Received: 5 April 2020 | Revised: 24 August 2021 | Accepted: 1 September 2021

DOI: 10.1111/geb.13409

Global Ecology and Biogeography | A Journal of Macroecology | WILEY

METHOD

A framework for quantifying deviations from dynamic equilibrium theory

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Funding information
University of Michigan, Grant/Award Number: Michigan Life Sciences Fellowship Program; Israel Academy of Sciences and Humanities, Grant/Award Number: Adams Fellowship Program

Editor: Petr Keil

Abstract

Aim: In an age of increased anthropogenic changes, it is crucially important to understand how and why ecological communities change. Community assembly is governed by colonization and extinction processes, and the simplest model describing it is dynamic equilibrium (DE), which assumes that communities are shaped solely by stochastic colonization and extinction events. Deviations from this model can point to the role of species life histories, niches or human stressors acting on communities. Despite its potential to serve as a null model for community dynamics, there is currently no accepted methodology for identifying and measuring such deviations.

Innovation: Here we propose a new, easily applicable methodology for testing and quantifying deviations of empirically observed time series of community dynamics from the predictions and assumptions of the classical DE model, in which assemblages of independent species undergo stochastic colonization–extinction dynamics with constant rates. The methodology consists of a novel randomization-based null model to generate synthetic time series (PARIS) and a set of statistics that quantify and test how different facets of community dynamics deviate from DE. These statistics are designed to test the assumptions of the theory, namely species independence and constancy of colonization and extinction rates, and the predictions of the theory regarding the magnitude of changes in species richness and composition.

Main conclusions: Tested against simulated data and a case study, the proposed methodology is shown to have good statistical properties: acceptable type I error rates, good statistical power and robustness against errors in the data. We discuss alternative methods and present guidelines for practical use of the methodology, hoping it will enhance the applicability of DE as a reference for studying changes in ecological communities.

KEYWORDS

colonization, community assembly, community dynamics, dynamic equilibrium, extinction, island biogeography, null models, species composition, species richness, temporal beta diversity

1 | INTRODUCTION

The dynamics of ecological communities reflect the processes that shape them. Although understanding these processes has been a primary focus of ecological research for decades (Diamond, 1969; Gotelli et al., 2017; Hutchinson, 1961), most studies examine how such processes shape static patterns (e.g., the dependence of species diversity on environmental heterogeneity, productivity etc.; Kadmon & Allouche, 2007; Rosenzweig, 1995). In contrast, in recent years there has been a growing interest in understanding temporal patterns of community dynamics and change (Dornelas et al., 2014; Kalyuzhny et al., 2015; Kalyuzhny, Schreiber, et al., 2014; Magurran et al., 2015; Vellend et al., 2013). It is increasingly understood that temporal patterns hold much valuable information on how ecological communities are assembled (Chisholm et al., 2014) and on the mechanisms underlying their responses to anthropogenic effects (Elahi et al., 2015; Magurran et al., 2015).

Despite its promise, the analysis of empirically observed community dynamics has proved complex (Dornelas et al., 2013). Community time series (where the abundance or presence of a set of species is recorded over time) are inherently high dimensional, frequently short, temporally autocorrelated, noisy and prone to observation errors. Although the last point is true for most ecological data, given that the aim in time-series analysis is often to estimate changes or variances, ignoring errors or mistreating them inherently introduces BIASES (on top of the errors), sometimes severe (Kalyuzhny, Seri, et al., 2014; Knape & de Valpine, 2012). Even if these issues are dealt with, interpreting patterns of community dynamics is difficult without having some reference (Magurran, 2016). This is because many ecological theories predict that communities undergo constant changes (Hubbell, 2001; MacArthur & Wilson, 1967; May, 1976); therefore, rejecting a null expectation that temporal changes or differences would be "zero", in analogy to many approaches in traditional statistics, would not be informative. Hence, the observed dynamics should be compared with the expected dynamics under some model.

A variety of such null or "reference" models for ecological dynamics have been proposed, differing in the assumptions on the nature of the "null dynamics". One approach is to use randomization-based null models, in analogy to null models for spatial patterns. An example of such a model is the cyclic shift algorithm, which shifts the time series of every species by a random number of time units, independently of other species (Hallett et al., 2014). This null model has been used to examine temporal trends in species richness and composition (Demars et al., 2014; Magurran et al., 2018). Generally, although randomization-based null models are easy to apply to real data, it has been argued that they do not explicitly incorporate or eliminate any processes (e.g., stochastic extinctions), raising questions on the proper interpretation of their predictions (Gotelli & Graves, 1996; Roughgarden, 1983).

An alternative approach is to use explicit stochastic process-based models (Gotelli & Ulrich, 2012). Perhaps the most basic dynamic null model is that the abundances (Knape & de Valpine, 2012; Murdoch, 1994) and diversity (Goheen et al., 2005; Gotelli et al., 2017) of species undergo a random walk. This null model is often used and rejected in favour of some form of stabilization, often attributed to intra- and interspecific interactions (Goheen et al., 2005; Knape & de Valpine, 2012; Murdoch, 1994). However, both abundances and diversity may be stabilized even in the absence of ecological interactions, simply owing to immigration from an external species pool (Hubbell, 1997; MacArthur & Wilson, 1967; Nichols et al., 2006). This immigration-generated stabilization was incorporated into two classical models, namely the dynamic equilibrium (DE) model (the simplest version of island biogeography theory; MacArthur & Wilson, 1967; Simberloff, 1969), which studies communities at the level of species presence and absence, and the neutral theory of biodiversity (Hubbell, 2001), which considers changes in abundance explicitly. These models have been used to analyse static patterns, such as abundance distributions (Hubbell, 2001; McGill, 2003) and species-isolation relationships (Schoener, 2010), and as null models of community dynamics for analysing temporal changes in multiple communities (Clark & McLachlan, 2003; Dornelas et al., 2014; McGill et al., 2005; Simberloff, 1969, 1983). Rejection of these null models highlights the role of niches and interactions beyond stochastic dynamics and immigration, making them a valuable tool for analysis of temporal changes in ecological communities. However, because of the increased complexity of these models, there is no consensus on the best practices of applying them to community time series (Boecklen & Nocedal, 1991; Kalyuzhny et al., 2015; Tomasovych & Kidwell, 2010). Alas, the complexity of fitting stochastic process-based models is viewed as a justification for using the simpler, randomization-based approach (Gotelli & Ulrich, 2012).

Here, we propose a new methodology for analysing temporal changes in species richness and composition that relies on the DE model, using randomizations of presence–absence time series. This classical model has been used as a conceptual framework in hundreds if not thousands of empirical studies (reviewed by Schoener, 2010), but only a few studies have tested explicitly whether the dynamics of natural communities are consistent with the model. We believe that a major reason for this gap is the absence of a tested and accepted methodology for doing so. We propose a novel methodology that attempts to cope with this challenge, allowing the user to answer, for the first time: to what degree and in what aspects do the dynamics of an ecological community deviate from a stochastic colonization–extinction process?

2 | THE DYNAMIC EQUILIBRIUM MODEL

The simplest dynamic model of ecological communities is the DE model (MacArthur & Wilson, 1967), portraying communities as assemblages of independent species that undergo stochastic colonization–extinction dynamics. The most applicable version of this model is the discrete-time, species-level formulation (Diamond & May, 1977; Simberloff, 1983) considering a local community (island) that receives immigrants from a regional pool (mainland) with

S_{reg} species. For every species i, if the species was absent (represented as "0") at time t it will immigrate and colonize the community by time $t + 1$ with probability C_i, whereas if it was present ("1") it will go extinct with probability E_i. Hence, the probability that species i is present at time $t + 1$, $R_{i,t+1}$, is given by (for definitions of all terms in this work, see glossary in Supporting Information Appendix S1, Table S1):

$$R_{i,t+1} = (1 - E_i)R_{i,t} + C_i(1 - R_{i,t}). \quad (1)$$

Hence, DE assumes that individual species undergo colonization and extinction dynamics at constant rates and transition probabilities (i.e., colonization and extinction probabilities; for a summary of the assumptions and predictions, see Table 1), also known as a two-state first order Markov process, which gives rise to geometric distributions of the durations of presence and absence periods. Consequently, the steady-state probability that species i is present (which is equivalent to the mean of the 0–1 time series) is:

$$\overline{R}_i = \frac{C_i}{C_i + E_i}, \quad (2)$$

and the temporal variance is:

$$\mathrm{var}(R_i) = \frac{C_i E_i}{(C_i + E_i)^2}. \quad (3)$$

At the community level, species richness $S(t)$ is simply the sum of all presences:

$$S(t) = \sum_{S_{reg}} R_{i,t}. \quad (4)$$

TABLE 1 Overview of the assumptions and predictions of the Dynamic Equilibrium (DE) model, examples of studies that have tested them and the statistics that we propose for that purpose

Property	Manifestation in DE model	Examples of studies on this property	Statistic quantifying deviations	Interpretation of positive/negative deviation
Assumptions				
Species are idependent of each other	C_i and E_i are independent of other species	Pielou and Robson (1972), Schluter (1984)	$\overline{cov}$: Average covariance between time series of individual species	Positive/negative association; species appear and disappear together (positive) or appear when others disappear (negative)
Constant colonization and extinction rates	C_i and E_i are constant	Bertuzzo et al. (2011)	var_{ex} and var_{col} (Equations 9 and 10): Mean standardized effect size of variance of presence and absence periods, *pr* and *pa*, respectively	High/low variance in presence/absence periods; positive: some periods very short, some very long; negative: species persist or are absent for fixed amounts of time
Predictions				
Temporal stability of species richness	$\mathrm{var}(S) = \sum_{S_{reg}} \frac{C_i E_i}{(C_i+E_i)^2}$	Diamond (1969), Dornelas et al. (2014), Simberloff (1983)	*ds* (Equation 7): Maximal change in richness, beyound expected change under DE	Larger/smaller changes in richness than expected (e.g., owing to responses to environmental changes)
Limited compositional turnover	See Equation S4 in Supporting Information (Appendix S2)	Diamond (1969), Dornelas et al. (2014)	*dj* (Equation 8): Maximal deviation from expected dissimilarity, beyond DE expectation	Changes in composition are too fast (only positive deviations are considered)

Abbreviation: DE, dynamic equilibrium.

Furthermore, DE assumes that the S_{reg} species are independent of each other and characterized by their probabilities C_i and E_i, which are determined by properties of the species and the environment. Based on these two core assumptions, namely constant rates (and transition probabilities) and independent species, the model predicts that species richness would fluctuate around a stable equilibrium, with temporal mean, $\overline{S}$:

$$\overline{S} = \sum_{S_{reg}} \overline{R}_i \quad (5)$$

and variance, var(S):

$$\mathrm{var}(S) = \sum_{S_{reg}} \mathrm{var}(R_i) \quad (6)$$

(Diamond & May, 1977). Composition is predicted to undergo some turnover, and this can be quantified by computing the Jaccard dissimilarity of the community at every time t to $t = 0$ (e.g., Dornelas et al., 2014; Magurran et al., 2018), which we term the Jaccard through time curve [$J(t)$]. For short time-scales the community would undergo little turnover, which would increase with time to an asymptote, representing the dissimilarity of the initial composition to a temporally independent community [for more information on $J(t)$, see Supporting Information Appendix S2; Figure S1].

Previous tests of DE were either qualitative (Diamond, 1969) or used ad-hoc quantitative methods whose properties have not been studied adequately (see Discussion; for a summary of references testing the assumptions and predictions, see Table 1; for the performance of alternative approaches, see Supporting Information Appendix S3). To fulfil the potential of DE to inform research on community dynamics, there is a need for a methodology that would allow quantification of deviations from both the predictions and assumptions of DE and the statistical significance of such deviations. Such a methodology should satisfy the following requirements:

1. For data generated by DE, the quantified magnitude of deviations from DE should be zero.
2. For such data, the type I error rate of the statistical test for the significance of these deviations should not exceed the preset level (we used $\alpha = .05$ for all analyses).
3. For data NOT generated by DE, the methodology should have good power to detect and quantify the deviation(s).
4. Given that empirical community dynamics might show deviations from DE in some respects and no deviations in other respects (and such differences might be informative), the methodology should be able to detect different deviations specifically and to distinguish between them.
5. The methodology should be robust to issues with the data, such as false or incomplete detection of species and missing years.
6. The methodology should be easily applicable.

Here, we propose a methodology that attempts to satisfy all these requirements. The proposed methodology tests both the assumptions and the predictions of DE by comparing a set of statistics indicating key aspects of community dynamics with an appropriate randomization-based null model. A comprehensive analysis using simulated data and a case study indicate that it has good statistical properties (both type I error rate and power) and is highly robust to typical issues of empirical data. To facilitate the use of the proposed methodology, we provide a full MATLAB and R code for its practical application and guidelines for optimal use of the methodology.

In the next section, we describe our methodology, focusing on its two basic elements, namely the null model and the statistics used for testing the assumptions and predictions of the DE model. We then provide a detailed analysis of the performance of the methodology, in particular its type I error rate (the realized α) and its robustness and power to detect deviations from DE under an alternative model. We also use our approach to reanalyse the data from the most classical test of the DE model (the Florida Keys defaunation experiment; Simberloff & Wilson, 1969). Based on these analyses, we provide key guidelines for practical applications of the methodology. We conclude by discussing the interpretation of outputs of the methodology and a comparison of our methodology with several previously proposed methods.

3 | THE METHODOLOGICAL FRAMEWORK

Our approach for testing DE consists of two components, which are, in principle, independent (i.e., each can be altered separately): a null model for generating synthetic community time series, and statistics that characterize various dynamical aspects and are compared with the null model. The basic assumption is that samples of presence/absence of species in the community are taken at discrete regular time intervals (years or any other time unit) and that some of the samples might be missing.

3.1 | The PARIS null model

The aim of the "Presence–Absence Randomization wIthin periodS" (PARIS) null model is to generate synthetic time series of community composition that resemble the original time series but adhere to the assumptions of DE, namely, species independence and constant colonization and extinction probabilities. This could be done by estimating the colonization and extinction probabilities for every species and simulating DE dynamics (e.g., Clark & Rosenzweig, 1994; Diamond & May, 1977; Simberloff, 1983), but this approach suffers from severe bias issues (see Supporting Information Appendix S3.1; Boecklen & Nocedal, 1991). PARIS circumvents this problem by using a key property of DE. Suppose that species i was present for r_{tot} years and absent for a_{tot} years, during which e_{tot} extinction events and c_{tot} colonization events have occurred. Then, these events could happen after each year of presence and absence (except for the last one),

respectively, WITH EQUAL PROBABILITY (with some constraints; see below and Supporting Information Appendix S4; see also the glossary in Supporting Information Table S1). This is because the probabilities of colonization and extinction are temporally constant under DE. To generate this property, for each species independently, PARIS randomizes the timing of the colonization and extinction events while keeping r_{tot}, a_{tot}, e_{tot}, c_{tot} and the initial and final states of the time series. In the Supporting Information (Appendix S4), we explain in more depth the equivalence of PARIS and DE and justify the algorithm further.

Consider that there were r_{tot} years of presence in the empirical time series, divided by extinction events (that initiate periods of absence) into pr_{tot} periods of presence, and a_{tot} years of absence, divided by colonization events into pa_{tot} periods of absence (see example below and Figure 1). The algorithm chooses $pr_{tot} - 1$ out of the first $r_{tot} - 1$ years of presence without replacement, simultaneously. Next, the extinctions events are assigned to happen after the chosen years (Figure 1c). The analogous procedure is applied when $pa_{tot} - 1$ colonization events are assigned randomly after the first $a_{tot} - 1$ years of absence. If a species was present and/or absent continuously, the presence and/or absence will not be changed in all realizations. Missing years are removed before the algorithm is applied and are then put back at their original timing (the implications of this are tested below). After randomizing the timing of the colonization and extinction events, and therefore the durations of every presence and absence period, the algorithm combines the presence and absence periods, beginning with the initial state (Figure 1d). To avoid confusion, we emphasize that the algorithm directly reshuffles the colonization and extinctions events with equal probabilities and not the presence and absence years.

The algorithm is exemplified in Figure 1, where the original time series is [1 1 1 0 0 0 1 1 0 1], where "1" stands for a year of presence and "0" for a year of absence. Here, $r_{tot} = 6$, $a_{tot} = 4$, $pr_{tot} = 3$ and $pa_{tot} = 2$, meaning that two extinction events and one colonization event should be assigned. Note that this is one colonization less than observed, in accordance with the definition of the algorithm above. This is because the last colonization must occur after the final year of absence, to ensure that the species is present in the final year of the time series. To examplify the algorithm, choosing extinction to occur after the first and second years of presence and colonization to occur after the second year of absence will lead to the following synthetic time series: [1 0 0 1 0 0 1 1 1 1], as in the upper example in Figure 1d. All such possible randomizations are equiprobable.

This algorithm generates independent species time series because it is applied to single species independently and is constructed to be equivalent to a process with constant transition probabilities, as explained above. Hence, the PARIS model satisfies the two core assumptions of DE and can be used to generate multiple synthetic time series that "force" these assumptions on the data. It is important to note that this model preserves the initial state of the community, in addition to the final state (the presence and absence of each species in the first and final year in the data). See the Discussion for implications of this.

3.2 | Summary statistics

Data describing the species composition of a community through time are inherently high dimensional and can therefore be summarized in multiple ways. The statistics we propose quantify core aspects of the dynamics relative to the expectations of DE. The significance of their deviation from DE can be calculated by comparing their observed value with the distribution of expected values under the null model. We define five statistics: two statistics refer to the predictions (changes in richness and composition), and three statistics refer to the assumptions (species independence and constancy of colonization and extinction). All statistics are constructed such that their mean if DE is true is zero. Other statistics can also be defined and tested in the same manner within the framework. For a description of these statistics and their interpretation, see Table 1.

3.2.1 | Quantifying temporal changes in richness (*ds*)

The most basic prediction of DE is that species richness should be relatively stable through time at steady state (Equation 6). To test it, we developed the statistic *ds*, which quantifies the magnitude of maximal temporal changes in species richness, beyond the expectation of DE (Figure 2a):

$$ds^{(k)} = max\left(S_{obs}^{(k)}\right) - min\left(S_{obs}^{(k)}\right) - \overline{\left[max\left(S_{null}^{(k)}\right) - min\left(S_{null}^{(k)}\right)\right]}. \quad (7)$$

Here, k is a hyper-parameter indicating the proportion of initial and final samples that are ignored (more on this later), and $S_{obs}^{(k)}$ and $S_{null}^{(k)}$ are the observed and randomized richness time series, in which the minimum and maximum richness are computed and the overbar represents averaging over PARIS randomizations.

Under the PARIS null model, richness in the first and last year in every realization precisely equals the observed values (because the presence/absence of all species in the first and final years are preserved), which can lower power. For this reason, it is useful to perform the calculation of *ds* for the central part of the time series, after "cutting" a proportion k of the years on both sides in the empirical data and in the PARIS randomizations. This is the meaning of the superscript "k" in Equation 7.

Positive *ds* indicates that the temporal changes in species richness are larger than expected, which could be caused by environmental fluctuations having a similar effect on many species or by mutualistic interactions. Negative *ds* indicates smaller changes, potentially caused by competition for limited niches that determine richness (Simberloff, 1983), or by contrasting responses to environmental changes. The temporal scale at which these changes are different from DE is not defined, meaning that a large *ds* can result from any combination of long-term trends and short-term variation, giving maximal power to detect deviations. This is similar conceptually to temporal variance, but our preliminary analysis revealed that it has more statistical power. Finally, given that *ds* may depend on average

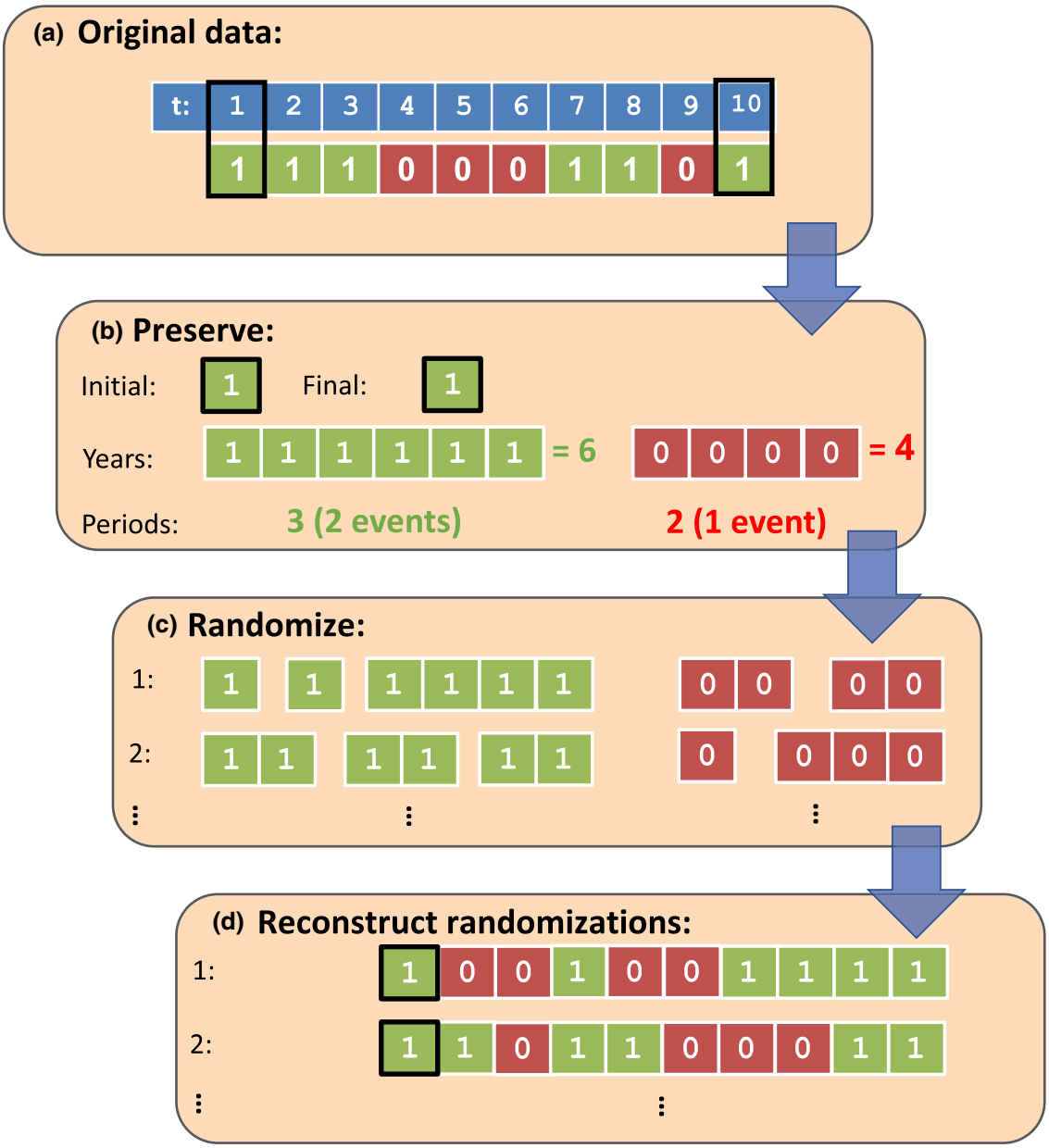

FIGURE 1 Example application of the "Presence–Absence Randomization wIthin periodS" (PARIS) null model to an observed time series. (a) The algorithm has as input a single-species time series of presence ("1") and absence ("0"). (b) The algorithm preserves the initial and final states (black boxes), the number of years of presence (r_{tot}) and absence (a_{tot}) and the number of periods they are divided into (pr_{tot} and pa_{tot}). This is done separately for presence and absence. (c) Next, the presence and absence periods are randomized by dividing the total time of presence and absence at $pr_{tot} - 1$ and $pa_{tot} - 1$ random time points (extinction and colonization events, respectively). (d) Finally, the time series is reconstructed by adding the presence and absence periods consecutively, beginning with the initial state

richness and to facilitate comparison and interpretation, it is also possible to examine $ds/\overline{S}$.

3.2.2 | Quantifying temporal changes in composition (*dj*)

The statistic *dj* quantifies the magnitude of temporal changes in composition, beyond the predictions of DE (Figure 2b):

$$dj = max\left(J_{obs} - \overline{J_{null}}\right) - \overline{max\left(J_{null} - \overline{J_{null}}\right)}, \quad (8)$$

where J is the Jaccard through time curve (Supporting Information Appendix S2), J_{obs} is this curve for the observed data, and J_{null} is computed for a single realization of the null model. The difference between any two J curves is computed for the year when it is maximal. The second term, averaging over realizations of the null, represents stochastic deviations from the expected J curve under the null, and subtracting

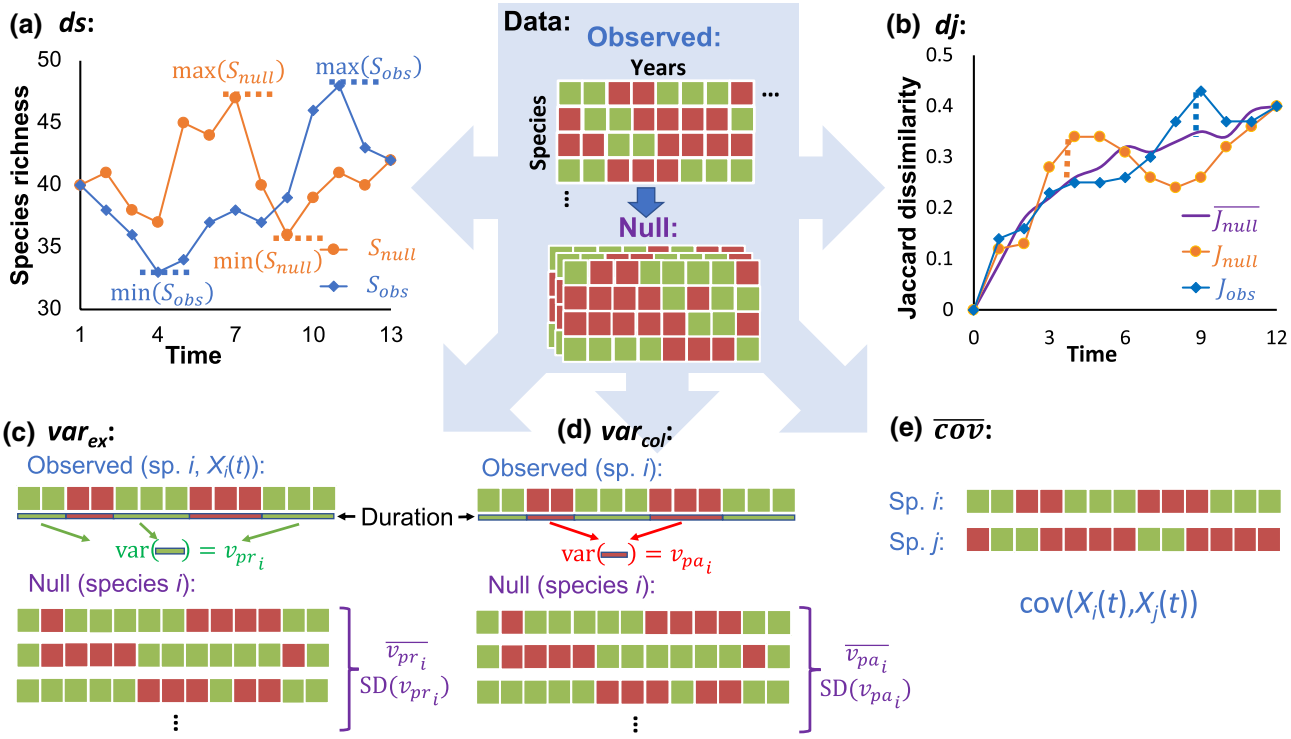

FIGURE 2 Computation of the five proposed statistics, which are based on the observed and null community time series of presence (green) and absence (red). Only one or a few randomized null communities are illustrated. In (a), excessive changes in richness (*ds*) are computed by comparing the maximal change in richness in the observed (blue) time series with the null (orange) time series. In (b), excessive compositional changes are computed by comparing the maximal upward deviations (dashed lines) of: (1) the observed Jaccard curve (blue) from the expected curve under the null model (purple); and (2) a single randomized community curve (orange) from the expected curve. In (c,d), the rate uniformity of extinction and colonization statistics (var_{ex} and var_{col}) are computed using the variance of presence (v_{pri}) and absence (v_{pai}) period durations, standardized using the means and variances computed using the null model. This computation is shown for only a single species, and these standardized measures should also be averaged over species. (e) Finally the temporal covariance of a pair of species is presented, and this should be averaged over all pairs to obtain $\overline{cov}$

it makes the expected $dj = 0$ under DE. In analogy to *ds*, *dj* does not specify a priori a temporal scale at which the deviations from DE are examined.

3.2.3 | Quantifying inconstancy of colonization (var_{col}) and extinction (var_{ex}) rates

To test the assumptions of DE that colonization and extinction probabilities are constant, we use the theorem that, under a discrete stochastic process with a constant probability of an event (colonization/extinction), the duration of time to the event is geometrically distributed. Hence, the variance in the durations of continuous presence periods (*pr*) and absence periods (*pa*) can be used to devise a test statistic for the constancy of extinction and colonization rates, respectively. For example, a time series where the durations of presence periods are $pr = \{1 \text{ year}, 30 \text{ years}\}$ is not likely to be a result of extinction occurring at a constant probability owing to the high variance of *pr*. Given that each species *i* has its own transition probabilities and variances of presence and absence durations [$v_{pri} = \text{var}(pr)$ and $v_{pai} = \text{var}(pa)$, respectively], we propose the statistics var_{col} and var_{ex} (Figure 2c,d), which average (across species) the standardized v_{pr} and v_{pa}. Hence:

$$\text{var}_{\text{ex}} = \frac{1}{\left|S_{pr}\right|} \sum_{i \in S_{pr}} \frac{v_{pri} - \overline{v_{pri}}}{\text{SD}(v_{pri})}, \tag{9}$$

and

$$\text{var}_{\text{col}} = \frac{1}{\left|S_{pa}\right|} \sum_{i \in S_{pa}} \frac{v_{pai} - \overline{v_{pai}}}{\text{SD}(v_{pai})}, \tag{10}$$

where the expectations and standard deviations (SD) of v_{pri} and v_{pai} are calculated over realizations of the null model (as in a standardized effect size). These formulae use only the subsets of species that have at least two presence periods, S_{pr}, or absence periods, S_{pa}, because only for them would randomizations generate data different from the input.

Positive values of var_{col} and var_{ex} indicate that the variation in the duration of absence and presence periods, respectively, is higher than expected under a stochastic process with constant transition probabilities. For example, if some time periods have higher extinction rates, we will sometimes see periods of short presence and

sometimes of long presence, leading to $var_{ex} > 0$. Negative values would indicate that the variation is too small (e.g., hypothetically, the species is always observed for 5 years and then it disappears, periodically). A value of "1" indicates that on average (across species), the variance in the durations of presence or absence periods is higher than expected by one unit of standard deviation.

3.2.4 | Quantifying species dependence ($\overline{cov}$)

To test the assumption of the independence of species, we compute the covariance between every pair of species time series and average over the pairs to obtain the average covariance statistic ($\overline{cov}$; Figure 2e). Positive covariance indicates that species appear and disappear together in the data, on average, whereas negative covariance indicates that species replace each other. For the sake of interpreting the magnitude of deviations in this respect, it is noteworthy that the maximal possible covariance is .25 (possibly slightly higher if covariance is normalized by $n - 1$ rather than n), if all the species are perfectly correlated and present half of the time.

All these statistics are expected to have a mean of zero under DE by construction. A small exception is average covariance, which may have a positive value if the community is far from equilibrium initially. For all statistics except *dj*, a two-sided test is performed by comparing the observed statistic with the distribution of the statistic in multiple PARIS randomizations and computing the *p*-values. For *dj*, the test is one sided.

3.3 | Application to multiple communities

If data for several similar local communities are available within some dataset, it might be of interest to calculate the average statistics (over communities) and their significance at the dataset level. This can be done by recording the statistics produced by PARIS for each community separately. The test is then performed by comparing the observed average (over communities) statistic with the distribution of averaged randomized statistics. For example, if a dataset consists of 10 communities, we initially compute the average *dj* (over the communities). We then compute and record 2×10^4 PARIS-generated values of *dj* for each of the communities. Next, we average the randomized statistics over the communities to obtain 2×10^4 average values of *dj* that will serve as the null distribution for the test. Importantly, this approach assumes that the communities are independent. Alternatively, pooling the presence across all communities is possible to generate a single time series.

4 | TESTING THE PERFORMANCE OF THE METHODOLOGY

We test three aspects of the methodology under different scenarios. Initially, we consider the behaviour of all statistical tests under DE, asking: is the type I error rate of each test excessive? And are the deviations roughly zero? Next, we ask whether these properties are robust to issues with the data, specifically false detection, incomplete detection and missing years. Finally, we examine the ability of the methodology to detect and quantify deviations under an alternative model. Based on the results in this section, we provide recommendations on the application of the methodology. Full details of the testing procedure are presented in the Supporting Information (Appendix S5). Briefly, we considered all combinations of:

- Three levels of regional species pool sizes (S_{reg}): 30, 90 and 270 species;
- Two distributions of colonization rates: C_i ~High and C_i ~Low;
- Two distributions of extinction rates: E_i ~High and E_i ~Low; and
- Two levels of $\rho(C_i, E_i)$, where ρ is Spearman's rank correlation: $\rho(C_i, E_i) = 0$ and $\rho(C_i, E_i) = -1$.

For each of the 24 scenarios above, we generated 5,000 synthetic communities using Equation 1 and calculated the five statistics and their *p*-values using 500 PARIS randomizations (of each community). To test the robustness of the methodology, we introduced errors into the data. For every presence record in every community, there was a probability P_{miss} of falsely missing the species (incomplete detection). Alternatively, we introduced a probability P_{false} to detect falsely a species that is not observed in the data. Finally, we transformed a given number of years into missing years. The statistics and their *p*-values were recorded at different levels of these parameters, and we examined the realized α (the proportion of tests where $p < .05$). Finally, we tested the behaviour of the methodology under an alternative community dynamics model that we developed for this purpose, the state-dependent extinction (SDE) model. This model assumes that extinction rates change through time and that species might respond synchronously to these fluctuations (for more details, see Supporting Information Appendix S5.3).

An initial examination revealed that calculating *ds* for the "central" part of the time series (removing a proportion *k* of the initial and final years; see above) has similar type I error rates and more power than $k = 0$, hence we used $k = 0.06$ throughout this work.

5 | RESULTS: PERFORMANCE OF THE METHODOLOGY

We found that under the multiple scenarios we considered, type I error rates for all the summary statistics were mostly close to .05 (Figure 3), and the magnitude of deviations was also close to zero (Supporting Information Figures S2 and S3). The addition of incomplete detection, false detection and missing years to the data (Figure 4; Supporting Information Figures S4–S9) introduced some errors into the inference, but many of the statistics were robust. Most noticeably, var_{col} and var_{ex} were highly sensitive to incomplete and false detection, respectively. These errors introduce short periods (typically a year) of absence and presence, therefore strongly

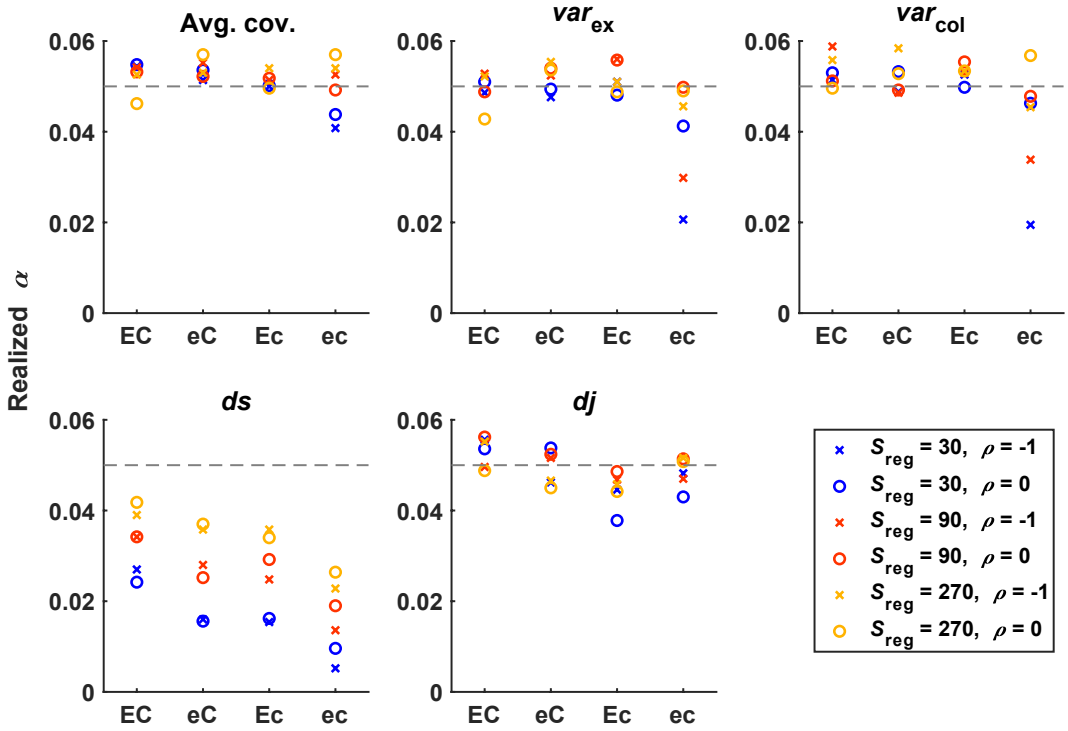

FIGURE 3 Proportion of rejected statistics under dynamic equilibrium (DE; type I errors, realized α) with various parameter regimes. Four combinations of rates are considered: high and low average colonization (C and c, respectively) and high and low average extinction (E and e, respectively). Simulations were run for each combination of rates, correlation between colonization and extinction ("o" = no correlation; "x" = negative correlation) and size of the species pool (30 = blue; 90 = orange; 270 = yellow). Every point represents one of these combinations, and the proportion of significant results was calculated over 5,000 synthetic communities. The grey dashed line represents a rejection probability of .05

inflating the variances in the duration of absence and presence periods. Moreover, *dj* was sensitive to issues with the data, mostly if regional richness is high (hundreds of species) and the issues are severe (many missing years, many short presence or absence periods owing to errors). In some cases, errors also generated negative values of *ds* and *dj* but this did not inflate type I error rates. Nevertheless, in most of the conditions we considered, the methodology was robust. Figure 4 provides some reference for considering the possible effect of issues with the data when interpreting results. For example, Figure 4 shows that $\overline{cov}$ may have a type I error rate between .075 and .1 for low incomplete detection or high false detection.

Under the alternative SDE model, the methodology exhibited several desired properties (see detailed analysis in Supporting Information Appendix S6). Generally, we found that the methodology has the power to detect deviations from DE, and this power increases with the number of species in the pool, the transition probabilities (since that more events mean more informative input to the methodology) and the magnitude of the deviations. We also examined cases in which only some of the assumptions are violated (e.g., the species are independent, but the transition probabilities are not constant), finding that a statistic quantifying violations from some assumption is mostly specific to this assumption and insensitive to the violation of other assumptions. Given that, in the alternative model, the transition probabilities fluctuate in time, some of the scenarios we model lead to trends in species richness over decadal time scales, and the model detects them with high power (see Supporting Information Appendix S6).

Finally, we have examined the ability of our methodology to detect meaningful deviations from DE in a real dataset, the classical Florida Keys experiment (Schoener, 2010; Simberloff & Wilson, 1969). This dataset has a relatively short temporal extent (13–16 surveys; see Supporting Information Appendix S7 and Figure S10 and Table S2 therein) and is often considered a classical system that supports DE qualitatively. In contrast to this long-standing interpretation, our analysis of the data using the PARIS model reveals significant excessive richness changes, in addition to deviations from the assumptions of DE (Supporting Information Figure S10; Table S2). This result confirms the power of our methodology to detect deviations from DE even in short time series from a system that has previously been suggested to support DE.

6 | GUIDELINES FOR PRACTICAL APPLICATION OF THE METHODOLOGY

Based on these and other tests of the performance, we provide a few guidelines for the application of the methodological framework. We recommend using data with ≥10 samples in time (years), observed

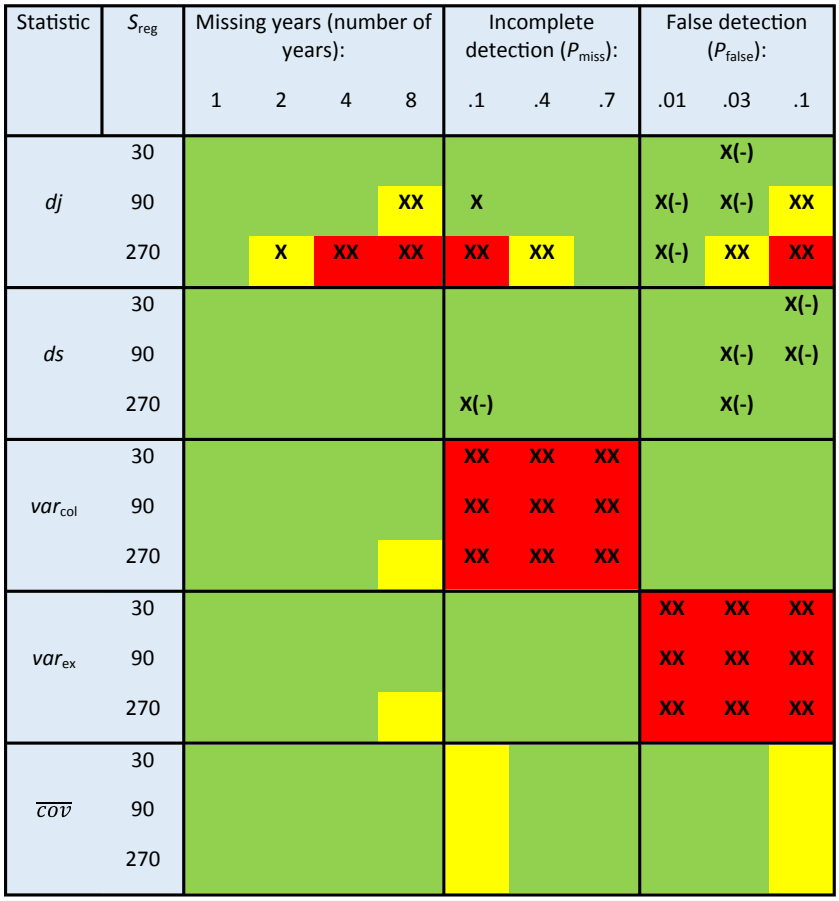

FIGURE 4 Sensitivity of the five statistics with the "Presence–Absence Randomization wIthin periodS" (PARIS) null model to issues with the data. Each cell represents the worst-case scenario (over eight settings for the colonization and extinction rates) for different levels of regional richness (S_{reg}) and different levels of missing years, incomplete detection probability (P_{miss}) and false detection probability (P_{false}). The colour represents the probability of type I error (which should ideally be *c*. .05). Green: realized $\alpha < .075$; yellow: $.075 \leq$ realized $\alpha < .1$; red: realized $\alpha \geq .1$. The symbol represents the resulting standardized effect size (SES, which ideally should be *c*. 0). No symbol: SES < 0.1; **X**: 0.1 ≤ SES < 0.2; **XX**: SES ≥ 0.2. The symbol (-) represents a negative SES

in the same season(s) or without seasonal effects across samples, and with ≥20–30 species observed. This will provide at least minimal power to detect deviations. Furthermore, having at least two periods of presence and two periods of absence (not necessarily for the same species) for some species is crucial for the PARIS null model to work. We further recommend using at least a few hundred PARIS randomizations (Efron & Tibshirani, 1994), and $k \approx .06$ (cutting 6% of samples on each side, which would give 1 year at the beginning and the end for a 10-year record) for the calculation of *ds*. Generally, higher values of "*k*" are better if changes in composition are slow, as is expected if colonization and extinction probabilities are low (Supporting Information Appendix S2). Moreover, the values and significance of var_{ex} and var_{col} should be taken with caution in the presence of sampling errors, although they may still be useful to compare between different communities with similar levels of sampling errors. With regard to missing years, if type I errors for *dj* are a concern, we recommend using Figure 4 as a guideline for the maximal percentage of missing samples to be used. We recommend 5%–15%, depending on the total number of species observed. If type I errors for $\overline{cov}$ are a concern, a threshold of $p = .08$ can be used for significant results.

The Supporting Information (Appendix S8) includes the full MATLAB code used in our analyses. In particular, the *test_all4* function has as input the number of randomizations to perform, the hyper-parameter *k* and a matrix of the composition of species (columns) on years (rows), where "1" represents presence, "0" represents absence, and a row of "NaN" values represents a missing year. The function calls the null2_comm3 function, which randomizes the communities using the PARIS algorithm and exports the values and the significances of the five statistics. A simple example code ("EXAMPLE.m") is included in the Supporting Information (Appendix S8). An R version ("PARIS.R") is also included.

7 | DISCUSSION

In line with the requirements that we set for our methodology, we found it to have good type I error rates, robustness to issues with the data and power to detect deviations from the assumptions and predictions of DE in a generic alternative model and in empirical data. In the Supporting Information (Appendix S3), we compare our methodology with five different approaches that have been suggested to test DE: (1) simulating DE with estimated transition probabilities (Clark & Rosenzweig, 1994; Diamond & May, 1977; Simberloff, 1969, 1981, 1983); (2) the ratio of variance to mean richness (MacArthur & Wilson, 1967; Schoener, 2010); (3) the ratio of variance to the expected variance if species are independent, used to study species interdependence and changes in species richness (Pielou & Robson, 1972; Schluter, 1984); (4) ordinary least squares regression to test for trends in richness (Brown et al., 2001; Dornelas et al., 2014; Magurran et al., 2015; Rosenzweig, 1995); and (5) a global null model for compositional changes (Dornelas et al., 2014).

We generally find that in most situations, alternative methodologies have (sometimes highly) elevated type I error rates or less power (Supporting Information Appendix S3).

More broadly, null models can be classified as randomization based or process based (Gotelli & Ulrich, 2012). DE is one of the two classical process-based null models, along with the neutral theory of biodiversity (NTB; Hubbell, 2001). Both are "dispersal–assembly" models, postulating that the presence and absence of species are dictated by stochastic colonization and extinction. Although NTB has become very popular in recent years, because it models population-level processes, it must make much stricter assumptions about the dynamics (e.g., zero sum, the magnitude of demographic stochasticity, the exact form of the regional specied abundance distribution, full ecological equivalence), which might lead to rejection owing to an auxiliary assumption (Connolly et al., 2017). Moreover, fitting neutral models to time series is much more technically demanding, requiring the estimation of multiple parameters, and is especially sensitive to the parameterization of time in the model (Kalyuzhny et al., 2015; Tomasovych & Kidwell, 2010). We believe that our new, easily applicable methodology would help to promote DE as a viable complementary approach for testing the deviations from dispersal–assembly.

Contrary to process-based null models, randomization-based null models are easy to apply to data, making them attractive. For time series data, the cyclic-shift algorithm, "shifting" each species independently in time, has been proposed and used for testing excessive compositional changes and trends in richness (Hallett et al., 2014; Magurran et al., 2018). However, this method has been shown to inflate type I errors because it does not preserve the initial state of the community and the autocorrelation structure (even of individual species; Kalyuzhny, 2020). Moreover, although a null model should eliminate a process of interest (Gotelli & Graves, 1996), it is unclear what processes are preserved or eliminated by the cyclic-shift, as is the case with randomization-based null models (Roughgarden, 1983). Another approach, recently proposed by Legendre (2019), proposes randomizing the species in different sites in two time periods to create a distribution of expected temporal turnover rates across sites. Here, again, it is not clear what is the mechanistic interpretation of an "excessive turnover". From this broader perspective, the PARIS null model lies in a unique "sweet spot", in that it is a randomization-based model, avoiding biased parameter estimation (Boecklen & Nocedal, 1991; Supporting Information Appendix S3.1) and being easy to apply, whereas it "imitates" a process-based model that makes minimalistic assumptions (unlike NTB) and has a clear ecological interpretation: What would the dynamics look like under stochastic colonization–extinction dynamics?

Several additional points regarding the interpretation of our methodology and its advantages and limitations need to be made. An essential property of our methodology is that it is applied to single communities. A possible limitation of this approach is that it cannot detect the signal of effects that are constant in time and show no temporal variation. Examples include species that are always present and exert strong effects on other species; temporally constant environmental conditions that shape assembly, and so forth. These factors have no randomizable effect on the composition–time matrix, meaning that their signal will be preserved in all randomizations and incorporated into the null expectations for all statistics. For similar reasons, if a rare species influences other species, the power to detect this will be low. It is also crucial to note that the rates which the null model uses ARE ALREADY AFFECTED by the biotic and abiotic environment, including potential intraspecific interactions. This is analogous to introducing competition "through the back door" by preserving species frequencies and richness in spatial null models (the "Narcissus effect"; Colwell & Winkler, 1984). Therefore, good agreement with the null model does not exclude effects of competition and certainly not temporally constant environmental filtering.

Although considering only one community in time precludes the detection of patterns of assembly that are observed across multiple communities in space, this also has advantages. Community assembly studies that consider spatial variation in presence/absence (Diamond, 1975; Gotelli & McCabe, 2002; Lyons et al., 2016) typically assume that the probability of a species to arrive in each community is identical. However, spatial structure in the species pool can lead to violations of this assumption. Our methodology, in contrast, makes no assumptions regarding the pool. Another point to mention is that PARIS preserves the initial state of the community, on which the observed dynamics depend. As a result, our methodology will not identify deviations from the steady state or equilibrium as violations of DE. For example, richness trends and fast compositional turnover are expected if the community is initially not at steady state (e.g., the defaunation experiment in Florida Keys; Simberloff & Wilson, 1969), and our methodology allows the detection of deviations beyond the dynamics that are expected based on the initial state (e.g., recovery of the islands from defaunation; Supporting Information Figure S10). Finally, although our methodology is applied to different communities separately, we believe it facilitates comparisons between communities. Communities can differ in colonization and extinction rates for a host of reasons, including differences in size and isolation (MacArthur & Wilson, 1967), potentially creating substantial differences in the observed dynamics. Our methodology eliminates these differences, revealing only the magnitude of deviations from DE, which we view as a form of standardization. Another aspect that facilitates comparative studies is the ability to quantify multiple deviations simultaneously, from both the assumptions and the predictions, in multiple communities. This might be used to reveal the underlying causes of such deviations across communities.

We believe that our framework has the potential to be applied widely and extended to include other aspects of community dynamics. For example, it is possible to compare subsets of species or periods, to examine the temporal variance or trends of species richness (Dornelas et al., 2014; Magurran et al., 2015), or to study the degree to which richness is regulated (tends to return to equilibrium; Gotelli et al., 2017). Such analyses should have acceptable type I error levels under DE because of the equivalence between DE and PARIS, but their robustness to issues with the data needs to be examined. We hope that the ease, good statistical properties

and sound interpretation offered by our approach should facilitate its extension and application for the empirical study of community dynamics.

ACKNOWLEDGMENTS

We thank Micha Mandel for his help and consultation on the development of the methodological framework and Eyal Ben-Hur for his assistance in the graphical presentation of results. M.K. was supported by the Adams Fellowship Program of the Israel Academy of Sciences and Humanities and by the Michigan Life Sciences Fellowship Program.

DATA ACCESSIBILITY STATEMENT

All code used to generate results is supplied in the Supporting Information. The data used in this work are available in the paper by Simberloff & Wilson (1969).

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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 in the online version of the article at the publisher's website.

How to cite this article: Kalyuzhny, M., Flather C. H., Shnerb N. M., & Kadmon R. (2022). A framework for quantifying deviations from dynamic equilibrium theory. *Global Ecology and Biogeography*, 31, 183–195. https://doi.org/10.1111/geb.13409