LETTER

A game-theory–inspired decomposition of interspecific interaction matrices

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A game-theory–inspired decomposition of interspecific interaction matrices

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Abstract – In evolutionary game theory, pair interactions are usually defined through so-called payoff matrices, which can be decomposed as linear combinations of basis matrices that represent just four different orthogonal interaction types. In this paper, we take the first steps in exploring the utility of this decomposition in ecology. We introduce the componental cosines of the irrelevant, external, coordination, and conflict components of matrices to measure the relative weight of the different interaction types, and use them to analyse the composition of 33 experimentally obtained interspecific interaction matrices compiled from the literature, which reveals statistically significant correlations both between different components and some components and community productivity and biodiversity.

Understanding the relationships between species interactions, biodiversity, and how ecosystems function is one of the main problems of ecology [1,2]. What factors govern species relative abundances in a community [3] and what determines species diversity [4] are among the related long-standing open questions. Apart from their fundamental scientific interest, these questions are of vital importance in assessing how human activities threatening biodiversity, such as changes in land use, overexploitation of biological resources, pollution, and climate change [5], impact food and water security.

Organisms in ecological communities compete for resources, eat each other, and engage in mutually beneficial relationships. There has been recent progress in linking species abundances and species diversity with measurable parameters, such as pairwise interaction coefficients, in real communities where, for instance, interactions are dominantly competitive [6] or restricted to being either purely predator-prey [7] or purely mutualistic in character [8]. Establishing such a connection, however, remains a pending issue in the general case of many species interacting simultaneously through more than one of the above-mentioned interaction types. Filling this gap will require a major interdisciplinary effort combining the development of new theories with experimental work and comparative analyses [7].

It was recently shown in the realm of evolutionary games that square payoff matrices can be decomposed as linear combinations of elementary matrices of just four orthogonal classes, each representing fundamental interaction types [9,10]. This approach provides a framework for a systematic investigation of any system involving interaction matrices, such as Lotka-Volterra models and random matrix models. By the same token, any $S \times S$ interaction matrix tabulating the interaction coefficients of a community of S coexisting species can also be submitted to this decomposition analysis and subsequently characterised based on its composition.

In the research reported in this paper, we employed the decomposition method to analyse the structure of the interaction matrices of real ecological communities. We identified characteristic statistical patterns in the relative weights of the four elementary interaction types as measured by the componental cosines of the interaction matrices onto the subspaces of the elementary interaction types. We also found apparent correlations between some of the componental cosines and a pair of community observables commonly used in ecology to characterise the relative species abundances and species diversities.

The decomposition method. – In game theory, pair interactions are usually defined through so-called payoff matrices, which tabulate the possible winnings or losses of a player by arranging them into rows and columns

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according to the player's and her opponent's choice of strategy [11,12]. Players are often assumed to be identical to each other in the sense that they choose from the same set of strategies and derive the same payoff from the same outcome, which allows establishing the rules of the game using a single square payoff matrix. A recently introduced technique [9,10] decomposes such payoff matrices into linear combinations of elementary matrices that describe just a few fundamental interaction situations.

One of the possible decomposition schemes identifies the following four elementary interaction types: *irrelevant games*, *external benefit games*, *coordination-type games*, and *zero-sum conflict games*. In an irrelevant game, each player always receives the same payoff regardless of her or her opponent's choice of strategy. In an elementary external benefit game, a player's payoff is proportional to the number of players choosing a specific available strategy, as if the players were rewarded as a group by an outside actor for choosing that startegy. In an elementary coordination game, the players both receive zero payoff unless they both choose either one of two coordinated strategies: if they pick matching coordinated strategies, they both gain a unit of payoff, whereas if they choose opposing coordinated strategies, they both lose the same amount. Finally, in an elementary conflict game, there is a winning and a losing strategy: the winner gets to take a unit of payoff away from the loser, while all other strategy pairings yield zero payoff to both players.

In linear algebraic terms, the above-described decomposition scheme exploits the fact that any $S \times S$ square matrix $\mathbf{A}$ —whose i-th row, j-th column element is denoted by A_{ij}— can be expressed as a linear combination of the following set of $S \times S$ matrices:

– the all-ones matrix $\mathbf{m}(S)$ with entries

$$m_{ij}(S) = 1, \tag{1}$$

which represents the elemenetary irrelevant game;

– S matrices $\mathbf{f}(k; S)$ $(k = 1, 2, \ldots, S)$ with

$$f_{ij}(k; S) = \begin{cases} 1, & \text{for } i = k \text{ and } j \neq k, \\ 1, & \text{for } i \neq k \text{ and } j = k, \\ 2, & \text{for } i = k \text{ and } j = k, \\ 0, & \text{otherwise,} \end{cases} \tag{2}$$

which correspond to elementary external benefit games;

– $\binom{S}{2}$ matrices $\mathbf{d}(k, l; S)$ $(k, l = 1, 2, \ldots, S; k < l)$ with

$$d_{ij}(k, l; S) = \begin{cases} 1, & \text{for } i = j = k, \\ 1, & \text{for } i = j = l, \\ -1, & \text{for } i = k \text{ and } j = l, \\ -1, & \text{for } i = l \text{ and } j = k, \\ 0, & \text{otherwise,} \end{cases} \tag{3}$$

which define elementary coordination games;

– $\binom{S}{2}$ matrices $\mathbf{c}(k, l; S)$ $(k, l = 1, 2, \ldots, S; k < l)$ with

$$c_{ij}(k, l; S) = \begin{cases} 1, & \text{for } i = k \text{ and } j = l. \\ -1, & \text{for } i = l \text{ and } j = k, \\ 0, & \text{otherwise,} \end{cases} \tag{4}$$

which describe elementary conflict games.

Formally, the decomposition reads

$$\begin{aligned} \mathbf{A} &= \mu \mathbf{m}(S) + \sum_{1 \leq k < l \leq S} \nu_{kl} \mathbf{d}(k, l; S) \\ &+ \sum_{k=1}^{S} \varphi_k \mathbf{f}(k; S) + \sum_{1 \leq k < l \leq S} \psi_{kl} \mathbf{c}(k, l; S), \end{aligned} \tag{5}$$

where the greek letters denote the expansion coefficients of the elementary games.

The matrix $\mathbf{m}(S)$ and the set of all $\mathbf{f}(k; S)$ are not linearly independent because

$$2\mathbf{m}(S) = \sum_{k=1}^{S} \mathbf{f}(k; S). \tag{6}$$

As a result, the decomposition is not unique, but it can be made so by fixing one of the expansion coefficients. An appealing way to do this is to set the expansion coefficient of $\mathbf{m}(S)$ as

$$\mu = \frac{1}{S^2} \sum_{i,j=1}^{S} A_{ij}, \tag{7}$$

because $\mu \mathbf{m}(S)$ then becomes the average component $\mathbf{A}^{(\text{av})}$ of the game, which invariably yields the payoff both players should expect to win when they both choose their strategy completely randomly, while

$$\varphi_k = \frac{1}{2S} \sum_{j=1}^{S} (A_{kj} + A_{jk}) - \mu \tag{8}$$

turns out to be the average payoff they can expect to gain on top of μ when at least one of them chooses strategy k. Notice that, in line with this interpretation, the φ_k coefficients add up to 0. In the following, we will refer to $\mathbf{A}^{(\text{ex})} = \sum \varphi_k \mathbf{f}(k; S)$ as the external benefit component of the game $\mathbf{A}$. In the remaining components, neither player can unilaterally set the expectation value of the sum of the players' payoffs. The coordination component $\mathbf{A}^{(\text{co})} = \sum \nu_{kl} \mathbf{d}(k, l; S)$ provides the same payoff to both players, so individual and community interests coincide in it, just as they do in the average and external benefit components. The conflict component $\mathbf{A}^{(\text{as})} = \sum \psi_{kl} \mathbf{c}(k, l; S)$, on the other hand, does the opposite: it is a zero-sum game, so it does not contribute to the total payoff of the community, it only affects how the total payoff is distributed among players following different strategies. The expansion coefficients of elementary coordination and

conflict games in a general matrix game can be derived from the off-diagonal elements of the symmetric and anti-symmetric parts of its payoff matrix as

$$\nu_{kl} = \mu + \varphi_k + \varphi_l - \frac{A_{kl} + A_{lk}}{2}, \qquad (9)$$

$$\psi_{kl} = \frac{A_{kl} - A_{lk}}{2}. \qquad (10)$$

To characterise the composition of payoff matrices, we introduce the componental cosines of matrix components modeled on the directional cosines of vectors as

$$P^{(i)} = \frac{\mathbf{A}^{(i)} \cdot \mathbf{A}}{||\mathbf{A}^{(i)}|| \, ||\mathbf{A}||}, \qquad (11)$$

where (i) stands for the label (av), (ex), (co), or (as) to indicate the average, external benefit, coordination, or conflict components, respectively;

$$\mathbf{A} \cdot \mathbf{B} = \sum_{i,j=1}^{S} A_{ij} B_{ij} \qquad (12)$$

is the Hilbert-Schmidt inner product of the two matrices, and $||\mathbf{A}|| = \sqrt{\mathbf{A} \cdot \mathbf{A}}$ is the norm of $\mathbf{A}$. Since the four components are orthogonal to each other ($\mathbf{A}^{(i)} \cdot \mathbf{A}^{(j)} = 0$ if (i) and (j) are different labels) and the Hilbert-Schmidt inner product is distributive over the addition of matrices, the expressions for the scalar products can be simplified to read

$$P^{(i)} = \frac{||\mathbf{A}^{(i)}||}{||\mathbf{A}||}. \qquad (13)$$

The norms satisfy a Pythagorean theorem, namely

$$||\mathbf{A}^{(av)}||^2 + ||\mathbf{A}^{(ex)}||^2 + ||\mathbf{A}^{(co)}||^2 + ||\mathbf{A}^{(as)}||^2 = ||\mathbf{A}||^2, \quad (14)$$

which, after division by $||\mathbf{A}||^2$, can be rewritten in terms of the componental cosines as

$$[P^{(av)}]^2 + [P^{(ex)}]^2 + [P^{(co)}]^2 + [P^{(as)}]^2 = 1. \qquad (15)$$

Unlike the usual directional cosines, these componental cosines do not measure the structure of a matrix with respect to fixed single-dimensional directions in the parameter space, but they compare its multidimensional projections to the matrix instead. As a result, the geometric meaning of directional cosines and componental cosines are somewhat different.

Results and discussion. – We analyse here a dataset of 33 multispecies experiments, which was recently compiled in ref. [13] from the literature [14–24]. Although this dataset covers several taxonomic groups, none of the experiments involved species from multiple trophic levels. For each experiment, both the yields Y_i of all S species forming the community in question and all their pairwise interaction coefficients α_{ij} $(i, j = 1 \dots S)$ were reported. In general, the $\boldsymbol{\alpha}$ interaction matrices included both negative and positive entries, the former indicating pairwise

competition, the latter indicating pairwise facilitation between the corresponding species. For more details about the dataset, see ref. [13] and the Supplementary Material (`empirical.txt`, `empirical_cosines_mry_h_data.txt`, `empirical_cosines_mry_h_corrs.txt`, `rawinteraction data.txt`, `rnd_-100_100.txt`, `rnd_-200_200.txt`, `rnd_-1000_1000.txt`, `uniform4dsphere.txt`, `corrref.cpp`, `interaction_matrix.cpp`, `randgen.cpp`, `utils.cpp`, `interaction_matrix.hpp`, `randgen.hpp`, `utils.h`, `fig1.gp`). Figure 1 shows the four componental cosines defined in eq. (11), $P^{(av)}$, $P^{(ex)}$, $P^{(co)}$, and $P^{(as)}$, for each empirical interaction matrix of the dataset. We also calculated the Spearman correlation coefficients between the componental cosines. The results are shown in table 1. We found the following patterns:

1) $P^{(ex)}$ is always smaller than $P^{(co)}$.

2) The smallest projection is either $P^{(ex)}$ or $P^{(av)}$.

3) The largest projection for the majority of these empirical matrices is $P^{(as)}$ (20 times out of 33) followed by $P^{(av)}$ (8) and $P^{(co)}$ (5). This is consistent with $P^{(as)}$ having the largest mean value.

4) $P^{(av)}$ is strongly anticorrelated with all of the other projections.

5) $P^{(ex)}$ is positively correlated with $P^{(as)}$.

In order to get an idea about which of these patterns are specifically characteristic of empirical interaction matrices, we compared our empirically obtained dataset to two randomly generated reference datasets. The first dataset consisted of the Cartesian coordinates of points selected with a uniform distribution from the positive orthant of a 4-dimensional unit sphere [25], while the other dataset was made up of the componental cosines of four-species interaction matrices with off-diagonal elements independently and uniformly drawn from the closed interval $[-1, 1]$. In both cases, we generated 33-data-point samples for direct comparability with the data in fig. 1 and table 1, calculated the same Spearman correlation coefficients and p-values, the number of apparently significant (with a significance level of 0.05) correlations, and how many times each component was the largest and the smallest, and then averaged them over 1000 iterations. The results are summarised in tables 2 and 3.

The coordinates of random points on the positive orthant of the 4-dimensional sphere model componental cosines that are as uncorrelated as possible, since these points are uniformly distributed on the surface defined by the two general properties of componental cosines, their non-negativity and the Pythagorean property equation (15). This claim is supported by the results reported in table 2. As expected, the four coordinates are statistically similar and they all turn out to be the largest or the smallest with equal probability. The pairwise correlation coefficients of the coordinates are also statistically similar
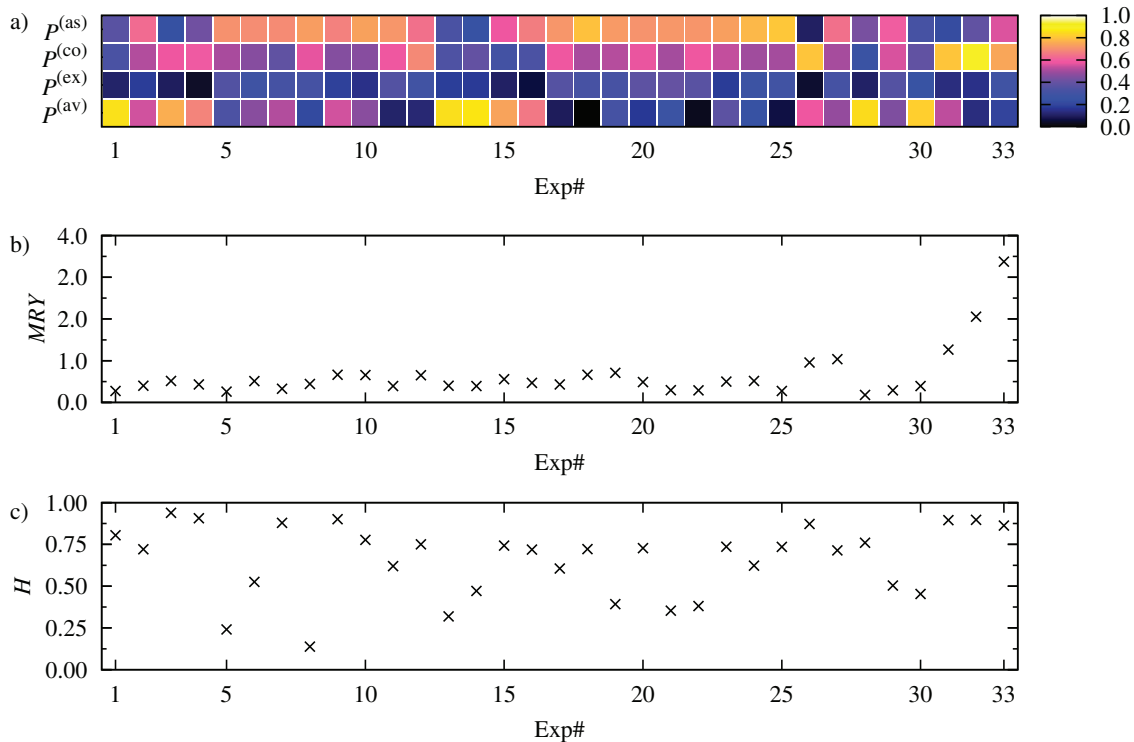
Fig. 1: (a) Componental cosines of the interaction matrices, (b) mean relative yields (MRY) and (c) Shannon equitabilities (H) in the 33 multispecies experiments compiled in ref. [13].

Table 1: Mean componental cosines and Spearman's rank correlation coefficients of empirical interaction matrices.

	Mean	Standard deviation	Times largest (out of 33 data points)	Times smallest (out of 33 data points)
$P^{(av)}$	0.436	0.269	8	14
$P^{(ex)}$	0.238	0.108	0	19
$P^{(co)}$	0.525	0.144	5	0
$P^{(as)}$	0.579	0.193	20	0

	Spearman's rank correlation	p-value	$p < 0.05$?
$P^{(av)}$–$P^{(ex)}$	-0.705	$5 \cdot 10^{-6}$	YES
$P^{(av)}$–$P^{(co)}$	-0.539	0.001	YES
$P^{(av)}$–$P^{(as)}$	-0.703	$5 \cdot 10^{-6}$	YES
$P^{(ex)}$–$P^{(co)}$	0.168	0.349	NO
$P^{(ex)}$–$P^{(as)}$	0.592	$3 \cdot 10^{-4}$	YES
$P^{(co)}$–$P^{(as)}$	-0.053	0.770	NO

Number of simultaneous $p < 0.05$ apparent correlations: 4

to each other. On average, they indicate weak anticorrelations between the componental cosines; each coordination seems significant about one out of three times, and the mean value of the ratio of apparently significantly correlated pairs is also about one-third. Taking larger samples provides further evidence of the presence of these weak correlations: the ratio of $p < 0.05$-significant correlations rises to about 80% when the size of individual samples is increased from 33 to 100, and it grows above 97% for a sample size of 200, without any noteworthy changes in the correlation coefficients but with a decrease in their standard deviations. The mean ratio of simultaneously detected significant correlations remains approximately equal to the overall ratio of significant-looking correlations in both cases, which suggests that the correlations are identified as significant by Spearman's method with the same (sample-size–dependent) probability and independently of each other.

Table 2: Mean componental cosines and Spearman's rank correlation coefficients when the componental cosines are randomly picked from the positive orthant of the 4-dimensional unit sphere.

	$\langle$Mean$\rangle$	$\langle$Standard deviation$\rangle$	$\left\langle\begin{array}{c}\text{Times largest}\\\text{(out of 33 data points)}\end{array}\right\rangle$	$\left\langle\begin{array}{c}\text{Times smallest}\\\text{(out of 33 data points)}\end{array}\right\rangle$
$P^{(av)}$	0.426 ± 0.046	0.259 ± 0.023	8.31 ± 2.42	8.11 ± 2.51
$P^{(ex)}$	0.425 ± 0.045	0.260 ± 0.023	8.29 ± 2.42	8.25 ± 2.51
$P^{(co)}$	0.425 ± 0.045	0.260 ± 0.023	8.32 ± 2.40	8.29 ± 2.64
$P^{(as)}$	0.422 ± 0.047	0.259 ± 0.024	8.08 ± 2.55	8.34 ± 2.49

	$\langle$Spearman's rank correlation$\rangle$	$\langle p\text{-value}\rangle$	Times $p < 0.05$ (out of 1000 samples)
$P^{(av)}$–$P^{(ex)}$	-0.263 ± 0.163	0.236 ± 0.261	320
$P^{(av)}$–$P^{(co)}$	-0.270 ± 0.166	0.232 ± 0.264	330
$P^{(av)}$–$P^{(as)}$	-0.269 ± 0.163	0.236 ± 0.266	333
$P^{(ex)}$–$P^{(co)}$	-0.269 ± 0.159	0.230 ± 0.261	339
$P^{(ex)}$–$P^{(as)}$	-0.264 ± 0.164	0.233 ± 0.260	327
$P^{(co)}$–$P^{(as)}$	-0.266 ± 0.166	0.232 ± 0.257	333
$\langle$Number of simultaneous $p < 0.05$ apparent correlations$\rangle$: 1.98 ± 0.80			

Table 3: Mean componental cosines and Spearman's rank correlation coefficients of four-species interaction matrices with random off-diagonal elements independently and uniformly drawn from $[-1, 1]$.

	$\langle$Mean$\rangle$	$\langle$Standard deviation$\rangle$	$\left\langle\begin{array}{c}\text{Times largest}\\\text{(out of 33 data points)}\end{array}\right\rangle$	$\left\langle\begin{array}{c}\text{Times smallest}\\\text{(out of 33 data points)}\end{array}\right\rangle$
$P^{(av)}$	0.359 ± 0.030	0.167 ± 0.018	2.63 ± 1.54	8.71 ± 2.55
$P^{(ex)}$	0.231 ± 0.015	0.087 ± 0.009	$0 \quad \pm 0$	22.72 ± 2.67
$P^{(co)}$	0.724 ± 0.019	0.101 ± 0.012	28.01 ± 2.14	$0 \quad \pm 0$
$P^{(as)}$	0.484 ± 0.021	0.107 ± 0.013	2.37 ± 1.54	1.57 ± 1.22

	$\langle$Spearman's rank correlation$\rangle$	$\langle p\text{-value}\rangle$	Times $p < 0.05$ (out of 1000 samples)
$P^{(av)}$–$P^{(ex)}$	-0.034 ± 0.175	0.496 ± 0.289	63
$P^{(av)}$–$P^{(co)}$	-0.785 ± 0.073	$4 \cdot 10^{-5} \pm 4 \cdot 10^{-4}$	1000
$P^{(av)}$–$P^{(as)}$	-0.040 ± 0.176	0.498 ± 0.293	54
$P^{(ex)}$–$P^{(co)}$	0.104 ± 0.177	0.445 ± 0.297	95
$P^{(ex)}$–$P^{(as)}$	-0.430 ± 0.152	0.067 ± 0.133	721
$P^{(co)}$–$P^{(as)}$	-0.447 ± 0.151	0.057 ± 0.125	745
$\langle$Number of simultaneous $p < 0.05$ apparent correlations$\rangle$: 2.68 ± 0.81			

By convention, the diagonal entries of interaction matrices are fixed at -1 [26]. This, of course, influences the elementary game composition of interaction matrices, namely it establishes a set of identities —one for each $k = 1, \ldots, S$— involving the expansion coefficients associated with elementary basis games, which can be written as

$$\sum_{\substack{l=1\\l\neq k}}^{S} \nu_{kl} + 2\varphi_k + \mu = -1, \tag{16}$$

where $\nu_{kl} = \nu_{lk}$ when $l < k$. These identities explicitly state that the external benefit, coordination, and average components of interaction matrices are not independent. At the same time, this expression says nothing about the expansion coefficients of the asymmetric conflict component of the matrix, so it does not introduce any further correlation between $P^{(as)}$ and the other componental cosines.

We tried to identify the impact of these relationships on the componental cosines by studying a simple four-species random interaction matrix model in which the off-diagonal entries are independently and uniformly drawn from the closed interval $[-1, 1]$. The results of our analysis are summarised by table 3. The smallest componental cosine turned out to be $P^{(ex)}$ most of the time, while $P^{(co)}$

Table 4: Spearman's rank correlation coefficients between the componental cosines of empirical interaction matrices and the global observables of the 33 multispecies experiments. Bold numbers highlight statistically significant ($p < 0.05$) correlations.

	$P^{(\mathrm{av})}$	$P^{(\mathrm{ex})}$	$P^{(\mathrm{co})}$	$P^{(\mathrm{as})}$
MRY	-0.1410 $p = 0.4337$	-0.2363 $p = 0.1855$	**0.4121** $p = \mathbf{0.0172}$	-0.0899 $p = 0.6188$
H	0.2072 $p = 0.2472$	$\mathbf{-0.5959}$ $p = \mathbf{0.0003}$	0.2009 $p = 0.2623$	$\mathbf{-0.3556}$ $p = \mathbf{0.0423}$

was never the smallest. The opposite can be said about the largest componental cosine: it is usually $P^{(\mathrm{co})}$ but never $P^{(\mathrm{ex})}$. In fact, we found that $P^{(\mathrm{co})}$ was always larger than $P^{(\mathrm{ex})}$. Notice that this is one of the characteristic patterns of our empirical interaction matrices as well.

The other patterns we listed above are clearly not universal. In the random interaction matrix model, $P^{(\mathrm{as})}$ can be the smallest componental cosine, albeit rarely when the matrix entries are picked from $[-1, 1]$, which does not occur for any of our empirical interaction matrices. Furthermore, the largest componental cosine in these random matrices is usually $P^{(\mathrm{co})}$, not $P^{(\mathrm{as})}$, which is typically the largest in empirical matrices. The correlations between the componental cosines also show marked differences. Whereas $P^{(\mathrm{av})}$ seems strongly anticorrelated with all other componental cosines in empirical matrices, it only has a significant, strong anticorrelation with $P^{(\mathrm{co})}$ in the random matrix samples. There is a moderately strong correlation between $P^{(\mathrm{ex})}$ and $P^{(\mathrm{as})}$ in both cases, but it is positive for the empirical and negative for the random matrices. In the latter case, our data indicate a similarly strong anticorrelation between $P^{(\mathrm{co})}$ and $P^{(\mathrm{as})}$ as well, which does not seem to be present in empirical matrices.

Changing the interval from which the random off-diagonal matrix elements are drawn leads to changes in the expected structure of the generated matrices, as shown by the results of our analyis for the intervals $[-2, 2]$ and $[-10, 10]$. The dissimilarities between the three cases include differences in the magnitudes and even rank orders of both the componental cosines themselves and their correlations. For example, $P^{(\mathrm{ex})}$ is much less likely and $P^{(\mathrm{av})}$ is much more likely to be the smallest componental cosine when the off-diagonal matrix elements are picked from $[-2, 2]$ or $[-10, 10]$ instead of $[-1, 1]$. As opposed to the other two cases, the correlation between $P^{(\mathrm{av})}$ and $P^{(\mathrm{co})}$ seems insignificant for $[-10, 10]$.

In conclusion, our results indicate that empirical interspecific interaction matrices have a more specific structure than having random off-diagonal entries independently and uniformly drawn from the same zero-centered interval.

We also analysed how the componental cosines are related to two different global community observables that characterise species relative abundance. There are several natural indices that quantify the intensity and various

effects of interspecies interactions [27]. Some of these indices are expressed in terms of *relative yields*, that is, the ratios of species yields in mixture to the same species yields in monoculture Y_i/M_i. $Y_i/M_i < 1$ indicates that species i performs worse in the community than in isolation, which means that this species, on average, faces stronger competition from the other species than its own intraspecific competition. Similarly, $Y_i/M_i > 1$ shows that species i performs better in the community, because, on balance, it is up against weaker than intraspecific competition or might even be facilitated by the presence of the other species. The simplest global community index is the mean relative yield or mean competitive response [27] defined as

$$MRY = \frac{1}{S} \sum_{i=1}^{S} \frac{Y_i}{M_i}. \qquad (17)$$

The mean relative yield allows comparing community productivity on a relative basis. An $MRY < 1/S$ indicates low productivity or *underyielding* [28] resulting from strong interspecific competition while an $MRY > 1/S$ indicates *overyielding*, that is, the species, on average, benefit from growing in the mixed community [28,29]. In particular, $MRY > 1$ shows very high productivity and implies that facilitation is the dominant form of interaction in the community. As a result, MRY can be used to assess the ability of ecosystems to provide ecological services related to biomass production.

Biodiversity can also be measured by a variety of different indices [1]. We looked at perhaps the most popular one, the Shannon equitability

$$H = -\frac{1}{\ln(S)} \sum_{i=1}^{S} p_i \ln(p_i), \qquad (18)$$

where $p_i = Y_i/\sum_{i=1}^{S} Y_i$. The more uniform the distribution of the yields is, the higher H becomes.

As table 4 shows, we found a positive correlation between the MRY and $P^{(\mathrm{co})}$, and negative correlations between H and both $P^{(\mathrm{as})}$ and $P^{(\mathrm{ex})}$, which indicates that these componental cosines can be used as predictors for MRY and H. These results are basically in line with the properties of the corresponding elementary games. An elementary coordination game equally encourages choosing a pair of strategies, but it either promotes the coexistence

(anticoordination) or the segregation and homogenisation (coordination) of these strategies depending on the sign of its interaction strength. The elementary conflict and external benefit games, on the other hand, penalise choosing certain strategies over others, decreasing their viability and thus their prevalence.

Conclusions. – In conclusion, we have statistically analysed the structure of a set of experimentally obtained interspecific interaction matrices. We have found that these empirical matrices have a non-trivial structure in terms of game theory's elementary game payoff matrices. The componental cosines of their irrelevant, external benefit, coordination-type, and conflict components show further correlations beyond those introduced by the mere definitions of these quantities, including a strong anticorrelation between the irrelevant component's componental cosine and those of the other components and a positive correlation between the external benefit and conflict componental cosines. Moreover, our analysis has revealed similar relationships between global observables of whole communities and the structure of their interaction matrices in the form of a positive correlation between the mean relative yield and the componental cosine of the coordination component and anticorrelations of the Shannon equitability with both the external benefit and the conflict componental cosines. These correlations reflect expectations based on the game theoretic interpretation of the elementary interaction matrices.

Being able to predict outcomes, or at least trends, in different communities could prove useful in practical applications such as optimising the productivity of crop mixtures in agriculture [30] or forecasting the impact of introducing foreign species on the species relative abundance of natural communities, a fundamental problem in environmental science [31,32]. Our findings are encouraging first steps in developing a new tool for making such predictions.

Data availability statement: All data that support the findings of this study are included within the article (and any supplementary files).

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