Directional trends in species composition over time can lead to a widespread overemphasis of year-to-year asynchrony

Running title: Directional trends effects on synchrony

Enrique Valencia[1*†], Francesco de Bello[2,3†], Jan Lepš[2,4], Thomas Galland[2,5], Anna E-Vojtkó[2,5], Luisa Conti[5,6], Jiří Danihelka[7,8], Jürgen Dengler[9,10,11], David J. Eldridge[12], Marc Estiarte[13,14], Ricardo García-González[15], Eric Garnier[16], Daniel Gómez[15], Susan Harrison[17], Tomas Herben[18,19], Ricardo Ibáñez[20], Anke Jentsch[21], Norbert Juergens[22], Miklós Kertész[23], Katja Klumpp[24], Frédérique Louault[24], Rob H. Marrs[25], Gábor Ónodi[23], Robin J. Pakeman[26], Meelis Pärtel[27], Begoña Peco[28], Josep Peñuelas[13,14], Marta Rueda[29], Wolfgang Schmidt[30], Ute Schmiedel[22], Martin Schuetz[31], Hana Skalova[8], Petr Šmilauer[32], Marie Šmilauerová[2], Christian Smit[33], Ming-Hua Song[34], Martin Stock[35], James Val[12], Vigdis Vandvik[36], Karsten Wesche[11,37,38], Ben A. Woodcock[39], Truman P. Young[40,41], Fei-Hai Yu[42], Martin Zobel[27], Lars Götzenberger[2,5].

[1] Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Móstoles, Spain.
[2] Department of Botany, Faculty of Sciences, University of South Bohemia, České Budějovice, Czech Republic.
[3] Centro de Investigaciones sobre Desertificación (CSIC-UV-GV), Valencia, Spain.
[4] Biology Research Centre, Institute of Entomology, Czech Academy of Sciences, České Budějovice, Czech Republic.
[5] Institute of Botany, Czech Academy of Sciences, Třeboň, Czech Republic.
[6] Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Praha, Czech Republic.
[7] Department of Botany and Zoology, Masaryk University, Brno, Czech Republic.
[8] Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice, Czech Republic.
[9] Vegetation Ecology Group, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland.
[10] Plant Ecology Group, Bayreuth Center for Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany.
[11] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany.
[12] Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia.
[13] CREAF, Cerdanyola del Vallès, Catalonia, Spain.
[14] CSIC, Global Ecology Unit CREAF-CSIC-UAB, Catalonia, Spain.
[15] Instituto Pirenaico de Ecología (IPE-CSIC), Jaca-Zaragoza, Spain.
[16] CEFE, CNRS, Univ Montpellier, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France.
[17] Department of Environmental Science and Policy, University of California Davis, CA, USA.
[18] Department of Botany, Faculty of Science, Charles University, Praha, Czech Republic.
[19] Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice, Czech Republic.

[20] Department of Environmental Biology, University of Navarra, Pamplona, Spain.
[21] Department of Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany.
[22] Research Unit Biodiversity, Evolution & Ecology (BEE) of Plants, Institute for Plant Science and Microbiology, University of Hamburg, Germany.
[23] MTA Centre for Ecological Research, Vácrátót, Hungary.
[24] INRA, VetAgro Sup, UCA, UMR Ecosystem Prairial, Clermont-Ferrand, France.
[25] University of Liverpool, Liverpool, UK.
[26] The James Hutton Institute, Craigiebuckler, Aberdeen, UK.
[27] Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia.
[28] Terrestrial Ecology Group (TEG), Department of Ecology, Institute for Biodiversity and Global Change, Autonomous University of Madrid, Madrid, Spain.
[29] Department of Conservation Biology, Estación Biológica de Doñana (EBD-CSIC), Sevilla, Spain.
[30] Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Germany.
[31] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Community Ecology, Switzerland.
[32] Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic.
[33] Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, Groningen, The Netherlands.
[34] Laboratory of Ecosystem Network Observation and Modelling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China.
[35] Wadden Sea National Park of Schleswig-Holstein, Tönning, Germany.
[36] Department of Biological Sciences, University of Bergen, Norway.
[37] Botany Department, Senckenberg, Natural History Museum Goerlitz, Görlitz, Germany.
[38] International Institute Zittau, Technische Universität Dresden, Dresden, Germany.
[39] NERC Centre for Ecology & Hydrology, Oxfordshire, UK.
[40] Department of Plant Sciences, University of California, Davis, USA.
[41] Mpala Research Centre, Nanyuki, Kenya.
[42] Institute of Wetland Ecology & Clone Ecology / Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China.

Correspondence

Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Móstoles, Spain.
Email: valencia.gomez.e@gmail.com

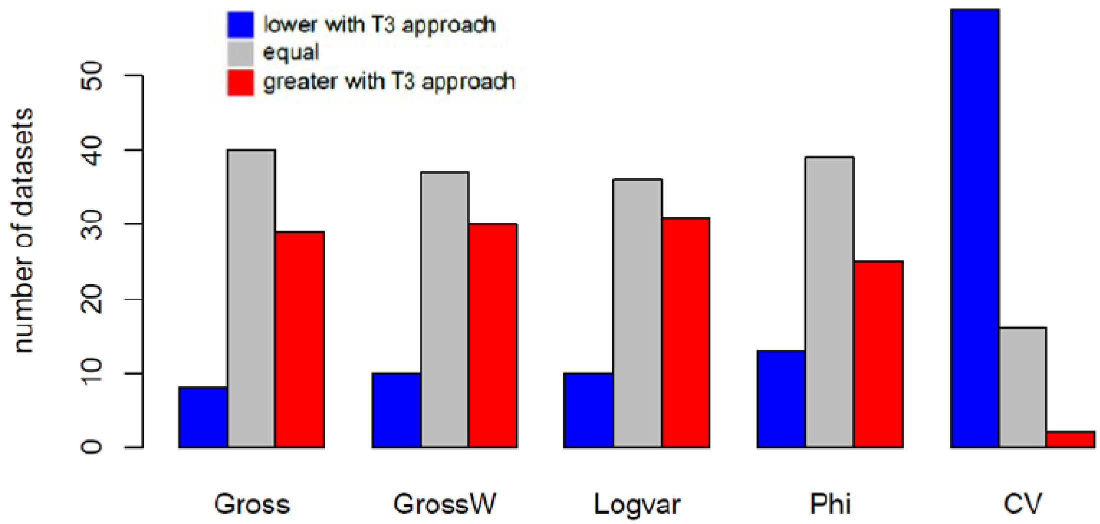
†Authors contributed equally

Funding information

Czech Science Foundation (GAČR). Grant Number: 16- 15012S.
Program for attracting and retaining talent of Comunidad de Madrid (EV). Grant Number: 2017-T2/AMB-5406

Web summary

Measures of community synchrony and stability aim at quantifying year-to-year fluctuations in species abundances. However, these indices reflect also long-term trends, potentially masking year-to-year signals. Using a large number of datasets with permanent vegetation plots we show a frequent greater synchrony and stability in year-to-year changes compared to when long-term trends are not taken into account.



Abstract

Questions

Compensatory dynamics are described as one of the main mechanisms that increase community stability, e.g. where decreases of some species on a year-to-year basis are offset by an increase in others. Deviations from perfect synchrony between species (asynchrony) have therefore been advocated as an important mechanism underlying biodiversity effects on stability. However, it is unclear to what extent existing measures of synchrony actually capture the signal of year-to-year species fluctuations in the presence of long-term directional trends in both species abundance and composition (species directional trends hereafter). Such directional trends may lead to a misinterpretation of indices commonly used to reflect year-to-year synchrony.

Methods

An approach based on three-term local quadrat variance (T3) which assess population variability in a three-year moving window, was used to overcome species directional trend effects. This 'detrending' approach was applied to common indices of synchrony across a Worldwide collection of 77 temporal plant community datasets comprising almost 7800 individual plots sampled for at least 6 years. Plots included were either maintained under constant 'control' conditions over time or were subjected to different management or disturbances treatments.

Results

Accounting for directional trends increased the detection of year-to-year synchronous patterns in all synchrony indices considered. Specifically, synchrony values increased significantly in ~40% of the datasets with the T3 detrending approach while in ~10% synchrony decreased. For the 38 studies with both control and manipulated conditions,

the increase in synchrony values was stronger for longer-time series, particularly following experimental manipulation.

Conclusions

Species long-term directional trends can affect synchrony and stability measures potentially masking the ecological mechanism causing year-to-year fluctuations. As such, previous studies on community stability might have overemphasised the role of compensatory dynamic in real-world ecosystems, and particularly in manipulative conditions, when not considering the possible overriding effects of long-term directional trends.

Keywords: asynchrony, biodiversity, stability, synchrony, temporal dynamics, year-to-year fluctuation.

Introduction

Given the challenges posed by rapidly changing environments in the context of global change, it is crucial to understand how biological diversity is maintained over time (Cardinale et al. 2007; Tomimatsu et al. 2013; Tilman, Isbell, & Cowles 2014). There is a general consensus toward the role that synchrony (or lack of) in, e.g., year-to-year population fluctuations between co-existing species plays on species diversity and community stability (Hautier et al. 2014; Craven et al. 2018). On the one hand, a common response to environmental fluctuations (for example changes in temperature or precipitation from one year to another) of most species (synchrony) will tend to destabilize the community biomass or abundance. On the other hand, the opposite pattern (compensatory dynamics, i.e. increases or decreases in the relative abundance of some species that are offset by changes in the relative abundance of others; Hubbell 2001; Gonzalez & Loreau 2009) will lead to higher community stability. In this sense asynchrony, i.e. the extent of the deviation from lack of perfect synchrony between species, has been advocated as an important and widespread mechanism that contributes to stability (Loreau & de Mazancourt 2013).

While there is a lively debate on the importance of compensatory dynamics on the stability of communities (Houlahan et al. 2007; Blüthgen et al. 2016; Lepš et al. 2018) there are also important methodological aspects that can influence the detection of the underlying biological patterns. Recently, Lepš et al. (2019) demonstrated that the study of synchrony between species has traditionally disregarded the possible effects of long-term directional compositional trends in the analysed communities (i.e. a tendency of some species to increase or decrease over time, or to fluctuate cyclically, Wu et al. 2007). Species directional trends occur when the abundances of species respond not only to short-term environmental fluctuations, but also to the presence of monotonic or cyclical tendencies over the whole time series considered. Short term environmental fluctuations (Rabotnov 1974), for example on a year-to-year basis, are expected to affect species abundance but also to be largely reversible, so that species would not show long-term directional trends in their abundances. In contrast, long-term environmental changes, such as climate change, nutrient deposition and changes in land use (e.g. abandonment or intensification of agricultural land), generally cause long-term species directional trends (Stevens et al. 2011; Walter et al. 2018). Long-term directional trends can also be the result of the impact of undetermined drivers (Milchunas, Lauenroth, & Burkeal 1998). As repeatedly reported by many authors, long term trends in species abundance are probably omnipresent, and have been demonstrated even in, now, more than 160 years of the Park Grass Experiment (Silvertown et al. 2006).

To gain a better understanding of the underlying mechanisms regulating changes in species abundance, short-term fluctuations and long-term trends effects on synchrony should be disentangled. Unfortunately, this differentiation has been rare in studies assessing drivers of synchrony and stability (but see Vasseur & Gaedke 2007; Tredennick et al. 2017; and the review by Lepš et al. 2019). Indeed, using simulations and simple case studies Lepš et al. (2019) showed that species directional trends can mask year-to-year fluctuations among species. This has the potential to result in a biased estimation of asynchrony when using many widely used synchrony indices. Such directional trends could lead to either overestimation of year-to-year synchrony when the majority of species concomitantly increase or decrease over time, as well as overestimation of year-to-year asynchrony when some species increase and some others decrease over time.

Multiple indices have been developed to evaluate the level of synchrony among species in a community (Loreau & de Mazancourt 2008; Gross et al. 2014; Blüthgen et al. 2016; Lepš et al. 2018). Further methodologies have also been developed to assess directional trends, such as spectral or wavelet analyses, however, they are applicable only to very long or highly resolved time series (see Lepš et al. 2019 for an overview of these methods). None of the classically used synchrony indices disentangle, *a priori,* the actual year-to-year fluctuations from the directional trends. However, such indices can be 'detrended' using different methods (Wu et al. 2007; Lepš et al. 2019). One appealing a simple solution includes computing synchrony indices over moveable windows of three consecutive years (three-term local variance, 'T3', Hill 1973) instead of over the whole sampling period (Lepš et al. 2019). This 'detrending' approach, which we call T3 detrending approach, could allow testing the generality of the effect of directional trends on synchrony indices. If the focus of the research is on year-to-year fluctuations, then the minimum number of years to exclude trends and consider yearly fluctuations is 3 years, hence the three-term local variance. With bigger windows the computation of a common linear trend over the time window, and the focus on the deviation from this trend, does recall on the other method proposed by Lepš et al. (2019), using residuals of fitted linear models over a given time period. The first approach has the advantage that it can be computed with any existing index of synchrony and does not require the knowledge of the shape of possible linear trends in species abundance.

A widespread assessment of the effect of species directional trends on synchrony has been limited by the scarcity of available long-term data. Indeed, the study of temporal dynamics requires a substantial sampling effort to obtain meaningful data for temporal analyses. Although there are networks and independent groups with long-term ecological data around the world, no major efforts have been made to compile and standardize the existing data in order to achieve a worldwide perspective. Consequently, a global-scale analysis would improve our understanding of both directional trends and year-to-year species fluctuations among the different synchrony indices and across diverse habitats, as well as how they are related with different types of disturbances or stressors. To face this challenge, we compiled plant community data from 77 temporal datasets with at least six sampling years, including almost 7800 vegetation plots distributed across the world. First, we evaluated to what extent year-to-year synchrony could be masked by long-term trends, by using the T3 detrending approach for temporal series proposed by Lepš et al. (2019) on commonly used indices of synchrony. Second, we assessed whether synchrony patterns changed in plots in which initial conditions were maintained ('control') vs. plots in which new conditions were applied ('manipulated' plots, see methods), assuming that these new conditions would trigger compositional changes and therefore generate a trend. Third, we evaluated how detrended synchrony values are affected by the duration of the sampling. Finally, we asked if relationships that are commonly assessed in the literature regarding synchrony indices, i.e. the correlation between synchrony and species richness and the correlation between synchrony and community stability, changed markedly depending on whether the T3 detrending approach was applied. Additionally, beside the validation of the T3 approach introduced by Lepš et al. (2019), we further validated (using simulations) the functionality of the approach in the case of both monotonic and cyclical long-term trends and depending on the time series length (Appendix S1). We expect that: (1) directional trends in our datasets can overshadow either asynchrony or synchrony depending on the type of trend; (2) manipulative experiments can give rise to directional trends and therefore reinforce the need for detrended metrics to accurately evaluate and compare community dynamics; (3) longer time series would provide greater chances to detect species directional trends; and (4) the presence of directional trends may affect the strength of the relationship between synchrony indices and species richness or community stability.

Methods

We collected 77 worldwide datasets of aboveground dry biomass, cover percentage, or frequencies of natural or semi-natural plant communities. These datasets consist of 7788 permanent and semi-permanent plots sampled between 6 to 53 times over periods of 6 to 99 years. These datasets included plots with different treatments or manipulations. The plots were thus grouped into two categories: control vs. manipulated. In total 38 datasets presented both control and manipulated plots. Control includes those plots where the long-term conditions prior to the establishment of the sampling scheme were maintained throughout the sampling. For example, if the historical conditions in a given site include periodic mowing, this represents the 'control'. The 'manipulated' plots were exposed to different treatments that altered the long-term conditions in their respective sites. These treatments included introduction or exclusion of grazing, mowing, removal of dominant species, fire, fertilization and climate change treatments. These wide categories allowed us to perform broad comparisons between different land-use and management conditions that are expected to influence species trends. The list of datasets, their characteristics in habitat, vegetation type and their available data on location and main manipulations is provided in Appendix S2.

Synchrony measures

For each of the 7788 plots, we computed the most common indices of community-level synchrony from existing literature. The main indices fall into two families. The first one is based on correlations between species' abundances and includes two indices: the one proposed by Gross et al. (2014) and then this modified by Blüthgen et al. (2016), which weighs the contribution of species to community synchrony in terms of their abundance. We call these indices ‘Gross’ and ‘GrossW’, respectively. The second family of indices is based on variance ratios, i.e. the variance in species fluctuations is compared against the null model of independent fluctuations of individual populations, and includes two indices: log variance ratio (‘Logvar’, Lepš et al. 2018) and φ (‘Phi’, Loreau & de Mazancourt 2008).

The Gross and GrossW indices range from -1 to +1 and Logvar from -*Inf* to +ln(*nsp*), with *nsp* being the number of species in a community. High values indicate a common response of the species (synchrony), while any deviation from perfect synchrony indicates asynchrony; the lowest and negative values indicate that the increases or decreases in some species are compensated by opposite changes in others. For all, Gross, GrossW and Logvar, zero corresponds to a situation where the species fluctuate completely independently of each other. Finally, Phi ranges from 0 to 1, 1 being perfect synchrony and any deviation from this value means asynchrony.

For each plot we also computed the average number of species in the plots across years, as well as the coefficient of variation (*CV*) of species abundances (standard deviation of the total sum of abundances or biomass across years divided by the mean of abundances or biomass across years). CV of total community abundance is a common measure of community (in)stability, where high values of CV indicate low stability in the community.

All measures of synchrony (and the CV) can be computed using the three-term local variance (*T3; see* Lepš et al. 2019 for an explanation of how to apply this method to the synchrony measures), originally introduced by Hill (1973) in the context of spatial pattern analysis. T3 is then calculated as:

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

where n is the number of years in the time-series, i is the year index, and x_i is the abundance recorded in year i. Consequently, T3 computes the variance by averaging variance estimates within a moving window of three consecutive years over the data. Any eventual increase in window size needs to be considered with respect to the limits imposed by total length of the series (Lepš 1990). In this context that the minimum length of the time series in our collection of datasets was 6 years, a movable window of 3 years seemed as a reasonable solution.

For the three-year window used in the calculations, the variance (which is needed in all existing index of synchrony) is estimated from the squared difference of the middle year and average of the years before and after. Therefore, if there is a perfect linear trend within these three years, the difference is zero. If there is no temporal trend in the time series analysed, 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; Lepš et al. 2019). For each plot, each synchrony index (Gross, GrossW, Logvar and Phi) as well as the CV were calculated both with and without the T3 detrending method.

Data analysis

To assess to what extent the synchrony indices were affected by directional trends we followed different approaches. First, we correlated (across plots within each dataset) synchrony values with and without the T3 detrending approach. Specifically, for each dataset we retained a Rho coefficient from the Spearman correlation between indices calculated using the T3 detrending approach and their respective indices calculated without the T3 approach. Then, to test consistency across datasets another Spearman test was run on the average of each synchrony index per dataset to test if the ranking in synchrony between datasets was maintained.

Second, we determined in how many datasets the T3 detrending approach significantly increased, or decreased, the synchrony values. For this we ran a series of paired t-tests, with a correction of the resulting p-values using the Benjamini–Hochberg approach (Benjamini & Hochberg 1995) for false discovery rates ($n = 77$ tests for each index). To assess how the T3 detrending approach affected overall community stability, this test was also applied to the CV. For each of the assessed synchrony indices, we also retained for each dataset the t-statistic of the paired t-test, which indicates the strength and the direction of the effect (positive values implying T3 increased synchrony, negative ones when T3 decreased synchrony). Additionally, we evaluated how globally the synchrony values responded to the T3 detrending approach using Linear Mixed Models (LMM). In one approach, we computed for each plot two separate synchrony values (synchrony with and without the T3 detrending approach). The LMM contained one categorical variable (TraT3) as explanatory variable, specifying if the index was calculated with the T3 detrending approach or not. Plots nested in each dataset were considered as a random factor. Also, we computed for each plot the difference between the synchrony values with the T3 detrending approach and the values without it. Then, we evaluated how the effect of detrending (i.e. the difference between synchrony with and without T3) varied across habitat types and the biomes by fitting a LMM in which the dataset identity was considered as a random factor.

Third, we assessed whether synchrony values were affected by directional trends depending on the presence of an experimental manipulation changing abruptly the ecological conditions in a plot. To do this, we evaluated the effect of T3 using the t-statistic of the paired t-test within dataset (see above), separately in control and manipulated plots within datasets. This analysis was restricted to those 38 datasets (out of 77) in which both control and manipulated plots were present and with at least three plots in each category. The same approach was used to test the effect of the duration (number of years) of the sampling period. This was undertaken using a linear model to test the relationship between the t-statistic (resulting from the paired-test) and number of years sampled in each dataset. We also used a similar LMM as described above to jointly evaluate the effects of the duration of the sampling period and experimental manipulation on the difference between the synchrony values with and without the T3 detrending approach in these 38 datasets. In this model, we used the number of years of sampling, the experimental manipulation (manipulated vs. control plots) and their interaction as fixed factor, while each dataset was considered as a random factor. When a significant interaction was found, we split the database in control and manipulated plots and evaluated the effects of duration of the sampling period on both groups of plots.

Finally, to assess changes in strength of the commonly found ecological relationships involving synchrony with or without the use of the T3 detrending approach, we tested for each dataset using paired t-tests how strong were the (Pearson) correlations between synchrony and (i) species richness and (ii) community stability. For each of these two correlations, we considered the Pearson r and tested through a paired t-test if this r value (one for each dataset) was greater or smaller when using the T3 approach compared to when not using the T3 approach.

For simplicity, we mostly present the results of one index (GrossW) in the main text because it is widely applied in the literature. However, most of the results for the other indices considered are shown in Appendix (S3 and S4). Similarly, all results concerning simulations are also included as Supporting Information material (Appendix S1). All the analysis were run in R (R Development Core Team 2018).

Results

The ranking of synchrony values with and without the T3 detrending approach was relatively consistent, both within and across datasets (Fig. 1). The Spearman Rho values computed within each of the 77 datasets were mostly positive and significant (Fig. 1a, for GrossW as an example; similar patterns were obtained for the other indices, Appendix S3). For example, in 44 out of the 77 datasets, the Spearman Rho was above 0.5. This indicates a moderate correspondence in the ranking in synchronicity values across plots within datasets. Nevertheless, notable exceptions were present, for example in six datasets (~8% of the cases) Rho was below 0.1. However, in five out of these six datasets, either the number of manipulated plots was greater than the control plots, or the control plots were entirely absent. Overall, the Spearman ranking test done on the mean synchrony values indicated that greater synchrony without the T3 approach also provided greater synchrony with the T3 approach (Fig. 1b: Rho = 0.81 and $p < 0.001$). Most importantly, synchrony mean values were frequently greater where the T3 detrending approach was applied than without its use (paired t-test $p < 0.001$; Fig. 1b and Appendix S3).

We generally found a greater synchrony when accounting for long-terms trends with the T3 methods than without. A significant increase in synchrony values was found for over 1/3 of the datasets (~30 datasets of 77, i.e. in ~40% of datasets synchrony significantly increase, $p < 0.05$, after correcting p-values for multiple tests with the Benjamini & Hochberg correction for false discovery rate within each synchrony index, Fig. 2; all significant tests reported in this section account for this p-value correction). Conversely, in around 10 datasets (13%, depending on the indices) synchrony values decreased using the T3 approach. In total around 50% of the datasets showed a significant change in synchrony values when using or not using the T3 detrending approach. The pattern described for GrossW index was similar for all other synchrony indices. The number of datasets showing greater synchrony with the T3 approach was lower using Phi, which also showed a higher number of datasets showing lower synchrony with the T3 approach. In the majority of datasets (around 60) the CV computed using the T3 approach was significantly lower compared to the one computed without the T3 approach.

The LMM on the whole dataset showed a significant difference between the use of synchrony with and without the T3 detrending approach ($p < 0.001$) with an overall increase in synchrony with T3, meaning that the T3 detrending approach generally led to increased synchrony values among all the plots (other synchrony indices yielded similar results). This result (which is similar to the significant deviation from the 1:1 line in Fig. 1b mentioned above) further confirms that across the whole dataset long-term trends generally blur the importance of synchrony between species.

The results of the LMM evaluating the effects of habitat type and biomes on the T3 difference (i.e. on the difference between indices of synchrony with and without T3 within a plot) showed a significant effect of the habitat type ($\chi^2 = 47.21$; $p < 0.001$), but no effect of the biomes. Grassland and savanna had in average positive values, meaning that a difference between T3 synchrony and synchrony without T3 were greater in these two habitats.

As expected, detrending had greater impacts on measures of synchrony in experimental plots than controls. Specifically evaluating ‘control’ vs. ‘manipulated’ plots (using 38 datasets in which there were both types of plots), showed a greater number of cases in which the T3 approach produced significant changes in synchrony in the manipulated than in the control plots (Fig. 3 for the GrossW and Appendix S4 for the other synchrony indices): 21 significant datasets (60%) in the manipulated plots but only 10 (27%) in the control plots. Moreover, the effect of the sampling period length (number of years plots were sampled) was significantly related to the change in mean synchrony with the T3 approach only in the case of the manipulated plots (Fig. 3, using, as dependent variable, the t-values resulting by comparing synchrony with and without T3 approach using the paired t-tests within plot described above). Specifically, in the manipulated plots a longer sampling period improved the predictive ability of the effect of T3 approach on synchrony (increased detection of synchrony over long-term periods and increased detection of asynchrony in short-time periods). We confirmed these results using an LMM in which the difference of synchrony with and without T3 were computed for each plot. This analyses showed a significant interaction between sampling period length and experimental manipulation. Sampling period length significantly increased the difference between synchrony values with and without the T3 approach only in manipulated plots ($\chi^2 = 10.37$; $p = 0.001$, n = 3414).

Finally, we found that overall the relationships between synchrony and both species richness and community stability were similar (Appendix S5). Nevertheless there were slightly more frequent significant cases after detrending for Gross and GrossW (Appendix S5). For instance, the relationship between species richness and synchrony (i.e. when considering GrossW) was found significant in 15 and 11 datasets (out of 77) respectively when using or not using the T3 detrending approach (in both cases correcting for false discovery rates). However, this relationship, with LogVar, was found significant in 4 datasets less when using the T3. Further, with GrossW the expected positive relationship between synchrony and community CV was significant in 58 and 54 datasets while using or not using the T3 detrending, respectively (we did not detect significant negative relationship between CV and synchrony). The strength of these relationships, however, was not affected by the detrending approach. In neither the (i) species richness and synchrony correlations, nor the (ii) community CV and synchrony correlations, did we detect significant differences when using or not using the T3 detrending approach (in both cases $p > 0.2$). This implies that the use of the T3 detrending approach did not systematically produce greater or weaker correlations when analyzing these common relationships.

Discussion

In this study we show that the synchrony patterns usually attributed to compensatory dynamics could be actually caused by trends in species composition. Without accounting for these trends effectively, it is possible that compensatory effects could be generally overemphasized (in 30% of our datasets) or even underemphasized (in 10% of our datasets). Previous studies of synchrony and compensatory dynamics have often overlooked the possible effects of directional trends on the studied communities. Only few studies, such as Vasseur and Gaedke (2007), Loreau & de Mazancourt (2008) and Tredennick et al. (2017), have effectively filtered out species trends (using wavelet based methods or considering growth rates of species in time, instead of raw abundances). Long-term trends in abundances, either directional or cyclical, indeed have the potential to bias the interpretation of synchrony with the most commonly used indices. The T3 detrending approach can account for this bias (see simulation in Lepš et al. 2019 and in Appendix S1). The advantages of the T3 approach, compared to other approaches, are its lower data requirement and consideration of all species in a community, not just the most frequent ones (Lepš et al. 2019).

In ~40% of the datasets, and in the overall model across all plots, synchrony using the T3 detrending approach was significantly greater than synchrony without using it (Fig. 2). The ~40% estimate is, furthermore, a conservative one as we account for Type I errors. Overall, the mean values of synchrony computed with the T3 detrending approach were higher than without it in the majority of cases, both within and across datasets (Fig. 1b, and LMM). This is an important finding because it suggests that our appreciation of the importance of asynchrony, and therefore compensatory dynamics, may have been possibly overestimated, leading to wrong conclusions about synchrony-asynchrony in communities. These findings highlight the necessity of evaluating the effects of possible directional trends on synchrony to accurately estimate the importance of ecological mechanisms regulating compensatory dynamics. The difference between the indices calculated using T3 detrending approach and without it were higher in grasslands and meadows, possibly because in the absence of slow-growing, less dynamic, woody species. In these communities temporal trends can thus be more easily detected compared to other types of vegetation. The increase in synchrony after detrending also suggests the presence of opposite trends of species abundances in time, such as when one species is decreasing steadily and another increasing. For example, trends could be the result of species responding differently to disturbance or to an increase in nutrient availability. Such opposite trends could be monotonic or following waves in time (Wu et al. 2007), e.g. resulting from periodic climate events such as “El Niño”, or intrinsic cycling of particular functional groups such as legumes (Herben et al. 2017). These results are partially expected because our datasets comprised natural or semi-natural well-established plant communities but included experimental conditions in which changes in abundance or composition of species are common.

When considering datasets with both control and manipulated plots (~50% of the datasets) the effect of the T3 approach was more frequently significant in manipulated plots than in control plots (Fig. 3). These plots were more prone to be affected by a directional trend promoted by the specific manipulation imposed. This result agrees with our hypothesis that events like soil-nutrient alteration (e.g. by fertilization) and recovery from disturbance might promote directional trends. This result was expected as some of the experimental manipulations were designed to directly alter species composition, in order to test their effects on community synchrony. However, such prompted changes, often due to colonization-competition trade-offs in species composition, can mask year-to-year fluctuations, and hence these experiments should disentangle these biologically different effects on synchrony. For these reasons, we recommend that any index of synchrony should be computed with and without the T3 approach to properly evaluate the corresponding effects of long-term experimental treatments and year-to-year fluctuations. Our result reinforces the assumption that the effect of the T3 approach could be stronger in changing environments/communities and the combination of indices with and without the T3 approach can be important to distinguish the mechanisms causing differential long-term species responses to changes in environmental conditions from the differential species responses to short-term species fluctuations on synchrony/asynchrony relationships.

The effect of detrending on synchrony values was particularly pronounced in the case of succession. During succession the majority of species will increase their abundance, which will cause them to be ultimately positively correlated in time. However, these same species can compensate each other or vary independently on a year-by-year basis, even if they all generally increase in time, so the existing synchrony indices would tend to overestimate their actual year-to-year synchrony between species within such communities. In fact, among the seven datasets with a Rho below 0.1 (Fig. 1a), the majority were characterised by being exposed to intense disturbance regimes that triggered some type of successional process. For instance, plots of four datasets had been exposed to a fire before or during the experiment, and two evaluated the effect of herbivory exclusion (where the reduction in grazing intensity allowed the development of higher vegetation like shrubs and trees). Both treatments are good examples of environmental conditions promoting species directional trends (Pardo et al. 2015) and thus affect synchrony values.

Interestingly, the effect of the T3 approach on the synchrony measured in manipulated plots depended on the period length of the sampling scheme. Manipulated plots sampled over longer time periods revealed higher synchrony values when using the T3 detrending approach (Fig. 3). In other words, the longer is the sampling period the greatest chance that there is a difference between T3 synchrony and synchrony without T3 in manipulated plots. Longer time series likely increased the chances that some species will have opposite trends in response to manipulation, with some increasing over time and others decreasing. In a shorter time series, on the contrary, the time lag in species responses (particularly extinction debt, Helm, Hanski, & Partel 2006; Lepš 2014) could cause that some species increase quickly in response to manipulation, while others might respond more slowly. The T3 detrending approach, therefore, will affect those species with a similar temporal trend in response to short-term manipulations. Consequently, the duration of the sampling period stands out as a key factor in the evaluation of temporal dynamics. We showed that, in the case of manipulated communities, classical methods tended to overestimate year-to-year synchrony when the sampling period was shorter, and underestimate it when the sampling period was longer. This highlights the importance of T3 approach for a correct evaluation of year-to-year synchrony between species. However, further research is required to find the causes and consequences of these results.

Finally, we generally found that the T3 detrending approach did not cause strong changes in the correlation between synchrony and both species richness and community stability, two of the most iconic relationships in temporal dynamics studies (Hautier et al. 2014; Blüthgen et al. 2016). However, there were more cases of significant correlations with the T3 approach and strength of the correlations could vary considerably (i.e. $R < 0.6$) across datasets. In summary, this suggests that while the applications of the T3 detrending approach did not produce systematically greater or weaker correlations on commonly used tests in ecology, the strength of the relationships could differ. These results confirm that the use of T3 approach to detrend the synchrony indices is far from trivial. As such, the conclusions obtained previously from studies that did not apply the method are not necessarily incorrect. Therefore, applying the detrended and non-detrended methods in a complementary way might bring us closer to understanding the directional changes in community dynamics. For instance, divergent trends, e.g. due to differential response to global warming with some species increasing and other decreasing, might stabilize communities and could maintain ecosystem functions unaltered in response to global warming, even if there are no short-term compensatory mechanisms between species. Hence, it is important to consider both the synchrony with and without detrending approach for teasing apart different causes of stability, or instability, in response to global change drivers.

The evaluation of synchrony with the T3 detrending method provides a feasible measure to reveal year-to-year fluctuations of species by removing the effect of directional trends. In comparison to methods using species growth rates, the T3 approach can be important because it enables the evaluation of the indices with and without the approach and also accounts for species which are not dominant and/or less frequent (in the case of the growth rates, log-transformation is needed, which might not be advisable in the case of zero abundances in specific years). This method has the advantage of evaluating both monotonic and non-monotonic directional trends, and can thus be used to detect year-to-year fluctuations in the face of cyclical periods, such as alternation between drought-wet periods (e.g. Riginos et al. 2018).

Acknowledgements

We thank multiple entities for the financial support necessary to obtain the different databases: the U.S. National Science Foundation under grant numbers DEB-8114302, DEB-8811884, DEB-9411972, DEB-0080382, DEB-0620652, DEB-1234162, DEB-9707477, DEB-0316402, DEB-08-16453, and DEB-12-56034, DEB-0618210, the Nutrient Network (http://www.nutnet.org) experiment from the National Science Foundation Research Coordination Network (NSF-DEB-1042132), the New Zealand National Vegetation Survey Databank, the Spanish MINECO (Project CGL2014-53789-R), the Madrid Regional Government (Projects REMEDINAL-3 and REMEDINAL-TE), the European Research Council Synergy grant 610028 (IMBALANCE-P), the Institute on the Environment (DG-0001-13), the SOERE-ACBB financed through French National Agency for Research (ANAEE, ANR-11-INBS-0001), the Estonian Research Council (IUT 20-28, IUT 20-29), Czech Science Foundation (GAČR 17-05506S), the European Regional Development Fund (Centre of Excellence EcolChange), the German Federal Environmental Foundation (DBU) for a grant to the NABU Hamburg (management experiment *Calamagrostis epigejos*), and the German Federal Ministry of Education and Research within the framework of the project BIOTA Southern Africa (promotion numbers 01LC0024, 01LC0024A and 01LC0624A2), Task 159 of SASSCAL (promotion number 01LG1201) and the Scottish Government's Rural and Environmental Science and Analytical Services division. Acknowledgement Data owned by NERC© Database Right/Copyright NERC. Further support was provided by the Jornada Basin Long-Term Ecological Research (LTER) project, Cedar Creek Ecosystem Science Reserve and the University of Minnesota. We also thank the Lawes Agricultural Trust and Rothamsted Research for data from the e-RA database. The Rothamsted Long-term Experiments National Capability (LTE-NCG) is supported by the UK Biotechnology and Biological Sciences Research Council (Grant BBS/E/C/000J0300) and the Lawes Agricultural Trust.

Author contributions: F.B., L.G. and J.L. conceived the project. All authors but E.V., F.B., T.G and L.G. collected the data used in this analysis. E.V. and T.G. assembled data. F.B. performed the analyses. E.V. and F.B. wrote the first draft of the manuscript and all the authors (especially L.G. and J. L.) contributed substantially to the revisions.

Data accessibility

The data that support the findings of this study are available at Figshare (Valencia et al. 2019).

References

Benjamini, Y., & Hochberg, Y. 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society: Series B (Methodological)* 57: 289–300.

Blüthgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., Boch, S., Fischer, M., Hölzel, N., Klaus, V.H., Kleinebecker, T., Tschapka, M., Weisser, W.W., & Gossner, M.M. 2016. Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nature Communications* 7: 10697.

Cardinale, B., Wright, J., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., & Weis, J.J. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America* 104: 18123–18128.

Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J.A., Cerabolini, B.E.L., Cornelissen, J.H.C., Craine, J.M., De Luca, E., Ebeling, A., Griffin, J.N., Hector, A., Hines, J., Jentsch, A., Kattge, J., Kreyling, J., Lanta, V., Lemoine, N., Meyer, S.T., Minden, V., Onipchenko, V., Polley, H.W., Reich, P.B., van Ruijven, J., Schamp, B., Smith, M.D., Soudzilovskaia, N.A., Tilman, D., Weigelt, A., Wilsey, B., & Manning, P. 2018. Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology and Evolution* 2: 1579–1587.

Gonzalez, A., & Loreau, M. 2009. The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* 40: 393–414.

Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Wayne Polley, H., Reich, P.B., & van Ruijven, J. 2014. Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *The American Naturalist* 183: 1–12.

Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H., Lind, E.M., MacDougall, A.S., Stevens, C.J., Bakker, J.D., Buckley, Y.M., Chu, C., Collins, S.L., Daleo, P., Damschen, E.I., Davies, K.F., Fay, P.A., Firn, J., Gruner, D.S., Jin, V.L., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Li, W., McCulley, R.L., Melbourne, B.A., Moore, J.L., O'Halloran, L.R., Prober, S.M., Risch, A.C., Sankaran, M., Schuetz, M., & Hector, A. 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* 508: 521–525.

Helm, A., Hanski, I., & Partel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters* 9: 72-77.

Herben, T., Mayerová, H., Skálová, H., Hadincová, V., Pecháčková, S., & Krahulec, F. 2017. Long-term time series of legume cycles in a semi-natural montane grassland: evidence for nitrogen-driven grass dynamics? (R. Ostertag, Ed.). *Functional Ecology* 31: 1430–1440.

Hill, M.O. 1973. The Intensity of spatial pattern in plant communities. *The Journal of Ecology* 61: 225.

Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Ernest, S.K.M., Findlay, C.S., Fuhlendorf, S.D., Gaedke, U., Legendre, P., Magnuson, J.J., McArdle, B.H., Muldavin, E.H., Noble, D., Russell, R., Stevens, R.D., Willis, T.J., Woiwod, I.P., & Wondzell, S.M. 2007. Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences* 104: 3273–3277.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Lepš, J. 1990. Comparison of transect methods for the analysis of spatial pattern. *Spatial processes in plant communities* 71-82.

Lepš, J. 2014. Scale- and time-dependent effects of fertilization, mowing and dominant removal on a grassland community during a 15-year experiment (S. Wan, Ed.). *Journal of Applied Ecology* 51: 978–987.

Lepš, J., Götzenberger, L., Valencia, E., & de Bello, F. 2019. Accounting for long-term directional trends on year-to-year synchrony in species fluctuations. *Ecography* 42: 1728-1741.

Lepš, J., Májeková, M., Vítová, A., Doležal, J., & de Bello, F. 2018. Stabilizing effects in temporal fluctuations: management, traits, and species richness in high-diversity communities. *Ecology* 99: 360–371.

Loreau, M., & de Mazancourt, C. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms (E. Duffy, Ed.). *Ecology Letters* 16: 106–115.

Loreau, M., & de Mazancourt, C. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist* 172: E48–E66.

Milchunas, D., Lauenroth, W., & Burke, I. 1998. Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos* 83: 65–74.

Pardo, I., Doak, D.F., García-González, R., Gómez, D., & García, M.B. 2015. Long-term response of plant communities to herbivore exclusion at high elevation grasslands. *Biodiversity and Conservation* 24: 3033–3047.

R Development Core Team. 2018. *R: A language and environment for statistical computing* (A. R Foundation for Statistical Computing, Vienna, Ed.). R Foundation for Statistical Computing, Vienna, Austria.

Rabotnov, T.A. 1974. Differences Between Fluctuations and Successions. In *Vegetation Dynamics*, pp. 19–24. Springer Netherlands, Dordrecht.

Riginos, C., Porensky, L.M., Veblen, K.E., & Young, T.P. 2018. Herbivory and drought generate short-term stochasticity and long-term stability in a savanna understory community. *Ecological Applications* 28: 323–335.

Silvertown, J., Poulton, P., Johnston, E., Edwards, G., Heard, M., & Biss, P.M. 2006. The Park Grass Experiment 1856–2006: its contribution to ecology. *Journal of Ecology* 94: 801–814.

Stevens, C., Duprè, C., Gaudnik, C., Dorland, E., Dise, N., Gowing, D., Bleeker, A., Alard, D., Bobbink, R., Fowler, D., Vandvik, V., Corcket, E., Mountford, J.O., Aarrestad, P.A., Muller, S., & Diekmann, M. 2011. Changes in species composition of European acid grasslands observed along a gradient of nitrogen deposition. *Journal of Vegetation Science* 22: 207–215.

Tilman, D., Isbell, F., & Cowles, J.M. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* 45: 471–493.

Tomimatsu, H., Sasaki, T., Kurokawa, H., Bridle, J.R., Fontaine, C., Kitano, J., Stouffer, D.B., Vellend, M., Martijn Bezemer, T., Fukami, T., Hadly, E.A., Van Der Heijden, M.G.A., Kawata, M., Efi, S.K., Kraft, N.J.B., Mccann, K.S., Mumby, P.J., Nakashizuka, T., Petchey, O.L., Romanuk, T.N., Suding, K.N., Takimoto, G., Urabe, J., & Yachi, S. 2013. Sustaining ecosystem functions in a changing world: a call for an integrated approach. *Journal of Applied Ecology* 50: 1124–1130.

Tredennick, A.T., de Mazancourt, C., Loreau, M., & Adler, P.B. 2017. Environmental responses, not species interactions, determine synchrony of dominant species in semiarid grasslands. *Ecology* 98: 971–981.

Valencia, E., de Bello, F., Lepš, J., Galland, T., E-Vojtkó, A., Conti, L., Danihelka, J., Dengler, J., Eldridge, D.J., Estiarte, M., García-González, R., Garnier, E., Gómez, D., Harrison, S., Herben, T., Ibáñez, R., Jentsch, A., Juergens, N., Kertész, M., Klumpp, K., Louault, F., Marrs, R.H., Ónodi, G., Pakeman, R.J., Pärtel, M., Peco, B., Peñuelas, J., Rueda, M., Schmidt, W., Schmiedel, U., Schuetz, M., Skalova, H., Šmilauer, P., Šmilauerová, M., Smit, C., Song, M., Stock, M., Val, J., Vandvik, V., Wesche, K., Woodcock, B.A., Young, T.P., Yu, F., Zobel, M., Götzenberger, L. 2020. Data from "Directional trends in species composition over time can lead to a widespread overemphasis of year-to-year asynchrony ". Figshare. https://doi.org/ 10.6084/m9.figshare.8276309.

Vasseur, D.A., & Gaedke, U. 2007. Spectral analysis unmasks synchronous and compensatory dynamics in plankton communities. *Ecology* 88: 2058–2071.

Walter, J.A., Ives, A.R., Tooker, J.F., & Johnson, D.M. 2018. Life history and habitat explain variation among insect pest populations subject to global change. *Ecosphere* 9: e02274.

Wu, Z., Huang, N.E., Long, S.R., & Peng, C.-K. 2007. On the trend, detrending, and variability of nonlinear and nonstationary time series. *Proceedings of the National Academy of Sciences of the United States of America* 104: 14889–14894.

Figure legend

Figure 1. Effects of the T3 detrending approach on synchrony, using the GrossW index (Blüthgen et al. 2016) as an example. In panel (a), a ranking correlation between synchrony values with and without detrending was computed for each of the 77 datasets considered. The histogram reports the 77 Rho values of the Spearman ranking correlations. Panel (b) reports, for each of the 77 datasets, the mean (+/- standard error) of the synchrony values with and without the T3 detrending approach. Vertical and horizontal dashed lines indicate zero synchrony (i.e. absence of synchrony). The solid line represents the 1:1 line above which, for example T3 synchrony was greater than synchrony without T3.

Figure 2. Summary of the directional effects of the T3 detrending approach on various synchrony indices and on CV. The bar plots indicate the numbers of datasets (n=77) in which the T3 approach significantly increased (red bars) or decreased (blue bars) synchrony values using a paired t-test after correction for false discovery rates. Grey bars indicate the number of datasets with non-significant paired t-tests.

Figure 3. Effects of the T3 detrending approach in manipulated vs. control plots. The plots report results of t-tests on 38 datasets in which there were both manipulated and control plots. For each dataset we used a pairwise t-test to compare synchrony values (using the GrossW synchrony index, Blüthgen et al. 2016) with and without the T3 approach (a: manipulated plots, and b: control plots). Positive values of the t-statistic indicate that the T3 approach increased synchrony and negative ones indicate that the T3 decreased synchrony. Values outside the grey area in each plot indicate significant t-tests after correction for false discovery rates (‘ns’ indicates $p > 0.05$). For each panel an R^2 for the relationship between t-statistic and number of years sampled in each dataset is provided together with the p-value of the regression model (the corresponding regression line is shown when significant). Syn: Synchrony.

Figure 1.

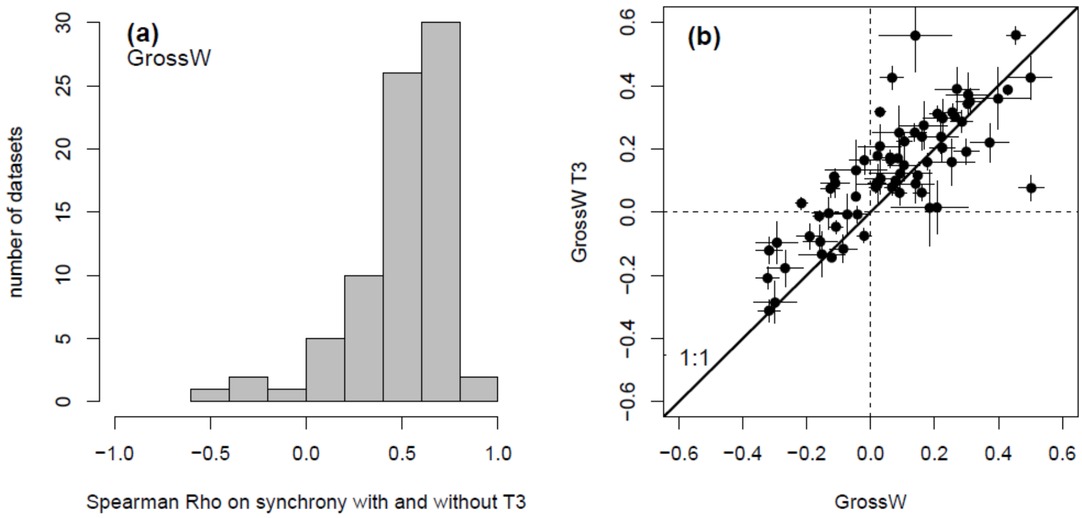

(a)
GrossW
number of datasets
0
5
10
15
20
25
30
−1.0
−0.5
0.0
0.5
1.0
Spearman Rho on synchrony with and without T3
(b)
1:1
GrossW T3
−0.6
−0.4
−0.2
0.0
0.2
0.4
0.6
GrossW

Figure 2.

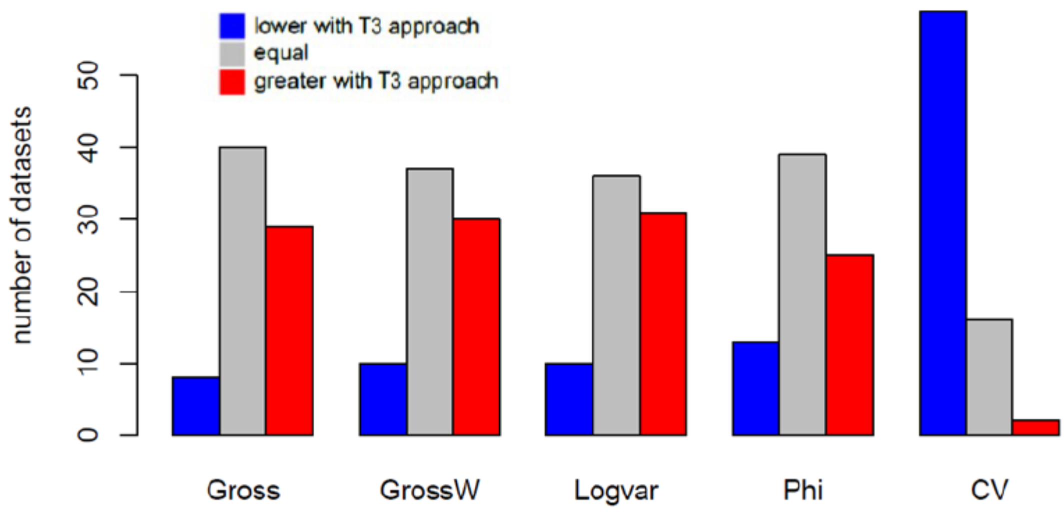
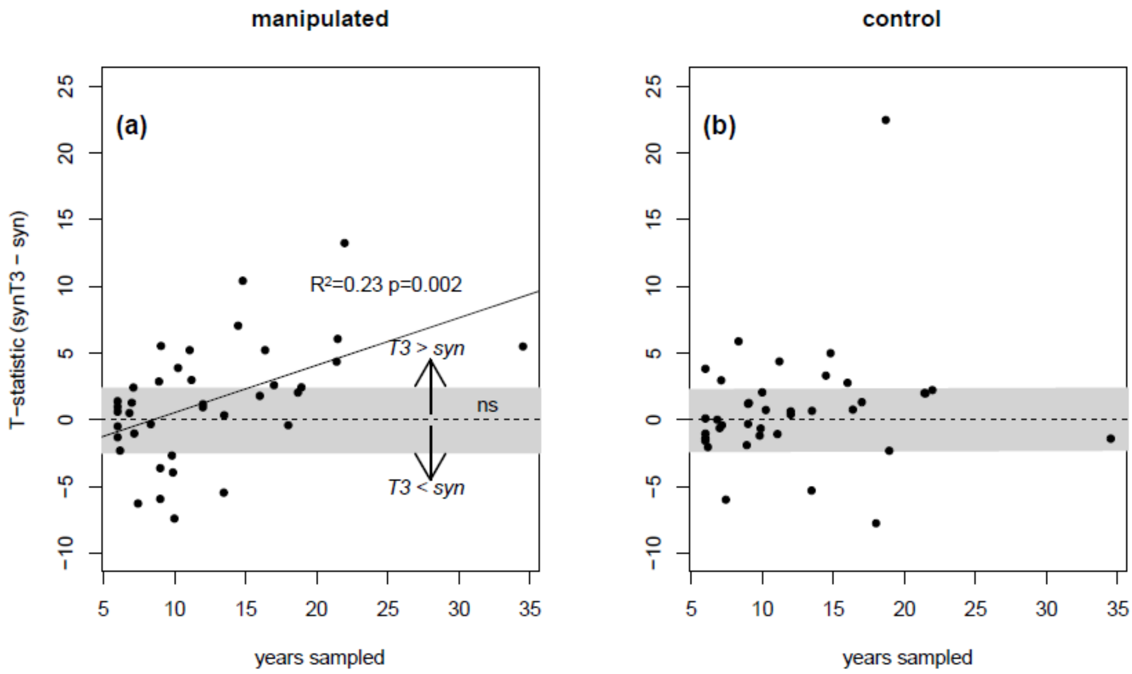

lower with T3 approach
equal
greater with T3 approach
number of datasets
0
10
20
30
40
50
Gross
GrossW
Logvar
Phi
CV

Figure 3.


manipulated
control
(a)
(b)
T−statistic (synT3 − syn)
R²=0.23 p=0.002
T3 > syn
ns
T3 < syn
years sampled
years sampled

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Simulating long term trends in artificial communities to validate effectiveness of the T3 approach

Appendix S2. Descriptions of each dataset, highlighting the treatments of the datasets with ‘control’ and ‘manipulated’ plots.

Appendix S3. Application of the analyses shown in Fig. 1 of the main text to the three remaining indices of synchrony.

Appendix S4. Application of the analyses shown in Fig. 3 of the main text to the three remaining indices of synchrony.

Appendix S5. Results of the correlation between synchrony indices with species richness or with the CV of total abundance.