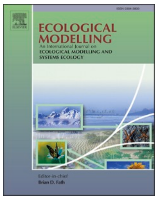
Ecological Modelling 491 (2024) 110695

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Reconsidering the Price equation: Benchmarking the analytical power of additive partitioning in ecology

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ARTICLE INFO

Keywords:
Community ecology
Null models
Price equation
Statistical testing
Trait expression

ABSTRACT

The Price approach allows the partitioning of composite variables into a set of additive components and has become an important tool in evolutionary and ecological research. However, because such components are not mutually independent and might be constrained by the inherent data structure, comparing and interpreting Price partitions among different datasets is not straightforward and has contributed to controversy in ecology.

Here we discuss and develop null model approaches that might be used as statistical standards to normalise partition values and reduce collinearity between partitions. We use a simulation approach to estimate Price partitions of artificial data and their randomisations. Using structural equation modelling we then reveal the degree of collinearity between raw and standardised partitions.

We first demonstrate that the degree of collinearity between partitions strongly depends on the data structure and then provide a general framework for null model selection. Null models that require limited additional information on the possible distribution of species richness and abundance perform best. These null models consistently reduce, but do not fully eliminate, collinearity between partitions. They assign separate type I and II error levels to each partition that differed among partitions.

We argue in favour of null models that strike a balance between information need (simplicity) and complexity of additional information, but we discourage the use of simple permutation approaches that have been successful for analysing other biodiversity measures such as species richness. We highlight that the interpretation of additive partitions of complex ecological data will benefit from analyses of the dependence among partitions.

1. Introduction

The partitioning of composite variables into a set of mutually exclusive, additive components is a popular method of analysis in ecology. For example, the total biodiversity represented in a set of samples (gamma diversity) can be decomposed into components representing diversity within samples (alpha diversity) and diversity among samples (beta diversity; Crist et al., 2003). Similarly, patterns of species co-occurrence across communities can be partitioned into the contribution of species richness differences and species turnover (Baselga, 2010). These analyses are comparable to a classic variance partitioning in the analysis of variance, in which the total sum of squares is decomposed into components of additive, interactive, and residual variation from different sources. To be properly interpreted, these ecological partitions should be compared to partitions generated by null or neutral models designed to mimic a random expectation while constraining important boundary conditions (Gotelli, 2000; Chase et al., 2011; Rosindell et al., 2012; Ulrich and Gotelli, 2013; Ulrich et al., 2017).

The Price equation is one such partition that has attracted a great deal of attention because the approach can be applied to problems from different disciplines (Luque, 2017). The partitions might be interpreted as being determined by separate mechanisms, similar to an analysis of variance. They are designed to logically separate several sources of change. but not causally separate them (Frank, 2012). In evolutionary biology, the Price equation decomposes the change in the mean value of a trait in one generation into components of transmission and selection. Within the biodiversity – ecosystem functioning (BEF) framework,

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https://doi.org/10.1016/j.ecolmodel.2024.110695
Received 19 December 2023; Accepted 16 March 2024
Available online 20 March 2024

Loreau & Hector (2001) adapted the Price equation in combination with a null model to decompose ecosystem function variables into components of complementarity (species richness effects) and selection (covariance of species composition and dominance effects). Fox (2006) and Fox & Kerr (2012) expanded this framework to incorporate species losses and gains. Recently, the Price equation has been adapted to disentangle the drivers of spatial or temporal change in species-level traits and abundances (Isbell et al., 2018; Lefcheck et al., 2021; Godsoe et al., 2022; Harrison et al., 2022; Ulrich et al., 2022). Fig. 1 specifies the possible processes involved in trait change within an evolutionary and an ecological context.

In spite of the popularity of the Price Equation, it's use in evolutionary ecology has been controversial in part because the components of a partition are not statistically independent of one another (Fox and Kerr, 2012; Pillai and Gouhier, 2019). For example, if there is no difference in mean trait values between two assemblages ($\Delta T = 0$ in Eq. (1)) the complementarity component(Δ_{Comp}) will be perfectly negatively correlated with the selection component (Δ_{Cov}.) However, an important issue that has received comparatively little attention is to what extent the partitions are constrained by the inherent data structure, for example by measurement precision. In the analysis of ecological community assembly, these constraints (e.g. community richness, total abundances, site occupation) often covary closely with traditional measures of diversity and community composition (Gotelli and Ulrich, 2012; Ulrich et al., 2017). This collinearity complicates the interpretation and applicability of the Price equation (Barry et al., 2019; Loreau and Hector, 2019; Gardner, 2020; Luque and Baravalle, 2021; Van Veelen, 2020; Bourat et al., 2023; Box 1). For instance, Isbell et al. (2018) and Bannar-Martin et al. (2018), using the 2-partition complementary approach of Loreau & Hector) and the 3-partition assembly approach of Fox & Kerr (2012), respectively, explained the components of ecosystem functioning in terms of external covariates and functional trade-offs between partitions. However, their discussion did not consider collinearity effects due to internal constraints. Moreover, absolute partition components cannot be compared directly because they are constrained by constant multipliers that guarantee additivity. For example in Eq. (3) of Box 1, four of the five partitions are multiplied by total abundance N or by N and the richness difference ΔS (implicitly the same holds for Eq. (2)). Consequently, partitions are not scale invariant and depend (often non-linearly) on the spatial extent at which N has been estimated. The use of scale invariant relative abundances (e.g. Fox, 2006) does not fully solve this issue because part of the partitions of Eq. (3) then become dependent on total richness, which also increases non-linearly with spatial (and temporal) extent (Ulrich et al., 2022). This scale dependence directly affects comparisons and the subsequent interpretation of Price partitions might be misleading (Govaert et al., 2016). Consequently, we argue that any Price approach needs a statistical standard for comparison that accounts for the inherent scale dependent collinearity of the resulting partitions.

Null model simulations and constrained randomisations can provide an effective benchmark for determining whether empirical patterns of diversity and community composition differ more than expected by chance or simple sampling effects. Here we ask what is the null expectation for Price partitions. In other words, what are the expected sizes of the partitions and their variances when compared to expectations based on assumptions of random assembly with constraints? Answering this question requires a systematic comparison of the partitions obtained for empirical or simulated data with the partitions obtained from a null model in which some elements of the original data are randomised and others are constrained. These null models can range from pattern-based statistical randomisations to process-based neutral models (Gotelli and Ulrich, 2012; Bausman, 2018; Molina and Stone, 2019).

As in other null-model analyses, the choice of the metric and the randomisation algorithm used are important determinants of pattern detection and interpretation (Gotelli and Ulrich, 2012; Strona et al., 2018; Molina and Stone, 2019). Because the individual components of Price partitions are not independent of one another, it is important to consider how the observed set of partitions collectively deviate from the expected partitions in the null model. Moreover, because some of the obvious constraints in null model analysis, such as the number of species or the abundance, are themselves part of the recipe for calculating the different components, the problem is more complex than in previous null model analyses. These are usually based on the analysis of simple, univariate response metrics (such as average species co-occurrence or

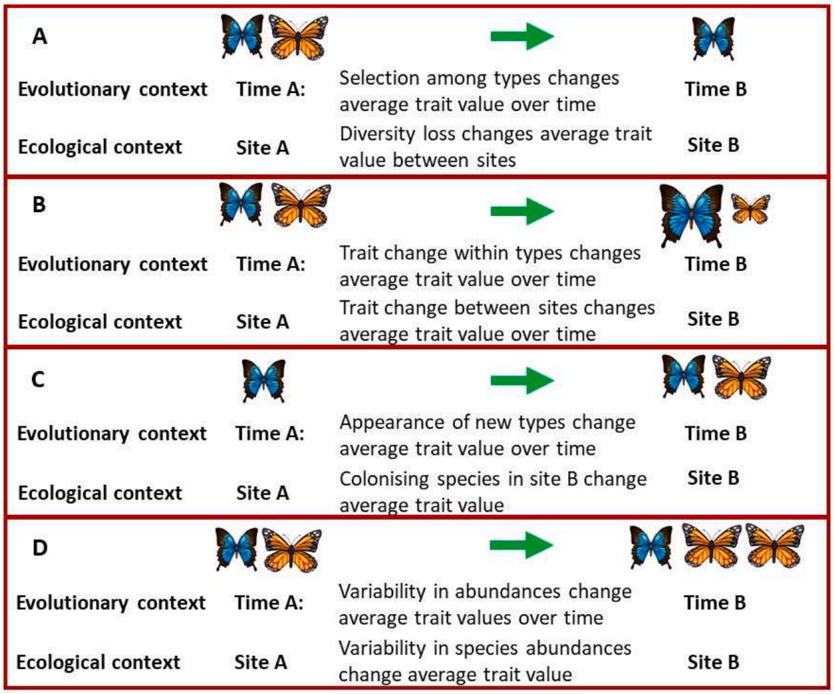


Fig. 1. The change in the average expression of a trait in a community from time *A* to time *B* within an evolutionary or from site *A* to site *B* within an ecological context.

nestedness).

Some of these issues were anticipated by Fox and Kerr (2012), who used empirical data for comparison; by Clark et al. (2019), who considered incomplete monoculture sampling, and by Frank (2014, 2018), who discussed possible constraints on partitions. More recently, Lefcheck et al. (2021) and Ulrich et al. (2022) used resampling of species identity or trait data, respectively, to compare effect sizes of each partition and to generate null expectations, although their methods did not fully account for differences in species richness and trait variability. In spite of more than 20 year of usage of Price partitioning in ecology, there are still no accepted statistical standards for Price partitions.

To better understand the implications of non-independence for Price equation partitions, we investigate this behaviour in simulated species occurrence matrices. That have typical patterns of species richness and relative abundance, but do not explicitly model strong biological processes such as density dependence, species interactions, or niche complementarity. Next, we use this set of matrices to explore correlations among the components of the Price partition, and to benchmark the performance null models and Markov chain models as baselines for Price partitions. We analysed both a classical 2-part partition comparable to the original BEF framework (Loreau and Hector, 2001) and a more recent 5-part partition (Ulrich et al., 2022) of ecological trait and abundance data. Our results emphasise that the partitions of the Price equation in ecology are likely to be non-independent, with consequences for interpretation. Below we discuss which available algorithms are able to account for this non-independence. Our analyses provide insight into the non-independence of partitions and could aid researchers in the analysis and interpretation of ecological Price partitions.

2. Methods

We first describe the statistical simulation of a set of artificial community matrices that have typical univariate patterns of relative abundance, species richness, and inter- and intra-specific variation in trait values. Next, we consider 10 possible statistical standards that could be used with Price partitions: broken stick randomisation, parametric trait randomisation, Monte Carlo Markov chain (*mcmc*), reshuffling of species identity, reshuffling of species trait and abundances using additional empirical data (*rshuff*), proportional resampling from the species pool, reshuffling across additional empirical data (*rsamp*), bootstrapping, Bayesian parameter estimation, and neutral modelling (Fig. 2, Table 1).

Box 1

The Price approach partitions the change in a variable of interest. It can be derived using a generalisation of the product rule from calculus for problems with discrete changes (Frank, 2018). For example, let S_A and S_B denote the species richness in communities A and B, S the total species richness, and $\bar{t}$ the mean expression of an ecological trait T. The change the trait value $\Delta T = \Delta(\bar{t}S)$ can be partitioned by

$$\begin{aligned}\Delta T = \Delta(\bar{t}S) = \overline{t_B}S_B - \overline{t_A}S_A = \overline{t_A}\Delta S + S_A\Delta\bar{t} + \Delta\bar{t}\Delta S = \overline{t_A}\Delta S + S_B\Delta\bar{t} \\ = \overline{t_A}\Delta S + (\Delta\bar{t}\Delta S + \Delta\bar{t}(S_B - \Delta S)) = \Delta_{Comp} + \Delta_{Cov}\end{aligned} \tag{1}$$

where $\Delta_{Comp} = \overline{t_A}\Delta S$ and $\Delta_{Cov} = \Delta\bar{t}\Delta S + \Delta\bar{t}(S_B - \Delta S)$

In an ecological context the expression of a trait c_i of species i with the relative abundance p_i can be expressed by $t_i = c_i p_i$. Eq. (1) can then be rewritten in an explicit form to show the hidden parameters of Eq. (1) (Ulrich et al., 2022)

$$\Delta T = \Delta\left(N\sum_i p_i c_i\right) = \frac{N_A}{S_A}\sum_i p_i c_i)\Delta S + S_B\sum_i \Delta\left(\frac{N}{S}p_i c_i\right) \tag{2}$$

N_A denotes the total number of individuals (abundance) in community A. Loreau and Hector (2001), using the definition of covariance applied to $\Delta T = \Delta(\bar{t}S)$ and comparing observed plant biomass with a specific null assumption, interpreted the resulting two-partition form of Eq. (1) (in red) in terms of complementary (richness and relative abundance effect) and selection (covariance effect). Fox (2006) interpreted the three partition form (in blue) in terms of richness, habitat context (including random effects), and community composition (covariance), respectively.

Ulrich et al. (2022) proposed a 5-partition framework that allows for the disentangling of richness, abundance, trait expression, and joint abundance – trait effects

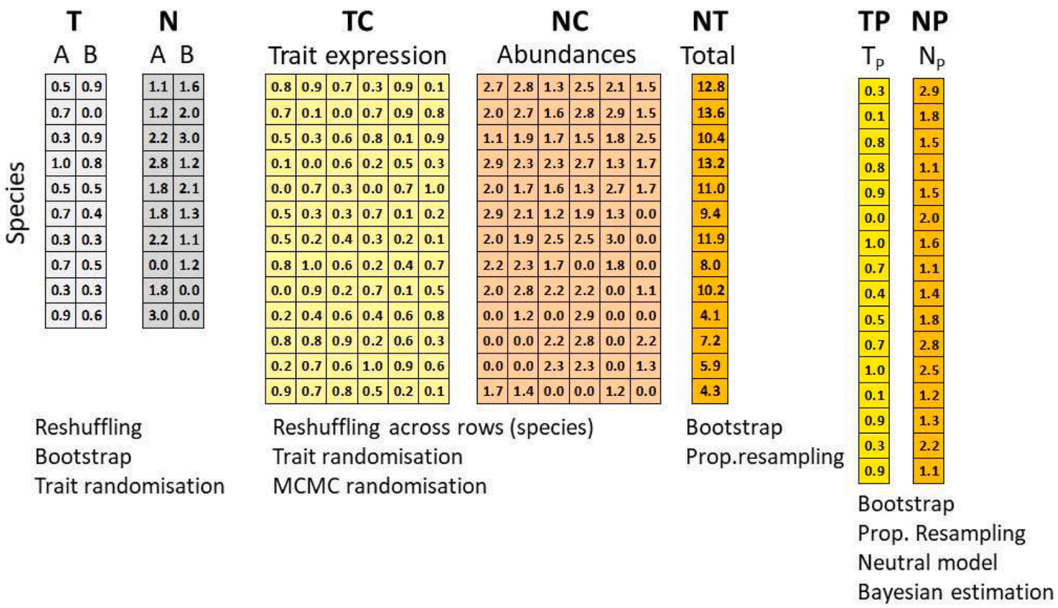
$$\Delta T = z_A\Delta S + N_B\sum_i \Delta p_i\Delta c_i + N_B\sum_i p_{A,i}\Delta c_i + N_B\sum_i \Delta p_i c_{A,i} + \left(N_B - N_A\frac{S_B}{S_A}\right)\sum_i p_{A,i}c_{A,i} \tag{3}$$

where $p_{A,i}$ and $c_{A,i}$ denote the relative abundance and trait expression of species i in community A. $z_A = \frac{N_A}{S_A}\sum_i p_{A,i}c_{A,i}$ is the mean trait expression in A. Here, we term these partitions Δ_{Comp}, $\Delta p\Delta c$, Δc, Δp, and ΔN.

We add that an algebraic reordering of Eq. (3) gives

$$\begin{aligned}\Delta T = z_A\frac{S_B - \Delta S}{N_A}\Delta N + N_B\left(\sum_i \Delta p_i\Delta c_i + \sum_i p_{A,i}\Delta c_i + \sum_i \Delta p_i c_{A,i}\right) \\ = z_A\frac{S_B - \Delta S}{N_A}\Delta N + N_B\left(\sum_i p_{i,B}c_{i,B-}p_{i,A}c_{i,A}\right) = f(\Delta S, \Delta N) + N_B\Delta(cp)\end{aligned} \tag{4}$$

Eq. (4) contains a two-partition solution equivalent to the red part in Eq. (1). The first term of Eq. (4) covers the change in community size (richness and abundance), while the second part subsumes the change in community structure. This modified two partition solution differs from the 2-partition for of Eq. (2) and both terms have a different interpretation. Particularly, the first partition does no longer solely quantify the change in richness but covers the covariance of richness and abundance.



T A	T B	N A	N B
0.5	0.9	1.1	1.6
0.7	0.0	1.2	2.0
0.3	0.9	2.2	3.0
1.0	0.8	2.8	1.2
0.5	0.5	1.8	2.1
0.7	0.4	1.8	1.3
0.3	0.3	2.2	1.1
0.7	0.5	0.0	1.2
0.3	0.3	1.8	0.0
0.9	0.6	3.0	0.0

TC						NC						NT
0.8	0.9	0.7	0.3	0.9	0.1	2.7	2.8	1.3	2.5	2.1	1.5	12.8
0.7	0.1	0.0	0.7	0.9	0.8	2.0	2.7	1.6	2.8	2.9	1.5	13.6
0.5	0.3	0.6	0.8	0.1	0.9	1.1	1.9	1.7	1.5	1.8	2.5	10.4
0.1	0.0	0.6	0.2	0.5	0.3	2.9	2.3	2.3	2.7	1.3	1.7	13.2
0.0	0.7	0.3	0.0	0.7	1.0	2.0	1.7	1.6	1.3	2.7	1.7	11.0
0.5	0.3	0.3	0.7	0.1	0.2	2.9	2.1	1.2	1.9	1.3	0.0	9.4
0.5	0.2	0.4	0.3	0.2	0.1	2.0	1.9	2.5	2.5	3.0	0.0	11.9
0.8	1.0	0.6	0.2	0.4	0.7	2.2	2.3	1.7	0.0	1.8	0.0	8.0
0.0	0.9	0.2	0.7	0.1	0.5	2.0	2.8	2.2	2.2	0.0	1.1	10.2
0.2	0.4	0.6	0.4	0.6	0.8	0.0	1.2	0.0	2.9	0.0	0.0	4.1
0.8	0.8	0.9	0.2	0.6	0.3	0.0	0.0	2.2	2.8	0.0	2.2	7.2
0.2	0.7	0.6	1.0	0.9	0.6	0.0	0.0	2.3	2.3	0.0	1.3	5.9
0.9	0.7	0.8	0.5	0.2	0.1	1.7	1.4	0.0	0.0	1.2	0.0	4.3

TP	NP
0.3	2.9
0.1	1.8
0.8	1.5
0.8	1.1
0.9	1.5
0.0	2.0
1.0	1.6
0.7	1.1
0.4	1.4
0.5	1.8
0.7	2.8
1.0	2.5
0.1	1.2
0.9	1.3
0.3	2.2
0.9	1.1

Fig. 2. Possible data used for null model randomisation approaches to Price partitions. Matrices: ***T*** and ***N***: trait expressions T_A and T_B and abundances N_A and N_B in communities *A* and *B* used in the Price partitioning. Matrices **TC** and **NC**: additional observed trait expression (T_C) and abundance (N_C) matrices from comparable communities. **NT**: vector of row totals of **NC. TP** and **NP**: Average trait expressions T_P and abundances N_P in the species pool. Possible randomisation methods are given below the matrices for which they are suited.

Table 1

Possible approaches to obtain null distributions for Price partitions. Abbreviations: as in Fig. 2. *S* refers to the observed richness in the null communities, *T* and *N* to the respective species trait expressions and abundances. ***Q*** denotes the transition matrix of *mcmc*. Detailed discussion of each model in Appendix A.

Approach	Randomisation model	Randomisation of		Assumptions	Constraints	Behaviour	Bias towards
		Abundance	Trait				
Parametric	Broken stick distribution	–	–	Equal probability for partition values	No constraints on *T, S* and *N*	Large standard error of the null distribution. Low discriminant power	Type II errors
	Resampling from a parametric trait distribution	–	***T***	Trait variability follows a predefined probability distribution	*S* and *N* fixed	Lack of discriminant power for richness variation	Type II errors
	Markov chain Monte Carlo randomisation (*mcmc*)	Transition matrix ***Q***		Fixed probability distribution for ***Q***	No constraints on *T, S* and *N* within observed values	Variability of partitions dependent on the choice of the distribution of *Q* values	Not obvious
Reshuffling	Equiprobable reshuffling species identity	***N***	–	Equal probability of trait expression across species, no functional or phylogenetic covariance	*S, T, N* fixed	Lack of discriminant power for richness variation	Type II errors
	Equiprobable reshuffling species trait and abundance values (*rshuff*)	**NC**	**TC**	**TC** and **NC** cover possible species trait and abundance space	No constraints on *T, S* and *N* within observed values	Site specific trait expression often not available	Not obvious
Resampling	Proportional resampling from the species pool	**NP**	**TP**	No variability in SAD	N_A and N_B fixed	Pool composition often not available. Filter effects excluded	Type I errors
	Proportional resampling (*rsamp*)	**NT**	**TC**	No variability in SAD	No constraints on *T, S* and *N* within observed values	Site specific trait expression often not available Reduced variability in N_A and N_B	Not obvious
	Bootstrapping	*N*, NT, or NP	–	No variability in species trait expression and abundances	Dominance order fixed	Dominant species often removed Collinearity among partitions not removed	Type II errors
Bayesian estimation	Bayesian parameter estimation	**NP**	**TP**	log-series SAD in **NP**	*T* and *S* linearly dependent on N. Biased null distributions	Pool composition often unknown	Type I errors
Assembly models	Neutral modelling	**NP**	–	log-series SAD in **NP**	No constraints on *T, S* and *N*	Low abundance variability in A and B at equilibrium	Type I errors

For each approach we briefly discuss the underlying assumptions, the resulting constraints on the Price parameters, and the potential effects on the frequency of Type I (false positive) and Type II (false negative) statistical errors. We then use simulations to compare the behaviour of the three most promising approaches (*mcmc, rsamp*, and *rshuff*).

2.1. Simulation of artificial matrices

In order to assess the behaviour of Price partitions for changes in traits between two communities we first generated 80 species × sites matrices ***N***, each having between 5 and 50 species (integers drawn from an equiprobable distribution) and 20 sites. In 40 of these matrices species abundances per site were sampled from a lognormal distribution with equiprobably-assigned shape parameters in the range of $1.0 < \alpha < 2.0$. Matrix fill (number of occupied cells) ranged between 20 % and 80 %. Occurrences of half of these matrices were re-arranged to yield a pattern of species nestedness (reflecting a gradient in species richness); the other half were re-arranged to yield a pattern species segregation (reflecting a high species turnover across sites). These arrangements generated considerable variation of species richness and total abundances across the sites, whereas both matrix types differed in the pattern of species co-occurrence. In the remaining 40 $\boldsymbol{N}$ matrices, species abundances were assigned by linear random numbers in the range [1,10]. To allow for a variation in richness across sites, abundances less than 0.01 were set to zero.

To model species' traits in each community we generated an additional matrix of trait values $\boldsymbol{T}$ associated to each species × site matrix. With respect to the 40 nested and segregated matrices, and to 20 of the random $\boldsymbol{N}$ matrices each column of the $\boldsymbol{T}$ matrix contained a continuous trait value drawn from an equiprobable random distribution within the arbitrary range [1,10]. This range was chosen to obtain realistic variation in trait values. For the 20 remaining $\boldsymbol{T}$ matrices trait values in the first site were again taken from a linear random number [1,10], while the trait expressions t_i of consecutive sites i came from $t_i = t_1 i^{1.5}$. Therefore, average trait expression in the 20th site was on average 90 times larger than in the first site. Since the trait values of each species are selected independently, there is no need to evoke complex mechanisms such as species interactions, niche complementarity, or density dependence.

The simulated matrices covered four type of trait species occurrence combinations: random trait × nested species occurrence, random trait × segregated species occurrence, random trait × random species occurrence, and trait increase × random species occurrence. These patterns correspond to wide range of observed community structures and trait variability that should have influenced the associated Price partitions in specific ways.

The null models should identify the Δ_{Comp} and Δ_{Cov} partitions (Eq. (1)), and the Δc and ΔN partition (Eq. (3)) of the segregated, nested and trait gradient $\boldsymbol{N}$–$\boldsymbol{T}$ matrix combinations as being non-random. In the 5-partition framework the Δc and $\Delta c \Delta p$, partitions of the nested and segregated matrices should have been within the random expectation, while the significances for the Δp partition should have depended on the pattern of species co-occurrence and dominance.

The *rshuff* null and *rsamp* null models require additional data about trait and abundance variability from which random expectations are derived. Randomisation of the *rshuff* null model was based on equiprobably reshuffled species abundances across the rows of $\boldsymbol{N}$. For the *rsamp* null model procedure, we resampled communities A and B by assigning species with probabilities proportional to the species' total prevalence across communities (i.e. based on the vector **NT** of Fig. 1, corresponding to the marginal row sums of the $\boldsymbol{N}$ matrix). Total abundances in A and B were assigned equiprobably among the simulated abundances in matrix $\boldsymbol{N}$ (the column totals). For *rsamp* and *rshuff* we randomly assigned species trait values in A and B from a truncated ($-2\sigma \leq x \leq 2\sigma$) Poisson distribution with $\sigma^2 = \mu$ centred around the mean simulated trait value of each species.

The present *mcmc* randomisation approach uses the fact that the vectors $\boldsymbol{T}_{\mathrm{B}}$ and $\boldsymbol{N}_{\mathrm{B}}$ of communities A and B are generated from $\boldsymbol{T}_{\mathrm{A}}$ and $\boldsymbol{N}_{\mathrm{A}}$ by

$$T_B^T N_B = P T_A R N_A = T_A^T P R N_A = T_A^T Q N_A \tag{5}$$

$\boldsymbol{P}$ and $\boldsymbol{R}$ the associated transition matrices, in the simplest case diagonal matrices defining the magnitude of change in $\boldsymbol{T}$ and $\boldsymbol{N}$. They collapse into a transition matrix $\mathbf{Q}$ (Appendix A). The elements x of the $\boldsymbol{Q}$ matrix were again sampled from a truncated ($-2\sigma \leq x \leq 2\sigma$) Poisson distribution with $\sigma^2 = \mu$.

First, we assessed the validity of the Price partitions and the degree of collinearity among partitions. For this task, we generated for each matrix Prices partitions for each unique pair of communities A and B, leading to a total of 11,400 pairwise matrix comparisons. For each comparison, we calculated the numbers of species, total abundances, and total trait expression, as well as the Bray–Curtis index of community similarity. We used Spearman's rank order correlations to infer the degree of collinearity among partitions. Structural equation modelling with maximum likelihood parameter estimation served to reveal the mutual dependencies of ΔT and its partitions on important constraining variables: absolute trait value T, species richness S, total abundances N, and the pattern of species co-occurrence quantified by the Bray–Curtis index. We expected the null models to detect correlations between the change in total trait expression ΔT, the differences in trait expression, richness, and total abundance of communities A and B.

In a next step we assessed the performance of the three null models (*rshuff, rsamp, mcmc*). To be additive the partitions of Eqs. (2) and (3) have constant multipliers that hinder direct comparisons of absolute values between partitions. In order to calculate effect sizes the Price partitions need to be rescaled. The mentioned null model algorithms randomise not only the parameter changes but also these multipliers, which generates increased co-variance among partitions making unequivocal interpretation of unscaled effect sizes challenging. Further, any bias in the randomised abundance and trait values would also bias the resulting significance levels. Therefore, to calculate standardised effect sizes (SES) and confidence limits we normalised the partitions dividing the Δ_{Comp} and ΔN partitions of Eqs. (2) and (3) by total trait value T, the Δ_{Cov}, $\Delta p \Delta c$, Δc, and Δp partitions by total abundance (N_{B}), and the total trait changes ΔT by $T \times N_{\mathrm{B}}$. For all three null models, we used for each pair of communities A and B, 1000 randomisations to obtain respective null model distributions, 99 % confidence limits, and standardised effect sizes (SES). Null model distributions ideally should be unbiased with respect to observed ranges of species richness and abundances. To test this, we calculated for each null community Shannon diversity and evenness and compared the values for $\boldsymbol{N}_{\mathrm{B}}$ with the respective randomised $\boldsymbol{N}_{\mathrm{B}}$ communities.

3. Results

3.1. Collinearity between partition values

With respect to the 2-partition Price equation, the present simulations indicated that both partitions were negatively correlated, while the strength depended on the pattern of species co-occurrences (Figs. 2a and 3). In segregated communities both partitions were strongly negatively and in nested communities moderately negatively correlated. The Δ_{Comp} partition of both frameworks and Δ_{Cov} contain mean trait expression (z_{A}) as a factor. Consequently, we observed a negative effect of initial trait expression on both richness partitions (Fig. 4). Within the 5-partition framework, Δ_{Comp} and ΔN were negatively correlated, strongly so in the case of nested communities (Figs. 3a and 4e). There were close correlative relationships between $\Delta p \Delta c$, Δc, and Δp and between ΔS and ΔN (Figs. 3 and 4g).

The use of standardised effect sizes (SES) reduced, on average, the collinearity between the partitions (Fig. 3, Fig. 4g–i) and the dependencies on constraining factors (Fig. 4d–f). Still visible was the influence of absolute trait value (T_{A}) on the Δ_{Cov} partition (Fig. 4b, c).

3.2. Comparison of null model behaviour

Null models based on the information contained only in communities A and B tended to be underpowered (Table 1). The parametric Broken stick model would return large standard errors for each partition leading to high type II errors (Table 1). The reshuffling of species identities randomises the trait - abundance association but retains *S, T*, and *N*, as well as the relative abundances. This model has low discrimination

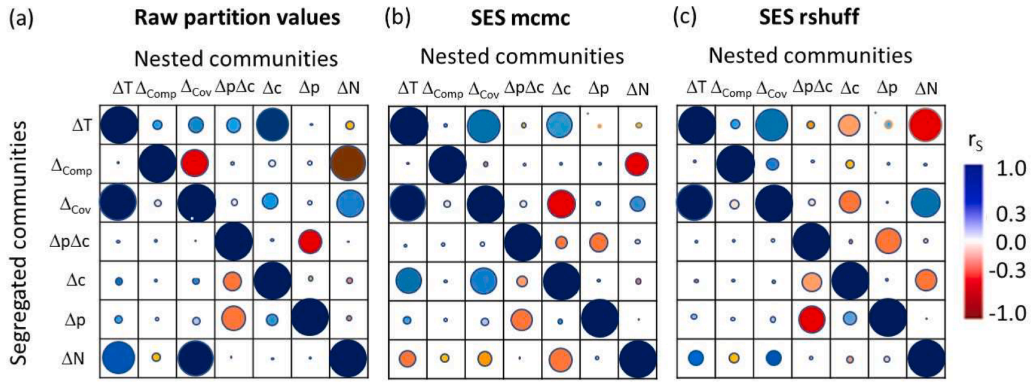


Fig. 3. Dot plots of mean Spearman's rank order correlations (r_S) of raw values (a) and respective standardised effect sizes of the *mcmc* (b) an the *rshuff* (c) null models of ΔT and six partitions (Δ_{Comp} and Δ_{Cov} cover to the 2-partition solution, Δ_{Comp}, ΔpDc, Δc, Δp, and ΔN cover the 5-partition solution, Box 1) for 3800 matrices each of different degrees of nestedness and species segregation. Because *rshuff* and *rsamp* performed similarly (Fig. 5), the results of *rshuff* are presented, only.

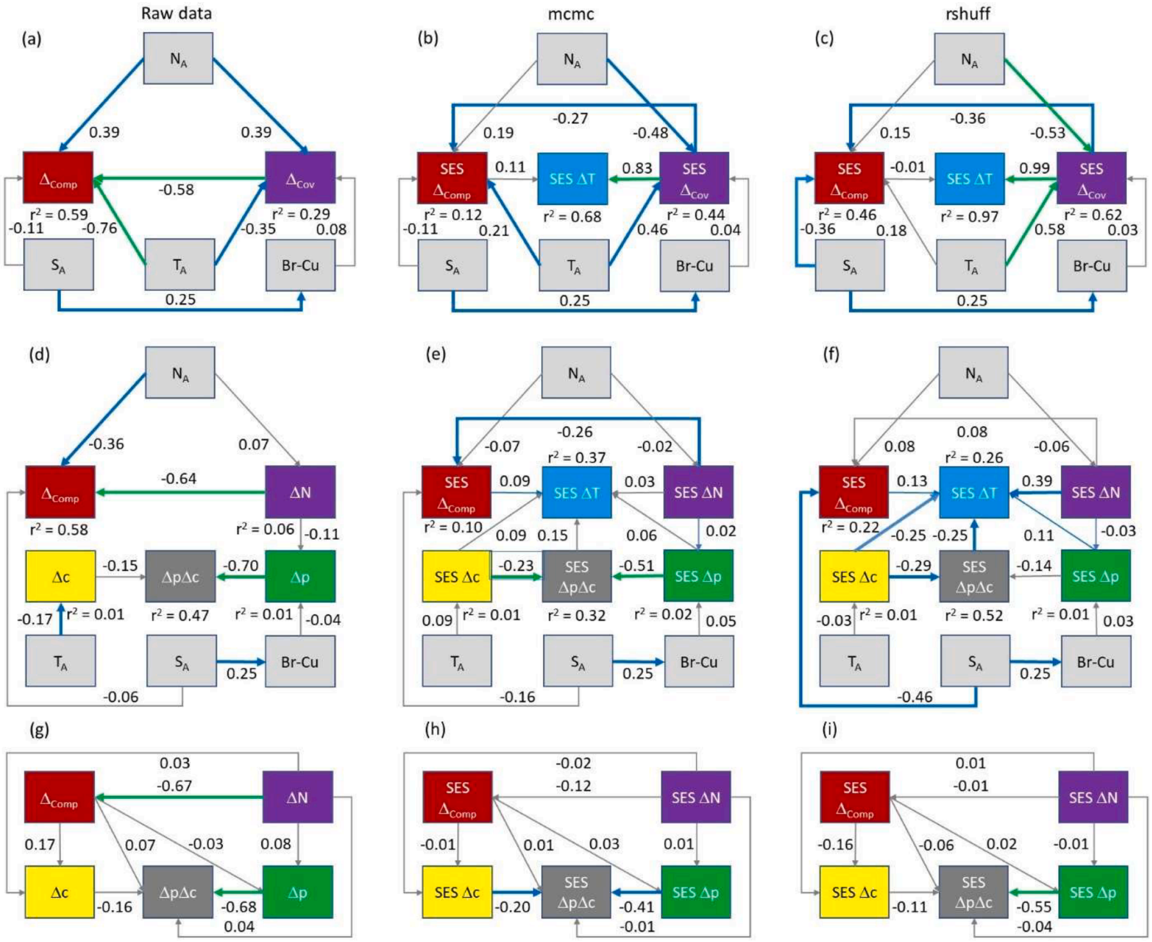


Fig. 4. path coefficients (arrows) and explained variances (numbers) for the relationships between raw Price partitions (Box 1) and the respective SES values of the *mcmc* and *rshuff* null models ($N = 7600$ each using results for segregated and nested matrices as input) in dependence on community constraints: trait value in site A (T_A), abundance in A (N_A), richness in A (S_A), and Bray–Curtis similarity between A and B (Br–Cu). Strong paths (coefficients > 0.5) in bold green, intermediate coefficients (0.2–0.5) in bold blue, weak coefficients (< 0.2) in thin grey. Because *rshuff* and *rsamp* performed similarly (Fig. 5), the results of *rshuff* are presented, only.

power for these parameters and therefore high type II error rates. Similarly, bootstrapping does not randomise the trait - abundance association and retains relative abundances (Table 1). Bootstrapping does not account for variability in richness between A and B.

Resampling, bootstrapping, and neutral modelling approaches based on species pools need additional information about pool sizes, relative abundances, extinction, colonisation and dispersal probabilities in A and B (Table 1). This information would need to be estimated from independent sources of data. Because relative abundances in the source pool will often differ from the observed ones in A and B, the models are inherently prone to type I errors (Table 1). Bayesian parameter estimation based on priors taken from the species pool suffers from the same problem of high false positives rates. Consequently, below we restrict our comparisons to the performance of three remaining null models (*mcmc, rshuff*, and *rsamp*) that represent a realistic compromise between realistic parameter ranges and additional empirical information. Two of these models (*rshuff*, and *rsamp*) require empirical data from more than two communities to obtain realistic ranges within which the Price parameters might vary.

3.3. Statistical performance of Markov, reshuffling, and resampling null models

The *mcmc* approach retains observed species relative abundances in the randomised B communities (Table B1). Reshuffling and resampling generated randomised communities with more even abundance distributions and higher mean diversity (Table B1).

The *mcmc* approach identified less than 50 % of the ΔT values as being non-random (Fig. 5). These low values resulted from compensatory effects of the Δ_{Comp}, Δ_{Cov}, and ΔN partitions (Fig. 4e). With respect to the 5-partition solution less than 10 % of the $\Delta p\Delta c$, Δc, and Δp partitions each of the nested (Fig. 5a, b), segregated (Fig. 5c, d), and random (Fig. 5e, f) matrices were detected as having non-random partitions (Fig. 5). In turn, between 23.3 % (random) and 69.2 % (nested) of the respective ΔN partitions appeared to be non-random. The *mcmc* model correctly identified the decrease in richness across sites in the nested matrices (Fig. 5a, b), while it was unable to detect the gradient in trait values expressed in the Δc and $\Delta p\Delta c$ partitions (Fig. 5g, h).

Reshuffling and resampling had similar performance (Fig. 5). Irrespective of matrix type, both approaches detected more than 80 % of ΔT partitions as being non-random and correctly identified the decrease in richness in the nested communities (Fig. 5). Contrary to *mcmc* and *rshuff*, the *rsamp* model correctly did not point to non-random changes in richness in the segregated communities. In turn, *rshuff* and *rsamp* indicated strong changes in the communities with randomly assigned abundances (Fig. 4c, d). *rsamp* correctly indicated the higher level of changes in the relative species abundances from community A to B ($>$ 20 % of comparisons) in the segregated communities (Fig. 5). *mcmc* and *rshuff* did not detect this difference (Fig. 5).

Structural equation modelling showed that a null model approach using SES values reduced the dependencies of Price partitions on community constraints, particularly the impact of total abundances (Fig. 3). Null models did not consistently reduce the collinearity between partitions (Fig. 4). The specific pattern of collinearity was dependent on the structure of species co-occurrences (Fig. 4).

4. Discussion

Using a null modelling approach we show that the Price equation is susceptible to collinearity among partitions. This is important because collinearity influence the absolute and relative values of partitions. Similar to non-orthogonal factor analyses, collinearity complicates interpretation. We show that the resulting bias can be mitigated by the incorporation of additional information about the possible variability of the variables, boundary conditions, and associated null expectations. Importantly, our results have general implications that go beyond the Price example studied here. Null models are a now well-established tool in the analysis of ecological patterns (Ulrich and Gotelli, 2013; Molina and Stone, 2019; Neal et al., 2023). So far, these model have been used to set random expectations for simple univariate metrics mainly of community composition and patterns of spatial species distributions (Gotelli and Ulrich, 2012). Importantly, our results have general implications for null model development and interpretation that go beyond the Price example studied here.

Classical null models for pattern detection in community assembly focus on a single metric and randomise the data without the need for additional information on, for example, community composition and colonisation dynamics (Gotelli and Ulrich, 2012; Neal et al., 2023). However, the recent finding that such randomisation might not fully eliminate biases due to the inherent non-independence of observed and randomised data (the Narcissus effect) indicated that in more complex situations data randomisation alone might not suffice for unequivocal

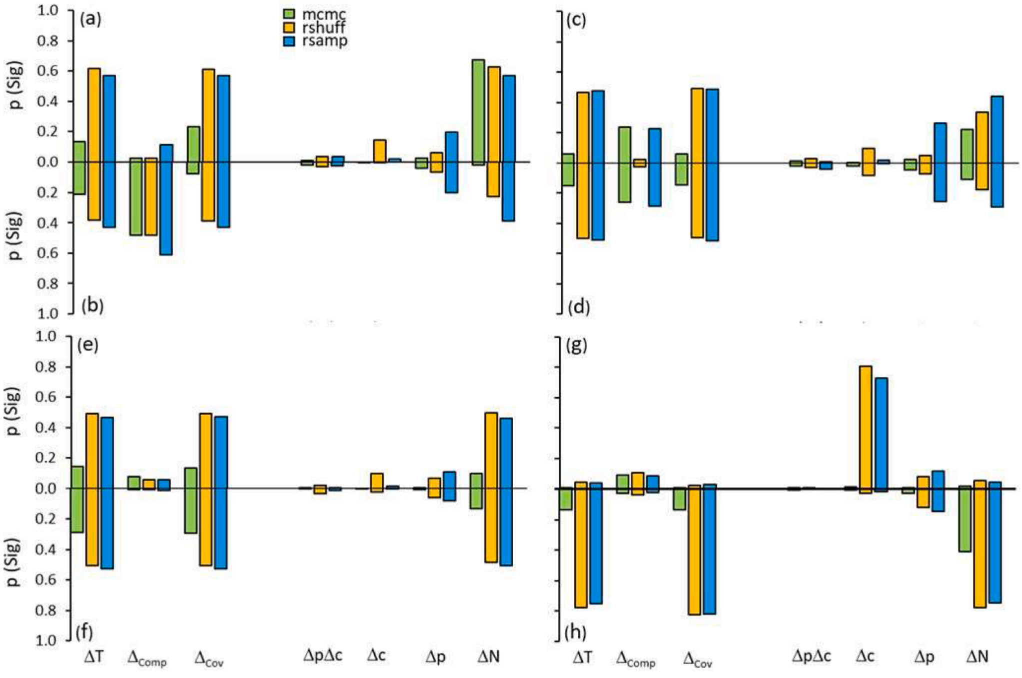


Fig. 5. Proportions of significantly positive (a, c) or negative (b, d) partitions (two-sided 5 % error level) of nested (a, b) and segregated (c, d), equiprobably random (e, f), and trait change (g, h) artificial communities (total of 3800 single pairs of sites each). Green: Monte Carlo Markov Chains (*mcmc*), Orange: reshuffling (*rshuff*), blue: resampling (*rsamp*). Nomenclature as in Box 1.

pattern detection (Ulrich et al., 2017, 2018). Indeed, the randomisations of our simulated data based on the reshuffling of species (trait) identity and on the randomisation of observed dominance orders appeared to be unsuited to serve as standards for Price partitions (Table 1). Only the Monte Carlo Markov chain approach appeared to be potentially suited (Fig. 4). This class of models uses observed data in combination with a predefined empirically guided transition rule. Here we assumed that abundances and trait values are a truncated Poisson distributed. Ideally, the transition rule might be based on observations about trait and abundance variability. We also assumed that species richness and abundances varied within observed boundaries. This need of additional information makes *mcmc* data driven similar to the present *rshuff* and *rsamp* null models. *mcmc* might only be an alternative if not additional empirical data is available.

The comparative analysis of null models demonstrated suitability of those models that compromise between information need (simplicity) and complexity of additional information. Null models that randomise observed data of communities A and B only are simple but face the Narcissus syndrome (Ulrich et al., 2017). Process based null models relying on ecological processes of community assembly (colonisation / extinction dynamics) are complex and need information of species pools and dispersal. Such information is often not available and has to be estimated. Therefore, our results strongly indicate that realistic and appropriate null distributions are best obtained using empirical data from additional sets of comparable communities. These are the input data for the *rshuff* and *rsamp* null models and also might serve to feed the transition matric of the *mcmc* null model.

Our work suggests that empirical analyses using the Price equation can be improved by including additional information sources. Classical parameter comparisons rely on statistical tests using estimates of standard errors. With respect to Price partitions it would be desirable to have an appropriate error propagation included in the partitions, for instance from simulated variation of ΔT. However, this would need the same information about the possible variability in ΔT (Eq. (1), trait expression, richness, and abundances) as required for the discussed null models. Additionally, the use of standard errors of partitions does not solve the inherent questions about collinearity and scale dependence as such standard errors would also covary with spatial and temporal extent.

Fox & Kerr (2012) used a different approach and created Price partitions for pairs of control and N-enriched plots in a grassland nitrogen enrichment experiment to quantify the effects of species additions and losses. The challenge is that not all plots differ in traits, species, or abundances, so it may be hard to tease apart the direct and indirect effects of these factors on the resulting Price partitions. Additionally, community parameters from controlled experiments such as total richness and relative abundances are often constrained and collinearity among the replicated plots is frequently high. This is an issue which is common in most biodiversity – ecosystem functioning studies; artificially reduced variability in the system might increase type II error rates. Finally, in many biogeographic cases trait and abundance data will not be fully available. In these cases additional data mainly serve to estimate the variability in richness, trait space, and abundances as an input to generate randomised communities. Unfortunately, only few studies provided respective data on intraspecific abundance and trait variability at the community level (e.g. Lamb et al., 2009; DeCock et al., 2021). In this respect our work should be read as a call for community analyses based on the trait variability of individual species.

Previous comparative work on null models tried to assign type I and II error levels for a single estimate of interest (Ulrich and Gotelli, 2007, 2013). More nuance is needed for methods that estimate several processes such as partitions. In the present case, we found the *rshuff* and *rsamp* models to properly detect differences in abundances and trait values while performing worse in detecting differences in richness (Fig. 5a, b, d). The lack of difference in trait values was correctly detected by all three null models (Fig. 5) while difference in trait values was only detected by *rshuff* and *rsamp*. An explanation demands the behaviour of all the model with respect to the communities, for which trait and abundance values were simple linearly distributed random numbers (Fig. 5c). Such an assignment introduces some degree of variability in total abundances across communities while species total abundances across sites asymptotically equalise with increasing number of sites. Consequently, random samples from the respective marginal totals (and also reshuffling) generate random communities with a comparatively lower variability in abundance than observed in comparisons of two communities A and B. This stochastic effect might make *rshuff* and *rsamp* less suited to detect non-randomness in the ΔN and also in the Δ_{Cov} partitions (Fig. 5). In this respect *mcmc* performed better although this model too had increased type II error rates (Fig. 5c, d).

An important task of null models is to reduce covariation of focal variables with constraining factors. The three null models studied here performed well in this respect when using standardised effect sizes (Fig. 4). In the 2-partition version Δ_{Cov} still was highly positively correlated with total abundances (Fig. 4b, c). Fortunately, this covariance would not change interpretation of the Δ_{Comp} partition and therefore the positive correlation of ecosystem performance and diversity within the BEF framework. Collinearity between the SES values of partitions was also consistently reduced in comparison to the raw partition values (Fig. 4g–i). Collinearity was one point of criticism against the use of Price partitioning in ecology (Pillai and Gouhier, 2019; van Veelen, 2020; Bourat et al., 2023). Indeed, in our simulated nested data D_{Comp} and D_{Cov} were strongly correlated ($r_S = 0.70$, Fig. 3) while the respective SES values were much weaker correlated, particularly for the *mcmc* model ($r_S = 0.17$). Importantly, the high collinearity of the Δ_{Comp} and ΔN partitions under certain data structures (here, segregated species occurrences) demonstrates that it might be difficult to disentangle the joint effects of total abundance and richness on the change of community properties, particularly functioning. Further, absolute trait values (yield in the case of BEF) had a high impact on the Δ_{Comp} partition in our simulations in comparison to the Δ_{Cov} partition. Any interpretation of the relative strength of both partitions needs to account for these collinearities. The alternative partition as derived in Eq. (4) might perform better in this respect.

CRediT authorship contribution statement

Werner Ulrich: Conceptualization, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. **Nicholas J. Gotelli:** Methodology, Validation, Writing – review & editing. **Giovanni Strona:** Methodology, Validation, Writing – review & editing. **William Godsoe:** Methodology, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

Authors declare no conflict of interest.

Data availability

No data was used for the research described in the article.

Acknowledgements

W.U. acknowledges funding by an institutional NCU grant within the Polish Excellence initiative.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2024.110695.

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