Global Ecology and Biogeography   A Journal of Macroecology   WILEY

Null models for community dynamics: Beware of the cyclic shift algorithm

Michael Kalyuzhny 🆔

Department of Ecology, Evolution and Behavior, Hebrew University of Jerusalem, Givat-Ram, Jerusalem, 91904, Israel

Correspondence
Michael Kalyuzhny, Department of Ecology, Evolution and Behavior, Institute of Life Sciences, Hebrew University of Jerusalem, Givat-Ram, Jerusalem 91904, Israel.
Email: michael.kalyuzhny@mail.huji.ac.il

Present address
Michael Kalyuzhny, Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan

Abstract

Aim: Temporal patterns of community dynamics are drawing increasing interest due to their potential to shed light on assembly processes and anthropogenic effects. However, interpreting such patterns considerably benefits from comparing observed dynamics to the reference of a null model. For that aim, the cyclic shift permutations algorithm, which generates randomized null communities based on empirically observed time series, has recently been proposed. This algorithm, borrowed from the spatial analysis literature, shifts each species time series randomly in time, and this is claimed to preserve the temporal autocorrelation of single species. Hence it has been used to test the significance of various community patterns, in particular excessive compositional changes, biodiversity trends and community stability.

Innovation: Here I critically study the properties of the cyclic shift algorithm for the first time. I show that, unlike previously suggested, this algorithm does not preserve temporal autocorrelation due to the need to 'wrap' the time series and assign the last observations to the first years. Moreover, this algorithm scrambles the initial state of the community, making any dynamics that result from deviations from equilibrium seem excessive. I exemplify that these two issues lead to a highly elevated type I error rate in tests for excessive compositional changes and richness trends.

Conclusions: Caution is needed when using the cyclic shift permutation algorithm and interpreting results obtained using it. Interpretation is further complicated because the algorithm removes all correlations between species. I suggest guidelines for using this method and discuss several possible alternative approaches. The non-preservation of autocorrelation also raises questions regarding the use of the analogous spatial null model, the torus-translation.

KEYWORDS

community dynamics, compositional changes, cyclic shift, null models, permutations, randomization methods, richness trends, species richness, statistical ecology, torus-translation

1 | INTRODUCTION

One of the main approaches for the study of community ecology is documenting patterns of variation in ecological communities and underpinning the mechanistic basis for these patterns (Rosenzweig, 1995). Some of the most commonly studied patterns are species–area relationships (e.g. Preston, 1960; Rosindell & Cornell, 2007), latitudinal diversity gradients (e.g. Hillebrand, 2004; Usinowicz et al., 2017) and productivity–diversity relationships (e.g. Kondoh, 2001; Tilman & Pacala, 1993). Multiple

explanations have been suggested for these patterns and studying them has shed light on the mechanisms determining species diversity in ecological communities (e.g. DeMalach, Zaady, & Kadmon, 2017; Usinowicz et al., 2017).

However, all the aforementioned patterns have a thing in common: they are static, representing 'snapshots' or time averages of ecological communities, without any temporal dimension. While interest in these patterns continues, in recent years there has been growing interest in understanding temporal patterns in communities (Dornelas et al., 2013; Loreau & de Mazancourt, 2013; Magurran, 2016; McGill, Dornelas, Gotelli, & Magurran, 2015). It is believed that some of these patterns, which represent community dynamics and assembly 'in action', may reveal new insights on the processes shaping ecological communities (Chisholm et al., 2014; Kalyuzhny, Seri, et al., 2014). For example, studies on the scaling of the magnitude of population fluctuations with abundance revealed the central role of temporal environmental variability in shaping ecological communities (Chisholm et al., 2014; Jabot & Lohier, 2016; Kalyuzhny, Kadmon, & Shnerb, 2015; Kalyuzhny, Schreiber, et al., 2014), and studies focusing on long-term changes in abundance and diversity revealed that population-level regulation is often weak (Kalyuzhny, Seri, et al., 2014; Knape & de Valpine, 2012; Ziebarth, Abbott, & Ives, 2010), while total abundance and species diversity are indeed regulated (Brown, Ernest, Parody, & Haskell, 2001; Goheen, White, Ernest, & Brown, 2005;

Gotelli et al., 2017; Magurran & Henderson, 2018). Moreover, in recent years there has been increasing interest in understanding richness trends and compositional turnover, partly motivated by concerns over the effect of anthropogenic activities on ecological communities (Elahi et al., 2015; Magurran et al., 2018; McGill et al., 2015; Vellend et al., 2013). Several studies have shown that while some local communities show richness trends, negative and positive changes may cancel out in multiple communities worldwide (Dornelas et al., 2014; Vellend et al., 2013). Moreover, many ecological communities show large compositional turnover (Dornelas et al., 2014; Magurran et al., 2018).

This immediately raises the question: what qualifies as a 'large' change in richness or composition? Stochastic community models generally predict that ecological communities undergo constant changes at steady state (Lande, Engen, & Saether, 2003), and so do some deterministic models of nonlinear dynamics (May, 1976). Importantly, these models also predict that community properties, such as species richness, will have considerable temporal-auto correlation, which may generate spurious 'trends' on decadal time-scales (see Figure 1a,b for an example). This is true even for the simplest and most minimalistic models of community dynamics such as the Neutral Theory of Biodiversity (Hubbell, 2001). Consequently, and in analogy to null models of community patterns in space, temporal patterns should be compared to some null model to evaluate whether they deviate from the expectations under a minimalistic set
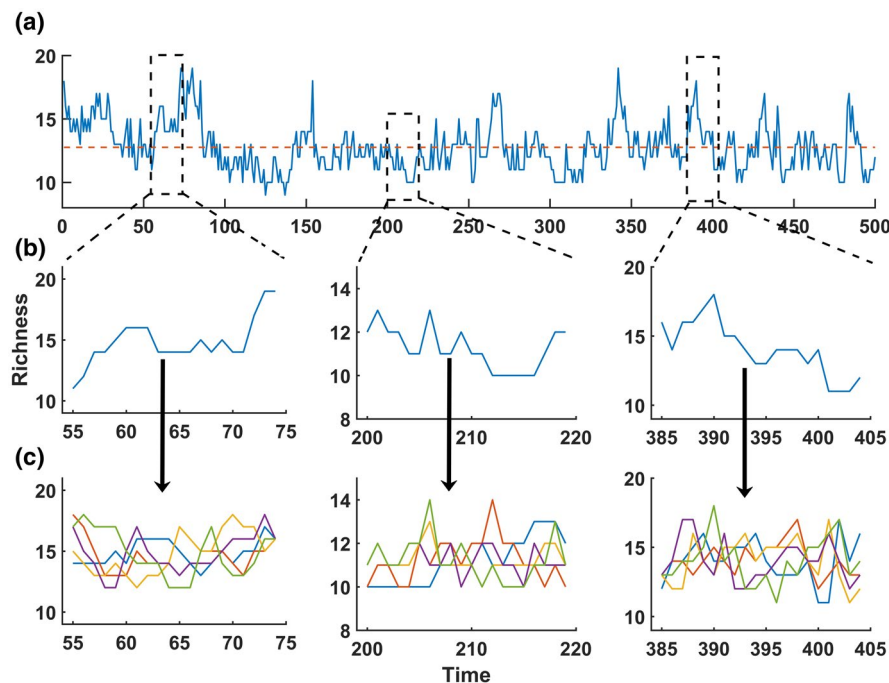
FIGURE 1 The challenges in analysing community time series, as exemplified with species richness through time. In (a), richness in 500 time steps of a Ricker model at steady state in the default non-neutral competition regime is presented (blue), along with the long-term average (red). Note the 'noisiness', the degree of temporal autocorrelation and the observation that the system can stay away from the equilibrium richness for long times. Zooming in on three sections (b), it is noticeable that some may show spurious 'trends', which are solely a result of this autocorrelation, as the system is in steady state with fixed parameters. However, time series produced by applying the cyclic shift null model to these short time series (five resamples for each time series, presented in (c)) would lack such 'trends' and make the observations in (b) seem excessive [Colour figure can be viewed at wileyonlinelibrary.com]

KALYUZHNY

Global Ecology
and **Biogeography**

A Journal of
Macroecology

-**WILEY**- 1087

of mechanisms (Gotelli & Graves, 1996; Gotelli & McCabe, 2002). Such null models preserve some aspects of the data and randomize others.

A recent suggestion for a null model of community dynamics is the cyclic shift permutations algorithm (Hallett et al., 2014), originally proposed for spatial analysis (Harms, Condit, Hubbell, & Foster, 2001). This algorithm gets as an input a matrix of the abundance, presence/absence or biomass of species by years (or other temporal units). In each realization of the algorithm, the time series of every species is shifted forwards in time a random number of years *y*, independently of other species. The last *y* data points are then assigned to the first *y* years, hence 'wrapping' the time series like a loop. For example, two possible resamples of the time series [1 2 3 4 5] could be [5 1 2 3 4] or [3 4 5 1 2] with equal probability. This approach has been claimed to preserve the autocorrelation structure and the abundance distribution of each species' time series (Hallett et al., 2014; Lamy et al., 2019; Magurran et al., 2018), which result from the ecological dynamics of this species, while removing all correlations between species. Hence, the cyclic shift algorithm was designed to test whether patterns of community dynamics differ from the expectations of an independent-species, temporally autocorrelated process.

Cyclic shift permutations have been used as a null model for richness and compositional changes (Demars et al., 2014; Magurran et al., 2018), changes in dominance (Jones & Magurran, 2018), and compensatory dynamics and stability of species diversity and total biomass (Gotelli et al., 2017; Hallett et al., 2014; Lamy et al., 2019;

Magurran & Henderson, 2018). The application of the cyclic shift null model is greatly facilitated by the available implementation of this algorithm within the open source R package Codyn (Hallett et al., 2016).

Here I would like to point out two important issues with the use of cyclic shift permutations and investigate their implications for statistical tests of temporal patterns. I claim that (a) cyclic shift permutations do not preserve the autocorrelation structure of single species' time series, especially on the time-scales of the length of the time series; and (b) cyclic shift permutations scramble the initial state of the community, making any dynamics that result from initial deviations from equilibrium seem excessive. See Figure 1 for examples of such deviations and for the effect of cyclic shifts on them. I show that these two properties lead to seriously inflated type I error rates when testing for excessive compositional changes and richness trends.

Here I point out two issues, I generate synthetic community time series using a flexible multispecies Ricker model (Kalyuzhny & Shnerb, 2017; Kilpatrick & Ives, 2003) in multiple parameter regimes under three scenarios assuming that species (a) are independent; (b) compete neutrally (i.e. all species are identical) and (c) compete and are different. See Figure 2 for examples of simulated time series. For these synthetic time series, richness trends and compositional changes are compared to the predictions of cyclic shift permutations. If the cyclic shift algorithm works properly, it should generate patterns similar to those of the independent species model (since the algorithm breaks intraspecific correlations),
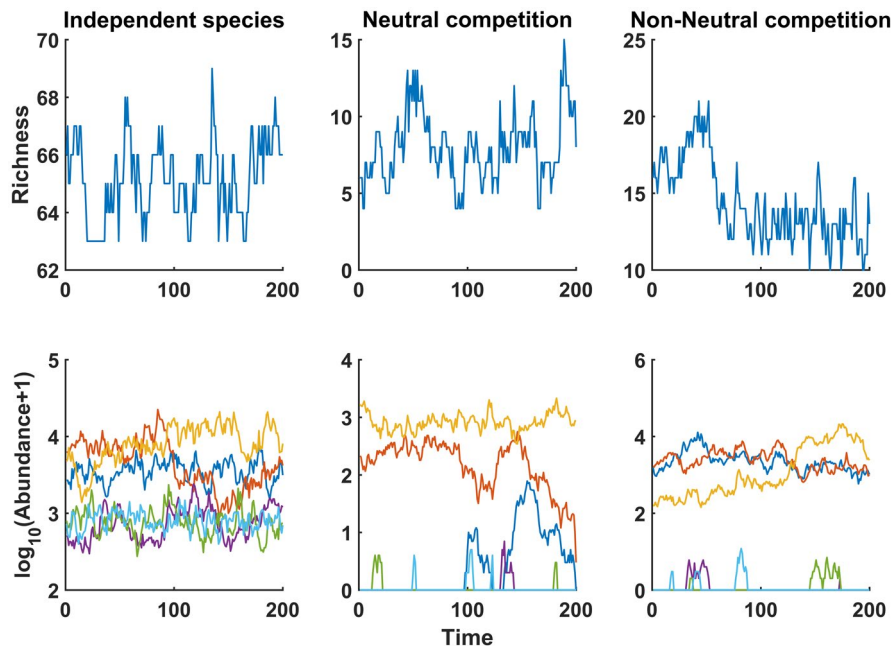
FIGURE 2 Examples of time series of species richness and abundance under the default parameter regime with the three interactions modes—independent species, neutrally competing species and non-neutrally competing species. The abundances presented below are of the three most common species and the three species around the 75th percentile of abundance. Time series produced under this (and other) parameter regimes were used for testing trends and excessive compositional changes in this work. Since these models are stationary, none of these 'trends' result from real changes in the communities, but are only a result of the autocorrelation of the process. See Methods for details about the simulations and their parameter regimes. The species pool has 100 species in all cases [Colour figure can be viewed at wileyonlinelibrary.com]

and more variable than those of the non-neutral competition model due to its stabilizing processes. While this could lead to acceptable or even reduced levels of type I errors, the aforementioned methodological issues are prevalent.

I conclude by discussing the possible applications of the cyclic shift algorithm and other community null models.

2 | DO CYCLIC SHIFT PERMUTATIONS PRESERVE TEMPORAL AUTOCORRELATION?

The most important argument raised for using the cyclic shift permutations algorithm is that it preserves the temporal autocorrelation of the data (Hallett et al., 2014; Lamy et al., 2019; Magurran et al., 2018). While this argument is highly intuitive, it ignores a crucial aspect of the algorithm—the 'wrapping' procedure, where the last y data points (where y is the number of years that the time series has been shifted) are assigned to the first y years.

Consider the first and last year data points in the resampled time series. It is highly likely that in the original time series, those were *consecutive* years, now maximally *separated* by the 'wrapping' of the time series. Assuming the original time series had positive short-term temporal autocorrelation, this results in the last data point in the resample resembling considerably the first data point. This is generalizable, to some degree, to the first several data points resembling the final several data points. Moreover, the wrapping 'attaches' a pair of years that were originally maximally separated in time, also distorting autocorrelation at short time-scales.

Given data that were generated by some process, the goal of bootstrap resampling is generating more data that should resemble new data that would have been generated by repeating that process. Many ecological models, and the Ricker (for parameter regimes

where nonlinear effects do not take place) in particular, predict that consecutive time points will be relatively similar, and as time passes dissimilarity will monotonously increase (Kalyuzhny et al., 2015). Figure 3 exemplifies this for communities of independent species (Figure 3a) and for species that compete neutrally (Figure 3b) and non-neutrally (Figure 3c). In all three cases, time series resampled using the cyclic shift permutations show a unimodal pattern of Bray–Curtis dissimilarity, very different from the original time series. Dissimilarity indeed initially increases, but then, after half the time-series duration, begins to symmetrically decrease, so that the last time points are quite similar in composition to the first time points. Moreover, For the first time points in the resamples, dissimilarity increases too fast, due to the 'attachment' of maximally separated years. Other parameter regimes and the Jaccard dissimilarity index show similar behaviours (Supporting Information Figures S1–S2), emphasizing that this is a general issue not limited to a narrow set of conditions and models. See Methods for details about the simulations and the parameter regimes.

I conclude that the 'wrapping' of the time series inherently distorts the temporal autocorrelation structure of ecological processes. This effect is dramatic on time-scales that are on the order of the length of the time series, and less dramatic for shorter time-scales. This raises the question—what are the implications of this, and of the 'scrambling' of the initial state that was mentioned earlier, for the performance of statistical tests?

3 | TYPE I ERRORS OF RICHNESS TRENDS AND EXCESSIVE TURNOVER

I exemplify the consequences of these properties for the testing of two fundamental patterns of community dynamics—temporal trends in diversity and compositional turnover. These are quantified by calculating the linear regression slope of (a) species richness
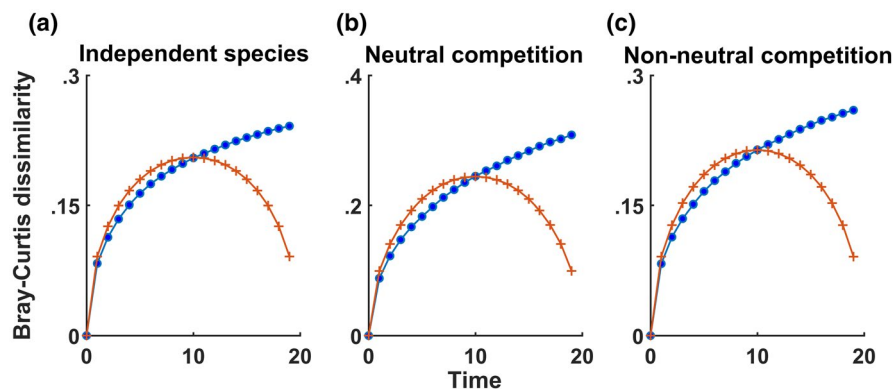
FIGURE 3 Comparison of Bray–Curtis community self-dissimilarity with time between 'empirical' simulated time series and their resamples, obtained using the cyclic shift algorithm. For each scenario [independent species (a), neutral competition (b) and non-neutral competition (c)], 10^4 synthetic time series were generated and Bray–Curtis compositional dissimilarity was computed between every year and the initial year for the empirical communities and resamples. For every empirical time series, 500 resamples were calculated and the results are averaged over the time series and resamples for every time point. The differences between the empirical and resampled average patterns is highly significant for every point but the middle and zero (*t* test, $p < 10^{-9}$). While the 'default' parameter regime is presented, other regimes and the Jaccard index (Supporting Information Figures S1–S2) show similar results [Colour figure can be viewed at wileyonlinelibrary.com]

and (b) the dissimilarity of species composition of each year with respect to the initial year; both versus time. These patterns have been studied in various communities and compared to the expectations under cyclic shift permutations to test for significance (Demars et al., 2014; Magurran et al., 2018). To examine the performance of the cyclic shift permutations null model I generated 10^4 synthetic communities under several parameter regimes using the Ricker model, assuming one of three modes of interspecific interactions: (a) no interactions; (b) neutral competition and (c) non-neutral competition. I then applied the cyclic shift algorithm 500 times to each community and compared the observed compositional and richness slopes in the time series generated by the model to the distribution of slopes under the cyclic shift algorithm. This allows me to calculate the significance of the observed slopes for each community.

Since simulations began at steady state, and since the parameters of the simulations remain fixed, there are no real trends in species richness (beyond the spurious trends generated by temporal autocorrelation, see Figure 1a,b). For this reason, detected trends are false-positive results (type I errors), and their proportion should be close to .05 if the null model is appropriate. This is particularly true for the non-interacting species case, since the breaking of correlations imposed by cyclic shift permutations should have no effect. However, I found that under all parameter regimes, type I errors were considerably inflated (Figure 4).

Type I errors for compositional changes were very high (.15–1) under all parameter regimes, interaction types and using either the Jaccard or Bray–Curtis indices (yellow and blue, respectively, in Figure 4a). These results are the consequences of the unimodal pattern of dissimilarity with time that is generated by cyclic shift permutations (Figure 3). The distribution of linear slopes fitted to this unimodal pattern is very different from the slope of the actual data, leading inevitably to a strong inflation of type I errors. In several cases it appears that type I errors increase with the number of species, leading to communities with more immigration and less environmental stochasticity having more errors. However, this also depends on the shape of the dissimilarity versus time curve, which is more complex.

Regarding richness trends, communities starting at the equilibrium species richness had elevated type I errors (.08–.14, Figure 4b). However, the most pronounced result is that communities whose richness in the first year deviated from equilibrium, even by a few species, had a much higher type I error probability, reaching .3–.7 in some parameter regimes. Moreover, type I error probabilities increased sharply with the magnitude of the initial deviation from equilibrium. It is important to emphasize that I did not intentionally initiate the communities at a deviation from equilibrium richness. Rather, deviations were a result merely of stochastic dynamics at steady state. These results hold under all parameter regimes and interaction modes, implying that such deviations, and the resulting inflation in type I errors, are to be expected in natural ecological communities.

The sharp increase in type I error rates as initial community richness moves away from equilibrium is a result of the 'scrambling' of
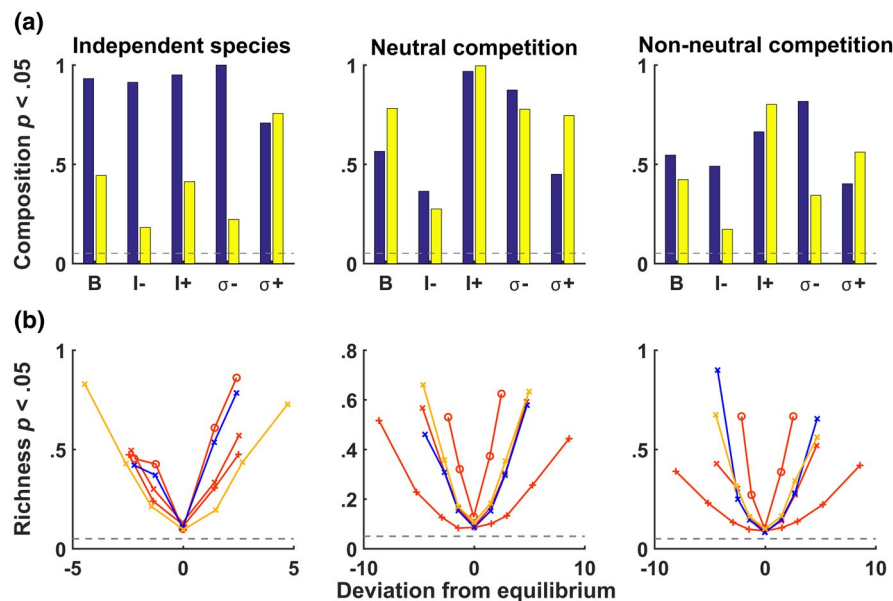
FIGURE 4 Proportion of false positive tests (at α = .05) for excessive compositional changes (a) and richness trends (b) for data generated by the multispecies Ricker model. 10^4 synthetic time series were generated for each parameter regime and mode of interspecific interactions. For each time series, the slopes versus time of compositional dissimilarity compared to the first year and of specie richness were calculated. They were then compared with the distributions of slopes for 500 resamples (using the cyclic shift algorithm and a two-sided test) of the synthetic time series to obtain a p value. The parameter regimes are denoted as 'B' or orange × for baseline; 'I-' or orange ○ for low immigration, 'I+' or orange + for high immigration; 'σ-' or blue × for no environmental stochasticity, and 'σ+' or yellow × for high environmental stochasticity. In (a) Jaccard (yellow) and Bray–Curtis (blue) dissimilarity were calculated. In (b) communities were assigned to bins based on the deviation of initial richness from equilibrium, and the proportion was calculated in each bin. The dashed grey line marks a proportion of .05 [Colour figure can be viewed at wileyonlinelibrary.com]

the initial state. Fairly generally for communities in steady state, if some community property (richness, in this case, but without loss of generality) has an equilibrium value, and we find it initially at a different value, it is expected to return to that equilibrium. However, the cyclic shift permutation eliminates the initial state of the community, and as a result any trend towards equilibrium would seem excessive. Figure 1 shows how the spurious trends that result from the autocorrelation and from beginning not at equilibrium (Figure 1b) are eliminated by the cyclic shift randomization (Figure 1c).

4 | DISCUSSION

The cyclic shift algorithm is a generalistic and easy to apply null model, making it an appealing approach for testing a variety of different patterns. However, as I have shown, this approach has two fundamental undesired properties. First, it distorts the autocorrelation structure so that the end of the resampled time series for each species closely resembles its beginning. The short-term autocorrelation (for the first several years, less than half the length of the time series) is also affected, but to a lesser degree. Moreover, the cyclic shift randomization 'scrambles' the initial state of the community, making any dynamics that result from properties of this initial state seem unlikely. I have further exemplified that these fundamental limitations have severe consequences for type I error rates in tests for trends in species richness and excessive compositional changes under a broad set of parameters, emphasizing the generality of the results. I believe that the fundamental nature of the issues with the cyclic shift null model would have negative consequences for tests that may be developed for other patterns as well. For this reason, I recommend using this null model with extra caution.

Another aspect that must be considered carefully before using the cyclic shift algorithm is the implications of removing the correlations between species. If the goal of the analysis is testing for the significance of such correlations (e.g. Hallett et al., 2014) then using a null with no correlations definitely makes sense. However, other aspects of the dynamics, such as temporal changes in diversity, composition and dominance, may very well be affected by correlations between species. These correlations could be caused by biotic interactions or responses to environmental changes, and the interpretation of finding excessive changes compared to such a null of independent species should be carefully considered. Even more so, one should be cautious about using cyclic shift permutations on data that are available at a resolution of less than a year (e.g. Magurran et al., 2018; Magurran & Henderson, 2018). In such data, correlation between species may be the result of seasonality, and randomly shifting each species independently of other species removes its effect. Consequently, the likely strong effects of seasonality on community composition will be detected as excessive changes.

These issues do not lessen, however, the need that led to the development of the cyclic shift algorithm. Indeed, I believe that the interest in temporal patterns will continue to grow, along with the need for a null model to serve as a reference for them. I would like to suggest several possible directions for addressing this need.

An alternative approach that has been suggested as a null model for community dynamics is neutral models (Dornelas et al., 2014; Gotelli & McGill, 2006; Hubbell, 2001), whose predicted dynamics have been compared to observed dynamical patterns on decadal (e.g. Dornelas et al., 2014; Kalyuzhny et al., 2015) or palaeobiological time-scales (e.g. Clark & McLachlan, 2003; McGill, Hadly & Maurer, 2005). However, the dynamic predictions of neutral models are quite sensitive to the level of immigration (e.g. Dornelas et al., 2014; Hubbell, 1997) and temporal resolution (Tomašových & Kidwell, 2010; Kalyuzhny et al., 2015), which are often unknown or difficult to parameterize. Furthermore, it has been shown that neutral models where stochastic events affect individuals independently (known as 'demographic stochasticity' or 'ecological drift'), such as the classical Unified Neutral Theory of Biodiversity and Biogeography (Hubbell, 2001), predict considerably smaller changes than observed in multiple communities (Dornelas et al., 2014; Kalyuzhny, Schreiber, et al., 2014; Kalyuzhny, Seri, et al., 2014). It has been shown that this is the result of ignoring environmental fluctuations, which affect the growth rate of entire populations synchronously (Chisholm et al., 2014; Fung, O'Dwyer, Rahman, Fletcher, & Chisholm, 2016; Jabot & Lohier, 2016; Kalyuzhny et al., 2015). Hence, a neutral model with environmental fluctuations would be a much more appropriate null (Jabot & Lohier, 2016; Kalyuzhny et al., 2015). Furthermore, neutral theories impose compensatory dynamics, or negative correlations, between species, which stem from the zero-sum assumption. This makes them not necessarily the best choice as a null model (Gotelli & McGill, 2006). Overall, using neutral theories as a dynamic null model involves multiple non-trivial challenges. Another alternative would be to try to fit multispecies autoregressive models (Ives, Dennis, Cottingham, & Carpenter, 2003). This framework is more flexible, and one may decide to preserve (or not to preserve) multiple properties such as the autocorrelation structure of the data, the magnitude of fluctuations, the correlations between species and the initial state of the community. This approach has not been studied much as a null model to this day.

Finally, a null model for presence–absence data named Presence-Absence Resampling wIthin periodS (PARIS) has recently been suggested as a methodology to generate synthetic communities where each species independently undergoes colonization and extinction dynamics at fixed rates (Kalyuzhny, Flather, Shnerb & Kadmon, 2019). While this approach imposes the autocorrelation structure of a Poisson process and species independence, it preserves the initial state of the community and has recently been shown to have excellent statistical properties: acceptable type I error rates, robustness to problems in the data and statistical power under alternative assumptions (Kalyuzhny et al., 2019). PARIS is also very easy to apply to ecological time series because, like the cyclic shift algorithm, it is a randomization-based methodology with publicly available code.

It is noteworthy that the cyclic shift algorithm was initially borrowed from the literature on spatial analysis (Harms et al., 2001, named 'torus-translation'), where the preservation

of autocorrelation argument was initially raised. Since its proposition, tests based on this torus-translation have been published in dozens of works (e.g. Hall, McKenna, Ashton, & Gregoire, 2004; Lan et al., 2012; Yamada et al., 2007). The finding that the temporal analogue, the cyclic shift algorithm, does not preserve temporal autocorrelation, implies that the torus-translation does not preserve spatial autocorrelation as well. This casts doubt on the justification for the torus-translation. I hope future works will examine the implications of this non-preservation of autocorrelation for the performance of statistical tests using the torus-translation as a spatial null model.

Overall, I believe that studying temporal patterns has great promise to shed light on the processes shaping ecological communities. This promise is amplified by the increasing availability of extensive datasets of temporal community dynamics (Dornelas et al., 2018). However, more research is required on how to appropriately analyse such data, and in particular on the best practices for applying null models of community dynamics. I hope this work will reduce the improper application of such null models and help guide the use and development of more appropriate null models for temporal community dynamics.

5 | METHODS

5.1 | Models

I studied the statistical performance of the cyclic shift permutations algorithm by applying it to synthetic time series generated using a discrete-time multispecies Ricker model (Kalyuzhny & Shnerb, 2017; Kilpatrick & Ives, 2003), whose flexibility allows generating of a variety of dynamic regimes.

In the multispecies Ricker model, the expected population of species i at time $t + 1$, $N_{i,t+1}$, in the absence of immigration is:

$$E\left(N_{i,t+1}\right) = N_{i,t}\exp\left(r_i\frac{K_i - N_{i,t} - \sum_{j\neq i}\alpha_{ij}N_{j,t}}{K_i} + \varepsilon_{i,t}\right), \qquad (1)$$

where r_i and K_i are the growth rate and carrying capacity of species i, respectively, α_{ij} is the per capita effect of an individual of species j on the growth of species i, representing interspecific interactions, and $\varepsilon_{i,t}$ represents stochastic fluctuations in growth rate due to environmental changes. $\varepsilon_{i,t}$ is normally distributed with a mean of 0 and variance of σ_e^2.

While Equation (1) represents the expected population of species i at time t, the actual population size is drawn from a Poisson distribution: $N_{i,t+1} \sim \text{Poisson}\left(E\left(N_{i,t+1}\right)\right)$. This introduces demographic stochasticity, that is, random variation between individuals in demography, as well as the discreteness of individual, which allows species to go stochastically extinct. Finally, after the local demography step described above, a Poisson distributed number of immigrants (with mean I, representing immigration rate)

are introduces and are chosen at random with equal probability from among the S_{reg} species available in the species pool.

The flexibility of the Ricker model allows the consideration of multiple parameter regimes and modes of interspecific interactions. I have used three such general modes of interactions: First, to be as consistent as possible with the properties of the cyclic shift algorithm, I considered communities of non-interacting species by setting all α_{ij}s to zero. I further assumed that the K_is of species are lognormally distributed with mean 1,000 and SD of 2,000, and the r_is are exponentially distributed with mean 0.1. To resemble neutral models, which are also used as null models, I assumed all $\alpha_{ij} = 1$, all $K_i = 1,000$ and all $r_i = 0.1$. In this case, all the species are identical, subject to one community-wide carrying capacity $K = K_i$ and to demographic and possibly environmental stochasticity. Hence, this model is analogous to classic neutral theory, but with the community carrying capacity subject to fluctuations rather than being a fixed number. Finally, to generate more complex and realistic dynamics I considered non-neutrally competing species. In this case, I assumed that the α_{ij}s are gamma distributed with mean and SD of 0.1, and the K_is and r_is are distributed similarly to the case of independent species.

In all three modes of interactions, I considered five parameter regimes. Under the baseline regime, $I = 1$ and $\sigma_e = 0.2$. Under the high immigration and low immigration regimes, I was set to 0.2 and 10, respectively, and under the low stochasticity and high stochasticity regimes σ_e was set to 0 and 0.5, respectively. Communities were initiated with each species at its carrying capacity K_i, or at K_i/S_{reg} in the neutral interactions regime and were given $20*S_{reg}/I$ time steps to equilibrate before being recorded for 20 time steps (unless otherwise presented). This equilibration time is meant to allow 20 immigration events (on average) for each species before I consider the community as at steady state.

For all models, I considered two levels of S_{reg}, 20 and 100 species. The results were qualitatively similar but more pronounced for the 100 species (because there are more changes overall), so I present the result for $S_{reg} = 100$ in all cases. Examples of time series generated under the models in the three interaction modes are given in Figure 1

5.2 | Statistical tests

I am interested in examining the performance of tests for excessive compositional turnover and richness trends. For compositional turnover, I computed the Jaccard and Bray–Curtis dissimilarity indices of every year with respect to the initial year (as in Figure 3) and used the linear slope of dissimilarity versus time as the test statistic. For richness trends, I computed the slope of the regression of richness versus time. For every synthetic community generated by the multispecies Ricker model I calculated these two test statistics, generated 500 resampled communities by applying cyclic shift permutations to the original data, and then compared the observed statistics to their distribution in the resampled communities using a two-sided

test. This gave the p value of both statistics for every community. This procedure is in line with the approach of Magurran et al. (2018).

To evaluate the performance of the statistics, I calculated the proportion of cases falling in the tails (using $\alpha = .05$). Since I expect no excessive changes, this proportion can be thought of as the type I error rate, which should not exceed α. For examining the tests of compositional changes (Figure 4a), the proportion was calculated over all 10^4 synthetic communities in a given parameter regime. For examining the tests of richness trends, I first assigned the communities to bins according to their initial deviation from equilibrium richness. Equilibrium richness was calculated as the average richness in the 20-year data for the sake of simplicity and resemblance to empirical analyses, where the real equilibrium is unknown. The bins that were used were $D \leq -7$, $-7 < D \leq -4$, $-4 < D \leq -2$, $-2 < D \leq -1$, $-1 < D \leq 1$, $1 < D \leq 2$, $2 < D \leq 4$, $4 < D \leq 7$, $7 < D$, where D is initial deviation from richness equilibrium. In each bin, I calculated the average D (presented on the x axis), and the proportion of false positive results among the communities in the bin (presented on the y axis). Bins with fewer than 10 communities were discarded.

All analyses were performed in MATLAB 2016a (The Mathworks, Inc., Natick, Massachusetts) with the full code supplied in Supporting Information Appendix S1.

ACKNOWLEDGMENTS

DATA AVAILABILITY STATEMENT

The manuscript does not use data. All the code is available in the Supporting Information Appendix S1.

ORCID

Michael Kalyuzhny https://orcid.org/0000-0002-5574-0079

REFERENCES

Brown, J. H., Ernest, S. K. M., Parody, J. M., & Haskell, J. P. (2001). Regulation of diversity: Maintenance of species richness in changing environments. _Oecologia_, _126_(3), 321–332. https://doi.org/10.1007/s004420000536

Chisholm, R. A., Condit, R., Rahman, K. A., Baker, P. J., Bunyavejchewin, S., Chen, Y.-Y., ... Yap, S. (2014). Temporal variability of forest communities: Empirical estimates of population change in 4000 tree species. _Ecology Letters_, _17_(7), 855–865. https://doi.org/10.1111/ele.12296

Clark, J. S., & McLachlan, J. S. (2003). Stability of forest biodiversity. _Nature_, _423_, 635–638. https://doi.org/10.1038/nature01632

DeMalach, N., Zaady, E., & Kadmon, R. (2017). Light asymmetry explains the effect of nutrient enrichment on grassland diversity. _Ecology Letters_, _20_(1), 60–69. https://doi.org/10.1111/ele.12706

Demars, B. O. L., Wiegleb, G., Harper, D. M., Broring, U., Brux, H., & Herr, W. (2014). Aquatic plant dynamics in lowland river networks: Connectivity, management and climate change. _Water_, _6_(4), 868–911. https://doi.org/10.3390/w6040868

Dornelas, M., Antao, L. H., Moyes, F., Bates, A. E., Magurran, A. E., Adam, D., ... Zettler, M. L. (2018). BioTIME: A database of biodiversity time series for the Anthropocene. _Global Ecology and Biogeography_, _27_(7), 760–786.

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. _Science_, _344_(6), 296–299. https://doi.org/10.1126/science.1248484

Dornelas, M., Magurran, A. E., Buckland, S. T., Chao, A., Chazdon, R. L., Colwell, R. K., ... Vellend, M. (2013). Quantifying temporal change in biodiversity: Challenges and opportunities. _Proceedings of the Royal Society B: Biological Sciences_, _280_(1750), 20121931. https://doi.org/10.1098/rspb.2012.1931

Elahi, R., O'Connor, M. I., Byrnes, J. E. K., Dunic, J., Eriksson, B. K., Hensel, M. J. S., & Kearns, P. J. (2015). Recent trends in local-scale marine biodiversity reflect community structure and human impacts. _Current Biology_, _25_(14), 1938–1943. https://doi.org/10.1016/j.cub.2015.05.030

Fung, T., O'Dwyer, J. P., Rahman, K. A., Fletcher, C. D., & Chisholm, R. A. (2016). Reproducing static and dynamic biodiversity patterns in tropical forests: The critical role of environmental variance. _Ecology_, _97_(5), 1207–1217. https://doi.org/10.1890/15-0984.1

Goheen, J. R., White, E. P., Ernest, S. K. M., & Brown, J. H. (2005). Intra-guild compensation regulates species richness in desert rodents. _Ecology_, _86_(3), 567–573. https://doi.org/10.1890/04-1475

Gotelli, N. J., & Graves, G. R. (1996). _Null models in ecology_. Washington, DC: Smithsonian Institution Press.

Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. _Ecology_, _83_(8), 2091–2096. https://doi.org/10.1890/0012-9658(2002)083[2091:scoama]2.0.co;2

Gotelli, N. J., & McGill, B. J. (2006). Null versus neutral models: What's the difference? _Ecography_, _29_(5), 793–800. https://doi.org/10.1111/j.2006.0906-7590.04714.x

Gotelli, N. J., Shimadzu, H., Dornelas, M., McGill, B., Moyes, F., & Magurran, A. E. (2017). Community-level regulation of temporal trends in biodiversity. _Science Advances_, _3_(7), e1700315. https://doi.org/10.1126/sciadv.1700315

Hall, J. S., McKenna, J. J., Ashton, P. M. S., & Gregoire, T. G. (2004). Habitat characterizations underestimate the role of edaphic factors controlling the distribution of Entandrophragma. _Ecology_, _85_, 2171–2183. https://doi.org/10.1890/03-0043

Hallett, L. M., Hsu, J. S., Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., ... Suding, K. N. (2014). Biotic mechanisms of community stability shift along a precipitation gradient. _Ecology_, _95_(6), 1693–1700. https://doi.org/10.1890/13-0895.1

Hallett, L. M., Jones, S. K., MacDonald, A. A. M., Jones, M. B., Flynn, D. F. B., Ripplinger, J., ... Collins, S. L. (2016). CODYN: An R package of community dynamics metrics. _Methods in Ecology and Evolution_, _7_(10), 1146–1151. https://doi.org/10.1111/2041-210x.12569

Harms, K. E., Condit, R., Hubbell, S. P., & Foster, R. B. (2001). Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. _Journal of Ecology_, _89_(6), 947–959. https://doi.org/10.1111/j.1365-2745.2001.00615.x

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. _The American Naturalist_, _163_(2), 192–211. https://doi.org/10.1086/381004

Hubbell, S. P. (1997). A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. _Coral Reefs_, _16_, S9–S21. https://doi.org/10.1007/s003380050237

Hubbell, S. P. (2001). _The unified neutral theory of biodiversity and biogeography_ (Vol. _32_). New Jersey: Princeton University Press.

Ives, A. R., Dennis, B., Cottingham, K. L., & Carpenter, S. R. (2003). Estimating community stability and ecological interactions from

time-series data. *Ecological Monographs*, *73*(2), 301–330. https://doi.org/10.1890/0012-9615(2003)073[0301:ecsaei]2.0.co;2

Jabot, F., & Lohier, T. (2016). Non-random correlation of species dynamics in tropical tree communities. *Oikos*, *125*(12), 1733–1742. https://doi.org/10.1111/oik.03103

Jones, F. A. M., & Magurran, A. E. (2018). Dominance structure of assemblages is regulated over a period of rapid environmental change. *Biology Letters*, *14*, 20180187. https://doi.org/10.1098/rsbl.2018.0187

Kalyuzhny, M., Flather, C. H., Shnerb, N. M., & Kadmon, R. (2019). A framework for quantifying deviations from dynamic equilibrium theory. *bioRxiv*, 755645. https://doi.org/10.1101/755645

Kalyuzhny, M. K., Kadmon, R., & Shnerb, N. M. (2015). A neutral theory with environmental stochasticity explains static and dynamic properties of ecological communities. *Ecology Letters*, *18*(6), 572–580. https://doi.org/10.1111/ele.12439

Kalyuzhny, M., Schreiber, Y., Chocron, R., Flather, C. H., Kadmon, R., Kessler, D. A., & Shnerb, N. M. (2014). Temporal fluctuation scaling in populations and communities. *Ecology*, *95*(6), 1701–1709.

Kalyuzhny, M., Seri, E., Chocron, R., Flather, C. H., Kadmon, R., & Shnerb, N. M. (2014). Niche versus neutrality: A dynamical analysis. *The American Naturalist*, *184*(4), 439–446. https://doi.org/10.1086/677930

Kalyuzhny, M., & Shnerb, N. M. (2017). Dissimilarity-overlap analysis of community dynamics: Opportunities and pitfalls. *Methods in Ecology and Evolution*, *8*(12), 1764–1773. https://doi.org/10.1111/2041-210x.12809

Kilpatrick, A. M., & Ives, A. R. (2003). Species interactions can explain Taylor's power law for ecological time series. *Nature*, *422*(6927), 65–68. https://doi.org/10.1038/nature01471

Knape, J., & de Valpine, P. (2012). Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance? *Ecology Letters*, *15*(1), 17–23. https://doi.org/10.1111/j.1461-0248.2011.01702.x

Kondoh, M. (2001). Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1464), 269–271. https://doi.org/10.1098/rspb.2000.1384

Lamy, T., Wang, S. P., Renard, D., Lafferty, K. D., Reed, D. C., & Miller, R. J. (2019). Species insurance trumps spatial insurance in stabilizing biomass of a marine macroalgal metacommunity. *Ecology*, *100*(7), e02719. https://doi.org/10.1002/ecy.2719

Lan, G., Getzin, S., Wiegand, T., Hu, Y., Xie, G., Zhu, H., & Cao, M. (2012). Spatial distribution and interspecific associations of tree species in a tropical seasonal rain forest of China. *PLoS ONE*, *7*(9), e46074. https://doi.org/10.1371/journal.pone.0046074

Lande, R., Engen, S., & Saether, B.-E. (2003). *Stochastic population dynamics in ecology and conservation*. New York, NY: Oxford University Press.

Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, *16*, 106–115. https://doi.org/10.1111/ele.12073

Magurran, A. E. (2016). How ecosystems change. *Science*, *351*(6272), 448–449. https://doi.org/10.1126/science.aad6758

Magurran, A. E., Deacon, A. E., Moyes, F., Shimadzu, H., Dornelas, M., Phillip, D. A. T., & Ramnarine, I. W. (2018). Divergent biodiversity change within ecosystems. *Proceedings of the National Academy of Sciences USA*, *115*(8), 1843–1847. https://doi.org/10.1073/pnas.1712594115

Magurran, A. E., & Henderson, P. A. (2018). More than the sum of the parts: Annual partitioning within spatial guilds underpins community regulation. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1883), 20180659. https://doi.org/10.1098/rspb.2018.0659

May, R. M. (1976). Simple mathematical-models with very complicated dynamics. *Nature*, *261*(5560), 459–467. https://doi.org/10.1038/261459a0

McGill, B. J., Dornelas, M., Gotelli, N. J., & Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology and Evolution*, *30*(2), 104–113. https://doi.org/10.1016/j.tree.2014.11.006

McGill, B. J., Hadly, E. A., & Maurer, B. A. (2005). Community inertia of Quaternary small mammal assemblages in North America. *Proceedings of the National Academy of Sciences USA*, *102*(46), 16701–16706.

Preston, F. W. (1960). Time and space and the variation of species. *Ecology*, *41*(4), 612–627. https://doi.org/10.2307/1931793

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge, UK: Cambridge University Press.

Rosindell, J., & Cornell, S. J. (2007). Species-area relationships from a spatially explicit neutral model in an infinite landscape. *Ecology Letters*, *10*(7), 586–595. https://doi.org/10.1111/j.1461-0248.2007.01050.x

Tilman, D., & Pacala, S. (1993). The maintenance of species richness in plant communities. In R. E. Ricklefs & D. Schluter (Eds.), *Species diversity in ecological communities* (pp. 13–25). Chicago, IL: University of Chicago Press.

Tomašových, A., & Kidwell, S. M. (2010). The effects of temporal resolution on species turnover and on testing metacommunity models. *The American Naturalist*, *175*(5), 587–606. https://doi.org/10.1086/651661

Usinowicz, J., Chang-Yang, C.-H., Chen, Y.-Y., Clark, J. S., Fletcher, C., Garwood, N. C., … Wright, S. J. (2017). Temporal coexistence mechanisms contribute to the latitudinal gradient in forest diversity. *Nature*, *550*(7674), 105–108. https://doi.org/10.1038/nature24038

Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beausejour, R., Brown, C. D., … Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences USA*, *110*(48), 19456–19459. https://doi.org/10.1073/pnas.1312779110

Yamada, T., Zuidema, P. A., Itoh, A., Yamakura, T., Ohkubo, T., Kanzaki, M., … Ashton, P. S. (2007). Strong habitat preference of a tropical rain forest tree does not imply large differences in population dynamics across habitats. *Journal of Ecology*, *95*, 332–342. https://doi.org/10.1111/j.1365-2745.2006.01209.x

Ziebarth, N. L., Abbott, K. C., & Ives, A. R. (2010). Weak population regulation in ecological time series. *Ecology Letters*, *13*(1), 21–31. https://doi.org/10.1111/j.1461-0248.2009.01393.x

BIOSKETCH

Michael Kalyuzhny performed the study as a PhD student in the Hebrew University of Jerusalem. He is interested in understanding the processes that shape species diversity and ecological dynamics, changes and stability.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.