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Accounting for long-term directional trends on year-to-year synchrony in species fluctuations

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What determines the stability of communities under environmental fluctuations remains one of the most debated questions in ecology. Scholars generally agree that the similarity in year-to-year fluctuations between species is an important determinant of this stability. Concordant fluctuations in species abundances through time (synchrony) decrease stability while discordance in fluctuations (anti-synchrony) should stabilize communities. Researchers have interpreted the community-wide degree of synchrony in temporal fluctuations as the outcome of different processes. However, existing synchrony measures depend not only on year-to-year species fluctuations, but also on long-term directional trends in species composition, for example due to land-use or climate change. The neglected effect of directional trends in species composition could cause an apparent increase in synchrony that is not due to year-to-year fluctuations, as species that simultaneously increase (or decrease) in abundance over time will appear correlated, even if they fluctuate discordantly from year to year. The opposite pattern is also conceivable, where different species show contrasting trends in their abundances, thus overestimating year-to-year anti-synchrony. Therefore, trends in species composition may limit our understanding of potential ecological mechanisms behind synchrony between species. We propose two easily implementable solutions, with corresponding R functions, for testing and accounting for the effect of trends in species composition on overall synchrony. The first approach is based on computing synchrony over the residuals of fitted species trends over time. The second approach, applicable to already existing indices, is based on three-terms local variance, i.e. computing variance over three-years-long, movable windows. We demonstrate these methods using simulations and data from real plant communities under long-term directional changes, discussing when one approach can be preferred. We show that accounting for long-term temporal trends is necessary and that separation of effect of trends and year-to-year fluctuation provides a better understanding of ecological mechanisms and their connections with ecological theory.

Keywords: anti-synchrony, compensatory dynamics, stability, temporal trend, three-term local variance, year-to-year fluctuations

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Introduction

Ecosystems are subject to temporal variations in environmental conditions including various stressors and disturbance events. An important aspect of the functioning of ecosystems is their temporal stability, which incorporates their responsiveness to these factors. Despite historical interest in the effect of biodiversity on the temporal stability of communities, relatively little consensus has been achieved on the importance of different mechanisms regulating stability. Both theoretical considerations and empirical data show that the degree of year-to-year synchrony in temporal fluctuations between species, i.e. of sizes of individual populations, is an important determinant of community stability (McCann 2000, Hautier et al. 2014, Song and Yu 2015). A higher synchrony between populations (i.e. concordant fluctuations of species abundances through time) leads to lower stability. On the contrary, when the fluctuations are discordant, and particularly when one species is compensated by another, a higher stability is expected. Any lack of perfect synchrony in a community is generally referred to as 'asynchrony', with greater asynchrony causing greater stability. The maximization of asynchrony in a community (i.e. when negative covariation and compensation between species dominate) can be referred to as 'anti-synchrony'.

Several indices of synchrony have been suggested and applied to both communities along environmental gradients and biodiversity experiments (Houlahan et al. 2007, 2018, Loreau and de Mazancourt 2008, Gross et al. 2014, Lepš et al. 2018). Researchers have interpreted the community-wide degree of synchrony in temporal abundance fluctuations as the outcome of different ecological processes. It is usually expected that high synchrony can be caused by concordant species responses to fluctuations in environmental conditions (Loreau and de Mazancourt 2008). Because soil conditions are usually considered stable (at least in natural and semi-natural systems), the main driver of population fluctuations, and thus also of synchrony, is likely weather fluctuations across individual years (Craine et al. 2012). In temperate systems, most species have a generally concordant physiological response to favourable and unfavourable conditions. For example, most species prefer warm springs with sufficient precipitation and will all increase in abundance when these favourable conditions exist, and vice versa. Such concordance in response is never perfect, leading to some degree of asynchrony, partially due to demographic stochasticity or partially discordant responses of individual species to the combination of weather conditions in a given year (Loreau and de Mazancourt 2008). In contrast, competition among species is generally expected to increase asynchrony, or even anti-synchrony, specifically leading to compensatory dynamics (Tilman 1996, Gross et al. 2014, Brown et al. 2016); then, years with unfavourable weather conditions might be advantageous for weak competitors if such conditions harm superior competitors. These effects would cause negative correlations among species (anti-synchrony) and

potentially lead to compensatory dynamics, although this hypothesis has generated some controversy (McCann 2000, Houlahan et al. 2007).

While existing indices should respond well to year-to-year species fluctuations and the mechanisms producing them (Götzenberger et al. unpubl.), there is an often-neglected mechanism that has the potential to both increase and decrease the values of synchrony indices, irrespective of year-to-year fluctuations: the effect of directional trends in species composition (Fig. 1). If this is the case, the values provided by the existing synchrony indices will not reflect only year-to-year fluctuations. For example, successional changes after some disturbance (Osbornová et al. 1990), or long-term effects of increasing nitrogen depositions (Stevens et al. 2011), often lead to directional changes in species composition. In many cases of secondary succession, the decline of early successional species is compensated for by an increase of late successional species and the total biomass remains quasi-constant (Osbornová et al. 1990). In this case, the directional changes in species composition cause a negative correlation between early and late successional species, leading to negative synchrony measure values, which would 'wrongly' indicate compensatory dynamics, even if species are fluctuating synchronously from year to year. On the contrary, in many primary successions, particularly in harsh conditions, the community starts with (sometimes extremely) low biomass of all species, and most of the species increase during the first years of succession. If this pattern is analysed using classical synchrony indices, we will obtain highly positive synchrony values even if the year-to-year fluctuations between species are independent of each other or even compensatory (Fig. 1). The reason for this potential bias effect of long-term directional trends is that synchrony indices are usually calculated from time series but do not take into account the order of the observations. Consequently, they often cannot distinguish year-to-year variability from the potential effect of directional trends.

Such long-term directional trends, potentially masking year-to-year synchrony in species fluctuations, are very probably quite omnipresent, even in communities that are generally considered stable. For example, in a 14-yr time series of moth light trap data from an alder carr undisturbed forest (where no successional trends were expected), both positive and negative trends were found in many more species than expected by chance (Lepš et al. 1998). Similarly, in analyses of various time series of agricultural and forest pest insect populations in the United States Walter et al. (2018) found that half of the time series exhibited a long-term trend. Thus, synchrony values can also be affected by these trends. Fast species turnover, or directional dynamics, can also be observed after establishment of experimental treatments (Lepš 1999) – some species are supported by the treatments and some are suppressed. When sowing species mixtures (typical for biodiversity–ecosystem function, BEF, experiments), some species establish fast, but due to colonization/competition tradeoffs, they might be outcompeted/suppressed by slowly growing

Figure 1. Conceptual figure depicting one case where long-term species trends could mask year-to-year fluctuations and how the two proposed methods account for this by detrending. Each species is represented by a set of dots of the same colour, with one dot per year. For each species a line interpolating these points is displayed, representing the overall fitted trend. In the case shown, the common positive trend across species would cause an overall synchrony signal through the sampling period, even if the species fluctuate in an opposing manner to each other in all years except one, which should result in anti-synchrony between the two species. The first method is based on the residuals of the fitted line for each species, shown in the panel below. Negative covariation between these residuals would indicate anti-synchrony. The second method is based on a movable three-year window computing covariation only across three consecutive years ('three-terms local variance').

ones through time. Thus, even in short-term experimental setups (often used to evaluate patterns of species synchrony and the resulting stability) directional trends could have overwhelming effects on BEFs, which have not been accounted for to date in the literature.

The importance of directional trends in time series calls for specific methods to disentangle the effect of such trends and year-to-year fluctuations on synchrony indices. Several approaches have been developed in ecological studies for dealing with different directional trend types. In this study, after reviewing such earlier approaches, we propose two easily implementable solutions, with corresponding R functions, designed to work with typical time series in ecological studies. We test the performance of these two methods using artificially generated data where we know what patterns the methods should detect. Finally, we illustrate the use, and importance, of the methods using two time-series data from our own experiments and discuss when one approach can be preferred over the other.

Previous approaches

The idea of correcting directional trends in time-series or spatially structured data has a decent tradition in ecology. Cattadori et al. (2000) used detrended time series to describe the spatial patterns of fluctuations in (log-transformed) abundance of gamebird from the Dolomitic Alps. They did so because most of the time series exhibited a decreasing trend. Such trend was removed by fitting a polynomial model and using the residuals for consequent temporal and spatial synchrony analysis. A similar reasoning was applied by Morrongiello and Thresher (2015) when assessing spatial and temporal synchrony between individuals of a commercially exploited fish in southeast Australia. They detected both age effects on individual growth and a regionally coherent signal of increasing average growth rate through time, a trend related to oceanic warming. They 'corrected' for these effects by considering year and individual age in their modelling approach and thus focusing on the magnitude of individual-specific deviations from average growth in each time interval. This approach was explicitly related to already existing methods such as time-series-based chronological methods (including dendrochronological studies of tree rings), which detrend individuals' increments by removing age-related trends (Black 2009). The identification of climatic trends, and the use of deviation from such trends (by analysing the corresponding residuals), represents a similar approach which has been used in climatology (Wu et al. 2007).

Following the theoretical framework of Loreau and de Mazancourt (2008), Tredennick et al. (2017), used population growth rates, rather than raw abundances, as the input variable for measuring synchrony. Because the growth rate is calculated from subsequent abundances (if time step, Δt , is one year, for example, then growth rate = $\ln(\text{abundance}_{t+1}) - \ln(\text{abundance}_t)$), this approach filters out the effects of concordant/discordant trends. However, growth rates cannot be calculated if the time series contain zeroes (i.e. if a species is absent from a sampling point in a given time period), because the log-transformation is applied. Moreover the estimates of growth rate could be rather imprecise for species with low abundances (because the measurement error might

be comparable with the extend of real dynamics). This makes such approach useful for studies on frequent and dominant species (Tredennick et al. 2017), but not suitable for measuring synchrony when more infrequent or rarer species are involved.

Another approach that has proven useful is to assess synchrony at different temporal scales, based on classical methods of time series analysis, such as spectral or wavelet analyses. For example, Vasseur and Gaedke (2007) considered different temporal scales, from approximately one month to one year, to capture recurrent dynamical patterns and ignore variance generated from long term changes in the eutrophication status of Lake Constance. They show compensatory dynamics for phytoplankton and zooplankton species which occurs regularly at scales ranging from six months to one year while synchronous dynamics dominate at most other scales. Spectral analysis, and similarly wavelet analyses (Vasseur et al. 2014) enables data measured over time (or other dimensions, e.g. geographical space) to be represented as the sum of many sine waves of different frequency. In a similar fashion, temporal patterns in pest populations were characterized using a combination of wavelet analyses and autoregressive moving-average model fitting (Walter et al. 2018). The wavelet and spectral analyses estimate the amount of variation in a time series attributable to a particular frequency (scale) at a particular point in time. Unfortunately, because these approaches require very long data series (i.e. either data at a very high temporal resolution or of very long time duration), they usually cannot be applied to data collected once a year (usually at the top of vegetation season), which are frequently collected in ecological research, because they are too short.

The last set of methods we review here, and which are among the methods proposed later in this study, are derived from analyses of species spatial associations. Traditionally, these methods analysed abundances of species in transects (belts of small quadrats), attempting to find scales of clumping by changing spatial scales. Later these methods were extended to analyse also scales of species spatial associations and to filter out the spatial trends (Hill 1973, Lepš 1990, Dale 2000). In this sense, Hill (1973) introduced the concept of two-term and three-term local variances, in which variance is computed from the differences between neighbouring quadrats (two neighbouring quadrats in the case of two-term local variance, and from deviation of the central quadrat from the linear trend within three neighbouring quadrats for three-term local variances). These two methods are very similar to each other and give also very similar results (Supplementary material Appendix 1). Common indices of synchrony, which are also based on measures of species variance, can therefore be computed with a similar approach, where instead of contiguous quadrats, contiguous sampling periods could be used (method 2 below). In principle, the two-term local variance resembles conceptually and computationally the approach by Tredennick et al. (2017) using population growth rates, because both these methods use the difference between

neighbouring observations (in Tredennick's et al. 2017 case after log transformation).

Method 1 – decomposition of trend and detrended synchrony

One group of useful indices of synchrony are those that compare the actual synchrony in fluctuations against the null model of independent fluctuations of individual populations. This null model is used consistently, e.g. in the formulation of the stabilizing effect of species richness due to the portfolio effect of Doak et al. (1998). These indices include that of Gross et al. (2014), its weighted form (Bluethgen et al. 2016) and the log(variance ratio). The latter is the log-transformed ratio of variance of community biomass and expected variance if the individual populations fluctuate independently (Lepš et al. 2018), based on the original variance ratio of Schluter (1984). For all of these indices, zero corresponds to the situation where the individual populations fluctuate completely independently of each other (or positive and negative covariances compensate for each other), positive values mean partial synchronization (i.e. prevalence of positive correlations/covariances among populations) and negative values mean anti-synchrony (i.e. prevalence of negative correlations).

Though these indices partially differ among one another, they are based on covariances (or correlations, which are derived from covariances) among species (or among species and the rest of the community). In the case of ecological community data, the individual variables are generally biomass values of individual species (x_i), and the sum is total community biomass (other measure of abundance, as number of individuals can be considered as well; here we consider biomass as an example). If species fluctuate independently, then:

$$\text{var}\left(\sum_{i=1}^{nsp} x_i\right) = \sum_{i=1}^{nsp} \text{var}(x_i) \quad (1)$$

where x_i is biomass of species i , and $\sum x_i$ is biomass of the whole community. This indicates that the variation in total community biomass is equal to the sum of variances of individual species. If there is some correlation structure, meaning that there are some non-zero off-diagonal elements in the variance–covariance matrix, then:

$$\text{var}\left(\sum_{i=1}^{nsp} x_i\right) = \sum_{i=1}^{nsp} \text{var}(x_i) + 2 \sum_{i,j>1}^{nsp} \text{covar}(x_{ij}) \quad (2)$$

Variance and covariance corresponds here to variability over time (and does not take into account the order of the observations). The difference between the observed variance of community biomass and the variance expected under the assumption of independence (called expected variance) corresponds to the sum of covariances in the variance–covariance matrix. Note that the common correlation coefficient,

Pearson r , is in fact covariance standardized by the variances of the two variables, so that the synchrony measures based on correlations (Gross et al. 2014) and covariances are closely related. We consider using covariances advantageous because this implicitly includes weighting the importance of each species by its proportion in the community (though the correlation-based methods can also be weighted, see Bluethgen et al. 2016).

The first method proposed in this study is based on the idea of separating the effect of directional trends on synchrony from a 'detrended' component. This is similar to some of the approaches already discussed in the 'Previous approaches' section above but it further allows to attribute temporal (co)variation to either trends and detrended components. For this we propose using the decomposition of the sum of squares in a regression. The first step is to calculate the simple linear regression of the values on time with n observations in the time series. Then, the total sum of squares (i.e. sum of squares of deviations of individual observations from the mean) can be decomposed into the regression and residual sum of squares (Zar 2010):

$$SS_{\text{Tot}} = SS_{\text{Regr}} + SS_{\text{Resid}} \quad (3)$$

If we divide the SS by $n - 1$, we get:

$$\text{var}_{\text{Tot}} = \text{var}_{\text{Regr}} + \text{var}_{\text{Resid}} \quad (4)$$

where var_{Tot} is the variance of the observed values, var_{Regr} is the variance of fitted values (note that here we divide SS_{Regr} by $n - 1$, so we get variance of the fitted values, not the MS_{Regr} obtained by dividing by corresponding df in a classical ANOVA of the regression model), and $\text{var}_{\text{Resid}}$ is the variance of residuals.

We can define a synchrony measure ($Stotal$ – total synchrony) as the sum of all (above- and below-diagonal) covariances (i.e. the difference between observed and expected variances of the total) divided by the expected variance, i.e.

$$Stotal = \frac{\text{var}\left(\sum_{i=1}^{nsp} x_i\right) - \sum_{i=1}^{nsp} \text{var}(x_i)}{\sum_{i=1}^{nsp} \text{var}(x_i)} = \frac{2 \sum_{i,j>i}^{nsp} \text{covar}(x_{ij})}{\sum_{i=1}^{nsp} \text{var}(x_i)} \quad (5)$$

Positive values mean (partial) synchrony (i.e. prevalence of positive covariances), and negative values anti-synchrony (i.e. prevalence of negative covariances). If instead of the covariance of original values we use the covariance of the fitted values (i.e. of values predicted by the linear regression on time), we will get the part of synchrony that can be ascribed to the directional trend, $Strend$. If we use the covariance of residuals of this regression, we will capture the characteristics of the synchrony of the residuals, i.e. the synchrony not due to trends, which we call $Sdetrended$. Note, that all the values are standardized by the expected variance of the total, so that the denominator remains the same for all three synchrony

measures, $Stot$, $Strend$ and $Sdetrended$. As it follows from Eq. 4, we can decompose total synchrony into two components:

$$Stotal = Strend + Sdetrended \quad (6)$$

so that we decompose synchrony values into the part that is due to the trend and the part that is due to residual variation ('detrended'). The latter can be, with some caution, interpreted as the year-to-year variation.

The S value is not symmetric, and it is positively skewed. Its minimum value is -1 , whereas positive values are not restricted (or are restricted only by the number of species and relative variability and representation of individual species). The closely related index of log variance ratio (i.e. $\log\left(\text{var}\left(\sum_{i=1}^{nsp} x_i\right) / \sum_{i=1}^{nsp} \text{var}(x_i)\right)$) is better centred on zero and the two indices can be transformed into each other, e.g. $\log \text{variance ratio} = \log(1 + Stotal)$, which allows centring around zero. This is important for statistical testing as values centred around zero allow for symmetrical properties, i.e. we expect that values will be roughly symmetrical around zero, if the fluctuations are independent. However, with the log-transformation, the values are no longer additive, and so decomposition into the trend and detrend is not possible. Consequently, for descriptive purposes, we keep the formulation in Eq. 6 (to enable the decomposition of the total value of synchrony into the year-by-year and trend components), whereas, for statistical testing of deviation of the S value from zero, we suggest using the transformation $\log(1 + S)$ (for values of S close to zero, these values are linearly related with $\log(\text{variance ratio})$).

Method 2 – three-term local variance

Another possible approach to filter out the pervasive effects of directional trends on synchrony is the use of the three-term local variance (T3), originally introduced by Hill (1973) in the context of spatial pattern analysis. As we show here, it can be adopted for use with temporal data. T3 is then calculated as:

$$T3 = \frac{\sum_i^{n-2} (x_i - 2x_{i+1} + x_{i+2})^2}{6(n-2)} \quad (7)$$

where n is the number of years in the time-series, i is the year index and x_i is the abundance of a species in year i . Thus, T3 does not compute variance as the average of squared deviations from the overall mean, but averages variance estimates by moving a window over the data (of three years in the case of temporal data). Within the three-year window, the variance is estimated from the squared difference of the middle year and average of the year before and after (so that, if there is a perfect linear trend within these three years, the difference is zero). If there is no temporal trend in the data, then T3 is an estimate of classic variance (i.e. for long-time series without a trend the values of T3 and classical variance will

converge; see below). In other words, we expect that in the case of no temporal trends and long-term data, the results will not be affected by using T3 instead of the classic measure of variance.

We can then use T3 to calculate synchrony, so it is important to be aware that, differently from method 1 described above, this T3 approach can be used for all already existing indices of synchrony, including Loreau and de Mazancourt's (2008) ϕ , just by replacing the way variance and covariance are computed. For the correlation-based indices (such as η of Gross et al 2014), or its weighted form (Bluethgen et al. 2016), in the general formula for the correlation coefficient:

$$r_{xy} = \frac{\text{cov}_{xy}}{\sqrt{\text{var}_x \text{var}_y}} \quad (8)$$

with

$$\text{cov}_{xy} = \frac{\text{var}_{x+y} - (\text{var}_x + \text{var}_y)}{2} \quad (9)$$

the variances are replaced by T3. In case of the variance ratio, to obtain the same range of values as for S in the decomposition method above, we can present a variance ratio – 1, and use $\log(\text{var ratio})$ for testing. As such:

$$\text{ST3} = \frac{\text{T3}\left(\sum_{i=1}^{nsp} x_i\right) - \sum_{i=1}^{nsp} \text{T3}(x_i)}{\sum_{i=1}^{nsp} \text{T3}(x_i)} \quad (10)$$

The three-term local variance (T3) is a minor extension of two-term local variance. Both have been proposed for the same purpose of detrending spatial data by Hill (1973). Their results are highly correlated (Supplementary material Appendix 1), but both theoretical considerations, and also the analyses of simulated data (Lepš 1990) show that T3 is slightly more efficient in removing trends. We thus decided here to use the three-term version (T3) only. The R script for both the methods is provided in the Supplementary material Appendix 2.

Data used for testing

Simulated data

We simulated simple communities with desired patterns of temporal fluctuations, following a simulation model developed by Götzenberger et al. (unpubl.; see Supplementary material Appendix 2 for the R script). The total number of species in the community was set to either 10 ('low richness') or 30 species ('high richness'). Each species was randomly assigned a mean abundance value stemming from a geometric series, representing its mean abundance over the years. The relative abundance of the most dominant species was equal to 0.4. To each mean abundance, a variance was assigned according to a hypothetical relationship between the mean and the

variance of the species abundances in the community (mean–variance scaling; Taylor 1961, Lepš 1993). This relationship of mean with variance was quantified by the slope of the linear dependence of $\log(\text{variance})$ on $\log(\text{mean})$, and was equal to 1.6, similar to frequently observed values in nature. We also considered simulations with different patterns for dominance structure and mean–variance scaling to explore a more complete parameter space (Götzenberger et al. unpubl.), but here we just present typical values after verifying that results were consistent after changing simulations parameters.

Once species richness and the species' overall means and variance of abundances were defined, they were used as the basis to simulate species fluctuations. For this, we created an annual environmental cue representing, for example, annual rainfall, sampled randomly from three possibilities, each occurring with a probability 0.33: representing negative deviation (–0.5), normal (0) and positive deviation (+0.5) from the long-term mean. For each species we determined how strong its abundance fluctuates according to this environmental cue by assigning a species response (R_i) to this environmental cue. The species response, R_i , was drawn from a normal distribution whose parameters depended on one of three possible scenarios: synchrony, anti-synchrony, or random fluctuations at the community level. To simulate synchrony, the majority of species had a similar response to the environmental cue, i.e. R_i had a mean and standard deviation equal to 1 (which means that most species would increase when the environmental cue increases and vice versa). To simulate anti-synchrony, R_i had mean equal to 1 for one half of the species, and –1 for the other half with a standard deviation equal to 1 for both, creating two species groups that mostly respond oppositely to the environmental fluctuations. In addition, a species' affiliation to these two groups depended on species' abundance rank, so that, for example, the two species that are closest in the abundance ranking have opposite R_i values. In this way, replacement/competition between similarly abundant species was approximated as an additional process underlying asynchronous fluctuations. To simulate the random scenario, R_i was set to 0 for all species so that the environmental cue was absent and species only fluctuated randomly according their value of mean abundance and standard deviation, i.e. the abundance of species i in year j was a random draw from a normal distribution with the species-specific mean abundance and standard variation. For the non-random scenarios, the mean was multiplied by the term combining environmental cue and species response, i.e.

$$A_{ij} = N\left(\mu = a_i \times (1 + r_j \times R_i), \sigma = s_i\right) \quad (11)$$

Where A_{ij} is the abundance of species i in year j , a_i is the mean abundance of that species, R_i its environmental response, r_j the yearly environmental cue and s_i the standard deviation around the mean a_i , as defined by the mean–variance scaling. Simulating A_{ij} in the described way can lead to negative abundance values, in which case A_{ij} was set to zero, which

represents the case of several species which are frequent in a community but do not appear within every sampling.

To test the effects of long-term directional trends and measuring synchrony with the proposed methods, we simulated long-term trends for part of the simulated data. Instead of simulating only an environmental cue that would stochastically change from positive to negative across years (resulting in ‘up and down’ fluctuations of species), the cue was a vector of constantly increasing values with time. Each species responded to this cue with a species-specific response, T_i , that was drawn from the same three different distributions as R_i to create three cases: a case where most species had a long-term positive trend, leading to a steady increase of individual species abundances over time (‘common trend’); had no long-term trends (‘no trend’); or half of the species would increase over time and the other half decrease (‘contrasted trends’). This resulted in additional terms in Eq. 11, namely T_i and t_j as the trend response of species i and t_j for the yearly increase in biomass compared to t_{j-1} :

$$A_{ij} = N(\mu = a_i \times (1 + r_j \times R_i) \times (1 + t_j \times T_i), \sigma = s_i) \quad (12)$$

The three scenarios of year-to-year species fluctuations (producing synchrony, anti-synchrony or random fluctuations) were then crossed with the three types of long-term directional trends (i.e. common trend, no trend, contrasting trend), resulting in nine possible combinations of trend–fluctuation scenarios. Within each scenario, 100 replicate communities for each of the two predefined richness settings (i.e. 10 and 30 species) were created by simulating fluctuations for a period of 40 yr.

Field data: Ohražení species-rich, semi-natural meadow

We used data from the Ohražení experiment, established in South Bohemia, Czech Republic (48°57'0"N, 14°36'0"E, altitude 510 m). The experiment was established in 1994, but in a recent analysis of synchrony in the experimental communities (Lepš et al. 2018), only data from 1999 to 2014 was used firstly, to avoid initial trends that resulted from introduction of the treatment before 1999, and secondly, because the sampling was fully consistent between 1999 and 2014. We thus consider this period most suitable for allowing comparisons and assume that the data should be trend-free (i.e. without any a priori effect of trends). The experiment was established in factorial design, with two treatments – 1) fertilization consisting of annual application of 65 g m⁻² of a commercial NPK fertilizer (12% N as nitrate and ammonium, 19% P as P₂O₅ and 19% K as K₂O), and 2) removal of the dominant species *Molinia caerulea*. This yields four factorial combinations, and we replicated each three times. The experiment was established in a traditionally managed species-rich meadow (regularly mown), and the biomass was determined each year from the central 0.5 × 0.5 m quadrat of 2 × 2 m plots, permanently marked in the field (i.e. results are not confounded

by spatial variability). Each year, the biomass was cut at the peak of the vegetation season (corresponding to the time of traditional mowing), all the biomass was sorted into species, oven-dried and weighed. We thus have a continuous series of biomass values of all species for 16 yr.

In addition to analysing the complete time series, we also split the 16-yr period into three periods within the 1999–2014 range; the first six years, the second six years (from year 7 to year 12) and the final six years (from year 11 to year 16, thus with two years of overlap with the second period).

A two-way ANOVA was used to test the effect of fertilization and *Molinia caerulea* removal on the different computations of synchrony. We also tested whether the grand mean (overall mean across all observations) is different from zero (i.e. whether on average, the communities show synchrony or anti-synchrony). The grand mean difference for zero was tested against the residual variability in the two-way ANOVA.

Field data 2: Benešov long-term biodiversity sowing experiment

We used data from the Czech site of the CLUE experiment (Van der Putten et al. 2000). The experiment was designed as a biodiversity ecosystem function (BEF) experiment, sowing species mixtures of varying species richness. However, unlike most other BEF experiments the experimental plots were open to natural colonization, as colonizers were not weeded. There were three treatments: 1) natural colonization, where the plots were left without any sowing open to natural colonization, 2) sowing a high-diversity seed mixture, composed of 15 species (five grasses, five legumes, five non-leguminous forbs) and 3) a low-diversity mixture, where mixtures of four species were sown (two grasses, one legume and one forb, which were taken from the set of the 15 species sown in mixtures, different in each replicate). The community composition thus concerns both sown species (that with time also spread to plots where they were not sown) and natural (unsown) colonizers.

These plots have undergone quite pronounced successional changes (Van der Putten et al. 2000), typical for old-field succession, with replacement of arable weeds with more competitive species. Such competitive species, in sown plots, interfered with establishment and/or maintenance of sown species, particularly in years 3–8 of the experiment (i.e. 1998–2003). We selected these years to demonstrate the ability of the decomposition method to separate trend and year-to-year variation effects, and also to show that the contributions of trend and year-to-year variation might differ among the treatments.

The experiment was established in five blocks. Each block contained three 10 × 10 m plots with one treatment each. In each of these plots, cover was visually estimated in 12 permanent 1 m² quadrats. To minimize observer error, the values of the 12 quadrats were averaged, and provide the estimate of species composition in the main 10 × 10 m plot. We thus analysed the time series of six years (1998–2003) in five plots of each treatment (15 plots together). We expect

pronounced successional dynamics in these plots, with their effects possibly differing between the treatments. Preliminary constrained ordination analyses (RDA, Šmilauer and Lepš 2014) has shown that time, as a quantitative variable (reflecting the linear trend in species composition), was a significant predictor in all the treatments, but explained most of the within-plot variation in the natural colonization treatment (66%), less in the high-diversity treatment (54%) and least in the low-diversity treatment (25%). The low values of explained variability were probably a result of large inter-plot variation caused by the fact that in each block a different seed combination was sown.

To test the effect of the new methods in the analyses we tested the difference between the three treatments within each synchrony measure (Stotal, Strend, Sdetrended, ST3) using an ANOVA and a corresponding Tukey's honest significant difference test.

Data deposition

Plot data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.6054537>> (Lepš et al. 2019). R-code to simulate temporal communities as described in 'Simulated data' section is available in Supplementary material Appendix 2, together with R code to calculate synchrony indices, corresponding help files, and a vignette. Code also available from <<https://github.com/larsito/tempo>>.

Results

Simulated data

The analyses of simulated data showed that the methods considered performed well (Fig. 2). In the case of no long-term trends ('no trend', Fig. 2A) we expected the synchrony in the random scenarios not to be different from zero, which was indeed the case for all measures of synchrony (i.e. Stotal, Strend, Sdetrended and ST3). Similarly, the simulated scenarios of synchrony and anti-synchrony were convincingly detected by the indices (positive synchrony in the first case and negative in the second case) and results were consistent between Stotal, Sdetrended and ST3. In fact, in the absence of trends we expect similar results whether or not we use the new methods proposed. There was, however, a very small but significant deviation from zero of average synchrony values in the Strend case: positive for the synchrony scenario and negative for the anti-synchrony scenario. We will consider these cases in the discussion.

Results for the case of species having a 'common trend' show the desired effects of the methods proposed (Fig. 2B). For example, random species fluctuations would be 'classified' as synchronous without using the methods proposed (Fig. 2B, Stotal, red boxplot, with positive values). Similarly, for Stotal, all synchrony values were, on average, positive, irrespective of the fluctuation scenario considered. In other words, even anti-synchrony in year-to-year fluctuations

Figure 2. Results of the simulations. The three different panels report results for the following scenarios: a lack of long-term trends (A: no trend), one where species have a common trend (B: all species increasing in time) and one with contrasted trends (C: half the species increasing in time and the other half decreasing). Within each of these scenarios we considered three scenarios: species would fluctuate randomly ('random'), would covary positively ('synchrony'), or negatively ('anti-synchrony'). For each case we calculated an overall synchrony (Stotal) and decomposed this into the components due to long-term trends (Strend) and the effect beyond these trends (Sdetrended). We also computed the three-terms local variance (ST3). Asterisks below each boxplot reflect cases which, on average, were significantly different from zero (two-tailed tests). Black asterisks, or lack of them, indicate results expected by the methods proposed, i.e. to reliably remove trend effects. Red asterisks indicate significance not expected under the perfect functioning of the indices. These panels report the case with communities having a total of 10 species (for the 30-species case see Supplementary material Appendix 3).

would be ‘classified’ as synchronous using traditional indices: a case also exemplified in the conceptual example in Fig. 1, where a common trend would mask year-to-year fluctuations. Using the detrending approach, the values became, on average, very close to zero and with ST3 the values were not different from zero for the random scenario. In the case of Sdetrended values the detrending does not seem to be able to completely remove the effect of species trends but produces values very close to zero anyway.

In the case of species having ‘contrasted trends’ (Fig. 2C) the methods proposed worked as well as in the case of a ‘common trend’. Random species fluctuations would be detected as anti-synchronous (Stotal, red boxplot, with negative values). Using the detrending approach (Sdetrended) the values became very close to zero and with ST3 the values were not different from zero. In the case of Sdetrended values the detrending does not seem to be able to completely remove the effect of species contrasted trends but does produce values very close to zero. The synchrony due to trends (Strend) was always negative, as expected, irrespective of the fluctuation scenario considered. In the case of contrasted trends and synchrony between species (grey boxplots Fig. 2C), clear positive values of synchrony were only detected with the Sdetrended and ST3 approaches, as expected. With anti-synchrony and contrasting trends between species (blue boxplots Fig. 2C) a large part of the negative synchrony between species was also removed by detrending (Sdetrended) and both ST3 and Sdetrended values were still significantly lower than zero. The case of contrasting trends produced the only differences between simulations using a richness of 10 species (Fig. 2) and a richness of 30 species (Supplementary material Appendix 3 Fig. A1). In the latter case, negative synchrony (anti-synchrony) was more difficult to detect compared to the former: an issue which, as we discuss below, applies to most indices of synchrony (Götzenberger et al. unpubl.).

Field data – Ohrazení

Across the three different periods considered, and all the periods together, fertilization was the main driver of changes in synchrony between species, and mostly decreased the value of synchrony indices (Fig. 3). These results confirm those already published by Lepš et al. (2018). In general, except for the first six-year period, the effect of fertilization was not due to common or contrasted species trends. In the first six years though, the effect of fertilization disappeared when considering Sdetrended and ST3 values. This suggests that the greater asynchrony in fertilized versus unfertilized conditions was likely due to the increase of some species and decrease of others following the beginning of the fertilization in the first years of the experiment.

While the second six years considered gave results similar to all 16 yr together, the last six years generally showed negative synchrony (anti-synchrony) between species caused by both contrasted species trends (Strend values below zero) and also Sdetrended values (also below zero), irrespective of the treatments. With T3 this negative synchrony was less marked

and overall synchrony was not different from zero, although there were also no treatment effects. Overall, using ST3 we observed fewer negative, or more positive synchrony values using all years together, in the first period only and in the last period only.

Field data – Benešov

The analyses demonstrated that in all treatments negative synchrony prevailed, suggesting some compensatory dynamics (Fig. 4). When the total variation was used (Stotal) there were significant differences among treatments, with natural colonization showing the most negative synchrony, and the high-diversity seed mixture showed the least negative synchrony values. However, when we decomposed synchrony values, the anti-synchrony caused by trends was actually most pronounced in natural colonization, and less for the high-diversity mixture (similarly as the Stotal). On the contrary, the differences in Sdetrended synchrony are not significant, and ST3 values also do not differ among treatments. Thus, the decomposition demonstrated that the highest total anti-synchrony in natural colonization is not based on species year-to-year fluctuations, but mostly governed by opposite trends (concordant with the most pronounced successional dynamics).

Discussion

We show that correcting for long-term directional trends when evaluating synchrony in year-to-year fluctuations in natural communities is both necessary, and feasible, with the methods proposed. The analysis of simulated data demonstrated the ability of the proposed methods to detect year-to-year species fluctuations and to decompose total synchrony into those parts caused by the trend and by the year-to-year fluctuations. The analyses of empirical field data demonstrated that the contribution of concordant and discordant trends to the overall synchrony is not negligible and can crucially affect biological conclusions when not taken into account.

Although the analyses of simulated data demonstrated the ability of the methods to disentangle the effect of directional trends and year-to-year variation, still the methods are not able to separate these effects completely. This is not surprising. Even in those cases in which the environmental cue is generated without any trend, its values might be, by chance, positively or negatively correlated with time (the sample correlation coefficient will be a random variable with normal distribution, mean zero and variance $1/(n-2)$, where n is the length of the series). If we were to calculate the average of correlation coefficients, we would get a value close to zero. However, if the year-to-year fluctuations are simulated as synchronous, the higher the correlation, and the more synchronous the species trends will be (and similarly for asynchronous year-by-year fluctuations). Thus, even in those cases in which no trend is nominally simulated, there are

Figure 3. Results from the field sampling over 16 yr. For each period considered an overall synchrony (Stotal) was computed and it was decomposed into the components due to long-term trends (Strend) and the effect beyond these trends (Sdetrended). We also computed the synchrony using three-terms local variance (ST3). Analyses were run for all 16 yr together and then the 16-yr data was split into three periods: the first six years, the second six years (from year 7 to years 12) and the final six years (from year 11 to year 16). In each panel we report statistical results about the effect of fertilization (F) and removal (R) and their interactions. We also tested whether the grand means of index values were significantly above or below zero, see main text ('Sync > 0' indicates values significantly above zero and 'Sync < 0' the opposite; '***' implies $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$). Red dots and lines reflect the effect of fertilization ('Fert +') while blue lines reflect the scenario in plots without fertilization ('Fert -'). Rem+ and Rem- indicates remove, or not, of the dominant species in the community. Note that the lines do not mean interpolation, but their deviation from parallelism visualizes the interaction (in the typical interaction plot style).

Figure 4. Results from the sowing experiment in Benešov (1998–2003), with natural colonization, low-diversity sowing mixtures and high-diversity sowing mixtures. Results are shown for overall synchrony (Stotal), which was decomposed into the components due to long-term trends (Strend) and the effect beyond these trends (Sdetrended), and using three-term local variance (ST3). Letters below the boxplots indicate, for each of these four synchrony measures, differences between natural colonization, low-diversity sowing mixtures and high-diversity sowing mixtures using a Tukey post hoc test (with different letter indicating $p < 0.05$).

cases when we must expect a small proportion of the year-to-year synchrony to form a synchrony of trends. Also, note that we have used 100 replicates for each scenario, which leads to rather high test power (so that even very small deviations from the null model become significant).

The analysis of the Ohrazení data has shown that in several cases the synchrony caused by trends (Strend) was negative, suggesting successional dynamics, whereas the Sdetrended values and the year-to-year variation ascertained by the ST3 methods were positive, or less negative (e.g. unfertilized plots in the second period). Accordingly, the year-to-year variation was considerably more synchronous than was suggested by ordinary synchrony measures, which do not separate the effect of directional trends. Particularly in the first period considered, when the effect of the establishment of the experiment (e.g. starting of fertilization) was potentially more marked, it also appeared that variation in Stotal due to fertilization was actually due to directional trends in species composition, with some species increasing in abundance after starting fertilization and others decreasing. We originally expected that the omission of the first five years after establishment of the experiment was enough to be sure that the dynamics were affected mainly by year-to-year fluctuations, but we show here that these directional trend effects could be more pervasive in time. This is extremely important because most experimental worldwide testing of the effect of eutrophication has so far used short-term fertilization experiments, without considering the potential directional trends effects.

The difference in ecological interpretation was very pronounced in the analysis of the Benešov data. Should we rely on classical synchrony measures, we would conclude that the most pronounced compensatory dynamics are in the natural colonization plots, and the least pronounced in the high-diversity sown plots. However, the decomposition of total synchrony demonstrated that the differences are caused by anti-synchronous trends, most pronounced in natural colonization, and least with sowing high-diversity seed mixtures, whereas the year-to-year variation (as shown by either the detrended results, or by T3) are comparably anti-synchronous in all three treatments. This pattern can be well explained – vegetation dynamics in natural colonization are mostly affected by typical secondary succession, driven by the colonization–competition tradeoff. Early colonizers are outcompeted by competitively stronger species, leading to a negative temporal trend for the early colonizers, while the competitors increase their cover over the years resulting in a positive temporal trend. In the sown treatments, the trends are less pronounced because stronger competitors were sown at the start of the experiment. Nevertheless, even in these treatments, the trends form a non-negligible part of the dynamics. Results from the Benešov data suggest that BEF-like experiments should carefully take directional trends into account when measuring synchrony. We can expect that colonization–competition tradeoffs will be frequent and thus possibly cause ‘false’ compensatory dynamics. Using measures of synchrony that account for directional trends might thus contribute to a better understanding of mechanisms of stability of ecological communities using sowing experiments.

So far we have considered the viewpoint that accounting for directional trends when computing synchrony indices is a desirable feature. However, depending on the specific questions asked, directional changes produced by trends could also be considered a mechanism that allows the total biomass to be kept constant, despite the pronounced dynamics of individual populations. For example, biomass during succession, under directional trends, can be quasi-constant due to long-term replacement of species (Osbornová et al. 1990). Also, we might imagine a case in which the community biomass is rather constant despite increasing chronic industrial pollution, and the long-term stability has maintained the increase of some species abundance in time and the decrease of others. In such cases, the presence of long-term directional trends could stabilize communities across years. This case, at the same time, reinforces the idea that the separation of the effects of year-to-year fluctuations and trend will provide meaningful help in interpreting the results of community stability and will reveal the underlying mechanisms. Disentangling the effect of concordant/discordant trends and year-to-year asynchrony in fluctuations might help to better connect the analyses of the temporal series with ecological theory. Whereas in many cases we can expect some successional dynamics, the temporal trends asynchrony will be probably connected with the colonization–competition tradeoffs, the year-to-year variation will be connected

with reaction of individual species to weather in individual years. The method 1 proposed here helps to distinguish these effects in a way that was not considered before, hence opening new opportunities to test, more consistently, several leading ecological theories.

Comparison of the two methods and perspectives

The Sdetrended and ST3 approaches have the same objective: provide a community wide measure of the year-to-year fluctuations of species from which the effect of directional trends has been filtered-out. Do we need both? Are they not superfluous? The correspondence between the two approaches is highest for the simulated data. This is expected, because in the simulated data the linear trend and the residual variation are the only sources of variability, and there is no other positive or negative autocorrelation in the data. On the contrary, in real data sets, the residuals of the linear trend might be autocorrelated, which would mean that there are trends more complicated than a simple linear one. In the Benešov data the results using Sdetrended and ST3 were generally similar but not always for the Ohrazení data. The Sdetrended approach corresponds to synchrony of residuals, whereas the synchrony based on T3 is 'purely' synchrony of year-to-year abundance fluctuations and the shape and possible periodicity of trends is irrelevant. In cases when there is some discrepancy between these two, we suspect that there might be some common non-linear, or even non-monotonic, trends. The combined use of Sdetrended and ST3, in this sense allows verification of the nature of directional trends in species compositions. In the case of non-monotonic trends, like for example in the presence of cyclical periods (like el Niño, or similar) only the use of ST3 will reflect the year-to-year fluctuations. From a practical point of view, it is important to note also that ST3 provides just a simple detrending, whereas the decomposition method disentangles the trend and year-to-year components and thus it is also able to evaluate the effect of concordant/discordant trends on the overall synchrony. The second might be extremely important where the (a)synchrony of trends is not a nuisance caused by the experimental setup, but a part of the phenomenon studied. Because ST3 reflects the year-to-year abundance fluctuations, its use assumes a complete continuous time series (i.e. no gap years), whereas the decomposition method expects just a linear trend, and missing data in terms of missing years are not problematic.

We believe that our methods will help to separate various mechanisms that lead to synchrony on various temporal scales, and very probably these mechanisms will lead to trends that are more complicated than simple linear ones. Probably the most frequently studied data type when assessing stability and synchrony patterns is plant biomass at the peak of the vegetation season in herbaceous temperate communities (Lepš et al. 2018). In these cases, we can speak about the stability or synchrony of aboveground production – in temperate herbaceous vegetation we expect that

all herbaceous biomass dies towards the winter and sampled aboveground production coincides with the period of peak biomass. But this interpretation must be taken with great caution when we attempt causal inference. In permanent grasslands, the yearly aboveground production is partially determined by photosynthesis in a given year, but in many species also by mobilization of reserves from the previous year(s), that are stored in belowground organs (Janeček and Klimešová 2014). These belowground reserves might react rather slowly to changes in management and cause long-term trends and 'waves' in species abundances (Pecháčková and Krahulec 1995).

With the decomposition method, we attempted here to separate the effects of year-to-year fluctuations from monotonic trends. As the basic rule $SS_{Tot} = SS_{Regr} + SS_{Resid}$ applies for various forms of regression, not only the linear case, the approach can be further extended to non-linear trends. However, most of the currently available time series for estimating synchrony are relatively short-term, enabling reasonably reliable estimation only of the linear trend. We therefore decided to only present the case of the linear trend. Should more complicated trends require fitting, we would need to decide on the degree of complexity of the involved regression (e.g. using the Huisman–Olf–Fresco 1993 approach), or whether to use the same complexity for all the species or use some stepwise procedure for each species separately. Other approaches like wavelet analyses or spectral analyses (Wu et al. 2007) potentially allow the revealing of cyclic changes in vegetation data, but typically data from permanent plots do not provide time series long enough to reasonably estimate parameters detrended from periodic trends.

It might be useful to further investigate the methods used for the analysis of transect data to determine the dimensions of spatial clumping (Hill 1973, Lepš 1990, Dale 2000) for further applications on temporal analyses. These methods form blocks of adjacent units to find the dimensions of the maximum degree of clumping, or maximum degree of correlation among species or between a species and an environmental variable. In an analogous way it would be possible to attempt to find the length of time periods of positive or negative correlation among species, or some periodicity in fluctuations of individual species. We can also apply similar approaches as used here to other problems connected with the assessment of variability from time-series data. Previous studies have already applied the two-term local quadrat variance (a simpler analogue of T3, Hill 1973) to detrend various indices of population stability, including CV, in the analyses of fluctuations of moth populations (Spitzer and Lepš 1988, Lepš et al. 1998). Also, if we would first fit a linear trend and then calculate indices of variability as a measure of overall stability (e.g. the coefficient of variation CV) from the fitted data and residuals, we could again obtain the separate effects of trend and residual variation. For CV however, the components will not be additive, because the sums of squares and

not their square roots used to calculate the standard deviation are additive.

The synchrony in population size variability can be decomposed into synchrony of directional trends and synchrony of year-to-year fluctuations. The two components are likely to be governed by different mechanisms. We propose two methods that are able to disentangle these two components and, using simulated data, we have demonstrated their efficiency. The analysis of real data demonstrates that trends (and their synchrony) form a non-negligible part of community dynamics. These analyses reinforce the idea that the separation of the effects of year-to-year fluctuations and trend will provide meaningful help in interpreting the results of community stability and will reveal underlying mechanisms.

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- Supplementary material (available online as Appendix ecog-04528 at <www.ecography.org/appendix/ecog-04528>). Appendix 1–3.