LETTER

Correlation between interaction strengths drives stability in large ecological networks

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Abstract

Food webs have markedly non-random network structure. Ecologists maintain that this non-random structure is key for stability, since large random ecological networks would invariably be unstable and thus should not be observed empirically. Here we show that a simple yet overlooked feature of natural food webs, the correlation between the effects of consumers on resources and those of resources on consumers, substantially accounts for their stability. Remarkably, random food webs built by preserving just the distribution and correlation of interaction strengths have stability properties similar to those of the corresponding empirical systems. Surprisingly, we find that the effect of topological network structure on stability, which has been the focus of countless studies, is small compared to that of correlation. Hence, any study of the effects of network structure on stability must first take into account the distribution and correlation of interaction strengths.

Keywords

Complexity, food webs, stability, pairwise correlation, population dynamics.

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INTRODUCTION

Food webs can be modelled as dynamical systems: the abundance of each species depends on those of the other species and the environmental conditions (May 1972). To fully determine the trajectories of populations in the community, we would need to parameterise dynamical equations – often involving quantities that are difficult to measure empirically – and precisely estimate the initial conditions and external forcing. Because of this difficulty, ecologists have studied the more tractable case of equilibrium-based asymptotic local stability, despite the fact that many natural populations persist out-of-equilibrium and persistence of species does not necessarily require stability (McCann 2000).

Local asymptotic stability (henceforth, stability) measures whether a system resting at an equilibrium state will return to it after small perturbations. Mathematically, an equilibrium point of a dynamical system is stable when its community matrix **M**, describing the effect of the column-species on the row-species at equilibrium, yields eigenvalues all having negative real parts (May 1972). The coefficients of **M** can be interpreted as interaction strengths (Berlow *et al.* 2004).

The structure of food webs is central to the study of ecology and evolutionary biology and has been investigated for more than a century (Camerano 1880). In 1972, May challenged the prevailing view that large communities would be more stable than small or poorly connected ones by showing that large complex systems would almost certainly be unstable (May 1972). May's results relied on random network structure, an assumption rightly criticised as unrealistic (Yodzis 1981): food webs have markedly non-random structure, setting them apart from Erdős-Rényi random graphs and scale-free networks (Dunne *et al.* 2002). Ecologists maintain that this non-random food web structure is key for their stability (Neutel *et al.*

2002; Krause *et al.* 2003; Rooney *et al.* 2006; Neutel *et al.* 2007; Gross *et al.* 2009; Stouffer & Bascompte 2011).

The large community matrices studied by May contained fixed proportions of interaction types, with mutualism (pairs of (+,+) coefficients) having the same frequency of competition (−,−), and half of the frequency of consumer-resource interactions (+,−). Allesina & Tang (2012) extended May's criterion to cases in which networks have any proportion of interaction types (e.g., food webs composed exclusively of consumer-resource (+,−) pairs), and showed that a preponderance of consumer-resource interactions would produce a negative correlation between them. Here we further generalise their stability criteria to show that the correlation between the interaction strengths of consumer-resource pairs can greatly affect the stability of real food webs, while all other structural features combined have much smaller influence. This correlation is strongly influenced by the scaling of species abundance with body size: scaling values close to the so-called 'Damuth's law' (Reuman *et al.* 2009; Pawar *et al.* 2012) yield a strong, negative correlation between pairs of interaction strengths, thereby maximising stability. We find that random networks conserving the pairwise correlation have stability properties similar to those of empirical systems. Hence, measuring the distribution and correlation of pairwise interaction strengths can inform us about the stability of whole ecological communities.

MATERIALS AND METHODS

Take a large community matrix **M** composed of *S* species randomly interacting with each other. This matrix is the Jacobian of the dynamical system describing the ecological community, evaluated at a feasible equilibrium point. M_{ij} measures the effect of a slight increase of species *j* on the growth rate of *i*,

and thus the coefficients of **M** can be thought as an estimate of the strengths of the interactions between species. The mean of the off-diagonal coefficients of **M** is $E < 0$, their variance is V, and E_2 is the mean of the products of the off-diagonal pairs $(M_{ij}, M_{ji})_{i \neq j}$. The quantity $(E_2 - E^2)/V$, denoted by ρ, is the overall pairwise correlation between the coefficients $(M_{ij}, M_{ji})_{i \neq j}$. The diagonal elements M_{ii} are sampled from a distribution with mean $-d$ and small variance (Appendix 7). Then, for a large community, the equilibrium is stable with high probability whenever:

$$\sqrt{SV}(1 + (E_2 - E^2)/V) - E < d \qquad (1)$$

We took fifteen published food webs (Jacob 2005; Jacob *et al.* 2011; Hechinger *et al.* 2011; Riede *et al.* 2010; 2011; Optiz 1996; Brose *et al.* 2005; Eklöf *et al.* 2013; Christian & Luczkovich 1999; Hall & Raffaelli 1991; Emmerson & Raffaelli 2004; Hudson *et al.* 2013; Jonsson *et al.* 2005; Yodzis 1998; Woodward *et al.* 2005), and for each web we parameterised an empirical community matrix **M** using body size (metabolic) scaling theory. Because metabolic scaling relationships hold only approximately, we performed multiple parameterisations for each food web. For each matrix **M** in the collection of empirically parameterised community matrices associated with each food web, we computed the real part of the leading eigenvalue $\Re(\lambda_{max}^{\mathbf{M}})$, thus obtaining an empirical distribution for $\Re(\lambda_{max}^{\mathbf{M}})$. Then, using randomisations (Table 1), we probed the effect on stability of each of the three main characteristics of the structure of **M**: the pairing of consumers and resources ('$(+,-)$-pairing'), the topological network structure (i.e., the 'skeleton' of the underlying food web) and the correlation between pairs of interaction strengths ρ.

Parameterisation of the community matrix

The empirical parameterisation of **M** suffers from the same problems found when trying to determine the exact trajectories of the populations: to estimate **M**, we would need to postulate a functional form, and precisely measure all parameters and the equilibrium. These problems are alleviated by the fact that the quantities determining the coefficients M_{ij} tend to scale with body size (Peters 1986; Brown *et al.* 2004; Brose *et al.* 2006; Pawar *et al.* 2012): knowing body size, we can estimate the search rate of consumer i for resource j (a_{ij}) and the corresponding handling time (h_{ij}).

The equilibrium abundance x_i^* itself also scales with body size, as shown by extensive studies on empirical food webs (Reuman *et al.* 2009; Pawar *et al.* 2012). We, therefore, estimated x_i^* by sampling the abundance scaling exponent from

the range of empirically observed values (Reuman *et al.* 2009). Finally, we need to determine the efficiency of conversion from resource biomass into consumer biomass (e_{ij}), which we chose arbitrarily between zero and one (the results are robust to this choice, see Appendix 5). Using these relations, and defining a functional form (Holling's type I or II), we estimate the off-diagonal terms of the matrix **M** for fifteen published food webs (Appendix 2). Naturally, the scaling relations are only approximate. Therefore, for each food web, we generated multiple parameterisations of the community matrix **M** by independently sampling the scaling exponents for each species from the corresponding distributions (Appendix 2). We find that the results are robust to variability in the parameterisation (Appendix 5).

The diagonal terms of the matrix **M** are also essential to determine its stability. For sufficiently large networks, the diagonal solely defines the center of mass of the eigenvalue distribution, without appreciable effects on its shape (Allesina & Tang 2012). For smaller networks, the approximation of Eqn 1 is accurate as long as the variance of the diagonal elements of the matrix is no larger than V (Appendix 7). In what follows, we set the diagonal to zero to concentrate on the effects of the off-diagonal terms, while we use simulations to probe the effect of having non-constant diagonal terms with large variance in Appendix 7.

Five randomisation tests

For each empirical food web, we parameterised 500 community matrices **M** and built a distribution for the real part of their leading eigenvalues $\Re(\lambda_{max}^{\mathbf{M}})$. The mean value of the distribution, $\overline{\Re(\lambda_{max}^{\mathbf{M}})}$ was recorded and used to normalise the distribution of $\Re(\lambda_{max}^{\mathbf{M}})$ so that the distribution was centered at one. To assess the effect of the arrangement of the off-diagonal coefficients in **M** on stability, we performed five different randomisation tests for the arrangement of the off-diagonal coefficients (Table 1). Each randomisation test preserves (or forgoes) some of the following features in the empirical community matrix **M**: (1) the pairing of positive and negative coefficients in the matrix ($(+,-)$-pairing), (2) the pairwise correlation ρ, and (3) the topological food web structure (i.e., 'who eats whom'). We denote the randomised matrix by **M**$'$: **M**$'$ contains the same coefficients found in **M**, but the position of the coefficients is different in each randomised matrix. For each empirical parameterisation of **M** and each test, the randomisations were repeated 50 times. Hence, the distribution for the real parts of the leading eigenvalues of **M**$'$, $\Re(\lambda_{max}^{\mathbf{M}'})$ was constructed using 500×50 values (also normalised by the mean of the empirical distribution $\overline{\Re(\lambda_{max}^{\mathbf{M}})}$). The difference between the distributions of $\Re(\lambda_{max}^{\mathbf{M}})$ and $\Re(\lambda_{max}^{\mathbf{M}'})$ represents a stabilising or destabilising effect, which can be attributed to the features that are originally in **M** but are destroyed in **M**$'$ due to the randomisation.

For simplicity, all five randomisation tests are explained here using a type I functional response, in which every positive M_{ij} (effect of the resource on the consumer) is paired with a negative M_{ji} (effect of consumer on resource) in the

Table 1 Features of **M** preserved or destroyed in each randomisation.

Preserves	Randomisation tests				
	1	2	3	4	5
$(+,-)$-pairing		✔	✔	✔	✔
pairwise correlation ρ				✔	✔
topological structure			✔		✔

community matrix $\mathbf{M}$. The tests can be extended to the more complex case of a type II functional response, in which two resources i and j sharing the same consumer produce a pair of positive interaction coefficients $(M_{ij}, M_{ji})_{i \neq j}$ (Appendix 3).

Test 1: Random case. In test 1, the least conservative test, following May (1972), we determine each interaction strength $M'_{ij, i \neq j}$ in $\mathbf{M}'$ by sampling it, independently and without replacement, from the set of all off-diagonal entries in $\mathbf{M}$ (including the zeros). Thus, in the randomised matrices, the topological structure is destroyed (i.e., $\mathbf{M}'$ represents an Erdős-Rényi random directed graph), and the pairwise correlation ρ and the $(+,-)$-pairing of matrix $\mathbf{M}$ are also lost.

Test 2: Keeping sign-pairing. Test 2 is slightly more conservative than test 1. The off-diagonal entries of $\mathbf{M}'$ are still determined by randomly sampling from the set of all off-diagonal entries in $\mathbf{M}$. However, for each pair $(M'_{ij}, M'_{ji})_{i \neq j}$, we always force the two coefficients to be either opposite in sign (i.e., $(+,-)$-pairing), or both zeros (i.e., no interaction). This test is in the spirit of Allesina & Tang (2012), as all interactions are constrained to be of the consumer-resource type. The link positions and directions in $\mathbf{M}'$ are still randomly determined, hence the topological network structure is lost in the randomisation. In addition, each non-zero pair $(M'_{ij}, M'_{ji})_{i \neq j}$ is specified by randomly pairing one positive coefficient with one negative coefficient $\mathbf{M}$, hence the pairwise correlation is lost.

Test 3: Keeping topological structure. In test 3, in addition to preserving the $(+,-)$-pairing as in test 2, we pre-determine the link positions and directions in $\mathbf{M}'$ to be those originally present in $\mathbf{M}$. By doing so, the topological structure (and hence the degree distribution of the species) is preserved. However, the positive and negative effects associated with each link are still assigned randomly, without replacement, from the sets of all positive effects and all negative effects in $\mathbf{M}$ respectively. Thus, the pairwise interaction correlation is not preserved.

Test 4: Keeping correlation. In test 4, not only do we keep $(+,-)$-pairing as in test 2, but we also fix the pair of coefficients ('weights') for each link. However, the direction and position for each link are randomly assigned among species. Thus, the topological network structure is lost in the randomisation. As such, $\mathbf{M}'$ can be thought of as the network obtained by randomly rewiring the links in $\mathbf{M}$. In this test, the pairwise interaction correlation ρ is preserved, since the set of pairs $(M'_{ij}, M'_{ji})_{i \neq j}$ in $\mathbf{M}'$ is the same as that in $\mathbf{M}$. However, since the link positions are randomly determined, the network structure of $\mathbf{M}'$ is again an Erdős-Rényi random directed graph.

Test 5: Keeping topological structure and correlation. In test 5, we conserve both the topological structure (as in test 3) and the pairwise interaction correlation (as in test 4), making it the most conservative test. This can be achieved by repeatedly swapping the links in $\mathbf{M}$ among themselves.

RESULTS

Strong negative pairwise correlation

In all parameterised food webs, we found a strong, negative pairwise correlation ρ (Fig. 1 and Appendix 4). The pairwise correlation ρ strongly depends on the scaling between body size and equilibrium abundance, thus directly linking body size scaling theory and stability. Specifically, we find that scaling exponents for species abundance close to $-3/4$ ('Damuth's law', Reuman *et al.* (2009); Pawar *et al.* (2012)) maximise the strength of correlation and thus are expected to be beneficial for network stability (Appendix 4).

Randomisation tests

For each food web, the normalised distribution of $\Re(\lambda^{\mathbf{M}}_{max})$ for the empirically parameterised community matrix $\mathbf{M}$ is reported in Fig. 2 (black), along with the corresponding distributions of $\Re(\lambda^{\mathbf{M}'}_{max})$ for the five randomisation tests. In test 1,
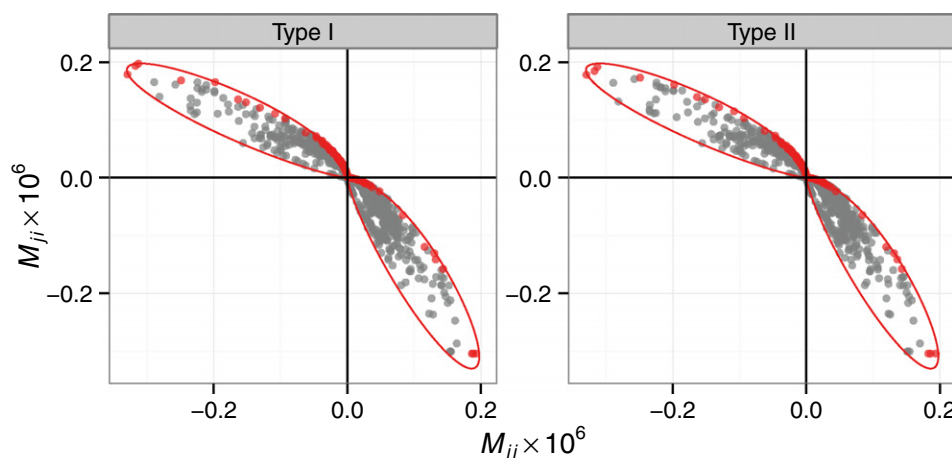

Figure 1 The distribution of pairs of interaction strengths in the Coral Reef (Optiz 1996) food web. We plot all the (M_{ij}, M_{ji}), for $i \neq j$. Both type I and type II functional responses show a strong negative correlation. The interactions involving a single generalist consumer are highlighted in red, to illustrate the fact that all the coefficients belonging to the same species are correlated ('species-level correlation'), and fall on a curve whose shape is determined by body size scaling parameters (Appendix 2).
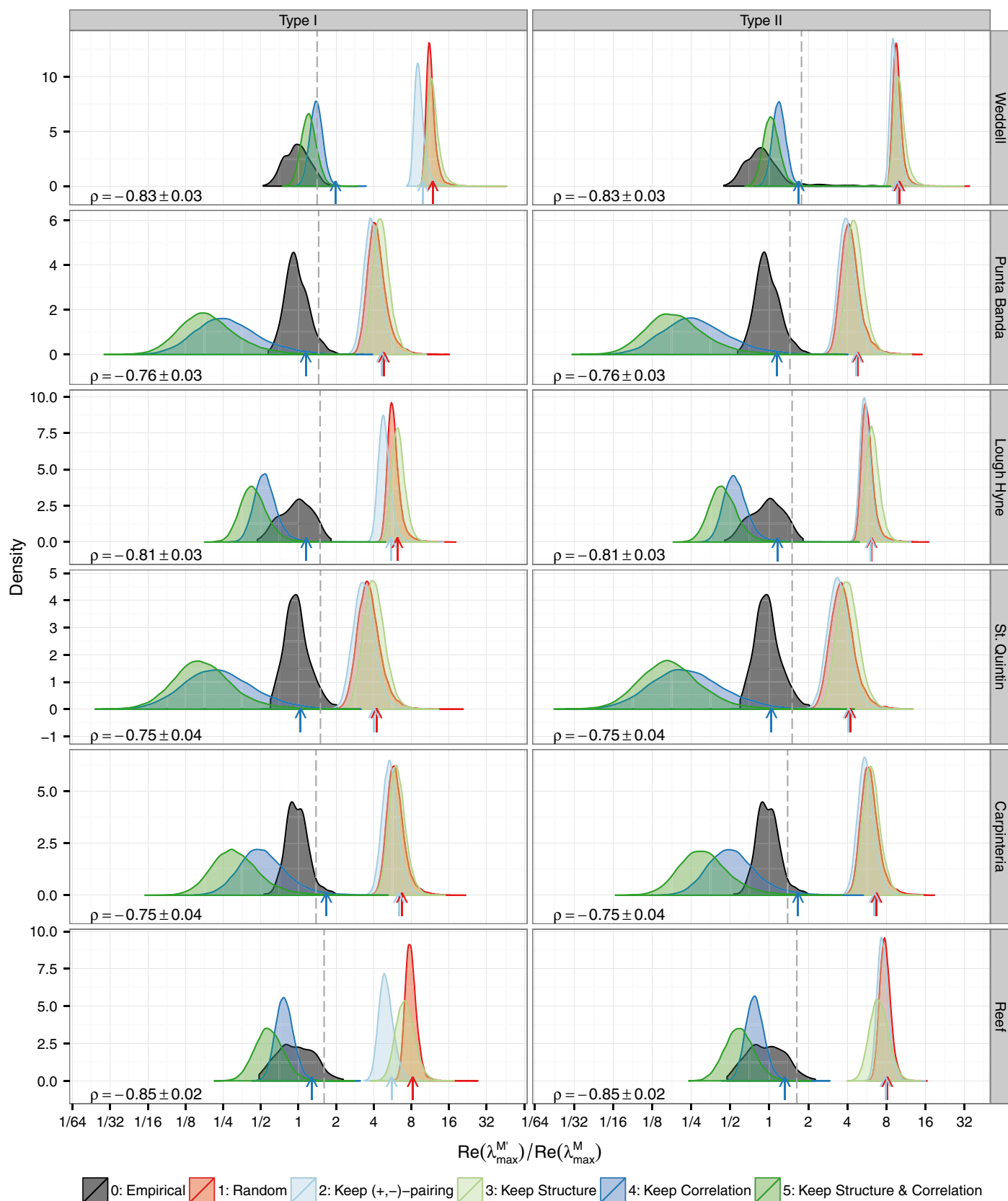
Figure 2 Density plot for the relative folds of leading eigenvalues (real part) in the empirical matrices ($\Re(\lambda_{max}^{\mathbf{M}})$) and in each randomisation test ($\Re(\lambda_{max}^{\mathbf{M'}})$), normalised dividing by the mean of the empirical distribution ($\Re(\lambda_{max}^{\mathbf{M}})$). The dashed line marks the 95th percentile for the empirical values. The arrows represent the analytic predictions for the corresponding test. Six webs (Jacob 2005; Jacob *et al*. 2011; Hechinger *et al*. 2011; Riede *et al*. 2010; 2011; Optiz 1996) are reported here. Similar results are obtained for other webs (Appendix 5).

the randomisation results in a large rightward shift of the leading eigenvalues (Fig. 2, red) relative to the normalised empirical distribution $\Re(\lambda_{\max}^{\mathbf{M}})$, meaning that the randomised networks are much less likely to be stable than the empirical ones. In test 2, the distribution of $\Re(\lambda_{\max}^{\mathbf{M}'})$ (Fig. 2, light blue) also lies to the right of the distribution for the empirical networks. However, it is slightly closer than that of test 1, indicating that arranging interactions as consumer-resource pairs slightly stabilises the network, as expected (Allesina & Tang 2012). In test 3 (Fig. 2, light green), constraining the network topological structure in addition to the consumer-resource pattern (i.e., the (+−)-pairing) has little effect on the distribution of the leading eigenvalues. The distribution of $\Re(\lambda_{\max}^{\mathbf{M}'})$ lies slightly to the right (i.e., less likely to be stable) of the unstructured consumer-resource case (test 2).

Note that in all of the first three tests, the pairwise interaction correlation is not preserved. Moreover, in all three tests, the distribution of $\Re(\lambda_{\max}^{\mathbf{M}'})$ lies to the right of the distribution of $\Re(\lambda_{\max}^{\mathbf{M}})$, indicating that the randomised networks are less likely to be stable than the empirically parameterised network.

In the fourth test, the empirical pairwise correlation ρ is preserved in addition to the (+,−)-pairing, which is conserved in test 2. This leads to a leftwards shift of the distributions of $\Re(\lambda_{\max}^{\mathbf{M}'})$, relative to the distribution for test 2. Surprisingly, although the topological structure of $\mathbf{M}$ is lost during the rewiring, the distribution of the real part of the leading eigenvalue (Fig. 2, dark blue) largely overlaps with that for the empirical matrices. Finally, in test 5, conserving the topological structure has little effect on the distribution of $\Re(\lambda_{\max}^{\mathbf{M}'})$, which largely overlaps with that for test 4 and that for the empirical matrices.

To summarise, the position of the distributions for the real parts of the leading eigenvalues (Fig. 2) reflects the probability of stability of the networks in each randomisation test (Table 1). Matrices built in test 1 (May 1972) are the least likely to be stable, closely followed by those in test 2; the distance between the two distributions measures the effect of imposing the (+,−)-pairing (Allesina & Tang 2012). Conserving the pairwise correlation (test 4), further enhances stability, producing matrices that are often more likely to be stable than the corresponding empirical one. Interestingly, compared to the distributions obtained in test 2 and test 4, tests 3 and 5 show that preserving the topological network structure has little effect on stability, no matter whether the correlation ρ is conserved or not. These effects are consistent for both type I and type II functional responses, and qualitatively robust to changes in the parameterisation (Appendix 5).

Eigenvalue distributions

The randomisation tests above show that preserving pairwise correlation between interaction strengths largely accounts for the stability of empirical networks. This is evident when inspecting the eigenvalue distribution (Fig. 3), which starts as a disk for matrices built in test 1 and becomes a vertically stretched ellipse for test 2 (Allesina & Tang 2012). Preserving the pairwise correlation (test 4) further stretches the ellipse vertically, in which the largest real part is similar to that found for the empirical matrix. Conserving the topological network structure (tests 3 and 5) greatly impacts the imaginary parts (making

the distributions more similar to the peculiar 'waxing-crescent moon' shape found for the empirical matrix) but leaves the largest real part almost unaffected. Hence, the topological network structure of food webs seems to play a secondary role in determining stability compared to the large effect due to the correlation between pairwise interaction strengths.

Predicting stability

Knowing that the topological network structure has relatively little effect on the largest real part of the eigenvalues of the community matrix $\mathbf{M}$, we can use its randomised version $\mathbf{M}'$ to approximate its stability. For each matrix, we computed the five parameters that are relevant for stability (S, V, E, E_2, and d, Appendix 6) and used these values to predict center of the distribution for the real parts of the leading eigenvalues (Fig. 2, arrows).

Each test preserves S, V, E and d, but alters the value of ρ. In test 1, $E_2 \simeq E^2$, and therefore the correlation is $\simeq 0$. In tests 2 and 3, if we denote by μ_1 the mean of the positive coefficients and μ_2 that of the negatives, $E_2 = C\mu_1\mu_2$ (C is the connectance, the fraction of all possible interactions that are realised). Finally, in tests 4 and 5, E_2 is exactly that found in the empirical matrix, as all pairs in $\mathbf{M}$ are preserved.

As such, in the five tests, all quantities needed for the stability criterion are preserved except E_2, which determines the correlation. ρ goes from approximately 0 (test 1), to slightly negative (tests 2 and 3), to strongly negative (tests 4 and 5 and empirical matrices). Fig. 2 shows that our analytic criterion successfully predicts results of the first two randomisations, while the prediction for test 4 overestimates the observed values, because of the large variability in the species-level correlation (Appendix 4). In fact, the stability criterion above assumes that pairs of interactions are sampled independently from the same distribution, while in our empirical parameterisations this is not the case. As such, the criterion is an approximation, yielding better results for distributions that are closer to this assumption.

An advantage of having derived an analytic criterion for the stability of randomly constructed matrices is that we can take derivatives. Doing so, we find that increasing S, V, or E_2 is always destabilising, and increasing the strength of the self regulation d is always stabilising. The stability criterion also shows that stronger pairwise correlation (i.e., $|\rho|$ large) is destabilising if the correlation is positive ($\rho > 0$) and stabilising if the correlation is negative ($\rho < 0$). Because we have seen that randomised matrices conserving all five quantities in test 4 largely capture the stability property of the empirical community matrices, we expect the same relation to hold for empirical communities as well.

DISCUSSION

We have shown that empirically parameterised community matrices display a strong, negative pairwise correlation between interaction strengths (Fig. 1), and that this correlation is key for stability.

In food webs, all the coefficients describing the effects of one species on all its resources and consumers are necessarily
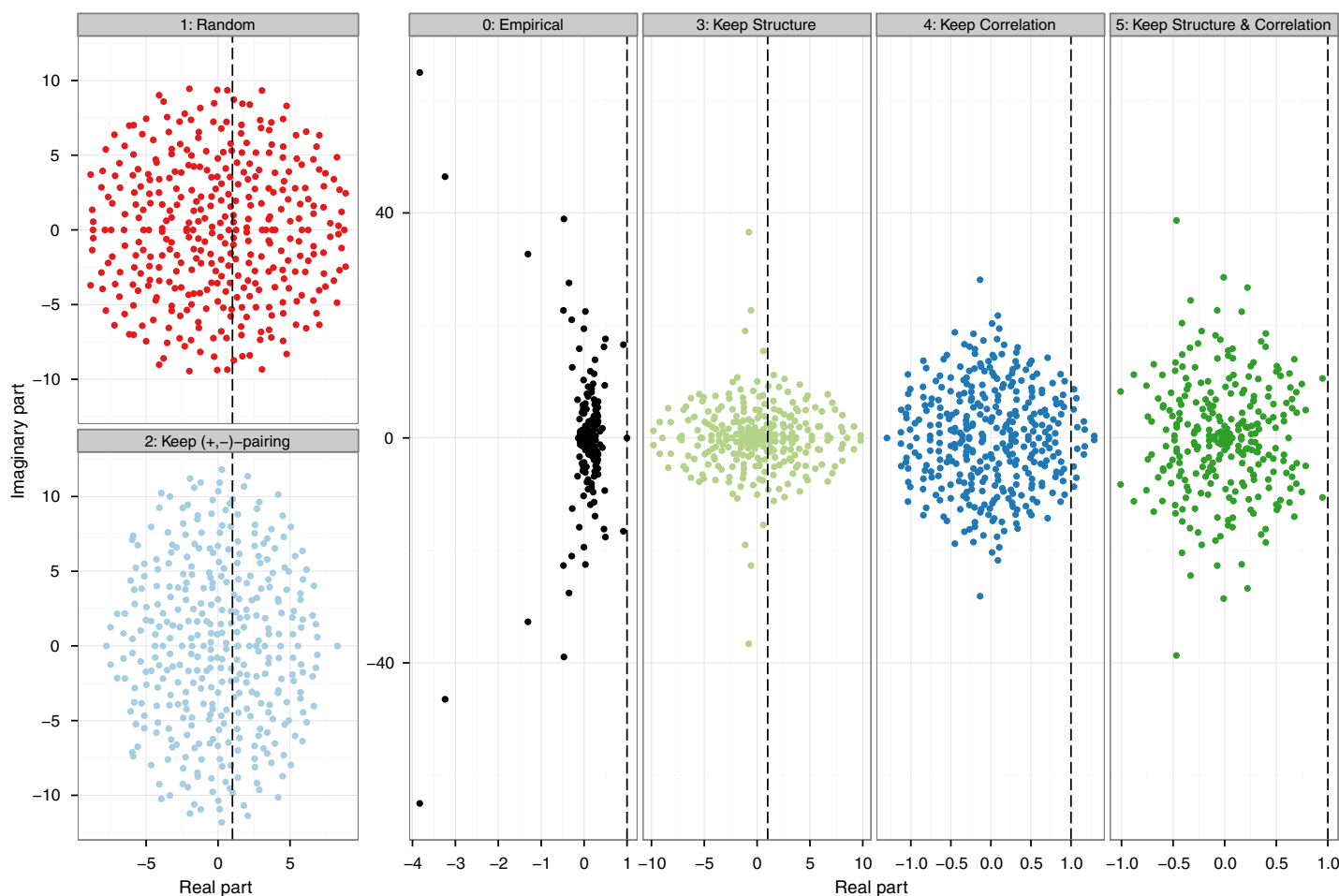
Figure 3 The distribution of eigenvalues for one randomisation of the Weddell Sea food web (Jacob 2005; Jacob *et al.* 2011). Moving from test 1 to 5, the eigenvalues are included in a circle (red), a vertically stretched ellipse (light blue), an ellipse with some vertical scatter (light green) and a very thin vertical ellipse (dark green). The eigenvalues start curving with test 5 (dark blue), which is the pattern most similar to the empirical distribution (black). The vertical dashed line marks the real part of the leading eigenvalue $\lambda_{\max}^{\mathbf{M}}$, which determines stability of the empirical matrix.

correlated ('species-level' correlation, Fig. 1), and the overall pairwise correlation ρ computed using all species descends from it. The importance of the pairwise correlation ρ for stability illuminates previous results showing the stabilising effects of allometric scaling (Brose *et al.* 2006). In particular, we find that conversion efficiency and scaling of equilibrium abundance play a dominant role in determining ρ, and therefore stability. Interestingly, the strength of the negative correlation is maximised for values of the scaling parameter close to the 'Damuth's Law' (Reuman *et al.* 2009; Pawar *et al.* 2012) and the values found in empirical systems (Appendix 4).

Negative correlation in interaction strengths causes the distribution of the eigenvalues of the randomised community matrix to be vertically stretched. A random network preserving five key quantities (the number of species S, the mean and variance of interaction strengths E and V, the pairwise correlation ρ, and the mean strength of self-limitation d) displays a leading eigenvalue similar to that of the corresponding empirical system.

Our results show that the topological network structure has limited influence on stability, compared to the contribution of correlation: adding or removing the topological network

structure only slightly shifts the distribution for the leading eigenvalues, compared to the unstructured case. As such, any study on the effects of network topology on stability must preserve the distribution of interaction strengths and their correlation – only in this case can the subtle effect of network structure be accurately assessed.

Finally, although a full parameterisation of large systems is still beyond the reach of ecologists, we have shown that estimating the mean, variance and pairwise correlation of the distribution of interactions strengths – a much easier task – can help us determine stability of whole communities.

AUTHORSHIP

S.T. processed the data and implemented the empirical parameterisations. S.T. and S.A. wrote and ran the

randomisation tests, and analysed the results. S.P. analysed the relationship between pairwise interaction coefficients. S.A. drafted the main text and prepared the figures. S.T. and S.P. drafted the Supporting Information. The analytic derivation was performed by S.T. All authors discussed the results at all stages and took part in writing the manuscript.

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