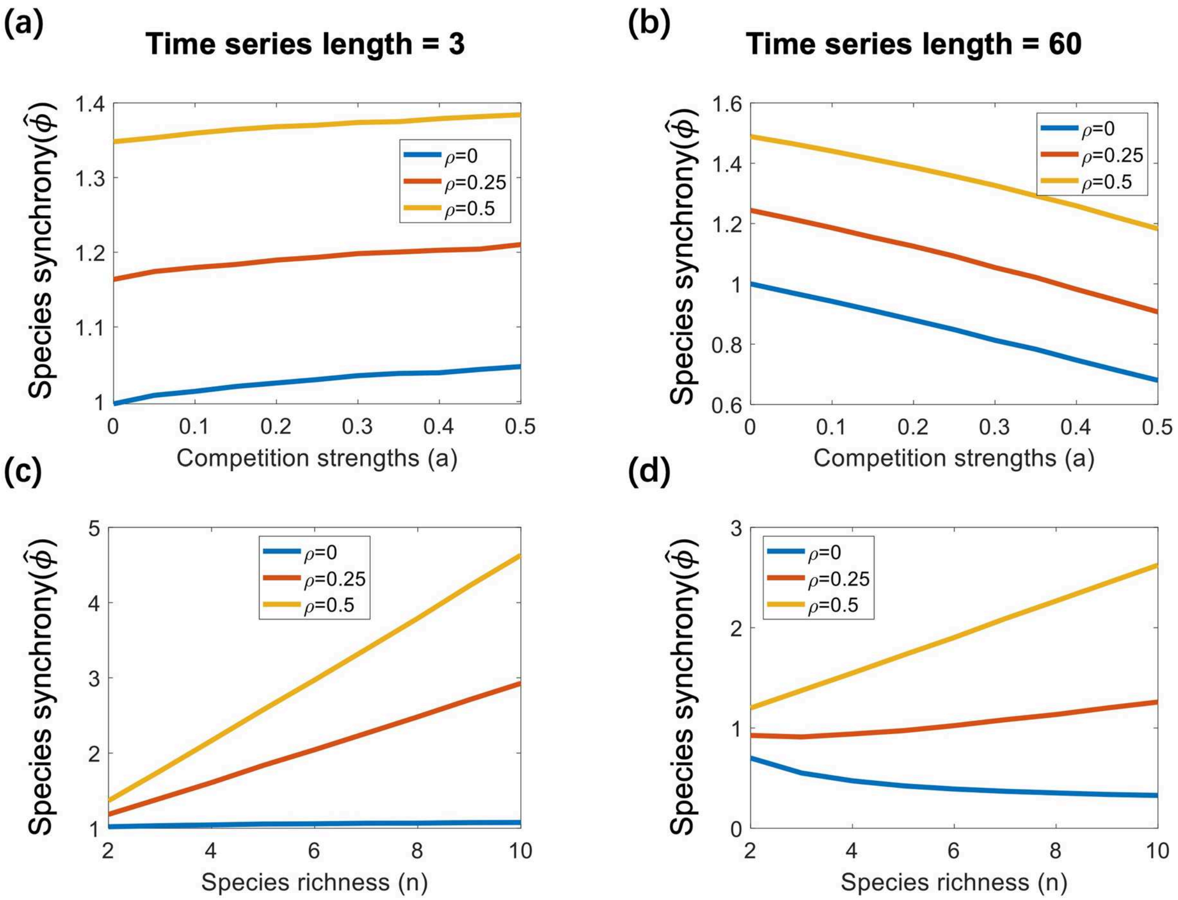
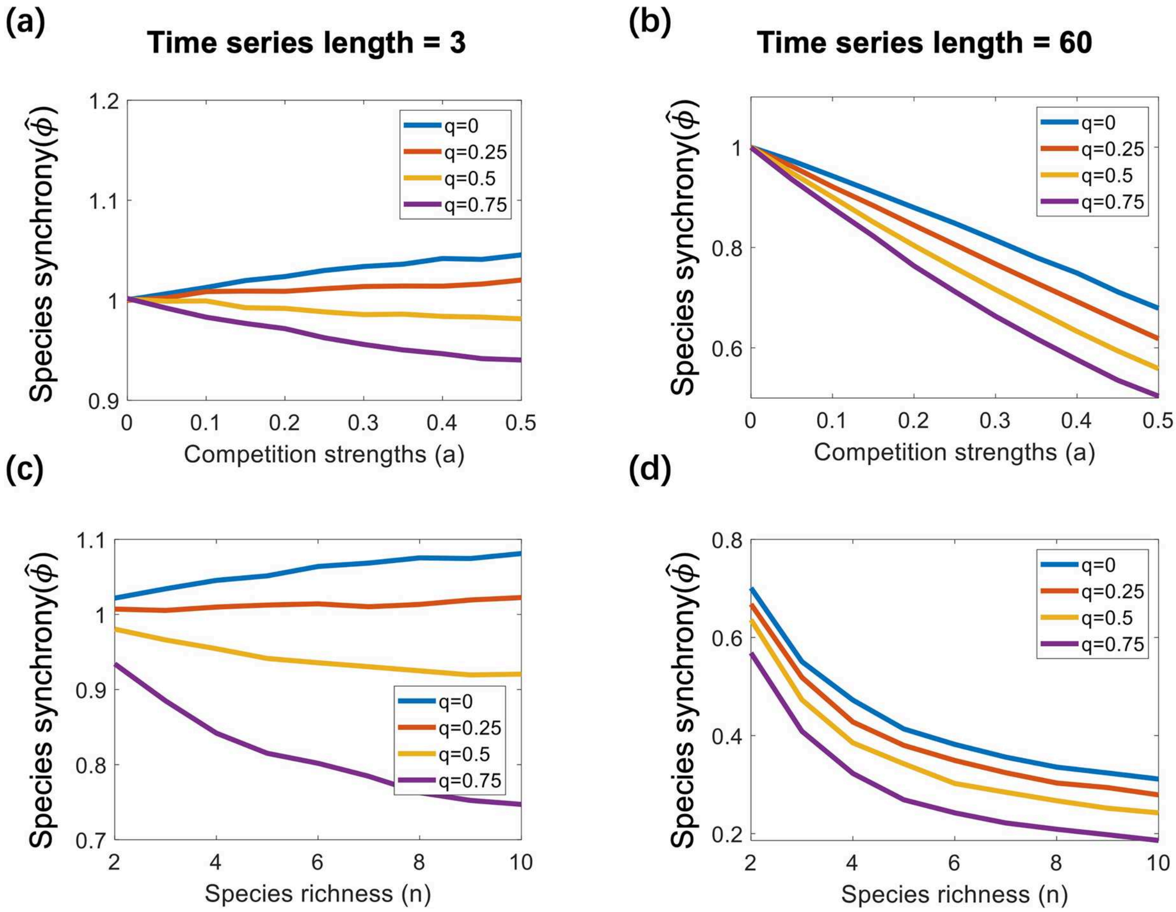


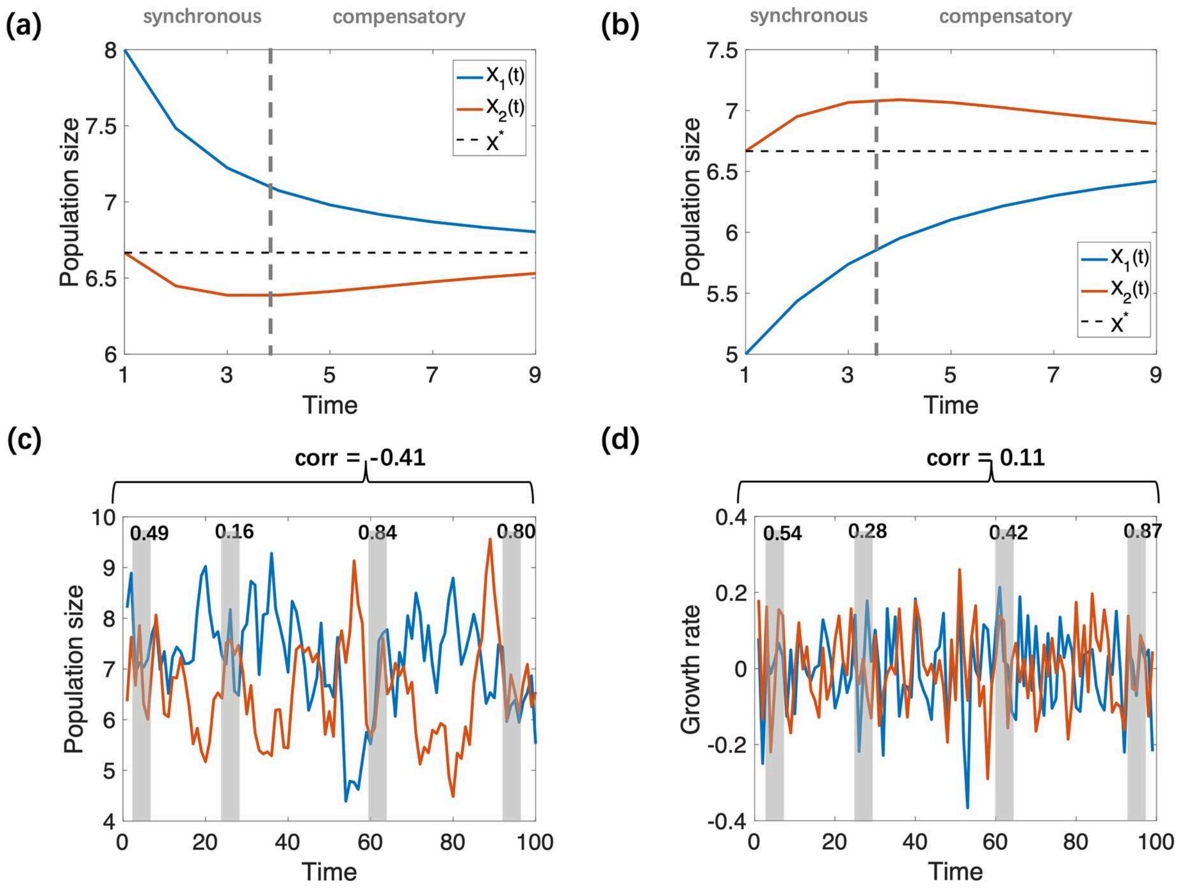
Extended Data Fig. 1 | Effects of time series length on synchrony under different scenarios of environmental noises. Effects of time series length on species synchrony in two-species symmetric Lotka-Volterra competition models under different scenarios of correlation in species environmental drivers (**a**) and temporal autocorrelation in environmental noise (**b**). Other parameters are same as in Fig. 2.



Extended Data Fig. 2 | Effects of competition strength and species richness on species synchrony in short and long time series under different degrees of species correlation in environmental response. Effects of competition strength (**a**,**b**) and species richness (**c**,**d**) on species synchrony in symmetric Lotka-Volterra competition models under different scenarios of correlation in species environmental response (ρ), in short (**a**,**c**) and long (**b**,**d**) time series. Other parameters are same as in Fig. 2.



Extended Data Fig. 3 | Effects of competition strength and species richness on species synchrony in short and long time series under different degrees of temporal autocorrelation in environmental noise. Effects of competition strength (**a**,**b**) and species richness (**c**,**d**) on species synchrony in two-species symmetric Lotka-Volterra competition models under different scenarios of temporal autocorrelation in environmental noise (q), in short (**a**,**c**) and long (**b**,**d**) time series. Other parameters are same as in Fig. 2.



Extended Data Fig. 4 | Competition-driven synchrony over short timescales versus compensatory dynamics over long timescales. (**a**) and (**b**) illustrates the responses of a two-species community to a pulse perturbation, with the blue and red curves representing the abundances of two species in a deterministic Lotka-Volterra competition model (that is without environmental noises; other parameters are same as for Fig. 2). Starting from equilibrium (both species at population size $X^* = 6.67$), a perturbation occurs that suddenly increased (**a**) or decreased (**b**) the abundance of species 1. Taking (**a**) for example. Following the perturbation, the two species both decreased, leading to synchronous dynamics in the short term. These synchronous dynamics were followed by compensatory dynamics in the long term, where the species 2 begins to increase once the abundance of the species 1 recover to a certain level. (**c**) and (**d**) illustrates the responses of the community to continuous random perturbations (that is, environmental noises). In (**c**), the population dynamics of the two species are positively correlated at short terms (for example, grey areas) but negatively correlated at long terms. The numbers above the grey areas represented the correlation coefficients during the observational window. In (**d**), the population growth rates of the two species are positively correlated at both short and long terms.

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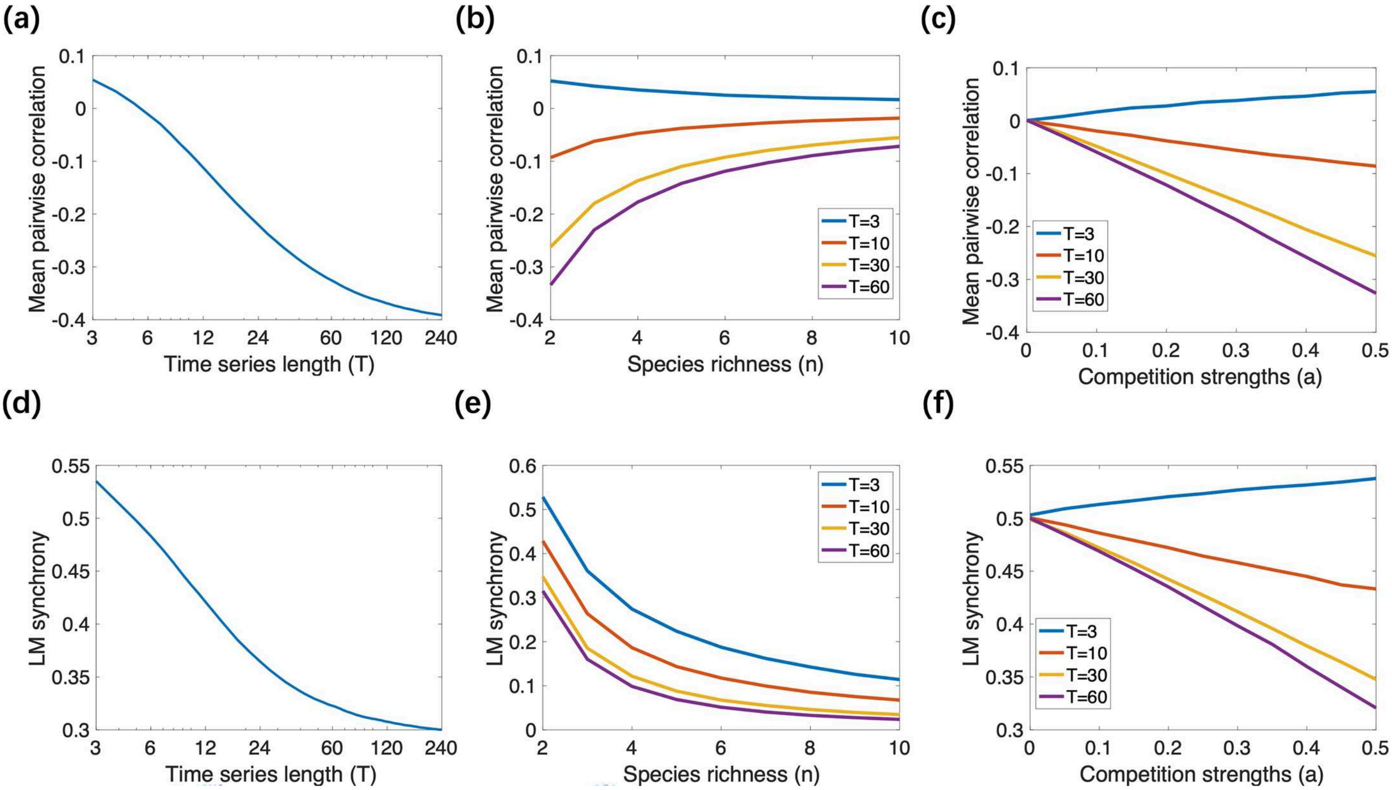
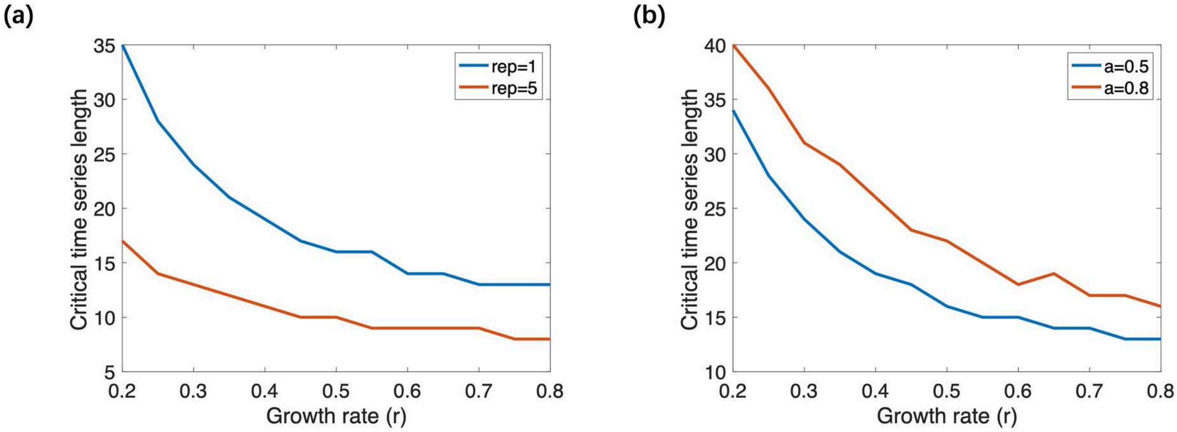


Extended Data Fig. 5 | Effects of time series length on two alternative synchrony metrics. Effects of time series length on two alternative synchrony metrics: the mean pairwise correlation coefficients (**a**-**c**), and the LM synchrony metric developed by ref. 14 (**b**-**d**). (**a,d**) show the change in synchrony with increasing time series length. (**b,c**) show the relationship of synchrony with species richness, and (**c,f**) show the relationship of synchrony with competition strengths. In (**a,d**), competition strength = 0.5 and species richness = 2; in (**b,e**), species richness = 2; in (**c,f**), competition strength = 0.5. Other parameters are same as in Fig. 2.



Extended Data Fig. 6 | The critical time series length for observing a negative regression slope between species diversity and synchrony. Relationship between the critical time series length and the population growth rate, under different scenarios of experimental replicates (**a**) or competition strength (**b**). Based on our symmetric competition models, the critical time series length is determined as the minimum time series length with more than 80% chance of observing a negative regression slope between diversity and synchrony. In (**a**), a number of replicates (1 or 5) was simulated for each level of species richness (S = 2, 3, …, 10), and the synchrony-diversity relationships were constructed across all simulated communities under given time series length. In (**b**), results under two different competition strengths were presented. Other parameters are same as for Fig. 2.

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Data collection	No software was used in data collection
Data analysis	Matlab and R codes to perform numerical simulations and data analyses are available at Figshare (Figshare link: https://figshare.com/s/52cd8c1a35f7cb8d801c).

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Reporting on sex and gender	Human participants, their data, or biological material are not involved in our research.
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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Our study uses theoretical approaches to explore the effects of time series length on species synchrony and tests the theoretical predictions by published empirical data. We uses published time series data of the biomasses and abundances of the species in nature and experimental plant communities.
Research sample	To test our theoretical findings, we uses published time series data of the biomasses and abundances of the species in nature and experimental plant communities with a total number of 2076 multivariate time series from different published datasets. Original datasets are available at https://cedarcreek.umn.edu/research/experiments/e120, https://cedarcreek.umn.edu/research/experiments/e141, and Supplementary Text S4 in https://www.pnas.org/doi/10.1073/pnas.1920405117#supplementary-materials.
Sampling strategy	To study the effects of time series lengths on the species synchrony in empirical data, for a community time series data of length T, we calculated the species synchrony of all subsetted time series of length t<T and use the mean value to represent the outcome of synchrony in time series length of t. Because we want to study the trend for each communities, we applied linear mixed-effects models to access the effects of time series lengths on the outcomes of species synchrony, with communities and studies (communities are nested in studies) as random factors.
Data collection	To study the species synchrony, we collected the multivariate time series data of biomasses or abundances of the communities with at least 10 time steps and more than one species have non-zero biomass or abundance in at least 3 time steps.
Timing and spatial scale	Timing and spatial scales vary in studies. We used annual and inter-annual time series data with more than 10 time steps. And the time span of the used time series are at least 15 years.
Data exclusions	Time series data with less than 15 years or less than 10 time steps are excluded. And the communities with only one species occurs in at least 3 time steps are excluded.
Reproducibility	Not applicable because published data were used and we did not perform experiments or observations..
Randomization	Multivariate time series data of communities are allocated into the studies where they were extracted from. When study the effects of time series lengths on the outcomes of species synchrony, we applied linear mixed-effects models with communities and studies as random factors.
Blinding	Not applicable because published data were used and we did not perform experiments or observations.

Did the study involve field work? ☐ Yes ☒ No

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☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
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☒	☐ Flow cytometry
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Plants

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